THESIS

INVASIVE WALLEYE DEMOGRAPHICS AND PREDATION ON RARE NATIVE FISH IN THE UPPER COLORADO RIVER BASIN

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ABSTRACT

INVASIVE WALLEYE DEMOGRAPHICS AND PREDATION ON RARE NATIVE FISH IN THE UPPER COLORADO RIVER BASIN

Invasive Walleye, *Sander vitreus*, pose a threat to endangered native fishes in the upper Colorado River basin, including Colorado Pikeminnow *Ptychocheilus lucius*. We evaluated Walleye demographic characteristics and used bioenergetics modeling to quantify their predation on native fishes in the lower Green and Colorado Rivers, Utah.

Walleye were sampled via electrofishing in 2021 and 2022. Age and growth were assessed from sagittal otoliths, and diet composition was determined from stomach contents of 643 individuals. Demographic data and estimated Walleye abundance informed bioenergetics simulations under four scenarios: baseline conditions (Baseline Scenario), a 2°C temperature increase (Climate Change Scenario), increased Colorado Pikeminnow abundance (Recovery Scenario), and abundance reductions of Walleye (Removal Scenario).

Walleye grew rapidly, reaching an average total length (TL) of 250 mm at age-1 and approximately 347 mm by age-2. Females exhibited a maximum predicted size of 611 mm TL and males were 507 mm TL. Most fish sampled were 3-5 years old and 412 – 501 mm TL. Diets were 87% nonnative fish by weight, but native species (12%) included Colorado Pikeminnow, Bonytail *Gila elegans,* other *Gila*, native suckers, and Speckled Dace *Rhinichthys osculus*. Bioenergetics modeling estimated that Walleye consumed 7875.8 kg of prey over two years under Baseline Scenario conditions, including 14,872 age-0 Colorado Pikeminnow. A 2°C increase in river temperature raised Walleye consumption of native fish by 141 kg, including 3,333 more age-0 Colorado Pikeminnow. If Colorado Pikeminnow abundance returned to historical levels and represented 5% of fish consumed by Walleye, modeled consumption would exceed 497949 age-0 individuals over the two-year simulation. Reducing Walleye abundance by 75% lowered age-0 Pikeminnow consumption by 11,282 individuals.

Walleye in the lower Green and Colorado Rivers present a significant predation risk to threatened and endangered native fishes. Management actions such as population suppression and immigration control are necessary to conserve Colorado Pikeminnow and other imperiled Upper Colorado River Basin species.

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Colorado River, providing invaluable insights into the Walleye. Additionally, Chris Smith and Kate Lawry from the USFWS Vernal office, and Sam Brockdorff and Katie Creighton from the UDWR Moab Field Station. These individuals played a crucial role in collecting the samples for the project on the Green River. I will be forever grateful and cherish the memories and knowledge I gained on the river with all these individuals in such a breathtaking area. I also want to thank the field technicians who were a part of this sampling for their diligence and for taking on the extra work of collecting the samples for me. This was an additional burden on top of the difficult and long field days they had, and I appreciate their close attention to detail in ensuring everything was collected accurately. I also want to thank Chris Michaud from the Upper Colorado River Endangered Fish Recovery Program. Chris was also the Fisheries Biologist focusing on Walleye at the Moab Field Station when I first started, and he helped facilitate the acquisition of samples for me. In his new role, he facilitated gathering historic data on Walleye in the basin.

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INTRODUCTION

Freshwater ecosystems are one of the planet's most diverse and threatened biomes (Dias et al., 2017; Garcia-Moreno et al., 2014; Ricciardi & Rasmussen, 1999; WWF, 2020). These ecosystems cover only 0.8% of the Earth's surface yet support a disproportionate share—approximately 33%—of vertebrate species (Dudgeon et al., 2006; Garcia-Moreno et al., 2014; Strayer & Dudgeon, 2010), many of those fishes. The reduction and disappearance of freshwater fishes are mainly due to habitat degradation and loss, overexploitation, chemical pollution, and negative effects of nonnative species (Dias et al., 2017; Jelks et al., 2008; Reid et al., 2018). Reductions in North America have been acute, especially in arid areas such as the Colorado River Basin, which has the second-highest native fish extinction rate of any river basin in the USA and Europe (Dias et al., 2017). The Colorado River Basin currently has three extinct species, and twenty-three species or subspecies federally listed as threatened or endangered out of thirty-five taxa thought historically native (Bestgen et al., 2020).

Riverine habitat in the Colorado River Basin has been modified heavily over the past century via construction of diversions, dams, and subsequent downstream flow modifications (Stanford, 1994). These structures block fish migration, alter flow, water temperature, and sediment supplies, facilitate the establishment of invasive fish, and generally reduce the survival of native species (Olden et al., 2006; Poff & Hart, 2002; Poff et al., 1997; Stanford et al., 1996). The Upper Colorado River basin (UCRB, upstream of Glen Canyon Dam, which impounds Lake Powell), where several threatened and endangered endemic riverine fish species remain, has been a focus of recovery activities since the early 1980s. Endangered Colorado Pikeminnow *Ptychocheilus lucius*, which historically extended from Wyoming downstream throughout warm water reaches of the Colorado River Basin to the Gulf of California, now occurs only in the UCRB, where fewer than 2,000 adult fish presently reside (Figure 1) (Bestgen et al., 2018; Elverud et al., 2020; U.S. Fish and Wildlife Service, 2002). Although prescribed flows, nonnative fish removal, habitat restoration, and other recovery actions have been implemented, rare fish populations continue to decline, perhaps due to several large-bodied nonnative piscivores, including Northern Pike *Esox lucius*, Smallmouth Bass *Micropterus dolomieu*, Channel Catfish *Ictalurus punctatus*, and Walleye *Sander vitreus* (Johnson et al., 2008; Wolff et al., 2012). Over the last decade, managers have become increasingly concerned about expansion of Walleye and their predatory effects on endangered fish because, unlike most of the other piscivores mentioned, their distribution overlaps with all life stages of Colorado Pikeminnow, including the two primary nursery habitat reaches where most young fish in the UCRB are produced (Bestgen et al., 2018; Elverud et al., 2020; Michaud et al., 2018, 2019). Predation by Walleye on young Colorado Pikeminnow has been documented (Elverud et al., 2020; Michaud et al., 2019; K. R. Bestgen, pers. comm., 2022), and competition for food resources from these piscivores is also possible, but population-level effects of these factors are unknown. Because the predatory impact of Walleye is assumed but not quantified, a more in-depth analysis of predation effects on Colorado Pikeminnow would help agencies prioritize nonnative fish removal and other management efforts for maximum conservation benefit.

One approach to understanding the predatory impact of Walleye is bioenergetics modeling. Such models have been applied to a wide range of freshwater species to understand a variety of issues, including individual and population growth rates, food web interactions, consumptive requirements, and predator-prey dynamics (Deslauriers et al., 2017; Kitchell et al., 1977; Lyons & Magnuson, 1987). The basic bioenergetics theory is rooted in the first law of thermodynamics, where modeling quantifies a fish’s energy budget (Deslauriers et al., 2017; Kitchell et al., 1977). This is accomplished by balancing energy intake from prey Walleye consume, with energy loss due to metabolism, waste, growth, and reproduction (Deslauriers et al., 2017; Hartman & Brandt, 1995). Physiological parameter estimates, derived from laboratory experiments and field data, enable users to manipulate the model to determine an individual fish's consumption and, by extrapolation, population-level effects (Deslauriers et al., 2017; Kitchell et al., 1977). Bioenergetics models are increasingly being applied to estimate the consumption of native fish by nonnative predators (Johnson et al., 2008, Johnson et al. 2017; Muhlfeld et al., 2008). These models often require location-specific demographic and environmental data for both predators and prey to parameterize the model. If such data were available, a bioenergetics model would be a valuable tool to assess the predatory impact of Walleye on Colorado Pikeminnow and other native fish in UCRB.

Therefore, the first objective of this study was to determine demographic characteristics of Walleye populations in the UCRB, specifically the lower Green and Colorado Rivers, where they were most abundant. Data gathered included age and growth, size structure, and Walleye diet quantification via examination of stomach contents. A second objective was to use demographic data in bioenergetics modeling, which, when coupled with Walleye abundance estimates, allowed for quantification of their predatory impact on Colorado Pikeminnow and other rare native species. Quantifying consumption demand will assist managers who must, among many other competing demands, prioritize recovery actions, including nonnative fish removal, to determine the most effective conservation strategies for native Colorado Pikeminnow and other fishes.

METHODS

Study area

The study area consisted of the lower Green and lower Colorado rivers in eastern Utah, in the UCRB upstream of Lake Powell (Figure 1). Both rivers have a snowmelt hydrograph with high peak flows in spring and early summer and lower baseflows in late summer through winter. Upstream impoundments reduce streamflow and alter water temperature each year because of water storage. Water temperatures are temperate and similar across the two rivers in most years (Figure 2). Lake Powell has supported a popular Walleye fishery for decades (Bolmmer & Gustaveson, 2021), but since about 2010, increasing numbers of Walleye have been documented upstream in our study area, prompting agencies interested in native fish conservation to initiate Walleye removal (Amidon et al., 2024). Walleye removal sampling is conducted everywhere but is focused on the Green River from downstream of Tusher Diversion, upstream of Green River, Utah, to 206 km downstream to its confluence with the Colorado River in Canyonlands National Park. In the Colorado River, removal sampling was conducted from the downstream end of Westwater Canyon near Cisco, Utah, and continued 180 km downstream to the confluence of the Green River in Canyonlands National Park. These river reaches supported the main riverine populations of Walleye in the entire upper Colorado River basin (Michaud et al., 2019); however, they were present in upstream reaches in lower numbers. Those same lower river reaches just described were critical nursery habitats and support the highest abundances of age-0 and larger juvenile Colorado Pikeminnow in the basin while also supporting other native and nonnative fish.

Fish sampling and diet analysis

Personnel from the U.S. Fish and Wildlife Service and the Utah Division of Wildlife Resources removed Walleye using electrofishing units mounted on inflatable rafts or flat-bottomed aluminum boats, with gear dependent on river flows and whitewater conditions. Crews removed Walleye during targeted efforts in the spring and summer-fall on the Colorado River and spring only on the Green River. Differences in river accessibility resulted in greater numbers of Walleye being available for analysis from the Colorado River. During those efforts, electrofishing time was recorded, and the catch of Walleye per hour of sampling (CPUE) was computed, which was used to estimate their abundance (below). Additionally, Walleye were captured during basin-wide sampling for Colorado Pikeminnow abundance estimation in 2021 in the Colorado River and the Green River in 2022. Following capture, Walleye were euthanized, a unique identifying tag was attached to each fish and placed in coolers on dry ice for later dissection in the Fisheries Ecology Laboratory, Colorado State University.

Stomach contents were removed and prey items were identified to the lowest taxonomic level possible. To identify partially digested food items, osteological structures, including pharyngeal arches, cleithra, and spines, were used. To identify prey items using osteological structures, we used a combination of known-identity reference specimens housed in the Colorado State University Larval Fish Laboratory collection, and the literature (Anderson et al., 2019; James et al., 2012; Parrish et al., 2006; Sublette et al., 1990; Traynor et al., 2010). When possible, prey fish standard lengths were recorded because the caudal fin was typically digested; standard lengths were converted to total length (TL) based on species-specific equations (Froese et al., 2014; Parrish et al., 2006). Lengths of partially digested prey fish were calculated using the species-specific relationships between backbone length, number of vertebrae, and standard length (Hansel et al., 1988; B. M. Johnson, unpublished data). The TL of prey was converted to wet weight in grams using species-specific length-weight equations to estimate the mean weight-based diet composition for bioenergetics simulations (Froese et al., 2014; Rees et al., 2005; Vanicek & Kramer, 1969). Prey energy density for bioenergetics simulations was estimated from the literature (Table 1).

Age, growth, and condition

Walleye ages were estimated by sectioning and polishing sagittal otoliths and counting annual increments (Heidinger & Clodfelter, 1987; Secor et al., 1992). Before reading, mineral oil was applied to otoliths to fill surface imperfections and enhance clarity. Digital images were obtained using a compound microscope at 40 - 100x magnification. Annuli were counted independently by two readers, and ages were assigned without knowledge of fish length. The final ages for each fish were consensus-based, where differences in age determinations were discussed and a final age determined. We were unable to age approximately 5% (30 fish) of Walleye otoliths due to unclear sections, so for those, we created an age-length key to assign age (Ogle et. al., 2023).

To estimate growth rate of an individual Walleye throughout its life, we back-calculated length-at-age from measurements of otolith annulus radii. We computed growth rates separately by sex because of dimorphic growth rates and size differences in Walleye (Henderson et al., 2003; Wszola et al., 2022). Schirripa (2002) compared models to estimate Walleye otolith radius to total length relationship (OR-TL) and found that a Weibull Cumulative Distribution Function (WCDF) was most useful as follows:

$$L_{ci} = (K \ \ (1 - e^{\left[-(\frac{r_{ci}}{a})\right]^{\beta}})$$

where L_{ci} was the TL at capture for fish *i*, and r_{ci} was the otolith radius at capture for fish *i.* The *K* was the asymptotic parameter, and α and β are estimated parameters. The WCDF was fitted using maximum likelihood procedures for sex separately, accounting for increased variation (Bolker & R Core Team, 2010; Farrell et al., 2021). Due to a smaller sample size in the Green River, specimens from both years were combined with Colorado River fish to evaluate age and growth, which was justified based on similarities of temperature and the prey fish communities of the two rivers (Figure 2; Breen & Fennell, 2022; Breen & Michaud, 2021).

Next, an individually corrected WCDF back-calculation model with an asymptotic OR-TL relationship was applied to each fish (Farrell et al., 2021; Schirripa, 2002) as follows:

$$L_{it} = (K\left(\frac{L_c}{L_P}\right))(1 - e^{\left[-(\frac{r_{ci}}{a})\right]^{\beta}})$$

where L_{it} was the estimated back-calculated total length for fish *i* at annulus *t*, L_c was the capture length, and L_p was the theoretical length predicted using the Weibull function OR-TL relationship. The *K* was the mean maximum total length for the sample; r_{ci}, α, and β were described above.

Predicted back-calculated lengths at each annulus were used to fit the Pütter-von Bertalanffy (Farrell et al., 2025; Kearney, 2021) growth model for each sex as follows:

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

where L_t was the average length at annulus (or age) *t*, L_∞ was the asymptotic average length, *K* was the Brody growth coefficient, and t_0 was a modeling artifact that represented the age when a fish's length was zero (von Bertalanffy, 1938). Given the inherent repeated measures nature of back-calculated growth data, a hierarchical mixed effects model was used with the random effect of individual fish and sex as a fixed effect owing to divergent growth trajectories after sexual maturity (Ogle et al., 2017). Individual growth trajectories were created for each fish in the sample using the Pütter-von Bertalanffy growth function. The individual growth trajectories were then used to create an average growth curve for male and female Walleye in our system. These lengths were then transformed into wet weights using the length-weight relationship observed from our Walleyes and used to calculate the wet weight of the fish without the gonads.

Walleye Condition

We used relative weight (W_r; Neumann et al., 2012) to compare Walleye body condition across rivers, years, and sexes. We used only spring samples, due to lack of fish from the Green River during summer and fall seasons. These spring samples represented post-spawning body condition because only a single non-spent (gravid) female was observed. To assess differences in W_r, we fit a linear model in RStudio (R Core Team, 2021) that included interactions between river, sex, and year. In the analysis, sex was not statistically significant, and no statistically significant interactions were found among river and year, river and sex, year and sex, or the three-way interaction between river, year, and sex. As a result, sex and the interaction terms were removed from the analysis. A simplified additive linear model including only river and year as predictors was subsequently fit to the data. Cohen's d (*d*) was performed to assess the difference between the groups and show the effective size difference between groups (Ben-Shachar et al., 2020).

Walleye abundance

Estimating realistic predator abundance in the wild for a bioenergetics study is important but difficult to obtain due to the costs and logistics of field sampling. Ideally, abundance would be estimated from a tag-recapture study, but conducting such in our study area was prohibitively expensive and undesirable due to the need to release tagged but predatory Walleye, rather than removing them. Instead, we estimated Walleye abundance by relating their CPUE in removal sampling to Colorado Pikeminnow CPUE and capture-recapture abundance estimates conducted in the same Colorado and Green River reaches (Bestgen et al., 2018; Elverud et al., 2020). To accomplish this, we fit a regression model of estimated Colorado Pikeminnow abundance as a function of CPUE for each of the Green and Colorado Rivers. We then solved for Walleye abundance by inserting their measured CPUE values for each river and year of sampling and solving the regression equation to estimate abundance, with the assumption that Walleye and Colorado Pikeminnow CPUE were similar. We deemed this a reasonable assumption because each species had a relatively large body size and fusiform shape, which made them susceptible to electrofishing capture, and they were commonly captured in the same riverine habitat types, including eddies, runs, deep backwaters, and pools during sampling. This abundance estimation technique was further supported by a close correlation between CPUE and estimated abundance for adult Colorado Pikeminnow (r = 0.85, Bestgen et al. 2018), indicating that CPUE of Walleye should be a reliable indicator of their estimated abundance.

Two estimates of CPUE were used for Walleye in the Green River because higher abundance was documented in the upper 50 km section from Tusher Wash downstream to Ruby Ranch (2021 CPUE = 3.33; 2022 CPUE = 2.82), where coarser substrate and deeper pools were present. Based on more limited data, only a single abundance estimate (CPUE = 0.315) was used for the more sandy-bottomed lower 156 km reach. Due to the homogeneity of habitat, we used a single Colorado River estimate of CPUE for the entire reach in 2021 (CPUE = 1.06) and 2022 (CPUE= 0.73). The regression equation of estimated abundance as a function of CPUE for the lower Colorado River ($y = 1{,}534x + 152.35$, $r^2 = 0.62$) yielded an estimated number of Walleyes in 2021 and 2022 of 1,148 and 824, respectively. The regression equation of estimated abundance as a function of CPUE, converted to Walleyes per river km to account for slightly different removal reach river lengths and CPUE values, was $y = 3.36x + 1.64$, $r^2 = 0.74$, where x is CPUE, and yielded an estimated number of Walleyes in the lower Green River in 2021 and 2022, of 1,062, and 976 fish, respectively.

As a consistency check on the efficacy of using abundance estimates for Walleye derived from Colorado Pikeminnow CPUE and abundance estimates, we used predator-productivity relationships presented by McGarvey et al. (2010) to determine potential predator densities. They used existing Colorado Pikeminnow abundances from 2001-2003 (Bestgen et al., 2007) as well as productivity estimates from the lower Green River and compared those to other predator density estimates for cold (trout) and warm water (Smallmouth Bass) predators in other stream systems in North America and estimated the lower Green River would support 0.45 predators/ha. We calculated the area of the lower Green River reach as 1,972 ha, based on river length of 193 km where estimates from Bestgen et al. (2007) were derived, and mean width of 102.6 m (20 equidistant transects of river width measured from October 2022 Google Earth images) and calculated the biomass of predators the reach would support (1,490 kg) so we could tailor it to the existing Walleye population. Walleye in the reach had an average TL of about 479 mm, and a length-conversion indicated average weight was 1.18 kg. Dividing that quantity into total predator biomass hypothetically supported by the reach resulted in an estimated Walleye abundance of 1,267, a value reasonably consistent with our estimates of 1,062, and 976, in 2021 and 2022, respectively, based on estimates derived from Colorado Pikeminnow data. The relative consistency of estimates gave us confidence that Walleye abundance estimates calculated for both river reaches were reasonable and could be used in bioenergetics simulations. Sex ratio in the total catch for both rivers and years was approximately 50:50. This allowed for an estimate of the population level consumption for Walleye during the study period in both rivers.

Mortality

We used a Poisson generalized linear model approach to estimate mortality rates from catch curve data (Mainguy & Moral, 2021) because traditional linear regression estimates of *Z* using log-transformed age-frequency catch data (Miranda & Bettoli, 2007; Ricker, 1975) can underestimate mortality (Mainguy et al., 2024). This approach also allowed 0's to fill missing, typically older, age class numbers; thus, truncation of older classes and data transformations were unnecessary. We used the peak censor approach, which eliminated fish ≤ 3 years old because they may not be fully recruited to the sampling gear. We included an overdispersion parameter in the model because deviances exceeded recommended values (assumes variance ≈ mean). This corrected for underestimated SE's of the slopes used here for Walleye mortality rate comparisons among rivers. Small sample size forced pooling of Green River data across years, and after adding the overdispersion parameter, confidence limits for slope estimates among rivers overlapped broadly. Thus, we used a single GLM estimate of mortality for both rivers during the two years.

Bioenergetics simulations

Field data were used to inform Fish Bioenergetics 4.0 (FB4) to estimate Walleye consumption of juvenile Colorado Pikeminnow, other rare native species, and nonnative taxa during the study years (Baseline Scenario). Additionally, three hypothetical scenarios were simulated and compared to Baseline Scenario results: one forecasting effects of climate change by increasing water temperature by 2 °C (Climate Change Scenario), one that increased Colorado Pikeminnow abundance to historical levels by increasing their proportion in the Walleye diets

(Recovery Scenario), and one with intensified Walleye removal rates (Removal Scenario) to simulate Walleye consumption and impacts to native fishes. Bioenergetics models are the mathematical representation of a fish's energy budget (Deslauriers et al., 2017) and assume that energy consumed must equal energy used for metabolism (M), waste (W), and growth (G) as follows:

$$C = M + W + G.$$

Metabolism, waste, and growth can be separated further as:

$$C = (R + A + SDA) + (F + U) + (SG + GG),$$

where metabolism is split into respiration (R), activity energy (A), and specific dynamic action (SDA; energy required to digest food). Waste is separated into energy lost in egestion (F) and excretion (U). The remaining energy is allocated to somatic growth (SG) and gonadal growth (GG) required for reproduction (Deslauriers et al., 2017).

Baseline Scenario

We modeled female age-classes 1-10 and male age-classes 1-8; age-10 and older females represented less than 2% of the overall populations in both rivers and no males > age-8 were observed. Simulations began on 1 April 2021, for the subsequent 12-month period (the first year of the simulation) and began again on 1 April 2022 (the second year of the simulation). These intervals represented the approximate end of spawning each year and were designated as such because ripe fish were rare after 31 March. Annual mean daily thermal regimes experienced by Walleye were modeled for the simulation period using nearby U. S. Geological Survey (USGS) stream gauges on the Colorado River (09180500) and the Green River (09315000) (Figure 2). Energetics parameters were taken from (Deslauriers et al., 2017) and used to estimate consumption, respiration, egestion, and excretion. Predator energy content was modeled as the sum of somatic and gonadal tissue values. Somatic energy density (4,186 J/g WW, Kitchell et al., 1977) was constant over the simulation period. To account for gonadal energy content explicitly, daily gonadal development was estimated based on Henderson et al. (1996), and gonad energy density values for males and females were used to estimate energy allocated to gonads over the year for each day of the simulation (Farrell et al., 2021). Age at maturity was determined as the first age class where more than 50% of sampled fish were classified as reproductive, based on examination of the gonads, according to Duffy et al. (2000). Consequently, males were assumed to be mature at age 2 or older, and females at age 3 or older. The GSI values from Henderson et al. (1996) were multiplied by the estimated weight from the growth curve to find gonad weight. Gonad weight was added to the somatic weight to calculate the final weight of mature fish at the end of each age class.

The simulation diet proportions were broken into four periods to reflect seasonal changes: Spring (April 1st to July 1st), Summer/Fall (July 2nd to November 30th), Winter (December 1st to January 31st), and Late Winter/Early Spring (February 1st to March 31st). Green River diet samples were available only for Spring. We used Colorado River diet composition in Summer and Fall for the Green River as well because sampling (Project 138, Interagency Standardized Monitoring Program https://coloradoriverrecovery.org/uc/documents/work-plan-documents/annual-reports/) indicated that prey community composition was similar, except that Gizzard Shad *Dorosoma cepedianum* were rare in the Green River (Breen and Fennell 2022; Breen and Michaud 2021). To account for this, the proportion of the diet Gizzard Shad represented was added to the nonnative fish category. For the Winter period, we used Colorado River diet data from the latest Summer/Fall collections for both rivers, so diet information was available for both rivers year-round. Annual consumption estimates from the Baseline Scenario were summed over years and rivers for comparison to these sums estimated in the other scenario simulations (below).

Climate Change Scenario

This scenario investigated how global warming may affect Walleye consumption. Air temperature in this arid desert region is expected to rise over the next several decades, so we chose to model a river temperature increase of 2°C, a level realistic for this region (Christensen et al., 2004; Fraser et al., 2019; McCabe & Wolock, 2007). To accomplish this, Baseline Scenario parameters (including growth) were held constant, except that 2°C was added each day to the thermal regime. Walleye consumption was then summed for the two rivers during the two year period and compared to Baseline estimates to determine Climate Scenario consumption changes.

Pikeminnow Recovery Scenario

Realistic estimates of historical potential Walleye consumption of small Colorado Pikeminnow were hindered by their extremely low abundance during our study years, which likely explained their low frequency in stomach samples. For example, mean percent catch of Colorado Pikeminnow in fall backwater seine sampling over our 2021-2022 study period in the Green and Colorado Rivers was only 0.08% and 0.78 % of captures, respectively (Breen and Michaud, 2021; Breen and Fennell, 2022), compared to overall estimates from 1986-2022, where they were 2.5% and 8.6% of captures, respectively (Project 138, Interagency Standardized Monitoring Program sampling https://coloradoriverrecovery.org/uc/documents/work-plan-documents/annual-reports/; K. R. Bestgen, unpublished data). To evaluate whether current Walleye predation intensity could reduce Colorado Pikeminnow population abundance compared to the pre-Walleye abundance era when they were more abundant (described below), we increased the Walleye diet proportion of Colorado Pikeminnow to 5% to reflect the higher average historical proportion in each river over the entire year in our simulations. The diet proportions for other prey categories were reduced accordingly on a weighted basis by 5% to balance diet proportions, and all other variables were held constant from the Baseline Scenario. Consumption of Colorado Pikeminnow (kg) was calculated for each of the two years and for the Green and Colorado Rivers.

Walleye Removal Scenario

To evaluate the effect of increased Walleye removal on prey consumption, we simulated population reductions in 25% increments up to 75% of Baseline Scenario abundance, while holding all other inputs constant. Consumption estimates at each removal level were then summed for both years and rivers to simulate how changes in population abundance would reduce biomass consumed and increase endangered fish abundance. Consumption changes were compared to Baseline estimates to determine the benefits of Walleye removal on native fishes.

Prey-sized Colorado Pikeminnow abundance

Understanding abundance of wild Colorado Pikeminnow at different sizes and ages in our study reaches was essential to realistically estimate the predatory impact that Walleye may have, and this information was available from historical research. For age-0 Colorado Pikeminnow, typically 25-60 mm TL in autumn, we used estimates of their abundance from 1994 and 1995 in the lower Green River obtained using a mark-recapture study (Haines et al., 1998). Their robust estimates from autumn in each of those years were 3,793 (95% CI 3001-4864) and 2,199 (1623-3031), respectively, in a 32 km river-reach. We calculated the mean of the two estimates and when extrapolated to the entire reach length of 193.2 river km (the reach length where estimated CPUE data were gathered) for each year resulted in mean abundance of 18,088 (mean of 22,900 and 13,276 in 1994 and 1995, respectively), or 93.6 age-0 Colorado Pikeminnow per km. To estimate the mean abundance of wild age-0 Colorado Pikeminnow during this study, we divided the mean backwater seine capture densities obtained in 2021-2022 by the mean from 1994-1995 to obtain 0.30 (mean = 1.745 Pikeminnow/100 m^2 seined in 2021-2022 divided by the mean = 5.8 Pikeminnow/100 m^2 seined in 1994-95; ratio = 0.30, (https://coloradoriverrecovery.org/uc/documents/work-plan-documents/annual-reports/) and multiplied that by the 1994-1995 mean abundance of 18,088 to get a 2021-2022 estimate of 5,480 age-0 Colorado Pikeminnow in the lower Green River. To obtain the estimated age-0 abundance in the lower Colorado River in 2021-2022, we computed the ratio of the capture densities in each river in the same years (2021-2022 Colorado River mean = 2.55 Pikeminnow/100 m^2 seined/Green River mean = 1.745 Pikeminnow/100 m^2 seined, = 1.46), multiplied that by the estimated Green River abundance of 5,480 (result was 8,008 age-0 fish), and reduced that by the slightly shorter reach length (180 river km/193.2 river km = 0.93*8,008) to get an adjusted abundance estimate of 7,461.

To obtain biomass of age-0 Colorado Pikeminnow available for consumption, abundance was multiplied by 0.39 g, the weight of a 40 mm TL fish at the end of their first growing season (Bestgen et al. 2006; https://coloradoriverrecovery.org/uc/documents/work-plan-documents/annual-reports/). The 0.39 g value was confirmed by measuring the weight of preserved Colorado Pikeminnow of that same length (0.37 g). This method of abundance estimation makes assumptions about habitat similarity and sampling among the two rivers, which we think were reasonable based on river proximity, temperature similarities, observations of similar backwater frequency, and consistency of sampling crews. The number of age-0 Colorado Pikeminnow consumed by the Walleye population was estimated by dividing the total annual bioenergetics consumption of Colorado Pikeminnow by Walleye by the average individual wet-weight of an age-0 fish.

Following from above, we used mark-recapture estimates of larger and older juvenile Colorado Pikeminnow to determine their abundance and estimated biomass available as Walleye prey in the wild. Those ongoing monitoring program estimates (Green River 2016-2018; juveniles = 100-399 mm TL: Colorado River 2013-2015, 250-399 mm TL) were calculated when that Colorado Pikeminnow life stage was still relatively abundant and in the earlier phase of the Walleye invasion (Elverud et al. 2020; K. R. Bestgen, unpublished data). We used the mean abundance of juveniles per year over the three years from each reach (lower Green River, n = 922; lower Colorado River n = 354) and multiplied that value by their average weight (Green River, 273 g; Colorado River, 331 g) to obtain an estimated biomass of Colorado Pikeminnow juvenile prey available for Walleye in each river. Based on wet weight of prey (age-0 or juveniles), we then estimated the proportion of Colorado Pikeminnow biomass that Walleye could consume annually.

Estimated size of Bonytail consumed

To estimate predation by Walleye on Bonytail, we translated biomass consumed to the number of individual fish consumed at a specific size. This conversion was relatively straightforward because natural reproduction of Bonytail was rare (Bestgen et al. 2017), and all individuals present in the lower Green and lower Colorado rivers were presumed stocked fish tagged with PIT tags prior to release. The minimum stocking size was 200 mm TL with a weight of 62 g based on the length-weight relationship of Vanicek and Kramer (1969). Walleye were observed consuming prey up to 60% of their body length (C. Michaud unpublished data, U. S. Fish and Wildlife Service, Upper Colorado River Recovery Program, Denver, CO), so the average Walleye in our study should be large enough to consume most of the Bonytail that are stocked.

RESULTS

In the 2021 and 2022 field seasons, we captured 643 Walleye, 522 from the Colorado River and 121 from the Green River; reduced accessibility and lower effort rather than differences in Walleye abundance were responsible for numbers sampled from each location. The mean size of Walleye in the Colorado River was 473 mm TL (260-690 mm TL) and 1,173 g (156-3,825 g) (Figure 3). The mean size of Walleye in the Green River was 460 mm TL (209-710 mm TL) and 987 g (109-3,570 g).

Age, growth, and condition

Independent age estimates showed 87% agreement between the two readers. Differences in age estimates among the remaining 13% of Walleyes were resolved after discussion. The age range for 613 fish was 1-15 years; fish aged 3-5 were the most common and comprised 61% of all Walleyes (Figure 4). The maximum observed female age was 15 years compared to 8 years for males, but 98% of females in the sample were ≤ age-10.

The Pütter-von Bertalanffy growth curve (Figure 5) predicted similar average back-calculated length of Walleye at age-1 for females (251 mm TL) and males (249 mm TL) but females grew at faster rates at older ages. The asymptotic length, L_∞, for females, was 611 mm TL (2,284.0 g), and for males 507 mm TL (1,315.8 g).

Walleye W_r was significantly higher in the Colorado River (mean = 96.3, SD ± 11.2) than in the Green River (mean = 87.6, SD ± 9.8; Figure 6). This difference corresponded to a large effect size (Cohen's $d = 0.82$, 95% CI [0.56, 1.07]) and was supported by linear model results showing a significant negative effect for the Green River on W_r ($\beta = –6.45 \pm 1.11$ SE, *t*-value 5.79, $P < 0.001$, n = 268) . Additionally, W_r was significantly higher in 2021 (mean = 99.1, SD ± 10.5) compared to 2022 (mean = 86.3, SD ± 8.1), with a large effect size ($d = 1.40$, 95% CI [1.13, 1.67]). The linear model confirmed the difference with a significant negative effect of year 2022 ($\beta = –11.96 \pm 1.09$ SE, *t*-value 10.94, $P < 0.001$, n = 268). Observations during dissections also showed Walleye from the Colorado River were in better condition, based on greater quantities of visceral fat, compared to Green River fish.

Mortality

Initial Walleye mortality estimates were higher in the Colorado River ($Z = 0.53$, SE ± 0.031) than in the Green River ($Z = 0.37$, SE ± 0.045) but estimates showed overdispersion, so subsequent the Quasi-Poisson GLM resulted in broader and overlapping confidence limits among the rivers (Colorado River $Z = 0.53$ SE ±0.049 Green River $Z = 0.37$ SE ± 0.076). Thus, we combined data across rivers and estimated a single instantaneous mortality rate $Z = 0.49$ (SE ± 0.025), with annual survival rate of 0.61.

Diet composition

Of the 643 Walleye stomachs examined, 39% were empty, and the remainder contained 16 fish taxa and two aquatic invertebrate taxa. We found that nonnative fish accounted for 87% of the Walleye diet by weight and 74% by count. The most common prey taxa were nonnative minnows (Table 2), which included Fathead Minnow *Pimephales promelas*, Red Shiner *Cyprinella lutrensis*, and Sand Shiner *Miniellus stramineus*. Nonnative sport fish, primarily centrarchids and ictalurids, comprised 13.9% of the diet by weight and 12.5% by count. Gizzard Shad, another nonnative species common in the Colorado River, was 11.0% of the diet by weight and 9.7% by count. Overall, native fish comprised 12% of the diet by weight and 9% by count. The two most common native species were suckers, either Bluehead Sucker or Flannelmouth Sucker, along with Speckled Dace. Imperiled species made up 3.7% of the diet by weight and 3.3% by count; we observed two juvenile Colorado Pikeminnow (0.2% by weight and 0.05% by count), five Bonytails (1.2% by weight and 1% by count), and 11 chubs in the genus *Gila* (2.3% by weight and 1.8% by count).

Seasonally, nonnative cyprinids dominated Walleye diets on a weight basis in the Colorado River during Spring 2021 (82.8%), Summer-Fall of 2021 (57.9%) and Spring of 2022 (54.5%), then declined in Summer-Fall of 2022 (16.1%; Table 3), where nonnative sport fish and Gizzard Shad were dominant. Gizzard Shad were absent in the Colorado River diets in Spring of both years. Walleye consumed more native species in the Colorado River during 2021 than they did in 2022 (Table 3). Two Colorado Pikeminnow were found in the diet during Spring 2021 only (0.6% by weight), and Bonytail were in the diet during Spring 2022 (4.5% by weight). Unidentified *Gila* were only observed in 2021, and Speckled Dace were rarely observed in Walleye from the Colorado River. In the Green River, during Spring 2021 and 2022, nonnative cyprinids were the dominant (46.0% and 68.0% by weight, respectively) prey taxa in Walleye diets (Table 4), as they were in the Colorado River. Colorado Pikeminnow were not observed in Green River Walleye diets, but Bonytail were present in 2021 (3.0%) and 2022 (4.7%). *Gila* other than Bonytail, were only observed in the diet in 2021, as in the Colorado River. Gizzard Shad were less common in Green River Walleye diets (≤ 4.4%) than they were in the Colorado River. Speckled Dace contributed 34% of the diet in 2021 but none were observed in 2022 (Table 4).

Bioenergetics modeling

Baseline Simulation

Using demographic and diet data described above and bioenergetics modeling, we estimated that individual female Walleyes consumed 32.5 kg (0.37-4.9 kg/yr) of prey over their 10-year lifespan (Table 5). Individual lifetime consumption by male Walleyes was lower at 14.6 kg over their 8-year lifespan (0.36-2.6 kg/yr) due to smaller size and lower maximum age. We estimated total fish consumption by male and female Walleyes in the Green and Colorado Rivers was 1,464.8-2,274.7 kg/yr, with variation based on different annual estimated abundances (Tables 6 and 7). Females accounted for 69% of total consumption. Over the two-year period in the Green and Colorado Rivers, Walleyes collectively consumed an estimated 7,442.9 kg of prey.

The two Pikeminnow found in the Walleye diets in the Colorado River, expanded out to a year with bioenergetics simulations, had an estimated 5.87 kg of Colorado Pikeminnow in the first year (Table 8); none were consumed in the second year. Based on that estimate and the mean weight of age-0 Colorado Pikeminnow (0.39 g), Walleyes consumed the equivalent of 14,872 age-0 Colorado Pikeminnow.

Walleyes consumed no Bonytail in the Colorado River in 2021, but biomass consumed in the second year (29.0 kg) was similar to that in the Green River in both the first (27.3 kg) and second year of the simulation (35.3 kg) (Table 8). Walleye consumption of Bonytail over the two-year simulation period in both rivers was estimated at 91.6 kg (Table 8) or 1,477 individuals.

Climate Change Scenario

The 2°C increase in daily water temperatures resulted in increased Walleye consumption for the two simulation years by 221.3. kg in the Colorado River and 211.6 kg in the Green River, compared to the Baseline simulation. Consumption of native fish in both rivers and years increased by 141.0 kg, from 849.3.3 kg to 990.3 kg (Table 9). Consumption of age-0 Colorado Pikeminnow in the Colorado River increased by 1.3 kg or 3,333 individuals, increasing the estimated total number consumed to 18,205 individuals. Walleye consumption of stocked Bonytails increased by 25.3 kg (Table 9) in both rivers due to the higher water temperatures, which translated to an additional 408 stocked fish consumed.

Pikeminnow Recovery Scenario

This scenario estimated potential Walleye predation on age-0 Colorado Pikeminnow if their abundance had been similar to historical levels (about 5% of the fish community). In the Colorado River, the estimated consumption of Colorado Pikeminnow during the first and second years of the simulation was 120.2kg and 74.0 kg, respectively. This biomass equated to 308,205age-0 fish in the first year (functionally 2021) and 189,744 age-0 fish in the second year (mostly 2022), numbers far greater than were estimated present during the study period. In the first year, potential Walleye consumption of juveniles was 120.2 kg, which exceeded the standing stock biomass of juvenile Colorado Pikeminnow (100.3 kg) estimated from the mark-recapture studies during 2013-2015, which was 119.8% of the total juvenile biomass. Reduced Walleye abundance in the second year of the simulation resulted in lower potential predation on juveniles but was still substantial at 74.0 kg, accounting for 73.8% of the total juvenile biomass.

Although no Colorado Pikeminnow were found in the diets of Walleye in the Green River during the study, the simulated diets indicated that Walleye could have a significant predatory impact on the Colorado Pikeminnow population. For example, simulated diets estimated 101.9 kg of Colorado Pikeminnow consumption in 2021 that equaled 261,282 age-0 consumed, exceeding by 14.5 times the average estimated historical abundance of age-0 Colorado

Pikeminnow in the lower Green River (18,088 age-0 fish). Walleye consumption of larger juvenile Colorado Pikeminnow was 52% and 43% of historical abundance, based on Walleye abundance in 2021 and 2022, respectively. Because Colorado Pikeminnow remain juveniles and susceptible to consumption for 2-6 years, few would survive at those predation rates over that time span. For example, if 1,000 juveniles were initially present and the predation rate was 50% per year over a five-year period, only 31 Colorado Pikeminnow would survive.

Walleye Removal Scenario

Reducing Walleye abundance would have reduced their total consumption over the two-year period in both rivers by 1,860.7 kg per 25% removal increment (Table 10). Reduced Walleye abundance would also have lessened the impact of predation on Colorado Pikeminnow, where a 25% reduction in the Walleye population would result in a 1.5 kg (or 3,846 age-0 fish) reduction in estimated consumption of Colorado Pikeminnow. A 75% reduction in Walleye abundance would reduce consumption of age-0 Colorado Pikeminnow by 4.4 kg, or an estimated 11,282 age-0 fish.

DISCUSSION

Bioenergetics modeling based on newly acquired demographic information showed that Walleye are a significant threat to native fish persistence in the UCRB. Walleye are fast-growing, opportunistic piscivores that consume a wide variety of prey, including endangered fishes. This is especially problematic because Walleye are most abundant in the nursery habitats responsible for most recruitment of age-0 and juvenile Colorado Pikeminnow in the UCRB, the last remaining wild populations anywhere in the world. Therefore, Walleye control is critical to conserving endangered Colorado Pikeminnow and other rare native fish species. Below, we expand on aspects of Walleye demographics and energetics modeling, the first data of its kind since the introduction of this invasive species into the UCRB decades ago and discuss options for their future control.

Origin of Walleye in our study area is an important question because their source location influences control options. Sampling conducted during this study and before showed that few larval and early juvenile (age-1 fish) Walleye were present, which indicated that the adults we sampled likely originated from sources outside the river rather than from local reproduction. Earlier provenance studies using otolith microchemistry showed that some riverine Walleye were from smaller upstream reservoirs (Rifle Gap and Starvation reservoirs; Wolff et al., 2012). Further analysis by Johnson et al. (2014) revealed that Walleye from the lower Green River had immigrated from either Starvation Reservoir or Lake Powell; however, because the elemental signatures of those two potential locations overlapped, they were unable to pinpoint the exact source. As a result of that research, upstream reservoirs were screened to reduce the escapement of Walleye and other nonnative fish into downstream rivers. Occasional escapement was noted during high flow years, such as 2023, when juveniles were found downstream (Amidon et al., 2024) but their distribution and abundance was generally considered reduced. Because an abundant Walleye population was established in Lake Powell following the accidental introduction and establishment of Gizzard Shad (Blommer & Gustaveson, 2021; Pennock & Gido, 2021), and there is no barrier to upstream dispersal, Walleye in our study area were likely spawned in Lake Powell, grew there for a year or two, and then migrated upstream into the lower Green and Colorado Rivers. That scenario aligns with our age-frequency information, which indicated a low abundance of age-2 or younger Walleye in the lower Green and lower Colorado rivers.

Further support for origin of Walleye from Lake Powell was their growth rates. Walleye growth conditions were ideal in Lake Powell with excellent thermal conditions (Kitchell et al., 1977) and abundant Gizzard Shad, an important food source (Kerr, 2011). Based on our growth curves for river-captured Walleye, growth was especially rapid during the first six years, which aligned closely with conditions in Lake Powell and for other southern populations in their native and introduced ranges (Quist et al., 2003). Compared to North American average growth (Quist et al., 2003), Walleye in our system grew larger during the first six years (Figure 7). An invasive Walleye population in Lake Pend Oreille, Idaho, had growth similar to other southern populations with a mean back-calculated length of 225 mm at age-1 and 333 mm by age-2 (Frawley et al., 2024), slightly slower than our population, which were 250 mm TL by age-1 and 347 mm TL at age-2. Growth of Walleye in our study area slowed as they reached reproductive age.

Walleye condition was relatively high, especially considering fish used for the W_r analysis were in spring post-spawn condition, which was expected to be low. Pennock and Gido (2021) investigated trends in W_r of Walleye sampled during fall in Lake Powell over a 38-year period and found mean W_r of 90. In comparison, we found over the two years Walleye in the Colorado River had a higher average condition (W_r = 96.3) than those found in Lake Powell, while Walleye in the Green River were in similar condition (W_r = 87.6). Relatively high Walleye condition in our rivers indicated habitat and forage were sufficient to support their continued persistence in the UCRB. Walleye W_r differed slightly between the Green and Colorado Rivers and between years, perhaps because of food availability. For reasons we cannot explain, Gizzard

Shad were more abundant in the Colorado River, and more common in Walleye diets, which likely led to their higher condition compared to Green River fish. Higher flow conditions prevailed in 2022 when fish condition was slightly lower, compared to 2021, perhaps placing added energetic demands on Walleye, but water temperatures were similar across years, so the role of environmental factors on condition differences was not clear.

Our instantaneous Walleye mortality rate of 0.49 was modestly lower than other North American populations. For example, Walleye instantaneous mortality, converted from annual mortality, for several study populations across North America varied widely, ranging from 0.6 to 1.24 with a mean of 0.57 (Fielder, 2014; Hayden et al., 2018; Kocovsky & Carline, 2001; Nate et al., 2011; Quist et al., 2004; Weber & Flammang, 2019). Lower mortality and relatively good growth and condition suggested that density-dependent factors were not important in 2021-2022, and we would not expect increased removal intensity to result in compensatory reductions in natural mortality that would reduce the impact of removal on Walleye abundance and consumption.

Walleye consumed almost exclusively fish, and the wide variety of species found in their stomachs indicated they were opportunistic predators. This was supported by backwater fish community sampling data (Project 138, Interagency Standardized Monitoring Program sampling https://coloradoriverrecovery.org/uc/documents/work-plan-documents/annual-reports/) that showed high abundance of nonnative cyprinids in both rivers, taxa which dominated Walleye stomach contents. Fish community sampling data also showed relatively low abundance of native species, likely contributing to their relatively low occurrence as Walleye prey.

Low occurrence of native fishes in Walleye diets should not be equated with low overall potential predation rates. We documented predation on Colorado Pikeminnow in 2021, even in a year when young Pikeminnow were very rare. Additionally, stomach content observations indicated juveniles were consumed in several other years (Francis & Ryden, 2015; K. R. Bestgen, pers comm., 2022; C. Michaud, unpublished data). Our 2021 Baseline Simulation showed that Walleye could consume twice the estimated abundance of age-0 Colorado Pikeminnow in the Colorado River in that year and triple the estimated abundance in the Green River. The logical outcome of Walleye consumption exceeding the abundance of age-0 fish is eventual extinction, even in a long-lived taxon like Colorado Pikeminnow.

Walleye predation on juvenile Colorado Pikeminnow up to 60% of predator length has also been documented (C. Michaud, unpublished data), showing that fish larger than age-0 individuals are vulnerable. Thus, average length and largest Walleye captured in both rivers—467 mm TL, and 710 mm TL, respectively could consume Colorado Pikeminnow up to 280 mm and 426 mm TL. This is problematic because Colorado Pikeminnow are slow-growing, and fish of those lengths may be 3 to 6 years old (Osmundson et al., 1998, their growth rates verified by unpublished data, K. R. Bestgen). That extended window of predation susceptibility means that entire year classes of juvenile Colorado Pikeminnow are susceptible to elimination by abundant Walleyes of average or larger size over several years. Field evidence in mark-recapture studies also showed the substantial predation effected by Walleye on larger juveniles as well. This was evident for the 2011 year class, when a group of nearly 2,400 juvenile Colorado Pikeminnow in the lower Green River and Desolation Canyon reaches of the Green River was reduced 75% by 2012-2013, years coinciding with the first large invasion of Walleyes (Bestgen et al. 2018). High predation by Walleyes on Colorado Pikeminnow was likely a primary reason adult population abundance has continued to decline in the Green River system because young fish survival was insufficient to offset adult mortality (Bestgen et al., 2007, 2018; K. R. Bestgen, unpublished data).

McGarvey et al. (2010) indicated that the ecological space for apex predators in the Green River study area was limited. Using their calculated general predator biomass and converting to that to Colorado Pikeminnow individuals showed that the Green River could support one fish for every 2.2 river hectares, or 896 adult Colorado Pikeminnow in the lower Green River study area. Mean abundance of adult Colorado pikeminnow in that reach, based on 15 estimates in the interval 2001-2024, was 279, and only 191 since Walleye invaded the system (2011-2024, Bestgen et al. 2018; KRB unpublished data). Using the McGarvey et al. (2010) estimates of predator abundance, we calculated that the Green River could support 1,267 Walleye if they were the only predator in the system. Based on our Walleye abundance estimates from the 2020-2021 data, approximately 1,000 Walleye were present in the system each year. Abundance differences demonstrated that Walleye were filling most of the ecological space in this river reach, leaving little room for piscivorous adult Colorado Pikeminnow. Walleye and Colorado Pikeminnow have similar habitat use, as both occupy the same habitat in the river channel (Michaud et al., 2018) and have similar diets (Osmundson, 2023). Therefore, Walleye may also have a competitive impact on adult Colorado Pikeminnow, for habitat and food resources.

Walleye were also a threat to the endangered Bonytail, the rarest native fish species in the UCRB. Stocked Bonytail have low survival as most were rarely seen more than one year after stocking (Bestgen et al., 2008; Pennock et al., 2024), and our diet data indicated Walleye predation was a contributing factor. Walleye abundance is lower upstream of our Study Area, but they still pose a predation threat to other native fishes, including Humpback Chub *Gila cypha* (federally listed as threatened) and Roundtail Chub *Gila robusta* (state-listed in Colorado and

Utah), species which occur in substantial numbers in Westwater Canyon and Black Rocks Canyon of the Colorado River (Francis et al., 2016; Hines et al., 2020). Populations of these fishes are also present downstream in the Colorado River in Cataract Canyon, where Walleye pass through from Lake Powell.

Warming river temperatures may also increase Walleye predation on native fishes. The 2°C increase in daily temperatures in our Climate Change Scenario resulted in a 432.9 kg increase in Walleye biomass consumption, exceeding the total biomass of juvenile Colorado Pikeminnow present in any given year. Specific estimated consumption for the Climate Change Scenario of individual age-0 Colorado Pikeminnow in the Colorado River was almost three times the abundance we estimated present in 2021. Bonytail and other native fishes would also experience increased predation from thermally increased Walleye consumption. It should be noted that in our Climate Change simulations, there was a period during summer when Walleye lost weight due to high temperatures; however, their modeled annual growth was unaffected due to enhanced thermal conditions during fall and spring.

Under current conditions, the Walleye population in the Colorado and Green rivers was sufficient to stymie the recovery of Colorado Pikeminnow. For example, if age-0 Colorado Pikeminnow abundance had been closer to their historical level in the Green River, with a commensurate increase in their contribution to Walleye diet, Walleye consumption would still have been sufficient to eliminate them. In fact, the 2021-2022 Walleye population could consume 14.5 times the historical abundance of age-0 Colorado Pikeminnow each year if Colorado Pikeminnow comprised just 5% of the Walleye diet. These realistic predation projections indicated continued existence of Colorado Pikeminnow in the UCRB will require significant management interventions directed at Walleye.

Simulations showed that reducing Walleye abundance was a potentially effective tool to reduce predation on Colorado Pikeminnow and other endangered fish. For example, if 75% of the existing Walleye population was removed, consumption of age-0 Colorado Pikeminnow could be reduced from 14,872 to 3,846 fish in the Baseline Scenario simulation. The resulting difference, 11,026 age-0 Colorado Pikeminnow, was greater than the estimated age-0 population present in 2021 by a substantial margin, with obvious potential benefits to eventual recruitment. Other native taxa would similarly benefit by reducing Walleye abundance.

Management implications

Our simulations quantified the large negative impacts of Walleye predation on endangered fish, now and into the future. Below we discuss additional management actions that should be evaluated to reduce predation by Walleye.

First, increased in-river removal effort should be considered by managers to reduce Walleye abundance. This would be especially timely given that a relatively large population of juvenile Colorado Pikeminnow existed in the lower reaches of the Green River in 2024 (K.R. Bestgen, unpublished abundance estimates), the first of its kind in several years. The low number of adults that remain in the Green River basin—now substantially less than 1,000 fish—indicated the potential for future large juvenile year classes was low, so immediate action is imperative to increase their survival to bolster adult numbers in the future.

A second approach to reduce Walleye predation on native fishes is to reduce their immigration into nursery habitat. Screening upstream reservoirs has been conducted and may be at least partially responsible for recent reduced Walleye abundance in Green River reaches upstream of Tusher Diversion. Screens should be maintained or bolstered to withstand high flow events such as those in spring 2023, where some may have failed and allowed Walleye to escape, resulting in notable increases in downstream abundance (Amidon et al. 2024). A corollary need was ensuring that passage of juvenile Colorado Pikeminnow over the Tusher Diversion out of the high-Walleye-density areas in the lower Green River was occurring to repopulate upstream reaches, a known life history strategy (Bestgen et al. 2007). This assessment is needed because Colorado Pikeminnow movements over the relatively recently redesigned Tusher Diversion have not been verified.

It also seems clear, based on demographic evidence and other research (Johnson et al., 2014), that immigration upstream from Lake Powell was a main source of Walleye into adjacent riverine habitat. Walleye are typically disinclined to use upstream fish passage structures and move past barriers (Peake et al., 2000), so a barrier that excludes them is a potential option. However, screening the large, highly variable Colorado River to prevent upstream passage of fish, including Walleyes, may be challenging. At a minimum, knowing when upstream Walleye movements occurred and what motivated their movement within and among years would be useful information to guide possible strategies to reduce immigration and abundance in native fish nursery habitats.

Management to reduce abundance of Walleye in Lake Powell, the probable Walleye source population, may result in fewer fish available to move upstream. This could be accomplished by agency removals or incentivizing angler harvest in the reservoir. For instance, an angler incentive program was successful at removing about 5,000,000 predators in the Columbia River basin (Beamesderfer et al., 1996; Klein et al., 2023). Angler harvest incentive programs and in situ removals could occur across the entirety of Lake Powell, but a focus on the Colorado River arm where Walleye were most abundant (Blommer & Gustaveson, 2021; Pennock & Gido, 2021), may be most effective. A combination of angler and mechanical removals, similar to what was used at Buffalo Bill Reservoir, WY (Kaus, 2019) and Lake Pend Oreille, ID (Ryan et al., 2021) may also be an effective suppression option. Commercial fishery expertise, similar to that used in Yellowstone Lake to suppress invasive Lake Trout (Koel et al., 2020), is another suppression option.

Yet another in-lake management action to reduce Walleye may involve genetic biocontrol applications, including YY chromosome individuals (Armstrong et al., 2022; Gutierrez & Teem, 2006; Miller et al., 2024) or gene drive approaches (Teem et al., 2020). This technology is largely unproven, especially in large and open environments, but seems worthwhile to consider for a problem of this magnitude and importance.

We have demonstrated that Walleye predation was a potentially major contributor to the demise of native and endangered fishes in the Upper Colorado River Basin. Broadening our ecological knowledge of Walleye, which was largely unknown in this system until recently, would be productive to focus management efforts. Specific information to better inform Walleye management may include verification of abundance estimates, understanding drivers of recruitment to riverine populations, and linking Lake Powell and riverine population dynamics. Understanding movement patterns specific to when fish move in and from Lake Powell, and if seasonal patterns between the lake and rivers were apparent, would inform time-specific removal efforts, and perhaps, identify hotspots where barriers or suppression could be focused. Any in-lake suppression efforts, whether increased harvest or genetic applications, would require the support of state fish management agencies. Determining if Tusher Diversion is an upstream barrier would also be useful to know so that it can be maintained or enhanced. Meanwhile, increased removal efforts are urgently needed to temporarily suppress Walleye predation so juvenile Colorado Pikeminnow recruitment can supplement declining abundance of adults and forestall further declines toward extinction.

TABLES

Table 1. Energy density (J/g wet weight) of Walleye prey used in bioenergetics simulations.

Prey taxon	Energy density	Source
Bonytail	4,200	Hanson et al., 1997
Colorado Pikeminnow	3,743	Parrish et al., 2006
Other *Gila* spp.	4,200	Hanson et al., 1997
Native catostomids	3,639	Bryan et al., 1996
Speckled Dace	4,558	Parrish et al., 2006
Gizzard Shad	4,301	Pothoven et al., 2017
Nonnative cyprinids	4,417	Deslauriers et al., 2017, Bryan et al., 1996, Pothoven et al., 2017
Nonnative sport fish	5,246	Parrish et al., 2006, Deslauriers et al., 2017
Invertebrates	4,526	James et al., 2012

Table 2. Average diet composition (%) of Walleye from the Green and Colorado Rivers, Utah, during 2021 and 2022.

Prey taxon	By weight	By count
Bonytail	1.2	1.0
Colorado Pikeminnow	0.2	0.05
Other *Gila* spp.	2.3	1.8
Native catostomids	5.3	4.3
Speckled Dace	3.4	1.7
Gizzard Shad	11.0	9.7
Nonnative cyprinids	62.2	52.1
Nonnative sport fish	13.9	12.5
Invertebrates	0.6	0.4
Unidentified fish	NA	16.4

Table 3. Seasonal diet composition (% by weight) of Walleyes in the Colorado River, Utah, during 2021 and 2022.

Prey taxon	2021		2022	
	Spring	Summer-Fall	Spring	Summer-Fall
Bonytail	0.0	0.0	4.5	0.0
Colorado Pikeminnow	0.6	0.0	0.0	0.0
Other *Gila* spp.	3.7	2.6	0.0	0.0
Native catostomids	9.8	3.6	0.0	3.7
Speckled Dace	0.5	0.0	0.0	0.0
Gizzard Shad	0.0	24.8	0.0	30.7
Nonnative cyprinids	82.8	57.9	54.5	16.1
Nonnative sport fish	1.8	11.0	40.9	49.5
Invertebrates	0.9	0.0	0.0	0.0

Table 4. Diet composition (% by weight) of Walleyes in the Green River, Utah, during Spring 2021 and 2022.

Prey taxon	2021	2022
Bonytail	3.0	4.7
Colorado Pikeminnow	0.0	0
Other *Gila* spp.	3.3	0
Native catostomids	5.4	2.4
Speckled Dace	34.0	0
Gizzard Shad	0.0	4.4
Nonnative cyprinids	46.0	68
Nonnative sport fish	9.1	18
Invertebrates	0.0	2.4

Table 5. Individual consumption (kg) by female and male Walleye of each age averaged for the two-year simulation period in both rivers in the Baseline Scenario.

Age	Female	Male
1	0.37	0.36
2	1.13	1.05
3	2.12	1.58
4	2.87	1.96
5	3.47	2.22
6	3.95	2.34
7	4.31	2.49
8	4.58	2.58
9	4.79	
10	4.94	
Total	32.53	14.58

Table 6. Walleye population consumption of all prey (kg) in the Baseline Scenario simulation, by sex and age, in the Colorado River, Utah, over the two-year period.

	1st year			2nd year		
Age	Female	Male	Total	Female	Male	Total
1	3.0	2.9	6.0	2.0	1.9	3.9
2	63.9	59.6	123.4	41.2	38.4	79.6
3	213.0	158.7	371.7	138.5	102.7	241.3
4	307.2	211.7	518.9	198.0	135.5	333.5
5	290.0	187.1	477.1	188.6	120.6	309.2
6	209.4	126.1	335.4	135.2	80.5	215.7
7	164.6	96.2	260.8	106.0	61.4	167.4
8	106.7	62.7	169.4	68.4	38.4	106.8
9	8.0	0.0	8.0	3.6	0.0	3.6
10	4.1	0.0	4.1	3.7	0.0	3.7
Total	1369.9	904.9	2274.7	885.3	579.5	1464.8

Table 7. Walleye population consumption of all prey (kg) in the Baseline Scenario simulation, by sex and age, in the Green River, Utah, over the two-year period.

Age	1st year			2nd year		
	Female	Male	Total	Female	Male	Total
1	2.6	2.5	5.2	2.1	2.1	4.2
2	55.7	52	107.7	46.8	43.6	90.5
3	188.5	140.4	328.8	158.4	117.5	275.9
4	270.9	186.8	457.6	226.8	155.4	382.2
5	257.9	166.4	424.3	215.4	138.0	353.4
6	184.4	111.1	295.5	154.1	91.9	246.0
7	143.6	83.9	227.6	121.7	70.5	192.2
8	94.7	53.7	148.4	79.7	50.5	130.2
9	15.2	0	15.2	6.9	0.0	6.9
10	7.9	0	7.9	3.6	0.0	3.6
Total	1,221.4	796.8	2,018.2	1015.6	669.6	1685.2

Table 8. Walleye population consumption (kg) for the Baseline Scenario simulation in the Colorado and Green rivers, Utah, over the two-year period.

	Colorado River		Green River	
Prey Categories	1st year	2nd year	1st year	2nd year
Bonytail	-	29.0	27.3	35.3
Colorado Pikeminnow	5.8	-	-	-
Other *Gila* spp.	70.6	-	56.8	-
Native catostomids	144.9	30.6	89.0	52.5
Speckled Dace	4.7	-	302.7	-
Gizzard Shad	313.2	253.2	-	32.8
Nonnative cyprinids	1569.1	481.7	1059.6	658.4
Nonnative sport fish	156.9	670.2	482.9	888.3
Invertebrates	9.6	-	-	17.8
Total	2,207.2	1,412.9	2018.2	1685.2

Table 9. Estimated consumption of prey (kg) by the Walleye population in the Climate Change Scenario in the Colorado and Green rivers, Utah, summed over the two-year simulation period.

Prey Categories	Colorado River	Green River
Bonytail	37.4	79.5
Colorado Pikeminnow	7.2	-
Other *Gila* spp.	76.4	60.2
Native catostomids	191.2	150.7
Speckled Dace	5.8	381.9
Gizzard Shad	512.0	41.8
Nonnative cyprinids	2268.8	1870.2
Nonnative sport fish	850.3	1307.9
Invertebrate	11.8	22.8
Total	3960.8	3915.0

Table 10. Walleye consumption of native and nonnative fishes in the Removal Scenario compared to the Baseline, summed for the two-year period in the Colorado and Green Rivers, Utah.

Prey Category		Walleye abundance reduction		
	Baseline	25%	50%	75%
Bonytail	91.6	68.7	45.8	22.9
Colorado Pikeminnow	5.8	4.4	2.9	1.5
Other *Gila* spp.	127.4	95.6	63.7	31.9
Native catostomids	317.0	237.8	158.5	79.3
Speckled Dace	307.4	230.5	153.7	76.8
Gizzard Shad	599.2	449.4	299.6	149.8
Nonnative cyprinids	3768.8	2826.6	1884.4	942.2
Nonnative sport fish	2198.2	1648.7	1099.1	549.6
Invertebrates	27.4	20.6	13.7	6.9
Total	7442.9	5582.2	3721.4	1860.7

FIGURES

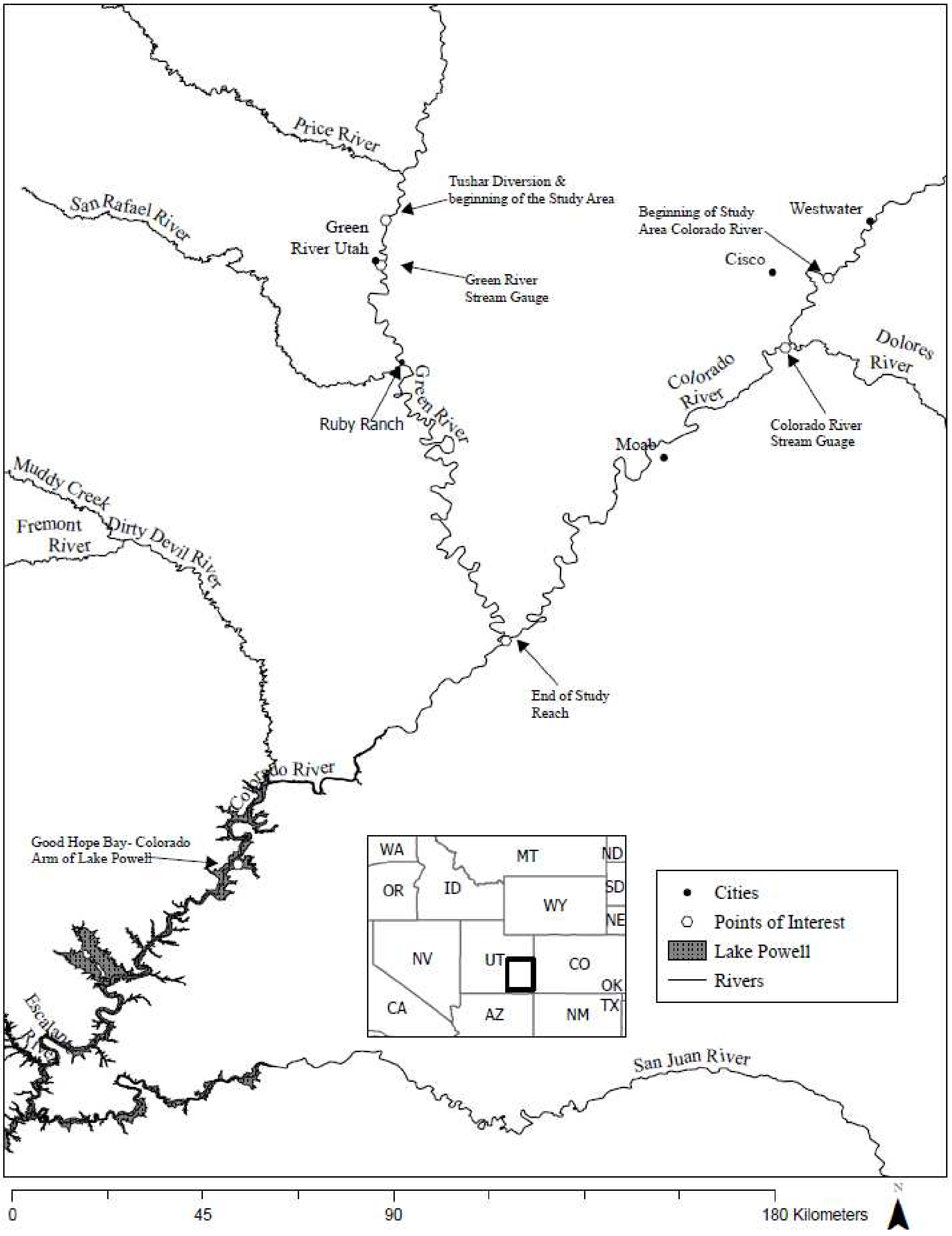

Figure 1. Map of study area, Upper Colorado River basin.

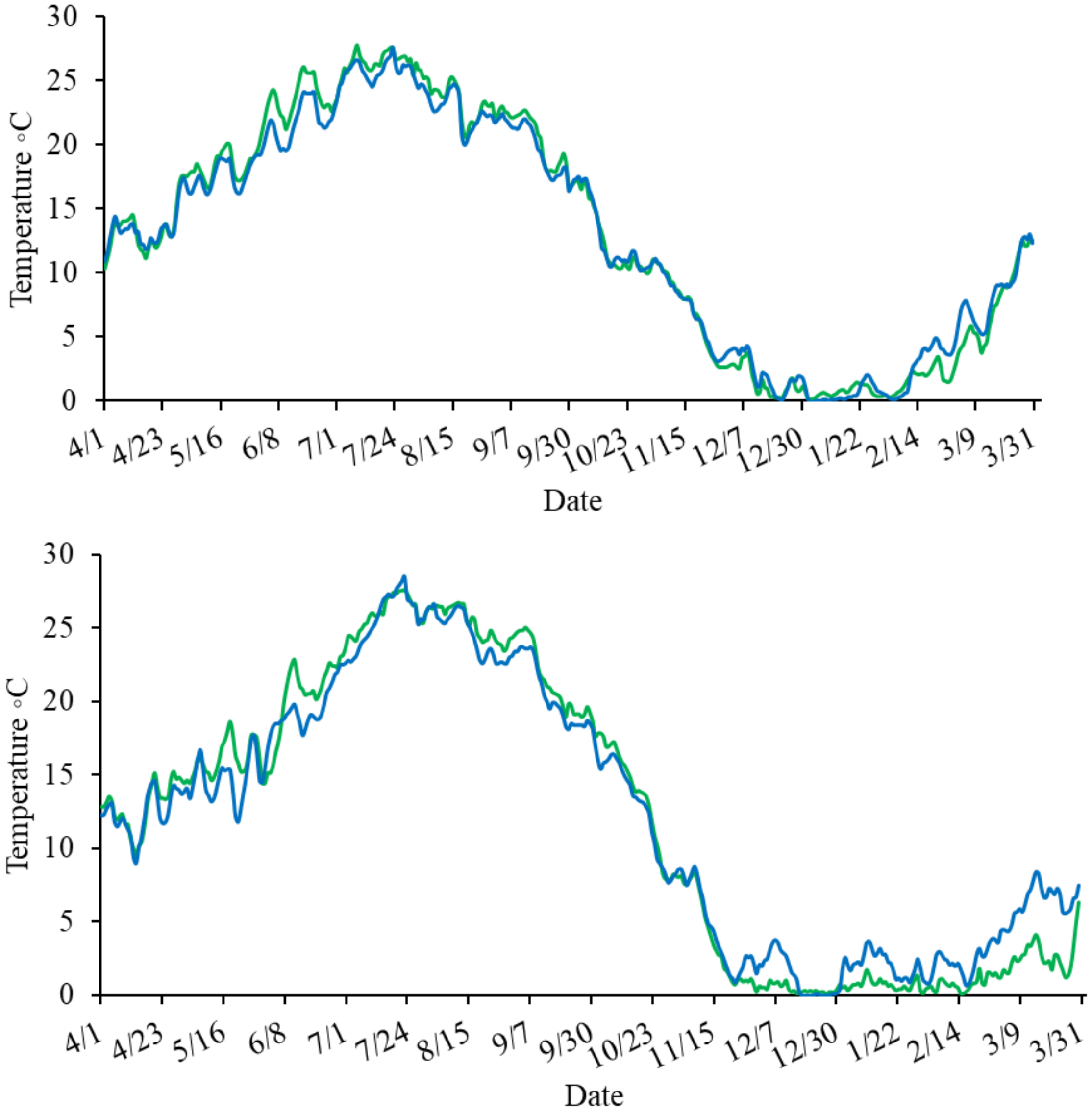

Figure 2. Thermographs for the Green (green lines) and Colorado (blue) Rivers, Utah, from April 1st, 2021, to March 31st, 2022 (top) and April 1st, 2022, to March 31st, 2023 (bottom). Data from U.S. Geological Survey stream gauges: Green River (09315000) and Colorado River (09180500).

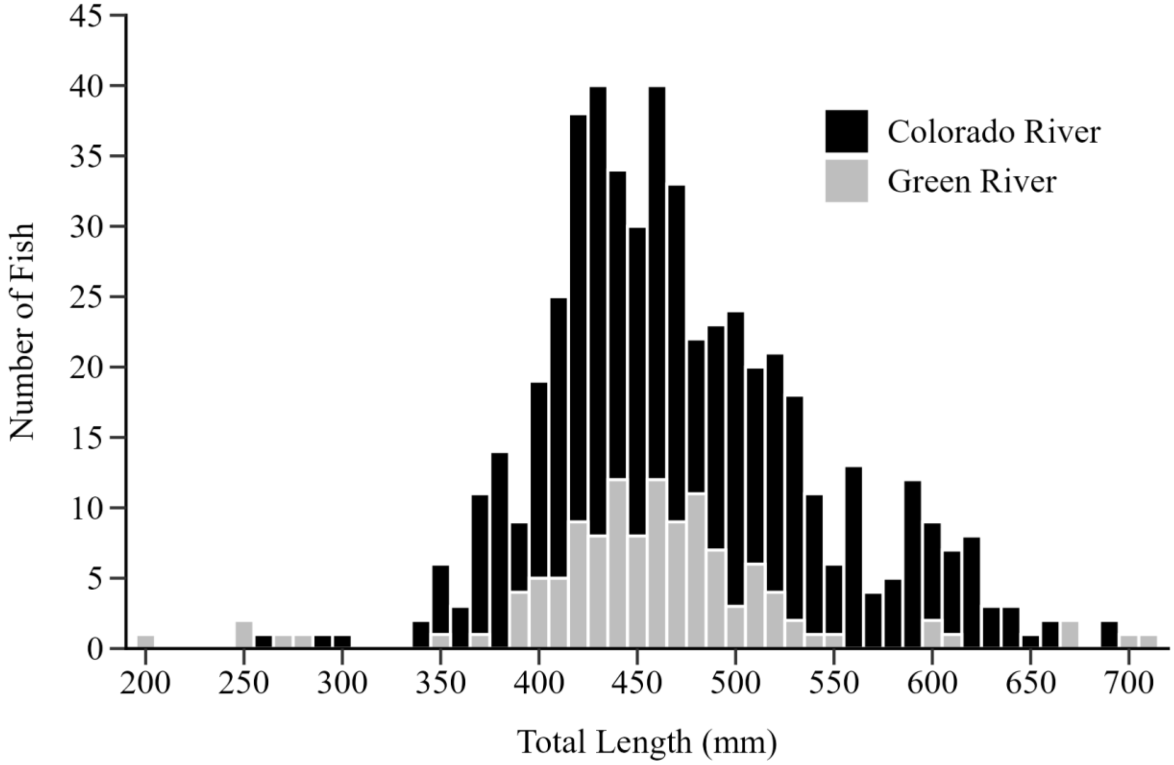

Figure 3. Length-frequency histogram for Walleyes sampled during 2021 and 2022, in the Green and Colorado Rivers, Utah.

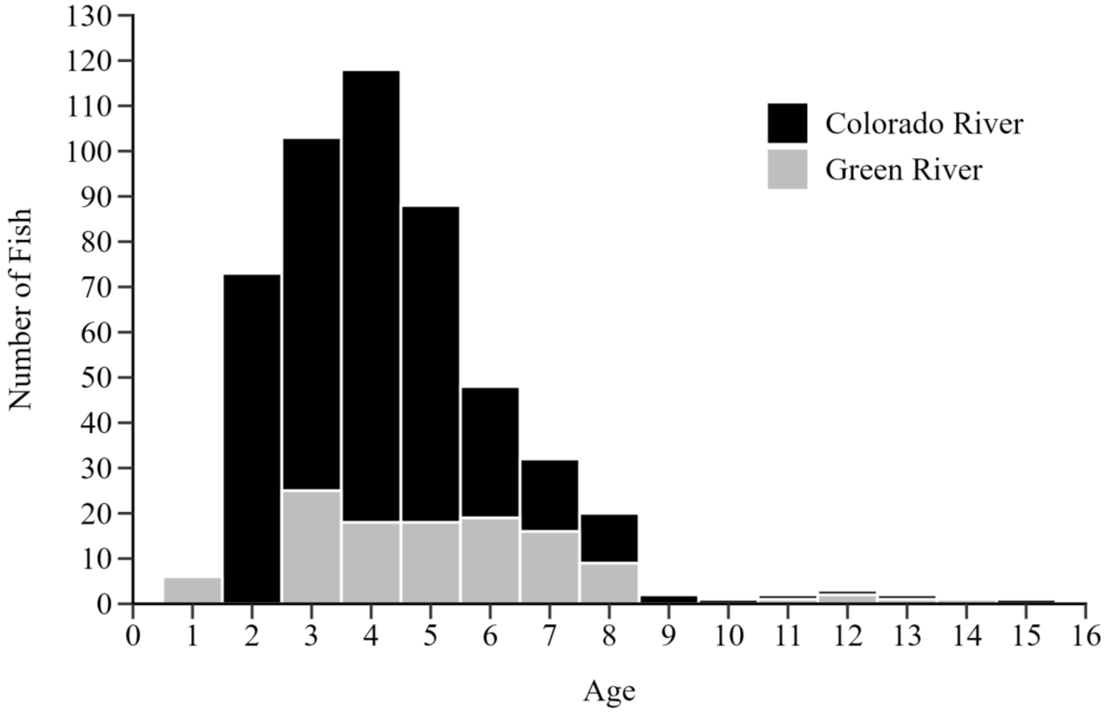

Figure 4. Age-frequency histogram for Walleyes sampled in the Green and Colorado Rivers, Utah, in 2021 and 2022.

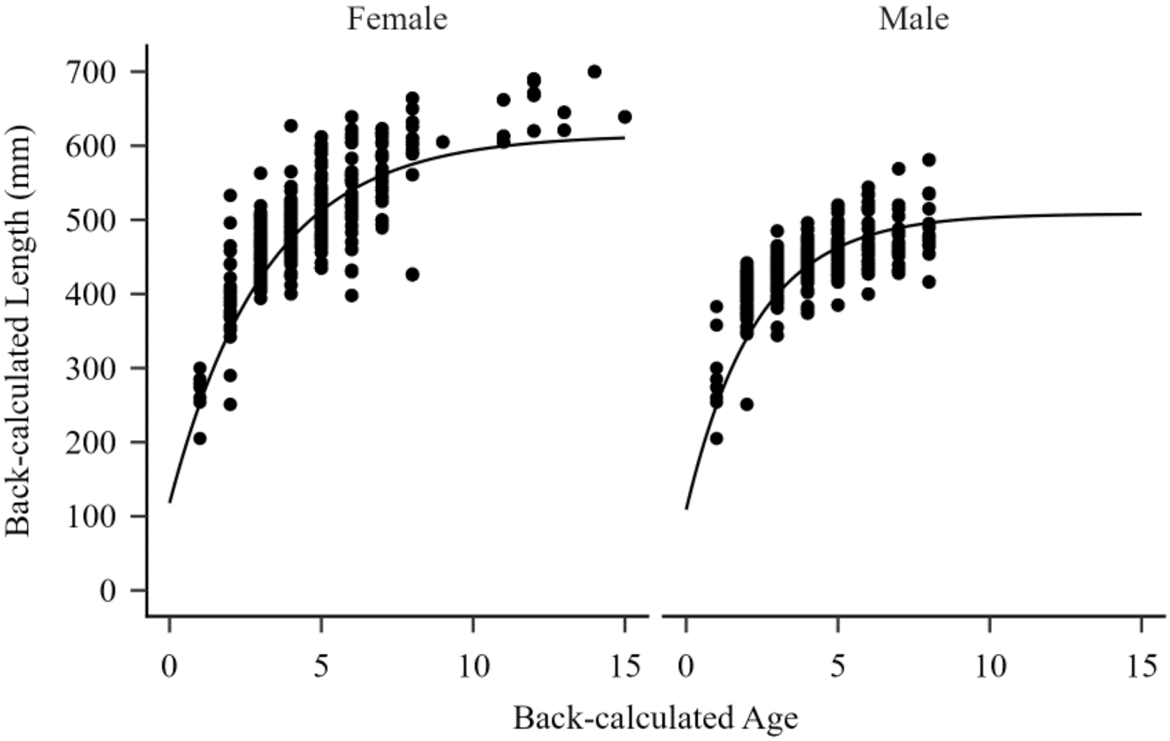

Figure 5. Pütter-von Bertalanffy growth model fits to back-calculated lengths-at-age for female and male Walleye sampled in the Colorado and Green Rivers, Utah.

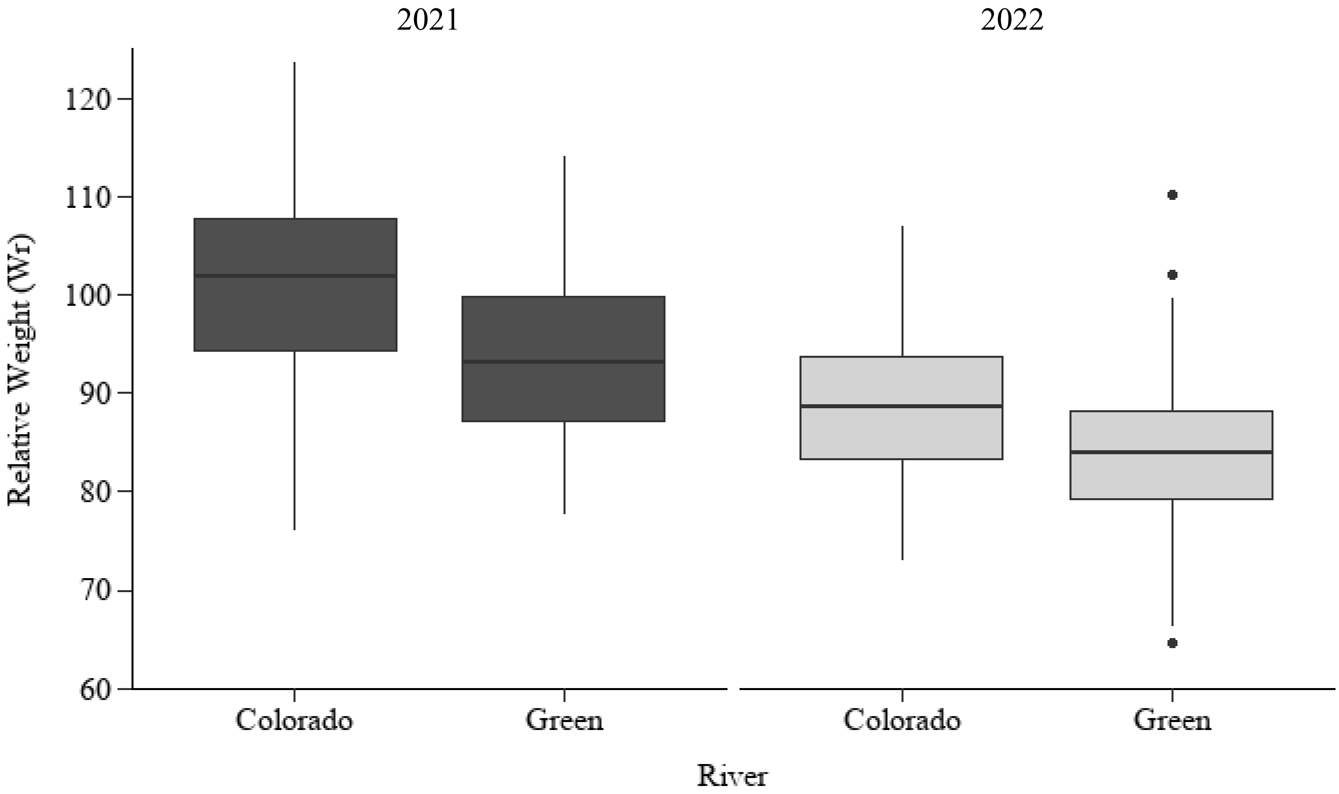

Figure 6. Relative weight (W_r) of post-spawn Walleyes sampled in the Colorado and Green Rivers, Utah, during spring 2021 and 2022.

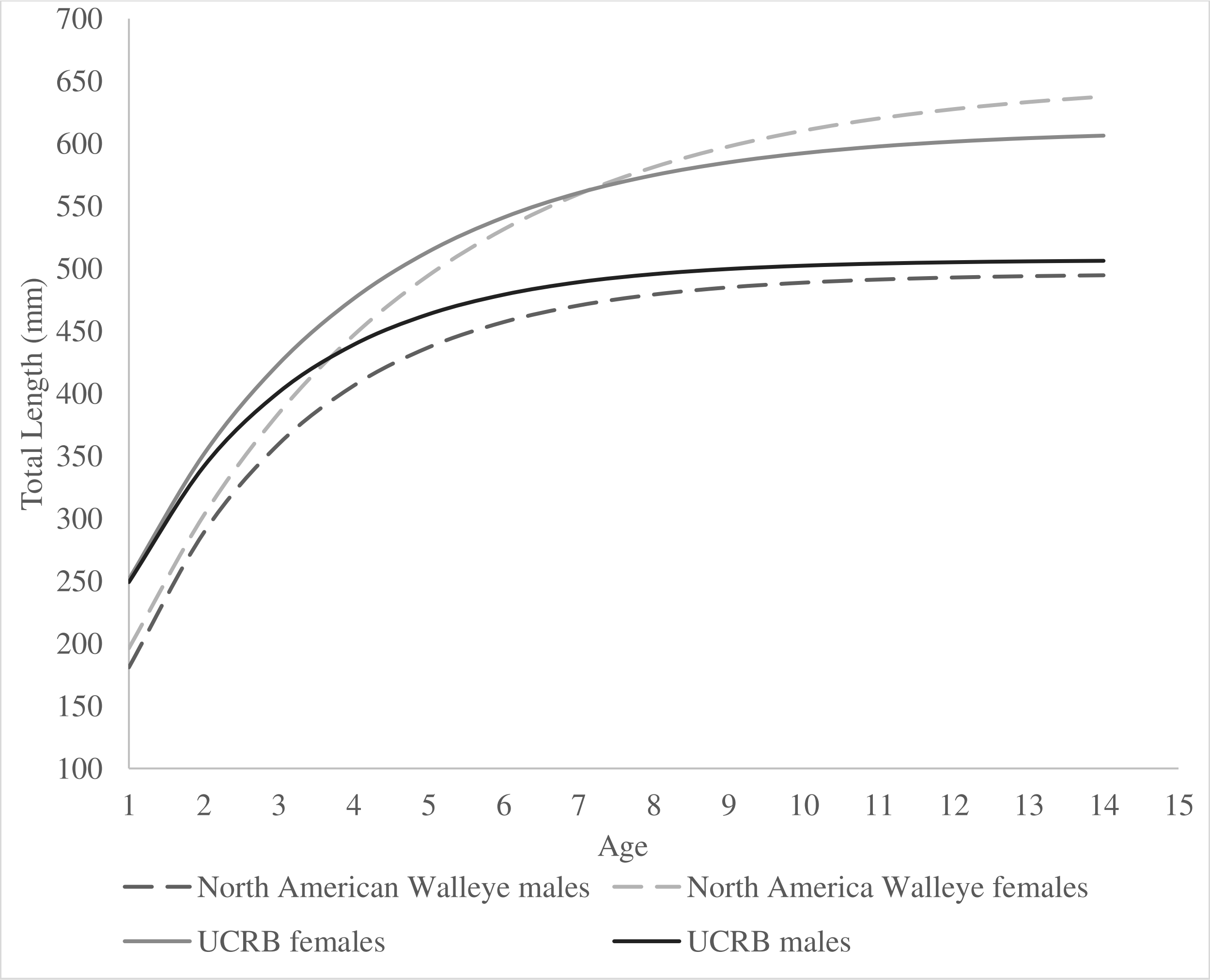

Figure 7. Pütter-von Bertalanffy growth curves for male and female Walleyes in the Upper Colorado River Basin (present study) and the averages for North American populations (Quist et al., 2003).

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