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Efficacy of Conservation Actions for Imperiled Colorado River Fishes in the Grand Canyon, Arizona

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EFFICACY OF CONSERVATION ACTIONS FOR IMPERILED

COLORADO RIVER FISHES IN THE

GRAND CANYON, ARIZONA

by

Brian D. Healy

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ABSTRACT

Efficacy of Conservation Actions for Imperiled Colorado River Fishes

in the Grand Canyon, Arizona

by

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Utah State University, 2022

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River regulation, human water use, and the introduction of invasive predators are primary factors leading to the imperilment of many fishes. In the Grand Canyon, Arizona, native fish conservation actions are in progress, including invasive fish suppression and translocations of the endangered humpback chub (*Gila cypha*) to habitats with natural flow regimes and fewer invasive fishes. Yet the population-level responses of both native and invasive fishes to these actions have been equivocal; environmental variability and ecosystem complexity have sometimes confounded the interpretation of outcomes. My research objectives were to assess the efficacy of these efforts in restoring native fish communities and mitigating threats of invasive species, by 1) quantifying the population-level effects of invasive trout suppression and environmental variability on the distribution and abundance of native fishes; 2) assessing factors driving the demographic vital rates (i.e., survival, recruitment, mortality) in translocated populations of humpback chub in small Colorado River tributaries; and, 3) evaluating alternative suppression strategies for an invasive brown trout (*Salmo trutta*) Colorado River and tributary metapopulation. In chapter 2, I found native species to increase by ~480% once trout

were suppressed by >60%, and the greatest increases in native fish abundance occurred in warmer reaches, in years with spring flooding and less-intense monsoon-driven flooding. In chapter 3, evidence supported hypotheses related to density-dependence in population growth, survival, and recruitment of translocated humpback chub, and invasive trout further limited somatic growth and recruitment. Somatic growth was higher in summers with greater flood-pulse frequency. My chapter 4 modeling showed metapopulation-scale suppression of all life stages was necessary to achieve rapid declines in brown trout – without intense suppression, metapopulation dynamics would allow for persistence of brown trout under warmer conditions related to water overallocation and climate change. Through quantitative analysis of commonly applied conservation strategies, species translocations and invasive species suppression, my research findings should inform native fish conservation in the Grand Canyon and elsewhere. I demonstrated the importance of mitigating limiting factors prior to initiating translocations to establish new populations, as well as the threat of introduced species to riverine native fish populations under plausible future conditions.

(283 pages)

PUBLIC ABSTRACT

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Many fishes are critically imperiled, particularly in their native rivers, due to

human water use and dam construction, which can dramatically alter habitats and block

fish migratory routes. The introduction of invasive sport-fishes that prey on native fish

further threatens native species that may be restricted to only a single river basin (i.e.,

"endemic"). To preserve native fishes in river systems with degraded habitats, managers

need to understand the effects of conservation actions to ensure limited resources are

applied effectively. Two commonly applied native fish conservation actions include

removal of invasive fishes, and translocations of native fish from one place into another

with suitable habitat to establish new populations. My primary research goals were 1) to

assess the population-level native fish responses to invasive fish removal, 2) understand

what factors lead to successful establishment of new endangered humpback chub

populations through translocations of juveniles, and 3) to investigate alternative strategies

for reducing invasive brown trout using angling, disturbance of eggs, and electrofishing,

in multiple connected populations (i.e., trout move between them) experiencing different

levels of warming and climate change. My research was conducted using data collected

over 10 years in the Colorado River and its tributaries in Grand Canyon National Park.

I found native fish populations increased by about 480% when invasive trout

populations were reduced by 60% or more. Increases in native fish were also greatest in

warmer areas in years when spring flooding occurred. Translocated humpback chub

populations were limited when numbers of introduced rainbow trout were higher and when floods washed ash from a fire into one stream in 2014. However, I found flooding was generally beneficial to humpback chub, which was probably because additional food was washed into their habitats. Finally, while future declines in Colorado River reservoir storage and warming of streamflow may reduce brown trout, successful Grand Canyon-wide reductions would require increasing trout removals throughout the river system particularly in tributary climate change refuges. In summary, translocations can contribute toward native fish conservation, but continued invasive fish removal and protection of natural river flow are also critical to meeting conservation goals.

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suppression projects – all of which are incredibly physically and mentally challenging, and often conducted in stressful working conditions. Emily, Robert, Rebecca, and Sarah Haas also covered many of my duties while I was on leave attending classes in Logan. I also appreciated the many hours of debate and discussion with Nic Medley and others that led to the hypotheses I explored in chapter 3.

The Grand Canyon backcountry is among the most difficult and environmentally-challenging environments in which to conduct field work. I am grateful for the thousands of hours spent collecting data by dozens of volunteers, NPS and ACE technicians (listed in the acknowledgments of my published chapter 2 manuscript), led by our skilled NFEC biologists and crew leads. I am grateful for the work of Santiago Garcia, who in my opinion fills the most important position in GCNP as database manager, and for the assistance of Rebecca Koller, for skillful and careful management of data I used in my research. Without the logistical support by boat operators, helicopter pilots and managers, trail crew, rangers, compliance specialists, and resource subject matter experts my research would not have been possible.

Many individuals from the Bureau of Reclamation, U. S. Fish and Wildlife Service, USGS-Grand Canyon Monitoring and Research Center, and Arizona Game and Fish Department provided technical and field assistance, recapture data used in chapter 3, and hatchery rearing of humpback chub. I am grateful for the assistance of Mike Yard, Kim Dibble, Maria Dzul, Dave Rogowski, Pilar Wolters, David Ward. Dr. Craig Paukert, University of Missouri, Dave Speas, Mark McKinstry, and Marianne Crawford (Reclamation), and Pam Sponholtz, Manual Ulibarri, Kirk Young, Randy Van Haverbeke, Dennis Stone, Mike Pillow, and Shaula Hedwall (USFWS) provided

align with the values of these tribes, but I hope my research leads to greater protection of the values they consider sacred.

Finally, and most importantly, without the support of my wife, Susie, I would not have been able to attend USU and complete my Ph.D. I am deeply grateful for her love, understanding, and patience, and for the support and encouragement provided by my family.

Brian D. Healy

CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Advancing our understanding of riverine ecosystem function (Palmer and Ruhi 2019, Tickner et al. 2020) and factors regulating populations (Strayer and Dudgeon 2010) is critical to effectively confront pervasive threats to native fishes. Invasive species introductions, degradation in water quality, a changing climate, and altered flood frequency and magnitude, continue to drive losses in native aquatic biodiversity (Poff et al. 1997, Palmer et al. 2008, Reid et al. 2019). Where opportunities exist for restoration of degraded aquatic ecosystems, knowledge of ecosystem function and a thorough evaluation of the consequences of management actions are critical to achieving restoration objectives (Schmidt et al. 1998), and predicting responses of future management actions (Nichols and Williams 2006). Yet, monitoring of management actions is often insufficient to determine outcomes, which is often the case in species reintroductions (Strayer and Dudgeon 2010, Nichols and Armstrong 2012). Management actions can also produce unexpected or equivocal results (Pine et al. 2009, Melis et al. 2015) that may be confounded by environmental variation, including invasive species suppression (Coggins et al. 2011). Given differences in how populations of species are regulated at low densities (i.e., density-dependent vs. density-independent drivers), responses to conservation programs including predator removal or managed relocations may differ. Thus, there exists a clear need to comprehensively evaluate species' population-level responses to conservation actions in order to adaptively manage restoration programs and develop and improve predictive science (Nichols and Williams 2006).

Life history models suggest species' life history traits evolved under specific ranges in environmental variability (Winemiller and Rose 1992), and persistent alterations outside this norm can alter regional species diversity and community structure (Lake 2000, Mims and Olden 2012). Demands for hydropower in dammed rivers can lead to increases in daily fluctuations and extirpation of aquatic biota (Kennedy et al. 2016), and homogenization of annual flow variability or shifts in thermal regimes may also disproportionately advantage invasive fishes (Olden et al. 2006, Poff et al. 2007, Dibble et al. 2021). For example, stable, more predictable annual flow regimes may favor "equilibrium" life history strategies where density-dependent biotic interactions, rather than stochastic or density-independent forces, regulate populations (Winemiller and Rose 1992, Olden et al. 2006, Mims and Olden 2012). Fishes having equilibrium life history strategies may include nonnative predatory fishes such as those that thrive in reservoirs, or where flood flows are now rare due to river regulation. River regulation and dam construction also fragment habitats and block migratory routes, which is also a critical aspect of adfluvial and fluvial life histories of many native fishes (reviewed in Liermann et al. 2012; e.g., bluehead sucker, Catostomus discobolus, Webber et al. 2012). In contrast, connectivity between suitable habitat patches in river networks can also benefit invasive species by promoting colonization and expansion (Milt et al. 2018). Consequently, there is a need to balance connectivity between sub-populations while preventing invasions, and understand how stressors, including invading species and water development, impact and regulate populations of native fishes. These research goals are particularly important for managing endangered fishes in dam-fragmented rivers with

highly altered flow and thermal regimes in vulnerable semi-arid to arid regions such as the Colorado River Basin.

The impacts to native fishes associated with water development and other land use changes may be exceptionally severe in desert regions (Williams et al. 1985, Sabo et al. 2010). In particular, the fishes of the Colorado River of the American Southwest are at risk as a result of regionally-widespread impacts (Minckley et al. 2003, Minkley and Marsh 2009). Across the Colorado River Basin, prominent changes in baseflow and peakflow have occurred due to trans-basin diversions for irrigation and municipal use, and dam construction for water storage and hydropower generation (Schmidt 2008) – water losses due to consumptive use now exceed supply (reviewed in Wheeler et al. 2021). Effects of water development to riverine fauna are compounded by the pervasiveness of nonnative fish introductions and invasions across the basin. Collectively, these habitat alterations have led to the decline and listing of several endemic Colorado River fishes under the U. S. Endangered Species Act (ESA; Minckley et al. 2003, Olden et al. 2006). ESA-listed fishes include the endemic humpback chub (*Gila cypha*), bonytail (*Gila elegans*), Colorado pikeminnow (*Ptychocheilus lucius*), and the razorback sucker (*Xyrauchen texanus*), but others are considered imperiled and predicted to decline with decreasing streamflow (Budy et al. 2015, Ruhí et al. 2016).

Predation by nonnative fishes is a primary obstacle to recovering the native fish fauna throughout the Colorado River Basin (Minckley et al. 2003, Mueller 2005, Bestgen et al. 2006) For example, almost complete losses of stocked endangered fishes have been noted due to predation (Schooley and Marsh 2007, Webber and Haines 2014, Bestgen et al. 2017). The Grand Canyon segment of the Colorado River is somewhat unique, in that

warmwater invasive fishes that threaten endangered fishes in other segments of the Basin have been relatively rare, and the altered, post-dam thermal regime was the primary impediment to native fish recovery (cf. Clarkson and Childs 2000, Yackulic et al. 2014, 2018). Recovery actions for the Colorado River endangered fishes have included nonnative fish control (Tyus and Saunders 2000, Coggins et al. 2011, Franssen et al. 2014, Zelasko et al. 2016, Pennock et al. 2018), translocations or relocations (Healy et al. 2020, Yackulic et al. 2021), stocking (Schooley and Marsh 2007, Franssen et al. 2016, Bestgen et al. 2017), flow manipulations to stabilize rearing habitats (Dodrill et al. 2015, Finch et al. 2016), and attempts to mimic natural flooding (Valdez et al. 2001, Propst and Gido 2004, Cross et al. 2011, Korman et al. 2011), among others.

The results of nonnative fish control have been equivocal; in some cases nonnative fish have increased dramatically following incomplete removal due to a release from density-dependence (Franssen et al. 2014, Zelasko et al. 2016, Pennock et al. 2018), or system-wide changes in environmental variables have occurred concurrently with control projects, confounding the interpretation of results (Coggins et al. 2011). Still others have achieved declines in nonnative fishes, but no responses to these declines were demonstrated in native species (Franssen et al. 2014, Pennock et al. 2018). However, translocations of endangered fishes in Grand Canyon have led to successful juvenile rearing (Spurgeon et al. 2015b, Stone et al. 2020), and reproduction in a translocated population (Healy et al. 2020). Given the varying levels of success demonstrated by these programs, there is a great need to understand the mechanisms behind successful or failed attempts to achieve conservation goals.

For my dissertation research, I critically evaluated the demographic response of both native and nonnative fishes to an invasive fish suppression program and translocations in the Grand Canyon, Arizona, while accounting for background environmental factors. In addition, a newly invading brown trout (*Salmo trutta*) population is becoming established in Glen Canyon, which is threatening native fishes in the Grand Canyon and challenging managers to develop and implement and effective suppression strategies (Runge et al. 2018). I also investigated potential suppression strategies for invasive brown trout, at a metapopulation scale.

For my second dissertation chapter, I investigated the responses of the fish assemblage to an intensive stream-wide invasive fish suppression effort conducted over eight years in Bright Angel Creek (Healy et al. 2022). Invasive fishes were removed, and native species were monitored, using electrofishing throughout Bright Angel Creek and a weir installed near the mouth of the creek. A comprehensive analysis was needed to understand the effects of suppression of brown trout and rainbow trout (*Oncorhynchus mykiss*), in the context of environmental variation, on the population dynamics (i.e., population growth rate) and distribution of native and invasive fishes. In addition, electrofishing can have lethal and sublethal effects on individual fish; I assessed the potentially harmful effects of repeated electrofishing (Ruppert and Muth 1997, Snyder 2003) on bluehead sucker and speckled dace (*Rhinicthys osculus*) in the context of population-scale benefits that may be incurred through reduced predation and competition with nonnative salmonids (Whiting et al. 2014, Spurgeon et al. 2015a). My analysis represents a rare and important example of a positive response in native fishes

following invasive species suppression, while accounting for the effects of environmental variation on population growth rates.

In my third chapter, I analyzed the abiotic and biotic drivers of somatic growth, survival, and recruitment of translocated humpback chub in Shinumo and Havasu creeks. I estimated survival while accounting for release site fidelity using both recaptures and detections at both translocation sites and from throughout the Colorado River ecosystem (Colorado River and its tributaries in the Grand Canyon). Differences in hydrology and temperature regimes, fish communities including abundances of invasive fishes, aquatic macroinvertebrate communities (Oberlin et al. 1999), and carrying capacities may exist between the release sites that could influence establishment of self-sustaining populations of humpback chub (Valdez et al. 2000, Pine et al. 2013). Only rarely are thorough analyses of the population dynamics of translocated populations of endangered fishes completed, and often these translocations fail (Nichols and Armstrong 2012). My research demonstrates how translocations can contribute to the recovery of large-river fishes by increasing population redundancy, and illuminated factors driving translocated fish population dynamics – knowledge that will inform conservation actions meant to stem global-scale biodiversity loss in freshwater ecosystems (Tickner et al. 2020).

For my fourth chapter, I explored alternative suppression strategies for a metapopulation of invasive brown trout inhabiting patches of differing size and habitat quality in Glen and Grand Canyons. The trajectory of habitat change may differ between the Colorado River and its tributaries related to water use and reservoir storage decisions and climate change – I accounted for these changes in simulated scenarios. I parameterized a matrix-based metapopulation model (Murphy et al. 2020) to compare the

effects of combinations of angler harvest, redd disruption (Korman et al. 2011), and mechanical removal (electrofishing; Yackulic et al. 2020, Healy et al. 2022) on brown trout population growth rates, minimum population size, and probability of attaining a quasi-extinction level (5% of carrying capacity). I used linear mixed-effects models to understand drivers of brown trout recruitment for modeled habitat suitability functions, and used both empirically-derived and literature-based vital rates (e.g., Budy et al. 2008, Grossman et al. 2017, Yackulic et al. 2020) to parameterize the model. The modeling approach I used has the advantage of incorporating stochastic processes, connectivity between subpopulations, and density-dependent effects of suppression scenarios on different life stages that may expose population vulnerabilities (van Poorten et al. 2019). By incorporating plausible future changes in habitat related to reservoir management and climate change, my research will be valuable for predicting fish invasion dynamics to inform the development of efficient and effective management strategies to conserve the unique endemic native fishes of the Grand Canyon.

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CHAPTER 2

REMARKABLE RESPONSE OF NATIVE FISHES TO INVASIVE TROUT

SUPPRESSION VARIES WITH TROUT DENSITY, TEMPERATURE,

AND ANNUAL HYDROLOGY[1,2]

Abstract

Recovery of imperiled fishes can be achieved through suppression of invasives, but outcomes may vary with environmental conditions. We studied the response of imperiled desert fishes to an invasive brown and rainbow trout suppression program in a Colorado River tributary, with natural flow and longitudinal variation in thermal characteristics. We investigated trends in fish populations related to suppression, and tested hypotheses about the impacts of salmonid densities, hydrologic variation, and spatial-thermal gradients on the distribution and abundance of native fish species using zero-inflated generalized-linear mixed-effects models. Between 2012 and 2018, salmonids declined 89%, and native fishes increased dramatically (~480%) once trout suppression surpassed ~60%. Temperature and trout density were consistently retained in the top models predicting the abundance and distribution of native fishes. The greatest increases occurred in warmer reaches and in years with spring flooding. Surprisingly, given the evolution of native fishes in disturbance-prone systems, intense, monsoon-driven flooding limited native fish recruitment. Applied concertedly, invasive species

suppression, and efforts to mimic natural flow and thermal regimes may allow rapid and widespread native fish recovery.

Introduction

Freshwater ecosystems are heavily modified world-wide, and consequently native fishes are threatened by a variety of persistent and emerging factors, including invasive species, hydropower generation and river regulation, climate change, and their interactive effects (reviewed in Reid et al. 2019). The impacts of invasive species have become a global economic, societal, and ecological crisis (Mack et al. 2000; Pejchar and Mooney 2009; Walsh et al. 2016), as widespread introductions have given rise to the loss or extirpation of native fishes (Gozlan et al. 2010; Strayer 2010), and homogenization of fish assemblages on a continental scale (Rahel 2002). Threats imposed by invasive fishes, including through predation and competition, may be compounded by habitat fragmentation and alteration of thermal and flow regimes (Poff et al. 1997a, 2007; Ruhí et al. 2016); with exacerbated synergies under continued climate change (Propst et al. 2008; Rahel and Olden 2008; Wenger et al. 2011). For example, warming thermal regimes may increase metabolic demand and consumption of native prey by invasive species (e.g., smallmouth bass and walleye predation upon native salmon, Rahel and Olden 2008).

Invading aquatic species are difficult to remove once established, and significant resources are expended to suppress or otherwise manage invasives and lessen their impacts on imperiled native fishes (Mueller 2005; Coggins et al. 2011; Franssen et al. 2014; Zelasko et al. 2016; Pennock et al. 2018). Nevertheless, unambiguous positive responses in populations of native fishes are not always achieved (Coggins et al. 2011;

Propst et al. 2015; Saunders et al. 2015; reviewed in Rytwinski et al. 2018). Suppression

efforts may be offset by compensatory survival of young-of-year (YOY) invasive species,

where recruitment is density-dependent (Meyer et al. 2006; Saunders et al. 2015; Zelasko

et al. 2016), or by immigration of invasive species (Franssen et al. 2014; Propst et al.

2015). Further, temporal variability in flow, turbidity and temperature, which may

mediate competition, predation, and other biotic interactions (Yard et al. 2011; Ward and

Morton-Starner 2015; Ward et al. 2016), may also confound interpretation of population

trends in native and invasive fishes following suppression (Coggins et al. 2011; Propst et

al. 2015). Thus, conservation of native fishes would benefit from improved understanding

of the ecological impact of species invasions in the context of environmental variability

(Cucherousset and Olden 2011), how patterns of distribution and abundance of native

fishes relate to those of invasive fishes, and how native fishes will respond to invasive

species suppression under different environmental conditions (Rytwinski et al. 2018).

Introduced for sport fishing, brown trout (*Salmo trutta*) and rainbow trout

(*Oncorhynchus mykiss*) are globally ubiquitous and damaging invaders, with populations

established in more than 30 countries (Crawford and Muir 2008; Budy and Gaeta 2018).

Invasions by brown trout can lead to top-down control on ecosystem function through the

alteration of nutrient dynamics in streams (Townsend 2003), and to declines or

extirpation of native fishes (Garman and Nielsen 1982; Townsend 2003; Young et al.

2010). Similarly, rainbow trout can alter stream and adjacent forest food webs through

trophic cascades (Baxter et al. 2004), eliminate native fishes (Crowl et al. 1992) and

amphibians (Knapp et al. 2007), and hybridize with native conspecifics (Weigel et al.

2003). Both species thrive in altered habitats, including in regulated dam tailwaters

comprised of colder hypolimnetic releases (McKinney et al. 2001; Dibble et al. 2015; Korman et al. 2016) where native fish assemblages are threatened (Pringle et al. 2000; Olden and Naiman 2010; Yackulic et al. 2018).

The magnitude of the impact of invasive salmonids may diminish at warmer extremes of their thermal tolerance (Ward and Morton-Starner 2015; Shelton et al. 2018; Yackulic et al. 2018), and natural thermal and flow regimes may allow native species to persist in salmonid-invaded habitats (Propst et al. 2008; Hayes et al. 2019), but outcomes of invasions may vary by species. For instance, in laboratory studies, rainbow trout piscivory was greatest in colder waters as the swimming ability of the obligate warmwater native prey species was hampered (Ward and Bonar 2003), whereas brown trout piscivory rates were always high over a range of water temperatures (Ward and Morton-Starner 2015). Additionally, discharge regimes may dictate the invasion success and population dynamics of these invading trout species (Fausch et al. 2001; Kawai et al. 2013; Dibble et al. 2015). For example, high flow variability in spring may limit brown trout invasions (Kawai et al. 2013), and natural flow regimes may confer resistance to the effects of biotic interactions to native fish assemblages uniquely adapted to extreme conditions (Hayes et al. 2019). Thus, environmental factors and invasive trout may interact to structure native fish communities, but the relationships among invasive trout, native fishes, and flow and thermal regimes are complex and not clearly understood.

In arid regions, including in the American Southwest, water use (Ruhí et al. 2016; Kominoski et al. 2018), altered sediment supply (Schmidt and Wilcock 2008), fragmentation (Fagan et al. 2002; Nilsson et al. 2005; Compton et al. 2008), and introduced species (Olden et al. 2006) have diminished the extent of riverine habitats and

increased extirpation risk of the native fauna (Poff et al. 1997b; Budy et al. 2015; Rolls et al. 2018), including in the Colorado River system (Dettinger et al. 2015). As a result, four of eight of the Colorado River large-river fishes, six of which are endemic, have been listed under the U.S. Endangered Species Act (ESA), while others, such as the bluehead sucker (*Pantosteus discobolus*) and flannelmouth sucker (*Catostomus latipinnis*), are considered imperiled and the subject of interagency conservation agreements and strategies following range-wide declines (e.g., Utah Division of Wildlife Resources 2006). These desert fishes are particularly vulnerable because they lack recreational value, inhabit regions with scarce water resources that are heavily appropriated for municipal use (reviewed in Budy et al. 2015), and possess unique and co-evolved ecological and life history traits to persist in highly variable environments with few native predators (Olden et al. 2006).

Introduced into spring-fed tributaries of the Colorado River in Grand Canyon National Park (GCNP), in Arizona, USA, during the mid-20th century (Williamson and Tyler 1932; Stricklin 1950), brown trout and rainbow trout expanded beyond tributaries once Glen Canyon Dam (GCD) was completed in 1963. Colder, hypolimnetic discharge lacking turbidity, created suitable habitat for rainbow trout introduced into the tailwater of the dam (McKinney et al. 2001), while inhibiting growth and reproduction of native fishes (Robinson and Childs 2001; Yackulic et al. 2014). Tributaries in Grand Canyon, which have less-modified thermal, flow, and sediment regimes, have become critical to maintaining populations of native fishes (Weiss et al. 1998; Walters et al. 2012; Yackulic et al. 2014); however, brown trout abundance increased in one tributary, Bright Angel Creek, beginning in the 1990s, while native fishes declined (Otis 1994; reviewed in

Runge et al. 2018). Piscivory by both salmonids on endangered humpback chub (*Gila cypha*) and native suckers has been documented in Grand Canyon and is thought to limit native fish recruitment (Marsh and Douglas 1997; Yard et al. 2011; Whiting et al. 2014), but population-level impacts of piscivory or competition are also difficult to quantify (Coggins et al. 2011; Walters et al. 2012; but see Yackulic et al. 2018).

To minimize threats of predation and competition posed to humpback chub in the Grand Canyon, invasive salmonids in the Colorado River and its tributaries have been the target of mechanical suppression programs, but with equivocal results (Coggins et al. 2011; Yard et al. 2011; Healy et al. 2018; Runge et al. 2018). A multi-year (2003-2006) trout suppression effort, using electrofishing, was implemented approximately 125 km downstream of GCD at the mouth of the Little Colorado River (Coggins et al. 2011); the primary tributary sustaining the Grand Canyon humpback chub population since the closure of GCD dam (Yackulic et al. 2014). Humpback chub increased as rainbow trout declined in abundance, but warming water temperatures that would benefit humpback chub recruitment over the removal period confounded the interpretation of results (Coggins et al. 2011). Brown trout were perceived to be a significant threat to humpback chub in Grand Canyon, due to high piscivory rates and observations of direct predation on humpback chub and other native fishes (Yard et al. 2011; Whiting et al. 2014). Bright Angel Creek was the target of a comprehensive suppression effort between 2010 and 2018 because of its importance to brown trout as the primary location of reproduction and recruitment (Omana Smith et al. 2012; Healy et al. 2018; Runge et al. 2018).

In this paper we quantify the population trends of both invasive and native fishes through the duration of this eight-year trout suppression effort in Bright Angel Creek.

This documentation allowed for a unique opportunity to study the effects of the removal of salmonids on the distribution and abundance of native fishes, while accounting for temporal and spatial variation in potential hydrologic and thermal drivers of fish population dynamics. We assess the following specific research objectives: 1) the effectiveness of suppression of invasive salmonids through mechanical removal to benefit native fish populations; and 2) the relationship among invasive salmonids, thermal variation, annual hydrology, and the distribution and abundance of native fishes. This study provides insights into the benefits of invasive species control across inherent environmental gradients potentially regulating populations.

Materials and Methods

Study Area

Our study focused on Bright Angel Creek, a spring-fed perennial tributary joining the Colorado River 168 km downstream of GCD, and draining approximately 260 km^{-2} (Oberlin et al. 1999) of the semi-arid North Rim of Grand Canyon, within the Kaibab Plateau in GCNP (Figure 2.1). Substrate composition is typical of a mountain stream, consisting of mixed cobble, boulder, sand, and gravels, within a variety of geomorphic habitat features including pools, riffles, runs, and cascades. Stream channel dimensions are displayed in Table 2.1.

The existence of minimally impacted hydrologic conditions and availability of continuous hydrograph data created an ideal setting to study the effects of flow variability on fish community dynamics. The annual average mean daily and baseflow discharge are 1.2 and 0.6 m$^3 \cdot$s^{-1}, respectively, with baseflow originating as groundwater from Roaring Springs and Angel Springs (Whiting et al. 2014). However, under existing management,

~ 0.08 m^3·s^{-1} (20%) of the baseflow is diverted to provide water for GCNP's visitors and

residents (Bair et al. 2019). Baseflow generally occurs during fall and winter months, but

during El Niño years, winter floods (November- February) can occur (Figure 2.2; U.S.

Geological Survey (USGS) gaging station 09403000; U.S. Geological Survey 2018). In

general, the annual hydrograph consists of a period of elevated flow during spring

snowmelt (March-May), followed by more frequent and ephemeral monsoonal floods

during the summer months (June or July – September) exceeding the maximum spring

discharge (Webb et al. 2000). More than half of flood events occur during the summer,

while approximately 1/3 occur during spring. Spring snowmelt driven floodwaters

discharged through the springs (reviewed in Bair et al. 2019) carry less fine sediment

than those in summer (Webb et al. 2000), but can be of longer duration (Figure 2.2).

Smaller tributaries to Bright Angel Creek can experience localized heavy rain events and

flash floods, which may not impact the entire stream. The maximum daily hydrograph for

the duration of the study is shown in Figure 2.2.

Continuous water temperature data, with the exception of May – August, 2010,

were available for the duration of the study period from USGS gaging station 09403000

located in Bright Angel Creek just upstream of the confluence with the Colorado River.

Water temperature data were available from four other locations distributed throughout

the study area, but were limited in duration to June 2013 through early August 2015

(Figure 2.1; Bair et al. 2019). Seasonal variation in stream water temperatures is

generally driven by discharge volume and solar radiation or air temperature (Bair et al.

2019). Over the course of our study, mean daily water temperatures near the mouth of

Bright Angel Creek varied seasonally, and ranged from 2 –24°C with an annual mean of

13.7°C (USGS gaging station 09403000). Water temperatures were consistently colder, and seasonal variation was dampened, closer to the headwater spring discharges, where mean water temperature was 11, and ranged between 6 - 14°C (Figure 2.1, reach 5; Bair et al. 2019).

Sampling of fishes in 2010 and 2011 by National Park Service (NPS) staff and volunteers documented the presence of two species of native fishes including speckled dace (*Rhinichthys osculus*), and bluehead sucker, as well as reproducing populations of invasive brown trout and rainbow trout (Omana Smith et al. 2012). Flannelmouth sucker has also been known to enter the stream seasonally as adults to spawn (Otis 1994; Weiss et al. 1998), but the presence of adults or juveniles outside of spring was not documented prior to this study in sampling by the NPS (Omana Smith et al. 2012), nor in a previous study characterizing the fish community in the early 1990s (Otis 1994). Stocking of rainbow trout into Bright Angel Creek was conducted by the NPS in 1923, 1924, 1932-42, 1947, 1950, 1958, and 1964 (reviewed in Runge et al. 2018). Brown trout were stocked in 1924, 1930, and 1934 (Williamson and Tyler 1932; Carothers and Minckley 1981; reviewed in Runge et al. 2018). While uncommon in Bright Angel Creek prior to 1984, an increase in brown trout abundance was followed by native fish declines (reviewed in Otis 1994). Both salmonids and native fishes freely move between the Colorado River and Bright Angel Creek, as no permanent barriers exist until approximately 13 km upstream of the mouth.

Invasive Trout Suppression and Field Data Collection

For analysis, we used fish capture data collected from between 2010 and 2018 during the implementation of an invasive salmonid suppression project conducted by the

NPS and U.S. Bureau of Reclamation involving multiple-pass depletion electrofishing, with additional single-pass electrofishing targeting areas of higher trout density, and the use of a weir (U.S. Department of the Interior 2013; Healy et al. 2018). We briefly summarize field sampling methods here (discussed in detail in Omana Smith et al. 2012, and Healy et al. 2018). Beginning in 2010, we conducted three-pass depletion sampling with a crew of 8-10 within block-netted stations distributed in the lower 3 km of Bright Angel Creek (approx. 1.5 km total; Table 2.1) each October and January, using paired Smith-Root© LR-20b backpack electrofishing units. In addition to electrofishing, we installed and operated a weir near the mouth of Bright Angel Creek from approximately October to December to intercept spawning runs of trout from the Colorado River (for weir results, see Healy et al. 2018).

In October 2012, and continuing through February 2018, we expanded both weir and electrofishing operations temporally or geographically to more fully encompass the seasonal timing of spawning runs or spatial distribution of salmonids. We expanded depletion electrofishing to the confluence of Angel and Roaring Springs creeks, tributaries of Bright Angel Creek, approximately 15.5 km upstream of the confluence with the Colorado River, and extended weir operations into February. We expected this expansion would enhance removal efficiency by targeting aggregating, spawning brown trout and disrupt fall and late winter spawning. Our electrofishing stations were nested within five reaches delineated from just upstream of the mouth (reach 1) to the upper limit of the study area (reach 5; Figure 2.1). We established reaches to represent changes in geomorphology or valley form, or where important tributaries joined Bright Angel Creek, and to capture spatial variability in habitat. In total, we sampled 877 stations using

three-pass depletion ranging in length from 37 to 255 m (mean = 115 m). Depending on

the availability of field crews and funding in a given year, we conducted additional

single-pass electrofishing without block nets, for the singular purpose of targeting and

removing salmonids found in higher density areas during three-pass depletion. We

weighed and measured fish to total length (TL) and fork length following standardized

protocols established for research in GCNP (Persons et al. 2013), with the exception that

we weighed and measured a subset of speckled dace, and humanely euthanized all

invasive fishes. This study was performed under the auspices of the Utah State University

Institutional Animal Care and Use Committee protocol number 10170.

Analyses

Abundance estimation

We estimated capture probabilities and station-specific abundances of rainbow

trout and brown trout using closed-population depletion models (Huggins data type;

Huggins 1989) in Program MARK (White 2008), following methodology described in

Saunders et al. (2011). To account for biases in capture probability related to behavior or

individual heterogeneity common in depletion sampling of fishes (Peterson et al. 2004;

Korman et al. 2009; Saunders et al. 2011), we constructed a series of reach- and species-

specific models incorporating individual (e.g., fish total length) and pass-specific (pass

number) covariates, as well as those with constant capture probability across passes. We

constrained recapture probabilities to zero for all models since all fishes were removed

from the stream between passes, and were unavailable for recapture. When captures were

low within a reach (i.e., a species was captured in < 5 stations), we pooled stations across

reaches to generate pass-specific pooled capture probability estimates, and derived

station-specific abundance. We compared models using Akaike's Information Criterion

adjusted for small sample size (AICc; Burnham and Anderson 2002; White 2008;

Saunders et al. 2011), and considered the model with the lowest AIC_c score the best

model. We assumed movement of previously captured native fishes between reaches,

subjecting them to double-counting, to be negligible because of the use of block-nets.

Our abundance estimation procedures for native fishes were similar; however, no

individual covariates were available to assess behavior and size-related biases for

speckled dace since only a subset were measured. In some years, low bluehead sucker

capture probability, likely due to gear size-selectivity, and flannelmouth sucker rarity,

resulted in depletion models that failed to converge (Healy et al. 2018). For example,

capture probability estimates for YOY bluehead suckers was < 0.05. We summed the

station-specific total captures across all three passes to define indices of abundance for

sucker species in our predictive models when depletion models for native suckers failed

to converge. For trout, we standardized abundance estimates for individual stations to

density by stream length (fish$\cdot 100$ m^{-1}).

Population growth rates

We quantified the annual population growth rate (λ) of fishes to assess the stream-

wide effect of mechanical suppression of invasive salmonids on fish community

dynamics. For trend assessment, we summed our abundance estimates ($\widehat{N}$) of native and

invasive fishes sampled at each station (i) by reach (j reaches = 1-5), and by year, when

stations throughout the entire stream were sampled (k years = 2012-2017). We estimated

the average λ, for each species, using linear regression, with natural log-transformed

annual incremental population growth rates as a function of time (Morris and Doak

2002). The estimated slope, and the mean squared residual from the regression model,

with an intercept constrained to zero, approximated the natural log of population growth

rate (Dennis et al. 1991; Morris et al. 1999; Morris and Doak 2002). A λ <1.0 indicates a

population in decline, λ >1.0 indicates an increasing population, and λ =1.0 is a stable

population (Morris and Doak 2002); however, when 95% confidence intervals in λ values

> or < 1 overlapped 1, we considered the population trend inconclusive.

Distribution and abundance of native fishes

We used generalized linear mixed effects models (GLMM) to investigate the

influence of trout density, spatial-thermal variation, annual stream discharge, and

electrofishing effort on the abundance and distribution of native fishes in Bright Angel

Creek. The dependent variables included species-specific and aggregated counts of native

fishes at 877 stations sampled throughout Bright Angel Creek between 2010 and 2018.

We used zero-inflated negative binomial (ZINB) GLMM, which has the flexibility to

model counts of rare species with overdispersion (Zuur et al. 2009; see Suplemental

Information, Figure 2-S1). A ZINB is a mixture model formed from the combination of a

binomial process and a negative binomial process, which was advantageous, in that we

could simultaneously test for the influence of covariates driving presence/absence (i.e.,

binomial) and count processes (Zuur et al. 2009). Under this model, the probability that

the count, $C_{i,j}$, in the ith station and jth year is zero is given by:

(1) $$P\big(C_{i,j} = 0\big) = \big(1 - \pi_{i,j}\big) + \pi_{i,j} * NB(0|y_{i,j}, \kappa)$$

where $\pi_{i,j}$ is the probability that a station is capable of a non-zero count, and

$NB(0|y_{i,j}, \kappa)$ represents the probability of counting zero even though the site is capable

of a non-zero count conditional on an expected density, $y_{i,j}$, and the overdispersion

parameter, κ. For counts greater than zero the probability is simply given by:

(2) $$P\big(C_{i,j} > 0\big) = \pi_{i,j} * NB\big(C_{i,j}|y_{i,j},\kappa\big)$$

We assumed κ to be constant and modelled $y_{i,j}$ and $\pi_{i,j}$ using a mixture of fixed

and random effects (i.e., using generalized linear mixed effects, GLMM, structure). For

$y_{i,j}$ and $\pi_{i,j}$ the most general structures considered were:

(3) $$logit(\pi_{i,j}) = \beta_0 + \boldsymbol{\beta}\boldsymbol{Z}_{ij} + \xi_{\boldsymbol{k[i],j}}\boldsymbol{z}_{ij} + \theta_{\boldsymbol{k[i],j}}$$

(4) $$log(y_{i,j}) = \alpha_0 + \boldsymbol{\alpha}\boldsymbol{X}_{ij} + \zeta_{\boldsymbol{k[i],j}}\boldsymbol{x}_{ij} + \eta_{\boldsymbol{k[i],j}}$$

where β_0 and α_0 are intercepts, $\boldsymbol{\beta}$ and $\boldsymbol{\alpha}$ are vectors of coefficients with lengths equal to

the number of covariates included in the corresponding portion of the model, $\mathbf{Z}$ and $\mathbf{X}$ are

arrays with dimensions given by the number of covariates, the number of stations and the

numbers of years, $\mathbf{z}$ and $\mathbf{x}$ are arrays that included only the subset of covariates with

varying slopes within reaches, $\xi_{\boldsymbol{k[i],j}}$ and $\zeta_{\boldsymbol{k[i],j}}$ are random slopes for the kth reach

(stations are nested within reaches) and j^{th} year, and $\theta_{\boldsymbol{k[i],j}}$ and $\eta_{k[i],j}$ are random effects

for the kth reach and j^{th} year. We constructed and evaluated candidate ZINB models with

the "glmmTMB" package (Brooks et al. 2017) in R version 3.5 (R Core Team 2019). All

models included the log of electrofishing station length as an offset term for

standardization of effort and catch. Prior to model fitting, we evaluated collinearity

among predictors using Pearson's correlation coefficients, and carefully considered those

predictors with coefficients greater than 0.60 for retention in models, to avoid variance

inflation. To avoid collinearity among trout variables (see below), candidate models did

not include more than one trout metric. As described below, we used principle

component analysis (PCA) to avoid multicollinearity among hydrology metrics.

The impact of invasive salmonids on the distribution of native fishes can depend

on the size-distribution of trout (McIntosh et al. 1994). Studies in two Grand Canyon

tributaries found a switch to higher incidence of piscivory occurs in trout between ~ 150-

250 mm TL (Whiting et al. 2014; Spurgeon et al. 2015). In addition to rainbow trout and

brown trout species-specific densities and total trout density (sum of density of both

species), we evaluated the density of large trout of both species (> 230 mm TL) as a

predictor of native fish (Table 2.2). We accounted for normal seasonal temperature

variation at a station in our analyses by proxy, as we lacked a continuous thermal record

for all reaches throughout the duration of the study. Bair et al. (2019) found air

temperature and the location of a station in Bright Angel Creek to be strong predictors of

water temperature, thus, our station-specific proxy for thermal variation, referred to as the

"spatial-thermal" predictor, was defined as the distance of each station from the Colorado

River.

To characterize annual flow variability, we calculated a suite of twelve annual

hydrology metrics (see Table 2.2) which have been shown to influence population

dynamics of both native and invasive fishes (Richter et al. 1996; Fausch et al. 2001).

Metrics represented inter-annual and seasonal flow variability in the water year prior to

annual fish sampling; flooding during spawning and emergence periods may reduce hatch

success or YOY survival of salmonids (Fausch et al. 2001; Cattanéo et al. 2002; Dibble et

al. 2015), and monsoon-driven flooding or drought may reduce densities of native fishes

(Yackulic et al. 2014; Gido et al. 2019). We calculated metrics across the water year

(October 1 – September 30) from continuous flow data collected at the USGS gaging

station located near the mouth of the Bright Angel Creek (USGS gaging station

09403000). We assumed data collected from this gauging station would approximate

flow variability throughout the creek; however, some tributary drainage characteristics

may be more prone to localized flooding than others (Griffiths et al. 2004), which could

result in variation in hydrology among reaches. We included "reach" as a random effect

to account for this potential source of variability (see below). We captured extreme

events by using maximum daily flows, rather than daily means, to calculate annual (water

year) and seasonal (spring – February through May, monsoon season – June through

September) coefficient of variation (CV) of flow metrics. We reduced dimensionality of

flow variables and described patterns of variation among them using PCA (Gauch 1982).

This method also reduced multicollinearity among variables used in the ZINB models

(described above; Graham 2003). We used PCA to summarize the flow metrics into

components accounting for the variation in hydrologic variables, and then used the

components in models as potential predictors of native fish abundance (Graham 2003).

The first (PC1) and second (PC2) principal components accounted for 43.2% and 22.1%

of hydrologic variation, respectively (Figure 2.3). PC1 represented a spring flood and

flow magnitude index (spring flood index) by accounting for a gradient of the annual

magnitude of spring flooding (April flow volume) and annual flow variability. The

magnitude of summer flows and monsoon flood variability was represented by PC2,

which was considered a monsoon flood frequency and magnitude index (monsoon index)

in our models. The monsoon index was negatively associated with PC2, such that high

PC2 scores represented weak monsoons.

Electrofishing can have deleterious effects on individual fish (Ruppert and Muth 1997; Snyder 2003), but population-level effects may be difficult to measure, as effects to individuals may be offset by the beneficial impacts of the suppression of invasive predators. We quantified electrofishing effort by reach and year, including for multiple-pass depletion, and targeted single-pass removal occurring at the end of each season, for evaluation in ZINB models. We recorded total electrofishing effort for both electrofishing units during each pass (seconds) in a station, converted seconds to hours, and summed the hours by reach. We applied the previous years' reach-scale electrofishing effort to models to predict native fish density, assuming the impacts of electrofishing the year prior to the census would be reflected in either beneficial effects of declines of invasive salmonids, or in injuries and potential population-scale negative effects to native fishes.

We accounted for repeated sampling and non-independence among stations within reaches and across years by including "reach" and "year" as multiplicative random effects (n = 32 levels) in ZINB models, where both intercepts and slopes were allowed to vary with trout density whenever possible (Gelman and Hill 2009; Harrison et al. 2018). While we strove for this complex random effects structure, in some cases models failed to converge, likely due to a lack of information to estimate some parameters (Brooks et al. 2017). We then opted for a simpler random effects structure (e.g., random intercept, constant slope) to seek model convergence. This structure accounted for potential spatial variation in geomorphology and thermal regime, and temporal variation in annual hydrology, which may differ among reaches (i.e., driven by tributary flood inputs). All continuous fixed effects were centered on their mean value and standardized by dividing by their standard deviation to aid in interpretation and allow for comparison among

predictors ("z-score"; Gelman and Hill 2009). A description of all fixed effect variables is provided in Table 2.2.

Model Selection

We took a multi-stage approach to model development and selection whereby competing models representing *a priori* hypotheses were developed following selection of the best combination of sub-models for each variable. This multi-stage approach was expected to yield the closest result to "true" parsimony as if all combinations of plausible models were fitted and compared (Morin et al. 2020). In the first stage, we compared up to six models for each variable to the intercept-only model, with *i*) the single predictor included in the count side of the model and an intercept only in the binomial model, and random intercepts, *ii*) the predictor included only on the binomial model, and random intercepts, *iii*) the predictor on both count and binomial elements of the model and random intercepts, and *iv – vi*) repeating the above models with the exception that the models included random slope interactions with trout density metrics. Only random intercepts were used in the first stage with hydrological, spatial-thermal, and electrofishing effort predictors. Bayesian Information Criteria (BIC) scores were used to compare models (BICtab function, R-package bbmle, Bolker and Team 2017), which we expected would select for models with the strongest relationship with native fish distribution and abundance (Burnham and Anderson 2002; Aho et al. 2014). All single-variable models within Δ5 BIC of the top model were carried forward into the next model selection stage (Morin et al. 2020).

In the second stage of model selection, we incorporated the best model structure for each predictor variable (Table 2-S1, Supplementary Information) into a global model

for each response variable (i.e., aggregated native fish counts, speckled dace, bluehead and flannelmouth suckers), and then constructed models incorporating combinations of predictors representing potential hypotheses explaining native fish distribution and abundance. Candidate models included combinations of trout density, the spatial-thermal variable, monsoon (PC2) and spring flooding (PC1) indices, and their first-order interactions. We added reach-scale electrofishing effort to models including trout density and spatial-thermal variables to evaluate whether electrofishing explained additional variation in native fish data.

Results

Population growth rate

Concurrent with intensive mechanical suppression of invasive salmonids, the predominant stream-wide composition of the fish community in Bright Angel Creek shifted from trout (65%) in 2012 to native fishes ($\geq$ 77%) as of 2015. By the end of the study in 2018, following the removal of 43 665 brown trout and 7 824 rainbow trout, native fishes represented 97% of the fish community, but remained absent from most of the extent of reaches 4 and 5. Population estimates for brown trout steadily declined between 2012 – 2018 from a high of 13 829 (95% C.I. = 13 061 – 15 385) to a low of 1 315 (95% C.I. = 1 249 – 1 706), resulting in a 91% reduction by the 2017 – 18 sampling season (Figure 2.4). Rainbow trout were a relatively small component of the fish community, representing < 1% in the last 2 years of the study, with a maximum of 13% of all fishes in the 2014-15 season. Annual trends in rainbow trout abundance were variable, with positive population trends occurring in two of five years, but by 2018 population estimates were 80% lower than in 2012 (Figure 2.4). The mean population

growth rate for brown trout suggested a decline ($\lambda = 0.71$, 95% C.I. = 0.44 – 1.14), but not for rainbow trout ($\lambda = 1.14$, 95% C.I. = 0.40 – 3.26). Nevertheless, trends were inconclusive, as confidence intervals for estimates of both salmonid species' population growth rates overlapped 1, likely owing to the relatively short timeframes of this study, ongoing removal of fish, and consequential effects on reproductive potential.

We observed the opposite pattern for native fishes; speckled dace increased almost five-fold (491%; $\lambda = 1.60$, 95% C.I. = 1.02 – 2.53), and both native suckers increased markedly during the last year of the study (Figure 2.4). Bluehead sucker almost doubled in the catch during the 2017 season compared to previous years, but although the estimate of $\lambda > 1$, confidence intervals overlapped 1.0 ($\lambda = 1.2$, 95% C.I. = 0.91 – 1.59), indicating uncertainty in the population trend. We were unable to calculate a population growth rate for flannelmouth sucker, but after the species' absence during the first three years, we consistently observed YOY and juveniles beginning in 2015, which was followed by a particularly strong cohort in 2017 (Figure 2.4). We began to observe large year-classes of native fishes in 2015, after a 63% decline in abundance of invasive fishes (68% and 62% decline in brown trout and rainbow trout, respectively). Beginning with the 2015 cohorts, we noted significant increases in speckled dace and flannelmouth sucker, followed by a large bluehead sucker cohort in 2017-18. We calculated a 480% increase in the total catch of suckers plus the abundance of speckled dace between 2012 and 2018.

Distribution and abundance of native fishes

There was a large proportion of zero-counts of native fishes in Bright Angel Creek through the duration of the study, and native species were distributed non-

randomly, but native fishes expanded upstream in the later years of the study. While

smaller-sized native fishes were likely under-represented in the catch due to size-specific

bias in capture probabilities (Healy et al. 2018), the frequency of occurrence for native

fishes in electrofishing stations, as an aggregate, was 0.55 (482 of 877 stations), including

occurrence of 0.52, 0.50, and 0.05 for speckled dace, bluehead sucker, and flannelmouth

sucker, respectively. Spatial-thermal variation in Bright Angel Creek was an important

predictor in top binomial models for all native fish as an aggregate response variable, and

for speckled dace, flannelmouth sucker, and bluehead sucker, suggesting colder

temperatures in upstream stations explained the high frequency of zero counts (Table

2.3). Only the most parsimonious binomial model for native fish included an additional

variable, which was the monsoon index (PC2), suggesting native fishes would be more

likely to be absent from stations following intense monsoon flood seasons. Flannelmouth

sucker binomial models including the full multiplicative year by reach random effects

structure failed to converge, and thus, we opted to include only a random intercept for

year in final model selection.

The best models predicting the abundance (counts) of native fishes included

combinations of spatial-thermal, invasive trout density, and stream flow variables (Table

2.3). Speckled dace and native fish count models included trout density (summed density

of both species), and brown trout was retained in the top model as a predictor of

flannelmouth sucker counts. Almost equal support (ΔBIC = 1.1) was given to the

flannelmouth sucker count model including only brown trout density and the spatial-

thermal variable, and an intercept-only binomial model. Counts of native fishes generally

declined with higher trout densities and further upstream, in stations closer to the cooler

headwater springs (Figure 2.5). Native fish counts were highest with greater spring

flooding in 2017, relative to the other years (PC1, Figure 2.5). Electrofishing effort was

not an important variable in any of the top models (i.e., ΔBIC <5). Similarly, rainbow

trout, which occurred in much lower abundance than brown trout, was not included in

any of the top models for native fishes. Rainbow trout were, however, represented in total

trout density, which was a better predictor than brown trout density alone for native fish

and speckled dace. We expected density of large piscivorous trout (>230 mm) would also

be an important influence, but as for rainbow trout, was not included in any top model.

While we tested first-order interactions among trout, spatial-thermal, and

hydrology variables, an interaction among spatial-thermal and trout density was retained

only in speckled dace count models. Nonetheless, the best-fitting random effects structure

for native fish and speckled dace count models included a varying slope interaction with

trout density, which improved BIC scores by 18.5 and 40.9, respectively, compared to a

simpler random intercept structure. We conducted *post hoc* tests to evaluate this simpler

random intercept structure without the trout by slope interaction. The improved model fit

with the random slope by trout density interaction suggests the strength of the influence

of trout density varied by year, reach, and longitudinally in the stream. Compared to the

null model, residuals calculated using the DHARMa package (Hartig 2018) indicated

significant improvements in model fit by including covariates on both the count and

binomial models (Supplementary information).

Discussion

Our analysis highlights several important findings, including that potential

density-dependent compensatory responses commonly associated with control programs

for invasive species (e.g., see Meyer et al. 2006; Saunders et al. 2015; Zelasko et al. 2016) can be overcome by large-scale and persistent mechanical suppression, for as long as it is maintained (Rytwinski et al. 2018). The suppression effort was designed to target migratory and resident life-history expressions and multiple life stages of trout through the use of electrofishing and a weir, which excluded migrants from spawning habitat. Brown trout, a harmful invader, declined by > 90%, while rainbow trout, one of the most widely introduced fishes in the world, but relatively rare in Bright Angel Creek, was reduced by more than 80% during our study. We provide strong evidence linking the community-wide increases in native fishes to declines in invasive fishes. A rapid shift occurred in the fish community from one dominated by invasive species, to 97% native fishes. Our results support the hypothesis that native fish populations were suppressed by invasive salmonids (Walters et al. 2012; Whiting et al. 2014), which were an important predictor of the abundance of native fishes.

Longitudinal variation in the temperature regime (Bair et al. 2019) was also a key regulator of native fish distribution. Our models predicted much lower probability of occurrence of native fishes in the colder upstream reaches. The temperature regime is likely a primary mediator of biotic interactions between desert fishes and invasive salmonids; colder temperatures may increase the vulnerability of native fishes to predation, partly due to decreased swimming ability of warm-water native species (Ward and Bonar 2003; Ward and Morton-Starner 2015), but also limit reproduction and growth (Robinson and Childs 2001; Yackulic et al. 2014; Dzul et al. 2016). Despite colder temperatures, native fishes expanded their range upstream as trout were suppressed, and large year-classes were evident during years with more intense spring runoff, and weak

monsoon seasons. Finally, while electrofishing can be injurious to fishes, we found only weak, but positive, relationships between reach-scale electrofishing effort and native fish distribution and abundance. This important finding suggests the benefits of invasive trout suppression outweighed potential population-level negative impacts.

The observed trends in the fish community, including increases in recruitment by native fishes as early as 2014, supports the hypothesis that complete removal of invasive fishes is not necessary to benefit imperiled desert fish populations, as long as suppression continues, and relatively unmodified flow and thermal regimes exist, as in Bright Angel Creek. Recruitment bottlenecks due to invasive fish piscivory are cited as a primary biological factor limiting populations of native Colorado River fishes (reviewed in Bestgen et al. 2006; Walters et al. 2012). We suggest dramatic benefits to native fish recruitment may occur when invasive salmonid abundance is reduced by ~60-65%, as this level of suppression coincided with an apparent increase in recruitment in native fishes as early as 2015, as well as positive population growth rates. Although not immediately obvious in bluehead sucker overall abundance, this pattern was consistent across all three native species present. Strong bluehead sucker YOY cohorts appeared in the catch for the first time in 2015 (Healy et al. 2018), and strong year classes continued through 2017-18 (R. Schelly, et al., NPS, written communication). Moreover, adult flannelmouth sucker were annually observed spawning prior to our study during spring, but juveniles had not been rearing in Bright Angel Creek (Otis 1994; Weiss et al. 1998) until 2015. Our findings are consistent with those of Walsworth and Budy (2015), suggesting complete eradication of invasive fishes is not necessary to secure benefits to imperiled flannelmouth and bluehead suckers. They predicted suppression of invasive

fishes of > 70% as a prerequisite to positive responses in a native long-lived cyprinid

(roundtail chub, *Gila robusta*), and a more pronounced decline of ≥ 90% before native

sucker populations would benefit. Mueller (2005) argued complete eradication is most

desirable, but surmised a threshold of at least 80% removal of invasive predators would

be necessary to achieve positive responses in native Colorado River fishes. Similarly,

Peterson et al. (2008) suggested that removal of >60% of brook trout (*Salvelinus*

fontinalis) would be the most cost-effective alternative to benefit native cutthroat trout.

This threshold is likely context-dependent, and the reaction of the native fish community

may depend on the strength and type of biotic interactions with invasive species, and

minimal flow regime modification that may provide an advantage to native species (Baltz

and Moyle 1993; Gido et al. 2013).

Regardless, we caution that suppression may be less effective where limited biotic

resistance from the native fish community exists, or where invasive species populations

exhibit strong density-dependent demographic responses (Meyer et al. 2006; Saunders et

al. 2015; Zelasko et al. 2016), unless near eradication is achieved. For example, the

proportion of brown trout annually removed through three-pass electrofishing in Bright

Angel Creek (>79%; Healy et al. 2018) exceeded removal in an experimental single-pass

brown trout removal project, where a compensatory response was observed (63-74%

suppression, Right Hand Fork of the Logan River in Utah, USA; Saunders et al. 2015).

The lack of a similar response in brown trout in our study could be due to density-

independent drivers of population dynamics (e.g., flow-related disturbances; Lobón-

Cerviá 2007; Budy et al. 2008), or biotic resistance (Baltz and Moyle 1993), including

through the uptake of resources previously sequestered by brown trout by both remaining

rainbow trout and native fishes. As evidence for a release from competition, a strong year-class of rainbow trout occurred in 2014 as the brown trout population declined sharply, but we admit drivers of trout population dynamics deserve further study.

Characteristics of brown trout and rainbow trout life history may lend themselves to successful control, relative to other invasive species. For example, new cohorts of brown trout in this study appeared to mature after 2 years (approx. 230 mm TL) allowing for two winter seasons of suppression attempts, and increasing the likelihood of removal prior to reproduction. Other invasive salmonids may reproduce during their first year, and at smaller sizes that are less susceptible to capture (reviewed in Saunders et al. 2011; Hedger et al. 2018), which may foster density-dependent compensatory responses that override removal efforts (e.g., brook trout; see Meyer et al. 2006). Nevertheless, variable population growth rates for trout, particularly for rainbow trout, indicate the potential for rapid growth if conditions are ideal and trout suppression is ceased. Finally, the operation of the weir near the mouth of Bright Angel Creek during the fall and winter months likely limited access to spawning habitat and reduced propagule pressure (see Colautti and MacIsaac 2004) that would otherwise occur through recolonization of Bright Angel Creek by larger, highly-fecund, migrants. Decreased fitness and population viability have been observed in other stream salmonid populations with the loss of large migratory individuals (Morita and Yokota 2002; Budy et al. 2017). Recolonization from outside of removal areas is a commonly cited cause of failure in invasive suppression efforts (e.g., Franssen et al. 2014; Bair et al. 2018).

Invasive trout densities were strong negative predictors of native fish abundance, after accounting for inherent spatial-thermal and temporal patterns in Bright Angel Creek.

Although the mechanism explaining these relationships cannot be directly discerned with our data, predation and competition by trout are implicated (Whiting et al. 2014). Piscivorous brown trout commonly thrive and grow to large sizes feeding on native fishes in novel habitats (Budy et al. 2013), including in our study area (max. size > 600 mm TL; Healy et al. 2018), suggesting the potential for strong predatory effects. Although surprisingly, the density of larger rainbow trout and brown trout (>230 mm TL), which are more likely to be piscivorous (Keeley and Grant 2001; Whiting et al. 2014; Spurgeon et al. 2015), was not a significant predictor of native fish occurrence, relative to smaller trout, flow, and spatial-thermal metrics. The significant positive response in the native fish community was likely related to a release from both the effects of competition with small trout and predation by larger trout, the latter of which has been hypothesized as a limiting factor in Bright Angel Creek based on food web and bioenergetic consumption estimates of native fishes (Whiting et al. 2014).

Numerous examples of displacement of native fishes around the world by invasive rainbow trout can be found in the literature (Krueger and May 1991; Crowl et al. 1992; Shelton et al. 2015), and rainbow trout negatively impact the survival of juvenile endangered cyprinids in Grand Canyon (Yackulic et al. 2018). Brown trout appeared to be more damaging to the native fish community in this study, as a significant driver of flannelmouth sucker, speckled dace and native fish response variables (also see Crowl et al. 1992; Young et al. 2010). However, the magnitude of the invasive species-specific impact may depend on the relative abundance of the two species. Yard et al. (2011) found the incidence of piscivory of native fishes by rainbow trout was much lower than that of brown trout, but hypothesized rainbow trout piscivory could have a much larger

population-scale effect on endangered humpback chub owing to the species' significantly

greater abundance in their study reaches. Rainbow trout comprised only 4-24% of the

annual salmonid abundance, and were similarly found to be less piscivorous than brown

trout in a Bright Angel Creek diet study (Whiting et al. 2014). In other areas where both

species were introduced, brown trout were proposed as a more damaging invader limiting

native fish distribution in South American (Young et al. 2010) and Australasian (Crowl et

al. 1992) waters. Disparate distributional data among the two species also suggest brown

trout may have depressed the abundance or constrained the distribution of rainbow trout

(see Figure 2.4; also Gatz et al. 1987), although we did not test interactions among trout

species in our models. Nonetheless, we cannot rule out the potential of rainbow trout to

influence native fish abundance in Bright Angel Creek. Rainbow trout exhibited

ontogenetic diet shifts toward larger prey, including fishes, and their diets overlapped—

and possibly constrained—the trophic niches of native fishes in Grand Canyon tributaries

(Whiting et al. 2014; Spurgeon et al. 2015).

Bright Angel Creek provided a unique opportunity to test interactions of invasive

salmonids along spatial-thermal gradients and across annual hydrological variation.

Unexpectedly, interactive effects were mostly weak, despite strong relationships between

native fish abundance and both temperature and trout density. Temperature can drive

recruitment of both trout (Eaton and Scheller 1996) and native desert fishes (Clarkson

and Childs 2000; Yackulic et al. 2014), and mediate biotic interactions between cold

water piscivores and warmwater fish (Yard et al. 2011; Ward and Morton-Starner 2015;

Yackulic et al. 2018). The pattern in native fish distribution and abundance identified

through our models was consistent with longitudinal variation in the Bright Angel Creek

thermal regime (Bair et al. 2019). Brown trout or trout predictors significantly improved model fits (e.g., $\Delta 13.9$ for native fish), but interactions between trout and temperature were only significant in the model predicting speckled dace abundance. Counterintuitively, the interaction was negative, suggesting the effects of trout on speckled dace weakened in colder reaches upstream, including in reach 2 where the most dramatic declines in brown trout were observed (98%), and the largest proportional increases in native fishes occurred (>4 000%). Even at lower brown trout abundance in later years, native fish density remained low in reach 3, but despite a 93% decline, reach 3 continued to support ten times the brown trout density compared to reach 2. These observed spatial and temporal trends suggest that in colder reaches, where habitat is less suitable for native fishes, a larger proportion of salmonids would need to be removed before benefits to native fish are realized, and temperature alone may inhibit native fish reproduction, recruitment, or immigration. The thermal regime may be nearing the lower limits of these vital demographic processes in upstream reaches.

Differences in life history traits and thermal requirements may explain variation in population responses to trout control as well. The strongest positive response was observed in lower reaches for speckled dace, which is a small, relatively short-lived and early maturing, ubiquitous species in western streams (traits described in Olden et al. 2006). Speckled dace have slightly warmer thermal requirements than native suckers (Huff et al. 2005; Utah Division of Wildlife Resources 2006; Valdez 2007), and the temperature regime of reach 3 may minimally support the species' reproductive needs. In contrast, both native suckers are slower growing, late maturing, long-lived fishes (reviewed in Walters et al. 2012). Bluehead suckers were found expanding into reach 3

during the study, but are also difficult to detect as YOY with electrofishing gear (Healy et

al. 2018). Moreover, the propensity of native fishes to drift downstream as larvae after

hatching (Robinson et al. 1998), combined with warmer temperatures and enhanced

recruitment to juvenile size (Clarkson and Childs 2000; Yackulic et al. 2014), would also

predispose downstream sites to support higher colonization rates, and ultimately

abundance, of native fishes. Thus, detectability, temperature, the effects of trout

predation, as well as life history, all contribute towards explaining the patterns we

observed in distribution and abundance of native fishes.

　　　The observed negative relationship between the monsoon flow variability and

native fish occurrence was somewhat surprising. We expected native fishes, which

evolved in arid-land streams characterized by extreme hydrologic events, would be

resistant to flow variability and monsoon flooding (Meffe and Minckley 1987), and have

a survival advantage over salmonids that thrive in more predictable hydrologic regimes.

The effects of flow could represent a spurious correlation in our relatively short-term

study, or longer time scales may be required for the detection of resilience in the

community (Matthews et al. 2013; Gido et al. 2019). The strength of monsoon flooding

weakened over time and covaried with declining brown trout abundance, while, perhaps

coincidentally, the largest spring flood and native fish cohort was evident in 2017.

Alternatively, the mostly stable, perennial baseflow, which is atypical for the region, was

likely ideal for rainbow trout and brown trout reproduction. Summer monsoon floods

could have scoured substrates and improved habitat for fall-spawners, as in the brown

trout's native range (Ortlepp and Mürle 2003), and indirectly impacted native fishes

through enhanced trout recruitment. Nonetheless, given the known resilience of desert

fishes to flood disturbances and sensitivity to drought documented in the literature (Budy et al. 2015; Gido et al. 2019), it was not unexpected to observe a large year-class of native fishes associated with the highest spring runoff volume in 2017.

Targeting life history stages thought to be most vulnerable (e.g., during reproduction), and controlling or containing the source of an invasive species rather than attempting removal under continuous immigration (Wolff et al. 2012; Bair et al. 2018), were our basic premises during the design of this study. Management objectives included minimizing the risk of predation by brown trout and rainbow trout to endangered fishes in Grand Canyon (U.S. Department of the Interior 2016), and enhancing the native fish community in Bright Angel Creek (U.S. Department of the Interior 2013). Our results, as well as annual monitoring data from the Colorado River in Grand Canyon showing the lowest brown trout catch since the program's inception in 2001 (Rogowski and Boyer 2019), provide evidence these objectives were accomplished and the effects of trout suppression may extend beyond Bright Angel Creek (i.e., as a primary source of brown trout to the Colorado River, Speas et al. 2003; Runge et al. 2018).

Our study further documents the damaging effects of globally-introduced salmonids (Crawford and Muir 2008; McIntosh et al. 2011; Budy and Gaeta 2018), but represents a promising example of successful mechanical suppression and positive response in highly imperiled desert native fishes. Our work provides a template for planning of similar efforts to conserve native fish assemblages in the context of social or logistical limitations on the use of chemical piscicides (reviewed in Peterson et al. 2008). Despite documented difficulties in achieving positive population-scale responses in native fishes through suppression of invasives, or in teasing apart confounding

environmental variation associated with these programs (Coggins et al. 2011; Franssen et al. 2014; Pennock et al. 2018), managers continue to implement mechanical removal of invasive fishes. Annual costs to agencies of stream-wide suppression in our study ranged from approximately USD $266 000 to $336 000. While suppression is difficult and costly, improvements in demographic vital rates of native or endangered fishes may be expected when invasive fishes are reduced in density (Peterson et al. 2008; Bair et al. 2018; Pennock et al. 2018). The suppression of invasive predators and competitors in shrinking aquatic habitats may be critical to the preservation or restoration of these unique and imperiled desert native fish assemblages (Williams et al. 1985; Mueller 2005; Propst et al. 2015). Examples of successful suppression of these invasive salmonids may also prove critical to conservation planning for range-restricted native salmonids, as climate-mediated invasions and loss of habitat exert additional stresses on their populations (reviewed in Budy et al. 2013; Hansen et al. 2019). Understanding the strength of abiotic and biotic factors in regulating ecological communities, particularly in the face of invasions, will be critical to conserving ecological services and values as aquatic biodiversity is increasingly stressed on a global scale.

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Table 2.1. Description of reach delineations and channel dimensions of reaches in Bright Angel Creek, Grand Canyon National Park.

Reach Number	Mean wetted width (m)	Minimum wetted width (m)	Maximum wetted width (m)	Reach length (km)	Description
1	7.0	3.4	8.7	2.9	Below Lower Bright Angel Campground Bridge, to Phantom Creek.
2	5.6	3.9	8.5	4.3	Phantom Creek confluence to Mint Spring
3	4.9	2.9	7.2	2.9	Mint Spring to Ribbon Falls Creek confluence
4	4.5	2.3	6.6	2.3	Ribbon Falls Creek to Transept Creek confluence
5	4.8	1.7	11.0	3.1	Transept Creek to Angel/Roaring Springs confluence

Table 2.2. Invasive trout, hydrology, electrofishing, and spatial-thermal variables hypothesized to predict the occurrence and density of native fishes in Bright Angel Creek, Grand Canyon, Arizona. Hydrologic variables were calculated using prior water data (see text).

Variables	Hypothesized effect (label)
Invasive trout variables	
Brown trout density/reach-scale abundance	Predation/competition
Rainbow trout density/reach-scale abundance	Predation/Competition
Total trout density/reach-scale abundance	Predation/Competition
Piscivore density/reach-scale abundance	Predation/Competition
Hydrology Variables	
Coefficient of variation (CV) of annual max daily flow	Annual variation in flow (Annual.CV)
30-day maximum flow volume	Annual flood magnitude (X30.day.max)
30-day minimum flow volume	Duration/magnitude of low flow (X30.day.min)
CV of spring max daily flow	Recruitment/emergence of salmonids (Feb-May) (SpringMxCV)
CV of max. daily flow, monsoon season	Monsoon (July-Sept.) flood freq./magnitude (MonsoonMxCV)
CV of max. daily flow, June	Flow variability – native fish spawning (JuneMxCV)
CV of max. daily flow, July	Flood disturbance to fish assemblage (JulyMxCV)
CV of max. daily flow, August	Flood disturbance to fish assemblage (AugustMxCV)

CV of max. daily flow, September	Flood disturbance to fish assemblage (SeptMxCV)
December median low-flow value (below 25th percentile)	Low winter flow, limiting habitat space (Dec.lowf)
June median low-flow value (below 25th percentile)	Low summer flow, limiting habitat (June.lowf)
April flow volume	Spring flow magnitude (April)

Other Variables

Previous year electrofishing effort	Deleterious effect of electrofishing
Spatial-thermal: distance of the station from the Colorado River	Temperature effect, proxy for temperature variation

Table 2.3. Estimates of generalized linear mixed effects, zero-inflated negative binomial model parameters, including BIC scores, for predicting the distribution and abundance of native fishes in Bright Angel Creek. The top five models are displayed for each response variable (aggregated native fishes, speckled dace, bluehead sucker, flannelmouth sucker abundance). Standard errors (SE) are given in parentheses with each coefficient.

Model rank	Conditional Model	Conditional model - coefficients (SE)					Zero-inflation model	Zero-inflation model – coefficients (SE)			df	ΔBIC
		α_1	α_2	α_3	α_4	α_5		β_1	β_2	β_3		
Native fishes												
1	α_1(Spatial-thermal) + α_2(Trout) + α_3(Spring flooding)	-2.63 (0.10)	-0.16 (0.17)	0.51 (0.15)			β_1(Spatial-thermal) + β_2(Monsoon)	8.47 (1.19	-1.89 (0.61)		12	0
2	α_1(Spatial-thermal) + α_2(Brown trout) + α_3(Spring flooding)	-2.53 (0.11)	-0.27 (0.21)	0.62 (0.15)			β_1(Spatial-thermal)	8.03 (1.18)			11	2.7
3	α_1(Spatial-thermal) + α_2(Brown trout) + α_3(Spring flooding)	-2.54 (0.11)	-0.24 (0.22)	0.62 (0.16)			β_1(Spatial-thermal) + β_2(Monsoon)	8.47 (1.16)	-1.88 (0.62)		12	2.8
4	α_1(Spatial-thermal) + α_2(Trout)	-2.64 (0.10)	-0.24 (0.19)				β_1(Spatial-thermal)	8.02 (1.21)			10	3.1
5	α_1(Spatial-thermal) + α_2(Trout) + α_3(Spring flooding) + α_4(Spatial-thermal × Trout)	-2.69 (0.11)	-0.24 (0.20)	0.49 (0.15)	-0.17 (0.15)		β_1(Spatial-thermal) + β_2(Monsoon)	8.38 (1.19)	-1.86 (0.62)		13	5.5

Speckled dace

		α						β			K	ΔAICc
1	α_1(Spatial-thermal) + α_2(Trout) + α_3(Spatial-thermal × Trout)	-3.23 (0.16)	-0.91 (0.35)	-0.86 (0.22)			β_1(Spatial-thermal)	10.96 (2.35)			11	0.0
2	α_1(Spatial-thermal) + α_2(Trout) + α_3(Spring flooding) + α_4(Spatial-thermal × Trout)	-3.19 (0.17)	-0.79 (0.34)	0.42 (0.22)	-0.81 (0.23)		β_1(Spatial-thermal)	11.00 (2.35)			12	3.5
3	α_1(Spatial-thermal) + α_2(Trout) + α_3(Spring flooding) + α_4(Spatial-thermal × Trout) + α_5(Spring flooding × Trout)	-3.21 (0.16)	-0.82 (0.31)	0.35 (0.21)	-0.81 (0.21)	-0.48 (0.29)	β_1(Spatial-thermal) + β_2(Monsoon) + β_3(Spring flooding)	10.67 (1.89)	-2.12 (0.57)	-0.64 (0.25)	15	4.1
4	α_1(Spatial-thermal) + α_2(Brown trout) + α_3(Spring flooding)	-2.65 (0.13)	-0.40 (0.31)	0.70 (0.23)			β_1(Spatial-thermal) + β_2(Monsoon)	10.55 (2.10)	-2.26 (0.65)		12	5.4
5	α_1(Spatial-thermal) + α_2(Trout) + α_3(Spring flooding)	-2.80 (0.12)	-0.13 (0.23)	0.54 (0.20)			β_1(Spatial-thermal) + β_2(Monsoon)	11.81 (2.39)	-2.55 (0.76)		12	7.4

Bluehead sucker

		α						β			K	ΔAICc
1	Intercept-only							β_1(Spatial-thermal)	9.11 (1.42)			6	0.0
2	α_1(Spring flooding)	0.18 (0.09)						β_1(Spatial-thermal)	9.11 (1.42)			7	2.9
3	Intercept-only							β_1(Spatial-thermal) + β_2(Large trout) + β_3(Spatial-thermal × Large trout)	9.52 (1.58)	1.65 (0.54)	-2.34 (0.70)	8	3.1
4	α_1(Trout)	-0.17 (0.09)						β_1(Spatial-thermal)	9.20 (1.45)			7	3.4

5	Intercept-only					β_1(Spatial-thermal) + β_2(Large trout)	8.03 (1.26)	0.76 (0.46)	7	4.2

Flannelmouth sucker

1	α_1(Spatial-thermal) + α_2(Brown trout)	-3.87 (0.61)	-9.02 (4.45)			β_1(Spatial-thermal)	21.4 (6.18)		8	0.0
2	α_1(Spatial-thermal) + α_2(Brown trout)	-4.70 (0.56)	-10.82 (4.07)			Intercept-only			7	1.1
3	α_1(Spatial-thermal) + α_2(Trout)	-3.86 (0.65)	-2.08 (2.64)			β_1(Spatial-thermal)	27.22 (8.80)		8	2.8
4	α_1(Spatial-thermal) + α_2(Spring flooding) + α_3(Rainbow trout) + α_4(Monsoon)	-4.26 (0.67)	2.21 (0.61)	-0.01 (0.06)	6.21 (2.40)	β_1(Spatial-thermal)	23.25 (13.60)		10	3.2
5	α_1(Spatial-thermal)	-5.22 (0.72)				Intercept-only			6	4.1
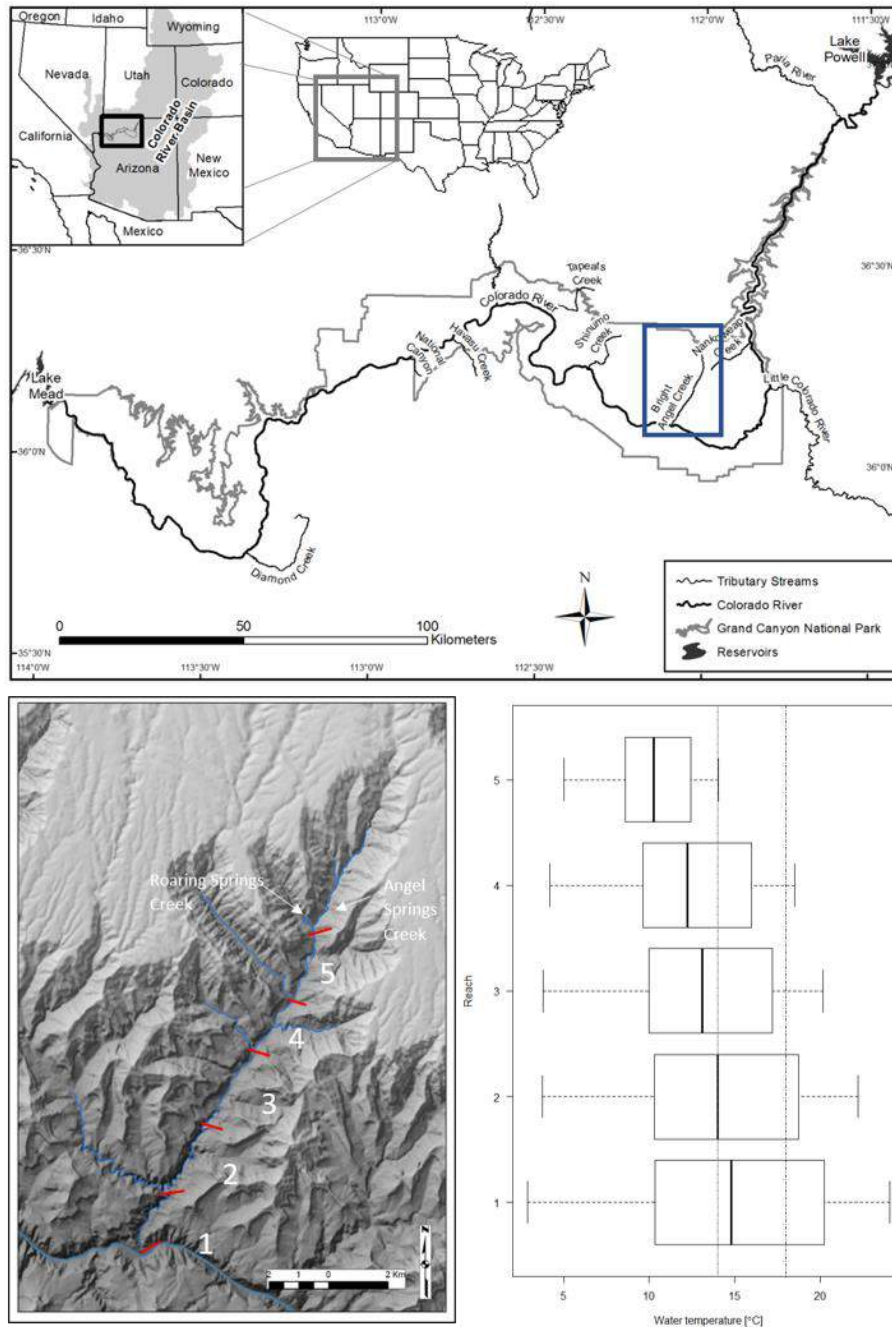
Figure 2.1. Bright Angel Creek study area in Grand Canyon National Park, Arizona. Insets indicate the location of Grand Canyon within the Colorado River basin, and topography and approximate reach delineations within the Bright Angel Creek watershed. Water temperature (°C) variation (25th, 75th percentiles, medians) in reaches one through five, June, 2013 – August, 2015 (data source: Bair et al. 2019), with dashed vertical lines representing approximate minimum spawning temperatures for speckled dace (18 °C, short-dash) and flannelmouth sucker (14 °C, long-dash; Valdez 2007), displayed in the lower right. Maps were created with ArcGIS Desktop (ArcMap) v. 10.6.1 (data source: National Park Service 2019, public data, no permission required for use).
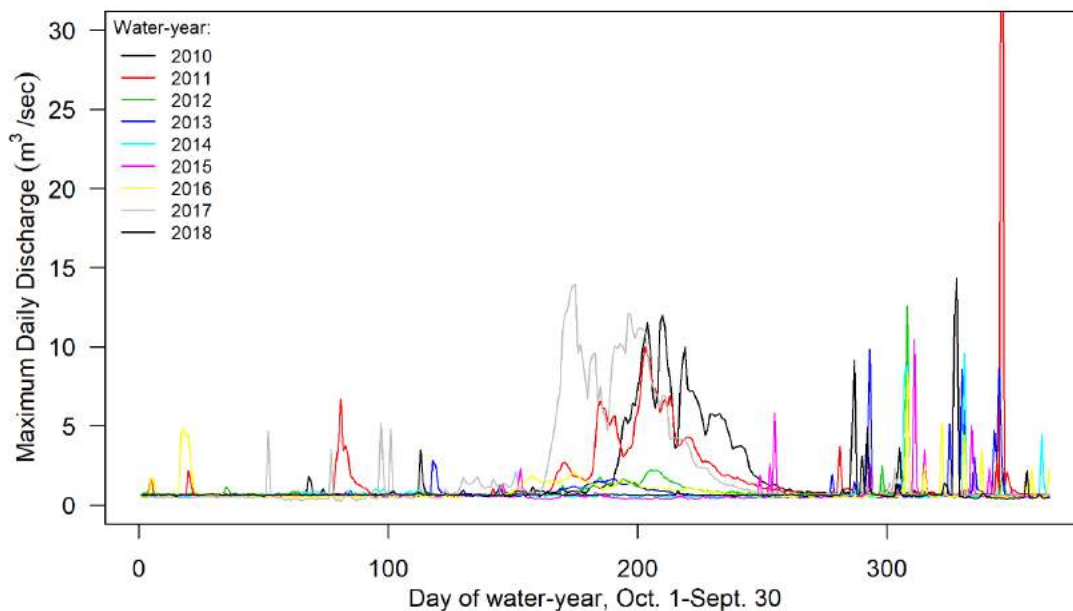
Figure 2.2. Maximum daily discharge (m3·s-1) of Bright Angel Creek, Grand Canyon, Arizona, measured near the mouth (USGS gaging station 09403000). Each water year is represented by a colored line, by day along the x-axis from October 1 through September 30. The extent of the y-axis is truncated to enable comparisons of typical water years, while the extreme hydrologic event in 2011 not pictured exceeded 75 (m3·s-1). Sampling occurred within the first 100-120 days of the water year, but we assumed estimated fish abundance reflected flow conditions during the previous water year.
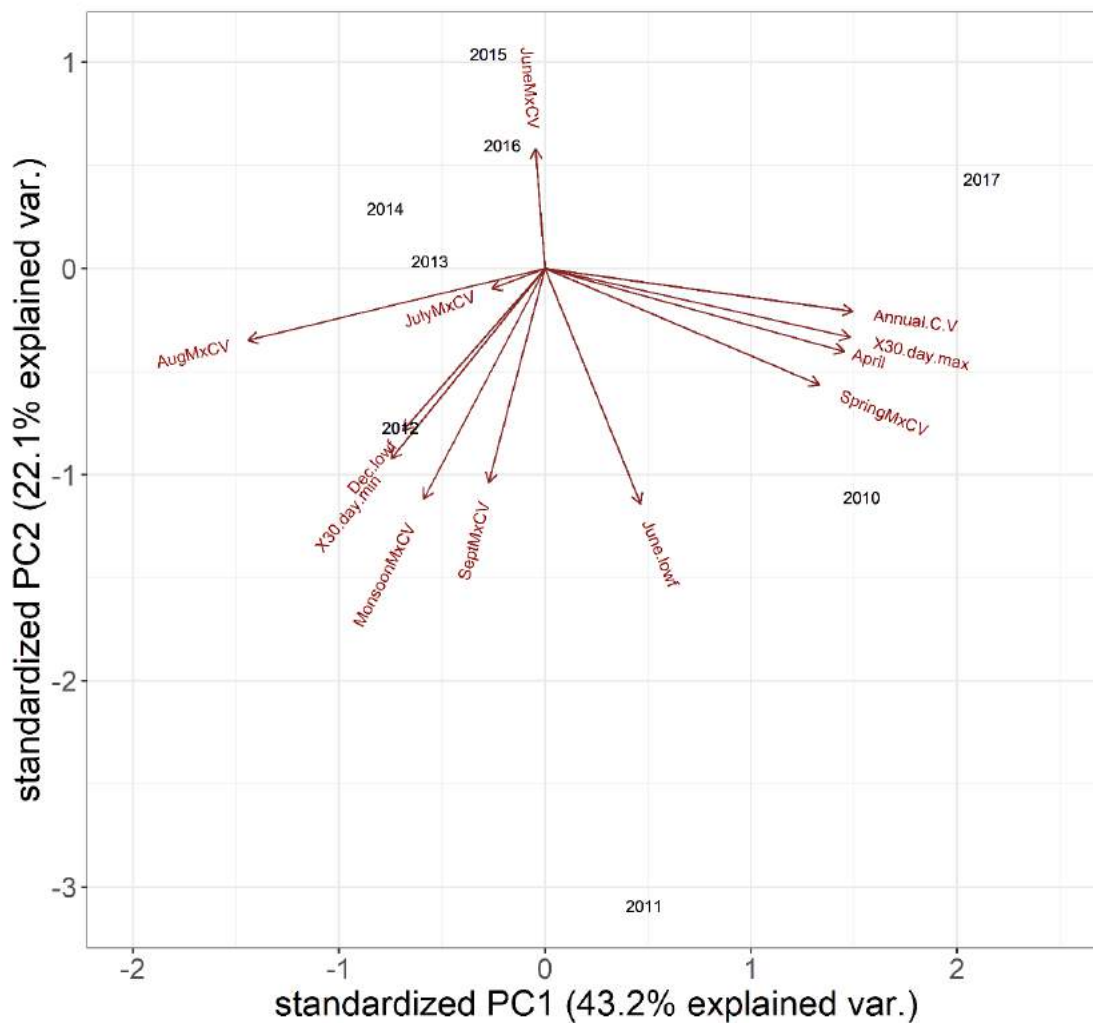
Figure 2.3. Principle component analysis results (PC1, PC2) for annual hydrologic variables, derived from maximum daily discharge data measured in Bright Angel Creek near Phantom Ranch (USGS gaging station 09403000, U.S. Geological Survey 2018), from water year 2010 through 2017. Loadings for individual years are displayed. Variable labels are listed in Table 2.2.
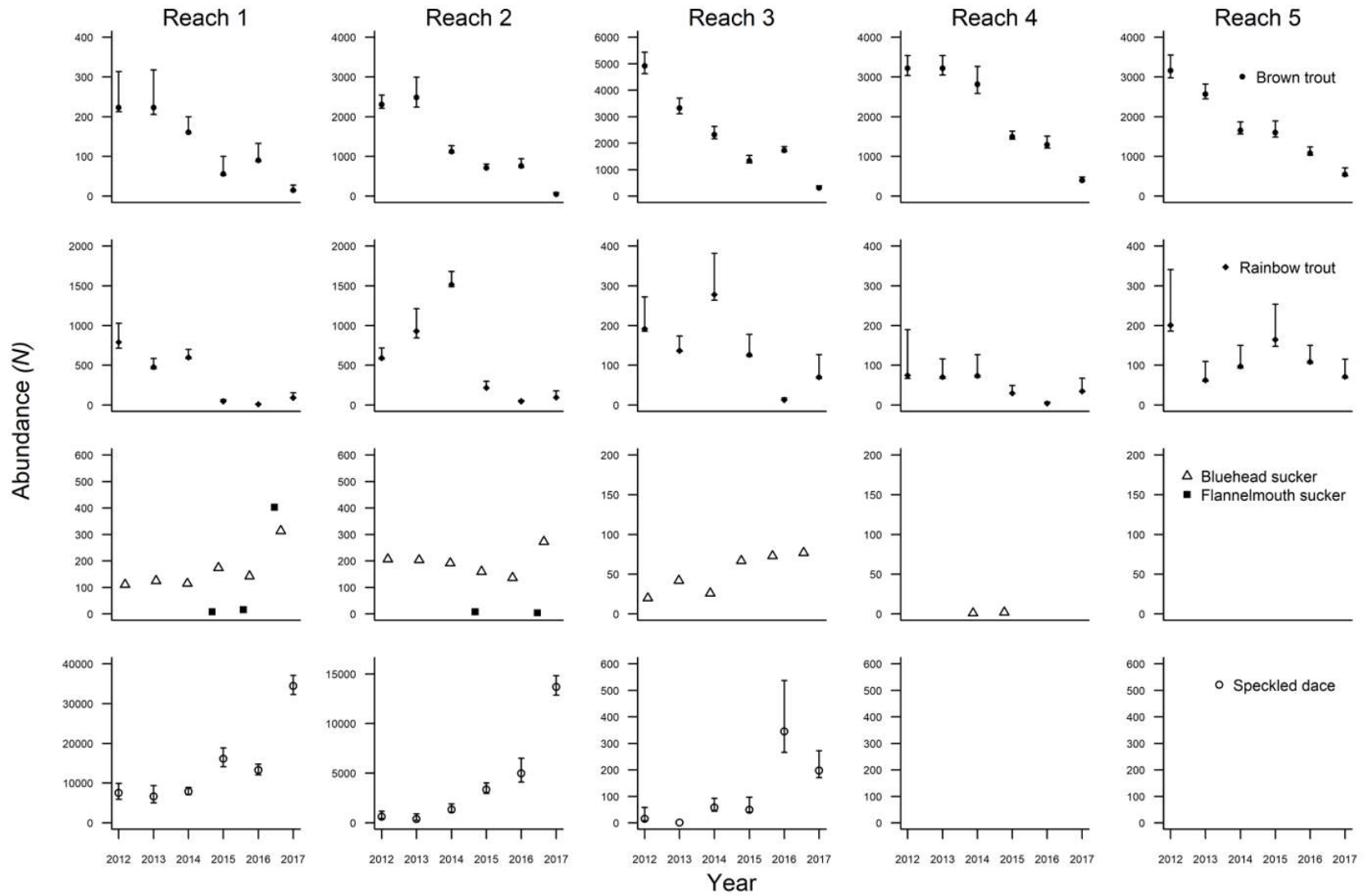
Figure 2.4. Reach-wide (15.5 km of stream) trends in abundance of brown trout, rainbow trout, and speckled dace, and trends in total catch of bluehead sucker and flannelmouth sucker, in Bright Angel Creek, Grand Canyon, Arizona, between 2012-2017 by reach, assessed using three-pass depletion electrofishing. Error bars indicate 95% confidence intervals for speckled dace and trout abundance estimates assessed using closed-population models in Program MARK. Shaded and tapered bar indicates the relationship between temperature and reach, with warmer and more seasonally variable thermal regimes (downstream) to the left.
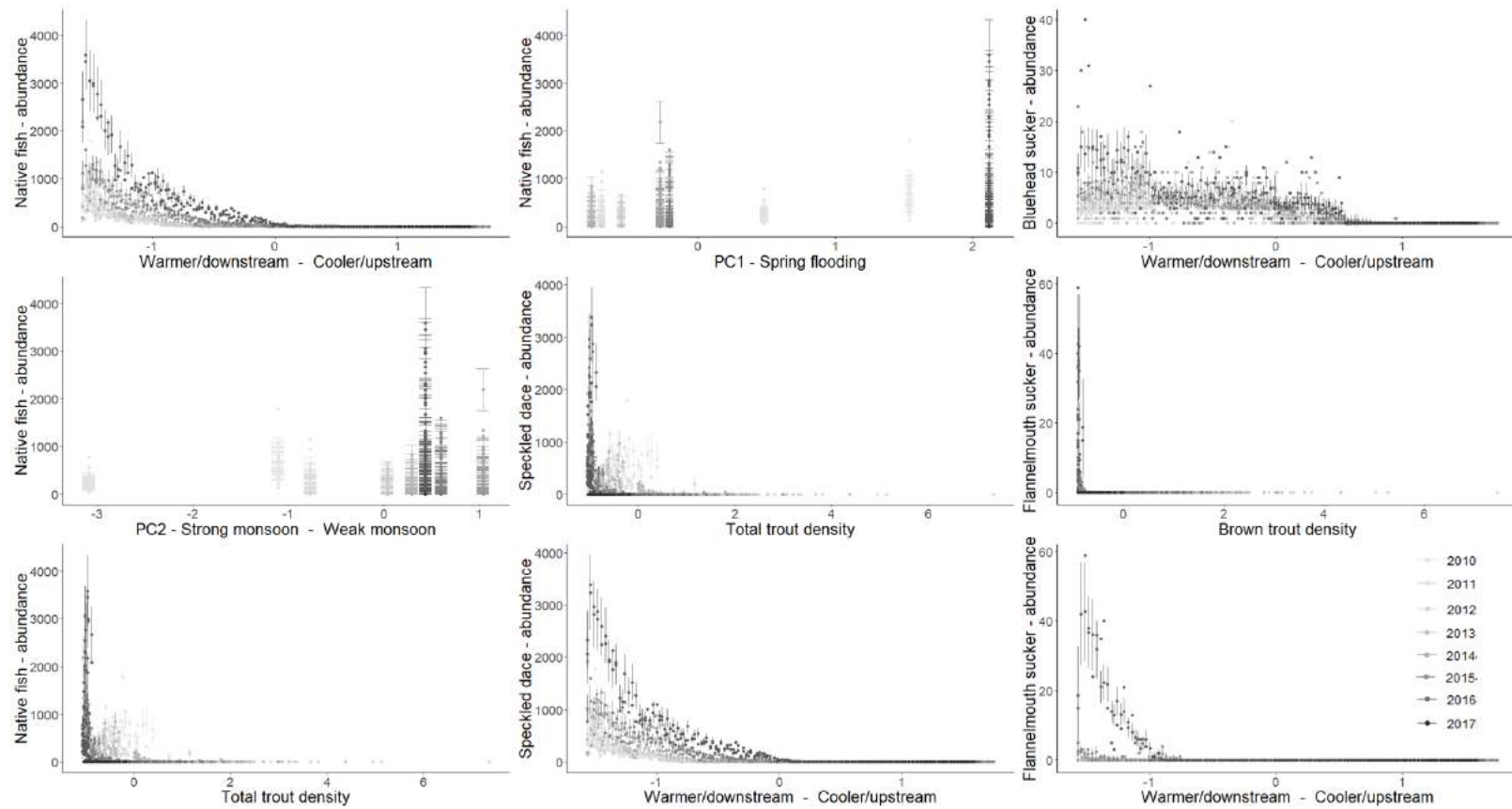
Figure 2.5. Relationship between average abundances for each native fish response variable and z-scored predictors selected for the GLMM with the lowest BIC score. Shading indicates year (i.e., later years are darker). Error bars are 95% confidence intervals of the predictions from the models.

CHAPTER 3

LIFE AND DEATH IN A DYNAMIC ENVIRONMENT: INVASIVE TROUT,

FLOODS, AND INTRA-SPECIFIC DRIVERS OF

TRANSLOCATED POPULATIONS[3,4]

Abstract

Understanding the relative strengths of intrinsic and extrinsic factors regulating populations is a longstanding focus of ecology and critical to advancing conservation programs for imperiled species. Conservation could benefit from an increased understanding of factors influencing vital rates (somatic growth, recruitment, survival) in small, translocated populations, which is lacking owing to difficulties in long-term monitoring of rare species. Translocations, herein defined as the transfer of wild-captured individuals from source populations to new habitats, are widely employed for species conservation, but outcomes are often minimally monitored, and translocations that are monitored often fail. To improve our understanding of how translocated populations respond to environmental variation, we developed and tested hypotheses related to intrinsic (density-dependent) and extrinsic (introduced rainbow trout *Oncorhynchus mykiss*, streamflow and temperature regime) causes of vital rate variation in endangered humpback chub (*Gila cypha*) populations translocated to Colorado River tributaries in Grand Canyon (GC), USA. Using biannual re-capture data from translocated populations over 10 years, we tested hypotheses related to seasonal somatic growth, and recruitment and population growth rates with linear mixed-effects models and temporal symmetry

(TSM) mark-recapture models. We combined data from re-captures and re-sights of dispersed fish (both physical captures and continuously recorded antenna detections) from throughout GC to test survival hypotheses, while accounting for site fidelity, using joint live-recapture/live-resight (JLRR) models. While recruitment only occurred in one site, which also drove population growth (relative to survival), evidence supported hypotheses related to density-dependence in growth, survival, and recruitment, and somatic growth and recruitment were further limited by introduced trout. Mixed-effects models explained between 67 – 86% of the variation in somatic growth, which showed increased growth rates with greater flood pulse frequency during monsoon season. Monthly survival was 0.56 – 0.99 and 0.80 – 0.99 in the two populations, with lower survival during periods of higher intra-specific abundance and low flood-frequency. Our results suggest translocations can contribute toward the recovery of large-river fishes, but continued suppression of invasive fishes to enhance recruitment may be required to ensure population resilience. Further, we demonstrate the importance of flooding to population demographics in food-depauperate, dynamic, invaded systems.

INTRODUCTION

The relative strengths of intrinsic and extrinsic factors regulating populations are a longstanding focus of ecological study and an important subject of debate for both ecologists and resource managers (Turchin 1999, Rose et al. 2001, Lobón-Cerviá 2014). Understanding population regulation is critical for both biodiversity conservation (Strayer

and Dudgeon 2010) and sustainable management of harvested species (Hilborn et al.

1995). Defining functional relationships between demographic vital rates (i.e., survival,

recruitment) and variation in extrinsic (e.g., density-independent predation, disturbances,

or harvest rates) and intrinsic (i.e., density-dependent) factors is essential for predicting

fluctuations in abundance and understanding factors limiting populations (Morris and

Doak 2002, Nichols and Armstrong 2012, Frederiksen et al. 2014). A vast body of

literature exists describing drivers of population dynamics of many economically-

important game or commercially-harvested species for the purpose of sustainable yield

calculation (e.g., Hilborn and Walters 1992). In comparison, knowledge of causes of

variation in vital rates in imperiled species' populations, which is critical for planning and

executing conservation actions, is generally lacking (Sibly and Hone 2002). This

understanding may be limited by misallocated monitoring (i.e., lack of focused

monitoring directed toward understanding critical uncertainties that if known, would

influence management decisions, Runge et al. 2011), the inherent rarity or behavioral

characteristics of imperiled species (Folt et al. 2020), and monitoring programs consisting

solely of count data or lacking long-term datasets (Wheeler et al. 2018, reviewed in

Margalida et al. 2020).

　　　As biodiversity loss may continue to accelerate with global change, expanded and

effective conservation programs, informed by knowledge of population regulation, are

critical (Hoffmann et al. 2010, Strayer and Dudgeon 2010, Reid et al. 2019). This need is

especially acute for obligate freshwater species which have suffered greater declines than

terrestrial or marine species (Strayer and Dudgeon 2010, Reid et al. 2019) – many

freshwater species may already occur at densities below thresholds of population viability

(Strayer and Dudgeon 2010). Novel or intensifying threats to riverine biota include, but are not limited to, climate change, species invasions, and expanding water and hydropower development to meet expanding human needs (Strayer and Dudgeon 2010, Reid et al. 2019, Albert et al. 2020). Among fishes, those inhabiting extensively fragmented arid- and semi-arid land river systems are among the most imperiled (Fagan et al. 2002). Expanding needs for human water development and threats imposed by invasive species introductions into environments with severely altered flow regimes require intensive conservation actions for arid-land species (Propst et al. 2008, Bond et al. 2015).

Reintroductions or translocations (hereafter translocations), defined herein as the movement of individuals from one source population to another area of a species' former range, could provide a means to recover imperiled species (reviewed in Armstrong and Reynolds 2012), including those inhabiting dry regions (Cahn et al. 2011, Lintermans 2013, Spurgeon et al. 2015b). Relative to terrestrial wildlife and birds, fewer translocations of fishes are reported in the literature (Brichieri-Colombi and Moehrenschlager 2016), in spite of 80% of endangered fish recovery programs in the USA including translocation as a recovery action (Williams et al. 1988, George et al. 2009). Nonetheless, translocations remain controversial given the potential to impact source populations (e.g., Pine et al. 2013, Lamothe et al. 2021), introduce disease, or cause other harmful negative impacts to the receiving ecosystems (George et al. 2009, Olden et al. 2011, Pérez et al. 2012).

Many translocations also fail, especially those involving endangered species (Griffith et al. 1989, reviewed in Cayuela et al. 2019). All too often, translocations are

inadequately planned or monitored (Strayer and Dudgeon 2010), or measurable objectives are not established to quantify and report outcomes (reviewed in Sheller et al. 2006, George et al. 2009, Galloway et al. 2016). When clear outcomes were reported, failures of translocations to establish self-sustaining populations were related to insufficient or unsuitable habitat (Griffith et al. 1989, Harig et al. 2000), limited duration of a program, the number (i.e., propagule pressure) and genetic origin of individuals translocated, the season of release (Sheller et al. 2006, Cochran-Biederman et al. 2015), predation by introduced fishes (Al-Chokhachy et al. 2009), and failure to address the initial cause of decline (e.g., continued presence of nonnative species; Cochran-Biederman et al. 2015). Assessment of demographic rates in translocated fish populations are also rare (Armstrong and Reynolds 2012, Vincenzi et al. 2012a). Given the prevalence of translocations in recovery plans, a clear need exists to evaluate translocation efficacy in recovering endangered or threatened species (Minckley 1995, Sheller et al. 2006, George et al. 2009, Olden et al. 2011), including the likelihood of persistence of translocated populations under varying environmental conditions in receiving habitats (Vincenzi et al. 2012a).

The context under which compensatory mechanisms confer population resilience in small translocated populations, including the drivers of variation in individual- or population-level growth within and among populations, are important uncertainties to be addressed (Sibly and Hone 2002, Winemiller 2005, Vincenzi et al. 2016). How populations compensate for high mortality related to disturbance, or losses due to invasive species predation, for example, will depend on how populations are regulated at low densities (Vincenzi et al. 2012a). Detection of density-dependence in vital rates can

also provide insights into the carrying capacity of habitats where translocations occur.

Once factors regulating populations are understood, managers can prioritize actions for

endangered species recovery in the context of environmental variation, and predict how

small populations may respond (Vincenzi et al. 2012a, e.g., Conner et al. 2018). For

instance, invasive species can limit populations of imperiled species through predation or

competition; however, environmental conditions, including those related to changing

climate, may mediate these impacts (reviewed in Rahel et al. 2008), or influence the

population-level response of native species to invasive species suppression (Healy et al.

2020b). Attempts to repatriate species may also be thwarted by severe floods or wildfire

(Vincenzi et al. 2012a, Hickerson and Walters 2019). The frequency and impact of such

catastrophic events must therefore be considered to understand long-term population

viability when planning conservation actions (Reed et al. 2003, Conner et al. 2018).

Monitoring that assesses vital rate relationships with environmental variables

(e.g., stream flow metrics, indices of invasive species abundance) or intraspecific density

are advantageous and underused for identifying the underlying mechanisms regulating

demographic variation (Wheeler et al. 2018). Mark-recapture techniques allow for

estimates of abundance, survival, recruitment, and temporary emigration – different

configurations of these translate to a given state (i.e., abundance at time t), and defining

the relative strength of each process in driving population growth rates can help focus

conservation (Armstrong and Reynolds 2012, Budy et al. 2017, Wheeler et al. 2018). For

example, restoring habitat in migratory routes and protecting large adults from harvest

was recommended for endangered Gulf of Mexico sturgeon (Acipenser oxyrinchus

desotoi, Pine et al. 2001) and bull trout (Salvelinus confluentus, Budy et al. 2017)

conservation, and placement of supplementary feeding sites to reduce negative density-dependent effects on adult survival was suggested to expand Bearded Vulture (*Gypaetus barbatus*, Margalida et al. 2020) populations – all species with population growth driven by adult survival.

Here, through the use of a multi-mark-recapture model approach, we examine demographic variation in translocated populations of a long-lived federally-endangered large-river cyprinid, humpback chub (*Gila cypha*), inhabiting the semi-arid Colorado River basin in the southwestern USA. Many native fishes of the region are imperiled due to the prevalence of dams and water diversions (Sabo et al. 2010) that fragment habitats and block migration routes (Fagan et al. 2002). Dramatically altered flow, sediment, and temperature regimes (Schmidt 2010) in the Colorado River also limit native fish reproduction and facilitate the replacement of native fauna by introduced invasive fishes (Holden and Stalnaker 1975, Olden et al. 2006). The largest remaining humpback chub population exists downstream of the Glen Canyon Dam within the Grand Canyon, Arizona, USA (USFWS 2018). The 1963 construction and operation of the Glen Canyon Dam altered or eliminated hmpback chub spawning habitat within Grand Canyon National Park (GCNP; Schmidt et al. 1998, Clarkson and Childs 2000), where humpback chub face predation and competition with introduced fishes (Marsh and Douglas 1997, Yard et al. 2011). Until recently (Van Haverbeke et al. 2017, Healy et al. 2020a), the Grand Canyon population was sustained almost solely by reproduction in a seasonally-warm tributary, the Little Colorado River (LCR; Valdez and Masslich 1999, reviewed in Pine et al. 2013). Managers initiated translocations to attempt to establish new populations in tributaries with more benign conditions (i.e., fewer predators, suitable

thermal regimes) than in the Colorado River, in order to increase population redundancy (Spurgeon et al. 2015b, Healy et al. 2020a) and reverse decadal-scale declines in abundance (Coggins et al. 2006). Knowledge of drivers of demographic rates in these populations could assist managers in planning translocations and mitigating additional stressors to endangered humpback chub and other imperiled fishes.

We assessed hypothesized mechanistic relationships between temporally varying environmental factors and humpback chub somatic growth, survival, recruitment, and emigration rates. Over a 10-year period, we studied responses in two populations of humpback chub translocated from the LCR to two small Colorado River tributaries. Specifically, our objectives were to a) evaluate hypothesized relationships between juvenile somatic growth, recruitment, survival, and fidelity rates with invasive rainbow trout (*Oncorhynchus mykiss*) abundance and seasonally-varying thermal and flow regimes; b) assess the degree of density-dependence in life-stage specific vital rates; and c), identify relative strengths of recruitment and survival in driving population growth rates among translocated fish and those produced *in situ*. We assessed evidence for the following hypothesized relationships between humpback chub vital rates and environmental drivers (additional humpback chub species information and study hypotheses are included in Appendix S1):

1) Individual growth, recruitment, and survival rates will vary with flood frequency, magnitude, timing, and duration. Growth of subadults would be constrained in winter (Dzul et al. 2016), but enhanced during summer months in years with higher frequency of floods (Behn and Baxter 2019). We predicted young-of-year (YOY) recruitment (survival from birth to age-1) would be limited during years with higher

monsoon flood frequency or intensity, as in the LCR (Yackulic et al. 2014). Once recruited into the sub-adult or adult population, we would expect minimal effects of flooding on survival, with the exception of ash-laden floods that may limit survival of southwestern US fishes (Gido et al. 2019).

2) We expect density-dependent growth and recruitment, but relationships between density and vital rates may be less important in sites with high food resources and with high emigration rates, compared to other drivers. The effects of negative density-dependence are assumed to weaken with size and age in the tributary humpback chub source population (Pine et al. 2013), but previous work found only weak support for density-dependent growth and survival in the Colorado River (Yackulic et al. 2018).

3) Rainbow trout will limit growth, survival (Yackulic et al. 2018), and ultimately recruitment of humpback chub in translocation sites, given high trophic niche overlap between the two species (Spurgeon et al. 2015a), and evidence of direct predation by rainbow trout upon YOY or sub-adult humpback chub (Yard et al. 2011).

METHODS

Study Area

Translocation sites were chosen in GCNP, on the semi-arid Colorado Plateau, which is bisected by 446 km of the Colorado River between Glen Canyon Dam and Lake Mead reservoir (Fig. 3.1). Havasu and Shinumo creeks, joining the Colorado River from the South Rim and North Rim of the Grand Canyon, respectively, were prioritized for translocations following an assessment of thermal characteristics, physical habitat, and biological conditions in several tributaries (Valdez et al. 2000, Spurgeon et al. 2015b, Healy et al. 2020a). Physical and chemical characteristics of Havasu Creek and the LCR

are thought to be most similar among GCNP tributaries, as calcium carbonate precipitates form large travertine dams and step-pools; however this unique water chemistry may also limit macroinvertebrate production (Oberlin et al. 1999), which was an order of magnitude lower in Havasu Creek relative to Shinumo Creek (Appendix S2: Fig. 3-S1).

The flow regimes in translocation sites differ; while the baseflow of both streams is driven by perennial groundwater discharge, during years with substantial snowpack at higher elevations on the North Rim, Shinumo Creek experiences spring snowmelt runoff, with intense, short-duration (< 1 day) monsoon-storm driven flooding in summer (~July-September; Tobin et al. 2018). Havasu Creek hydrology differs, as no prolonged spring snowmelt discharge occurs. Flooding in Havasu Creek is generally associated with monsoon-season storms, which can be intense (>280 $m^{-3} \cdot s$) but also of short duration (Melis et al. 1996). Baseflow discharge in the fall and winter in Shinumo Creek is ~0.26 $m^{-3} \cdot s$ (Spurgeon et al. 2015b), while Havasu Creek baseflow is 1.8 $m^{-3} \cdot s$ (Fig. 3.1; USGS data, gaging station 9404115). On July 28, 2014, an intense rainstorm on a freshly burned area comprising ~10% of the Shinumo Creek watershed triggered a massive flood that carried heavy loads of ash, destroying monitoring equipment and extirpating translocated humpback chub. Debris flows triggered by intense and localized rainfall that reorganize stream channels are also common (occurring in 18% of tributaries in 20 years) in Grand Canyon tributaries (Griffiths et al. 2004). While we lacked a long-term hydrologic record for Shinumo Creek, we assumed a flood of the magnitude observed in 2014 was a rare event, since it destroyed historic dwellings in existence for > 100 years (B. Healy, E. Omana Smith, personal observation).

Annual and seasonal variation in water temperatures (hereafter "temperature") in Shinumo Creek exceeds that of Havasu Creek (Voichick and Wright 2007), and while maximum temperatures are similar, Shinumo Creek has lower winter temperatures (Fig. 3.1). Havasu Creek water temperatures were suitable for humpback chub growth throughout the year (>12° C, Hamman 1982), with some exceptions, while Shinumo Creek was expected to provide seasonally-suitable temperatures (Fig. 3.1).

The fish assemblage in Havasu Creek consists primarily of native species with small numbers (averaging < 2% of fish) of rainbow trout captured (Healy et al. 2020a). Rainbow trout, an invasive salmonid introduced into GCNP in the 1920s (reviewed in Runge et al. 2018), was abundant in Shinumo Creek (Spurgeon et al. 2015a). Speckled dace (*Rhinichthys osculus*) were the most prevalent of native fishes in both streams during our study, followed by bluehead sucker (*Catostomus discobolus*), prior to extirpation from Shinumo Creek in 2014 (Spurgeon et al. 2015b, Healy et al. 2020a). A ~3 m waterfall near the mouth of Shinumo Creek, and steep cascades near the mouth of Havasu Creek, prevents immigration of fishes from the Colorado River, with the exception of a small number of humpback chub that presumably moved into Havasu Creek during high 2011 Colorado River discharge for reservoir storage equalization (discussed in Healy et al. 2020a). Historic, pre-dam fish survey data for tributaries prior to trout introductions in GCNP is limited to anecdotal reports that contain little species-specific information.

Translocation process

The process of collecting, rearing, and translocating humpback chub is described in detail in Spurgeon et al (2015b), and Healy et al. (2020a). In summary, we collected

wild YOY or juvenile humpback chub from the LCR in summer or fall months,

transferred the fish to a federal or state hatchery for parasite and disease treatment. Once

large enough (> 80-100 mm total length [length]; see Ward et al. 2015), humpback chub

were tagged with a 12-mm passive-integrated transponder (PIT) tag. We released a total

of 1,002 sub-adult humpback chub in groups of 200-302 individuals in Shinumo Creek

annually in June, between 2009 and 2013, with the exception of 2012 (Appendix S2:

Table S1). In Havasu Creek, we released a total of 1,955 humpback chub in groups of

243-305 in May, June, or July between 2011 and 2016. We completed translocations in

both May (300 fish) and July (209 fish) of 2014 to Havasu Creek – fish destined to be

released in June to Shinumo Creek were diverted to Havasu Creek in July to avoid

exposing fish to potential impacts of an active fire in the Shinumo Creek watershed.

Field Methods – Translocation Monitoring

Monitoring of translocated fish was conducted within translocation sites by crews

led by the authors, or throughout the Colorado River ecosystem (CRE; i.e., Colorado

River and its tributaries from Glen Canyon Dam to Lake Mead) during interagency

monitoring associated with the Glen Canyon Dam Adaptive Management Program

(GCDAMP). Sampling protocols for monitoring translocated populations are described in

Healy et al. (2020a) and Spurgeon et al. (2015b). In general, we monitored translocated

populations during biannual hoop-netting events conducted in spring or summer (pre-

monsoon season) and fall (post-monsoon) of each year, with 2 netting passes throughout

reaches accessible to translocated fish at least once per year. We were forced to cancel

one planned monitoring event in Havasu Creek during the suspension of US government

operations during October 2013, and sampling was disrupted by a late-monsoon season

Havasu Creek flood in October 2018. Otherwise, we consistently monitored between June 2009 and September 2014 in Shinumo Creek, and from June 2011 through October 2019 in Havasu Creek. Humpback chub dispersing from translocation sites were recaptured throughout the CRE during standardized river-wide electrofishing or hoop-netting administered through the GCDAMP (described in Van Haverbeke et al. 2017, Rogowski et al. 2018), or in the LCR (see Van Haverbeke et al. 2013 for details). Additional hoop-netting focused on the Havasu and Shinumo Creek inflow reaches of the Colorado River was also conducted consistently under the GCDAMP beginning in 2010 (Persons et al. 2017) or by our sampling crews after 2013 (~60 net sets per trip; Shinumo only). Handling and processing of native and invasive fish followed standardized protocols established for GCNP (Persons et al. 2013). We generally avoided tagging humpback chub < 100 mm and those 100 – 150 mm in length engorged with bait to minimize perforation of the gut and potential mortality (distribution of size of fish at tagging; Appendix S2: Fig. 3-S2).

We used continuously collected PIT-tag detection data from fixed passive interrogation antennas (PIAs) established prior to translocations in Shinumo Creek (June, 2009 – July, 2014), in Bright Angel Creek (May, 2018 – present), and in the LCR to augment capture histories for survival models (described below). PIAs in Shinumo and Bright Angel creeks spanned the width of their respective stream channels, and were installed as close to the mouth as possible (~200 m), but differed in the number of arrays; Shinumo Creek consisted of two antenna arrays installed 200 upstream of the waterfall, while three were installed in Bright Angel Creek for additional redundancy to improve detection rates. PIA operations were uninterrupted with some exceptions; due to power

supply issues and flood damage, the LCR PIA has operated intermittently since 2009

(Pearson et al. 2015) with more continuous operation between August 2017 – August

2019, and the Shinumo Creek PIA power failed briefly during winter of 2010. The

Shinumo PIA was destroyed during the flood of July 2014. We determined that powering

an antenna array at Havasu Creek was infeasible due to site characteristics, and relied

solely on recaptures in the Creek and Colorado River to populate encounter histories for

Havasu Creek fish. Beginning in 2014, the GCDAMP agencies began to deploy baited,

portable PIAs during river-wide monitoring excursions that also provided detections of

translocated fish. The spatial and temporal distribution of sampling effort generating data

for our study is depicted in Appendix S2: Fig. 3-S3.

     Environmental and Biological Predictors – We calculated physical and biological

variables to test hypothesized relationships with translocated humpback chub vital rates

(Table 3.1). Streamflow metrics represented flood duration, magnitude, timing, and

frequency, which are thought to drive the population dynamics of many stream fishes

(Poff and Ward 1989, Richter et al. 1996, Gido et al. 2013). Given differences in data

availability and stream discharge characteristics, streamflow metric calculation varied

between streams. Large flood events can rise and fall quickly within a day, and may not

be detectable when 15-minute flow records are averaged over a day. Therefore, we used

instantaneous maximum daily streamflow (m^3/s) from a USGS gaging station located

near the mouth of Havasu Creek (USGS data, gaging station 9404115), and lacking a

continuous hydrograph for Shinumo Creek, from a nearby gage on Bright Angel Creek

(USGS data, gaging station 9403000) subjected to similar regional-scale seasonal and

annual climatic patterns (Tillman et al. 2020). We assumed that Bright Angel Creek

baseflow and spring discharge was representative of seasonal hydrologic variation in Shinumo Creek, since the hydrology of both watersheds is driven by discharge from the same aquifer (e.g., synchronous spring snowmelt timing and magnitude; Tobin et al. 2018). Available daily discharge in both streams between January through June (2010-2016) was correlated ($p<0.001$, $R^2=0.93$, Appendix S2: Fig. 3-S4); however, spring discharge magnitude can be an order of magnitude higher in Bright Angel Creek. We assumed Shinumo Creek monsoon season flood frequency, but not magnitude and duration, would be represented by Bright Angel Creek discharge data. Thus, for Shinumo Creek, we defined flood-pulse frequency as the number of days the maximum daily flow exceeded 2 standard deviations greater than baseflow (>2.8 m^3/s), calculated from the streamflow record corresponding to our study period (Resh et al. 1988, Richter et al. 1996) in Bright Angel Creek.

Our approach to calculating Havasu Creek flow metrics differed from Shinumo Creek, given the rare and intense nature of floods (Melis et al. 1996), lack of spring snowmelt runoff, and availability of a complete flow record (USGS data, gaging station 9404115). The number of days flooding exceeded 2.8 m^3/s, and the number of days discharge exceeded 28 m^3/s for each interval between sampling events captured variation in flood frequency and magnitude, in addition to the maximum (peak) flow in each season. We calculated the number of days between translocations and the occurrence of a flood >28 m^3/s to understand how the timing of large floods following translocations would impact survival and fidelity (Table 3.1).

We represented seasonal (summer, winter) temperature variation in our models as cumulative degree-days (CDD, 10-degree C° base; Chezik et al. 2014) calculated from

mean daily temperatures measured at the Havasu Creek gaging station, and from a

temperature logger placed near the mouth of Shinumo Creek recording at hourly intervals

through the duration of our study. Summer and winter CDD were calculated between the

first days of each spring and fall sampling event (e.g., between spring 2012 and fall 2012,

and between fall 2012 and spring 2013, etc.).

We included biological variables in our models representing indices of abundance

of humpback chub, speckled dace, and rainbow trout. We used the total catch of speckled

dace, rainbow trout, and humpback chub during each sampling event at Shinumo Creek,

and the total catch of humpback chub (including untagged fish) on the first sampling pass

from Havasu Creek to account for differences in effort between spring and fall sampling

(single vs two-pass sampling). We included the number of humpback chub translocated

(at time t-1) as another measure to test for hypothesized density-dependent effects on

vital rates.

Data analysis

Modeling drivers of individual growth – We used linear mixed-effects models

(Gelman and Hill 2009, Weisberg et al. 2010, Dzul et al. 2017) to evaluate combinations

of predictors of individual somatic growth rates for summer and winter seasons of the

first year following translocation of each cohort of humpback chub. We calculated

individual growth rates for the 2013 Shinumo Creek cohort using the formula: growth

$_{season}$ = length$_{time-2}$ – length$_{time-1}$/Δ-day (Spurgeon et al. 2015b, Healy et al. 2020a), to

maintain consistency with published growth rates for juvenile humpback chub

translocated to Shinumo Creek from 2009 – 2011 (Spurgeon et al. 2015b), and Havasu

Creek between 2011 – 2016 (Healy et al. 2020a), minus the 2013 Havasu Creek cohort

(no data available in fall 2013). To avoid potential autocorrelation related to repeated measures of PIT-tagged individuals and assess the strength of temporally-variable environmental or biological fixed effects in predicting growth rates, we included random intercepts representing each individual humpback chub and the year of the interval in all models (Weisberg et al. 2010). We provide additional details and equations defining growth models in Appendix S2.

Growth model selection –We tested for effects of between- and within-stream temporal variation in temperature, flood-pulse frequency, and density-dependence on growth rates using combinations of covariates (Table 3.1) in models incorporating all cohorts from both streams. We included a categorical variable representing Shinumo and Havasu creeks in these models. We also separately evaluated the relationship between rainbow trout abundance and humpback chub growth rates, along with other covariates, within Havasu and Shinumo Creeks (Appendix S2: Table 3-S2). Prior to model fitting, we examined Pearson's (r) correlation coefficients between covariates and excluded covariates with correlations >0.70 to minimize inflated variance and difficulties in detecting effects (Zuur et al. 2010, Dormann et al. 2013). In cases where correlations between variables we deemed important for hypothesis testing exceeded this r threshold, we substituted another ecologically-similar variable. We included a categorical factor variable representing season in lieu of temperature, and avoided including humpback chub and rainbow trout abundance in the same model. To assess the potential for intra-specific density-dependent growth, and constraints on growth related to competition with trout, we included humpback chub and rainbow trout abundance covariates indexed at the end of each growth interval in models. Our base model, onto which we added other

covariates, included fixed effects of season and individual fish length, measured prior to release, to account for declining growth rates with size (Pine et al. 2017). In addition to additive models, we included two-way interactions between flood-pulse frequency and season, as well as between humpback chub or rainbow trout abundance and flood-pulse frequency and season, in other candidate growth hypothesis models.

We also calculated the variance inflation factor (VIF) for each of our top ranked models using the car package in R (Fox and Weisberg 2014, R Core Team 2019). We replaced interactions with additive terms for VIF testing. In cases where collinearity was evident or VIF > 3, we closely examined the effect of removing individual variables on collinearity (i.e., sensitivity of coefficient and SE estimates; Zuur et al. 2010) – further diagnostic procedures are described in Appendix S2. Predictors were z-scored to aid in interpretation of partial regression coefficients (Gelman and Hill 2009). We constructed all growth models using the lme4 package in R (Bates et al. 2015, R Core Team 2019), ranked models using AIC_c (Burnham and Anderson 2002) calculated with the bblme package (Bolker and Team 2017), and used R^2 calculated for the fixed effects in the models using the sjplot package (Lüdecke 2019) for model comparison.

Survival and fidelity – We used a joint live-recapture/live-resight (JLRR) model to estimate survival (probability of survival through interval i) and site fidelity (F_i, probability of remaining in tributaries) of translocated humpback chub (Barker 1997). This model is particularly useful for determining the fate of translocated individuals because it can incorporate continuously-collected data from PIAs and captures throughout the CRE during GCDAMP-interagency monitoring, which we considered "resights," as well as recaptures during targeted monitoring within translocations sites (e.

g., Horton and Letcher 2008, Conner et al. 2015). Additional parameters estimated by the

JLRR model include recapture probability (p_j) during translocation site monitoring

events, resight probability outside of translocations sites (R_i, i.e., probability of detection,

given the individual survives through interval i), temporary emigration (F'_j, the

probability a fish is not available for capture during j sampling event, but is available at

j+1), the probability of resighting prior to death (R'_i, probability of detection before an

individual dies during the interval i), and the probability an animal is found dead during

the interval (r_i). We set $r_i = 0$, since only 5 individuals (<0.002% of translocated fish)

were found dead during our study, and we assumed permanent emigration ($F' = 0$) due to

the presence of barriers near the mouths of both tributaries (Spurgeon et al. 2015b, see

Healy et al. 2020a). For the JLRR model, we included recaptures during summer and fall

netting events between June, 2009 and June, 2014, and June, 2011, and October, 2019,

for Shinumo and Havasu Creeks, respectively. Resights from GCDAMP monitoring trips

between June, 2009 and August, 2019 from anywhere in the CRE, and resights from the

Shinumo PIA between recapture events, were also included in encounter histories.

Following the extirpation of humpback chub from Shinumo Creek in July 2014, zero

recaptures occurred, but we created "dummy" post-flood recapture events with fixed p

=1, assuming certainty of humpback chub extirpation. We also defined two groups (g) of

humpback chub in Havasu Creek; translocated and non-translocated fish (either fish

produced in situ, or immigrated during elevated 2011 Colorado River discharge; Healy et

al. 2020a).

Due to the large number of potential combinations of parameters, our JLRR

model selection process proceeded in stages, which is described in detail in Supporting

Information (Appendix S2). In summary, we began by finding the best supported

structure on recapture and resight probabilities (*p, R, R'*) using combinations of time-

varying and constant parameters, and then compared combinations of models with time-

varying (*t*), constant, and group-specific fidelity and then survival. Finally, we combined

the most-supported model structure for *p*, *R, R'*, survival, and fidelity, and if top-ranked

models included *t*, we added combinations of environmental and biological covariates to

survival and fidelity parameters (replacing *t* from the base model). For each translocation

site, covariates were comprised of two synthetic variables (PC1 and PC2) constructed

using principle component analysis (PCA, Graham 2003), with the prcomp function and

default rotation in the stats package in R (R Core Team 2019). We determined PCA to be

advantageous over other multivariate methods given the underlying linear trends in our

continuous variables, which we centered and standardized (i.e., PCA based on a

correlation matrix) due to the differing scales of variables (Kenkel 2006). PC1 and PC2

represented 42% and 23%, of environmental and biological variation in Havasu Creek,

and 51.3% and 22.0% in Shinumo Creek (Fig. 3.2). For Havasu Creek, PC1 represented

variation in flood magnitude and frequency and temperature (−, i.e., greater flood

magnitude and temperature negatively associated with PC1), and PC2 represented indices

of abundance for humpback chub and the number of translocated chub (−), rainbow trout

abundance (+), and the timing of large (> 28 m^3/s) floods relative to translocation timing

(−, Fig. 3.2). PC1 for Shinumo Creek represented a gradient of rainbow trout, speckled

dace, and humpback chub abundance (−), and the total acres of fire below the canyon rim

in the watershed (+). Shinumo Creek PC2 represented flood-pulse frequency (−). For

Shinumo Creek, we also tested whether survival differed before and after the 2014 fire

and large flood event. We constructed and ranked models using Program MARK (White

and Burnham 1999) and Akaike Information Criteria adjusted for small sample sizes

(AICc, Burnham & Anderson 2002).

Recruitment – We used a temporal symmetry model (TSM; Pradel 1996) to assess

drivers of annual recruitment rates for humpback chub in Havasu Creek. The TSM is an

open-population model that simultaneously estimates apparent survival (φ, confounded

by emigration) using individual encounter histories, and estimates the relative

contributions of adult survival and recruitment (*f*) towards the population growth rate (λ)

that is interpretable through a "seniority probability" (γ) parameter (Pradel 1996, Nichols

et al. 2000, Budy et al. 2017). In the TSM, recruitment is defined as the number of new

adults at time $t + 1$ relative to the number of adults at time t, and we considered newly

PIT-tagged fish as recruits. Recruits averaged the approximate length ($\bar{X} = 204$ mm)

when fish begin to mature (i.e., defined as fish in spawning condition; size at tagging,

Fig. S2 Healy et al. 2020a). For unbiased estimates of *f*, the size of the study area and

sampling effort are held constant (Williams et al. 2002). We restricted our TSM analysis

to data collected during spring trips when 2 sampling passes were consistently conducted.

We were interested in TSM estimates of λ, *f*, and γ for non-translocated fish only

(*f* of translocated fish could be regulated by additional translocations), which we

separated from translocated cohorts by defining representative groups in the encounter

history matrix. Assigning individuals to groups (translocated and non-translocated)

allowed us to share p_j from both groups if appropriate (i.e., if no group-level differences

in p_j were found), while generating group-specific estimates of *f* and γ. We used the *φfp*

and the *$\varphi\gamma p$* parameterizations of the TSM in Program MARK (White and Burnham

1999) to construct models with all combinations of group, constant, and time-varying φ, p, and f, to assess the relative contributions of φ and f to population growth. We considered estimates of $\gamma > 0.5$ to indicate greater influence of f on λ, while $\gamma < 0.5$ indicated φ was more important for λ in a given year (Budy et al. 2017).

Given constraints related to annual time intervals and our inability to differentiate between seasonal variation, we limited our hypothesis testing to annual drivers of f during early life stages. We tested covariates including flood-pulse frequency, and humpback chub and rainbow trout abundance indices during the natal year, as drivers of f, using the top-ranked model (ranked using $QAIC_c$, see Appendix S2) without covariates described above. The humpback chub abundance index metric differed slightly from the metric used for survival hypothesis testing, in that we summed the number of humpback chub translocated and captured in the spring of the natal year for each cohort, which we defined as f year $t - 2$. The number of rainbow trout captured in spring, and flood-pulse frequency during the summer of the natal year were also tested.

RESULTS

All cohorts of humpback chub translocated to Shinumo Creek in 2009 – 2011 and 2013, and to Havasu Creek in 2011- 2016, were represented in recapture data collected during monitoring events conducted in both streams between 2009 – 2014 and 2011 – 2019, respectively. We detected 51% and 38% of all fish translocated to Havasu Creek and Shinumo Creek. Through May of 2019, we also captured and tagged 232 non-translocated humpback chub in Havasu Creek that were produced *in situ* or immigrated during 2011, but we did not capture unmarked humpback chub in Shinumo Creek upstream of Shinumo Falls.

Individual growth modeling – The top growth model including all cohorts had all the support (Akaike weight = 1.0, ΔAICc >10, Burnham & Anderson 2002). The top model indicated there were lower growth rates of humpback chub in winter (range 0 – 0.28 mm/d) compared to summer (0.04 – 0.78 mm/d), lower growth rates in Shinumo Creek (0 – 0.74 mm/d) relative to Havasu Creek (0 – 0.78 mm/d), and a negative relationship with humpback chub abundance and individual length (Table 3.2; fixed effects R^2 = 0.86). Top models for Shinumo and Havasu Creeks suggested that humpback chub growth rates were related to humpback chub abundance and flood pulse frequency or rainbow trout abundance, and there were interactions between flood-pulse frequency and season or rainbow trout abundance (Fig. 3.3, Table 3.2). The top growth model for Havasu Creek indicated growth rates were lower with higher humpback chub density, and decreased or increased in winters and summers, respectively, with higher flood-pulse frequency (i.e., flood-pulse frequency × season interaction; R^2 = 0.84, Table 3.2, Fig., 3.3). We observed little support for other models explaining variation in growth at Havasu (Akaike weight = 0.88, ΔAIC_c > 4.8); however, three models were supported explaining growth rates in Shinumo Creek (ΔAIC_c < 2, Akaike weights = 0.36, 0.19 and 0.16, Table 3.2). Rainbow trout abundance, season, flood-pulse frequency, and a rainbow trout × season interaction explained variation in growth rates in the top-ranked Shinumo Creek model (R^2 = 0.67, Table 3.2). Growth in Shinumo Creek was higher during summers with more frequent flood pulses, but growth declined with higher trout abundance during summer intervals (Fig. 3.3). Humpback chub abundance coefficients in the 2nd and 3rd ranked Shinumo Creek growth models had weak effects (large SEs).

Model fit diagnostics are included in Supporting Information (Appendix S2: Figs. 3-S5 – 3-S7).

Survival and fidelity – A total of 767 (76%) fish translocated to Shinumo Creek were resighted at the Shinumo Creek antenna array, and 21% of 1,102 fish released in Shinumo Creek were resighted in the Colorado River (228 total), LCR (12 total; 9 fish were detected in both CR and LCR), or in Bright Angel Creek, where a single fish was detected on the Bright Angel Creek PIA (June 4, 2019); 4% of fish translocated to Havasu Creek were detected in the Colorado River (72) or LCR (2 individuals; Fig. 3.4). Eleven of 232 humpback chub tagged in Havasu Creek (i.e., produced *in situ*) were resighted in the Colorado River.

Our JLRR results for Havasu Creek humpback chub indicated survival differed between groups, and that survival of translocated fish was negatively density-dependent (PC2) and positively associated with flooding and temperature (PC1). The top-ranked model included time-varying survival of translocated fish (range 0.71 – 0.99/month) that was a function of PC2 (0.80, SE=0.31), constant survival of non-translocated fish (0.69), and time-varying fidelity (range 0.40 – 0.89) with no difference between groups (Table 3.3, Fig. 3.5). Recapture probability (*p*) varied over time (0.47 – 0.89), as did resight probability (*R*, ~0 – 0.10), and the probability a tagged fish was resighted in the interval prior to death (*R'*) was constant in the top model (*R'* = 0.02; Appendix S2: Fig. S8). There was almost equal support (Akaike weight = 0.41, model likelihood = 0.80, Table 3.3) for a model with the same structure on fidelity, *p*, *R*, and *R'*, as in the top-ranked model, with survival as a function of both PC1 and PC2. The confidence interval on the PC1 coefficient (-0.67) overlapped zero (SE = 0.57, 95% confidence interval -1.80 –

0.45), but nonetheless, models including these covariates reduced AIC_c by >7 when compared to the time-varying survival model without covariates in the model. In both models, survival was lower in non-translocated fish (survival = 0.69, 95% confidence interval 0.54 - 0.80). Survival was also reduced for translocated fish when humpback chub catch was greatest during summer 2014 to 2016 intervals following the largest translocation event (2014), but increased during intervals with higher flood-frequency-intensity and temperature (Fig. 3.5). While no covariates were retained on fidelity in the top models, the lowest fidelity estimates were observed during intervals corresponding with the largest maximum flood events during the monsoon seasons of 2013 and 2018 (Fig. 3.5, see Fig. 3.1).

We conducted separate *post hoc* tests of individual covariates comprised of PCs 1 and 2 (Appendix S2: Table 3-S3) in an attempt to understand the relative importance of each composite environmental effect on survival in Havasu Creek. Of variables with PCA loadings > 0.4 or < -0.4 (the top 4) tested in separate models, rainbow trout ranked highest based on AIC_c, followed by the timing of large flood post-translocation, number of translocated chub – models were all within 2 ΔAIC_c of the top model, suggesting similar support.

Survival, *p* (pre-flood), *R*, and *R'* varied for humpback chub translocated to Shinumo Creek (Fig. 3.5); however, no covariates were retained in the top JLRR model (Table 3.3). Survival ranged from 0.56 – 0.99, with a sharp decline concurrent with the Galahad Fire and subsequent flooding in July 2014 (Fig. 3.5). Models with *p* = 1, and fidelity = 0 during post-fire recapture occasions would not converge, but we found the most support for time-invariant fidelity differing before (0.85, 95% C.I. 0.82 – 0.87) and

after (0.37, 95% C.I. 0.30 – 0.46) the 2014 fire and flood. Models with $F' = 0$ were ranked higher than those without constraints, supporting the assumption of high probability of emigration once individuals were detected at the PIA (Spurgeon et al. 2015b). With the exception of confounded or inestimable resight probability estimates for the last two intervals, R estimates were generally higher (range 0.03 – 0.12) than for Havasu Creek fish, and p ranged from 0.37 - 0.68 (Supplementary Information, Appendix S2: Fig. 3-S8).

Havasu Creek recruitment and population growth – Temporal symmetry models with time-varying annual apparent survival (φ) and recruitment (f), and without group effects on recapture probability (p_j; mean 0.72, range 0.26 –0.91), outperformed those with group-specific parameters (p_j; Table 3.3), which allowed us to leverage data from both groups (translocated and *in situ*-produced fish) and estimate f rates for fish produced *in situ* (recruits), while testing recruitment hypotheses using covariates (adjusted for overdispersion, median $\hat{c} = 2.33$, Table 3.3). Recruitment of the translocated group was directly related to translocations, and thus, ignored. The greatest annual population growth rate (λ) of *in situ*-produced humpback chub occurred in the last two years of our study in Havasu Creek, coinciding with the highest f rates (Fig. 3.6). Population growth rates were < 1 in the 2013-2014 interval, but were stable (λ 95% confidence intervals overlapped 1 in 3/8 intervals) or increasing ($\lambda > 1$, 4/8 intervals) in all other years. Of the 232 non-translocated individuals captured and tagged, we observed the highest numbers of recruits in spring of 2018 (29) and 2019 (52). Both natal year humpback chub (Coefficient = -0.84, SE=0.43) and rainbow trout (Coefficient = -0.32, SE=0.16) abundance were retained in the top model (Akaike weight=0.36, model likelihood = 1).

There was also support for models that included natal year flood-pulse frequency ($\Delta QAIC_c$ = 1.62; Akaike weight = 0.15, model likelihood = 0.44), in addition to humpback chub and rainbow trout abundance, and for a model without covariates on f ($\Delta QAIC_c$ = 1.88; Burnham and Anderson 2002; Table 3.3). However, the SE for the flood-pulse frequency covariate was large (Coefficient = -0.64, SE=1.01), and confidence intervals overlapped zero, suggesting a weak effect. Nonetheless, these results support density-dependence hypotheses of reduced f with higher age-1 or older humpback chub and invasive rainbow trout abundances during a cohort's natal year. In the top model, annual φ for all cohorts ranged 0.36 – 0.67, and our estimate of seniority (γ) indicated f was of greater importance to λ than φ in Havasu Creek in all years but two (i.e., f was proportionally more important than adult survival, $\gamma < 0.5$, and confidence intervals overlapped 0.5 in 2 years; Fig. 3.6).

DISCUSSION

Our study provides a rare example of robust demographic rate estimates and their relationships to intrinsic and extrinsic factors in small translocated populations of an imperiled fish. While translocations are often used for species recovery, very few are monitored effectively to allow for an assessment against predetermined objectives and adaptation of methodology (i.e., while accounting for detection probability, Nichols and Armstrong 2012). The flow regime, often described as the "master variable" driving processes in streams, was important for somatic growth in both translocation sites, and positively related to survival, with the exception of a catastrophic flood event following a fire. Documentation of quantitative relationships between high flows and growth and survival of non-salmonid fishes is limited (Rosenfeld 2017). We also provide strong

evidence supporting hypotheses of the negative impacts of invasive rainbow trout on humpback chub vital rates, and intra-specific density-dependence in survival, growth, and recruitment. Our study is unique in that research in arid or semi-arid watersheds with minimally-impacted hydrologic regimes has been largely directed toward understanding patterns of persistence in native and introduced fishes in these dynamic systems (e.g., Propst and Gido 2004, Stefferud et al. 2011), but few studies directly address potential mechanisms driving demographic rates, and analyses of translocations are rare.

Flooding can both limit and enhance the somatic growth rates of fishes (Arndt et al. 2002, Mallen-Cooper and Stuart 2003). We provide support for summer flooding as an important hypothesized seasonal driver of growth (Dzul et al. 2016, Behn and Baxter 2019). Growth in humpback chub was constrained during winter, as expected for other warmwater fishes (Pine et al. 2017, Matthias et al. 2018), but we also observed a negative relationship between flooding and growth during fall-winter months in both translocated populations. Dzul et al. (2016) reported a similar negative relationship to winter-spring flooding related to snowmelt or winter rains and higher turbidity, because spring flooding may also alter temperatures and impact growth (Dzul et al. 2017). Compared to the LCR, winter floods are generally of much shorter duration in Havasu Creek, and scouring during these intense winter floods may temporarily remove periphyton or invertebrates. Subsequent production would be limited in winter relative to summer, due to reduced solar insolation (Hall et al. 2015). While we are not certain of the mechanism (e.g., increased terrestrial-based allochthonous food delivery vs. instream autochthonous invertebrate production), our results support previous findings that food availability may be enhanced for desert fishes during monsoon flooding (Sabo et al. 2018, Behn and

Baxter 2019), and importantly, opportunistic feeding on allochthonous matter translates into greater growth. The mechanism driving the positive response in growth rates to flooding in our perennially-flowing systems likely differs from other arid-land rivers where intermittent floods promote autochthonous production in floodplains and waterholes (Arthington and Balcombe 2011). The importance of increased resource availability during floods for growth and recruitment is well-documented for rivers with floodplains (Power et al. 1995, reviewed in Humphries et al. 2020), and for littoral-dependent fishes in large rivers (Gutreuter et al. 1999), but less so in canyon-bound streams such as ours (Behn and Baxter 2019). Terrestrial-based diet items may be critical to sustain drift-foraging fishes in Havasu Creek (Garman 1991, Kawaguchi et al. 2003), where instream invertebrate production is limited due to travertine deposition (Oberlin et al. 1999, Rundio 2009). Monsoon flood-pulsed food in Havasu Creek may offset intra-specific, density-dependent negative effects on growth. Nonetheless, we suspect enhanced food availability in our sites would be short-lived, given the intensity and short-duration of monsoon flood events. Our results suggest the physiological capacity of humpback chub to process food evolved for boom and bust cycles (Armstrong and Schindler 2011), which warrants further study.

From a bioenergetic standpoint, consumption and demand for food, as well as intra – and inter – specific competition, would be higher during warmer summer periods (Taniguchi et al. 1998, Paukert and Petersen 2007). Temperature and food availability do in fact interact to influence growth of humpback chub in the LCR (Dzul et al. 2017), and in other species (reviewed in Ficke et al. 2007, e.g., Pennock et al. 2020). Rainbow trout are also known to aggressively defend foraging territories in streams (Keeley 2001),

potentially to the detriment of humpback chub growth and survival (Yackulic et al. 2018). Thus, bioenergetic interactions, which are driven in part by temperature, may explain the importance of the interactions of rainbow trout, season, and flooding on growth in Shinumo Creek, where substantial diet overlap was documented between the two species (Spurgeon et al. 2015a). Because growth rate-body size relationships are linked to survival and adult fecundity, understanding drivers of growth at early life stages that may manifest in the fitness of adult fishes (Vincenzi et al. 2012b, Nater et al. 2018) may be critical to the success of translocations. Faster growth may manifest in gape-limited predator avoidance (Urban 2007), earlier age-at-maturity (Stone et al. 2020), and increased fecundity, which would allow populations to recover quickly from losses due to predation or disturbance (Vincenzi et al. 2012b).

We identified functional relationships between annual humpback chub recruitment and age-1 and older humpback chub (i.e., density-dependent) and natal year rainbow trout abundances, and to a lesser extent, flood-frequency, in Havasu Creek. The largest year-classes of humpback chub recruited to the population in 2018 and 2019 (at age-2). These fish would have been produced *in situ* in 2016 and 2017 natal years, following cessation of translocations, declines in humpback chub, and when few trout were present. The occurrence of intra-specific density-dependent recruitment in fishes is commonly reported (Minto et al. 2008), but nonetheless controversial and potentially overridden by environmental conditions (Rose et al. 2001, Lobón-Cerviá 2014). Surprisingly, given the extremes in discharge observed during our study, flooding during the natal summer received less support in our recruitment models relative to hypothesized predation by rainbow trout (Coggins et al. 2011, Yard et al. 2011) or older conspecifics

(Stone and Gorman 2006). Nonetheless, monsoon flood magnitude during the natal year for the two largest cohorts ranked among the lowest ($< 14.3 \text{ m}^3/\text{s}$, median max. monsoon flood $= 29.6 \text{ m}^3/\text{s}$). High recruitment rates following years without intense monsoon floods suggests both flood magnitude and frequency may constrain recruitment (Healy et al. 2020b). In contrast, intense monsoon flooding may result in gains in recruitment in intermittent river systems flowing through arid-lands (Arthington and Balcombe 2011). Although we lacked data to test the relationship between the timing of flooding and recruitment (emergence timing is unknown in Havasu Creek), monsoon flooding may cause dispersal of YOY humpback chub (Yackulic et al. 2014). Dispersal of larval fishes through flooding may be an important adaptive mechanism for recruitment in systems with patchy distribution of resources (e.g., food; Winemiller and Rose 1992, Humphries et al. 2020). Flooding prior to spawning is also important for recruitment and persistence of stream fishes (Budy et al. 2015, Healy et al. 2020b). Floods maintain channel complexity and create aerated substrates for lithophilic spawners including salmonids (Bestgen et al. 2020) and humpback chub (Gorman and Stone 1999, Van Haverbeke et al. 2013).

Our results suggest invasive salmonids impacted recruitment and growth in Havasu Creek, as found for humpback chub in the Colorado River (Coggins et al. 2011, Yackulic et al. 2018). The likely mechanism explaining the relationship between recruitment and rainbow trout in Havasu Creek is related to rainbow trout predation upon juvenile humpback chub (Coggins et al. 2011, Yard et al. 2011). Rainbow trout are one of a suite of globally-introduced (Crawford and Muir 2008) invasive salmonids implicated in the suppression of native fish recruitment through piscivory (McDowall 2006, e.g.,

New Zealand, Jellyman and Mcintosh 2010, South Africa, Shelton et al. 2015) and other

multi-level ecological impacts (Simon and Townsend 2003, McIntosh et al. 2011,

Stanković et al. 2015, Hansen et al. 2019). While we can only speculate on the cause for

a lack of recruitment in Shinumo Creek prior to extirpation, rainbow trout predation on

larval chub is one hypothesis. Whiting et al. (2014) demonstrated that rainbow trout

could have a substantial impact on a small-bodied native fish population, and Spurgeon et

al. (2015a) found 75% of large rainbow trout stomachs to contain native fish in Shinumo

Creek. The highest incidence of piscivory corresponded to June, when native fishes

would be at their highest abundances following spawning (Spurgeon et al. 2015a). The

discovery of juvenile native suckers and large increases in native fish abundance

(~480%) following the suppression of rainbow trout and brown trout (*Salmo trutta*) in

another GCNP tributary also lends support to this hypothesis (Healy et al. 2020b).

Nonetheless, other authors have suggested the effects of warming temperatures in the

thermally-altered Colorado River may override or lessen trout predation risks to juvenile

humpback chub (Coggins et al. 2011, Ward and Morton-Starner 2015, Yackulic et al.

2018). Our findings appear contrary, since our study was conducted in naturally warmer

and more variable thermal regimes than in the Colorado River – temperatures only rarely

dropped below the approximate minimum threshold for growth in Havasu Creek, for

example. Projections suggest the consequences of basin-wide water storage decisions

may override climate change in governing future Colorado River temperatures (Dibble et

al. 2021). Future water management decisions that consider the impacts to endangered

fish could be informed by additional knowledge of the interactions between rainbow trout

and humpback chub across a broader temperature range than in previous laboratory (10-

20 °C, Ward and Morton-Starner 2015) or field studies (<15°C, Yackulic et al. 2018).

Our results provide further support for the eradication of invasive species to facilitate the

successful reintroduction or recovery of animal populations (e.g. salmonids, Al-

Chokhachy et al. 2009, amphibians, Bosch et al. 2019).

We found evidence of intra-specific density-dependence in survival, moderated

by flooding, in humpback chub translocated to Havasu Creek. The relationships between

survival and humpback chub abundance based on catch, the number of humpback chub

translocated, and the timing of a large flood event in relationship to translocation timing –

all correlated variables represented on Havasu Creek PC2 in our best-supported models –

provided evidence for the density-dependence survival hypotheses. Survival was lowest

during the summer intervals with the highest total number of humpback chub present

(2014-2016). The discovery of density-dependence in vital rates has important

implications for management of stocked or translocated populations since densities are

being directly manipulated (Lorenzen and Enberg 2002). Reintroducing or augmenting

populations with numbers that exceed the carrying capacity would thus be counter-

productive. However, detection of density-dependence in sub-adult or adult life stages,

and understanding how population dynamics are influenced can be difficult (reviewed in

Rose et al. 2001). Results of *post hoc* tests suggest complex and confounding

relationships that confuse the interpretation of mechanistic survival relationships. For

example, survival was positively, albeit less strongly (i.e., relatively weakly related to

PC2), related to rainbow trout abundance. Reduced body condition found following

intervals with greater humpback chub abundance (B. Healy, *unpublished relative weight

data*), and negative relationships between humpback chub abundance and individual

growth rates in this study, provide additional lines of evidence supporting the density-dependence hypotheses. Declining individual growth rates and body condition are linked to lower survival in fishes (Korman et al. 2021). Evidence for density-dependent survival has also been noted in the LCR population, but generally limited to juveniles (Pine et al. 2013, Van Haverbeke et al. 2013, Yackulic et al. 2018), as is common in other fishes (Lobón-Cerviá 2012 may be an exception, Vincenzi et al. 2016).

High mortality in humpback chub translocated to Shinumo Creek appeared to coincide with intense, ash-laden flooding. Despite the lack of covariates in our best Shinumo Creek survival models, we observed a sharp decline in interval-specific survival coinciding with the 2014 flood event, confirming high mortality predictions, rather than emigration from the Creek. In contrast, we observed relatively weak but positive relationships between survival and flooding in Havasu Creek, which is notable since extreme floods (i.e., > two orders of magnitude above baseflow) occurred in half the years, and sometimes multiple times within a year. The absence of a catastrophic effect of extreme flooding, or even a beneficial effect, suggests high resistance to flooding of sub-adult and older humpback chub in Havasu Creek. High resistance and resilience to flooding would be consistent with findings for native fishes in other arid-land systems (Pearsons et al. 1992, Propst et al. 2008, Rogosch et al. 2019). In contrast, ash-laden floods commonly extirpate aquatic biota in receiving waters due to hypoxia or toxic water chemistry (Bixby et al. 2015, Whitney et al. 2015). The extirpation of the Shinumo Creek population, as well as native resident bluehead sucker, suggests fire-related flood events – the type of event projected to increase in frequency under some future climate

scenarios (O'Donnell et al. 2018) – could lead to potential peril for small translocated populations.

Surprisingly, flow-related covariates were unimportant in explaining variation in fidelity in both translocation sites, despite high emigration rates found by Spurgeon et al (2015b) associated with higher stream stage in Shinumo Creek. We also noted much lower fidelity rates during intervals corresponding with the largest monsoon-driven Havasu Creek flood events during our study, occurring in the summers of 2013 and 2018. Covariates representing humpback chub abundance and the timing of large Havasu Creek flood events (>28 m^3/s) following translocations were corelated on PC2. This pattern simply suggests longer time periods between translocations and the occurrence of large floods led to higher numbers of humpback chub. We would expect newly released fish having been reared in a hatchery for up to a year to fare poorly in the face of a large disturbance or other stressful event. However, once established, native fishes appear to resist high flow events through morphological, physiological, or behavioral adaptations that may prove advantageous over invasive species (Ward et al. 2003, Moran et al. 2018).

Our ability to infer relationships between vital rates and abiotic and biotic drivers benefited from a biannual mark-recapture monitoring regime (sensu Wheeler et al. 2018) designed to answer questions related to the translocations developed *a priori* (e.g., Trammell et al. 2012); a practice uncommon in many reintroduction programs (Nichols and Williams 2006, Armstrong and Seddon 2008). Although our findings related to drivers of recruitment are supported in the literature (e.g., negative effects of flooding and invasive trout) as described above, we suggest additional years (~10 or more) of monitoring will allow for differentiation between sampling and process variation, and in

turn, stronger inference (Burnham and White 2002). High emigration immediately after

release (35% within 25 days, Spurgeon et al. 2015b), and short residence time prior to

extirpation likely limited our ability to estimate fidelity and test hypotheses for Shinumo

Creek humpback chub. In prior analyses, we observed that survival was related to size at

release; however, survival rate estimation was confounded by emigration (Spurgeon et al.

2015b, Healy et al. 2020a), which may be influenced by fish size or age (Yackulic et al.

2014). We leveraged detection data from multiple monitoring programs throughout the

CRE allowing for improved survival estimates accounting for emigration. These survival

estimates (annual mean survival = 0.60 and 0.35, Havasu and Shinumo, respectively)

were comparable to those found for juvenile humpback chub in the source population

(Yackulic et al. 2014, Dzul et al. 2016), and slightly lower, in the case of Shinumo, to

fish translocated to the upper LCR (Yackulic et al. 2021). We also estimated lower

survival for *in situ*-produced fish, which could have been a function of unaccounted for

tag-loss in the field. Alternatively, higher survival of translocated fish shows the

collection and rearing process was advantageous, and suggests mortality related to the

stress of transport to release sites and handling during the tempering and release process

were unimportant (Tennant et al. 2019) relative to natural conditions. Future work could

involve investigating the value of translocations to tributaries outside the LCR using vital

rates generated by our study, in a cost-benefit framework relative to other conservation

actions (Lamothe et al. 2021, Yackulic et al. 2021).

Implications for conservation

Our results provide further evidence for demographic resilience (Capdevila et al.

2020) of arid-land fishes adapted to relatively frequent flood-disturbances (Eby et al.

2003, Stefferud et al. 2011). Three of eight annual population growth rate estimates were high (λ>1.5) for humpback chub, suggesting the potential for rapid recovery under ideal conditions, such as following summers lacking intense monsoon flooding. The continued presence of invasive fishes may nonetheless limit demographic responses and reduce resiliency. Vincenzi et al. (2016) documented similar demographic responses to disturbance for populations of an imperiled salmonid, but resiliency to ash-laden flooding in arid-land streams may depend on the spatial location of disturbances and connectivity to sources for recolonization (Gido et al. 2019). Establishing populations with connections to broader stream networks would ensure population persistence. Smaller isolated tributary populations may take longer to recover to pre-disturbance levels than those with more direct connections to source populations in a mainstem river (Gido et al. 2019).,Continued monitoring would be necessary to understand how humpback chub demographic rates in translocated populations ultimately translate to long-term persistence.

The relationships between demographic rates and stream flow patterns we observed have important implications for conservation under climate change. The region is projected to become drier with increasing wildfire severity (O'Donnell et al. 2018) that could lead to more frequent ash-laden floods, and declining baseflows or spring flooding may limit humpback chub production (Van Haverbeke et al. 2013). If maintaining tributary populations in the fragmented CRE is a goal, occasional augmentation following disturbances, and focused mitigation of limiting factors, including removal of invasive species may be necessary. Regardless, the existence of density-dependence in vital rates reinforces the importance of the existing population size, carrying capacity, and invasive

species densities when planning augmentation and translocations programs. Reductions in spring flood magnitude and declining baseflow under extended drought scenarios projected for spring-fed tributaries (Tillman et al. 2020) would likely further constrain carrying capacities in our sites and others in arid-land systems. Warming temperatures with declining tributary baseflows (Bair et al. 2019) will also intensify consumptive demand and potentially increase competition for food between rainbow trout and humpback chub. Additional study is needed to understand how tributary flow and thermal regimes may change in future years, and how these novel regimes may mediate biotic interactions among native and introduced fishes. Despite these uncertainties, our findings derived from monitoring outcomes against *a priori* defined objectives can provide the basis for future adaptive management of translocated populations (Runge 2011, Runge et al. 2011).

In contrast to predictions of life history models suggesting a lack of density-dependence in recruitment ("periodic strategist", Winemiller 2005), we found population growth rates in endangered and long-lived humpback chub were driven primarily by density-dependent reproduction and recruitment in the early years of life. Studies finding density-dependence in recruitment are generally less common than those identifying density-dependent somatic growth in fishes (Grossman and Simon 2019). Adult survival was a less important component contributing to annual population growth rates of humpback chub in Havasu Creek compared to recruitment (all but 2 years), indicating management regimes aimed at mitigating factors limiting recruitment would lead to population maintenance or growth (Coggins et al. 2006). Protecting natural flow regimes in the Grand Canyon region will allow for continued pulses of food to both tributaries

and the mainstem (Sabo et al. 2018). Our work also supports the need to achieve

suppression of invasive fishes prior to translocations (Al-Chokhachy et al. 2009,

Cochran-Biederman et al. 2015).

In conclusion, we demonstrate how translocations can provide unique

opportunities to study ecological processes. With thorough monitoring and detailed

analyses, we provided additional knowledge of the life history and drivers of population

dynamics of an imperiled species that can assist in planning of recovery actions, and

inform further hypothesis testing through the use of models (Sarrazin and Barbault 1996,

Armstrong and Reynolds 2012). We also improved our knowledge of basic humpback

chub ecology and interactions of this endangered species with an introduced species and

its environment (Sarrazin and Barbault 1996). Our study presents a rare example of a

successful reintroduction effort of an endangered species, while also elucidating factors

preventing successful recruitment, and ultimate extirpation, of another translocated

population – both cases will inform future actions aimed at stemming global-scale

biodiversity loss (Tickner et al. 2020).

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Table 3.1. List of biological, hydrological, and other variables and their abbreviations used in figures, along with each variables' hypothesized relationship with humpback chub demographic rates.

Variables	*Abbreviation*	*Hypothesized Effect*	*Analyses*
Biological Variables			
Humpback chub catch-index of abundance	HBC.catch	density-dependence	Growth, Survival-fidelity, recruitment (Havasu only)
Number of humpback chub translocated	No.Transl	density-dependence	Growth, Survival-fidelity
Total length of individual (mm)	Total length	declining growth rate with size	Growth
Rainbow trout catch-index of abundance	RBT.catch	predation/competition	Growth, Survival-fidelity, recruitment (Havasu only)
Speckled dace catch-index of abundance	SPD.catch	food base indicator	Survival/fidelity
Hydrology Variables			
Flood pulse frequency (number of days discharge > 2.8 m^3/s)	Floodpulse	flood frequency/duration	Growth, Survival-fidelity, recruitment (Havasu only)
Number of days of flooding > 28 m^3/s	days.ov.1000	flood magnitude/duration, large disturbance/displacement	Survival-fidelity

Maximum flood size during interval	max.Flood	flood magnitude/timing, disturbance	Survival-fidelity
Number of days following a translocation before flood > 28 m^3/s occurs	No.daysto1000	flood timing/magnitude - large disturbance/displacement	Survival-fidelity
	Other Variables		
Season - summer or winter	Season	Represents seasonal differences in stream productivity and energetic demands	Growth, Survival-fidelity
Stream (Havasu or Shinumo creeks)	Stream	Represents differences in intrinsic conditions in translocation sites not captured by other variables	Growth
Acres of fire burned below the Canyon rim (Shinumo only, fires occurred in 2010, 2011, 2014)	Fire_brim	Ash limits survival	Survival (Shinumo only)
Temperature - cumulative degree days (base 10°C)	cDD	Temperature effect	Growth, Survival-fidelity

Table 3.2. Humpback chub growth model results for models incorporating growth rate (dependent variables) and environmental data (predictors) from all translocated cohorts, Havasu Creek, and Shinumo Creek. Partial regression coefficients (standard errors in parentheses), Akaike weights, and the coefficient of variation (R^2) are displayed for the top models (within ΔAICc< 2) for growth rates in each stream and both streams combined.

Model	Intercept	Stream	Season	Total length	Humpback chub catch	Rainbow trout catch	Flood pulse freq.	Interaction	Akaike weights	R^2
All cohorts/ streams	0.77 (0.04)	-0.5 (0.01)	-0.31 (0.001)	-0.001 (<0.001)	-0.11 (0.011)	–	–	–	1.0	0.86
Havasu Creek	0.72 (0.02)	–	-0.24 (0.01)	-0.002 (<0.001)	-0.01 (0.004)	–	0.14 (0.014)	Flood × Season -0.07 (0.01)	0.88	0.84
Shinumo Creek	0.67 (0.02)	–	-0.22 (0.01)	-0.001 (<0.001)	–	-0.11 (0.02)	0.03 (0.004)	RBT catch × Season -0.06 (0.01)	0.36	0.67
Shinumo Creek	0.65 (0.03)	-	-0.30 (0.01)	-0.001 (<0.001)	-0.007 (0.02)	-	-	HBC catch × Season -0.01 (0.01)	0.19	0.65
Shinumo Creek	0.67 (0.04)	–	-0.32 (0.02)	-0.0005 (<0.001)	0.02 (0.03)	-	-0.01 (0.008)	HBC catch × Season -0.04 (0.02)	0.16	0.64

Table 3.3. Model selection results for survival and fidelity (JLRR models) for Havasu and Shinumo Creek humpback chub, and for TSM model (apparent survival, recruitment, population growth rates and seniority) for Havasu Creek. The top ranked models supported by AIC_c for JLRR models and $QAIC_c$ for TSM models (model weights ≥ 0.01, or top 4), are displayed.

Model	ΔAICc/ ΔQAICc	AICc Weights	Model Likelihood	Num. Par	Deviance
Havasu Creek - survival and fidelity (JLRR model)					
S (g1(PCA2) g2(.) p(t) r=0 $R(t)$ R'(.) F(t) F'=0	0	0.51	1	44	1652.97
S (g1(PCA1+PCA2) g2(.) p(t) r=0 $R(t)$ R'(.) F(t) F'=0	0.42	0.41	0.81	45	1651.37
S(g1(PCA1) g2(.) p(t) r=0 $R(t)$ R'(.) F(t) F'=0	3.95	0.07	0.14	44	1656.92
S(g1(t) g2(.) p(t) r=0 $R(t)$ R'(.) F(t) F'=0	7.33	0.01	0.03	56	1636.05
Shinumo Creek - survival and fidelity (JLRR model)					
$S(t)$ $p(t$, years>2014=1) r=0) $R(t)$ $R'(t)$ F(.)pre-flood/F(.)post-flood F'=0	0	0.99	1	67	2993.17
$S(t)$ $p(t$, years>2014) r=0) $R(t)$ R'(t) $F(t)$pre-flood/F(.)post-flood F'=0	16.54	<0.001	<0.001	75	2948.86
S(pre-flood(t) S(post-flood(.)) $p(t$, years>2014) r=0) $R(t)$ $R'(t)$ $F(t)$ F'=0	22.39	<0.001	0	75	2954.70
$S(t)$ p(t) r=0) $R(t)$ $R'(t)$ $F(t)$ F'=0	29.26	0	0	82	2947.04
Havasu Creek – recruitment (TSM model)					
φ (t) $p(t)$ f(g1(t)g2(RBT catch +Chub natal period))	0	0.36	1	25	196.59
φ (t) $p(t)$ f(g1(t)g2 (RBT catch +Chub +Flooding natal period))	1.63	0.16	0.44	26	196.19
φ (t) $p(t)$ f(g*t)	1.89	0.14	0.39	29	190.35
φ (t) $p(t)$ f(g1(t)g2(RBT catch natal period))	2.08	0.13	0.35	24	200.71

φ (t) p(t) f(g1(t)g2 (RBT catch + Flooding natal period))	2.78	0.09	0.25	25	199.37
φ (t) p(t) f(g1(t)g2(Chub natal period))	3.27	0.07	0.19	24	201.89
φ (t) p(t) f(g1(t)g2 (Chub +Flooding natal period))	4.07	0.05	0.13	25	200.66
φ (t) p(t) f(g1(t)g2 (Flooding natal period))	9.45	<0.01	0.01	24	208.07

JLRR model annotation, $S = survival$, p = recapture probability, g=group membership (translocated or non-translocated), t=time-varying, r=probability of dead recovery, R=resight probability, R'= probability of detection before an individual dies during the interval, (.) =constant, F=site fidelity, F' = the probability a fish is not available for capture or temporary emigration; TSM specific annotation, φ=apparent survival, f=recruitment rate, RBT = rainbow trout. Refer to text for additional model details.
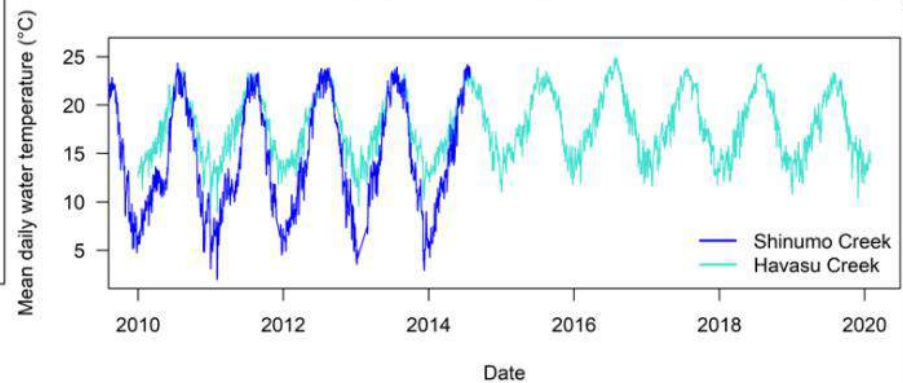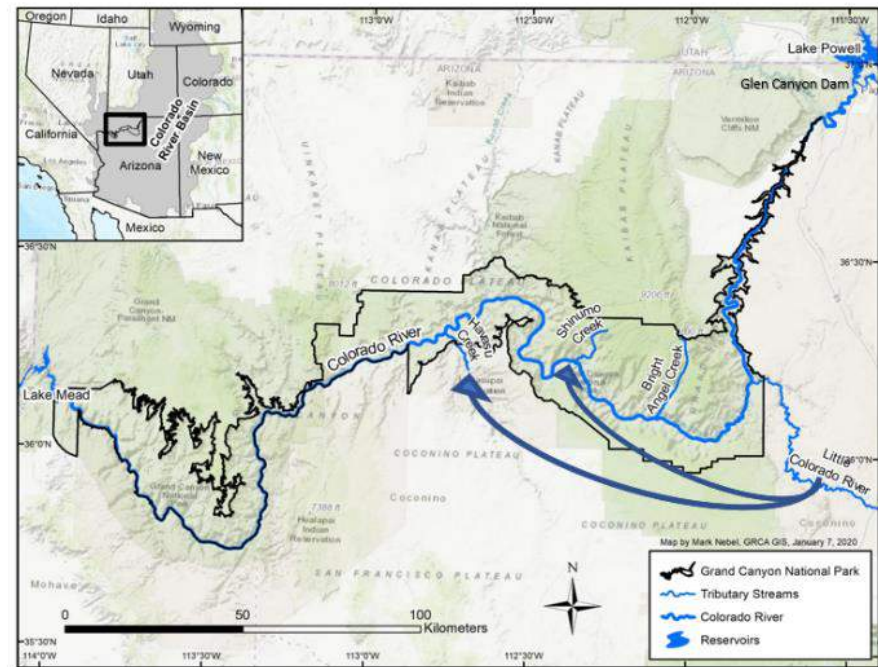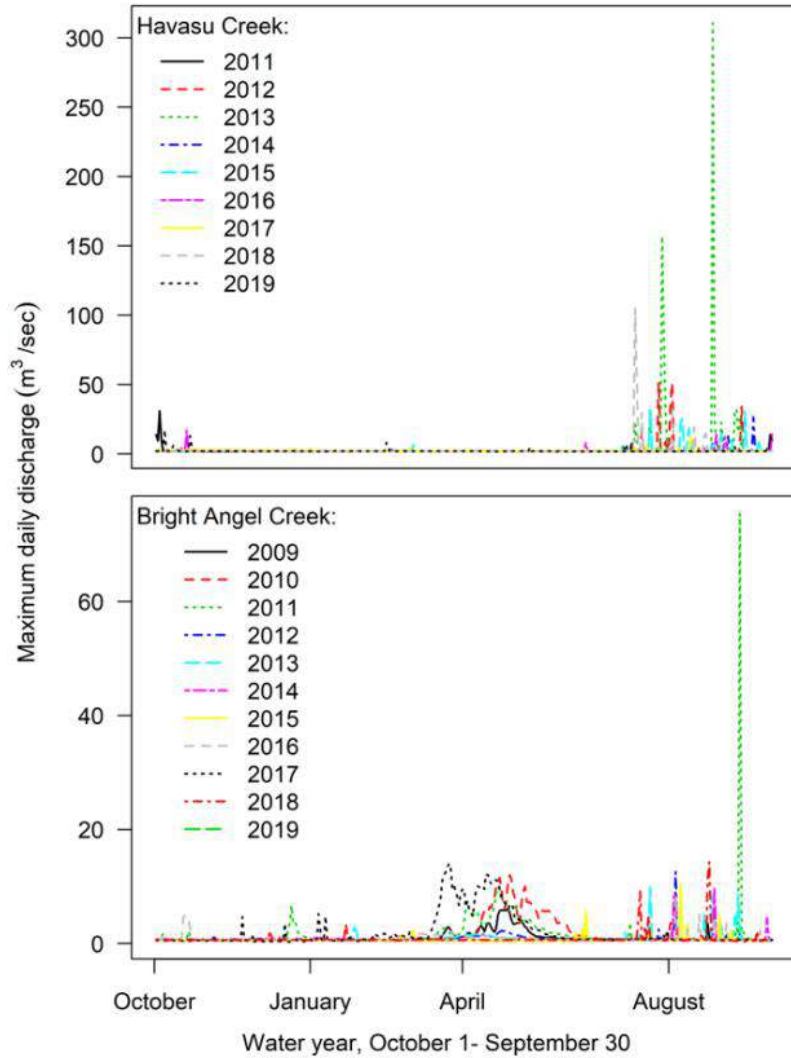
Fig. 3.1. Study area, with arrows depicting translocations of humpback chub from the Little Colorado River to Shinumo and Havasu creeks, within Grand Canyon National Park, Arizona, USA. Flow regimes (maximum daily discharge, m^3/sec, by water year) in Havasu and Bright Angel creeks, and temperature regimes (mean daily temperature °C) in Shinumo and Havasu creeks occurring during the duration of the study, as also displayed. Discharge data from Bright Angel Creek, an adjacent watershed to the east of Shinumo Creek, was used to calculate flood-pulse frequency to represent conditions in Shinumo Creek.
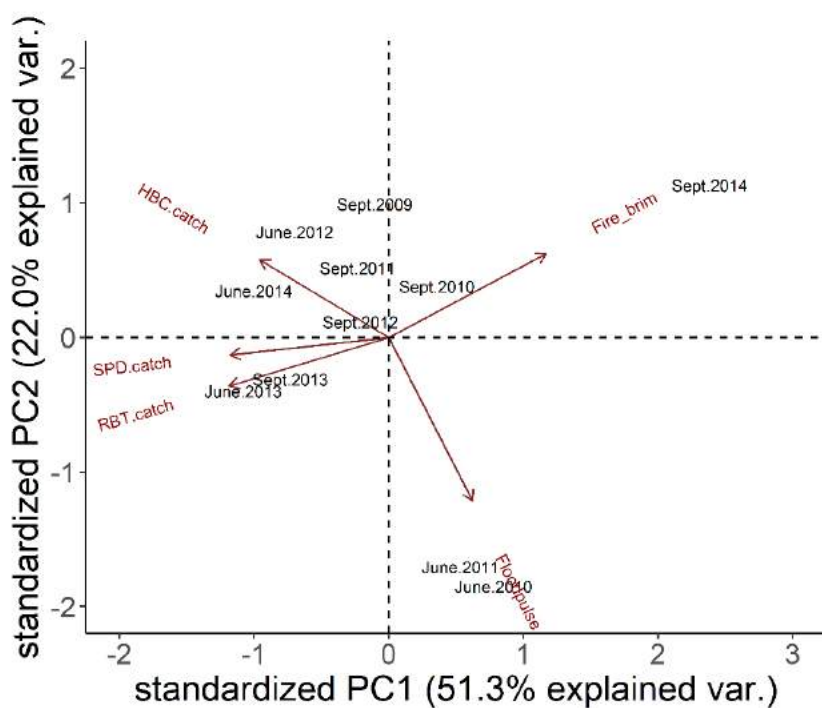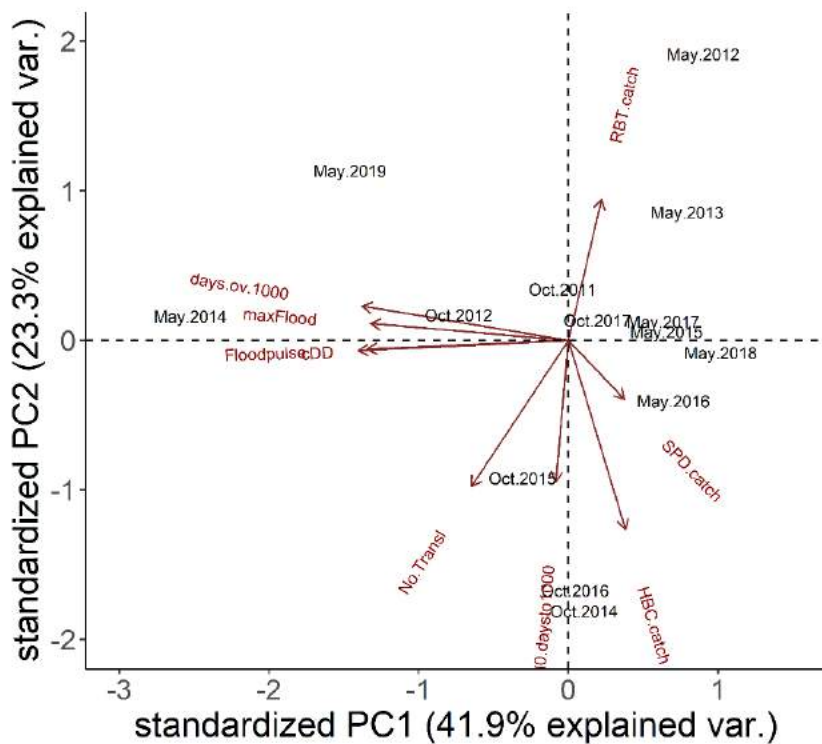
Fig. 3.2. Principle component analysis scores for Havasu Creek (top) and Shinumo Creek (bottom) environmental covariates used in joint live-resight/recapture models for survival-fidelity. Codes for each covariate are listed in Table 3.1.
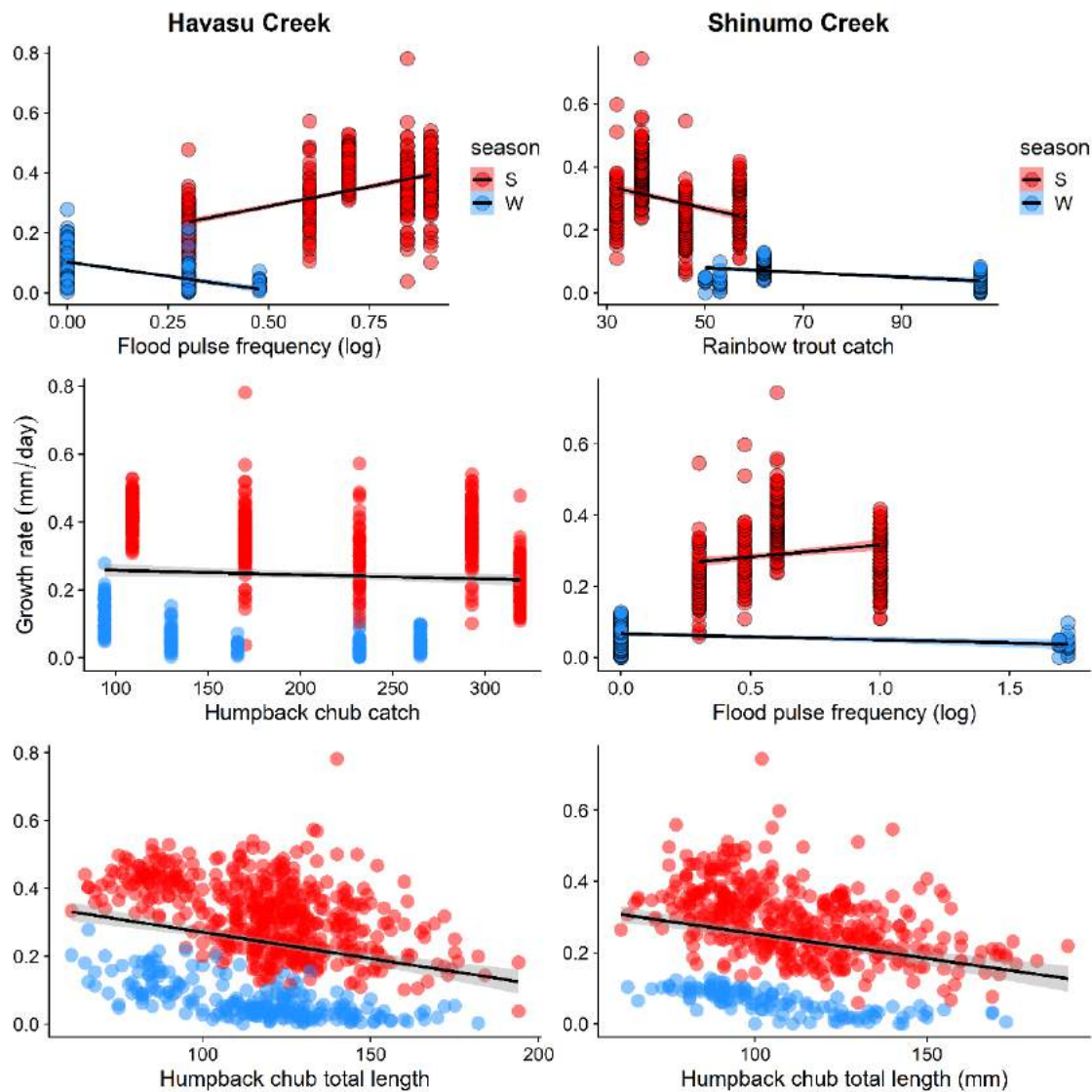
Fig. 3.3. Seasonal somatic growth model results (red points = summer, blue = winter) from the top models for Havasu Creek (left column) and Shinumo Creek (right column), including relationships between daily growth rates and flood-pulse frequency, intra-specific densities, and the interaction between season and rainbow trout abundance (upper right).
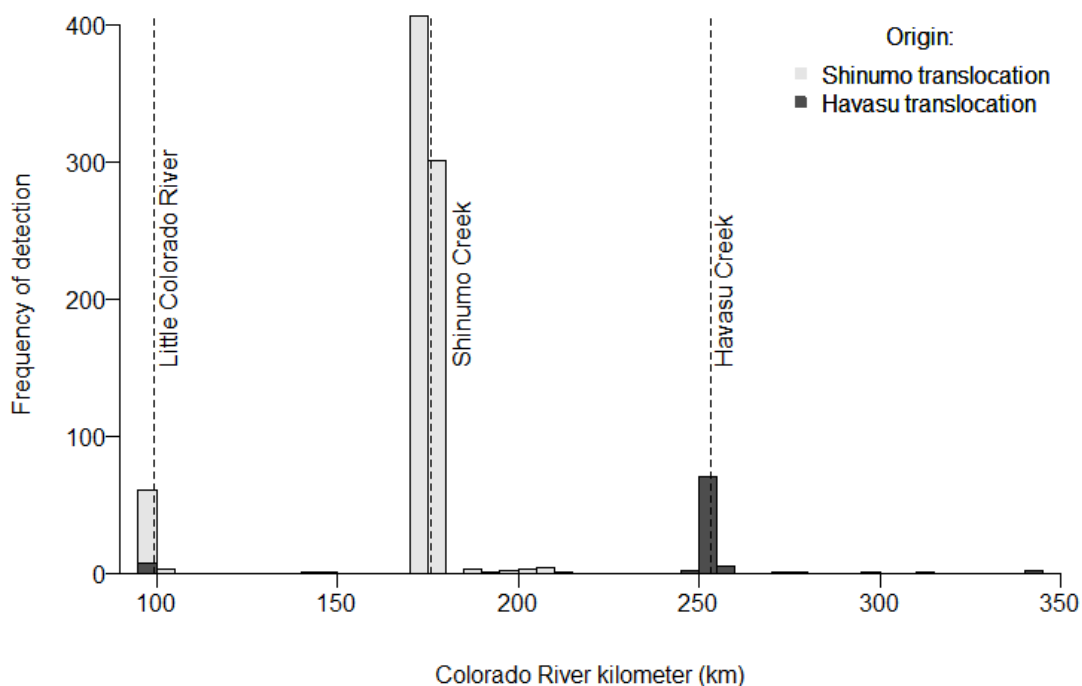
Fig. 3.4. Frequency of detections of translocated fish, dispersed from Shinumo (228 of 1,102 unique fish or 21%) or Havasu (73/1,954 or 4%) creeks, by Colorado River kilometer (km). Fish translocated to Havasu Creek were resighted outside of Havasu Creek in the Colorado River (72 total) or the LCR (2 total; one of which was also detected in the Colorado River). Upon leaving translocation sites, humpback chub dispersed upstream and downstream in the Colorado River – maximum dispersal distances from Shinumo Creek were 77 km upstream, and 34 km downstream, while fish from Havasu dispersed up to 154 km upstream through the Colorado River to the LCR and 89 km downstream. Detections include those of portable or fixed antennas or physical recaptures (i.e., netting or electrofishing) throughout the Colorado River ecosystem between Glen Canyon Dam (km -24) and Lake Mead (km 450). The river km of the confluence of tributaries where detections occurred outside of translocation sites are displayed. Dashed lines indicate the confluences of key tributaries.
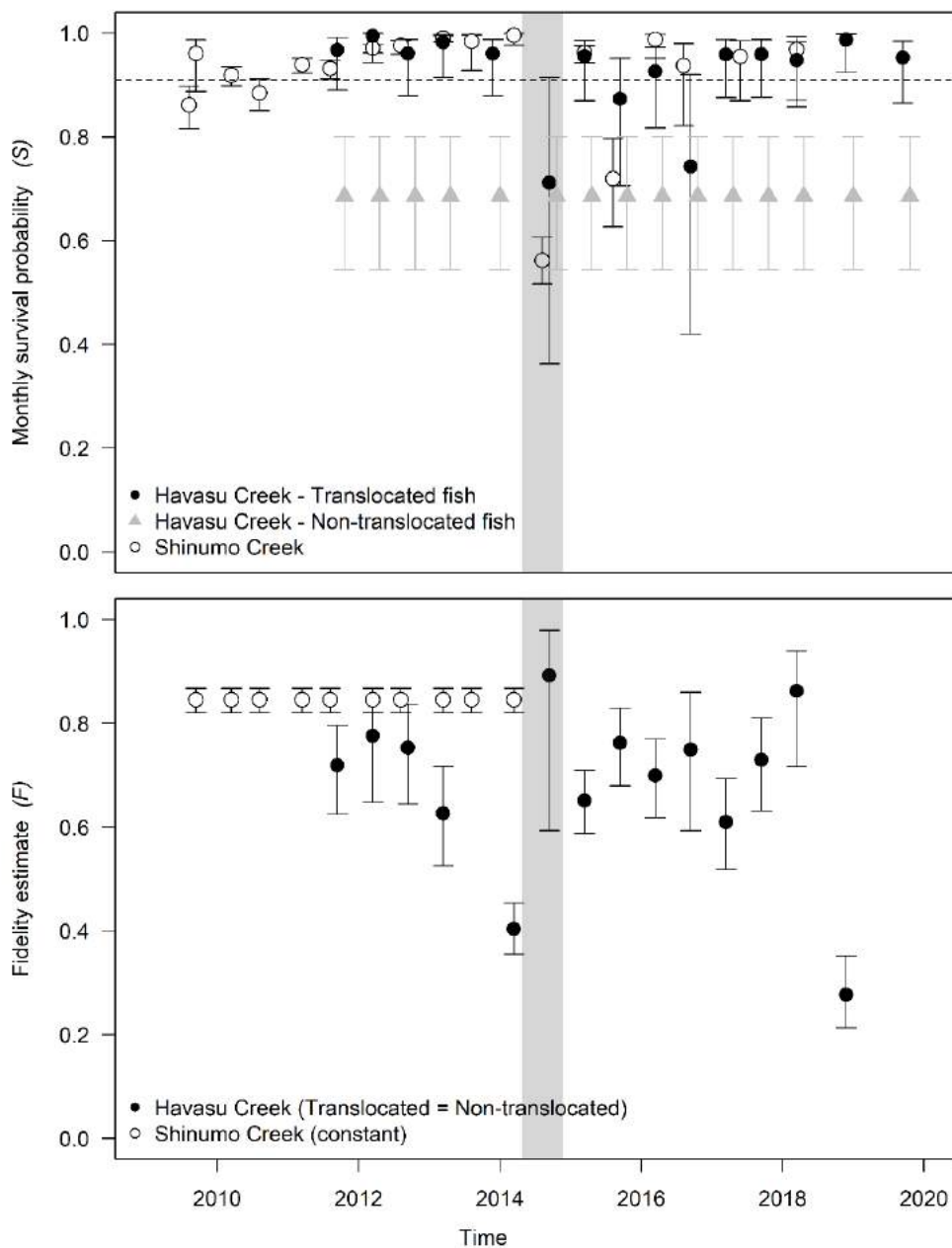
Fig. 3.5. Joint live-recapture-resight model monthly survival (upper) and fidelity (lower) estimates (with 95% confidence intervals) for humpback chub translocated to Shinumo and Havasu creeks, and non-translocated humpback chub initially tagged in Havasu Creek. On the survival plot, the dashed horizontal line indicates estimates of survival of small sub-adult humpback chub (total length 100-150 mm) in the Little Colorado River (translocation source population) 2009 – 2012 (Yackulic et al. 2014), and the interval corresponding to the Shinumo Creek ash-laden flood in August 2014 is denoted by the vertical gray band. Resight and recapture probability estimates are included in supplementary information (Figure S7).

Demographic rate
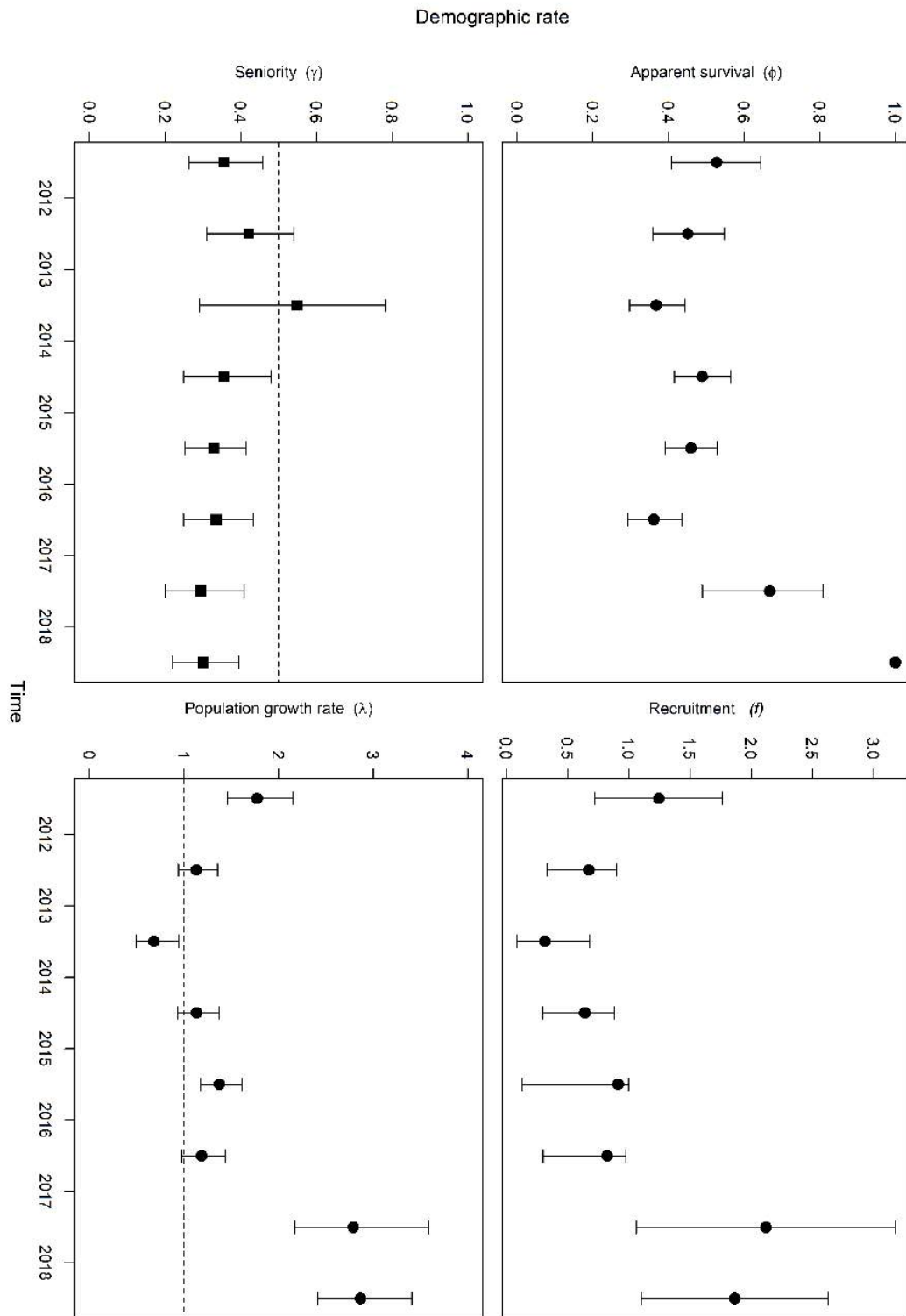
Fig. 3.6. Havasu Creek temporal symmetry model results including apparent survival for all cohorts (translocated and non-translocated fish), and seniority, recruitment, and population growth rate estimates for humpback chub produced *in situ* between 2011-12 through 2018-19. Note: the 2018-2019 apparent survival estimate is confounded.

CHAPTER 4

EXPLORING MANAGEMENT OPTIONS FOR A METAPOPULATION

OF A GLOBAL INVADER IN A RIVER NETWORK

UNDER CLIMATE CHANGE[5,6]

Abstract

Invasive species can dramatically alter ecosystems, but eradication is difficult, and suppression is expensive once they are established. Uncertainties in the potential for colonization and impacts by an invader can lead to delayed and inadequate suppression, allowing for establishment. Metapopulation viability models can aid in planning suppression actions to improve responses to invaders and lessen invasive species' impacts, which may be particularly important under climate change. We used a spatially-explicit metapopulation viability model to explore suppression strategies for an ecologically-damaging invasive fish, brown trout (*Salmo trutta*), established in the Colorado River and a tributary within Grand Canyon National Park. Our goals were to: 1) estimate the effectiveness of strategies targeting different life stages and subpopulations within a metapopulation, 2) quantify the effectiveness of a rapid response to a new invasion relative to waiting until establishment; and 3) estimate whether future hydrology and temperature regimes related to climate change and reservoir management affect metapopulation viability and alter the optimal management response. We included scenarios targeting different life-stages with spatially-varying intensities of electrofishing, redd destruction, incentivized angler harvest, piscicides, and a fish weir.

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Quasi-extinction (QE) was obtainable only with metapopulation-scale suppression targeting multiple life-stages; subpopulations were most sensitive to age-0 and large adult mortality. Importantly, the duration of suppression needed to reach QE for a large established subpopulation was triple compared to a rapid response to a new invasion. Isolated subpopulations were vulnerable to suppression; however, tributary subpopulations enhanced metapopulation persistence by serving as climate refuges and sources for recolonization. Water shortages driving changes in reservoir storage and subsequent warming would cause brown trout declines, but metapopulation QE was only achieved by re-focusing and increasing suppression. Our modeling approach improved our understanding of invasive brown trout metapopulation dynamics, which could lead to more focused and effective invasive species suppression strategies, and ultimately, maintenance of populations of endemic fishes.

Keywords: conservation, demographic rates, Lefkovitch matrix, population dynamics, flow-ecology, introduced species, nonnative salmonid

Article impact statement: An invasive brown trout metapopulation is predicted to persist in Grand Canyon under climate change, requiring adaption of current suppression strategies.

Introduction

Invasive species can extirpate natives and threaten ecosystem services (Mack et al. 2000; Pyšek et al. 2020); however, eradication of invasive species is difficult and suppression costs increase as populations become established and disperse across the landscape (Simberloff 2003). Once established, complete eradication is often infeasible

due to socio-political (Beever et al. 2019) or logistical constraints (Peterson et al. 2008), and costs (Mack et al. 2000; Baxter et al. 2008). Critical uncertainties can also limit decision-making and early intervention –the lack of future projections of dispersal or population growth rates, the extent of ecological or economical damage, or lack of resources needed to control invasive species legitimizes inaction. Consequently, costs may increase and the likelihood of success declines, if suppression is deferred to later stages of invasions when populations have fully established and are less vulnerable to stochastic events (Mack et al. 2000; Simberloff 2003; van Poorten et al. 2019). In addition, socio-economic beneficiaries (e.g., anglers of introduced salmonids) may resist control of invasive species populations (Beever et al. 2019).

Identifying abiotic and biotic drivers of invasive species' vital rates and planning control operations to target vulnerable or important life stages may improve the effectiveness of suppression strategies (Govindarajulu et al. 2005; van Poorten et al. 2019). This approach requires fundamental, but often uncertain knowledge of the species' population ecology and life history (Simberloff 2003). Knowledge of vital rates provides an advantage since the effectiveness of control or suppression techniques may be life stage or size-specific. For example, invasive amphibians have complex life cycles that may include aquatic egg or larval stages, metamorphosis to a juvenile stage, and sometimes a transition to upland adult habitats, which all vary in vulnerability to removal techniques (Govindarajulu et al. 2005). Fishing gears used to control invasive fishes such as electro-fishing or netting also select for larger (and thus older) individuals (Walsworth et al. 2020; Healy et al. 2020). Species with complex life histories including a partial or

fully migratory stage may also require a landscape-scale approach to control explicitly accounting for dispersal between populations (Milt et al. 2018).

Landscape-scale metapopulation conservation approaches are more often applied to imperiled species than to managing invasions or established nonnative species (With 2002; Bertolino et al. 2020). Nonetheless, dispersal rates between populations across spatially-heterogeneous landscapes may have important implications for resiliency of suppressed invasive species populations (With 2002; Pepin et al. 2019). Treating specific locations to eradicate or suppress an open and connected metapopulation of invasive species without a strategic approach, which is common, can lead to failure (Mack et al. 2000; Hock et al. 2016).

Matrix-based projection modeling and population viability analysis (PVA; Morris & Doak 2002), can be an effective approach for exploring drivers of population dynamics and the effects of management actions (e.g., Kareiva et al. 2000; Cahn et al. 2011) applied across a metapopulation (Murphy et al. 2020). PVA can be used in invasive species management applications, where the aim is to quantify the life history of invasive species and predict and compare the relative likelihood of suppression scenarios leading to eradication, time to extinction, or to meet a minimum population threshold (Berg 2012; van Poorten et al. 2019). Metapopulation-structured PVA models (mPVAs) are rarely applied to aquatic invasive species, which is surprising given the need to account for dispersal and connectivity between habitats in river networks (Murphy et al. 2020).

Future climate-driven changes in thermal or flow regimes propagating across dendritic stream networks may facilitate invasions of some, but hinder those of other aquatic species (Rahel & Olden 2008; Wenger et al. 2011). Recent research involving

temperature-sensitive fishes suggests tributary and mainstem habitats may provide a diversity of seasonal thermal regimes facilitating persistence of salmonids (Armstrong et al. 2021). Thus, there exists a need to employ spatially-explicit mPVAs incorporating spatial and temporal heterogeneity in habitat and connectivity when evaluating suppression scenarios for invasive aquatic species.

We investigated population vulnerabilities to inform suppression strategies for a worldwide ecologically-damaging, invasive salmonid, brown trout (*Salmo trutta*; McIntosh et al. 2011; Budy et al. 2013; Hansen et al. 2019). Brown trout have been introduced globally and are one of several introduced species responsible for widespread homogenization of fish diversity (Toussaint et al. 2016; Budy & Gaeta 2018). Brown trout mechanical suppression has rarely been effective (Caudron & Champigneulle 2011; Saunders et al. 2015), and only in small streams and sometimes at great expense over multiple years (Healy et al. 2020; Budy et al. 2021).

Our goal was to explore a range of planned and hypothetical brown trout suppression scenarios, including those targeting different life stages, in the context of a newly established metapopulation threatening native fishes in Grand Canyon National Park (GCNP), in order to: 1) understand the effectiveness of management strategies targeting different life stages and locations within a metapopulation, 2) quantify the effectiveness of a rapid response to a new invasion relative to delaying suppression until establishment; and 3) estimate whether future changes in hydrology and water temperature related to climate change and reservoir management affect metapopulation viability, requiring adaptation of suppression strategies. Our results will have wide implications given the

ubiquitous distribution of non-native salmonids and their worldwide potential to impact aquatic ecosystems and their inhabitants.

Methods

Study Area

Control of brown trout established in GCNP is a priority to mitigate threats of predation to imperiled native fishes in the Colorado River (CR) and its tributaries (Yard et al. 2011; Healy et al. 2020). The National Park Service (NPS) mandates removal of invasive species, where feasible, when natural or cultural resources are negatively affected (U.S. Department of the Interior 2006). Regardless of the fact that brown trout are non-native and negatively affect native fishes (Healy et al. 2020), aquatic life in GCNP is culturally- important to Traditionally Associated Indian Tribes (Runge et al. 2018), and brown trout are a recreationally and economically-important species prized by anglers (Budy & Gaeta 2018; Beever et al. 2019).

Brown trout were introduced into GCNP tributaries through stocking between the 1920-30s, and persisted primarily in one tributary, Bright Angel Creek (BAC). The species recently expanded ~147 km upstream through the CR into the Glen Canyon Dam tailwater where a second reproducing subpopulation became established (Figure 4.1 [reviewed in Runge et al. 2018]). Colonization of the tailwater from GCNP was likely facilitated by fall high flow experiments beginning in 2013 (Schelly et al. *in prep.*) – movement in salmonids is commonly stimulated by flow (Davis et al. 2015). Hypothesized mechanisms causing this brown trout expansion and further details of the history of the species in our study area are provided in Runge et al. (2018).

Bright Angel Creek is a perennial spring-fed stream with a seasonally and longitudinally-varying thermal regime (hereafter, temperature; Figure 4.1). Temperature is more stable and colder nearest the spring sources (~11°C, ~17 km from the mouth), while increasing seasonal variability and warmer summer temperatures characterize downstream reaches (2-25°C, Bair et al. 2019). Elevated spring snowmelt runoff and monsoon-driven flooding during summers occurs in most years (see Healy et al. 2020 for BAC hydrology).

Closure of the Glen Canyon Dam in 1963 and the creation of Lake Powell wrought profound temperature, flow, and sediment regime changes in the CR conducive to trout (Schmidt et al. 1998). Temperature in the mainstem CR is closely linked to water storage in Lake Powell, discharge volume, and air temperature, which in turn may influence fish population status(Dibble et al. 2021). Due to drought and aridification (Udall & Overpeck 2017), CR temperatures have warmed (2012-2020 range: 7-16°C, USGS Gaging Station 09380000) as reservoir storage has declined (Dibble et al. 2021), and these trends are expected to continue (Wheeler et al. 2021). Decisions regarding future reservoir water storage may lead to even more dramatic variation in temperatures (Dibble et al. 2021). At the same time, climate change is expected to warm temperatures and modify flow regimes in the unregulated tributaries in the Grand Canyon region (Tillman et al. 2020).

Population viability model

We used a matrix-based, stage-structured, spatially-explicit, stochastic, and partially mechanistic mPVA, the Dynamic Habitat Disturbance and Ecological Resilience model (DyHDER; Murphy et al. 2020) to assess suppression strategies and brown trout

metapopulation dynamics. The DyHDER was developed specifically to simulate disturbances that may differentially affect dynamics of subpopulations across a landscape, while also accounting for dispersal and connectively (Murphy et al. 2020; Supporting Information). The DyHDER model is ideal for simulating management scenarios in the context of future conditions brought about by press-disturbances such as climate change or reservoir storage decisions (hereafter, climate change), and including drought that may affect thermal and hydrologic regimes (Tillman et al. 2020; Dibble et al. 2021) often driving brown trout population dynamics (e.g., Lobón-Cerviá et al. 2018).

Model parameterization – Our modeled brown trout metapopulation included 4 sub-populations, including upper (BACU), middle (BACM), and lower (BACL) reaches of BAC, and the CR between Glen Canyon Dam and the Paria River (see spatial distribution, Figure 4.1). All sites are connected, except the BACU subpopulation is upstream of a waterfall impassable to upstream movement of fish, and dispersal to the site was accordingly restricted in the model. We defined 4 life stages of brown trout (age-0, juvenile, small adult, and large adult), and assigned subpopulation carrying capacities (*K*) based on baseline abundance estimates from suppression activities in BAC (Healy et al. 2020), and assumed the most recent abundance estimates approximated *K* for the CR (Table 4.1). We used a combination of empirically- or literature-derived stage-specific fecundity, vital rate, and dispersal rate estimates for introduced lotic brown trout populations (Table 4.1; also see Supplementary Information).

We incorporated habitat suitability (HS) curves (optimality functions, Murphy et al. 2020) into brown trout stage transition rates. To account for observed spatial (BAC, Bair et al. 2019; CR, USGS Gaging Station 09380000) and simulated temporal

temperature variation potentially constraining growth in salmonids (Railsback & Rose 1999), we applied a temperature HS curve to transition rates, with temporally-varying maximum observed summer mean daily temperatures for each subpopulation and scenario (Table 4.1; Supplementary Information). Fishes also seek temperatures to maximize growth (Hughes & Grand 2000); thus, we parameterized dispersal as a function of temperature.

Survival of fry may be particularly sensitive to extreme flow events (Lobón-Cerviá et al. 2018), and warm temperatures (Jonsson & Jonsson 2009). We used linear mixed-effects models to assess relationships between age-0 (S_{age-0}) brown trout abundance, using data collected between 2012 and 2019 (sampling described in Healy et al. 2020), and flow and temperature variation for HS survival curve development. In our candidate models, we included covariates representing temperature and flow volume (mean monthly or seasonal discharge) and flow variability (CV of monthly or seasonal discharge) during the winter egg incubation period, spring and summer emergence and growth periods for age-0 fish, and abundance of a potential predator or competitor (age-1 and older rainbow trout; Supporting Information). We used AIC_c to compare models, considering models within $\Delta AIC_c = 2$ of the top model to be equally supported (Burnham & Anderson 2002), and converted fitted relationships from the top model to HS curves for age-0 survival.

Simulated suppression and climate change scenarios – We simulated 30-year brown trout suppression scenarios targeting different life-stages across a range of intensity levels including hypothetical and ongoing management actions, a stable baseline (no suppression), and climate change with and without suppression. We compared

relative scenario outcomes using subpopulation growth rates (λ) during suppression, time

to quasi-extinction (QE, defined as abundance at 5% of *K*), and minimum metapopulation

densities (N_{min}). Demographic stochasticity is not represented in the model and errors are

not propagated over time; thus, outcomes should be interpreted relative to each other

(Murphy et al. 2020). We conducted a life-stage perturbation analysis by simulating 10,

20, and 30% suppression of each life stage by itself while holding others constant and

comparing median λ during suppression (30 years). We focused perturbation analysis on

the CR since different techniques may be available to target different life stages (e.g.,

dam operations to target incubating eggs [Korman et al. 2011], vs electrofishing for older

life stages); all life stages are susceptible to electrofishing in BAC (Healy et al. 2022). To

assess the importance of dispersal to metapopulation resiliency, we modeled suppression

in CR and BAC separately while maintaining baseline conditions in the non-suppressed

subpopulation, and then applied suppression to all subpopulations concurrently (Table

4.2).

We simulated CR-specific suppression involving incentivized harvest by anglers

(harvest), redd disruption (RD), and mechanical removal using boat-mounted

electrofishing (MR) – we included scenarios with actions applied singularly and in

combination. We simulated existing levels of harvest (November 2020 – March 2021)

calculated as an approximate proportion of harvest (NPS data) of the 2020 abundance

estimate, and then tripled the proportional harvest for other scenarios (Table 4.2). We

simulated RD by applying a 50% reduction in egg survival prior to the application of the

density-dependance function (Korman et al. 2011), and simulated MR by proportionately

removing CR life stages during the spawning season based on tripled single-pass

electrofishing capture probabilities (p̂; Yackulic et al. 2020).

Our simulations of BAC subpopulation suppression included life stage- and

electrofishing pass-specific $\hat{p}$ for each subpopulation (MR; Table 4.2) estimated from 3-

pass electrofishing (Healy et al. 2022). We also included a scenario with simulated

eradication of the BACU subpopulation using chemical piscicides, and the interception of

migratory trout achieved through weir operations (Healy et al. 2020). We assumed

complete disconnection of BAC from CR immigration during weir operations, although

this is less realistic.

We simulated a rapid response (RR) to a new brown trout invasion with

combinations of likely suppression approaches (MR and RD) applied to the CR as a small

subpopulation growing toward K (Table 4.2). For RR simulations, we did not apply

concurrent treatments to the BAC subpopulations to allow for maximum dispersal to the

CR. We compared the amount of time required and probability of achieving QE during

the 15-year RR scenario, to a scenario with similar suppression intensity applied to the

stable subpopulation at K.

We simulated 6 hypothetical climate futures by varying hydrology and maximum

temperatures (cf. Wenger et al. 2011) for 30-years (2021–2050) using predicted

maximum CR temperatures for basin-wide alternative water management options

(Wheeler et al. 2021) applied to CR brown trout transition rates. For BAC, we used

forecasted (RCP 4.5 emission scenario models; Figure 4.2a.) future spring discharge

variability and temperature effects on age-0 survival and transition rates. Extreme spring

peak discharge volumes limit age-0 brown trout recruitment (see Results; Lobón-Cerviá

et al. 2018). We adjusted future spring (February –April) discharge using projected

temperature and precipitation inputs from 2 CMIP5 project models representing high and

low inter-annual variability scenarios(hereafter, dry and wet scenarios; methods in Tercek

et al. 2021). We adjusted maximum annual BAC temperatures using projected air

temperature increases (2.8°C increase, Tillman et al. 2020) while accounting for

longitudinal variation in temperature for each subpopulation (Bair et al. 2019).

Wheeler et al. (2021) modeled the consequences of reservoir storage decisions

and climate change to CR temperatures discharged from Glen Canyon Dam; we used

projected maximum annual dam discharge temperatures based on recent observed trends

(Baseline2000) and potential reservoir storage options prioritizing storage in Lake Powell

(upstream, Fill-Powell-First) or Lake Mead (downstream, Fill-Mead-First) reservoirs

(Figure 4.2b). Thus, the 6 climate scenarios included both wet and dry BAC hydrologic

regimes combined with 3 maximum summer dam discharge temperatures for the CR.

Finally, we simulated 8 metapopulation suppression scenarios including combinations of

actions applied under the Baseline2000 resample scenario for the CR and wet hydrology

for BAC (see Table 4.2). Additional details of scenarios are provided in Supplementary

Information.

Results

The most effective metapopulation suppression scenarios included combinations

of all CR suppression methods with current BAC electrofishing (5.7 or 6.3 years to QE,

Table 4.2; Figure 4.3). Of 18 suppression scenarios under existing climatic conditions

(excluding rapid response), 6 led to a 100% likelihood of QE – all scenarios applying

suppression across the metapopulation led to QE, with the exception of 2020-21 levels of

harvest and 3-pass BAC electrofishing (Figure 4.3h, Table 4.2). Scenarios without MR, the only modeled method targeting age-0 and older life stages in the CR, reduced the probability of QE to 29% and prolonged the time to QE to >27 years (Table 4.2). Scenarios with MR combined with RD or harvest (triple 2020-21 levels) led to similar metapopulation suppression (~10 years to QE). In contrast to the CR, varying suppression intensity applied to BAC subpopulations led to similar metapopulation-scale outcomes, with the exception that severing BAC subpopulations from CR immigrants through the use of a weir delayed metapopulation QE (Table 4.2). Nonetheless, the weir reduced the λ for the BACL and BACM subpopulations (Figure.4 3b, 4.3c), demonstrating the importance of connectivity and dispersal to maintaining the BAC subpopulations and metapopulation resilience. Maintenance of N_{min} near K also provided evidence that the weir caused additional dispersal to the CR (Figure 4.3h), since it did not trap and remove fish in our model. With a waterfall barrier preventing immigration from downstream subpopulations, we found BACU $\lambda<1$ for all BAC suppression scenarios despite lower effectiveness of electrofishing there relative to BACM and BACL (Figure 4.3a).

Based on perturbation analysis, we predicted the CR subpopulation to be most sensitive to large adult and age-0 life stage suppression, which reduced mean λ to 0.975 and 0.979, respectively, from a stable λ ($\lambda=1$), when 30% suppression was applied (Figure 4.3g). Of the 3 suppression tools applied singly to the CR over 30 years, RD (~reduced egg survival) and harvest by anglers – both actions targeting a limited number of life stages – were the least effective in reducing λ and metapopulation abundance (Table 4.2, Figure 4.3d).

Rapid response scenarios applied to a newly invading CR subpopulation were predicted to reduce the time to QE (median 4 years, 5th and 95th percentiles, 1 – 7 years) compared to suppression starting with density at K (median 12 years to QE, 5th and 95th percentiles,11 - 13 years; Figure 4.3e). Targeting multiple life stages with a combination of approaches was important to quickly eliminate the subpopulation. A rapid response using only MR had a minimal effect on λ (0.91, 0.78 – 1.07), relative to the scenario with MR and 50% RD added (λ declined to 0.78, 0.74 – 0.84; Figure 4.3d).

Spring runoff discharge magnitude was an important predictor of brown trout age-0 abundance in BAC. We found similar support for 3 linear mixed-effects models representing relationships between peak spring discharge and age-0 brown trout abundance (ΔAICc <0.5), and no support for models with covariates representing summer temperature, rainbow trout abundance, or winter or monsoon discharge (ΔAIC$_c$ >6, Supplementary Information, Table 4-S1). The best model among those tested (R^2 = 0.30) included a 3rd order polynomial of April maximum discharge (Figure 4.4). Age-0 abundance was reduced following years with relatively high or low April discharge – this non-linear flow-recruitment relationship was included in the mPVA as a HS curve, and along with maximum summer temperature, formed the basis of our future climate change scenarios for BAC discussed above.

All future climate scenarios led to eventual declines in the metapopulation, although metapopulation QE was reached for only the Fill-Mead-First-dry BAC scenario (16.3 years to QE; Figs 3, 5, Table 4.2). The metapopulation N_{min} for climate scenarios ranged from 3% to 29% of K, with the largest reduction in Fill-Mead-First scenarios, followed by the Baseline2000-dry scenario (Table 4.2). BACU and BACM

subpopulations remained above QE for all climate scenarios, while CR and BACL

subpopulations fell below QE only under the Fill-Mead-First (Figure 4.5). Rapid

warming under the Fill-Mead-First reservoir storage scenarios exceeding our assumed

thermal limit for brown trout growth (>23°C) led to an abrupt and short-lived dispersal

pulse to BAC, preceding the decline and CR and BACL subpopulation QE. All

subpopulations remaining above QE nonetheless declined steadily to the end of the

modeled times series (Figure 4.5; Range of N_{min} for Fill-Powell-First or Baseline2000

scenarios: 8-37% of K, Table 4.2).

Due to the uncertainty in the relationship between peak snow-water-equivalent

and spring discharge used for BAC climate change scenarios, we conducted a sensitivity

analysis by adjusting thresholds for high and low flow HS thresholds by +/-10%. This

sensitivity analysis resulted in changes in the frequency of extreme spring discharge

events, and consequently we observed predicted changes in subpopulation N_{min} to average

-2.5% to 4.3% from the baseline (Supplementary Information, Table 4-S3).

We demonstrated the brown trout metapopulation could persist through 2050

under a plausible future climate change scenario (Baseline2000-wet) with 2020-21

suppression levels; however, QE was reached for all other scenarios we simulated with

higher suppression intensities (Figure 4.3f, 4.3h). We found CR MR and RD, applied in

combination with BAC stream-wide 3-pass electrofishing, or 4-pass electrofishing

applied only to BACM and with BACU piscicide application, to result in similar

outcomes. Despite each of these 2 scenarios reaching QE in ~9 years (Table 4.2), they

represent much different levels of effort – we assumed future temperatures in BACL

exceeding 23°C would forego the need for suppression, but with piscicide use, additional

suppression would be required only in BACM where future temperatures would remain

suitable. Without CR MR, scenarios with only RD or harvest (triple the current level) and

current BAC suppression would lead to QE in > 25 years (Table 4.2, Figure 4.3f).

Discussion

Our metapopulation PVA demonstrated important opportunities and limitations of

brown trout suppression approaches. We found quasi-extinction (QE) could be achieved

through a sustained metapopulation-wide suppression program targeting multiple life

stages. Conversely, scenarios which did not affect the age-0 life stage across the

metapopulation were least effective. Forgoing suppression at one subpopulation could

also negate the effects of suppression of another through dispersal of individuals from the

unsuppressed subpopulation. We also demonstrated advantages of a rapid response to

stem invasions, as other authors have (Simberloff 2003; van Poorten et al. 2019). Lastly,

by exploring metapopulation dynamics related to hypothetical habitat changes arising due

to climate change and reservoir storage decisions, we observed that declines in the

metapopulation were primarily driven by warming CR water temperatures; some future

scenarios may lessen the need for CR suppression, but BAC subpopulations would

persist.

Resilience of a metapopulation may depend on local environmental variation,

synchrony of dynamics in distinct subpopulations, and connectivity between them

allowing for recolonization following catastrophic events (Fagan et al. 2002; Elkin &

Possingham 2008). We demonstrate that understanding metapopulation dynamics and the

degree of connectivity can assist with prioritization of invasive species subpopulations

for control, and provide insights into vulnerabilities that could be exploited to improve

the likelihood of suppression (Hock et al. 2016; Pepin et al. 2020). We found relative

differences in λ and QE probability across subpopulations depended on connectivity.

Without immigrants, the upper tributary subpopulation was more likely to reach QE

despite reduced electrofishing effectiveness, relative to electrofishing other BAC

subpopulations (Healy et al. 2022). Maintenance of the BACL subpopulation occupying

marginal habitat was more dependent upon immigration, and as such, the restriction of

CR immigrants using a weir caused a significant subpopulation decline. Left

unsuppressed and without weir operation, dispersal from the much larger CR

subpopulation could negate BAC suppression efforts, particularly in the lower reaches,

which provide important habitat for native fishes (Healy et al. 2020). Our predictions are

consistent with others showing the importance of spatial connectivity to brown trout

population persistence, where a single barrier could influence density and population

structure in distant tributaries (González-Ferreras et al. 2019).

Large adults, which we hypothesized would move greater distances than other life

stages, also have greater capacity to contribute to reproduction (e.g., Goodwin et al.

2016). Accordingly, our results reflected the importance of controlling highly fecund

large adults and age-0 life stages, in order to reduce relative λ. Destruction of nests with

eggs or juveniles was more effective in suppressing invasive smallmouth bass

(*Micropterus dolomieui*), relative to angling removal of older life stages (van Poorten et

al. 2019). Similarly, our results suggest inclusion of early life stage suppression may be

an effective technique to control invasive fishes, especially when age-0 survival is high

and an important contributor to population growth (Simard et al. 2020). Brown trout

metapopulation sensitivity to age-0 or large adult mortality is unsurprising since

fecundity scales allometrically with body size, individual body size is generally

correlated with reproductive fitness (including in brown trout, Goodwin et al. 2016), and

salmonid population dynamics are often driven by young-of-year survival (e.g., Milner et

al. 2003; Lobón-Cerviá et al. 2018).

We demonstrated a dramatically shorter timeframe to QE when suppression was

applied early in the invasion process and to multiple life stages, while also depicting a

plausible range in density-dependent λ and the potential for environmental or

demographic stochastic QE (Liebhold & Bascompte 2003). A rapid response to a newly

establishing subpopulation could reduce the risk of ecological damage and lead to more

efficient and less costly suppression (Simberloff 2003; van Poorten et al. 2019; Pyšek et

al. 2020), compared to waiting to act until after an invader has grown in abundance and

dispersed (Bair et al. 2018). Successful invaders often possess life-history traits that

facilitate invasiveness or have well-studied invasion histories, including brown trout

(Kulhanek et al. 2017; Spear et al. 2021), and as we demonstrate, population growth is

likely. Salmonids generally demonstrate high potential population growth providing

resilience to catastrophic events through density-dependent demographic rates or

immigration from neighboring populations (Saunders et al. 2015; Vincenzi et al. 2016).

From a metapopulation perspective, the extent of high quality salmonid habitat in the

Glen Canyon Dam tailwater has the potential to support a much larger subpopulation

(potential K estimated between 20,000 and 150,000, Runge et al. 2018) that could confer

additional metapopulation resilience (i.e., a large "patch", Hanski 1998).

Outcomes of climate change scenarios demonstrated the importance of dispersal

and availability of refuge habitats to future metapopulation viability (Hanski 1998; Elkin

& Possingham 2008). We modeled how changes in the frequency of years with high spring stream discharge or drought may displace fry or reduce habitat space and increase competitive interactions, thereby limiting brown trout recruitment (Cattanéo et al. 2002; Lobón-Cerviá et al. 2018; this study). While limited data are currently available to assess drivers of CR recruitment (e.g., effects of current and future flows are unclear), we assumed warming would consistently, negatively affect metapopulation-wide demographics (Jonsson & Jonsson 2009; depending on changes in food production, Railsback 2021). Subpopulation responses to future scenarios differed due to longitudinal variation in BAC temperatures (Bair et al. 2019), the degree of subpopulation connectivity, and important differences in temperature resulting from reservoir operational decisions. Asynchronous variation in habitat quality between patches is often overlooked in metapopulation models applied to dendritic stream networks, despite the importance of dispersal to persistence, and vulnerability of stream organisms to fragmentation (Mari et al. 2014; Murphy et al. 2020). Asynchrony in subpopulation dynamics, as we demonstrated for brown trout, could lead to a higher likelihood of long-term metapopulation persistence (Hanski 1998; Elkin & Possingham 2008).

An important finding of our modeling was how declining upstream reservoir storage was predicted to result in dramatic declines in brown trout and the potential loss of the CR subpopulation – likely outcomes if shifts to reservoir water storage prioritizations occur, and dependant upon Upper Basin consumptive water use (Wheeler et al. 2021; Dibble et al. 2021). Similar to our study, where high initial dispersal rates to BAC refuges were evident as CR habitat suitability declined, others have observed higher rates of dispersal toward refuge patches leading to greater metapopulation viability (Elkin

& Possingham 2008). Nevertheless, with BAC as a refuge, combined with seasonal

diversity in temperature variation provided across the CR-BAC network (cf. Armstrong

et al. 2021; Hahlbeck et al. 2021), the metapopulation could be maintained under even

the most severe futures we simulated.

Our conservative approach to modeling metapopulation persistence under future

climate change may underestimate the likelihood of brown trout extirpation. For

example, we did not include catastrophic events in our simulations that can extirpate

tributary fishes (Healy et al. *in press*), used an optimistic carbon emission future (RCP

4.5), and assumed BAC baseflows would be maintained. Higher emission scenarios could

lead to higher temperatures, more extreme drought, and greater CR flow declines (up to -

55%, Udall & Overpeck 2017). Baseflow declines in BAC due to increased aridity and

air temperatures (Tillman et al. 2020) could exacerbate stream warming during summer

or fall (Bair et al. 2019), and increased winter rain and flooding could negatively affect

spawning adults or incubating eggs, thereby reducing reproductive output (Jonsson &

Jonsson 2009).

We simulated realistic ecological and demographic processes, future

environmental stochasticity, and potential management scenarios using a well-established

and parametrized model. Nonetheless, we recognize uncertainties exist in modeled

outcomes, which are driven by our parameterization choices and information gaps. Our

simulations could underrepresent compensatory, density-dependent survival and high λ

under optimum reproductive conditions, which could offset suppression effects (Saunders

et al. 2015). Age-0 brown trout increased dramatically in BACU in 2020 despite very low

spawning adult densities in 2019 (Appendix 4, Supplementary Information, Figure 4-S4)

for instance. Movement probabilities may also increase when stimulated by high flow

experiments (Schelly et al. *in prep.*), which could reduce the effectiveness of a rapid

response (through higher immigration). Nonetheless, observed declines in BAC

subpopulations (Healy et al. 2020) were generally matched by simulations, and simulated

and observed CR λ were similar (Supplementary Information, Figure 4-S4). Regardless,

outcomes of scenarios should be viewed relative to each other and the baseline scenarios,

rather than as absolutes when considering management options (Morris & Doak 2002).

Management Implications

Current (2020-21) metapopulation-scale suppression, while effective in

temporarily reducing tributary brown trout abundance (Healy et al. 2020), is unlikely to

lead to substantial metapopulation-wide declines, even under plausible climate change

scenarios resulting in degraded habitat quality in some subpopulations. Rather, if the

goal is to remove invasive brown trout, consistent with management policies (US DOI

2006), both dramatic increases in angler harvest and additional life stage suppression

would need to occur (also see Dux et al. 2019). Alternatively, managers may face

increasingly costly suppression operations to limit dispersal of brown trout to critical

endangered fish habitat, where suppression may be less effective (Bair et al. 2018).

Uncertainties in participation by anglers, the invulnerability of age-0 fish to angling, and

potential economic benefits provided by brown trout (Nuñez et al. 2012; Beever et al.

2019), may hinder angler harvest-based suppression efforts. Understanding and

quantifying operational uncertainty (method effectiveness uncertainty) in suppression

techniques, along with biological uncertainties could improve management outcomes (Li

et al. 2021). In addition to angler harvest, operational uncertainties in our study relate

primarily to RD or other untested age-0 suppression techniques. Research and development devoted to impacting age-0 invasive salmonids, which are generally less vulnerable to common fishing gears, could assist managers in refining suppression programs. For example, we hypothesize that the removal of invasive aquatic vegetation that may provide rearing habitat for age-0 salmonids (Marsh et al. 2021) may limit early-life stage survival. Nonetheless, our results suggest expanded CR subpopulation suppression, eradication of isolated climate-refuge subpopulations, re-focusing suppression efforts to other areas with future suitable habitat (e.g., BACM), and ensuring isolation of BAC from CR, could limit metapopulation persistence.

Given the world-wide prevalence of ecological damaging salmonids and other invasive fishes (McIntosh et al. 2011; Toussaint et al. 2016; Hansen et al. 2019), our results are broadly applicable to aquatic ecosystem conservation. Our metapopulation PVA approach is novel in that it allowed for the simulation of variation in dispersal and connectivity while accounting for realistic spatial and temporal heterogeneity in physical habitat (Murphy et al. 2020), in the context of invasive species management. The DyHDER model could easily be applied to a more complex interconnected system where invasive species eradication is perceived to be difficult or impossible. Functional eradication (the suppression level effectively maintaining highly valued ecological services or species) may be feasible even in difficult situations (Green & Grosholz 2020). For instance, only ~60% trout reduction may be necessary to maintain BAC native fish populations (Healy et al. 2020). We also demonstrated how predicting invasive species' distributional range constrictions or expansions (of warmwater species) with climate change could assist in prioritization of subpopulations for monitoring or response

planning (Rahel & Olden 2008). Relatively large, high-quality habitat patches would support rapid subpopulation establishment and future invasive species metapopulation resilience in the Grand Canyon – patches with similar attributes could be prioritized for early detection monitoring or targeted suppression (Simberloff 2014). Suppression of established invasive species may not be universally appropriate; however, we suggest that national parks and protected areas, where legal mandates and management objectives promote conservation of endemic species and naturally-functioning ecosystems, are areas likely considered top priority for active prevention and control of invasions (Lawrence et al. 2011; reviewed in Beever et al. 2019). Our spatially-explicit metapopulation approach can assist managers and conservationists in strategically prioritizing costly and often logistically challenging invasive species suppression in protected areas and elsewhere, particularly in open systems (Hock et al. 2016; van Poorten et al. 2019; Pepin et al. 2020).

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Table 4.1. Subpopulation-specific demographic parameters and source of information included in the brown trout metapopulation viability model.

Model parameter	Subpopulation-specific parameters			
Stage-specific survival[a]	Bright Angel Creek Lower (BACL)	Bright Angel Creek Middle (BACM)	Bright Angel Creek Upper (BACU)	Colorado River (CR)
Age-0, S_0	0.04	0.15	0.15	0.16
Juvenile, S_1	0.2	0.38	0.42	0.3
Small adult, S_2	0.2	0.38	0.42	0.3
Large adult, S_3	0.2	0.38	0.42	0.74
Transition rates[b]				
g_{01}	1	1	1	1
g_{12}	0.5	0.5	0.5	0.5
g_{23}	0.5	0.5	0.5	0.5
Reproduction rates[c]				
F_0	0	0	0	0
F_1	0	0	0	0
F_2	11	11	11	11
F_3	51	51	51	51
Temporal variance[b]				
s_{S0}	0.03	0.03	0.03	0.03
s_{S1}	0.03	0.03	0.03	0.03
s_{S2}	0.03	0.03	0.03	0.03
s_{S3}	0.03	0.03	0.03	0.03
σF_0	0.00	0.00	0.00	0.00
σF_1	0.00	0.00	0.00	0.00
σF_2	0.90	0.90	0.90	0.90
σF_3	1.50	1.50	1.50	1.50
Carrying capacity[d] (K)	4000	5000	3200	30000
Density-dependent parameters[b]				
$S_0 (N/K=1)$	0.05	0.05	0.05	0.05
$S_0 (N/K\sim0)$	0.15	0.15	0.15	0.15
Dispersal[e]				

q_{Age-0}	0.1	0.1	0.1	0.1
$q_{Juvenile}$	0.05	0.05	0.05	0.05
$q_{small\ adult}$	0.016	0.016	0.016	0.016
$q_{Large\ adult}$	0.016	0.016	0.016	0.016
Distance scalars for movement (km)[f]				
Age-0	0.5	0.5	0.5	0.5
Juvenile	4	4	4	4
Small adult	12	12	12	12
Large adult	20	20	20	20

[a]*BAC and age-0 CR, informed by literature as described in Supplementary Information, tuned to stable baseline; Mark-recapture estimates for CR based on methodology in Yackulic et al. (2020).*

[b]*Borrowed from Murphy et al (2020).*

[c]*Calculated using size-specific fecundity based on egg counts from sexually mature brown trout removed from BAC and a female:male ratio of 0.3 (NPS data), assuming mean size of small adults= 275 mm, large adults = 420 mm, and an egg-fry survival rate of 0.1. F = 0.3 female:male ratio x 368 or 1699 eggs/female x 0.1 egg-fry survival rate. See Supplemental Information.*

[d]*Baseline abundance from Healy et al. (2020) for BACM, BACU, 2020 abundance estimate for CR (methods in Yackulic et al. 2020); BACL adjusted to achieve stable baseline.*

[e] *Schelly et al. (in prep.) average movement probabilities for small and large adults. Literature review for age-0. Supplemental Information.*

[f]*Movement scalars based on best professional judgment and known movements of tagged fish in Grand Canyon. Assumed larger fish moved greater distances than small fish.*

Table 4.2. Description of suppression scenarios, intensity levels of suppression actions, and minimum metapopulation or subpopulation abundance (N_{min}) over 30 years, and time to quasi-extinction (QE) for each scenario.

Code	Scenario Description	Incent. harvest[a]	Redd disrupt. (age-0)	Mech. removal (CR)[b]	Mech. removal (BAC)[c]	Duration (years)	Meta-population N_{min}	BACL N_{min}	BACM N_{min}	BACU N_{min}	CR N_{min}	QE time
	Baseline/stable subpopulations at carrying capacity (K)	-	-	-	-	-	37529	3811	4305	2971	26317	-
	Colorado River suppression scenarios											
CR-Harvest	Incentivized angler harvest	3	-	-	-	30	19334	1117	3410	2998	11772	-
CR-Redd.Disrupt	Redd disruption	-	50%	-	-	30	19162	1127	3398	2995	11514	-
CR-Mech.Removal	Mechanical removal – boat-based electrofishing	-	-	3	-	30	8240	482	3201	2977	1483	-
CR-Harv.+Redd.Dis	Incentivized harvest + redd disruption	3	50%	-	-	30	9180	494	3214	2989	2317	-
CR-Redd.Dis.+Mech.Rem	Redd disruption + mechanical removal	-	50%	3	-	30	6679	454	3172	2974	12	-
CR-Harvest+Mech.Rem.	Incentivized harvest + mechanical removal	3	-	3	-	30	6669	454	3169	2990	12	-
CR-All.methods	Incentivized harvest + redd disruption+ mechanical removal	3	50%	3	-	30	6647	459	3193	2984	4	-
	Bright Angel Creek suppression scenarios											
BAC-3pass+Weir	Mechanical removal (3-pass electrofishing) with weir installation	-	-	-	3	30	40548	0	0	1	30000	-
BAC-3pass	Mechanical removal (3-pass electrofishing)	-	-	-	3	30	27795	1108	50	1	26617	-

BAC-3pass+Pisc	Mechanical removal (3-pass electrofishing) and piscicide applied to BACU	-	-	-	3	30	27844	1112	49	0	26647	-
BAC-4passes	Mechanical removal (4-pass electrofishing) stream-wide	-	-	-	4	30	27078	560	8	0	26510	-
	Metapopulation-scale suppression scenarios											
CR+BAC-CurrentSuppression	Incentivized harvest at current level and BAC 3-pass electrofishing stream-wide	1	-	-	3	30	21527	671	23	0	20830	-
CR-Redd.+Mech.Rem.+BAC-3pass	CR - Redd disruption and mechanical removal with 3-pass electrofishing stream wide		50%	3	3	30	0	0	0	0	0	10.0
CR-Harv.+Mech.+BAC-3pass	CR-incentivized harvest and mechanical removal with 3-pass stream wide electrofishing	3	-	3	3	30	0	0	0	0	0	10.3
CR-Harv.+Redd+BAC-3pass	CR-incentivized harvest and redd disruption with 3-pass stream wide electrofishing	3	50%	-	3	30	0	0	0	0	0	27.3
CR-All+BAC-3pass	CR-all suppression methods with 3-pass stream wide electrofishing	3	50%	3	3	30	0	0	0	0	0	6.3
CR-All+BAC-3pass+Pisc	CR-all suppression methods with 3-pass electrofishing with piscicides applied to BACU	3	50%	3	3	30	0	0	0	0	0	5.7

Scenario	Description											
CR-All+BAC-3pass+Pisc+Weir	CR-all suppression methods with 3-pass electrofishing with piscicides applied to BACU and weir installation	3	50%	3	3	30	0	0	0	0	0	11.4

Rapid response scenarios

Scenario	Description											
RapidRbaseline	CR- baseline unsuppressed growth for comparison to rapid response suppression	-	-	-	-	40	8871	549	3247	2974	1608	-
RapidR.3-pass	CR-Rapid response to small/increasing population using boat electrofishing	-	-	3	-	15	8043	478	3155	2991	1303	13
RapidR.3-pass+Redd	CR-Rapid response to small/increasing population using boat electrofishing and redd disruption	-	50%	3	-	15	6645	445	3134	2988	65	4
RapidK.3-pass+Redd	CR- boat electrofishing and redd disruption applied to stable subpopulation at carrying capacity	-	50%	3	-	15	6708	463	3198	2996	12	12

Climate change scenarios

Scenario	Description											
ClimateCRbasewet	Baseline2000 resample with annual max (based on means of 100 traces), BAC RCP 4.5 SWE and Tillman temp increases, with wetter model	-	-	-	-	30	10771	374	1575	1180	7505	-

ClimateCRbasedry	Baseline2000 resample with annual max (based on means of 100 traces), BAC RCP 4.5 SWE and Tillman temp increases, with drier model	-	-	-	-	30	9422	335	959	683	7416	-
ClimateCRFPFwet	Baseline2000 resample with FillPowellFirst, BAC RCP 4.5 SWE and Tillman temp increases, with wetter model	-	-	-	-	30	12408	528	1785	1173	8796	-
ClimateCRFPFdry	Baseline2000 resample with FillPowellFirst, BAC RCP 4.5 SWE and Tillman temp increases, with drier model	-	-	-	-	30	11100	491	1152	682	8775	-
ClimateCRFMFwet	Baseline2000 resample with FillMeadFirst, BAC RCP 4.5 SWE and Tillman temp increases, with wetter model	-	-	-	-	30	2708	48	1336	1141	0	-
ClimateCRFMFdry	Baseline2000 resample with FillMeadFirst, BAC RCP 4.5 SWE and Tillman temp increases, with drier model	-	-	-	-	30	1133	5	407	702	0	16.3
	Suppression scenarios with climate change											
Climate.CR+BAC-Current	Current level of suppression with	1	-	-	3	30	4550	64	45	0	4439	-

Climate.CR-3p+BAC-4p+Pisc+Weir	basewet climate scenario CR-3-pass mechanical removal, BACM 4-pass electrofishing, BACU piscicide application and weir installation	-	-	3	4	30	0	0	0	0	0	15.7
Climate.CR-3p+BAC-4p+Pisc	CR-3-pass mechanical removal, BACM 4-pass electrofishing, BACU piscicide application	-	-	3	4	30	0	0	0	0	0	14.5
Climate.CR-3p+Redd+BAC-4p+Pisc	CR-3-pass mechanical removal and redd disruption, BACM 4-pass electrofishing, BACU piscicide application	-	50%	3	4	30	0	0	0	0	0	9.0
Climate.CR-3p+Redd+BAC-3p	CR-3-pass mechanical removal and redd disruption, BAC 3-pass electrofishing	-	50%	3	3	30	0	0	0	0	0	9.2
Climate.CR-Redd+BAC-3p	CR-3- redd disruption, BAC 3-pass electrofishing	-	50%	-	3	-	30	0	0	0	0	27.6
Climate.CR-3p+BAC-3p	CR-3-pass mechanical removal and BAC 3-pass electrofishing	-	-	3	3	-	30	0	0	0	0	14.4
Climate.CR-Harvest+BAC-3p	CR-Incentivized harvest (3X current level) and BAC 3-pass electrofishing	3	-	-	3	-	30	0	0	0	0	25.7

[a]*Incentivized Harvest (IH) levels: 1, current harvest $\hat{p} = 0.08$ on large adults, 0.03 on small adults; level 3, triple ($\hat{p} = 0.24/0.12$).*

[b]*Mechanical removal levels -Colorado River/Glen Canyon: 3-pass $\hat{p}_{age\text{-}0} = 0.27$, $\hat{p}_{juveniles} = 0.17$, $\hat{p}_{small\ adults} = 0.17$, $\hat{p}_{large\ adults} = 0.30$ during spawning season.*

[c]*Mechanical removal levels - Bright Angel Creek: 3-pass electrofishing (current level of removal, during spawning season): $\hat{p}_{age\text{-}0}$ range= 0.30-0.58, $\hat{p}_{juveniles} = 0.38$-$0.74$, $\hat{p}_{small\ adults} = 0.40$-$0.79$, $\hat{p}_{large\ adults} = 0.43$-$0.85$; 4-pass electrofishing: $\hat{p}_{age\text{-}0}$ range= 0.44-0.78, $\hat{p}_{juveniles} = 0.54$-$0.89$, $\hat{p}_{small\ adults} = 0.56$-$0.93$, $\hat{p}_{large\ adults} = 0.60$-$0.96$. See Supplementary Information (Appendix 4) for more details.*
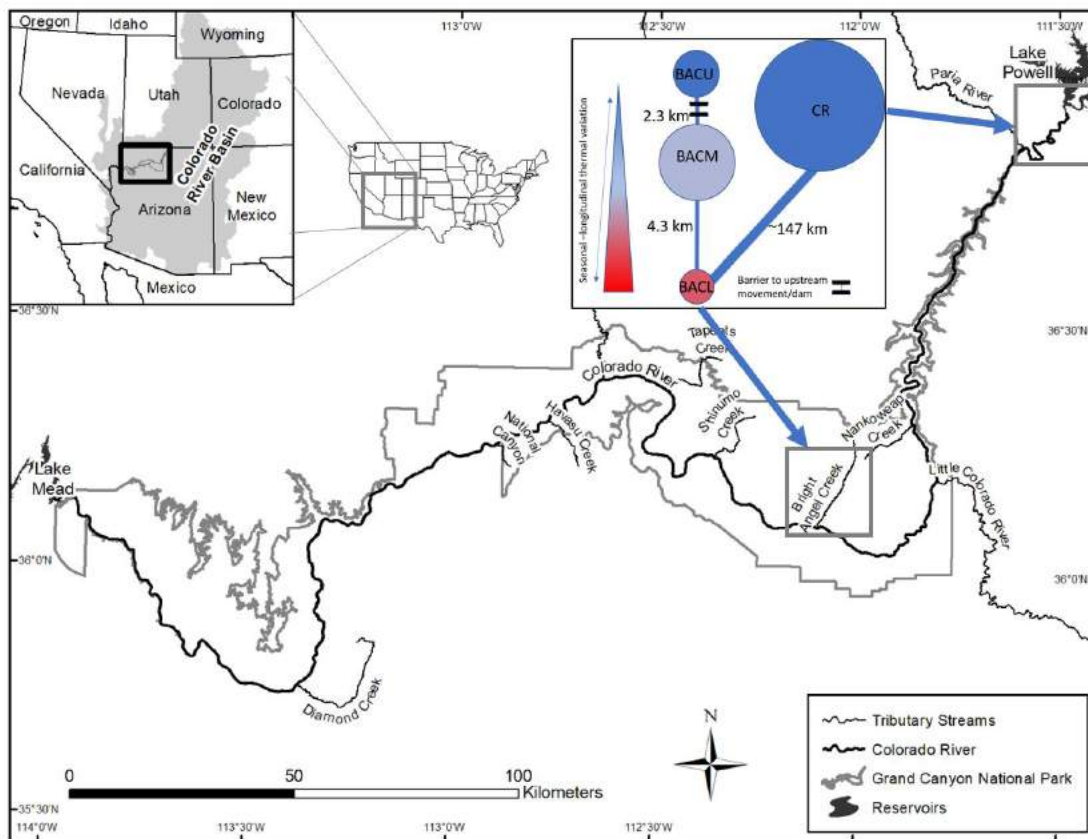
Figure 4.1. Study area showing the boundaries of Grand Canyon National Park, located with the Colorado River basin in the southwestern US. The inset shows a conceptual metapopulation model including the location of and dispersal distances between each subpopulation in Bright Angel Creek (BAC), including the lower (BACL), middle (BACM), and upper reaches (BACU) and the Colorado River (CR) downstream of Lake Powell and Glen Canyon Dam. The size of the circles in the conceptual diagram indicates the relative carrying capacity (K) for each subpopulation, and colors indicate maximum temperatures (see scale in inset).
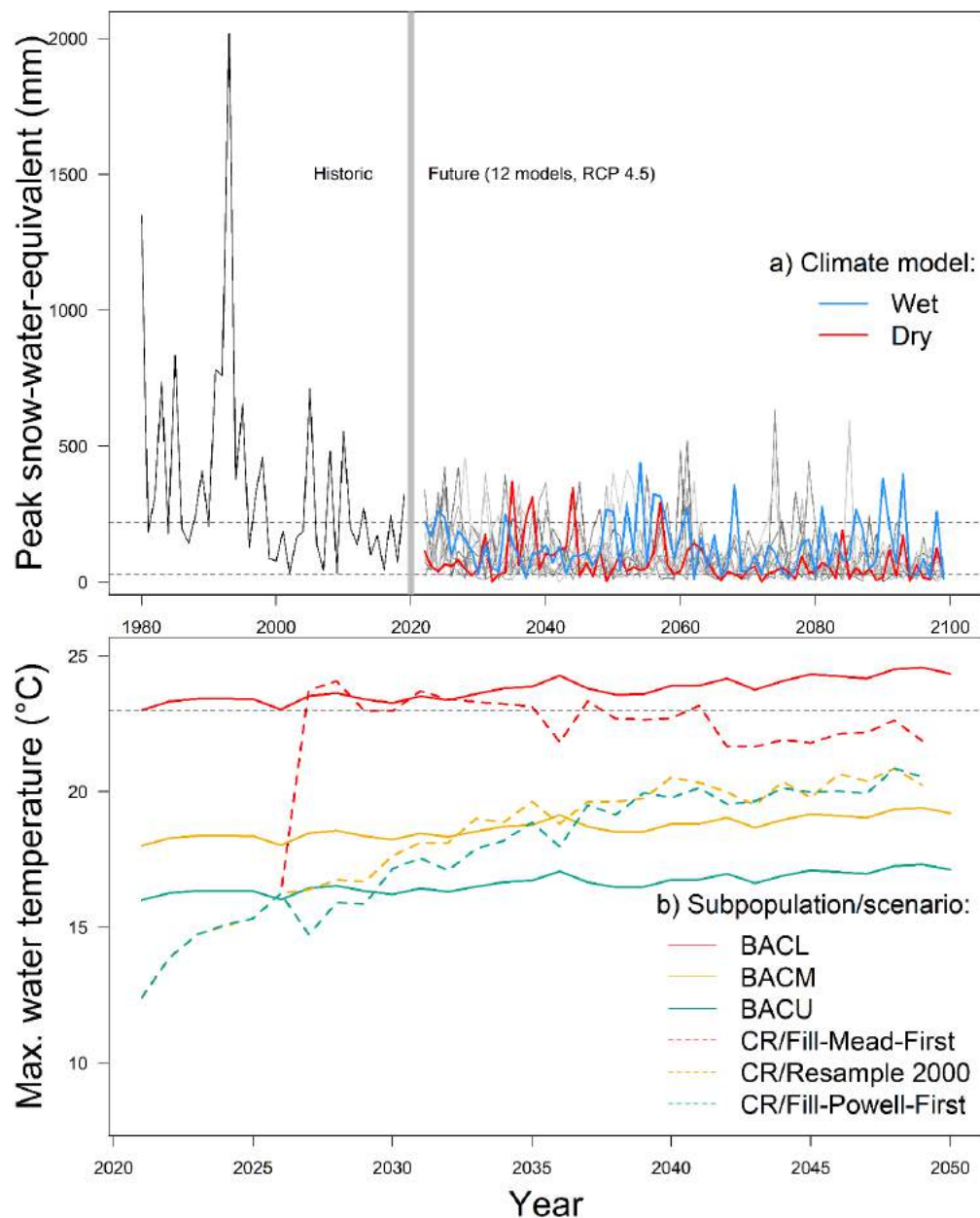
Figure 4.2. Historic and future peak snow-water-equivalent (peak SWE; left and right of the gray vertical bar, panel a) from downscaled water balance models (Tercek et al. 2021), with selected models used in the individual-model projection approach in red and blue to represent high and low peak spring runoff variability (occurrences of extreme high and low April peak discharge volumes in BAC based on hypothetical relationships between peak SWE and peak spring discharge are depicted by peak SWE values above or below black dashed lines); b) trends in maximum water temperature for Bright Angel Creek (BAC; methods in Supplemental Information) and Colorado River (CR) subpopulations under 3 different simulated climate change scenarios including Fill-Mead-First (FMF), Fill-Powell-First (FPF), and Baseline 2000 resample (data source: Wheeler et al. 2021).
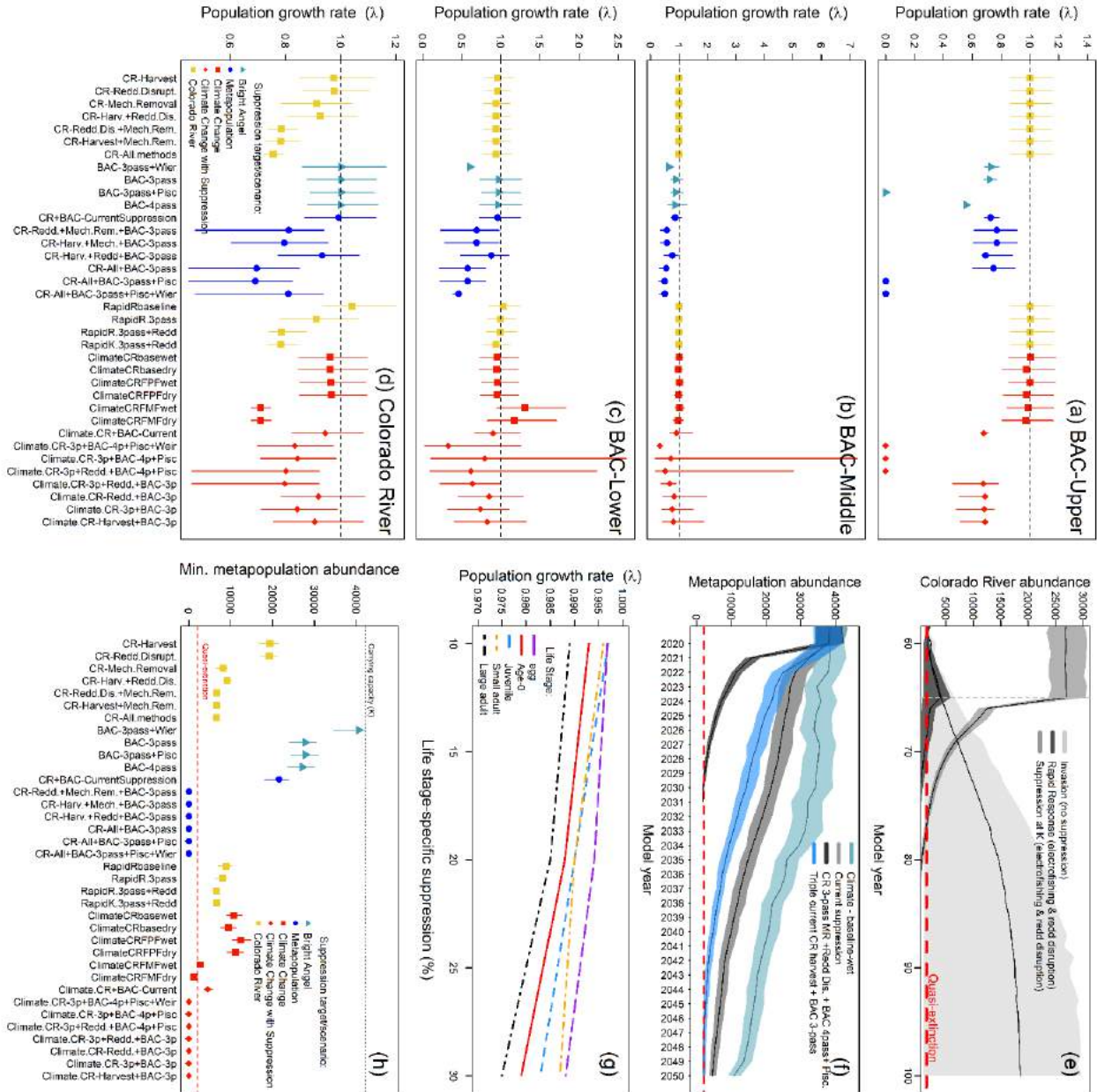
Figure 4.3. Results of metapopulation viability simulations for suppression and climate change scenarios, including relative comparisons of population growth rates (λ) for each subpopulation (panels a-d), a comparison of trends in Colorado River (CR) subpopulation abundance during early stages of invasion and following rapid response suppression or suppression of a stable subpopulation at carrying capacity (K; panel e), relative comparisons of simulated metapopulation abundance under the Baseline2000 climate change scenario with and without suppression (f), perturbation analysis to assess sensitivity of the CR subpopulation to life-stage-specific suppression (g), and minimum metapopulation abundance for all scenarios (h). A description of suppression is provided in table 4.2. Red dashed lines indicate the quasi-extinction threshold (5% of K, in panels e, f, and h).
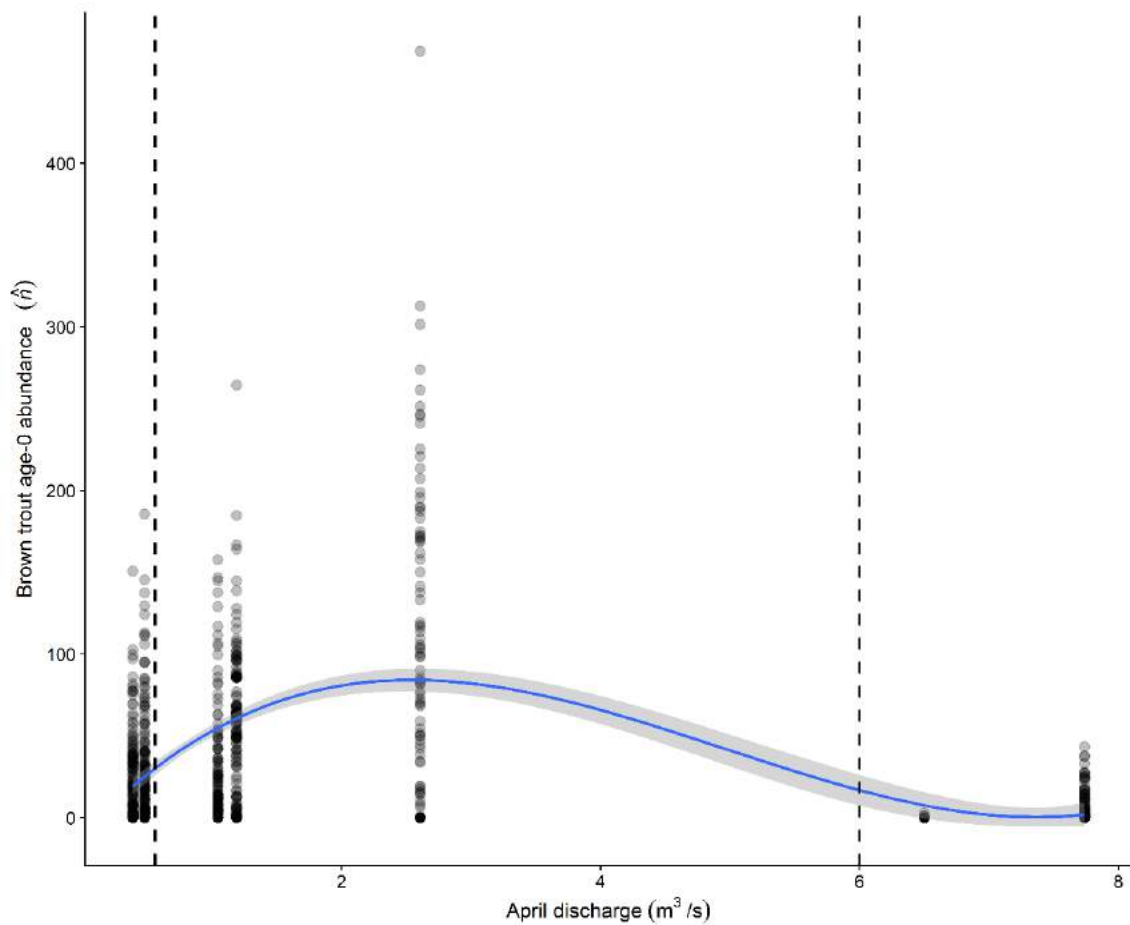
Figure 4.4. Results of linear-mixed effects modeling, showing the relationship between April Bright Angel Creek peak discharge magnitude and age-0 brown trout abundance estimated the following fall. Points are station-specific age-0 brown trout abundance estimates, and dashed vertical lines indicate thresholds for extreme low (left) and high (right) discharge modeled in climate change scenarios.
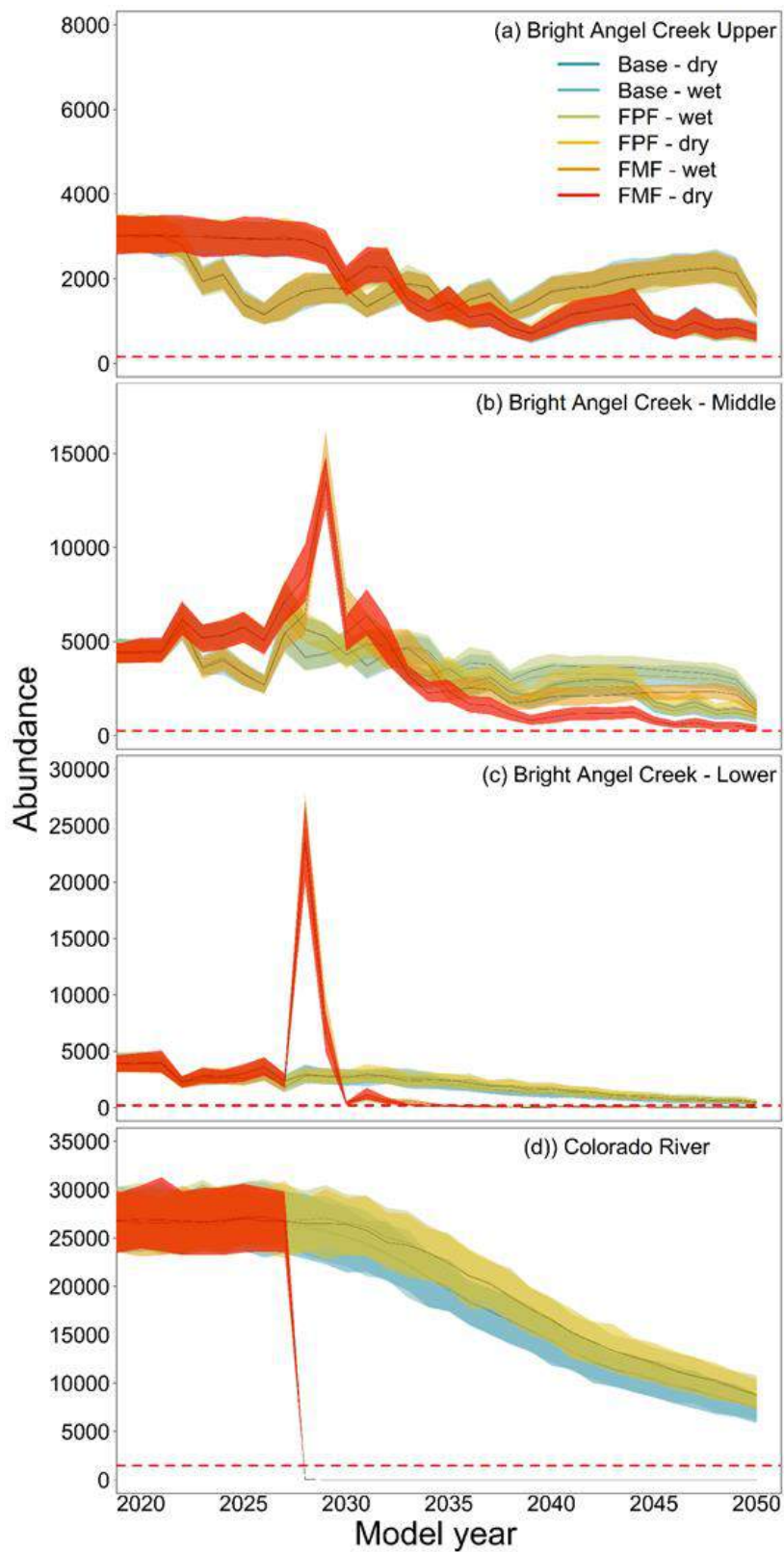
Figure 4.5. Time series of subpopulation abundance of brown trout in Bright Angel Creek (a-c) and the Colorado River (d) under 6 future climate change scenarios.

CHAPTER 5

SUMMARY AND CONCLUSIONS

Under a continuously warming climate and increasing anthropogenic stressors related to water development and introduced species leading to novel aquatic systems, society is increasingly challenged to develop, implement, and adapt conservation approaches. Challenges to conservation of aquatic biodiversity include habitat loss, water infrastructure development and diversion, and the widespread introductions of invasive species. Beyond the Grand Canyon, monitoring and quantification of trends in native fishes following actions meant to restore native aquatic communities are generally lacking. Understanding how both native and invasive species' population dynamics respond to these conservation actions can inform adaptive management. My dissertation research goals included: 1) quantifying the response of native fishes to the removal of globally-introduced rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) while accounting for temporal and spatial variation in environmental variables; 2) assessing the abiotic and biotic drivers of demographic rates in translocated populations of endangered humpback chub (*Gila cypha*); and 3) exploring the effectiveness of alternative brown trout suppression scenarios applied across a metapopulation experiencing the effects of climate change and water storage to aquatic habitats.

In chapter 2, I used generalized linear mixed-effects models to test the relative strengths of invasive trout abundance, longitudinally-varying temperature, and seasonally-varying hydrologic metrics influencing the abundance and distribution of native fishes. Fish abundance data included in my analyses were collected in a Colorado River tributary over 8 years concurrent with a stream-wide trout suppression program

(877 sampling and removal stations, of 37-255 meters of stream). I found native fish abundance increased dramatically (~480%) and distribution expanded once trout abundance was suppressed to approximately 40% of baseline levels. Native fish abundance was highest at sites with warmer water, fewer trout, and during years with greater spring flood magnitude –recruitment was limited by trout and monsoon flood magnitude. My findings provide a rare example of a positive response in native fishes as a result of invasive species suppression, and also highlight the importance of protecting natural flow and thermal regimes for conserving native fishes in tributaries of the Colorado River in the Grand Canyon.

Next, I studied intrinsic and extrinsic drivers of population dynamics of translocated humpback chub populations. I employed multiple mark-recapture/mark-resight models to estimate juvenile humpback chub survival and site fidelity throughout the ecosystem, and at a site where reproduction occurred (Havasu Creek), I estimated relative contributions of adult survival and juvenile recruitment to population growth rates. I also used linear mixed-effects models to assess abiotic and biotic factors affecting somatic growth. I found flooding to have an important influence on seasonal somatic growth, providing support for hypotheses related to increased food consumption associated with allochthonous food delivery during monsoon floods (Behn and Baxter 2019). While flooding and higher densities of adults and invasive trout during the natal year reduced recruitment in humpback chub, survival increased during years with greater flood-pulse frequency, except following periods when fires occurred in the watershed. My analysis confirmed that intense flooding following a fire in the Shinumo Creek watershed reduced survival and likely extirpated humpback chub from Shinumo Creek.

Population growth was driven more by juvenile recruitment than by adult survival in Havasu Creek. This suggests management actions to protect juvenile humpback chub survival, including trout suppression, could lead to positive population growth, but recruitment, as well as somatic growth and survival, were also density-dependent. My findings suggested humpback chub abundance approached carrying capacity in Havasu Creek during my study period, indicating that food delivery through flooding, and careful consideration of numbers of translocated fish, may be important to maintaining robust populations and achieving maximum conservation benefit through translocation programs.

I used a metapopulation population viability model to assess suppression scenarios for invasive brown trout for my fourth dissertation chapter. For parameterization of demographic rates and dispersal probabilities and distances in the model, I relied on long-term empirical data collected from within my Grand Canyon study area (Schelly et al. *in prep.*, Yackulic et al. 2020), as well as on literature derived rates from other introduced brown trout populations. To simulate plausible future habitat conditions in the Colorado River and in Bright Angel Creek that might affect brown trout metapopulation dynamics, I used projections of Colorado River water temperatures driven by reservoir levels (Wheeler et al. 2021) and plausible runoff (data supplied by M. Tercek, NPS Climate Change Response Program; methods in Tercek et al. 2021) and water temperature regimes in Bright Angel Creek. I also used estimates of electrofishing capture probability (Yackulic et al. 2020, Healy et al. 2022), actual angler harvest data (NPS data), and used results from previous studies (Korman et al. 2011) to simulate the effects of combinations of electrofishing removal, incentivized angler harvest, and redd

disruption using Glen Canyon Dam discharge. My findings suggest that current levels of electrofishing suppression in Bright Angel Creek and incentivized angler harvest in Glen Canyon will be insufficient to slow population growth or suppress brown trout at the metapopulation scale over the next 30 years. To reduce brown trout metapopulation resilience and persistence, increased intensity of metapopulation-scale suppression is necessary, including targeting multiple brown trout life stages (including age-0 in Glen Canyon) while reducing connectivity between sites, to reduce metapopulation resilience and persistence. My predictions suggest that as habitats degrade in some areas due to climate change and plausible future reservoir storage scenarios, other areas would act as refuges allowing for brown trout metapopulation persistence over the next 30 years without increased suppression intensity.

Through quantitative analysis of two commonly applied conservation strategies, species translocations and invasive species suppression, my dissertation research findings will inform future conservation of native fishes in the Grand Canyon and elsewhere. I demonstrated the importance of mitigating limiting factors prior to initiating translocations to establish new populations, as well as the threat of introduced species to riverine native fish populations. Catch rates of brown trout in the Colorado River declined concurrently with suppression in Bright Angel Creek (Rogowski and Boyer 2019), highlighting the need for focused suppression at reproduction areas to minimize the threat of invasive species dispersing throughout a river network. My research shows the effort that may be necessary to effectively suppress invasive fishes using a rarely-used metapopulation-scale approach in a river network (Murphy et al. 2020) – my methodology and findings will inform mitigation efforts for invasive species introduced

to aquatic habitats spanning the globe. Depending on the level of immigration of invasive species from adjacent reservoirs, a shift in the fish community toward warmwater invasive species is expected in the Grand Canyon, as reservoir storage declines and discharge from Glen Canyon Dam warms (Wheeler et al. 2021, Dibble et al. 2021). I demonstrated that a rapid response to a new invasion to avoid metapopulation establishment would be particularly important as tributary and mainstem Colorado River habitats become suitable to species such as smallmouth bass. My metapopulation approach could be applied to smallmouth bass and other warmwater species expanding through river networks (e. g., Columbia River basin, Rubenson and Olden 2020) as cold-water habitats warm with climate change (Rahel and Olden 2008). The effects of climate change and basin-wide consumptive water use on Colorado River water availability will force critical reservoir storage and water management decisions in the near future. The findings of my research will have important implications for the development of conservation strategies as managers deliberate the future of the Colorado River's ecological values and water needs for more than 30 million people.

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APPENDICES

Appendix A: Chapter 2 Supporting Information

Use of Zero-inflated Negative Binomial Model

Count data are normally modeled using a Poisson or negative-binomial error

distribution, where assumptions include spatially random distributions of counts and

variance equal to the mean (Poisson only; reviewed in Lindén and Mäntyniemi 2011).

Owing to the large number of zero counts of native fishes (Figure S1), variance far

exceeded the mean, which also suggested overdispersion in the data (aggregated native

fish count $\mu = 156.2$, $\sigma^2 = 120\ 263.2$; speckled dace $\mu = 152.9$, $\sigma^2 = 116\ 697.2$; bluehead

sucker $\mu = 18.0$, $\sigma^2 = 85.3$; flannelmouth sucker $\mu = 0.50$, $\sigma^2 = 14.6$). Zero counts can

arise from sampling or observer error ("false zeros"), design error (e.g., sampling for

migratory animals in a season when they are absent), structural error, meaning sampling

was conducted outside suitable habitat (Zuur et al. 2009), or environmental stochasticity,

which can effect both species presence and observation error (Lindén and Mäntyniemi

2011). In our study, while sampling error cannot be ignored, we assumed spatial

heterogeneity in occurrence and abundance was primarily related to structural error and

abiotic or biotic covariates. Rather than excluding count data in the uppermost reaches

where, for example, cold temperature (Bair et al. 2019) or potential barriers might limit

native fish distribution, we elected to include all data, and use zero-inflated negative

binomial (ZINB), two-part mixture models, which have the flexibility to model counts of

rare species with overdispersion (Cunningham and Lindenmayer 2005; Zuur et al. 2009;

Lindén and Mäntyniemi 2011; Burke et al. 2013). An advantage of this approach is the

ability to simultaneously test for the influence of covariates driving binomial (i.e.,

presence/absence) and count processes (Zuur et al. 2009).
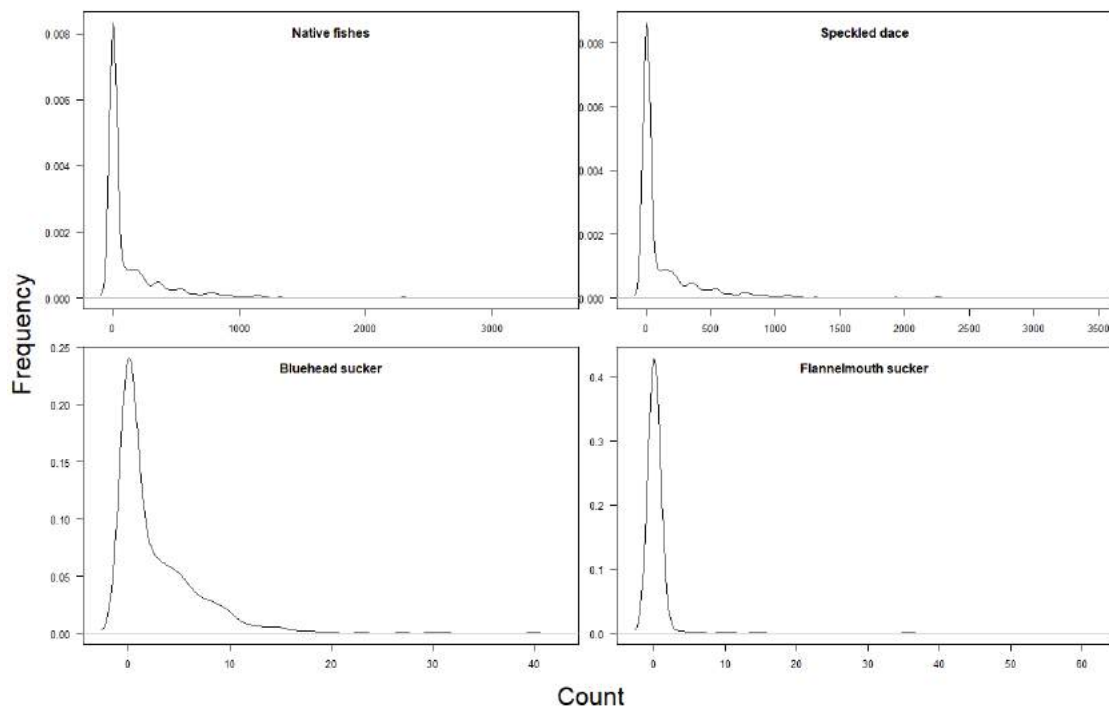
Figure 2-S1. Frequency distribution of counts of native fishes, speckled dace, bluehead sucker, and flannelmouth sucker from n=877 stations in Bright Angel Creek between 2010-2018.

Model Selection

Table 2-S1. Results of stage-1, single variable model selection for all potential predictors in zero-inflated, negative-binomial generalized linear mixed-effects models, using Bayesian Information Criterion (BIC). Values indicate ΔBIC in relation to the null (intercept-only) model, for single predictor variables included in the conditional (count), zero-inflation, and for the predictor included in both conditional and zero-inflation models. Bold values indicate the model structure for the variable of interest carried forward into stage-2 of model selection, and CF=convergence failure with the full multiplicative random effects structure. Models within +5 ΔBIC of the top model (lowest BIC score) were carried forward.

Predictor	Model type	Native fish	Speckled dace	Bluehead sucker	Flannelmouth sucker
Brown trout	Count	**-152.3**	**-154.3**	**2.1**	**-34.3**
	Zero-inflation	CF	9.2	5.9	CF
	Both	CF	-137.2	8.6	-28.1
Rainbow trout	Count	**-43.4**	**-39.3**	6.7	**-19.1**
	Zero-inflation	CF	7.6	**-1**	CF
	Both	CF	-26.1	5.8	-12.4

Total trout density	Count	**-90.1**	**-88.5**	**3.5**	**-26.5**
	Zero-inflation	CF	15.6	6.3	CF
	Both	CF	-69.3	10.1	CF
Large trout (>230 mm total length)	Count	**-6.6**	**-8.4**	4.6	**-18.8**
	Zero-inflation	**-3**	2.3	**-2.1**	CF
	Both	11.4	-2.7	3.6	-12.8
Spatial-thermal	Count	-472.1	-429.1	3.1	**-72.7**
	Zero-inflation	-109.1	-147.6	**-83.8**	-51
	Both	**-562**	**-546.2**	-78.7	CF
Spring flooding (PC1)	Count	**2.7**	**3.7**	**2.6**	**-21.1**
	Zero-inflation	6	**2.9**	6.3	**-19.2**
	Both	8.8	6.7	9.1	-14.6
Monsoon (PC2)	Count	6.1	6.6	6.5	**-20**
	Zero-inflation	**4.6**	**3.9**	6.8	CF
	Both	10.8	10.5	13.3	-14.2
electrofishing	Count	6.7	5.8	6.6	**-19.9**
	Zero-inflation	**4.9**	5.7	**3.9**	**-19.3**
	Both	11.6	11.5	10.6	CF

Stage-2 model selection example

This section includes an example of the R-code for the second stage of model section to predict native fish counts using variables and model structure carried forward from stage-1.

```
#Full model - total trout
globalmz<-
glmmTMB(Natives~zDist*ztotTroutdn+ztotTroutdn*zPCA1+ztotTroutdn*zPCA2+offset(log(EF_DISTA
NCE_METERS))+(ztotTroutdn|multiRE), ziformula = ~zDist+zPCA2+(1|multiRE),family=nbinom2, data
= MMix_mat)

globalmzE<-
glmmTMB(Natives~zDist*ztotTroutdn+ztotTroutdn*zPCA1+ztotTroutdn*zPCA2+offset(log(EF_DISTA
NCE_METERS))+(ztotTroutdn|multiRE), ziformula =
~zR.EFPrevYHours+zDist+zPCA2+(1|multiRE),family=nbinom2, data = MMix_mat)


#flow models
tot1z<-
glmmTMB(Natives~zDist*ztotTroutdn+zPCA1+offset(log(EF_DISTANCE_METERS))+(ztotTroutdn|mul
tiRE), ziformula = ~zDist+zPCA2+(1|multiRE),family=nbinom2, data = MMix_mat)

tot2z<-
glmmTMB(Natives~zDist*ztotTroutdn*zPCA1+offset(log(EF_DISTANCE_METERS))+(ztotTroutdn|mul
tiRE), ziformula = ~zDist+(1|multiRE),family=nbinom2, data = MMix_mat)
```

```
tot2zb<-
glmmTMB(Natives~zDist*ztotTroutdn*zPCA1+offset(log(EF_DISTANCE_METERS))+(ztotTroutdn|mul
tiRE), ziformula = ~zDist+zPCA2+(1|multiRE),family=nbinom2, data = MMix_mat)


tot3z<- glmmTMB(Natives~ztotTroutdn*zPCA1+
offset(log(EF_DISTANCE_METERS))+(ztotTroutdn|multiRE), ziformula =
~zPCA2+(1|multiRE),family=nbinom2, data = MMix_mat)


tot4z<-
glmmTMB(Natives~zDist+zPCA1+ztotTroutdn+offset(log(EF_DISTANCE_METERS))+(ztotTroutdn|mul
tiRE), ziformula = ~zDist+zPCA2+(1|multiRE),family=nbinom2, data = MMix_mat)


tot4zd<- glmmTMB(Natives~zDist+zPCA1+
ztotTroutdn+offset(log(EF_DISTANCE_METERS))+(1|multiRE), ziformula =
~zDist+zPCA2+(1|multiRE),family=nbinom2, data = MMix_mat)


tot4zb<- glmmTMB(Natives~zDist+zPCA1+ offset(log(EF_DISTANCE_METERS))+(1|multiRE),
ziformula = ~zDist+zPCA2+(1|multiRE),family=nbinom2, data = MMix_mat)


tot4zc<-
glmmTMB(Natives~zDist+zPCA1+zR.EFPrevYHours+offset(log(EF_DISTANCE_METERS))+(1|multiR
E), ziformula = ~zDist+zPCA2+(1|multiRE),family=nbinom2, data = MMix_mat)


#trout and temp
tot5z<- glmmTMB(Natives~zDist*ztotTroutdn+
offset(log(EF_DISTANCE_METERS))+(ztotTroutdn|multiRE), ziformula =
~zDist+(1|multiRE),family=nbinom2, data = MMix_mat)


tot6z<-
glmmTMB(Natives~zDist+ztotTroutdn+offset(log(EF_DISTANCE_METERS))+(ztotTroutdn|multiRE),
ziformula = ~zDist+(1|multiRE),family=nbinom2, data = MMix_mat)


tot6az<- glmmTMB(Natives~zDist+ztotTroutdn+offset(log(EF_DISTANCE_METERS))+(1|multiRE),
ziformula = ~zDist+(1|multiRE),family=nbinom2, data = MMix_mat)
#~~~~~~~~~~~~~~~~~~~~

# models above with efishing added to each

#flow models

tot1E<-
glmmTMB(Natives~zDist*ztotTroutdn+zPCA1+offset(log(EF_DISTANCE_METERS))+(ztotTroutdn|mul
tiRE), ziformula = ~zR.EFPrevYHours+zDist+zPCA2+(1|multiRE),family=nbinom2, data = MMix_mat)


tot2E<-
glmmTMB(Natives~zDist*ztotTroutdn*zPCA1+offset(log(EF_DISTANCE_METERS))+(ztotTroutdn|mul
tiRE), ziformula = ~zR.EFPrevYHours+zDist+(1|multiRE),family=nbinom2, data = MMix_mat)


tot2zE<-
glmmTMB(Natives~zDist*ztotTroutdn*zPCA1+offset(log(EF_DISTANCE_METERS))+(ztotTroutdn|mul
tiRE), ziformula = ~zR.EFPrevYHours+zDist+zPCA2+(1|multiRE),family=nbinom2, data = MMix_mat)


tot3E<- glmmTMB(Natives~ztotTroutdn*zPCA1+
offset(log(EF_DISTANCE_METERS))+(ztotTroutdn|multiRE), ziformula =
~zR.EFPrevYHours+zPCA2+(1|multiRE),family=nbinom2, data = MMix_mat)
```

tot4E<-
glmmTMB(Natives~zDist+zPCA1+ztotTroutdn+offset(log(EF_DISTANCE_METERS))+(ztotTroutdn|multiRE), ziformula = ~zR.EFPrevYHours+zDist+zPCA2+(1|multiRE),family=nbinom2, data = MMix_mat)

tot4zE1<- glmmTMB(Natives~zDist+zPCA1+
ztotTroutdn+offset(log(EF_DISTANCE_METERS))+(1|multiRE), ziformula =
~zR.EFPrevYHours+zDist+zPCA2+(1|multiRE),family=nbinom2, data = MMix_mat)

tot4zE2<- glmmTMB(Natives~zDist+zPCA1+ offset(log(EF_DISTANCE_METERS))+(1|multiRE),
ziformula = ~zR.EFPrevYHours+zDist+zPCA2+(1|multiRE),family=nbinom2, data = MMix_mat)

Trout and temperature models

tot5E<- glmmTMB(Natives~zDist*ztotTroutdn+
offset(log(EF_DISTANCE_METERS))+(ztotTroutdn|multiRE), ziformula =
~zR.EFPrevYHours+zDist+(1|multiRE),family=nbinom2, data = MMix_mat)

tot6E<-
glmmTMB(Natives~zDist+ztotTroutdn+offset(log(EF_DISTANCE_METERS))+(ztotTroutdn|multiRE),
ziformula = ~zR.EFPrevYHours+zDist+(1|multiRE),family=nbinom2, data = MMix_mat)

tot6aE<- glmmTMB(Natives~zDist+ztotTroutdn+offset(log(EF_DISTANCE_METERS))+(1|multiRE),
ziformula = ~zR.EFPrevYHours+zDist+(1|multiRE),family=nbinom2, data = MMix_mat)

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Appendix B: Chapter 3 Supporting Information

Brian D. Healy, Phaedra Budy, Mary M. Conner, Emily C. Omana Smith. 2022-*In press*. Life and death in a dynamic environment: invasive trout, floods, and intra-specific drivers of translocated populations. *Ecological Applications.*

Appendix S1. Study species and hypotheses

What is known of the population ecology and life history of humpback chub is based on studies in the LCR and adjacent Colorado River in Grand Canyon, which began in the 1980s (Kaeding and Zimmerman 1983, Valdez and Ryel 1995, Coggins et al. 2006, Yackulic et al. 2014). As expected for a long-lived (>30 years) organism, long-term mark-recapture studies have shown adult survival to be high (up to 82% annual survival, Coggins et al. 2006), but variable depending on primary residency in the LCR or Colorado Rivers (61% vs. 78%, Yackulic et al. 2014). Juvenile and young-of-year (YOY) survival can vary dramatically between years, and was thought to be particularly low for fish swept out of the LCR and into the colder Colorado River during monsoon flooding (Valdez and Ryel 1995, Robinson and Childs 2001). Cold hypolimnetic discharge from Glen Canyon Dam favors introduced salmonids, which compete with and prey upon humpback chub (Yard et al. 2011), leading to reduced growth and survival in the LCR inflow reach (Coggins et al. 2011, Yackulic et al. 2018). Yackulic et al. (2014) found high emigration rates of LCR juveniles during monsoon season (July to September) and survival of these emigrants near the Colorado-LCR confluence varied with the abundance of rainbow trout *Oncorhynchus mykiss* (Yackulic et al. 2018). Warmwater invasive fishes (Marsh and Douglas 1997), or introduced parasites (Campbell et al. 2019) may also threaten humpback chub in the LCR, where survival of all age-classes was surprisingly lower relative to the mainstem (Yackulic et al. 2014). Differences in growth of humpback

chub in the LCR and mainstem has been largely attributed to thermal regime differences, whereas the LCR is >6°C warmer (Yackulic et al. 2014), but variation in growth within the LCR may be driven by food availability as well as temperature (Dzul et al. 2017, Stone et al. 2020), and winter flooding may limit growth (Dzul et al. 2016).

Managers were prompted to consider means to establish new spawning populations in tributaries with more benign conditions, including through translocations, following decadal-scale declines in abundance of humpback chub (Coggins et al. 2006), persistent threats as described above, and the reliance of the population on reproduction in only the LCR (Valdez et al. 2000). Translocations of humpback chub were first initiated to vacant upstream reaches of the LCR in 2003, where fish remained and grew rapidly (Stone et al. 2020). Building on successes in the LCR, we initiated translocations to Shinumo (2009 - 2013, Spurgeon et al. 2015b) and Havasu Creeks (2011 - 2016, Trammell et al. 2012, Healy et al. 2020a; Table S1). Tributaries targeted for translocations are much smaller than others supporting humpback chub populations, but were thought to be suitable to support small populations with fewer threats from invasive fishes (Valdez et al. 2000, Pine et al. 2013).

Survival and growth rates in translocated populations in Shinumo and Havasu Creeks were estimated in two prior studies using mark-recapture methods (Spurgeon et al. 2015b, Healy et al. 2020a). While apparent survival (survival confounded by emigration) and individual growth rates in translocated populations were comparable to those of juvenile humpback chub in the LCR, neither study assessed environmental drivers of these vital rates, and study designs were inadequate to estimate true survival. Further, as determined through detections on a passive-integrated transponder (PIT) tag

antenna array, nearly half of translocated individuals left in Shinumo Creek within the first year, associated with increasing flow and temperature (Spurgeon et al. 2015b), which potentially limiting the establishment of the population (Pine et al. 2013). The remaining individuals were extirpated from Shinumo Creek during July – August of 2014, following a series of large flood events triggered by intense rainstorms on a fire. In contrast, we observed reproduction and recruitment in the Havasu Creek population, which persists through 2020. Survival of emigrants and fidelity rates are unknown for translocated cohorts due to imperfect detection, and our study aims to quantify these rates, which would not be possible without the inclusion of detections outside release sites (Barker 1997, Schaub and Royle 2014). Through monitoring conducted by cooperators throughout the Colorado River Ecosystem (CRE; US Geological Survey - Grand Canyon Monitoring and Research Center (GCMRC), unpublished data), defined as the Colorado River and its tributaries in Grand Canyon, and through our own monitoring in the Colorado River adjacent to Shinumo Creek, we have detected individuals that had emigrated from both translocation sites.

Based on these prior studies, we assessed evidence for the following hypothesized relationships between flow, thermal characteristics, and invasive salmonids, and translocated humpback chub population dynamics and individual growth:

1) Individual growth, and recruitment and survival rates will vary with flood frequency, magnitude, timing, and duration. Growth of subadults would be higher during summer months in years with higher frequency of floods that would deliver additional terrestrial diet items (Behn and Baxter 2019) or scour substrates to enhance invertebrate growth – of particular importance in Havasu Creek where invertebrate production

appears limited relative to other tributaries (Oberlin et al. 1999; Figure S1). While gut

fullness in humpback chub was found to be highest during periods of flooding in the LCR

(Behn and Baxter 2019), it is uncertain whether the addition of allochthonous food items

would translate into higher growth rates. Terrestrial-derived food quality may vary (Brett

et al. 2017), and in one translocated population of humpback chub, assimilation of

allochthonous diet items was low relative to others (e.g., fish, insects, algae; Spurgeon et

al. 2015a). Winter flooding may also limit growth, as in the LCR (Dzul et al. 2016).

We predicted recruitment would be limited during years with higher monsoon

flood frequency or intensity, as in the LCR where YOY are transported downstream to

the Colorado River (Yackulic et al. 2014). Unlike in the LCR, flood-dispersed juveniles

are unable to return to and recruit into translocated populations due to barrier falls near

the mouth of each tributary. Once recruited into the sub-adult or adult population, we

would expect minimal effects of flooding on survival, with the exception of ash-laden

floods following fires in the Shinumo Creek watershed. Southwestern native fishes vary

in their resistance to ash and intense flooding, and a congener was susceptible to ash

flows in another Colorado River tributary system (Gido et al. 2019). It is unclear if

humpback chub were flushed from Shinumo Creek or suffered high mortality rates during

the summer of 2014, but we suspected higher mortality rates occurred.

2) The strength of density-dependence in vital rates was assumed to be greater for

juveniles, and weaken with size and age in the LCR by Pine et al. (2013), but Yackulic et

al. (2018) found only weak support for density-dependent growth and survival in

humpback chub in the Colorado River. Nonetheless, following the onset of reproduction,

increasing annual abundance estimates of Havasu Creek humpback chub began to level

off, and somatic growth rates were lowest in the largest cohort translocated (2014), suggesting density dependence (Healy et al. 2020a). Therefore, we expect density-dependent growth and recruitment in Havasu Creek, but relationships between density and vital rates may be less important in Shinumo Creek compared to other drivers, given high emigration rates (Spurgeon et al. 2015b), and more abundant food (Figure S1; NPS unpublished data).

3) We hypothesize rainbow trout would limit growth, survival, and ultimately recruitment in translocation sites. Previous food web analysis showed high trophic niche overlap in Shinumo Creek between rainbow trout and humpback chub (Spurgeon et al. 2015a), suggesting potential competition for food. Higher rates of direct predation by rainbow trout upon YOY or sub-adult humpback chub (cf. Yard et al. 2011) would limit recruitment and survival in years when trout are abundant (Yackulic et al. 2018). Alternatively, trout densities appear to be low based on field observations and catch rates through the duration of our study in Havasu (also see apendix in Healy et al. 2020a) relative to Shinumo Creek, and thus trout may have minimal impact on vital rates in Havasu Creek. While no humpback chub were recovered from rainbow trout stomachs during monitoring in our translocation sites, bite scars were observed, piscivory upon other (more abundant) resident native fishes occurred (Whiting et al. 2014, Spurgeon et al. 2015a), and trout were found to suppress native cyprinid and catostomid distribution and abundance in another tributary (Healy et al. 2020b), suggesting the potential for negative interactions between the two species.

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Appendix S2. Somatic growth and mark-recapture modeling

Modeling drivers of individual growth – We used linear mixed-effects models (Gelman and Hill 2009, Weisberg et al. 2010, Dzul et al. 2017) to evaluate combinations of predictors of individual somatic growth rates for summer and winter seasons of the first year following translocation of each cohort of humpback chub. We calculated individual growth rates for the 2013 Shinumo Creek cohort using the formula: growth $_{season}$ = TL_{time-2} − TL_{time-1}/Δ-day (Spurgeon et al. 2015, Healy et al. 2020), to maintain consistency with published humpback chub growth rates in Shinumo Creek from 2009 – 2011 (Spurgeon et al. 2015), and those for juvenile humpback chub translocated to Havasu Creek between 2011 – 2014 in Healy et al. (2020), minus the 2013 Havasu Creek cohort (no data due to the fall 2013 U.S. government shutdown). To avoid potential

autocorrelation related to repeated measures of PIT-tagged individuals and assess the
strength of temporally-variable environmental or biological fixed effects in predicting
growth rates, we included a random intercept representing individual humpback chub in
all models (Weisberg et al. 2010). We attempted to include a random intercept
representing translocated cohort membership, and a random slope interaction with fish
size, however, our data did not always support this more complex random effects
structure. Instead, we included only a random intercept representing variation that may be
introduced related to the translocation year. We also included individual fish size
measured prior to release (total length) as a fixed effect in all models to account for
declining growth rates with size (Pine et al. 2017b):

$$y_{s,t} = \beta_0 + \beta_1 TL + \sum_k \boldsymbol{\beta_k} \times \boldsymbol{Z_{k,s,t}} + \xi_{0[i]} + \theta_{0[t]} + \varepsilon_{s,t}$$

$$(S1)$$

$$\xi_0 \sim N(0, \sigma_i^2)$$

$$\theta_0 \sim N(0, \sigma_t^2)$$

$$\varepsilon_{s,t} \sim N(0, \sigma^2)$$

where $y_{s,t}$ represents the modeled growth rates of humpback chub during season s and
year t (in Havasu or Shinumo creeks or both), β_0 is the intercept, $\beta_1 TL$ is the term
representing humpback chub total lengths included in all models as a fixed effect, $\boldsymbol{Z}$ denotes the
value(s) of environmental covariates $\boldsymbol{k}$ measured in intervals s of t and $\boldsymbol{\beta}$ represents values of
fixed effects coefficients. Random intercepts for individual humpback chub (i) released ($\xi_{0[i]}$),
and each year $\theta_{0[t]}$, are also included, and as for the model error term, $\varepsilon_{s,t}$, assumed to have a
normal distribution (N), with a mean of 0 and standard deviation of σ^2, σ_i^2 and σ_t^2.

We tested for effects of between- and within-stream temporal variation in temperature, flood-pulse frequency, and density-dependence on growth rates using combinations of covariates (Table 1) for models incorporating all cohorts from both streams. In addition, we separately evaluated the relationship between rainbow trout and humpback chub growth rates, along with other covariates, within Havasu and Shinumo Creeks. To assess the potential for intra-specific density-dependent growth, and growth relationships with trout, we included abundance indices from the monitoring event at the end of each seasonal interval as a covariate. Our base model, and all others tested, included temperature, or a variable representing season and stream as factors, except where collinearity was introduced with the inclusion of season and other predictors as explained below. In addition to additive models, we included interactions between flood pulse frequency and season, as well as between the humpback chub and rainbow trout abundance and flood-pulse frequency and season in candidate models. We minimized collinearity among our covariates by carefully considering the inclusion of predictors together in models with Pearson's (r) correlation coefficients >0.60 (see diagnostic process below), and replaced variables with r >0.70 (Zuur et al. 2010, Dormann et al. 2013). In the full dataset used to analyze predictors of growth in both streams, humpback chub abundance was correlated with temperature ($r = 0.73$) and rainbow trout ($r = 0.76$). High correlations were found among some Shinumo Creek covariates including between humpback chub abundance and temperature ($r = 0.86$), and between season and rainbow trout abundance ($r = 0.69$), and season and temperature ($r = 0.70$). Similarly, in the Havasu Creek dataset, the humpback chub abundance index was correlated with rainbow trout ($r = 0.74$), and flood-pulse frequency was correlated with both season ($r = 0.69$) and

temperature ($r = 0.77$). In cases where collinearity ($r>0.70$) was evident, we substituted another ecologically-similar variable which we assumed to represent the hypothesized environmental or biological driver of interest. We included season in lieu of temperature, and avoided including both humpback chub and rainbow trout abundance in the same model. We reasoned that the season covariate would represent wide variation in seasonal temperature known to influence growth in humpback chub (Pine et al. 2017a), which is a necessary effect for inclusion in models, while also eliminating multiple correlations between variables (temperature and flood-pulse frequency, rainbow trout abundance, humpback chub abundance).

Growth model selection and diagnostics – Predictors were z-scored to aid in interpretation of partial regression coefficients (Gelman and Hill 2009). We constructed all growth models with combinations of covariates using the lme4 package in R (Bates et al. 2015, R Core Team 2019), ranked models using AICc (Burnham and Anderson 2002) calculated with the bblme package (Bolker and Team 2017), and used R^2 calculated for the fixed effects in the models using the sjplot package (Lüdecke 2019) for model selection and comparison.

Following model selection, we calculated the variance inflation factor (VIF) for each of our top ranked models using the car package in R (Fox and Weisberg 2014, R Core Team 2019), and carefully examined coefficients and p-values in models with VIF > 3 (Zuur et al. 2010). For models with interactions, we excluded the interaction term and tested the additive models' VIF. Through this diagnostic process we found relatively high VIF scores for covariates in the top-ranked models for Shinumo Creek (e.g., rainbow trout abundance VIF = 13.4) and Havasu Creek growth (e.g., season VIF = 6.1). We

found that by removing the random intercept for translocation year, VIF scores decreased

to < 2.5, and the p-values and SEs for coefficients in the top-models with and without

translocation year as a random effect showed little difference, suggesting a minimal

effect of collinearity. The top-ranked growth models for the combined dataset for both

streams had VIF scores < 3 (combined dataset VIF < 2.76). Model fit was further by

examining model residuals (Fig. S4 – S6).

Survival and Emigration – We used a joint live-recapture/live-resight (JLRR)

model to estimate true survival (S_i, probability of survival through interval i) and site

fidelity (F_i) of translocated humpback chub (Barker 1997). This model is particularly

useful for determining the fate of translocated individuals because it can incorporate

continuously-collected data from PIAs and captures throughout the CRE during

GCDAMP-interagency monitoring, which we considered "resights," as well as

recaptures during targeted monitoring within translocations sites (e. g., Horton and

Letcher 2008, Conner et al. 2015). Additional parameters estimated by the JLRR model

include recapture probability (p_j) during translocation site monitoring events, resight

probability outside of translocations sites (R_i, i.e., probability of detection during the

interval i), temporary emigration (F'_j, the probability a fish is not available for capture

during j sampling event, but is available at $j+1$), the probability of resighting before an

individual dies during the interval (R'_i), and the probability an animal is found dead

during the interval (r_i).

For Shinumo Creek humpback chub *S* and *F* models, we included re-captures

during summer and fall netting events between June, 2009 and June, 2014, and resights

from the Shinumo PIA and CRE between recapture events from June, 2009 to May,

2019. Encounter histories were developed to represent positive and negative observations for individual fish, and those recaptured or resighted multiple times during a monitoring event or interval between events were only recorded once (i.e., "present"). We coded Shinumo PIA detections that occurred during the recapture sampling events (i.e., the ~5-7 days during summer and fall sampling) as recaptures. Following the extirpation of humpback chub from Shinumo Creek in July 2014, zero recaptures occurred, but we created "dummy" post-flood recapture events with fixed $p = 1$, assuming certainty of humpback chub extirpation. Creating dummy recapture events enabled the use of all available resight data from the CRE through 2019 to estimate monthly S of humpback chub that had emigrated from Shinumo Creek prior to the flood event, and assess the impact of the flood on S.

We estimated S and F for Havasu Creek humpback chub in a similar fashion, except no PIA detections at the mouth of Havasu Creek were available to augment resight encounter histories. Resights from GCDAMP monitoring trips between June, 2011 and August, 2019 from anywhere in the CRE, and recaptures from within Havasu Creek during spring and fall NPS monitoring trips between June, 2011, and October, 2019, were incorporated into the JLRR model. We also defined two groups (g) of humpback chub in Havasu Creek, including translocated and non-translocated fish (either fish produced *in situ*, or immigrated during elevated 2011 Colorado River discharge; Healy et al. 2020a), for estimation of S and F. We attempted to fit and age-cohort model, as described in Cooch and White (2011), to estimate survival of newly translocated humpback chub during the first two intervals following translocation; however, the data did not allow for estimation of most S parameters using the age-cohort structure.

Our JLRR model selection process proceeded in stages, where we began by finding the best supported structure on recapture and resight probabilities (p, R, R'), using combinations of time-varying and constant parameters, while maintaining flexibility on S and F (i.e., S_t, or $S_{g \times t}$, F_t). We assumed R and p probabilities were equal for both translocated and non-translocated groups in Havasu Creek based on previous analyses (Healy et al. 2020). We set $r_i = 0$, since only 5 individuals (<0.002% of translocated fish) were found dead during our study. We tested for permanent emigration of humpback chub from Shinumo Creek if an individual was detected on the PIA (cf. Spurgeon et al. 2015), which we accomplished by comparing a constant and time-varying F' to models with $F' = 0$. We assumed permanent emigration ($F' = 0$) in Havasu Creek models due to the presence of barriers near the mouth (see Healy et al. 2020). Using the established parsimonious model of p, $R,$ and R' probabilities from the first model-selection stage, we compared combinations of models with time-varying, constant, and group-specific F and then $S,$ while holding the other parameter flexible (F_t or S_t). Finally, we combined the most-supported model structure for p, R, R', S, and F, and then added combinations of environmental and biological covariates to S and F parameters. Ultimately, we retained flexibility (t) in p, R, S, and $F,$ and R' was held constant prior to the addition of covariates to F and S. We constructed and ranked models using Program MARK (White and Burnham 1999) and Akaike Information Criteria adjusted for small sample sizes (AIC$_c$, Burnham & Anderson 2002).

We opted to reduce dimensionality in our covariate data by using principle component analysis (PCA) to represent environmental and biological variation (Graham 2003), given correlations among covariates. This also avoided complications typically

arising from the almost infinite number of hydrologic metrics available for assessment, which are often correlated (Yarnell et al. 2020). We included combinations of the first two principal components (PCs), which are orthogonal vectors derived from linear combinations of covariates, representing 42% and 23% of variation in the covariates in Havasu Creek, and 51.3% and 22.0% in Shinumo Creek, as explanatory variables in JLRR models (Figure 2). For Havasu Creek, PC1 represented variation in flood magnitude and frequency and temperature (−), and PC2 represented indices of abundance for humpback chub and the number of translocated chub (−), rainbow trout abundance (+), and the timing of large (> 28 m^3/s) floods relative to translocation timing (−, Figure 2). PC1 for Shinumo Creek represented a gradient of rainbow trout, speckled dace, and humpback chub abundance (−), and the total acres of fire below the canyon rim in the watershed (+). Shinumo Creek PC2 represented flood-pulse frequency (−). The spatial and temporal distribution of sampling monitoring effort generating data for the JLRR model is depicted in Fig. S3.

Recruitment – To assess drivers of annual recruitment rates for humpback chub in Havasu Creek, we used a temporal symmetry model (TSM; Pradel 1996). The TSM is an open-population model that simultaneously estimates apparent survival (φ, confounded by emigration) using individual encounter histories, and estimates the relative contributions of adult survival and recruitment (ρ) towards the population growth rate (λ) that is interpretable through a "seniority probability" (γ) parameter estimated using the time-reversed encounter history (Pradel 1996, Nichols et al. 2000, Budy et al. 2017). Assumptions of the TSM, in addition to assumptions of typical demographically-open models (Lebreton et al. 1992), include the size of the study area and sampling effort are

held constant to avoid biasing ρ. We restricted our TSM analysis to mark-recapture data collected during spring trips when 2 sampling passes were consistently conducted. Effort differed slightly during the May 2014 sampling event, relative to other events, when logistical delays hindered our ability to complete both passes throughout the entire study site (Healy et al. 2020). Nonetheless, 2-passes were completed in the stream reach where >85% of humpback chub captures have been recaptured (2,915/3,390 total captures), and thus, we assumed this discrepancy would result in little bias in our ρ estimates.

We were interested in TSM estimates for only non-translocated fish, which we separated from translocated cohorts by defining representative groups in the encounter history matrix. Assigning individuals to groups (translocated and non-translocated) allowed us to share p_j from both groups if appropriate (i.e., if no group-level differences in p_j were found), while generating group-specific estimates of ρ and γ. In the TSM, recruitment is defined as the number of new adults at time $t + 1$ relative to the number of adults at time t, and we considered newly PIT-tagged fish as recruits. The average size at tagging was 204 mm TL, which corresponded to approximately age-2 (Healy et al. 2020) when fish begin to become mature (i.e., defined as fish in spawning condition; size at tagging, Figure S2). We ignored estimates of λ, ρ, and γ for the translocated group because those parameters were directly related to translocations. We used the $\varphi\rho p$ and the $\varphi\gamma p$ parameterizations of the TSM in Program MARK (White and Burnham 1999) to construct multiple models with combinations of constant and time-varying parameters, including comparisons of group, time-varying, and constant p, to generate recruitment estimates and assess the relative contributions of adult survival and recruitment to population growth. We considered estimates of $\gamma > 0.5$ to indicate greater influence of ρ on

λ, while γ<0.5 indicated φ was more important for λ in a given year (Budy et al. 2017).

To test for, and adjust for overdispersion in our TSM, we used a goodness-of-fit (median

$\hat{c}$) bootstrapping procedure in Program MARK using a fully-parameterized CJS model

($\varphi_{g \times t} p_t$). If estimated median $\hat{c}$ was >1 but < 3 (Lebreton et al. 1992), we made

adjustments to account for $\hat{c}$ before final model selection (i.e., quasi-AIC$_c$ [QAIC$_c$] values

were computed with the estimated median $\hat{c}$ value).

Given constraints related to annual time intervals and our inability to differentiate

between seasonal variation, we limited are hypothesis testing to annual drivers of

recruitment during early life stages. We tested covariates including flooding-pulse

frequency, and humpback chub and rainbow trout abundance indices during the natal

year, as drivers of recruitment. The humpback chub abundance index metric differed

slightly from the metric used for survival hypothesis testing, in that we summed the

number of humpback chub translocated and captured in the spring of the natal year for

each cohort, which we defined as recruitment year $t - 2$. The number of rainbow trout

captured in spring, and flood-pulse frequency during the summer of the natal year were

also tested.

Table 3-S1. Summary of average size, tag dates, release dates, and number of Humpback chub released into Shinumo and Havasu creeks from 2009-2018 (see Spurgeon et al. 2015, Schelly et al. 2019, Healy et al. 2020).

Tributary	Hatchery Tagging Date	Average Length (mm)	Average Weight (g)	Release Date	Number Translocated
Shinumo Creek	May 18, 2009	127.9	18.7	June 15, 2009	302
Shinumo Creek	June 10, 2010	121.1	15.3	June 23, 2010	300
Shinumo Creek	May 5, 2011	88.9	5.4	June 21, 2011	300
Shinumo Creek	June 10, 2013	123.3	14.8	June 15, 2013	200
Havasu Creek	May 5, 2011	86.1	4.8	June 28, 2011	243
Havasu Creek	May 10, 2012	124.7	16.7	May 13, 2012	298
Havasu Creek	May 9, 2013	123.1	14.9	May 14, 2013	300
Havasu Creek	May 14, June 5, 2014	123.5	16.4	May 14, 2014, June 5, 2014	300, 209
Havasu Creek	May 13, 2015	131	20.3	May 20, 2015	300
Havasu Creek	May 10, 2016	130	18.5	May 18, 2016	305
Bright Angel Creek	May 1, 2014	258	141	May 14, 2018	116*

*A hatchery tagging error led to an uncertain number of uniquely tagged fish released.

Table 3-S2. Somatic growth models and AICc ranking for humpback chub translocated to Shinumo and Havasu Creek (modeled using lme4). The top model is indicated by a ΔAIC_c =0, and 2 models that did not converge for Shinumo Creek are indicated by "NC". Key (z-scored) covariates for hypothesis testing included flood-pulse frequency (z_Flood), rainbow trout(z_RBT) and humpback chub abundance (z_HBC).

| Model	variables	Shinumo Creek ΔAIC_c	Havasu Creek ΔAIC_c
m0	growth_rate ~ Length.mm.+season+(1| PITTAG)+(1| transl.year)	28.4	383.4
m1	growth_rate ~ Length.mm.+season+z_Flood+(1| PITTAG)+(1| transl.year)	16.7	30.2
m2	growth_rate ~ Length.mm.+season+z_RBT+(1| PITTAG)+(1| transl.year)	29.6	115.2
m3	growth_rate ~ Length.mm.+season+z_Flood*z_HBC+(1| PITTAG)+(1| transl.year)	3.3	4.8
m4	growth_rate ~ Length.mm.+season+z_Flood*z_RBT+(1| PITTAG)+(1| transl.year)	NC	25.5
m5	growth_rate ~ Length.mm.+season*z_Flood+(1| PITTAG)+(1| transl.year)	8.7	5.5
m6	growth_rate ~ Length.mm.+season*z_Flood+z_HBC+(1| PITTAG)+(1| transl.year)	2.4	0
m7	growth_rate ~ Length.mm.+season*z_Flood+z_RBT+(1| PITTAG)+(1| transl.year)	10	6.5
m8	growth_rate ~ Length.mm.+season+z_Flood+z_HBC+(1| PITTAG)+(1| transl.year)	2.5	24.1
m9	growth_rate ~ Length.mm.+season+z_Flood+z_RBT+(1| PITTAG)+(1| transl.year)	9.1	32.1
m10	growth_rate ~ Length.mm.+season*z_HBC+z_Flood+(1| PITTAG)+(1| transl.year)	1.6	18.4
m11	growth_rate ~ Length.mm.+season*z_RBT+z_Flood+(1| PITTAG)+(1| transl.year)	0	23.8
m12	growth_rate ~ Length.mm.+season*z_HBC +(1| PITTAG)+(1| transl.year)	1.2	34.5
m13	growth_rate ~ Length.mm.+season*z_RBT+(1| PITTAG)+(1| transl.year)	8.7	108.9
m14	growth_rate ~ Length.mm.+ season + z_HBC +(1| PITTAG)+(1| transl.year)	NC	35.9
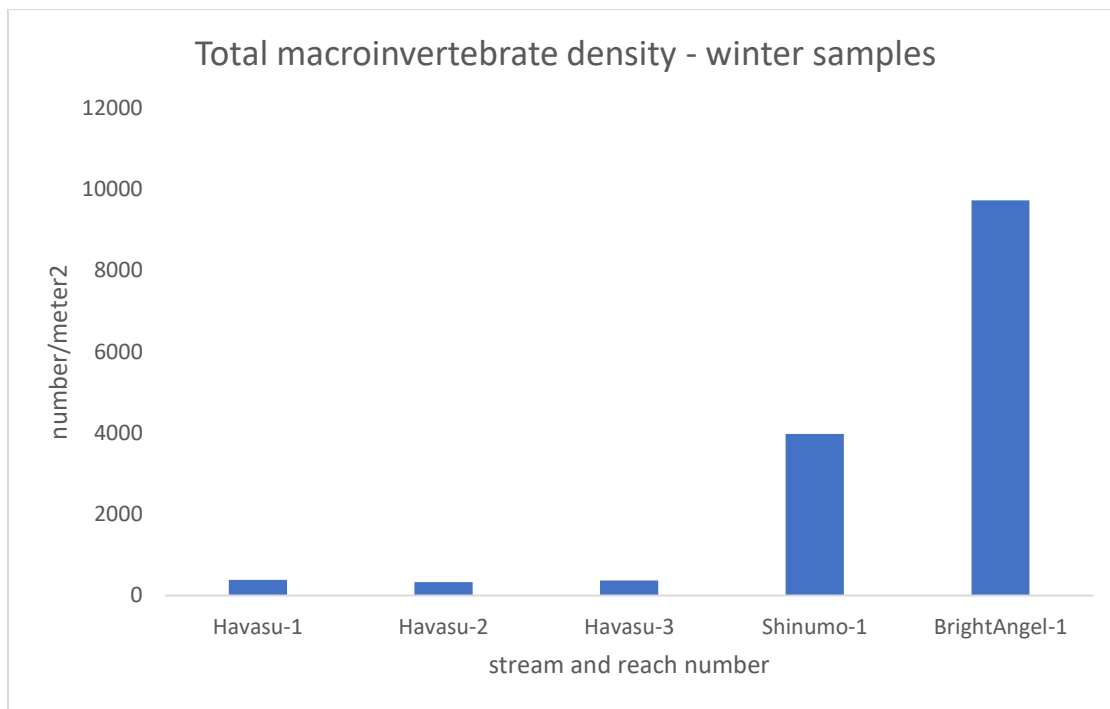
Fig. 3-S1. Macroinvertebrate density in translocation sites, from samples collected between 2011 and 2019.
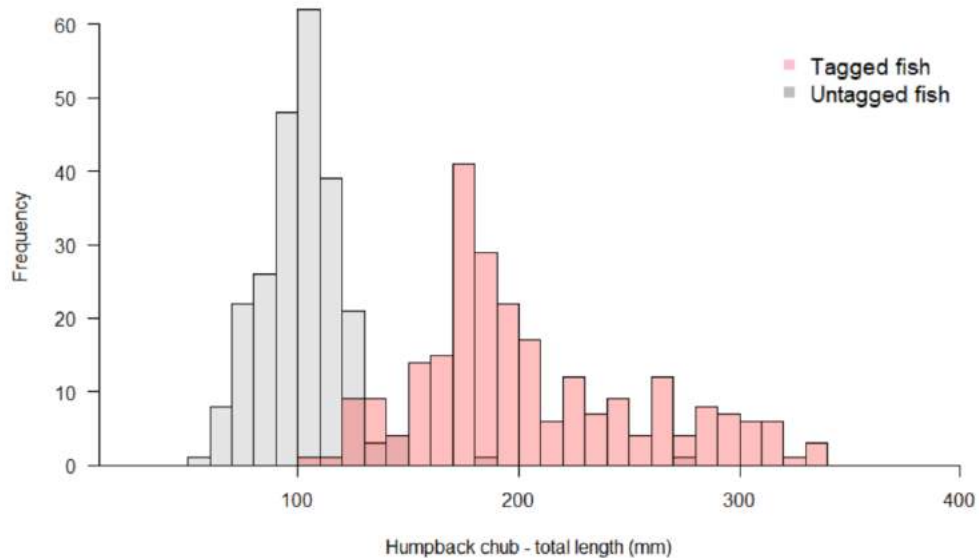
Fig. 3-S2. Havasu Creek tagging size - referenced in the Pradel model section- non-translocated fish.
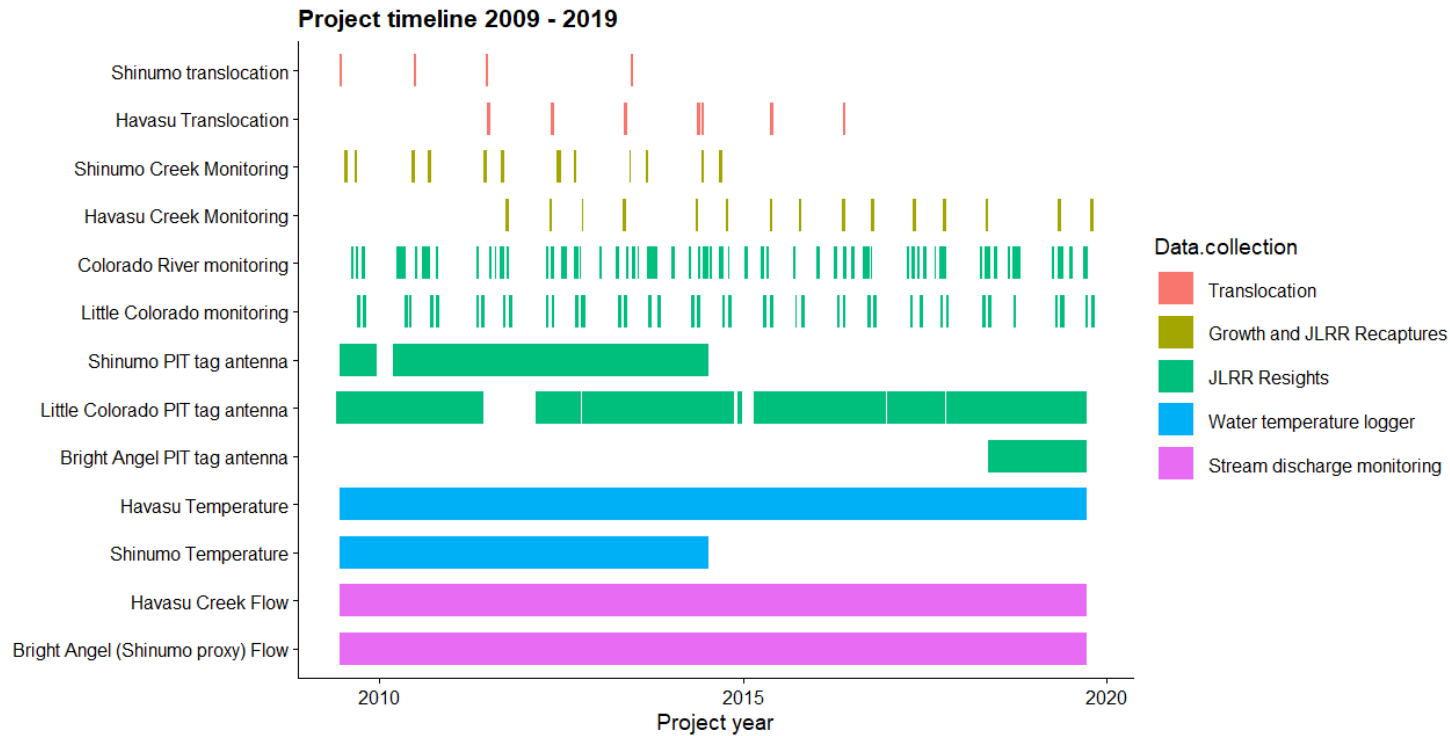
Fig. 3-S3. Timing of translocations to Shinumo and Havasu creeks, and the distribution of sampling by location and type. Sampling occasions color-coded as "Growth and JLRR Recaptures" included sampling within translocation sites to generate data for somatic growth modeling and physical recapture data to populate encounter histories for the JLRR model and TSM model (Havasu spring trips only). Samples coded as "JLRR resights" included capture (any gear type) or antenna detection data from outside translocation sites in the Colorado River ecosystem (including other tributaries). Gaps in PIT tag antenna coverage over time depict periods when flooding or power loss occurred; however, timing for the Little Colorado River antenna is approximate (data for actual operational periods between 2009-2011 were unavailable; see Pearson et al. 2015). Water temperature loggers were lost and the PIT tag antenna was destroyed during summer 2014. Abundance indices representing humpback chub, rainbow trout, or speckled dace were derived from catch data collected during JLRR recapture occasions, and applied to the previous interval for survival and somatic growth models.
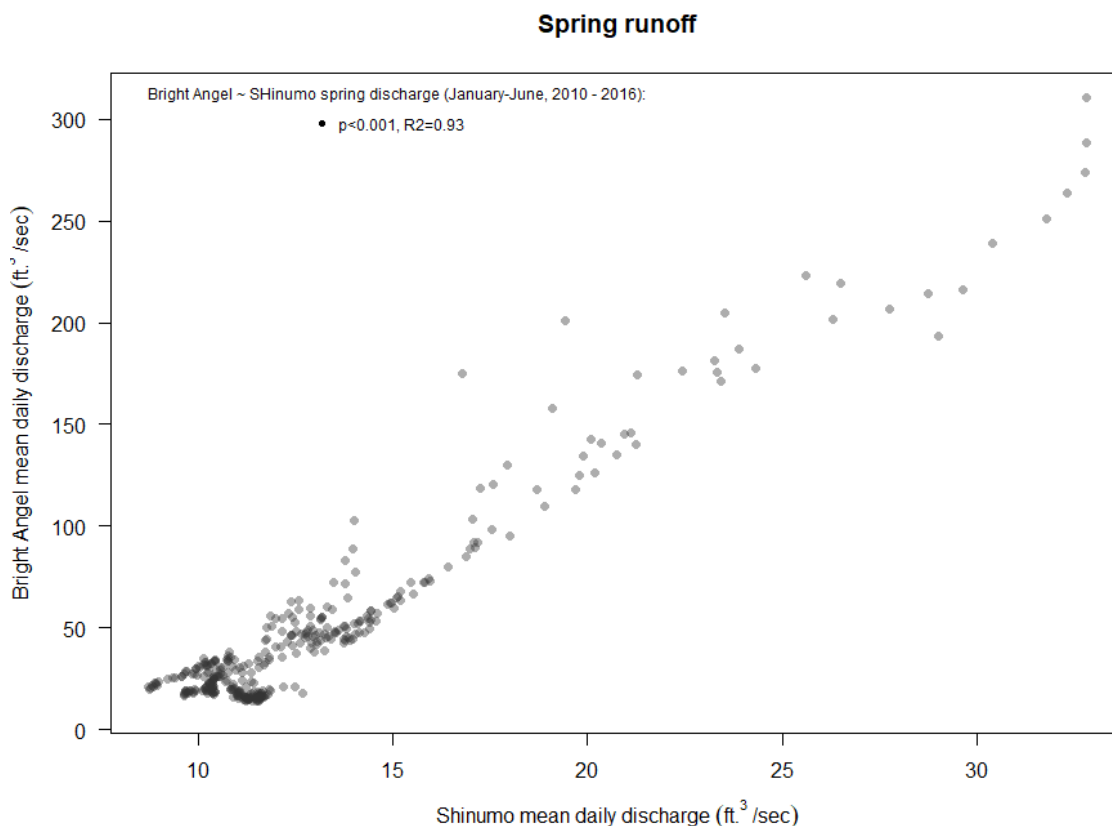
Fig. 3-S4. Correlation between available Shinumo Creek discharge data and Bright Angel Creek discharge data (USGS gaging station 9403000) during spring (January – June, 2010-2016). We used Bright Angel Creek hydrology data to calculate representative flood-pulse frequency for Shinumo Creek. Both streams flow from the North Rim of Grand Canyon National Park, and have similar watershed characteristics (forest type cover, elevation, climate, groundwater-fed). Few data were available for summer monsoon season from Shinumo Creek for comparison to Bright Angel Creek during the same season, due to damage to equipment related to floods. Remoteness of the site prevented crews from maintaining the stream gage outside of June and September.
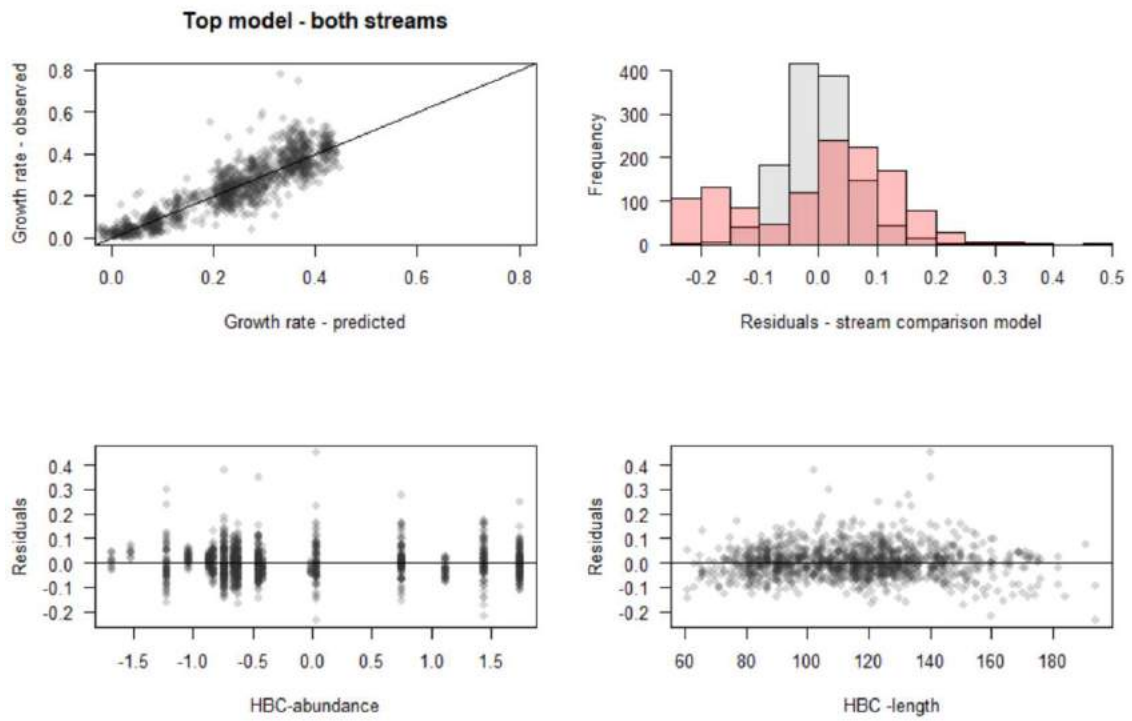
Fig. 3-S5. Model diagnostics/fit statistics for the top model (# g6y1) for growth including data for all streams/cohorts.
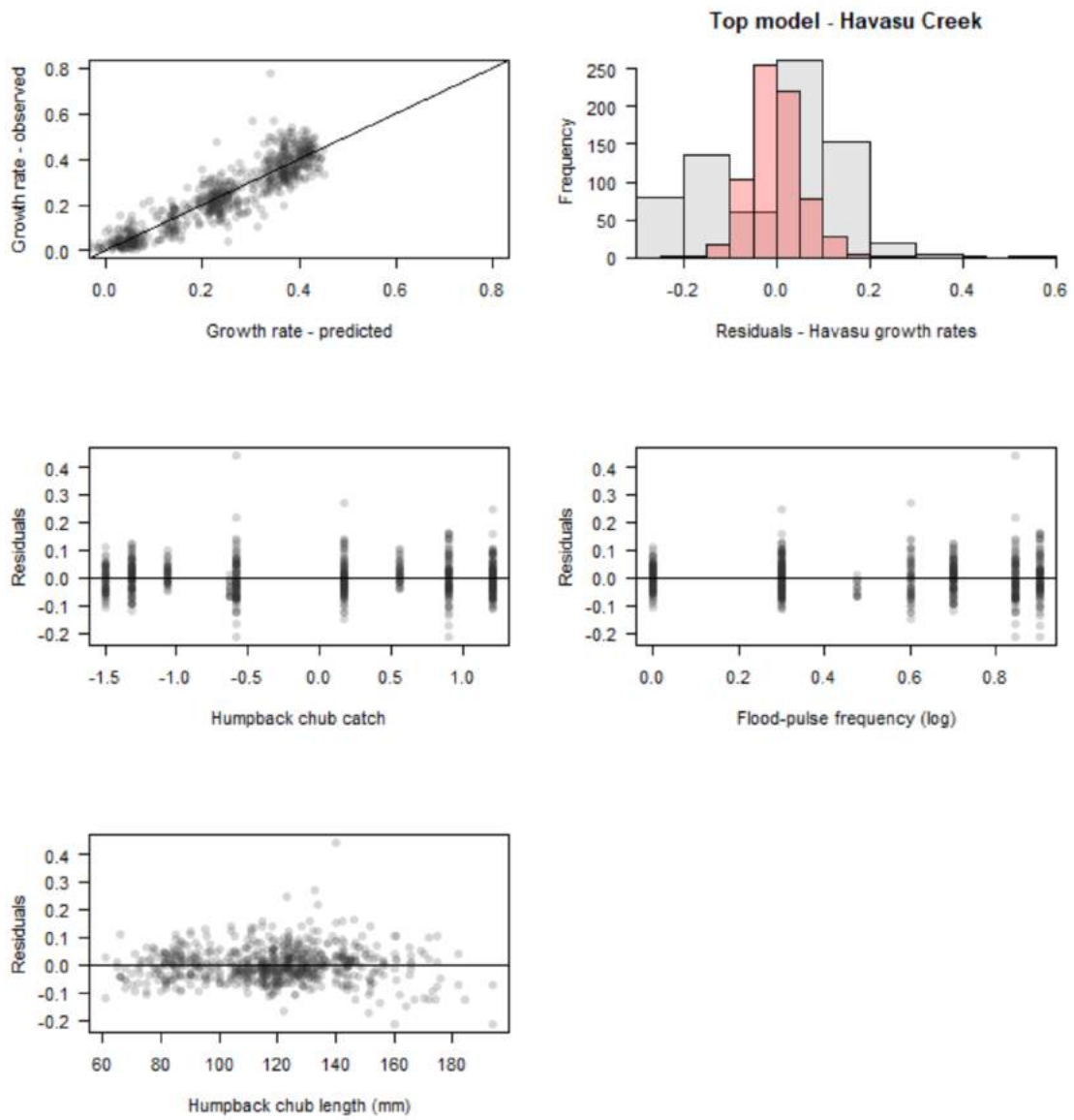
Fig. 3-S6. Model diagnostics for top model for Havasu Creek growth.
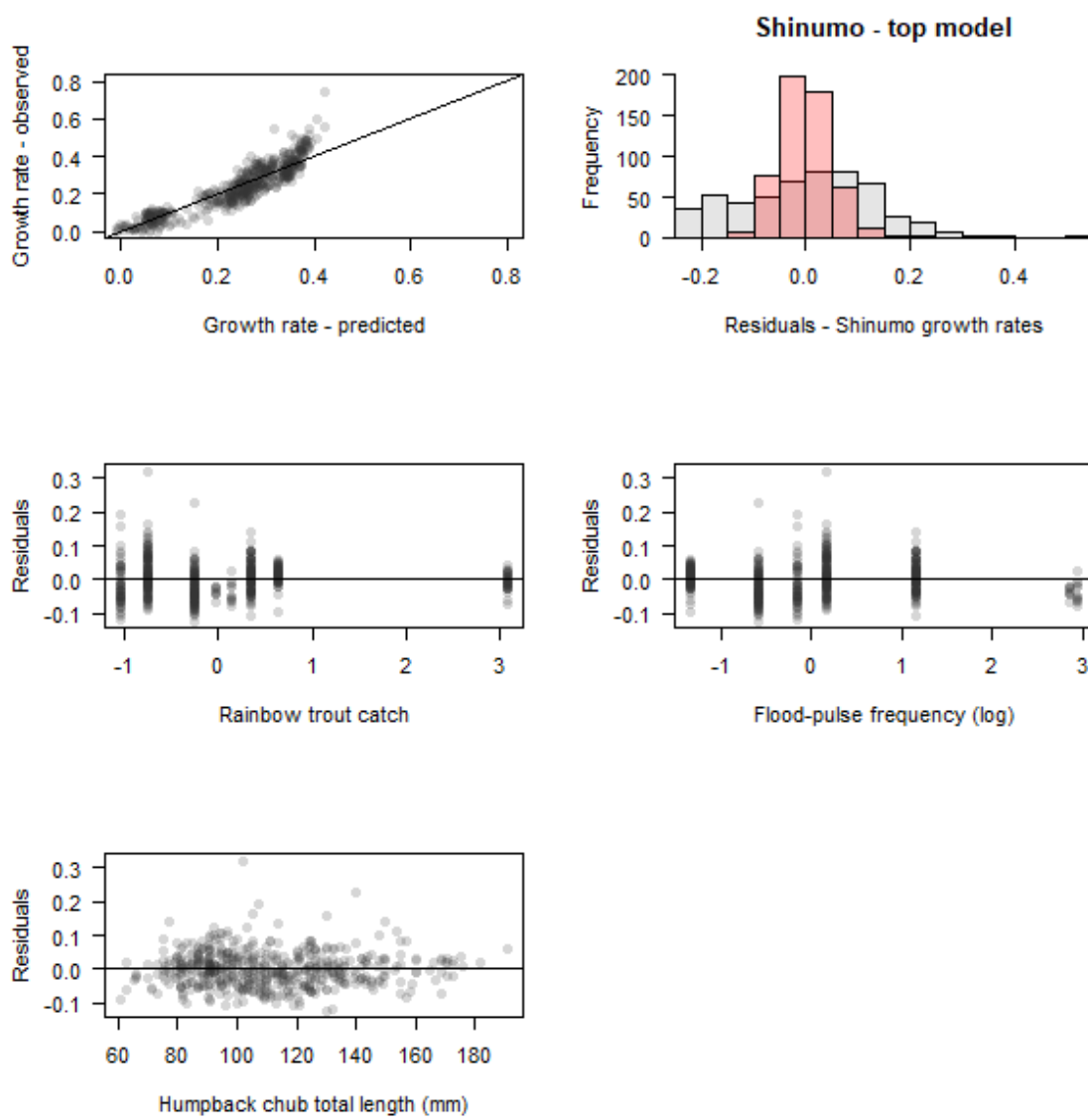
Fig. 3-S7. Model diagnostics for Shinumo Creek growth rates.
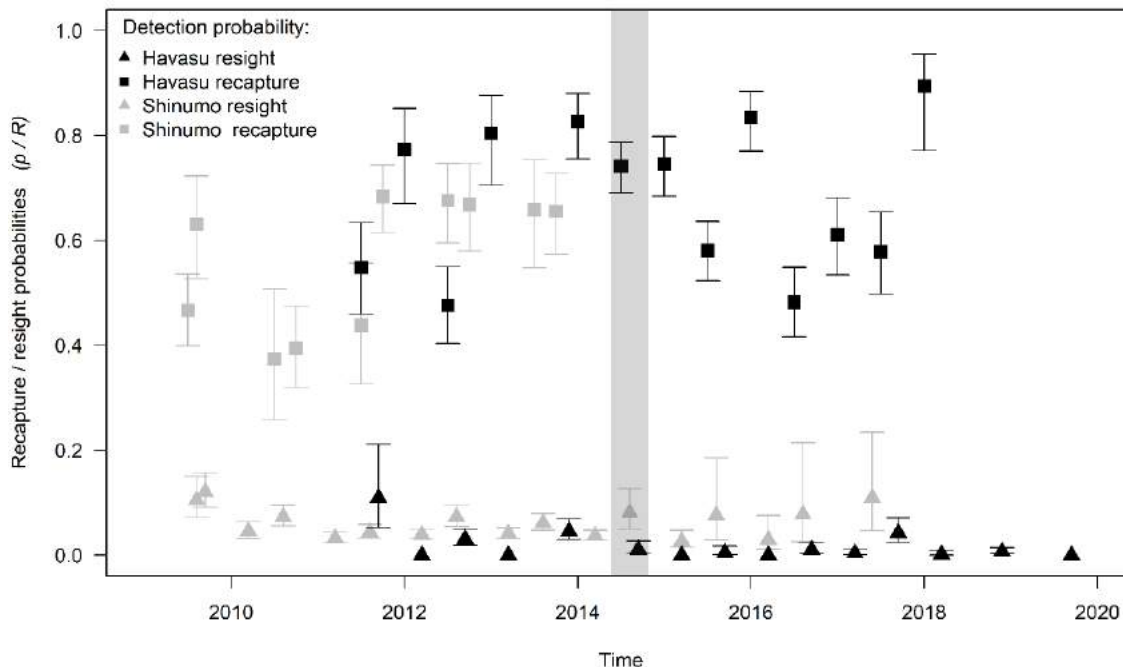
Fig. 3-S8. Recapture/resight probabilities from Havasu Creek joint live-recapture/resight model. Note the last estimate of R and p are confounded.

Table 3-S3. Supplementary info PCA scores for Havasu Creek environmental covariates.

Variable	Label	PC1	PC2	PC3
Number of translocated humpback chub	No.Transl	-0.23	**-0.46**	**0.41**
Number of days after translocation until flood > 1000 cfs/28 cms	No.daysto1000	-0.03	**-0.44**	**0.45**
Humpback chub catch (index of abundance)	HBC.catch	0.13	**-0.59**	-0.14
Flood-pulse frequency (log-transformed)	Floodpulse	**-0.47**	-0.03	-0.07
Rainbow trout catch (index of abundance)	RBT.catch	0.08	**0.44**	**0.49**
Speckled dace catch (index of abundance)	SPD.catch	0.13	-0.18	**-0.58**

Cumulative degree-days	cDD	**-0.49**	-0.03	-0.02
Maximum flood	maxFlood	**-0.46**	0.05	-0.15
Number of days discharge > 1000 cfs/28 cms	days.ov.1000	**-0.48**	0.11	-0.10
Principle component statistics				
Proportion of Variance		0.42	0.23	0.18
Cumulative Proportion		0.42	0.65	0.83

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Appendix C: Chapter 4 Supporting Information

Appendix 1: Model description

   The model operates by generating Lefkovitch (i.e., matrix based on ontogenetic stages, S_i) matrices for each subpopulation using stage-specific demographic rates, multiplied by habitat suitability (HS) values (Ψ_t) at each time step (t). Reproductive rates (F_i) are adjusted depending on the density (N) of each subpopulation at the end of t relative to the carrying capacity (K), where F_i decrease as N approaches K (i.e., S_0 [N/K=1]). Prior to the projection of the matrices into the next (annual) timestep, temporal variance is applied to the demographic rates (standard deviation of reproductive rate σF_i, and survival rates σ_i), and subpopulations that fall below a predetermined quasi-extinction (QE) probability are terminated. For all simulations, we set QE for the metapopulation and subpopulations to 5% of the K, or 10 individuals, whichever is greatest (see Murphy, Walsworth, Belmont, Conner, & Budy, 2020 for discussion of Allee effects). The next step in the projection involves simulated dispersal of individuals across subpopulations as a function of time-specific Ψ_t, connectivity, distances between sites, and stage-specific dispersal propensity (q_i). Dispersal probabilities increase as Ψ_t approaches zero and N increases in a subpopulation. Harvest or suppression scenarios are applied in the final step of the model following the application of the dispersal function. We included an additional function in the model for invasive species suppression that allows for the removal of a proportion ($\hat{p}$) of a life stage representing stage-specific gear capture efficiency generated from mark-recapture (CR, see methods in Yackulic, Dodrill, Dzul, Sanderlin, & Reid, 2020), or depletion data (BAC, see methods in Healy et al. *in review*, 2020), or estimated from angler harvest data for CR

(https://www.nps.gov/glca/planyourvisit/brown-trout-harvest.htm). We discuss details of

suppression scenarios, demographic rates and other parameters in Supplemental

Information.

Appendix 2: Model parameterization

Our modeled brown trout metapopulation included 4 sub-populations, including

upper (BACU), middle (BACM), and lower (BACL) reaches of BAC, and the CR reach

between Glen Canyon Dam and the Paria River (see Fig.1 in main text). Brown trout are

relatively rare in other tributaries (Runge et al., 2018) and the mainstem Colorado River

in Grand Canyon (Rogowski & Boyer, 2019); based on recent electrofishing surveys

completed by the National Park Service (NPS unpublished 2020-2021 data) showing

relatively low catch rates of brown trout in multiple tributaries (Nankoweap, Clear,

Crystal, Pipe, Shinumo, and Tapeats Creeks – those with suitable habitat for brown

trout), we assumed BAC and the CR reach of Glen Canyon were primary areas of

reproduction. All sites are accessible to brown trout dispersing between subpopulations,

except the BACU subpopulation is upstream of a waterfall impassable to movement of

fish, and movement to the site was accordingly restricted in the model. The CR site is

~147 km from BACL, and BACM and BACU are 4.3 and 9.5 km from BACL. We

considered baseline BAC abundance estimates from 2012 (Healy et al., 2020) as carrying

capacity (*K*) for each subpopulation, with the exception of BACL, where we adjusted *K*

upward to 4000 to stabilize the model. The CR *K* is less understood since the

subpopulation is newly establishing (Runge et al., 2018), and continues to grow. We

approximated *K* assuming that the most recent population estimates are near carrying

capacity (see main text Table 1). We defined 4 life stages of brown trout based on fish

size-at-maturity observed during annual spawning season suppression activities in BAC,

beginning in 2010 (Healy et al., 2020). Adult brown trout spawn during fall-winter

months and eggs hatch and fry emerge from gravels sometime during spring. We

considered age-0 brown trout those <175 mm total length (TL), fish from 176-230 mm as

the juvenile life stage, small adults were between 231-300, and large adults were >300

(median sizes by life stage = 133, 200, 275, 420 mm TL).

Where we lacked empirical data to estimate vital rates, we used literature-derived

estimates for introduced lotic brown trout population; survival rates of 0.15 for age-0

(S_0), and 0.38-0.42 in older life stages (S_{1-3}) resulted in a stable baseline (i.e., $\lambda \sim 1$) in

modeled BAC subpopulations (Table 1) and were within the range reported in the

literature (Budy, Thiede, McHugh, Hansen, & Wood, 2008; Grossman, Carline, &

Wagner, 2017). Due to disturbance by visitors, including angling, and habitat limitations,

we expected BACL to have slightly lower age-0 (S_0 =0.04), and juvenile and adult

survival (S_{1-3} =0.2). Survival rates for age-1 to large adult CR brown trout were estimated

using methods in Yackulic et al. (2020). Age-0 survival in the CR was adjusted (to S_0

=0.16; Table 1) to stabilize the CR population near K. While S_0 =0.16 may appear higher

than other published estimates in established populations (e.g., up to 0.08%, Jorgensen &

Berg, 1991), early life stage survival is often difficult to estimate, can drive populations

of invasive species, and may exceed 6 times the rate in an invasive salmonids' native

range (Syslo et al., 2020).

We calculated reproductive rates (F) using size-specific fecundity based on egg

counts for each reproductive age-class (small adult = 368 eggs/female, F_3 = 11; large

adults 1699 eggs/female, F_4=51) and a female : male ratio of 0.3 from brown trout

sacrificed in BAC, multiplied by an egg-to-fry survival of 0.10 (range 0.053 - 0.10;

Syrjänen et al., 2017). Fecundity was assigned to each reproductive age class using egg

counts from brown trout sacrificed in BAC by one of the authors (mode for small adults

= 275 mm, 368 eggs/female; large adults = 420 mm, 1699 eggs/female), and an egg-fork

length relationship (Fig. S1; 0.3 females x 0.1 egg-to-fry survival x 368 or 1699

eggs/female = 11 or 51). It was difficult to decide what mean size to use for large adults

since mean sizes range from 280-560 mm between ages 3 and 6+, as estimated using

mixed distribution models (Macdonald & Pitcher, 1979), and we assumed 420 mm would

represent commonly-sized large migratory adults (larger adults were rare).

Brown trout stage-specific dispersal rates and life-history strategies are highly

variable and flexible, with both migratory and resident life history expressions common

within a single population (Birnie-Gauvin, Thorstad, & Aarestrup, 2019; Cucherousset,

Ombredane, Charles, Marchand, & Baglinière, 2005; Goodwin, Andrew King, Iwan

Jones, Ibbotson, & Stevens, 2016). Movement probabilities (q) were available for small

and large adult brown trout ($q_{small, large adult} = 0.016$) in our study metapopulation from a

20-year mark-recapture dataset (Schelly et al. *in prep.*). Lacking data for early life-stages,

we scaled $q_{age-0, juvenile}$ assuming higher dispersal probabilities of age-0 ($q_{age-0} = 0.10$;

Vatland & Caudron 2015) and juvenile brown trout ($q_{juvenile} = 0.05$) than adults (cf.

Ciepiela & Walters, 2019). We lacked stage-specific dispersal distances; however, we

have recaptured or detected large brown trout in BAC that were tagged in the CR (>147

km away), indicating long-distance dispersal is possible. We scaled dispersal distance to

500 m for age-0 fish (Eisenhauer et al., 2020; Vøllestad et al., 2012), and then set

distance scalers for juveniles, small adults, and large adults to 4, 12, 20 km assuming

larger fish would move longer distances (Radinger & Wolter, 2014). We borrowed

process variance estimates, transition rates, and parameters to adjust density-dependent

reproductive rates (i.e., Beverton-Holt parameters) from Murphy et al. (2020) based on a

long time series of empirical data.

Appendix 3: Linear mixed-effects modeling results for brown trout recruitment and simulation scenario development

Habitat suitability functions– We incorporated habitat suitability (HS) indices

(optimality function, Murphy et al., 2020) into survival and transition rates using both

empirical and literature derived mechanistic relationships between brown trout

demographic rates and environmental variables. Water temperature (hereafter, temperature)

is an important driver of life cycle processes in salmonids, including growth, reproductive rates,

and metabolic rates (Railsback & Rose, 1999). We used a HS curve (Railsback & Rose, 1999)

encompassing a liberal range of temperature for growth (5 - 23 °C, Forseth et al. 2009), assuming

piscine and macroinvertebrate prey is unlimited in BAC (Whiting, Paukert, Healy, & Spurgeon,

2014), CR brown trout consume high proportions of fish (Yard, Coggins, Baxter, Bennett, &

Korman, 2011), and optimum temperatures for growth may be 3-4°C higher for piscivorous trout

(reviewed in Jonsson & Jonsson, 2009). For instance, optimum temperatures for growth may

be 3-4°C higher for trout feeding on fish than those consuming invertebrates (reviewed in

Jonsson & Jonsson, 2009). To account for observed spatial (BAC, Bair et al., 2019; CR, USGS

Gaging Station 09380000) and simulated temporal temperature variation potentially constraining

growth, we applied a temperature HS curve to transition rates, with maximum observed summer

mean daily temperatures for each subpopulation and scenario. The temperature HS curve

applied to brown trout, assuming optimum temperature is 14°C, which is within the range

of optimal growth for fry reported in the literature (reviewed in Jonsson & Jonsson, 2009;

no growth occurred above 23.1°C; displayed in Figure 6 in Murphy et al. [2020]). Fishes

may also distribute themselves to maximize growth based on temperature and resource

availability (Hughes & Grand, 2000); thus dispersal was also a function of temperature

($\Psi_{temp,t}$).

Predictors of age-0 brown trout – Population dynamics of salmonids are often

driven by survival from egg to age-1 (Lobón-Cerviá, 2009; Milner et al., 2003). To

understand drivers of brown trout recruitment to incorporate into our climate change

scenario HS curves, we compared linear mixed effects models including covariates

representing hypothesized relationships between environmental variables and abundance

of age-0, using data from BAC between 2012-2017 and 2019 (sampling described in

Healy et al., 2020). Mixed-effects modeling methods are similar to those described in

Healy et al. (2020) to predict native fish abundance in sampling sites, with the exception

that zero-inflation model components were excluded and a Poisson error distribution was

used for age-0 brown trout counts. Brown trout fry may be sensitive to extreme flow

events following absorption of yolk sacs and emergence from among interstitial spaces in

spawning gravels (Lobón-Cerviá, 2009; Lobón-Cerviá, Rasmussen, & Mortensen, 2018),

or to warm summer temperatures (Smialek, Pander, & Geist, 2021). We also

hypothesized that summer monsoon flooding could lead to reduced fall age-0 brown trout

survival and abundance. We tested a model including the coefficient of variation (CV) of

maximum daily flow in July-September as a covariate (Healy et al. 2020). Invasive

rainbow trout (*Oncorhynchus mykiss*) were the only other large-bodied piscivore present

in BAC (Whiting et al., 2014); we included adult (total length >230 mm) rainbow trout

abundance as a covariate in our models to test whether large rainbow trout limit brown

trout recruitment. Other tested models included covariates representing temperature and seasonal or monthly flow volume (mean monthly or seasonal discharge) and flow variability (CV of monthly or seasonal discharge) during spring and summer emergence (February – May) and growth (June) periods for age-0 fish. We also included the 30-day maximum discharge (Richter, Baumgartner, Powell, & Braun, 1996) and the number of days >12°C between April and July in separate models. To test for non-linear relationships (Rosenfeld, 2017) with age-0 brown trout abundance, we also included 2nd and 3rd order polynomials for models representing discharge hypotheses. Models included on offset term (log electrofishing station length) to standardize variable sampling station lengths (see Healy et al. 2020), and a random intercept for the year corresponding to the sampling year for each station. We used AIC_c to compare models, and considered models within $\Delta AIC = 2$ of the top model to be equally supported (Burnham & Anderson, 2002). Results of AIC_c rankings is shown in Table S1. We used the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) in R (R Core Team, 2019) for linear mixed-effects modeling.

In summary, we applied a temperature HS curve to transition rates in all scenarios and to age-0 survival in climate change scenarios, which also including future temperature variation from climate models. To represent results of linear mixed-effects modeling, we also included April mean discharge (3rd order polynomial) as a second optimality function driving age-0 survival (see Table S1, also see Fig. 2 in the main body of the manuscript). We selected the geometric mean fuzzy aggregation approach in DyHDER when both April discharge and temperature covariates were included in climate change scenarios (Murphy et al. 2020).

Table 4-S1. Rankings of linear mixed-effects models representing hypothesized relationships between environmental drivers of age-0 brown trout abundance (BNTyoyNhat) in Bright Angel Creek.

Model	ΔAICc	df	weight
BNTyoyNhat ~ April+I(April^2)+I(April^3)+offset(log(station length))+(1|year)	0	6	0.3146
BNTyoyNhat ~ 30day.max+I(X30day.max^2)+I(X30day.max^3)+offset(log(station length))+(1|year)	0.1	6	0.3025
BNTyoyNhat ~ 30day.max+I(X30day.max^2)+offset(log(station length))+(1|year)	0.5	5	0.2505
BNTyoyNhat ~ April+I(April^2)+ offset(log(station length)) +(1|year)	3.3	5	0.06
BNTyoyNhat ~ DaysOver12+offset(log(station length))+(1|year)	6.1	4	0.0151
BNTyoyNhat ~ 1 +offset(log(station length))+(1| year)	6.6	3	0.0113
BNTyoyNhat ~ Adult rainbow troutNhat+offset(log(station length))+(1|year)	7.3	4	0.0081
BNTyoyNhat ~ SpringMnQ+I(SpringMnQ^2)+offset(log(station length))+(1|year)	7.3	5	0.008
BNTyoyNhat ~ DaysOver12+I(DaysOver12^2)+offset(log(station length))+(1|year)	7.4	5	0.0076
BNTyoyNhat ~ February+I(February^2)+offset(log(station length))+(1|year)	7.6	5	0.007
BNTyoyNhat ~ SpringMxCV+I(SpringMxCV^2)+offset(log(station length))+(1|year)	7.9	5	0.0061
BNTyoyNhat ~ June+I(June^2)+offset(log(station length))+(1|year)	9	5	0.0035
BNTyoyNhat~MonsoonMxCV+I(MonsoonMxCV^2)+offset(log(station length))+(1|year)	9.3	5	0.003
BNTyoyNhat ~ March+I(March^2)+offset(log(station length))+(1|fyear)	9.5	5	0.0028

Management scenarios – We simulated 30-year brown trout suppression

scenarios targeting different life-stages across a range of intensity levels including

hypothetical and ongoing actions in management plans, a stable baseline (no

suppression), and climate change scenarios with and without suppression. We compared

outcomes of simulations using subpopulation growth rates (λ) during suppression, and

time to quasi-extinction (QE, defined as abundance at 5% of *K*) and minimum

metapopulation densities (N_{min}). We conducted a perturbation analysis to assess life-stage

specific sensitivity by simulating 10, 20, and 30% suppression of each life stage by itself

while holding others constant, and comparing median λ during suppression (30 years).

We focused perturbation analysis on the CR since different techniques may be available

to target different life stages (e.g., dam operations to target incubating eggs [Korman et

al. 2011], vs electrofishing for older life stages); all life stages are susceptible to

electrofishing in BAC [Healy et al. *in review*]). To assess the importance of dispersal

between subpopulations to metapopulation resiliency, we modeled brown trout

suppression in CR and BAC separately while maintaining baseline conditions in the non-

suppressed subpopulation, and then applied suppression to all subpopulations

concurrently (Table 2).

We simulated a CR-specific suppression program involving incentivized harvest

by anglers (harvest), redd disruption (RD), and mechanical removal using boat-mounted

electrofishing (MR) – we included scenarios with actions applied singly and in

combination. We simulated existing levels of harvest (November 2020 – March 2021) of

vulnerable life stages based on NPS harvest data

(https://www.nps.gov/glca/planyourvisit/brown-trout-harvest.htm) as an approximate

proportion of the 2020 abundance estimate (capture probability $[\hat{p}]$, $\hat{p}_{\text{small adults}} = 0.03$,

$\hat{p}_{\text{large adults}} = 0.08$), and then tripled the proportional harvest for other scenarios (Table 2).

We simulated RD by applying a 50% reduction in egg survival prior to the application of

the density-dependence function (Korman, Kaplinski, & Melis, 2011), and simulated MR

by proportionately removing CR life stages vulnerable to electrofishing by tripling the

stage-specific $\hat{p}$ estimates for single-passes of electrofishing throughout the

subpopulation ($\hat{p} = 1$-[1- single pass $p]^3$: $\hat{p}_{\text{age-0}} = 0.27$, $\hat{p}_{\text{juveniles}} = 0.17$, $\hat{p}_{\text{small adults}} = 0.17$,

$\hat{p}_{\text{large adults}} = 0.30$ during spawning season; Yackulic et al. 2020).

Our simulations of BAC subpopulation suppression included life stage- and

electrofishing pass-specific $\hat{p}$ for each subpopulation (MR; Table 2) estimated from 3-

pass electrofishing (Healy et al. *in review*) and validated against observed trout declines

(Healy et al. 2020; Supplemental Information). We adjusted electrofishing $\hat{p}$ upward to

simulate a 4th pass, and included a scenario with simulated eradication of the BACU

subpopulation using chemical piscicides (Table 2). To simulate the interception of

migratory trout achieved through weir operations (Healy et al., 2020), and to assess the

effect of dispersal in maintaining the metapopulation, we assumed complete

disconnection of BAC from CR immigration, although this unlikely to be completely

true.

We simulated a rapid response (RR) to a new brown trout invasion, where likely

suppression approaches (MR and RD) are applied to the CR as a small subpopulation

growing toward *K* (Table 2). For these simulations, we set the initial brown trout density

to QE, and then applied 3-pass MR alone, and with 50% RD for 15 years once the mean

simulated density had grown for 5 years. We did not apply concurrent treatments to the

BAC subpopulations to allow for maximum dispersal to the CR. The 15-year RR scenario

allowed us to compare the amount of time required and probability of achieving QE with

similar suppression intensity applied to the stable subpopulation at *K*.

  Climate change scenario development and sensitivity analysis – Historic and

future projected future Bright Angel Creek snow-water-equivalent (SWE) estimates were

provided by the NPS Climate Change Response Program (NPSCCRP,

https://www.nps.gov/orgs/ccrp/index.htm) using downscaled climate change projections

for a 4 km^2 grid (1 km^2 resolution) located on the North Kaibab Plateau. The area

selected was assumed to be representative of the groundwater recharge catchment for

Roaring Springs (a major source of Bright Angel Creek, Bair et al., 2019). Accumulated

daily SWE forecasts for the selected grid from 2022-2099 were estimated by NPSCCRP

staff using a water balance model (Tercek et al., 2021) with inputs of future precipitation

and temperatures from 12 CMIP5 general circulation models using relative concentration

pathway 4.5 (RCP 4.5). We calculated peak SWE from February to May using 2

(BNU.ESM, Ji et al., 2014; INMCM.4, Volodin, Dianskii, & Gusev, 2010) of the 12

available models, which were chosen to represent a range of future interannual flow

variability (high and low peak flow years). We used 2 selected models to ensure a

plausible range of interannual variability was captured, which is lost when model

averages are used. This individual (model) projection approach was found to better

represent a range in variability in future conditions than a model ensemble approach, for

instance (Lawrence, Runyon, Gross, Schuurman, & Miller, 2021). Ideally, we would use

relationships between historic peak SWE and peak spring stream discharge to develop

high and low flow thresholds driving age-0 brown trout survival; however, past SWE and

peak spring discharge (USGS gage 09403000) relationships in BAC (2006-2019) were

noisy (e.g., high SWE did not always correlate with high runoff, R^2= 0.42 see Fig. S2).

Spring runoff magnitude in Bright Angel Creek would be driven by many variables and

the relationship between the 2 variables are likely complicated by interannual variation in

winter rain frequency and amount, air temperature, soil moisture, and others (Hammond,

Saavedra, & Kampf, 2018; Stewart, 2009). We assumed peak SWE >220 and <30 mm

would represent high and low flows (~5.7 m^3/s or 0.57 m^3/s during spring runoff; see HS

curve in Figure 2 in main text), which we represented according to the future projected

frequency of high and low SWE. The frequency of high and low spring discharge

occurrences was then reflected in time series in climate scenarios based on peak SWE

from the 2 chosen models, with all other years' peak SWE falling between these

thresholds assumed to be optimum discharge for age-0 brown trout survival. Results of

the sensitivity analysis of these high and low thresholds are described below (and see

Table S3).

We used air temperature data provided in Tillman et al. (2020) to develop

maximum stream temperature scenarios for BAC. Air temperature increases of up to

3.4°C were forecasted for the Grand Canyon region by the end of the century, and 2.8°C

is projected by 2050 (Tillman et al., 2020). We used a subset of air temperature data for

2022 -2050 to match available years of data from Wheeler et al. (2021) for future

Alternative Management Paradigms for Colorado River reservoirs. We used a published

model developed to predict water temperature by location in BAC to convert maximum

air temperatures to maximum annual water temperature when water is or is not diverted

for human use from Roaring Springs (Bair et al., 2019):

$$BAC_{stream\ temp,\ subpop\ i.} = (3.615 - 1.710P) + 0.282D + (0.340 + 0.085P) \times A$$

where P = diversion pump on(1)/off(0), D=longitudinal distance from Roaring Springs, A=air temperature at Phantom Ranch (near the mouth of BAC). Some model calibration and assumptions were required to match maximum stream temperatures chosen to represent the baseline maximum temperature for the BACL, BACM, and BACU subpopulations from available NPS and USGS water temperature loggers placed along BAC. We assumed the diversion was constantly applied to represent reduced (~20%) future flows in BAC (Bair et al., 2019). Lacking future air temperature projections from across the range of BAC elevations, we generated % annual temperature increases from regional air temperature increases in Tillman et al. (2020) data (Fig. S3), and then applied those % increases to air temperature in the Bair et al. (2019) model for each subpopulation, starting with 35°C as a baseline air temperature (Table S2). Future temperatures for BAC subpopulations were included with annual discharge for climate changes scenarios as described above. R code to develop these temperature scenarios is included below.

Table 4-S2. Water temperature modeling results using maximum air temperature from Tillman et al. (2020)(MaxMnAnnTemp), and proportional increases (inc) applied to Phantom Ranch baseline air temperature (PRair; 35°C), which were used to generate subpopulation-specific proportional increases in water temperatures (right 3 columns) using the Bair et al. (2019) water temperature model from baselines of 16°C, 18°C, and 23°C for BACU, BACM, and BACL, respectively.

yr	MaxMnAnnTemp	inc	PRair	BACU-temp	BACM-temp	BACL-temp	BACU-temp.adj	BACM-temp.adj	BACL-temp.adj
2021	26.99	0.00	35.00	17.06	17.91	20.45	16.00	18.00	23.00
2022	27.65	0.66	35.66	17.34	18.19	20.73	16.26	18.28	23.31
2023	27.86	0.87	35.87	17.43	18.28	20.81	16.34	18.37	23.41
2024	27.87	0.88	35.88	17.44	18.28	20.82	16.35	18.38	23.42
2025	27.83	0.84	35.84	17.42	18.26	20.80	16.33	18.36	23.40
2026	27.05	0.06	35.06	17.09	17.93	20.47	16.02	18.02	23.03
2027	28.08	1.09	36.09	17.53	18.37	20.91	16.43	18.46	23.52
2028	28.31	1.32	36.32	17.62	18.47	21.01	16.52	18.56	23.63
2029	27.82	0.83	35.83	17.42	18.26	20.80	16.33	18.35	23.40
2030	27.53	0.54	35.54	17.29	18.14	20.67	16.21	18.23	23.25
2031	28.07	1.08	36.08	17.52	18.37	20.91	16.43	18.46	23.52
2032	27.76	0.77	35.77	17.39	18.23	20.77	16.30	18.33	23.36
2033	28.23	1.24	36.24	17.59	18.44	20.97	16.49	18.53	23.59
2034	28.66	1.67	36.67	17.77	18.62	21.16	16.66	18.71	23.80
2035	28.80	1.81	36.81	17.83	18.68	21.22	16.72	18.77	23.86
2036	29.65	2.66	37.66	18.19	19.04	21.58	17.06	19.13	24.27
2037	28.64	1.65	36.65	17.77	18.61	21.15	16.66	18.71	23.79
2038	28.19	1.20	36.20	17.57	18.42	20.96	16.48	18.51	23.57
2039	28.21	1.22	36.22	17.58	18.43	20.96	16.48	18.52	23.58
2040	28.87	1.88	36.88	17.86	18.71	21.24	16.75	18.80	23.89
2041	28.89	1.90	36.90	17.87	18.71	21.25	16.75	18.81	23.90
2042	29.42	2.43	37.43	18.09	18.94	21.48	16.97	19.04	24.16
2043	28.56	1.57	36.57	17.73	18.57	21.11	16.62	18.67	23.75

2044	29.24	2.25	37.25	18.02	18.86	21.40	16.89	18.96	24.07
2045	29.75	2.76	37.76	18.23	19.08	21.62	17.10	19.18	24.32
2046	29.59	2.60	37.60	18.17	19.01	21.55	17.04	19.11	24.24
2047	29.42	2.43	37.43	18.09	18.94	21.48	16.97	19.04	24.16
2048	30.15	3.16	38.16	18.40	19.25	21.79	17.26	19.35	24.51
2049	30.28	3.29	38.29	18.46	19.31	21.84	17.31	19.40	24.57
2050	29.80	2.81	37.81	18.25	19.10	21.64	17.12	19.20	24.34

GCregionTemps<-read.csv("C:/Users/.../GC_area_TMEAN_monthly_MEAN_F.csv",header=TRUE)

library(frost)

GCregionTemps$cels <- convert.temperature(from="F",to="C",GCregionTemps$avgTemp)

GCregionmaxtemp<- ddply(GCregionTemps,.(yr), summarise,MaxMnAnnTemp=max(cels, na.rm=TRUE))

plot(MaxMnAnnTemp~yr,data=GCregionmaxtemp, type="l", las=1, xlab="Year",ylab="Max. annual air temperature (\u00B0C)")

GCregionmaxtemp2050<-subset(GCregionmaxtemp, yr>2020 &yr<2051)

#calculate annual temp increase from baseline 26.99 air temp in 2021

GCregionmaxtemp2050$inc<-GCregionmaxtemp2050$MaxMnAnnTemp-26.99

#calc Phantom Ranch future air temp from baseline 35 from Bair et al.

GCregionmaxtemp2050$PRair<-GCregionmaxtemp2050$inc+35
#calc future water temp for each Subpopulation by adding to temp used in base model (with pump on)

GCregionmaxtemp2050$BACUtemp<-(3.615-1.71*1)+(0.282*1)+((0.34+0.085*1)*GCregionmaxtemp2050$PRair)

GCregionmaxtemp2050$BACMtemp<-(3.615-1.71*1)+(0.282*4)+((0.34+0.085*1)*GCregionmaxtemp2050$PRair)

GCregionmaxtemp2050$BACLtemp<-(3.615-1.71*1)+(0.282*13)+((0.34+0.085*1)*GCregionmaxtemp2050$PRair)

Perturbation - sensitivity analysis – Due to uncertainty in relationships between North Kaibab Plateau peak SWE and BAC discharge, and a large number of assumptions related to climate change scenarios, we conducted a sensitivity analysis to understand how varying peak SWE thresholds representing extreme high and low spring discharge years would affect age-0 brown trout survival. We increased or decreased (10% and 20%) the assumed peak SWE values that would represent high and low spring peak discharge (5.7 and 0.57 m^3/s) from baselines of >220 or <30 mm SWE. We used the CR resample 2000 baseline model (assumes status quo reservoir management) for all sensitivity analysis scenarios. Results of sensitivity analysis, comparing minimum population sizes (N_{min}) between baseline wet (INMCM.4) and dry (BNU.ESM) models, are shown in Table S3. N_{min} values generally deviated little from baseline models when thresholds were changed, and BACU, was most sensitive to changes in thresholds (-2.9% to 14.6%).

Table 4-S3. Results of climate change scenario sensitivity analysis, involving adjustment of peak snow-water-equivalent and peak spring Bright Angel Creek discharge relationships so that dry and wet scenario thresholds are +/-10% or +/- 20% of the baseline. The upper section of the table shows the number of occurrences of high or low spring peak flows (above and below optimum range for brown trout age-0 survival) with changes in thresholds, and the lower portion of the table represents % changes in minimum population abundance for the metapopulation and each subpopulation, with changes in thresholds.

|	Climate-CRbasewet	Wet, threshold -10%	Wet, threshold +10%	Wet, threshold -20%	Wet, threshold +20%	Climate-CRbasedry	Dry, threshold -10%	Dry, threshold +10%	Dry, threshold -20%	Dry, threshold +20%
High and low spring peak runoff frequency (number/30 years)										
Low flows	2	1	3	1	3	6	5	6	4	6
High flows	6	6	4	7	1	4	4	3	5	3
Total disturbances	8	7	7	8	4	10	9	9	9	9
Minimum metapopulation and subpopulation abundances and % change from baseline model										
Meta	10771	1.42%	-2.50%	1.78%	0.87%	9422	1.58%	1.05%	2.51%	2.66%
BACL	374	3.61%	-1.63%	3.86%	0.00%	335	1.18%	-0.30%	4.83%	2.90%
BACM	1575	3.85%	-9.38%	4.95%	2.05%	959	2.74%	5.70%	4.67%	6.71%
BACU	1180	-2.88%	0.84%	-9.87%	14.62%	683	8.45%	12.21%	3.94%	14.30%
CR	7505	1.20%	0.07%	0.91%	-0.07%	7416	1.12%	-0.31%	2.37%	1.25%
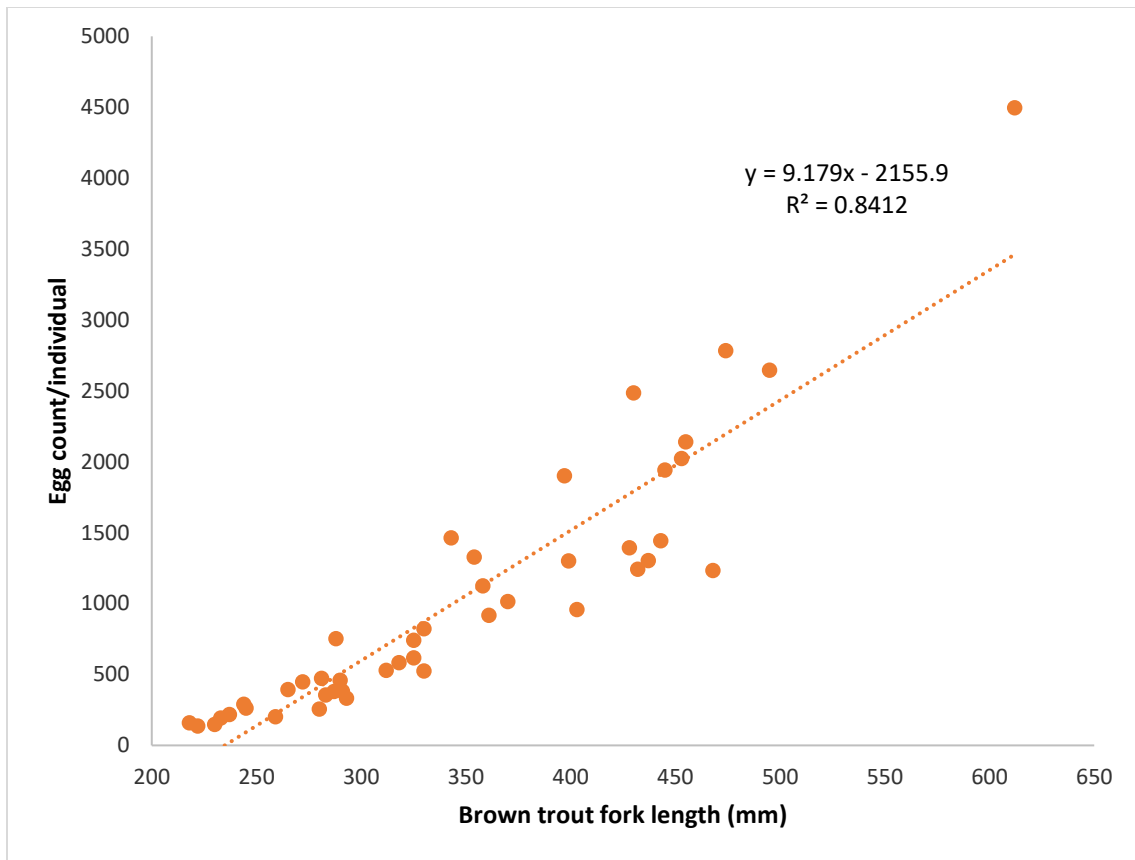
Figure 4-S1. Relationship between female brown trout fork length and fecundity.
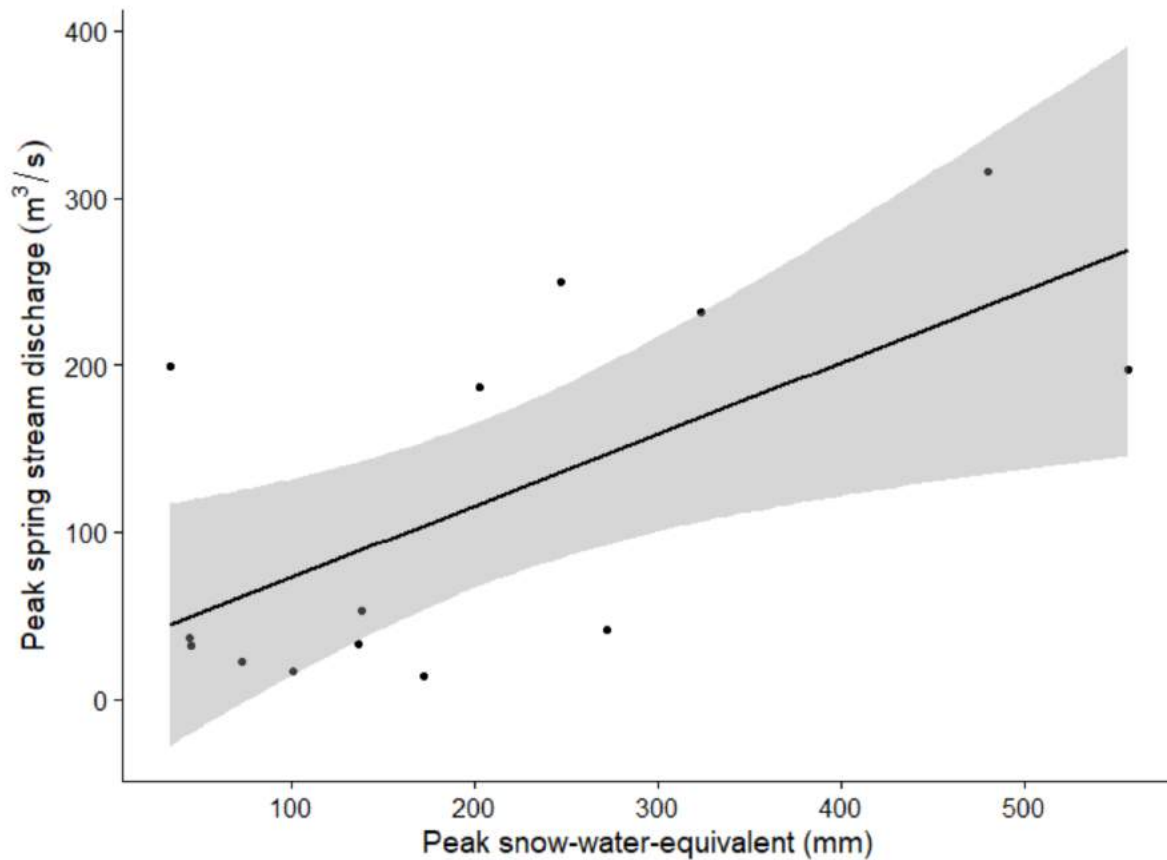
Figure 4-S2. Relationship between peak snow-water-equivalent, generated using a water balance model (Tercek et al. 2021), and peak spring Bright Angel Creek discharge (USGS gage 09403000 data).
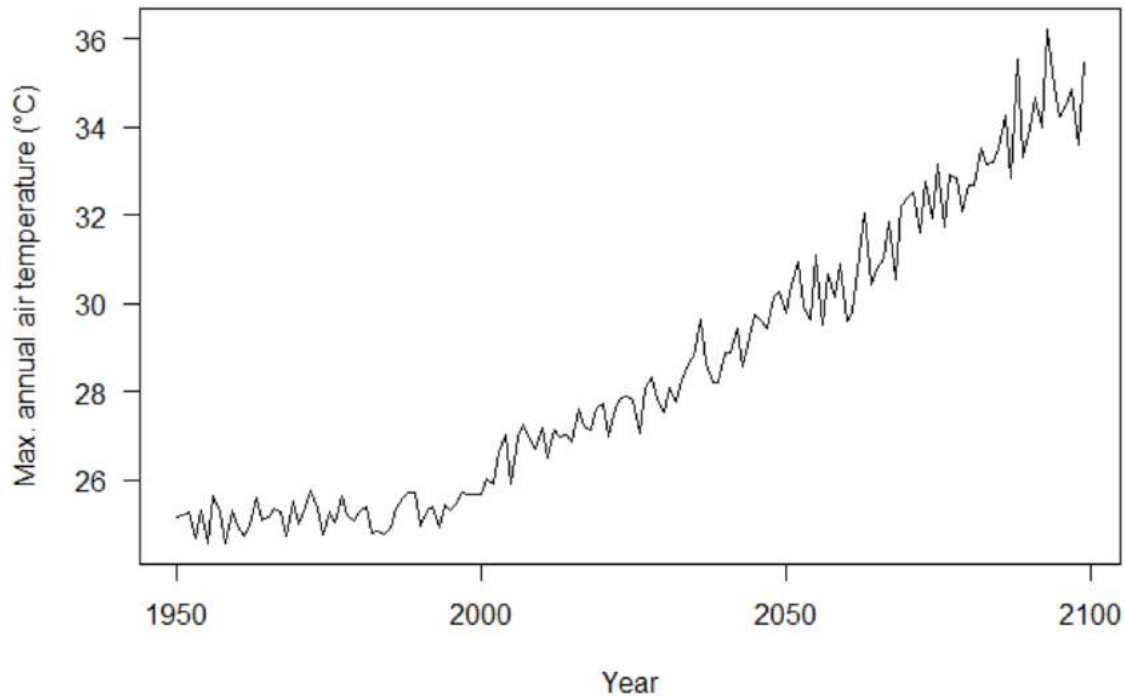
Figure 4-S3. Monthly max air temperatures using Tillman et al. (2020) data from USGS website (converted to average from 370 grids, then to Celsius). These data were subset from 2021-2050 for use in BAC water temp models.

Appendix 4: Validation of the PVA results using observed vs simulated trends in Bright Angel Creek abundance.

We used data from long-term suppression activities in BAC (Healy et al., *in review*, 2020) for estimating size- (age) specific electrofishing capture probability ($\hat{p}$) to be used in BAC suppression scenarios. Initial model tests using estimates of $\hat{p}$ taken from Healy et al. (*in review*) caused the BAC subpopulations to reach quasi-extinction (QE) at a faster rate than observed in BAC (Healy et al., 2020). Thus, we made adjustments until declines approximated observed declines in BAC (Fig. S4). Results of analysis of environmental and spatial variation in $\hat{p}$ (Healy et al., *in revision*) found 15% and 49% reductions in $\hat{p}$ for BACM and BACU subpopulations relative to BACL, and we adjusted subpopulation $\hat{p}$ accordingly (Table S4). Comparing observed and simulated

abundance over 7 years of suppression in BAC suggested similar outcomes could be

represented by our PVA, although observed declines were greater than simulated in

BACL, which is likely due to immigration from the CR subpopulation. We also note that

2020-21 abundance increased substantially, likely due to optimum flows for age-0

recruitment, corresponding to year 8 in Fig. S4.

Table 4-S4. Cumulative capture probability ($\hat{p}$) values used for BAC brown trout
subpopulation suppression scenarios for 2-4 electrofishing passes.

|	2-pass $\hat{p}$	3-pass $\hat{p}$	4-pass $\hat{p}$
Bright Angel Creek - lower subpopulation			
Age0	0.48	0.58	0.78
Juvenile	0.61	0.74	0.89
Small Adult	0.65	0.79	0.93
Large Adult	0.70	0.85	0.96
Bright Angel Creek - middle subpopulation			
Age0	0.38	0.49	0.68
Juvenile	0.49	0.63	0.81
Small Adult	0.52	0.67	0.84
Large Adult	0.56	0.72	0.87
Bright Angel Creek - upper subpopulation			
Age0	0.20	0.30	0.44
Juvenile	0.26	0.38	0.54
Small Adult	0.28	0.40	0.56
Large Adult	0.30	0.43	0.60
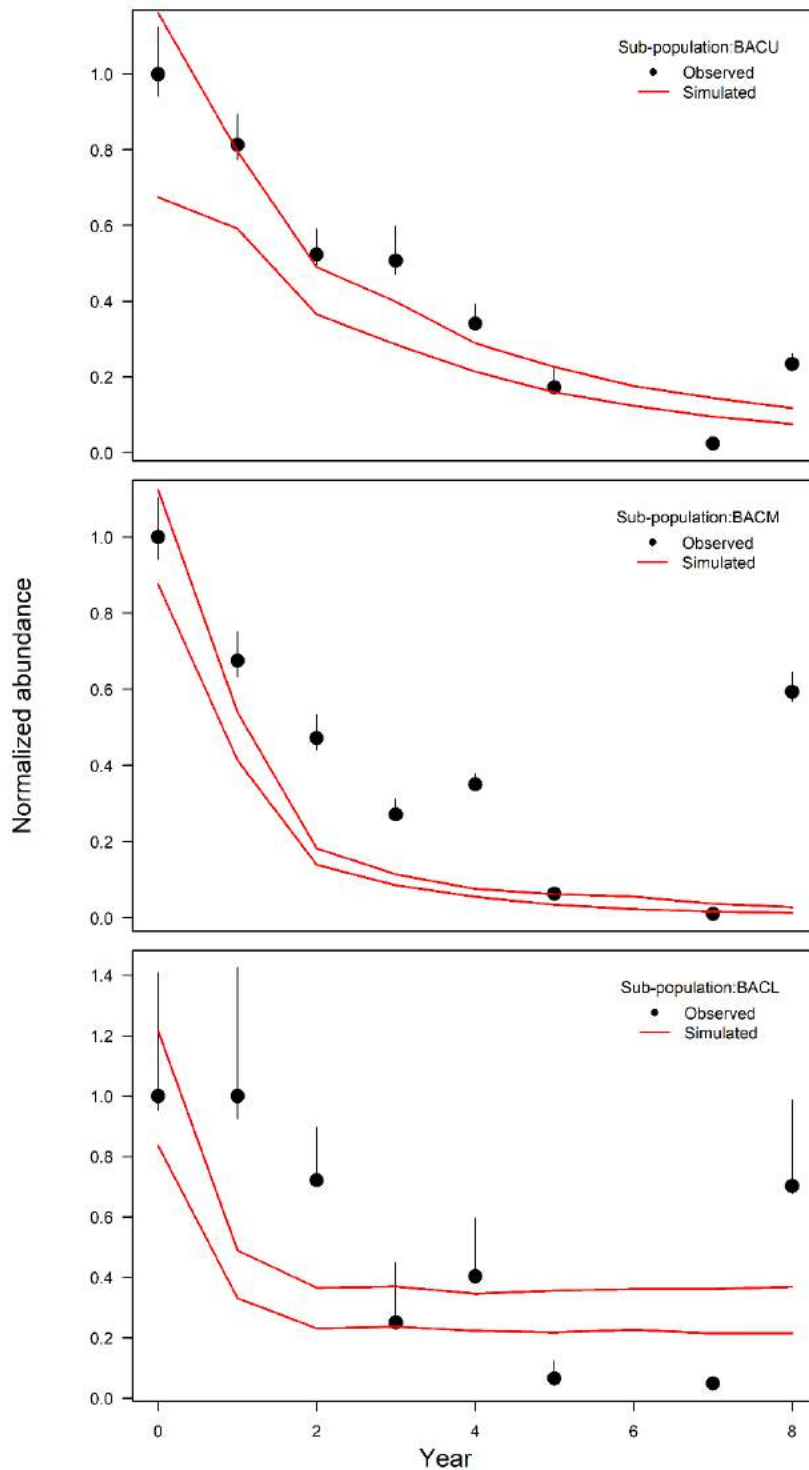
Figure 4-S4. Validation plots of observed for reaches 1, 3, and 5 through spring 2021 (Healy et al. 2020, NPS unpublished 2020-21 abundance data) compared to simulated trends in normalized abundance (abundance trends normalized to % of carrying capacity) for BACL, BACM, BACU subpopulations.

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Appendix D: Permission Letters

26 February 2022

Brian Healy
4115 Canyon Loop
Flagstaff, AZ 86005
970-471-3407, brianhealy31@yahoo.com

Robert Schelly, Native Fish Ecology and Conservation Program, Grand Canyon National Park

Dear Robert Schelly,

I am in the process of preparing and finalizing my dissertation in the Department of Watershed Sciences and the Ecology Center at Utah State University.

I am requesting your permission to include our coauthored papers, "Remarkable response of native fishes to invasive trout suppression varies with trout density, temperature, and annual hydrology," and "Exploring management options for a metapopulation of a global invader in a river network under climate change" in my PhD dissertation, as per graduate school requirements. You will be cited as a coauthor on the first page of each corresponding dissertation chapter (chapters 2 and 4).

Please indicate your approval of this request by signing in the space provided. By signing this letter, you acknowledge that the work leading to the completed papers was primarily my own.

Please contact me with any questions.
Thank you in advance,
Brian Healy

I hereby give permission to Brian D. Healy to reprint the following material in his PhD dissertation:

Healy, Brian D., Robert C. Schelly, Charles B. Yackulic, Emily C. Omana Smith, and Phaedra Budy. "Remarkable Response of Native Fishes to Invasive Trout Suppression Varies with Trout Density, Temperature, and Annual Hydrology." *Canadian Journal of Fisheries and Aquatic Sciences* 77, no. 9 (September 2020): 1446–62. https://doi.org/10.1139/cjfas-2020-0028.

Healy, Brian D., Phaedra Budy, Charles B. Yackulic, Brendan P. Murphy, Robert C. Schelly, and Mark C Mckinstry. *In preparation.* "Exploring Management Options for a Metapopulation of a Global Invader in a River Network under Climate Change." *Conservation Biology.*

Signature: _Robert Schelly_   Date: _2/28/2022_

26 February 2022

Brian Healy
4115 Canyon Loop
Flagstaff, AZ 86005
970-471-3407, brianhealy31@yahoo.com

Brendan Murphy, School of Environmental Science, Simon Fraser University

Dear Brendan Murphy,

I am in the process of preparing and finalizing my dissertation in the Department of Watershed Sciences and the Ecology Center at Utah State University.

I am requesting your permission to include our coauthored paper, "Exploring management options for a metapopulation of a global invader in a river network under climate change" in my PhD dissertation, as per graduate school requirements. I intend to submit the paper to Conservation Biology or a similar outlet this spring and will include you as a coauthor. You will also be cited as a coauthor on the first page of my corresponding dissertation chapter (chapter 4).

Please indicate your approval of this request by signing in the space provided. By signing this letter, you acknowledge that the work leading to the completed papers was primarily my own.

Please contact me with any questions.
Thank you in advance,
Brian Healy

I hereby give permission to Brian D. Healy to reprint the following material in his PhD dissertation:

Healy, Brian D., Phaedra Budy, Charles B. Yackulic, Brendan P. Murphy, Robert C. Schelly, and Mark C Mckinstry. *In preparation*. "Exploring Management Options for a Metapopulation of a Global Invader in a River Network under Climate Change." *Conservation Biology*.

Signature: _____   Date:____02/28/2022_____

26 February 2022

Brian Healy
4115 Canyon Loop
Flagstaff, AZ 86005
970-471-3407, brianhealy31@yahoo.com

Emily Omana Smith, Native Fish Ecology and Conservation Program, Grand Canyon National Park

Dear Emily Omana Smith,

I am in the process of preparing and finalizing my dissertation in the Department of Watershed Sciences and the Ecology Center at Utah State University.

I am requesting your permission to including our coauthored papers, "Remarkable response of native fishes to invasive trout suppression varies with trout density, temperature, and annual hydrology," and "Life and death in a dynamic environment: invasive trout, floods, and intra-specific drivers of translocated populations" in my PhD dissertation, as per graduate school requirements. You will be cited as a coauthor on the first page of each corresponding dissertation chapter (chapters 2 and 3).

Please indicate your approval of this request by signing in the space provided. By signing this letter, you acknowledge that the work leading to the completed papers was primarily my own.

Please contact me with any questions.
Thank you in advance,
Brian Healy

I hereby give permission to Brian D. Healy to reprint the following material in his PhD dissertation:

Healy, Brian D., Robert C. Schelly, Charles B. Yackulic, Emily C. Omana Smith, and Phaedra Budy. "Remarkable Response of Native Fishes to Invasive Trout Suppression Varies with Trout Density, Temperature, and Annual Hydrology." *Canadian Journal of Fisheries and Aquatic Sciences* 77, no. 9 (September 2020): 1446–62. https://doi.org/10.1139/cjfas-2020-0028.

Healy, Brian D., Phaedra Budy, Mary M. Conner, and Emily C. Omana Smith. *In press*. "Life and Death in a Dynamic Environment: Invasive Trout, Floods, and Intra-Specific Drivers of Translocated Populations." *Ecological Applications*.

Signature: *Emily Omana Smith*   Date: *3/10/2022*

Appendix E: Curriculum Vitae

Brian D. Healy

Program Manager, Native Fish Ecology and Conservation Program,
Division of Science and Resource Management,
Grand Canyon National Park
1824 S. Thompson Street, Suite 200, Flagstaff, Arizona 86001
Brian_Healy@nps.gov   928-638-7453 (office), 970-471-3407 (cell)

Education
Utah State University –Ph.D. in Aquatic Ecology, Watershed Sciences Department and the Ecology Center, May, 2022.
Dissertation: Efficacy of conservation actions for imperiled Colorado River fishes in the Grand Canyon, Arizona.

Texas A&M University – M.S. Fisheries Ecology and Management, Wildlife and Fisheries Sciences, August 2002
MS Thesis: Relationships of drought and biotic interactions to crayfish assemblage structure in gulf coastal headwater streams.

University of Wisconsin – Eau Claire – B. S. Biology, 1998

Professional Experience
Graduate Research Assistant/Colorado River Doctoral Scholar – Center for Colorado River Studies, Watershed Sciences Department, Utah State University
Logan, Utah
August 2018 - Present

Native Fish Ecology and Conservation Program Manager – Grand Canyon National Park, National Park Service
Flagstaff, Arizona
June 2009 – Present

East Zone Fisheries Biologist – White River National Forest, USDA Forest Service
Minturn, Colorado
September 2003 – June 2009

District Fisheries Biologist – Chippewa National Forest, USDA Forest Service
Blackduck, Minnesota
October 2002 – September 2003

Fisheries Biologist – Chippewa National Forest, USDA Forest Service
Cass Lake, Minnesota
August 2000 – October 2002

Graduate Research Assistant – Department of Wildlife and Fisheries Sciences, Texas A&M University
College Station, Texas

June 1999 – August 2000

Research Assistant – Department of Wildlife and Fisheries Sciences, Texas A&M University
College Station, Texas
May 1999 – October 1999

Graduate Research Assistant – Texas Cooperative Wildlife Collection, Texas A&M
University
College Station, Texas
June 1999 – September 1999

Graduate Teaching Assistant - Department of Wildlife and Fisheries Sciences, Texas A&M
University
College Station, Texas
January 1999 – May 1999

Fisheries Technician – Total Lake Management
Bryan, Texas
January, 1999 – May, 1999

Wildlife Technician (Volunteer) – U. S. Fish and Wildlife Service, Division of Migratory
Bird Management
Anchorage, Alaska
May 1998 – September 1998

Student Research Assistant – Department of Biology, University of Wisconsin – Eau Claire
Eau Claire, Wisconsin
January 1998 – September 1998

Student Research Assistant – Department of Biology, University of Wisconsin – Eau Claire
Eau Claire, Wisconsin
May 1995 – August 1997

Awards, Grants, and Scholarships

- **2021 Award for Outstanding Performance (5% of salary)**– National Park Service, Grand Canyon National Park
- **2021 STAR award ($750)** – National Park Service, award for extra effort related to Colorado River issues and leadership on climate change
- **2019 Travel Grant, Ecology Center, Utah State University ($800)** – grant for travel to the "Advances in Population Ecology of Stream Salmonids V Symposium," Granada, Spain, May, 2019.
- **2018 Grand Canyon Conservancy, E. L. Johnson Foundation Grant ($45,000)** – support for field technicians conducting Humpback Chub translocation monitoring and invasive trout control**.**
- **2018 Colorado River Doctoral Scholarship, Center for Colorado River Studies, Watershed Sciences Dept., Utah State University**
- **2017-2018 Conservation Achievement Award, Western Division of the American Fisheries Society** – awarded to the Grand Canyon National Park Fisheries Program, May, 2018.

- **2018 Horace M. Albright-Conrad L. Wirth Grant, National Park Foundation ($3,260)** – Tuition for graduate-level statistics course and support for manuscript publication.
- **2017-18 Grand Canyon Association Direct Aid Grants (total: $72,223)** – Support for interns, a documentary film, and endangered fish research and conservation projects.
- **2016 Grand Canyon Association Direct Aid Grant ($22,500)** – Support for brown trout telemetry study.
- **2016 Grand Canyon Association Direct Aid Grant ($3,000)** – Support for development of educational posters and brochures, Grand Canyon's native fishes.
- **2011 Regional Director's Award for Professional Excellence in Natural Resources**, National Park Service, Intermountain Region.
- **2011 Partnership Award**, awarded by the US Fish and Wildlife Service, Arizona Fish and Wildlife Conservation Office.
- **2011 Grand Canyon Small Grant ($2,264),** awarded by Grand Canyon National Park, Superintendent – continuing education grant to attend an Intermediate Program MARK workshop, June, 2011.
- **2009 Extra Effort Award**, for Leadership in Humpback Chub Translocations to Shinumo Creek, National Park Service, Grand Canyon National Park.
- **2006 Rise to the Future Award: Collaborative Aquatic Resource Stewardship** – awarded for collaborative work with the Eagle River Watershed Counsel, Avon, Colorado. USDA Forest Service.
- **2006 USDA Forest Service Merit Award (Quality Step Increase)**, White River National Forest.
- **2001 USDA Forest Service Merit Award**, Eastern Region.
- **2000 Graduate Student Research and Presentation Grant**, Texas A&M Office of Graduate Studies.
- **2000 Student Award**, Texas A&M Chapter of the American Fisheries Society.
- **1998 Terry Balding Scholarship**, University of Wisconsin-Eau Claire Foundation.
- **1998 Small Research Grant**, UW-Eau Claire, Office of University Research.
- **1996 Student/Faculty Collaboration Grant**, UW-Eau Claire, Office University Research.

Peer-reviewed Journal Articles

Healy, B. D., P. Budy, C. B. Yackulic, B. P. Murphy, R. C. Schelly, M. C. McKinstry. *In preparation.* Predicting eradication success of a global invader through a spatially-explicit stage-based metapopulation viability modeling approach. To submitted to Conservation Biology.

Healy, B. D., P. Budy, M. M. Conner, and E. C. Omana Smith. *In press.* Life and death in a dynamic environment: invasive trout, floods, and intra-specific drivers of translocated populations. Ecological Applications. Accepted February 24, 2022.

Healy, B. D., J. F. Moore, and W. E. Pine. 2022. Monitoring and managing fishes that are invisible and keep moving around: influences of an invasive species and environmental factors on capture probability. North American Journal of Fisheries Management. Published online January 29, 2022. DOI: 10.1002/nafm.10755.

Holton, P. B., D. Mattson, K. Ironside, and **B. D. Healy**. *In preparation.* Survival rates and causes of mortality within and surrounding a pseudo-protected ecosystem: Grand Canyon National Park. To be submitted to Journal of Wildlife Management.

Schelly, R. C., **B. D. Healy**, C. B. Yackulic. *In preparation.* Weir are you going? Experimental fall floods increase brown trout rates of immigration into a tailwater. To be submitted to North American Journal of Fisheries Management.

Healy, B. D., R. C. Schelly, C. B. Yackulic, E. C. Omana Smith, P. Budy. 2020. Remarkable response of native fishes to invasive trout suppression varies with trout density, temperature, and annual hydrology. Canadian Journal of Fisheries and Aquatic Sciences 77(9):1446-1462. https://doi.org/10.1139/cjfas-2020-0028

Healy, B. D., E. C. Omana Smith, M. Trammell, R. C. Schelly, C. B. Nelson. 2020. Establishment of a reproducing population of endangered Humpback Chub through translocations to a Colorado River tributary, Grand Canyon, Arizona. North American Journal of Fisheries Management 40: 278-292. DOI: 10.1002/nafm.10408.

Gilbert, E. I., W. H. Brandenburg, A. L. Barkalow, R. B. Kegerries, B. C. Albrecht, **B. D. Healy**, E. C. Omana Smith, J. R. Stolberg, M. C. McKinstry, and S. P. Platania. *In press.* Systematic larval fish surveys and abiotic correlates characterize extant native fish reproductive success in the Colorado River, Grand Canyon, Arizona. The Southwestern Naturalist.

Kegerries, R. B., B. Albrecht, M. C. McKinstry, R. A. Valdez, R. J. Rogers, A. L. Barkalow, E. I. Gilbert, H. Mohn, **B. Healy**., and E. Omana Smith. 2020. Small-bodied fish surveys demonstrate native fish dominate over three hundred kilometers of the Colorado River through Grand Canyon, Arizona. Western North American Naturalist 80(2). https://scholarsarchive.byu.edu/wnan/vol80/iss2/2

Bair, R., B. W. Tobin, **B. D. Healy**, H. Childres, C. Spangenburger, E. Schenk. 2019. Modeling temperature regime and physical habitat impacts from restored streamflow. Environmental Management 63(6): 718-731.

Albrecht, B., H. E. Mohn, R. Kegerries, M. C. McKinstry, R. Rogers, T. Frances., B. Hines, J. Stolberg, D. Ryden, D. Elverud, B. Schleicher, K. Creighton, **B. Healy**, and B. Senger. 2017. Use of inflow areas in two Colorado River Basin reservoirs by endangered razorback sucker (*Xyrauchen texanus*). Western North American Naturalist 77(4): 500-514.

Kegerries, R. B., B. C. Albrecht, E. I. Gilbert, W. H. Brandenburg, A. L. Barkalow, M. C. McKinstry, H. E. Mohn, **B. D. Healy**, J. R. Stolberg, E. C. Omana Smith, C. B. Nelson, and R. J. Rogers. 2017. Occurrence and Reproduction by Razorback Sucker (*Xyrauchen texanus*) in the Grand Canyon, Arizona. The Southwestern Naturalist 62(3):227- 232.

Spurgeon, J. J., C. P. Paukert, **B. D. Healy**, M. Trammell, D. Speas, E. Omana Smith. 2015. Translocation of Humpback Chub into Tributary Streams of the Colorado River: Implications for Conservation of Large-River Fishes. Transactions of the American Fisheries Society 144(3):502-514.

Whiting, D. P., C. P. Paukert., **B. D. Healy**, J. J. Spurgeon. 2014. Macroinvertebrate prey availability and food web dynamics of nonnative trout in a Colorado River tributary, Grand Canyon. Freshwater Science 33(3):872-884.

Spurgeon, J. J., C. P. Paukert, **B. D. Healy**, C. A. Kelley, D. P. Whiting. 2014. Can translocated native fishes retain their trophic niche when confronted with a resident invasive? Ecology of Freshwater Fish 24(3): 456-466.

Pine, W. E., III, **B. Healy**, E. Omana Smith, M. Trammell, D. Speas, R. Valdez, M. Yard, C. Walters, R. Ahrens, R. Van Haverbeke, D. Stone, W. Wilson. 2013. An Individual-Based Model for Population Viability Analysis of Humpback Chub in Grand Canyon. North American Journal of Fisheries Management 33(3): 626-641.

Gelwick, F. I., **B. D. Healy**, N. J. Dictson, R. Knipe. 2001. Fishes of the Keechi Creek Wildlife Management Area of east Texas. Texas Journal of Science 53(1):13-18.

Gelwick, F. I., **B. D. Healy**, N. J. Dictson, J. Cathey. 2000. Fishes of the Richland Creek Wildlife Management Area of east Texas. Texas Journal of Science 52(4):313-318.

Healy, B. D., and D. G. Lonzarich. 2000. Microhabitat use and behavior of overwintering juvenile Coho salmon in a Lake Superior tributary. Transactions of the American Fisheries Society 129: 866-872.

Peer-reviewed Technical Reports

Healy, B. D., R. Schelly, C. Nelson, E. Omana Smith, M. Trammell, R. Koller. 2018. A review of suppression of nonnative fishes in Bright Angel Creek, 2012-2017, and future recommendations for Humpback Chub translocation. Report prepared for the Upper Colorado River Region, Bureau of Reclamation, Interagency Agreement Number R12PG40034. Peer-review coordinated by the Glen Canyon Dam Adaptive Management Program – Science Advisors. 45 pages.

Van Haverbeke, D. R., K. L. Young, and **B. Healy**. 2016. Translocation and refuge framework for Humpback Chub (*Gila cypha*) in Grand Canyon. U.S. Fish and Wildlife Service, Arizona Fish and Wildlife Conservation Office. Flagstaff, Arizona. USFWS-AZFWCO-FL-16-03. 50 pages.

Trammell, M., **B. D. Healy**, E. Omana Smith, P. Sponholtz. 2012. Humpback chub translocation to Havasu Creek, Grand Canyon National Park: implementation and monitoring plan. Natural Resource Report NPS/GRCA/NRR—2012/586. U. S. Department of the Interior, National Park Service. Fort Collins, Colorado. 36 pages.

Omana Smith, E., **B. D. Healy**, W. C. Leibfried, D. P. Whiting. 2012. Bright Angel Creek trout reduction project: Winter 2010- 2011 Report. Natural Resource Technical Report NPS/GRCA/NRTR—2012/01. U. S. Department of Interior, National Park Service. Fort Collins, Colorado. 45 pages.

Zuellig, R. E., J. F. Bruce, **B. D. Healy**, C. A. Williams. 2010. Macroinvertebrate-based assessment of biological condition at selected sites in the Eagle River watershed, Colorado, 2000–07. U. S. Geological Survey Scientific Investigations Report 2010–5148. 19 pages.

Healy, B. D. 2002. Conservation assessment for the greater redhorse (*Moxostoma valenciennesi*). USDA Forest Service, Eastern Region, Milwaukee, Wisconsin. 34 pages. https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsm91_054277.pdf

Technical Reports (Selected)

Omana Smith, E., **B. D. Healy**, R. C. Schelly, and R. Koller. 2021. Monitoring humpback chub translocated to Grand Canyon tributaries: 2021 annual report. Report prepared for the Bureau of Reclamation, Upper Colorado River Region. National Park Service- Grand Canyon National Park.

Schelly, R., E. Omana Smith, R. Koller, and **B. Healy**. Bright Angel Creek comprehensive brown trout control project: October 1, 2020 - March 1, 2021, season report. Report Prepared for the Upper Colorado Region, Bureau of Reclamation, Interagency Agreement Number: R17PG00048. National Park Service - Grand Canyon National Park.

Healy, B. D., E. C. Omana Smith, R. C. Schelly, and R. Koller. 2020. Translocation of humpback chub to Grand Canyon tributaries: 2019 annual report. Annual Report prepared for the U. S. Bureau of Reclamation, Upper Colorado River Region, Interagency Agreement Number: R10PG40063. National Park Service - Grand Canyon National Park, Flagstaff, Arizona. 45 pages.

Healy, B. 2016. Evaluation of Rocky Mountain National Park's fisheries program: recommendations for future cooperative management. Report submitted to the U. S. Fish and Wildlife Service, Colorado Fish and Wildlife Conservation Office, in fulfillment of Interagency Agreement Number 4500094597. 18 pages.

Healy, B. D., E. Omana Smith, C. Nelson, M. Trammell. 2014. Translocations of humpback chub to Grand Canyon tributaries and related nonnative fish control activities: 2011-2013. Report prepared for Upper Colorado Region, Bureau of Reclamation, Interagency Agreement Number: 09-AA-40-2890. National Park Service, Grand Canyon National Park. 48 pages.

Healy, B. D., E. Omana Smith, J. J. Spurgeon, C. Paukert, J. Whittier, P. J. Sponholtz, and W. C. Leibfried. 2011. Translocation of humpback chub to Grand Canyon tributaries, and related nonnative fish control activities: 2010 annual report. Report prepared for Upper Colorado Region, Bureau of Reclamation, Interagency Agreement Number: 09-AA-40-2890 and Colorado Plateau Cooperative Ecosystems Studies Unit Coop. Agreement Number H1200-09-0005. Grand Canyon National Park. 94 pages.

Healy, B. 2009. Gore Creek aquatic habitat and macroinvertebrate monitoring – 2004-2007. Summary prepared for the Eagle River Watershed Council and the Town of Vail and Eagle County. White River National Forest, Minturn, Colorado. 16 pages.

Healy, B. D. 2008. Pennsylvania Mine and Lower Warden Gulch Mine, preliminary assessment – site investigation: macroinvertebrate monitoring, 2007. Report Prepared for the Rocky Mountain Region of the USDA Forest Service, submitted May 8, 2008, Lakewood, Colorado. 21 pages.

Healy, B. 2007. Straight Creek fish and macroinvertebrate monitoring report. Report submitted to the Dillon Ranger District of the White River National Forest, March 19, 2007, Silverthorne, Colorado. 16 pages.

Healy, B., and M. Grove. 2007. Gore Creek Macroinvertebrate and Stream Health Monitoring Report: 2004-2006 Monitoring. Report Prepared for the Eagle River Watershed Council, Funded in Part by the Town of Vail and Eagle County June 8, 2007. White River National Forest, Minturn Colorado. 16 pages.

Healy, B. 2005. Black Gore Creek Macroinvertebrate Biomonitoring Report. Report prepared for the Holy Cross Ranger District, White River National Forest, April 13, 2005, Minturn, Colorado. 26 pages.

<u>Selected Presentations</u>

Healy, B. D., P. Budy*, C, B. Yackulic, B. P. Murphy, R. C. Schelly, M. C. McKinstry. 2021. Exploring management options for a global fish invader in a river network using a mechanistic metapopulation population viability analysis approach. 2022 Researchers Meeting, Upper Colorado River Endangered Fish Recovery Program and San Juan River Basin Recovery Implementation Program (virtual). January 25 -26, 2022. *Presented by B. Budy.

Healy, B. D., P. Budy, C, B. Yackulic, B. P. Murphy. 2021. Towards a better understanding of the population dynamics of a global invader: a stage-based population viability model for predicting eradication success. 2021 Annual Meeting of the Ecological Society of America (virtual). August 2-6, 2021.

Healy, B. D., R. C. Schelly, C. B. Yackulic, E. C. Omana Smith, M. M. McKinstry, M. M. Conner, P. Budy. 2019. Native fish population responses to mechanical suppression of invasive brown trout in a Grand Canyon tributary. Conservation of North American freshwater native non-game fishes: presented by the Western Native Fish Committee, Desert Fish Habitat Partnership, and the Desert Fishes Council: Part II, Symposium. 149th Annual Meeting and Joint Conference with the Wildlife Society. Reno, Nevada, September 29-October 3, 2019.

Schelly, R. C., **B. D. Healy** C. B. Yackulic, M. J. Dodrill, C. B. Nelson, E. C. Omana Smith, M. M. McKinstry, S. K. Haas, P. Budy. 2019. Response of invasive brown trout to sustained mechanical removal in Bright Angel Creek, a Grand Canyon tributary, with an evaluation of movement in the main channel Colorado River. Invasive Fishes: Ecology and Management, Symposium. 149th Annual Meeting and Joint Conference with the Wildlife Society. Reno, Nevada, September 29-October 3, 2019.

Koller, R., **B. D. Healy**, R. C. Schelly, E. C. Omana Smith. 2019. Translocations to enhance redundancy of endangered humpback chub in Grand Canyon. The 3 R's of Fish and Wildlife Translocations: Rescue, Reinforcement, and Reintroduction, Symposium. 149th Annual Meeting and Joint Conference with the Wildlife Society. Reno, Nevada, September 29-October 3, 2019.

Healy, B. D., R. Schelly C. B. Yackulic, E. Omana Smith, and P. Budy. 2019. Rapid native fish recovery following salmonid suppression varies along environmental gradients in a Colorado River tributary in Grand Canyon, Arizona. Advances in the Population Ecology of Stream Salmonids V, Granada, Spain, May 20-24, 2019.

Healy, B., E. Omana Smith, C. Nelson, R. Koller, R. Schelly, M. Trammell, and M. Crawford. 2018. Translocations lead to a reproducing population of an endangered fish in Grand Canyon, Arizona. Western Native Fishes Symposium, 43rd Annual Meeting of the Alaska Chapter/Western Division American Fisheries Society, May 21-25, 2018.

Healy, B., R. Schelly, E. Omana Smith, C. Nelson, M. Trammell, R, Koller, M. Crawford. 2018. Mechanical suppression of nonnative trout leads to increases in abundance of native fishes in

Bright Angel Creek, Grand Canyon. 51st Joint Annual Meeting of the Arizona and New Mexico Chapters of the Wildlife Society and American Fisheries Society, February 1-3, 2018, Flagstaff, Arizona.

Schelly, R., **B. Healy**, C. Nelson, B. Vaage, D. Ward, B. Albrecht, R. Kegerries, H. Mohn, and J. Boyer. 2018. Brown trout telemetry at Lees Ferry and Grand Canyon, Arizona. 51st Joint Annual Meeting of the Arizona and New Mexico Chapters of the Wildlife Society and American Fisheries Society, February 1-3, 2018, Flagstaff, Arizona.

Schenk, E., **B. D. Healy**, E. O. Smith, B. W. Tobin, and N. Tanski. 2017. Impacts of a recent wildfire and major flash flood on endangered humpback chub habitat – Shinumo Creek, Grand Canyon. National Park Service Science, 14th Biennial Conference of Science and Management for the Colorado Plateau and Southwest Region, September 11-14, 2017, Flagstaff, Arizona.

Daubert, M. E., A. Ingram, M. A. Ford, J. D. Muehlbauer, T. A. Kennedy, and **B. D. Healy**. 2017. Aquatic invertebrate response to brown trout removal in Bright Angel Creek – study design and preliminary results. Society for Freshwater Science Annual Meeting – Designing our Freshwater Futures. Raleigh, North Carolina, June 4-8, 2017.

Koller, R. C., E. C. Omana Smith, R. Schelly, and **B. Healy**. 2017. Humpback chub translocations and nonnative fish control: Grand Canyon success stories. 14th Biennial Conference of Science and Management for the Colorado Plateau and Southwest Region, September 11-14, 2017, Flagstaff, Arizona.

Rogowski, D. L., **B. Healy**, and C. Nelson. 2016. Nonnative trout removal in a tributary stream: does it benefit native fish in the mainstem Colorado River? 49th Joint Annual Meeting of the Arizona/New Mexico Chapter of the American Fisheries Society, and Arizona and New Mexico Chapters of The Wildlife Society, February 4-6, 2016, Flagstaff, Arizona.

Healy, B. D. 2015. Mercury in Grand Canyon Trout. 2015. Presentation to the Glen Canyon Dam Adaptive Management Program - Technical Work Group (TWG), October 20-21, 2015, Phoenix, Arizona.

Kegerries , R., B. Albrecht, S. P. Platania, H. Brandenburg, A. Barkalow, M. McKinstry, **B. D. Healy**, and J. Stolberg. 2015. Razorback Sucker, *Xyrauchen texanus,* Presence and Reproduction in the Lower Grand Canyon, Arizona. 145th Annual Meeting of the American Fisheries Society, August 16-20, 2015, Portland, Oregon.

Barkstedt, J. M., A. L. Barkalow, S. P. Platania, R. B. Kegerries, B. Albrecht, **B. D. Healy**, J. R. Stolberg, M. C. McKinstry. 2014. Documentation of spawning by Razorback Sucker, Xyrauchen texanus, Razorback Sucker in the lower Grand Canyon during 2014. 46th Annual Meeting of the Desert Fishes Council, November, 19-23, 2014, San José del Cabo, Baja California Sur, México.

Kegerries, R. B., B. Albrecht, J. M. Barkstedt, W. H. Brandenburg, A. L. Barkalow, S. P. Platania, M. McKinstry, **B. D. Healy**. 2014. Razorback Sucker, *Xyrauchen texanus*, telemetry and small-bodied fish community sampling in the Lower Grand Canyon, Arizona. 46th Annual Meeting of the Desert Fishes Council, November, 19-23, 2014, San José del Cabo, Baja California Sur, México.

Omana Smith, E., **B. Healy**, C. Nelson, M. Trammell. 2013. Endangered humpback chub translocations to Colorado River tributaries in Grand Canyon National Park. 45th Annual Meeting of the Desert Fishes Council, November 20-24, 2013, Flagstaff, Arizona.

Healy, B. D., C. Nelson, E. Omana Smith, M. Trammell. 2013. Non-native fish control in Colorado River tributaries in Grand Canyon National Park. 45th Annual Meeting of the Desert Fishes Council, November 20-24, 2013, Flagstaff, Arizona.

Invited Presentations (Selected)

Healy, B. D., P. Budy, M. Conner, E. Omana Smith, R. Schelly, R. Koller. 2021. Drivers of demographic rates in translocated humpback chub populations and an annual update. (Invited) Presented at the Glen Canyon Dam Adaptive Management Program Annual Reporting Meeting 2020. January 20-21, 2021. Virtual/web presentation.

Healy, B. D., D. Ward, K. Young. 2020. Green sunfish – status and trends in the Western Grand Canyon. (Invited) Presented to the Glen Canyon Dam Adaptive Management Program, Technical Working Group, October 14-15, 2020. Virtual/web presentation.

Healy, B. D., R. Schelly, C. Nelson, E. Omana Smith, M. Trammell, R. Koller. 2017. Preliminary review of Bright Angel Creek trout control operations, 2012-2017. (Invited) Presented to the Glen Canyon Dam Adaptive Management Program, Brown Trout Workshop, September 21-22, 2017, Tempe, Arizona. September 21-22, 2017, Tempe, Arizona.

Healy, B. D., P. Budy, M. M. Conner, E. C. Omana Smith. 2020. Drivers of demographic rates in translocated populations of an endangered fish in Colorado River tributaries. 150th Annual Meeting of the American Fisheries Society (virtual). Getting it Right: A Guide to Successful Supplementation for Recreation, Restoration, and Recovery (invited). September 14-25, 2020.

Healy, B. D. 2020. The role of translocations and invasive species suppression in the conservation of native fishes in Grand Canyon. (Invited) Webinar/seminar. Collaborative Conservation Adaptation Strategy Toolbox, hosted by the University of Arizona and U.S. Fish and Wildlife Service. April 9, 2020.

Healy, B. D., M. M. Conner, R. C. Schelly, C. B. Yackulic, E. C. Omana Smith, R. Van Haverbeke, M. A. Trammell, P. Budy. 2020. Status and trends of native fish populations in Grand Canyon. Glen Canyon Dam Adaptive Management Program Annual Reporting Meeting 2020. January 13-14, 2020, Tempe, Arizona.

Haas, Sarah K., **B. D. Healy**, R. C. Schelly, R. C. Koller, E. Omana Smith. 2019. A review of a decade of conservation actions for imperiled desert fishes in Grand Canyon tributaries: implications for conservation of large-river fishes. (Invited) Presentation. Glen Canyon Dam Adaptive Management Program meets the Amazon Dams Network – International information exchange symposium, 15th Biennial Conference of Science & Management on the Colorado Plateau & Southwest Region, September 9-12, 2019.

Healy, B. D., R. C. Schelly, E. Omana Smith, M. Trammell, R. Koller, K. Evans, M. C. Conner, M. C. McKinstry, P. Budy. 2019. A stronghold for Colorado River native fishes: Grand Canyon conservation successes. (Invited) Presentation to the Grand Canyon River Guides, Guides Training Seminar, *100 years of "Grand": Celebrating the Past and Planning for the Future.* March 29-31, 2019, Marble Canyon, Arizona.

Healy, B. D., E. Omana Smith, R. C. Schelly, R. C. Koller, K. Evans, C. B. Yackulic, M. C. Conner, M. C. McKinstry, K. Young, P. Budy. 2019. Efficacy of humpback chub translocations and invasive trout control in Grand Canyon tributaries, 2012-2018. (Invited) Presentation to the Glen Canyon Dam Adaptive Management Program, Annual Reporting Meeting March 12-13, 2019, Phoenix, Arizona

Budy, P., M. McKinstry, C. Yackulic, T. Kennedy, **B. Healy**, Z. Ahrens, and J. Schmidt. 2018. The future of the fishes of the Colorado River and its tributaries. (Invited) Presentation. The Future of the Colorado River: a community symposium. Sponsored by the Center for Colorado River Studies, Quinney College of Natural Resources, Utah State University, October 13, 2018, Moab, Utah.

Omana Smith, E., **B. Healy**, R. Schelly, M. Crawford, M. McKinstry, K. Young. 2018. Translocation of Humpback Chub into Bright Angel Creek: a joint project of Grand Canyon National Park, Bureau of Reclamation, and U.S. Fish and Wildlife Service. (Invited) Presented to the Glen Canyon Dam Adaptive Management Work Group, May 22, 2018 (Webinar). https://www.usbr.gov/uc/rm/amp/amwg/mtgs/18may22/Attach_05.pdf

Healy, B. D., R. Schelly, C. Nelson, E. Omana Smith, M. Trammell, R. Koller. 2017. Preliminary review of Bright Angel Creek trout control operations, 2012-2017. (Invited) Presented to the Glen Canyon Dam Adaptive Management Program, Brown Trout Workshop, September 21-22, 2017, Tempe, Arizona. https://www.usbr.gov/uc/rm/amp/amwg/mtgs/17sep20/BT08.pdf

Healy, B. 2017. Brown trout management considerations: an update. (Invited) Presentation to the Glen Canyon Dam Adaptive Management Program – Technical Work Group Meeting, January 26, 2017, Phoenix, Arizona. https://www.usbr.gov/uc/rm/amp/twg/mtgs/17jan26/A10_Healy.pdf

Healy, B., E. Omana Smith, C. Nelson, R. Koller, R. Schelly, M. Trammell, M. Crawford. 2017. Bright Angel Creek brown trout control and humpback chub translocations. (Invited) Presentation to the Glen Canyon Dam Adaptive Management Program – Technical Work Group, Annual Reporting Meeting, January 25, 2017, Phoenix, Arizona. https://www.usbr.gov/uc/rm/amp/twg/mtgs/17jan26/AR22_Healy.pdf

Anderson, M., M. Anderson, M. Trammell, **B. Healy**, and R. Succec. 2016. Colorado River slough, green sunfish removal. (Invited) Presentation to the Glen Canyon Dam Adaptive Management Program – Technical Work Group, January 28, 2016, Phoenix, Arizona. https://www.usbr.gov/uc/rm/amp/twg/mtgs/16jan26/documents/Attach_05b.pdf

Nelson, C., **B. Healy**, E. Omana Smith, R. Koller, D. Ward. 2016. Bright Angel Creek non-native trout reduction, Grand Canyon National Park. (Invited) Presentation to the Glen Canyon Dam Adaptive Management Program – Technical Work Group, Annual Reporting Meeting, January 26-27, 2016, Phoenix, Arizona. https://www.usbr.gov/uc/rm/amp/twg/mtgs/16jan26/documents/AR21_Nelson.pdf

Omana Smith, E., **B. Healy**, C. Nelson, M. Trammell. 2016. Humpback chub translocations to Havasu and Shinumo creeks, Grand Canyon National Park. (Invited) Presentation to the Glen Canyon Dam Adaptive Management Program – Technical Work Group, Annual Reporting Meeting, January 26-27, 2016, Phoenix, Arizona.

Healy, **B.**, C. Nelson, E. Omana Smith, S. Blackburn, D. Ward. 2015. Bright Angel Creek nonnative trout reduction, Grand Canyon NP. (Invited) Presentation to the Glen Canyon Dam Adaptive Management – Technical Work Group, Annual Reporting Meeting, January 20-21, 2015, Phoenix, Arizona. https://www.usbr.gov/uc/rm/amp/twg/mtgs/15jan20/Attach_09.pdf

Healy, B., E. Omana Smith, C. Nelson, M. Trammell, M. McKinstry, B. Albrecht, R. Kegerries. 2014. Native fish population trends: Grand Canyon tributaries, and razorback sucker status and habitat use. (Invited) Presentation to the Glen Canyon Dam Adaptive Management – Technical Work Group, Annual Reporting Meeting, January 30, 2014, Phoenix, Arizona. https://www.usbr.gov/uc/rm/amp/twg/mtgs/14jan30/AR_Healy_NF&RBS.pdf

Healy, B., E. Omana Smith, C. Nelson, M. Trammell, C. Paukert, J. Spurgeon, M. Crawford, D. Speas. 2014. NPS fisheries program updates: humpback chub translocations to Grand Canyon tributaries. (Invited) Presentation to the Glen Canyon Dam Adaptive Management – Technical Work Group, Annual Reporting Meeting, January 30, 2014, Phoenix, Arizona. https://www.usbr.gov/uc/rm/amp/twg/mtgs/14jan30/AR_Healy_HBC_Translocation.pdf

Healy, B., E. Omana Smith, C. Nelson, M. Trammell, D. Ward, M. Yard, D. Speas, M. Crawford. 2014. Nonnative fish control in tributaries: Grand Canyon National Park. (Invited) Presentation to the Glen Canyon Dam Adaptive Management Program – Technical Work Group, Annual Reporting Meeting, January 30, 2014, Phoenix, Arizona. https://www.usbr.gov/uc/rm/amp/twg/mtgs/14jan30/AR_Healy_NNFC_GRCA.pdf

Poster Presentations

Healy, B., E. Omana Smith, R. Schelly, M. Trammell, R. Koller, and M. Crawford. 2018. Establishment of a reproducing population of Humpback Chub through translocations to Havasu Creek, Grand Canyon (poster). 51st Joint Annual Meeting of the Arizona and New Mexico Chapters of the Wildlife Society and American Fisheries Society, February 1-3, 2018, Flagstaff, Arizona.

M. Daubert, T. Kennedy, J. Muehlbauer, **B. Healy**. 2017. Aquatic invertebrate response to trout removal in Bright Angel Creek, Grand Canyon, Arizona (poster). Annual Meeting, Society for Freshwater Science, June 4-8, 2017, Raleigh, North Carolina.

Spurgeon, J., D. Whiting, C. Paukert, **B. Healy**, and C. Kelley. 2011. Trophic structure of fish communities in Grand Canyon National Park tributary streams (poster). 141st Annual American Fisheries Society Meeting, September 1-9, 2011, Seattle, Washington.

Spurgeon, J., C. Paukert, J. Whittier, and **B. Healy**. 2011. Translocation success of humpback chub into Shinumo Creek: implications for future management actions (poster). Arizona/New Mexico American Fisheries Society Meeting, February, 2011, Pinetop, Arizona.

Spurgeon, J., C. Paukert, J. Whittier, and **B. Healy**. 2010. Translocation success of humpback chub: implications for future management actions (poster). 71st Midwest Fish and Wildlife Conference, December, 2010, St. Paul, Minnesota.

Outreach Publications

Healy, B. D. 2022. Too much of a good thing? Climate warming and water overallocation may lead to new warmwater fish invasions that threaten the viability of Grand Canyon's native fishes. Canyon Views, a publication of the Grand Canyon Conservancy. In press. Spring, 2022.

Schelly, R., E. Omana Smith, R. Koller, and **B. Healy.** 2021. Might endangered Colorado pikeminnow be reintroduced to Grand Canyon? Boatman's Quarterly Review, the journal of the Grand Canyon River Guides, Inc., Vol. 34, No. 2/Summer, 2020, pages 10-11.

Healy, B., and P. Budy. 2019. Assisting Grand Canyon National Park with conservation actions for Colorado River endemic fishes. Research Brief, Utah, USGS Coop Catch-up, Newsletter for the U.S. Geological Survey Fish and Wildlife Cooperative Research Unit Program. March 2019, Issue 8.

Healy, B., R. Schelly, E. Omana Smith, R. Koller. 2018. Important milestones reached for native fish conservation in Grand Canyon. Boatman's Quarterly Review, the journal of the Grand Canyon River Guides, Inc., Vol. 31, No. 3/Fall, 2018, pages 20-21.

Trammell, M., and **B. Healy**. 2017. Grand Canyon has a robust population of humpback chub. Swimming Upstream. A publication of the Upper Colorado River Endangered Fish Recovery Program and the San Juan River Basin Recovery Implementation Program. Pages 4- 5, Field Report 2017. Lakewood, Colorado, and Albuquerque, New Mexico.

Healy, **B.**, and C. Nelson. 2013. Humpback chub translocations – an update, by the numbers. Boatman's Quarterly Review, the journal of the Grand Canyon River Guides, Inc. Summer, 2013, page 10.

Omana Smith, E., S. Ernenwein, **B. Healy**, and A. Mathis. 2012. Restoring humpback chub in Grand Canyon National Park. The Grand Canyon River Runner, Number 13 (Winter, 2012): pages 8-10. Grand Canyon River Runners Association, Sedona, Arizona.

Omana Smith, E., **B. Healy**, and A. Mathis. 2012. 2012 humpback chub translocation update. Boatman's Quarterly Review, the journal of the Grand Canyon River Guides, Inc., Vol. 25, No. 2/Summer 2012, pages 26-27.

Mathis, A., L. Makarick, **B. Healy**. 2012. Controlling invasive species along the Colorado River in Grand Canyon National Park. River Management Society Journal 25(2): 4-5, 15.

Mathis, A., and **B. Healy**. 2010. Conserving Grand Canyon's endangered humpback chub. Canyon Views, a publication of the Grand Canyon Association, Volume XVI, No. 2/Summer 2010, pages 2-3.

Mathis, A., and **B. Healy**. 2010. Flying fish continued – additional humpback chub to be translocated to Shinumo Creek. Boatman's Quarterly Review, the journal of the Grand Canyon River Guides, Inc., Volume 23, No. 1/Spring 2010, pages 10-12.

Testimony
2016 - Invited testimony before the U. S. House of Representatives, Full House Committee on Oversight and Government Reform. Examining Misconduct and Mismanagement at the National Park Service. September 22, 2016, Washington, D. C.
https://oversight.house.gov/hearing/examining-misconduct-mismanagement-national-park-service/

2008 – Responsive pre-hearing statement of the USDA Forest Service – White River National Forest, Eagle-Holy Cross Ranger District, Compiled by Brian D. Healy. Testimony to the

Colorado Water Control Commission. In the matter of proposed revisions to the water quality standards and temporary modifications for segments 5 and 7 of the Eagle River, in the classifications and numeric standards for the Upper Colorado River Basin and the North Platte River (Planning Region 12), Regulation #33 (5 CCR 1002-33).

Selected Technical Training & Activities

Introduction to Structural Equation Modeling – May 6-8, 2020, Curran-Bauer Analytics, online webinar.

Introduction to Computer Programming with R (FOR 6934) – Spring, 2018 semester, University of Florida, online course – 1 graduate credit.

Intermediate Program MARK Workshop – June 5-10, 2011, Colorado State University, Fort Collins, Colorado.

Principles of Modeling for Conservation Planning and Analysis – May 23-27, 2011. U. S. Fish and Wildlife Service, National Conservation Training Center, held in Flagstaff, Arizona.

Humpback Chub Population Viability Modeling Workshop – August, 2011 **-** Co-developed and hosted a workshop with Dr. Bill Pine, University of Florida, to develop a population viability model with an interagency panel of fisheries biologists for the purpose of assessing varying levels of "cropping" juvenile Humpback Chub and assessing stocking levels needed for successful translocations.

Colorado Aquatic Macroinvertebrate Multimetrix Index Development Workshop – September, 2008, Colorado Water Quality Control Division. Invited expert to contribute toward development of statewide metric for aquatic biomonitoring.

Freshwater Biomonitoring Using Macroinvertebrates – May 17- 21, 2004, US Fish and Wildlife Service National Conservation Training Center.

Applied Fluvial Geomorphology – January, 2003, Wildland Hydrology, Monterey, California.

Forest Hydrology Workshop – June 11, 2002, Cloquet Forestry Center, University of Minnesota, College Of Natural Resources, Cloquet, Minnesota.

Principles of Electro-fishing Training – March, 2001, Minnesota Department of Natural Resources, Hutchinson, Minnesota.

Geographical Information Systems for Aquatic Professionals I and II – May 22-23, 1999, North American Benthological Society Workshop, 47th Annual Meeting, Duluth, Minnesota.

Peer-reviews:
- Journal of the American Water Resources Association
- U.S. Geological Survey – internal reviewer
- North American Journal of Fisheries Management
- Canadian Journal of Fisheries and Aquatic Sciences
- National Park Service- invited peer reviewer for Devils Hole pupfish strategic plan, phase 1 and 2 – January, 2020
- Fisheries – monthly magazine of the American Fisheries Society

- River Research and Applications
- Ecology of Freshwater Fish
- U. S. Fish and Wildlife Service - Invited peer reviewer for the Humpback Chub Species Status Assessment – Summer 2017
- Hydrobiologia
- American Midland Naturalist
- Journal of the North American Benthological Society

Professional Society Activities and Memberships:
- **Ecological Society of America** – member since 2018
- **American Fisheries Society –** member since 1998
- **Utah Chapter of the American Fisheries Society** – member since 2018
- **Arizona/New Mexico Chapter of the American Fisheries Society** - member since 2009
- **Minnesota Chapter of the American Fisheries Society** – Membership Committee Chair, 2001; Federal Executive Committee representative, 2002
- **Texas A&M Chapter of the American Fisheries Society** – Vice-President, 1999-2000