Canadian Science Publishing | Canadian Journal of Fisheries and Aquatic Sciences

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Journal:	*Canadian Journal of Fisheries and Aquatic Sciences*
Manuscript ID	cjfas-2020-0028.R1
Manuscript Type:	Article
Date Submitted by the Author:	29-Apr-2020
Complete List of Authors:	Healy, Brian; Utah State University, Watershed Sciences and the Ecology Center; National Park Service, Grand Canyon National Park Schelly, Robert; National Park Service, Grand Canyon National Park Yackulic, Charles; USGS, Grand Canyon Monitoring and Research Center Omana Smith, Emily; National Park Service, Grand Canyon National Park Budy, Phaedra; USGS Utah Cooperative Fish and Wildlife Research Unit,
Keyword:	INVASIVE SPECIES < Organisms, FISHERY MANAGEMENT < General, HYDROLOGY < General, CONSERVATION < General, STREAMS < Environment/Habitat
Is the invited manuscript for consideration in a Special Issue? :	Not applicable (regular submission)

Remarkable response of native fishes to invasive trout suppression varies with trout density, temperature, and annual hydrology

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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.

Keywords: Invasive species, fishery management, hydrology, conservation, streams

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 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 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·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; 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). 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.

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 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 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 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 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 ($\hat{N}$) 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 $\lambda < 1.0$ indicates a population in decline, $\lambda > 1.0$ indicates an increasing population, and $\lambda = 1.0$ 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). 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) $$P(C_{i,j} = 0) = (1 - \pi_{i,j}) + \pi_{i,j} * NB(0|y_{i,j},\kappa)$$

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

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) $$logit(\pi_{i,j}) = \beta_0 + \boldsymbol{\beta Z_{ij}} + \xi_{\boldsymbol{k[i],j}}\boldsymbol{z_{ij}} + \theta_{\boldsymbol{k[i],j}}$$

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

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, **Z** and **X** are arrays with dimensions given by the number of covariates, the number of stations and the numbers of years, **z** and **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 jth year, and $\theta_{\boldsymbol{k[i],j}}$ and $\eta_{k[i],j}$

are random effects for the k^{th} 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). 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) 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 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.

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 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 (≥ 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 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 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 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 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 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 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 5). Native fish counts were highest with greater spring flooding in 2017, relative to the other years (PC1, Figure 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 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., Δ13.9 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.

Acknowledgements

Funding for this project was provided by the U. S. Bureau of Reclamation, National Park Service, Utah State University- Center for Colorado River Studies, Grand Canyon Conservancy, Arthur L. and Elaine V. Johnson Foundation, U.S. Geological Survey – Utah Cooperative Fish and Wildlife Research Unit and Grand Canyon Monitoring and Research Center (In-kind), and the Albright-Wirth Grant Program administered by the National Park Foundation and the NPS Learning and Development Program. T. Walsworth and J. Gaeta provided analytical assistance, T. Walsworth provided critical reviews of early drafts, and M. Nebel developed maps in Figure 1. M. Trammell, N. Medley, D. Speas, M. Yard, J.

Wullschleger, and M. Crawford provided input and guidance during the development of the project. C. Nelson coordinated, trained, and led crews in the field and provided key technical assistance during project development, and R. Koller provided key logistical support and crew training, and along with S. Garcia, provided invaluable expertise and attention to detail in managing the data and ensuring quality control. The NPS-GRCA Aviation staff and C. Brothers and staff provided key logistical support. D. Yurcik, A. Sherman, and L. Hendy, among others, provided security. The project could not have been completed without the support of numerous volunteers and technicians including, but not limited to D. Shein, A. Martin, S. Wood, A. Bachelier, Z. Ahrens, R. McGrew, R. Jurgen, J. Duff-Woodruff, B. Leibfried, K. Perterlein-Rogers, E. Frye, M. Frye, M. MacGregor, T. Melis, N. Alvord, K. Evans, A. Guenther, C. Veety, S. Till, D. Fay, D. O'Connel, E. Ludkey, J. Bailey, J. Miller, J. Gavlak, J. Richardson, J. Minott, K. Landry, K. Shollenberger, L. Duhamell, L. Smith, L. Gelczis, L. Kearsley, L. Vrogope, M. Severson, M. Webster, C. Kearney, M. Talbert, S. Healy, M. Aakland, M. Berg, M. Lancioni, M. Partlow, M. Kawski, N. Brodie, N. Salinas, N. Klein, P. Lunney, R. Ianniello, R. Allison, R. Manuel, S. Yates, S. Dowlatshahi, S. Northrup, T. Schreiner, W. Chang. S. Haas and J. Balsom provided key support that permitted this paper to be completed. The authors thank M. McKinstry, J. Schmidt, and M. Conner, and two anonymous reviewers of the manuscript for their constructive criticism which improved the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This study was performed under the auspices of the USU IACUC protocol number 10170, National Park Service Scientific Research and Collection Permit #GRCA-2018-SCI-0049, U.S. Fish and Wildlife Service ESA Section 10 permit #TE819473-1, and an MOA between the Arizona State Historic Preservation Office, consistent with Section 106 of the National Historic Preservation Act.

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Table 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. 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 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.

		Conditional model - coefficients (SE)						Zero-inflation model – coefficients (SE)				
Model rank	Conditional Model	α_1	α_2	α_3	α_4	α_5	Zero-inflation model	β_1	β_2	β_3	df	ΔBIC
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												
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												
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 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).

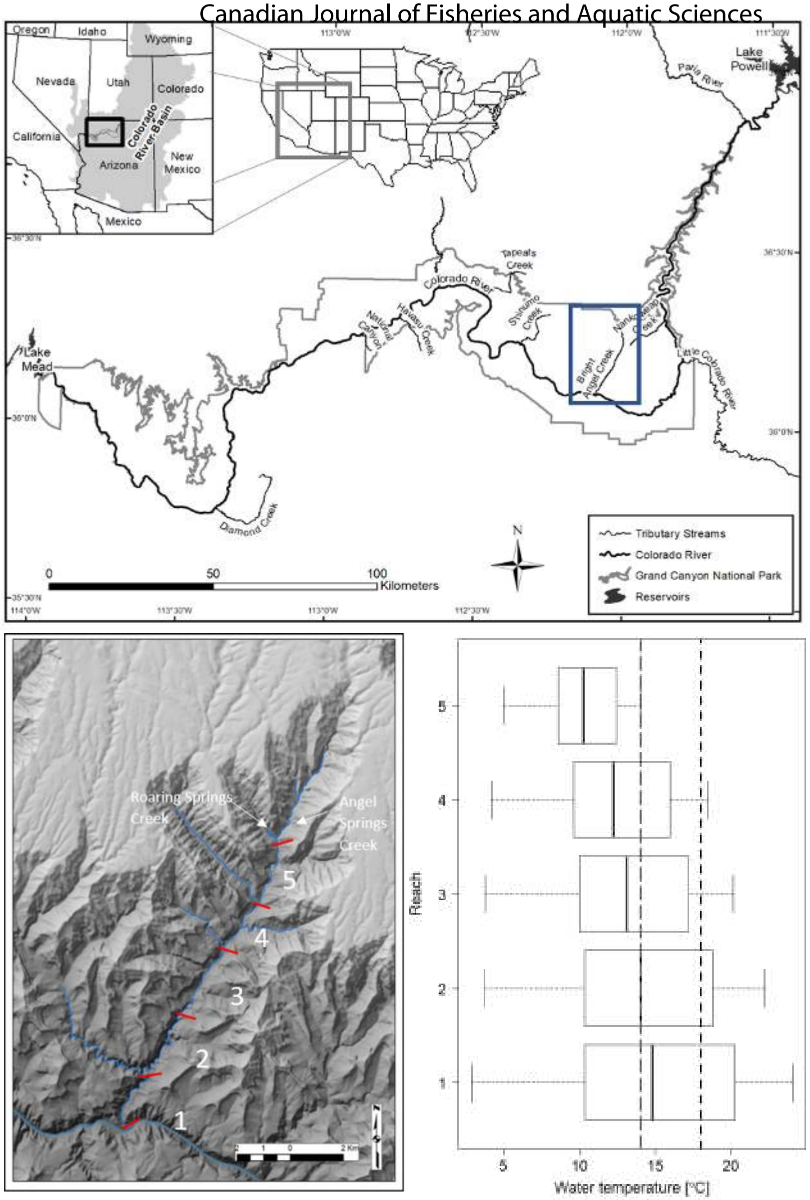
Figure 2. Maximum daily discharge ($m^3 \cdot s^{-1}$) of Bright Angel Creek, Grand Canyon, Arizona, measured near the mouth (USGS gaging station 09403000). Each water year is represented by a colored line, by day along the x-axis from October 1 through September 30. The extent of the y-axis is truncated to enable comparisons of typical water years, while the extreme hydrologic event in 2011 not pictured exceeded 75 ($m^3 \cdot s\text{-}^1$). 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 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.

Figure 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 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.


Oregon
Idaho
Wyoming
Nevada
Utah
Colorado
California
Colorado River Basin
Arizona
New Mexico
Mexico
113°0'W
112°30'W
112°0'W
111°30'W
Lake Powell
Paria River
36°30'N
36°0'N
35°30'N
Tapeats Creek
Colorado River
Shinumo Creek
Nankoweap Creek
National Canyon
Havasu Creek
Bright Angel Creek
Little Colorado River
Lake Mead
Diamond Creek
N
0
50
100
Kilometers
Tributary Streams
Colorado River
Grand Canyon National Park
Reservoirs
114°0'W
113°30'W
113°0'W
112°30'W
Roaring Springs Creek
Angel Springs Creek
5
4
3
2
1
2
1
0
2 Km
Reach
5
4
3
2
1
5
10
15
20
Water temperature [°C]

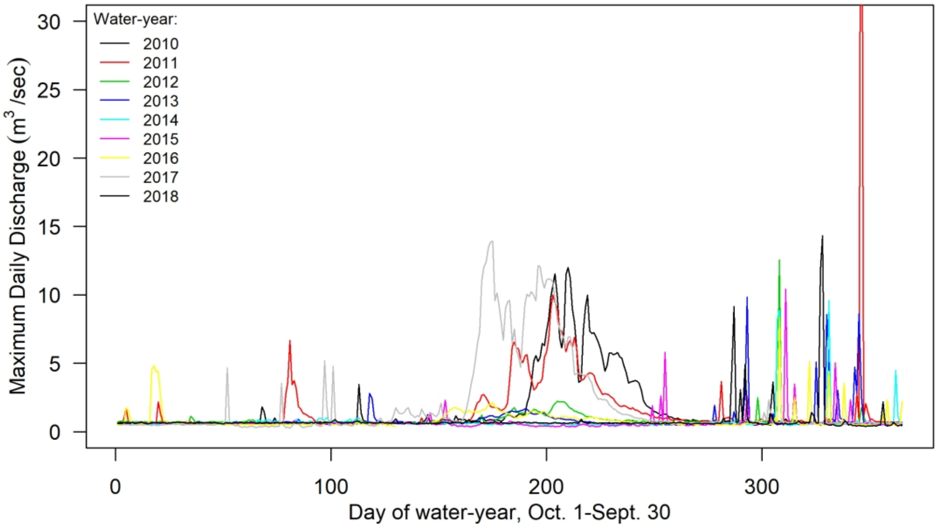


Figure 2. Maximum daily discharge (m3·s-1) of Bright Angel Creek, Grand Canyon, Arizona, measured near the mouth (USGS gaging station 09403000). Each water year is represented by a colored line, by day along the x-axis from October 1 through September 30. The extent of the y-axis is truncated to enable 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.

199x113mm (300 x 300 DPI)

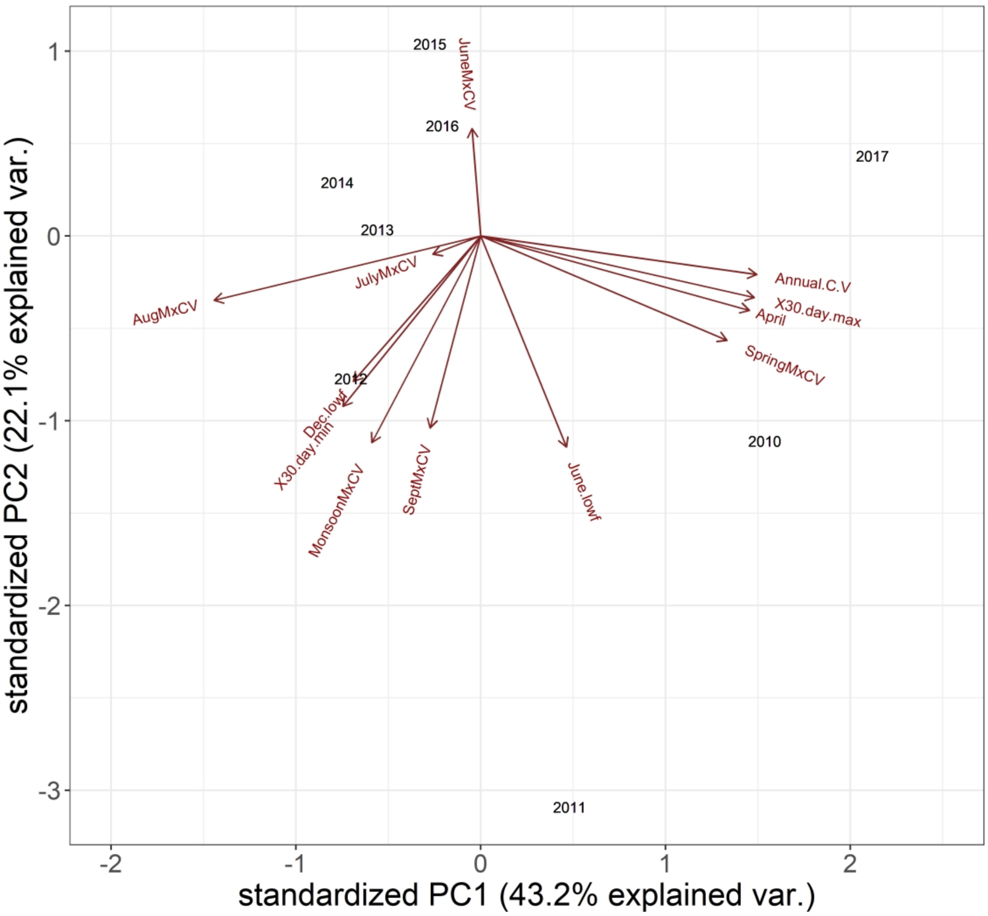


Figure 3. Principle component analysis results (PC1, PC2) for annual hydrologic variables, derived from maximum daily discharge data measured in Bright Angel Creek near Phantom Ranch (USGS gaging station 09403000, U.S. Geological Survey 2018), from water year 2010 through 2017. Loadings for individual years are displayed. Variable labels are listed in Table 2.

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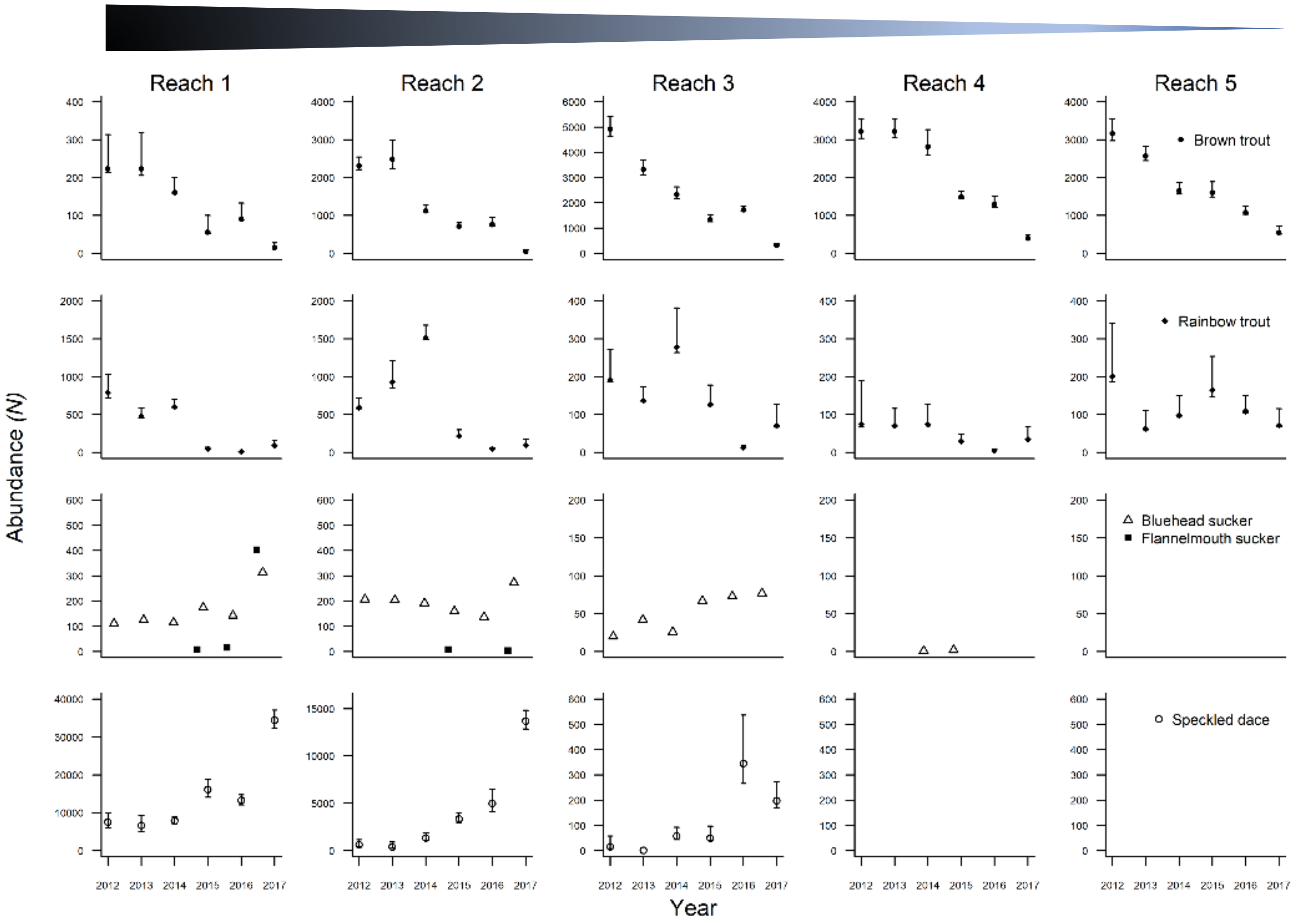
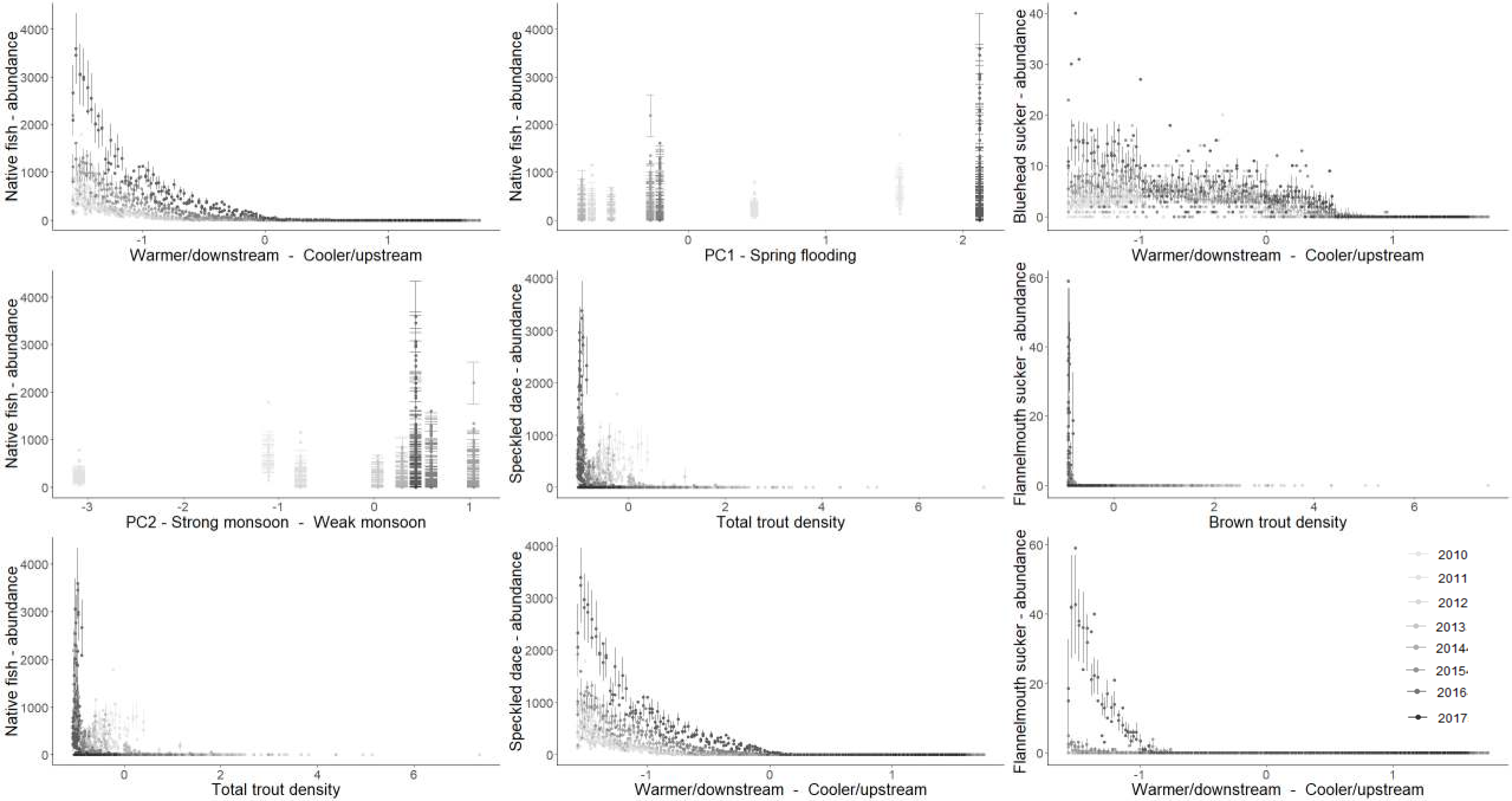

Reach 1
Reach 2
Reach 3
Reach 4
Reach 5
Brown trout
Rainbow trout
Bluehead sucker
Flannelmouth sucker
Speckled dace
Abundance (N)
Year
2012
2013
2014
2015
2016
2017
0
100
200
300
400
500
600
1000
1500
2000
3000
4000
5000
6000
10000
15000
20000
30000
40000
50
150


Native fish - abundance
Warmer/downstream - Cooler/upstream
PC1 - Spring flooding
Bluehead sucker - abundance
PC2 - Strong monsoon - Weak monsoon
Speckled dace - abundance
Total trout density
Flannelmouth sucker - abundance
Brown trout density
2010
2011
2012
2013
2014
2015
2016
2017