ORIGINAL PAPER

Climatic drivers and ecological impacts of a rapid range expansion by non-native smallmouth bass

Mark A. Kirk · Bryan M. Maitland · Brian T. Hickerson · Annika W. Walters · Frank J. Rahel

Abstract Smallmouth bass (*Micropterus dolomieu*) are a globally introduced fish species that have experienced widespread range expansions in recent decades and which can have deleterious effects on native fish communities. Rapidly assessing their expansions will aid conservation and management actions geared towards controlling their spread and mitigating their impacts. Smallmouth bass have recently experienced a rapid upstream expansion in a Great Plains river (Laramie River, Wyoming, USA), which provided an opportunity to evaluate the drivers and impacts of this expansion by using a modified before-after, control-impact (BACI) design. Our objectives were to test whether climatic drivers (temperature, precipitation, flow) were related to this range expansion and subsequent effects of the expansion on native fish communities. Smallmouth bass population size in Grayrocks Reservoir increased following a climatically extreme wet year, with statistically extreme amounts of spring-time and June precipitation creating high discharge events that coincided with the upstream expansion. Unlike previous studies highlighting the invasive nature of smallmouth bass, the modified BACI analysis revealed no declines in species richness induced by the expansion. However, there was evidence that native small-bodied minnow species (family *Leuciscidae*) declined in relative abundance and that community-level and species-level trophic niches were compressed for invaded sites. Our findings provide important insight into how climatic extremes can prompt biological invasions that can alter community composition and food web structure even if local extirpations do not occur.

Keywords BACI · Black bass · Climate change · Invasive fish · Isotopic niches

M. A. Kirk (✉) · B. M. Maitland ·
A. W. Walters · F. J. Rahel
Department of Zoology and Physiology, Program in Ecology, University of Wyoming, Laramie, WY 82072, USA
e-mail: kirkma18@gmail.com

B. T. Hickerson
Arizona Game and Fish Department, 5000 W Carefree Highway, Phoenix, AZ 85086, USA

A. W. Walters
U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82072, USA

Introduction

Freshwater systems are arguably the most invaded ecosystems on the planet due to widespread, human-assisted dispersal of species for economic purposes (e.g., aquaculture and recreational fisheries; Gozlan et al. 2010). The establishment and spread of aquatic, non-native species have been further facilitated by anthropogenic impacts, such as flow alterations, land use change, and climate change (Craig et al. 2017). For example, the impoundment of rivers through reservoir construction often benefits the life-history strategies of non-native species in these flow-altered environments (Gido et al. 2009, 2013), and climate warming will likely prompt future range expansions out of reservoirs (Kirk et al. 2020; Sun et al. 2020). Climatic extremes have been hypothesized to explain rapid and unpredicted biological invasions (Winder et al. 2011; Diez et al. 2012). Thus, the effects of continued anthropogenic change may act synergistically with the spread of non-native species to drive future changes in native freshwater diversity (e.g., Kuczynski et al. 2018).

Invasive, piscivorous fish are one group that appear to have this synergistic effect on freshwater diversity. Due to their large body size and predatory nature, invasive piscivores represent a "novel selective force" that can alter community structure and food web dynamics (Mitchell and Knouft 2009; Cucherousset and Olden 2011). Invasive piscivores displace native predators from high trophic positions (Vander Zanden et al. 2004), compress trophic niche space of native communities (Rogosch and Olden 2020), and reduce diversity of small-bodied species through consumptive and non-consumptive effects (Jackson and Mandrak 2000). One group of invasive fish in particular, black bass (*Micropterus spp.*), are considered among the world's most successful invasive species because of their strong antagonistic interactions with native species (Lowe et al. 2000; Loppnow et al. 2013; Pereira and Vitule 2019). Black bass have some of the fastest expansion rates from climate change (Comte et al. 2013). Hydropower development is also predicted to facilitate the spread of black bass species (Bae et al. 2018). Smallmouth bass (*Micropterus dolomieu*), in particular, appear poised to benefit from future flow alterations and climate warming, as evident by the increasing numbers of case studies on range expansions for this species (Alofs et al. 2014;

Lawrence et al. 2015; Van der Walt et al. 2016; Rubenson and Olden 2017; Peterson et al. 2020).

Although detecting the drivers and impacts of emerging black bass invasions is critical for developing management actions (e.g., Vander Zanden et al. 2004; Van der Walt 2016), identifying appropriate management responses can be difficult because many biological invasions are unanticipated (Ricciardi et al. 2011). Species traits provide one promising outlet for predicting invasions, and *Micropterus spp.* possess many of the traits (equilibrium life history, high temperature tolerance, high trophic position) associated with highly invasive fish species (Marchetti et al. 2004; Buckwalter et al. 2020). Biological invasions via range expansion involve an interaction between species traits and environmental change, the latter of which is far more unpredictable (e.g., climatic extremes; Smith 2011; Diez et al. 2012). While a mechanistic understanding of how environmental factors determine range limits can help anticipate gradual range expansions (Lawrence et al. 2015; Rubenson and Olden 2017), case studies on abrupt, rapid invasions are less common and more concerning.

A recent upstream expansion of non-native smallmouth bass in a Great Plains river of the central USA provided an opportunity to explore the impacts and drivers of an abrupt and rapid invasion. Smallmouth bass expanded 83 river kilometers upstream (269.5 m elevation gain) between 2008 and 2016, which coincided with an increase in the population size of smallmouth bass in a local reservoir in 2011 (Grayrocks Reservoir; Fig. 1, Fig. S1). Smallmouth bass now interact with a relatively naïve Great Plains fish assemblage that did not historically interact with large-bodied piscivores (Hickerson et al. 2019). Great Plains fish assemblages have experienced high degrees of biotic homogenization and a decline of endemic, plains-specialist species (Quist et al. 2004; Perkin et al. 2015; Kirk et al. 2020). Non-native species have been identified as a primary driver of those biological changes due to the magnitude of introductions and the high degree of flow and landscape alteration in plains rivers (Gido et al. 2006; Falke and Gido 2006; Stewart et al. 2016). Managing non-native species is thus a priority for conserving Great Plains fishes.

Using a combination of climate data, reservoir sampling data, and stream fish community data, our study addressed three objectives. Our first objective was to identify the potential climatic drivers
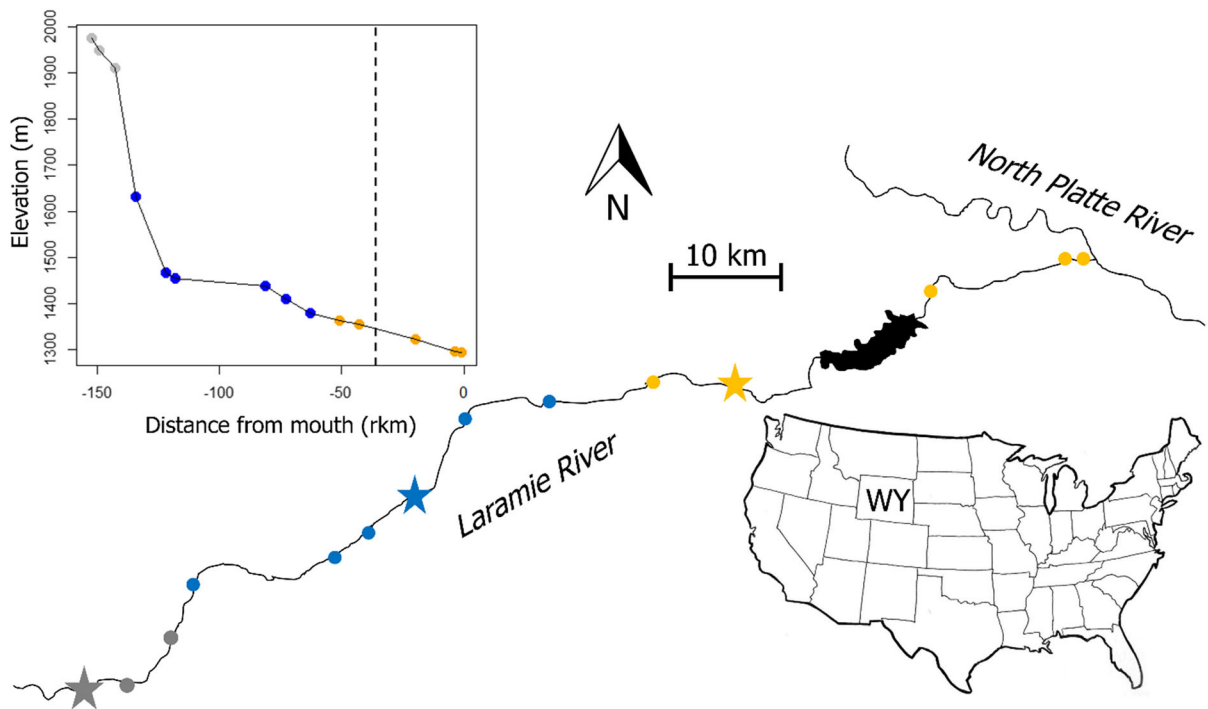
Fig. 1 Map of the Laramie River in southeastern Wyoming (WY, lower-right inset) and distribution of the 14 distinct sampling sites surveyed multiple times before and after the smallmouth bass expansion. Gold symbols represent sites with smallmouth bass present before and after the expansion (BI, AI-P), blue indicates newly invaded sites (BC, AI-N), and gray indicates sites that have not been invaded (BC, AC; see Fig. S2). Stars indicate collection sites for isotopic niche data. Upper-left inset shows the relationship between elevation and river kilometer (rkm) for the distinct sampling sites. Dashed black line indicates Grayrocks Reservoir and steepness of the line is indicative of stream gradient (e.g., channel steepness)

responsible for the rapid, upstream expansion of smallmouth bass. The second objective was to perform a modified before-after, control-impact (BACI) analysis on stream fish surveys performed pre- and post-expansion of smallmouth bass to determine if any community-level changes occurred. We hypothesized that community diversity metrics (richness and evenness) would decline and community structure would be altered following the smallmouth bass expansion. Our third objective was to use isotopic niche data to infer whether the presence of smallmouth bass induced community-level and species-level changes to trophic niche space. We hypothesized that the presence of smallmouth bass would reduce the trophic position of native species and compress trophic niche space (e.g., Rogosch and Olden 2020). Finally, we predicted that these community-level changes would be driven by declines in small-bodied minnow species (family *Leuciscidae*), which are highly susceptible to invasive piscivores (Alofs and Jackson 2015; Van der Walt et al. 2016; Kirk et al. 2017).

Methods

Study system

Our study encompassed a 152 km section of the Laramie River (elevation range: 1286–1977 m), which is a tributary of the North Platte River in southeastern Wyoming (Fig. 1). Smallmouth bass are non-native to Wyoming, and the construction of Grayrocks Reservoir (42.145°,–104.737°) in 1980 led to the introduction of smallmouth bass and other non-native gamefish species in the early 1980s. Grayrocks is a storage reservoir that provides cooling water for a coal-powered electrical facility, and no fish passage systems are present to connect fish populations upstream and downstream of the reservoir. Despite the lower Laramie River experiencing intensive water development for irrigation, agriculture and energy, the river has maintained an intact fish assemblage and only a few native species declines have

occurred since reservoir construction (Patton and Hubert 1996; Quist et al. 2005; Kirk et al. 2020).

Our study section is composed of two distinct stream geomorphologies, which we define as upstream and downstream sections. Downstream sites have low channel slopes (mean: 0.003 km elevation gain per km) with predominately warm-water fish assemblages and reservoir species occurring within 100 river kilometers (rkm) of the Laramie River's mouth (Fig. 1). Downstream sites within 50 rkms of the mouth have been historically occupied by smallmouth bass since reservoir construction (Quist et al. 2005). Upstream sites have high channel slopes (mean: 0.011 km/km) with large substrate types in the Laramie canyon dominated by more riverine, cool-water fish assemblages, which have only recently been invaded by smallmouth bass (Hickerson et al. 2019).

Objective 1: climatic drivers

We tested whether statistically extreme climatic conditions coincided with the 2011 peak of small-mouth bass abundance in Grayrocks Reservoir using long-term precipitation, temperature, and discharge data. Importantly, we used the relative abundance of smallmouth bass in Grayrocks Reservoir as the response variable for determining what climatic conditions elicited the upstream expansion (i.e., we assumed the increase in relative abundance was a proxy for expansion because the two events closely coincided with each other [see Fig. S1; Gale 2015; Hickerson et al. 2019; Wyoming Game and Fish Department 2011]). While we cannot pinpoint the specific year of the expansion, we know that the expansion occurred between 2010 and 2013. Intensive sampling on the Laramie River in 2014 documented smallmouth bass in a 55 km stretch of river that did not have them present in 2009.

We obtained daily estimates of precipitation (mm/day), maximum daily air temperature (°C), and minimum daily air temperature (°C) for Grayrocks Reservoir from 1980 to 2019 using the daily surface weather and climatological summaries database (DAYMET; Thornton et al. 2007). DAYMET provides daily climatic estimates for 1 km by 1 km gridded cells. Daily discharge data were downloaded for a U.S. Geological Survey stream gauge on the Laramie River from 1956 to 2019 (site number 06670500; U.S. Geological Survey [USGS], 2020),

which is located $\sim$ 23 rkm downstream of Grayrocks Reservoir. State agency data on discharge records from two locations in closer proximity to the reservoir, but with shorter time-series, revealed high correlation among the USGS stream gauge, a reservoir inflow gauge, and a reservoir outflow gauge (daily discharge correlations from 1985 to 2018; all $r > 0.92$). Because data on reservoir levels and storage capacity was not available for Grayrocks Reservoir, discharge was considered as a proxy for reservoir levels (e.g., high discharge corresponds to periods of high reservoir levels).

We averaged daily values of temperature, precipitation, and discharge into different time periods, which included annual, spring-time (defined as March 21–June 20), summer-time (June 21–September 20), and by month. We considered a time period as being a statistically extreme climatic event for precipitation (extreme wet versus dry) and temperature (extreme hot versus cold) if a value was two standard deviations greater than the mean value of the entire 1980–2019 period (sensu Boucek and Rehage 2014). We considered a time period as being a statistically extreme event for discharge (extreme high flow versus low flow) if a value was two standard deviations greater than the mean value of the reference period before the completion of Grayrocks Reservoir in 1980 (1956–1979).

We then individually regressed each annual, seasonal, and monthly climate variable against the annual relative abundance of smallmouth bass in Grayrocks Reservoir. The Wyoming Game and Fish Department conducts annual trend-netting surveys on reservoirs using experimental sinking gillnet sets composed of a standard mesh array to determine population status of gamefish species. While sampling was performed at similar locations across years, the number and duration of sets varied. Annual smallmouth bass relative abundance was thus standardized to catch per unit effort (CPUE) as the number of fish per gillnet per hour. Exploratory analyses revealed no linear trends between smallmouth bass CPUE and climate variables due to the non-linear nature of the CPUE data. We thus used exponential, non-linear regression models (package nlsLM; R version 3.4.2, R Development Core Team, 2017) to determine which climatic variables explained the sharp increase in smallmouth bass CPUE. We only tested univariate models with single predictors for current year climatic conditions (t), as

well as univariate models with lag effects for previous year climatic conditions (t—1) and two-year previous climatic conditions (t—2). We used Akaike information criteria (AIC) to determine the best climatic variables for explaining the 2011 increase in smallmouth bass CPUE from all candidate models ($n = 135$ total univariate models). We considered the best models to be those with ΔAIC values < 2 of the top model, with model weights (w_i) > 0.1, and those deemed significant ($P < 0.05$).

Objective 2: community effects

Stream fish community survey data were used in a modified BACI framework to determine if community composition changed after the smallmouth bass expansion (sensu Bellow et al. 2016; Christie et al. 2019). Fish community data were collated from numerous surveys performed by the Wyoming Game and Fish Department, Colorado State University, and the University of Wyoming. All sampling was performed with electrofishing methods and conducted during summer, low flow conditions. We attempted to correct for different sampling effort (e.g., pass number and reach length) across sources by standardizing relative abundance data to only first pass estimates when surveys were multi-pass and to an estimate of individuals per 100 m. We also required sampling events to have total fish captures > 50 individuals to accurately estimate proportional relative abundance (e.g., Kirk et al. 2017). Sampling events were aggregated into one km river segments (i.e., distinct sampling sites), and distinct sampling sites needed to be sampled at least once before (2002–2010) and after (2013–2019) the smallmouth bass expansion for inclusion. In total, 14 distinct sampling sites had 84 sampling events before (45) and after (39) the expansion.

Our modified BACI study design closely resembled a three × two factorial design with impacted (I) and non-impacted (C) sites being sampled before (B) and after (A) the invasion (sensu Christie et al. 2019; see Fig. S2), but instead consisted of five period by invasion categories: sampling events in the first period with smallmouth bass present (before-impacted [BI]; $n = 9$), events in the first period without smallmouth bass (before-control [BC]; $n = 36$), events in the second period where smallmouth bass were previously present (after-previously impacted [AI-P]; $n = 12$),

events in the second period where smallmouth bass newly invaded (i.e., smallmouth bass were absent in the first period; after-newly impacted [AI-N]; $n = 19$), and events in the second period where smallmouth bass have still not invaded (after-control [AC]; $n = 8$). Our modified BACI design was required because control and impacted sites differed profoundly in environmental characteristics that needed to be controlled for (e.g., rkm and stream geomorphology). High variance inflation factors (VIFs) were observed in exploratory models with traditional BACI treatment categories that prevented the inclusion of those confounding environmental co-variates (range of high VIFs: 5.0–7.2; Zuur et al. 2010).

We evaluated the impacts of smallmouth bass in the modified BACI study design using both multivariate and univariate descriptors of stream fish community composition (sensu Kirk et al. 2017). Multivariate analyses included non-metric multidimensional scaling (NMDS based on a Bray–Curtis dissimilarity matrix; metaMDS function; R v. 3.4.2) for characterizing the degree of dissimilarity in community composition among stream sampling events before and after the smallmouth bass expansion. NMDS was performed on transformed proportional relative abundance data ($\log[x + 1]$), which allowed for the visualization of both sampling events and fish species in ordination space. Species that occurred in less than five sampling events were excluded to reduce the influence that rare species have on multivariate approaches (4 of 34 species were excluded; see Table S1 for all 30 species). Stress plots indicated the first two NMDS axes were important for explaining community composition differences.

We also performed an indicator species analysis (multipatt function; R v. 3.4.2) to determine if the identity of species most likely to be associated with newly invaded sites differed between the pre-expansion and post-expansion period. The indicator value is calculated as the product of a species relative frequency and relative average abundance within time periods. We performed the analysis for only the six distinct sampling sites (consisting of 14 sampling events pre-expansion and 19 post-expansion) that were newly invaded by smallmouth bass during our study period (AI-N sites; blue symbols; Fig. 1). Species significance for a specific time period was assessed with a permutation procedure ($n = 5,000$; $P < 0.05$). The presumption is that species associated

with only the pre-expansion period are susceptible to smallmouth bass, whereas species associated with the post-expansion period are unaffected by smallmouth bass.

We calculated five univariate diversity metrics for each community survey: 1) total species richness, 2) native minnow richness (*Leuciscidae*; small-bodied minnows), 3) the Shannon diversity index for evenness, 4) the Simpson diversity index for evenness, and 5) the proportion of all individuals as minnow species based on relative abundance data. *Leuciscidae* was the only taxonomic family considered for independent analysis because it was the only family to have modestly high species richness ($\geq$ five species). Smallmouth bass were removed a priori from all multivariate and univariate calculations of community structure and diversity.

Our modified BACI framework was analogous to an analysis of covariance (ANCOVA), repeated measures design. We used generalized linear mixed-effects models (glmer function; R v. 3.4.2) to determine whether assemblage structure (quantified by scores along the two NMDS axes) and the five univariate community metrics changed following the smallmouth bass expansion. We used a mixed-effects model for NMDS data instead of traditional multivariate analyses (e.g., PERMANOVA) because of the need to account for the pseudoreplication of repeat sampling events at distinct survey sites within and between time periods as a random effect (i.e., repeated measures design). In addition to our modified BACI treatment variable (five treatment categories), the fixed-effects covariates in the ANCOVA were river kilometer and smallmouth bass abundance. River kilometer (rkm) tested for assemblage differences along the upstream–downstream gradient resulting from stream geomorphological differences among sites. Smallmouth bass abundance was included to test if biotic changes were driven by the abundance rather than simply the presence of this non-native species (e.g., Chick et al. 2020). Smallmouth bass abundance was standardized to the number per 100 m in the first sampling pass. Distinct sampling site ($n = 14$, Fig. 1) was included as a random intercept term to control for pseudoreplication in site-specific effects.

Mixed-effects models for richness metrics were fit with a Poisson distribution due to the non-normal distribution of count data, whereas evenness metrics,

proportional relative abundance of minnows, and NMDS axes were fit with a Gaussian (normal) distribution. Significant differences among the five BACI treatment categories were determined using Tukey's *post-hoc* test based on least square means comparisons (lsmeans package; R v. 3.4.2). VIFs indicated acceptable collinearity of predictor variables in the final models ($\leq$ 3.2). Diagnostic tests for normality and heteroscedasticity in model residuals indicated no violation of linear model assumptions and models were not over-dispersed (following Zuur et al. 2010). Fixed-effects variables were deemed significant based on $P < 0.05$.

Objective 3: isotopic niche data

We collected isotopic niche data in a design separate of our modified BACI community analysis. Stable isotope data were collected for fish species during three years of the post-expansion period (2015–2017) at three sites differing in invasion status—one that remains uninvaded (AC), one that was newly invaded (AI-N), and one that was previously invaded (AI-P; stars in Fig. 1). Isotopic niches were determined from stable isotope analyses based on carbon and nitrogen isotope ratios (δ^{13}C and δ^{15}N). Isotope samples were analyzed at the University of Wyoming Stable Isotope Facility and had corrected baselines, as detailed in Maitland (2020). We estimated community-level trophic diversity based on all fish species present using three metrics. The first two metrics were the carbon and nitrogen isotopic ranges, which quantify the realized trophic niche length along the horizontal and vertical axes of the δ^{13}C-δ^{15}N biplot space (Layman et al. 2007). The third metric, isotopic niche area, quantifies the amount of trophic niche space that all species occupy by summarizing the combination of the carbon and nitrogen isotopic ranges using the novel kernel utilization density (KUD) method as implemented in the rKIN package of R (Eckrich et al. 2019).

At the species-level, we again quantified isotopic niche area using the KUD approach, but only for eight species with at least five individuals sampled at a given site that were also sampled across multiple years. Given our limited sample sizes for years ($n = 2$–3) and sites ($n = 2$–3), we explored changes in trophic diversity (isotopic niche area, CR, and NR) using only descriptive statistics. For species-level patterns,

we determined site-level differences (i.e., uninvaded [AC], newly invaded [AI-N], previously invaded [AI-P]) in species isotopic niche area based on whether sites had overlapping niche areas (calculated as: mean site value $\pm$ standard deviation (SD) across years). Community-level relationships for isotopic area, carbon isotopic range, and nitrogen isotopic range for the three distinct sampling sites across the three years ($n = 7$) were related to smallmouth bass abundance using Pearson correlation coefficients.

Finally, we quantified changes in a species' trophic position across sites with the tRophicPosition package in R using $\delta^{15}N$ data (Quezada-Romegialli et al. 2018). Species trophic position was determined using the formula from Post (2002), which corrects for baseline levels of trophic level and $\delta^{15}N$. We then compared posterior samples of trophic position between all eight species and all three sites for each year using a Bayesian pairwise comparison. The Bayesian comparison calculates the probability that a given species at a site has a posterior trophic position that is different from the trophic position of other species-site combinations. Species' trophic position changes were interpreted for only descriptive purposes given small sample sizes.

Results

Climatic drivers

2010–2011 was marked by climatic extremes in precipitation and flow. While not statistically extreme, 2010 annual precipitation was the wettest year since reservoir construction. Spring precipitation and summer flow in 2010 were considered statistically extreme wet and high flow seasons, and 2011 was a statistically extreme high flow year, high flow spring, and high flow summer (Table S2; Fig. 2). Previous year June precipitation (2010) was the only significant temperature or precipitation variable to have a positive threshold effect on smallmouth bass CPUE in Grayrocks Reservoir ($w_i = 0.21$; $\Delta AIC = 0.98$; $P = 0.002$; Fig. 3), which was identified as a climatic extreme. Models for current year (2011) March flow ($w_i = 0.34$; $\Delta AIC = 0$; $P < 0.001$) and April flow ($w_i = 0.19$; $\Delta AIC = 1.15$; $P < 0.001$) were also positively correlated with the 2011 increase in smallmouth bass

CPUE; both of which were also climatic extremes (Table S2).

Community effects

The modified BACI analysis revealed few community changes in the Laramie River resulting from the smallmouth bass expansion. After accounting for decreasing total richness ($\beta = -0.64$, $P = 0.005$) and decreasing minnow richness ($\beta = -0.74$; $P = 0.010$) along the stream continuum, there was no evidence that sites newly invaded by smallmouth bass declined in richness (all pairwise comparisons with $P \geq 0.156$; Table 1). Local smallmouth bass abundance also did not have a negative effect on species richness and minnow richness (both $P \geq 0.579$). Shannon and Simpson diversity indices displayed similar patterns with no significant changes in community evenness among pre- and post-expansion treatment groups (all $P \geq 0.071$). However, there was evidence for a decline in the relative abundance of minnows after smallmouth bass invasion. Newly invaded sites had a significantly lower relative abundance of minnows (AI-N; mean = 0.46, SD = 0.14) compared to those same sites prior to the expansion (BC; mean = 0.69, SD = 0.16; pairwise $P = 0.029$; Fig. 4).

The NMDS ordination (2-D stress = 0.19) sorted sampling events and species on the first axis based on position along the stream continuum ($\beta = -0.91$; $P = 0.048$). Downstream sites with warm-water species associated with reservoir environments had positive values along axis one, whereas upstream sites with cool-water, riverine species had negative values along axis one (Fig. 5a). Sites were sorted along a similar stream continuum pattern for the second NMDS axis ($\beta = -0.80$; $P = 0.054$). After accounting for those stream continuum effects, there was a significant differentiation of newly invaded sites (AI-N; red convex hull) and previously uninvaded sites (BC; blue convex hull; Fig. 5b) along both axes (both $P \leq 0.014$; Table 1). This differentiation resulted in a shift of increasing similarity to downstream communities and decreasing similarity to upstream communities. There were also significant differences along axis two for newly invaded sites (AI-N) and still uninvaded sites (AC: black convex hull; $P = 0.010$), and for sites that had smallmouth bass present in both periods (AI-P vs. BI; $P = 0.003$; Table 1).
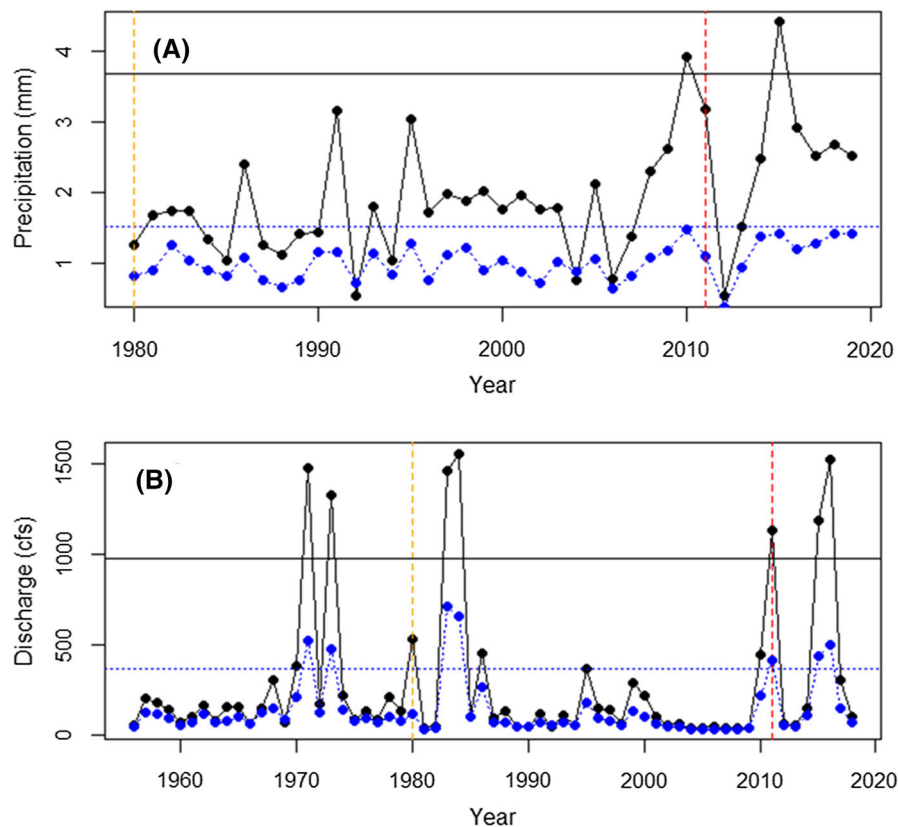
Fig. 2 Mean annual (dashed, blue lines) and mean spring-time (solid, black lines) A) precipitation (top panel; 1980–2019) and B) discharge (lower panel; 1956–2019) since the construction of Grayrocks Reservoir (dashed vertical orange line). The vertical, dashed red line indicates the year smallmouth bass increased in the reservoir (Fig. S1). Horizontal solid black and dashed blue lines correspond to values equal to two standard deviations (SD) of the mean across all years for precipitation and for two SD of the mean for reference, pre-reservoir conditions of discharge (1956–1979)

For newly invaded sites (AI-N), the indicator species analysis revealed that creek chub (*Semotilus atromaculatus*), fathead minnow (*Pimephales promelas*), johnny darter (*Etheostoma nigrum*), and longnose dace (*Rhinichthys cataractae*) were significantly more associated with pre-expansion fish communities (all $P \leq 0.034$). Common carp (*Cyprinus carpio*), common shiner (*Luxilus cornutus*), longnose sucker (*Catostomus catostomus*), shorthead redhorse (*Moxostoma macrolepidotum*), and stonecat (*Noturus flavus*) were significantly more associated with post-expansion communities (all $P \leq 0.045$).

Isotopic niche changes

Isotopic niche data supported these species-level changes. Creek chub exhibited strong compressions in isotopic niche area for the newly invaded (AI-N) and the previously invaded (AI-P) sites relative to the uninvaded site (AC, Fig. 6; Table 2). Furthermore, probabilities were frequently > 75% that the trophic position of creek chub at the newly invaded site was lower than the uninvaded site, where it occupied the highest trophic level (Fig. 6; Table S3). There was also weak evidence that white sucker (*Catostomus commersonii*) had compressed niche space and lower trophic positions for the newly invaded site. Common carp, longnose sucker, sand shiner (*Notropis stramineus*), and shorthead redhorse exhibited no evidence of compressions in isotopic niche area (Table 2), despite evidence that sand shiner and shorthead redhorse had high probabilities of occupying higher trophic positions at the previously invaded site (range: 75.2–90.2%; Table S3). The only species to show a different response between indicator species analysis and isotopic niches was stonecat, which increased in
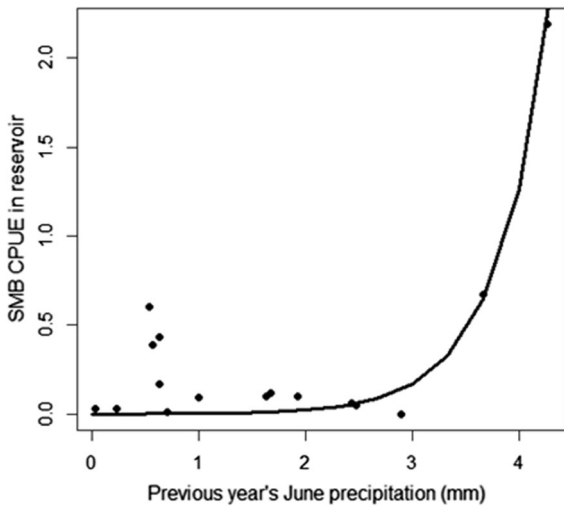
Fig. 3 Exponential relationship between relative abundance of smallmouth bass based on catch per unit effort (SMB CPUE) in Grayrocks Reservoir and the previous year's total June precipitation

relative abundance, but had a compression in isotopic niche area for the newly invaded site. Finally, these species-level patterns resulted in prominent community-level changes, as total community niche area decreased at sites with higher smallmouth bass abundances ($r = 0.75$; $P = 0.054$; Fig. S3). Community-level carbon isotopic range also decreased at sites with higher smallmouth bass abundance ($r = 0.66$;

$P = 0.110$), while community level nitrogen isotopic range increased ($r = 0.60$; $P = 0.155$; Fig. S3).

Discussion

Drivers of the expansion

Our results indicate that smallmouth bass have exhibited a rapid invasion that has caused a potential shift in native fish community composition. The swiftness of the expansion is similar to recent studies documenting expansions of smallmouth bass in the Columbia River basin, USA (Rubenson and Olden 2017, 2020). Managing biological invasions requires understanding what factors limit a species' invasion potential (Ibáñez et al. 2014; Lawrence et al. 2015). We identified extreme precipitation and high flow events as being correlated with the expansion of smallmouth bass's upstream distribution limit. The extreme wet year of 2010 likely created high in-flows that increased reservoir levels to maximum capacity, which required high discharge events in late 2010 and through 2011 to drop reservoir levels. Indeed, precipitation had been increasing annually from 2006 to 2010 while discharge remained low until 2011 (Fig. 2). Three mechanistic hypotheses are proposed below, as well as anecdotal evidence, to explain how the smallmouth

Table 1 Marginal R^2 (fixed effects only) and least square mean, pairwise comparisons (*P*-values) of the five BACI treatment categories for the seven community metrics evaluated in linear mixed-effects models. Bolded values indicate $P < 0.05$

Treatment comparisons	Total richness	Minnow richness	Shannon diversity	Simpson diversity	Minnow abundance	NMDS axis 1	NMDS axis 2
Marginal R^2	0.31	0.11	0.10	0.10	0.51	0.40	0.26
AI-N versus AC	0.884	0.999	0.999	0.953	0.977	0.090	**0.010**
AI-N versus AI-P	0.622	0.741	0.459	0.385	0.644	0.999	0.185
AI-N versus BC*	0.227	0.998	0.153	0.322	**0.029**	**0.014**	**0.001**
AI-N versus BI	0.156	0.478	0.765	0.900	0.931	0.982	0.999
AC vs AI-P	0.999	0.952	0.559	0.233	0.535	0.520	0.999
AC versus BC	0.995	0.996	0.244	0.071	0.341	0.989	0.893
AC versus BI	0.839	0.803	0.817	0.710	0.821	0.217	0.162
AI-P versus BC	0.998	0.630	0.983	0.909	**0.023**	0.536	0.999
AI-P versus BI	0.650	0.954	0.966	0.693	0.961	0.766	**0.003**
BC versus BI	0.841	0.398	0.999	0.999	0.125	0.199	0.223

* indicates the comparison of sampling events that were previously uninvaded and newly invaded by smallmouth bass (i.e., our central hypothesis)
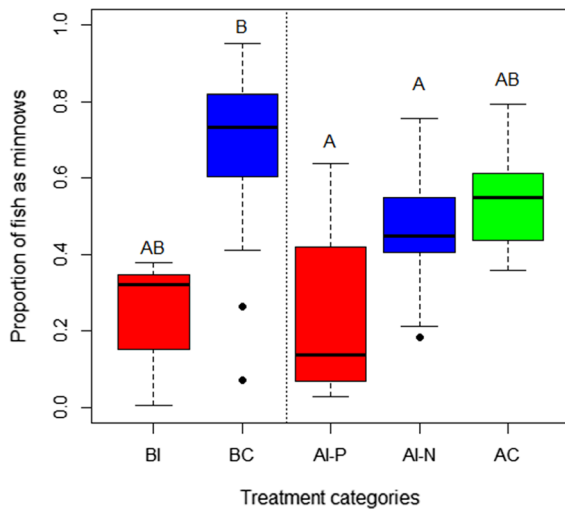
Fig. 4 Proportional relative abundance of individuals in the family *Leuciscidae* for 84 sampling events before and after the smallmouth bass range expansions. Red boxes compare sites with smallmouth bass present in both periods (AI-P vs. BI), blue compares sites newly invaded by smallmouth bass between periods (AI-N vs. BC; our central hypothesis), and green indicates sites not yet invaded by smallmouth bass (AC). Different letters indicate statistically different groups based on least square means comparisons (Table 1). Boxplots encompass 25th, 50th and 75 percentiles; whiskers represent values 1.5 times the interquartile range

bass expansion could be related to interactions among precipitation, discharge, and reservoir levels.

First, the high flow events may have prompted upstream spawning movements of smallmouth bass. Smallmouth bass tend to spawn in the late-spring, early-summer periods of May and June when water temperatures approach 16 °C (Graham and Orth 1986; Patton and Hubert 1996). This corresponds to the extreme wet conditions during the spring of 2010, as well as 2015. High spring discharge thus likely had a positive effect on smallmouth bass spawning. Indeed, smallmouth bass were the only non-native species to exhibit high population abundances in years of high spring discharge for streams of the American Southwest (Gido et al. 2013). Comparably, smallmouth bass were the only species to exhibit an upstream expansion during the extreme climatic conditions in the Laramie River. Two additional reservoir non-natives captured frequently during both periods of our study did not exhibit prominent upstream expansions (channel catfish [*Ictalurus punctatus*] = 8.7 km upstream shift; yellow perch [*Perca flavescens*] = 4.0 km downstream shift).
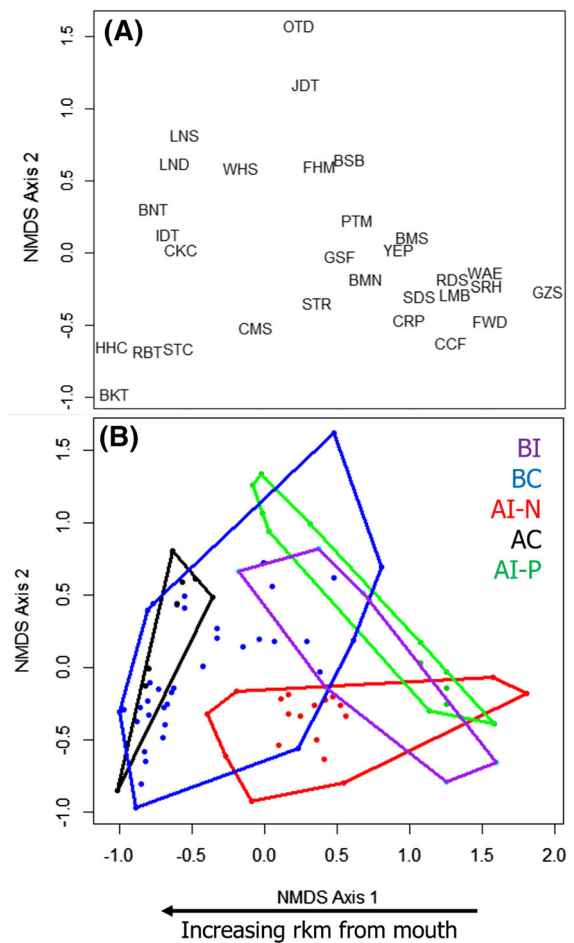

Fig. 5 Non-metric multidimensional scaling (NMDS) ordination plot based on relative abundance data for **a** 30 fish species and **b** 84 sample events before (BI, BC) and after (AC, AI-N, AI-P) the smallmouth bass expansion. Convex hulls are drawn around the five modified BACI treatment categories. Table 1 indicates significant differences among treatment categories. See Table S1 for species abbreviations

Second, the range expansion could have resulted from overcoming barriers that became passable during high flow conditions. This invasion is particularly noteworthy because it has involved dispersing into a high gradient stream section (Fig. 1), which can represent natural barriers that are difficult for smallmouth bass and even native species to disperse into (Gibson-Reinemer et al. 2017; Rubenson and Olden 2020). The immediate expansion was not solely related to overcoming an anthropogenic barrier because the nearest one was ∼ 26 km upstream of the species' pre-expansion limit. Smallmouth bass were able to overcome that anthropogenic barrier on
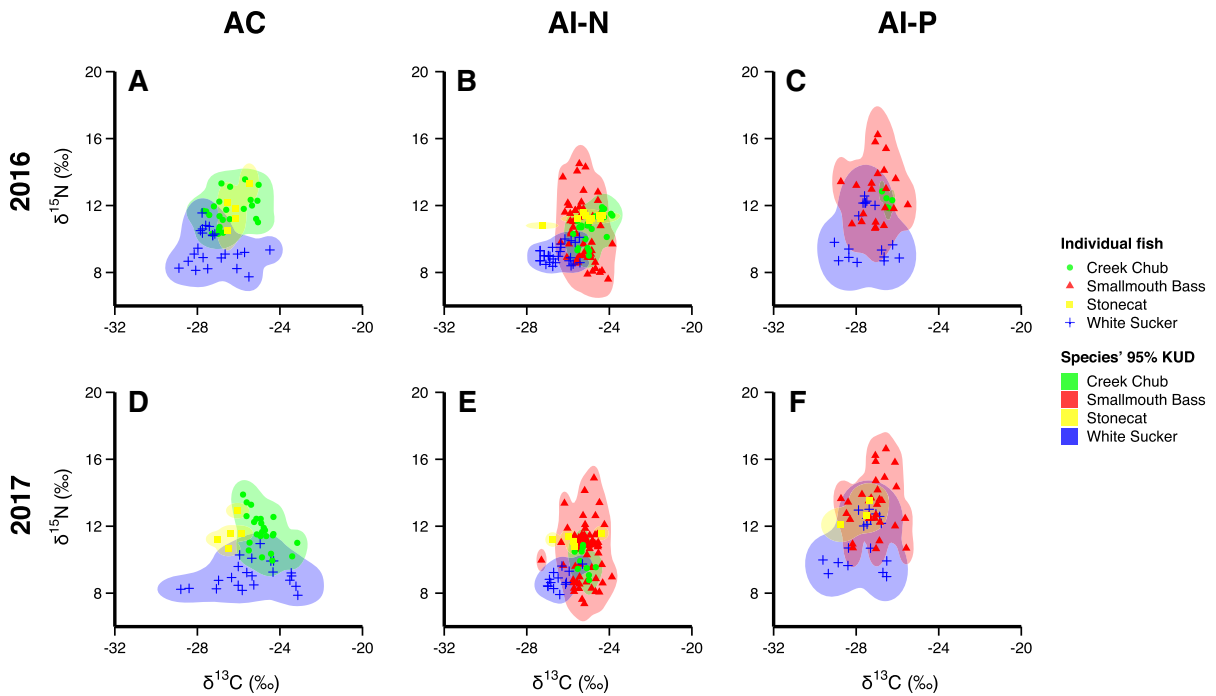
Fig. 6 Isotopic niche areas of four fish species during the years of 2016 and 2017 for an uninvaded site (AC; Panels A, D), a newly invaded site (AI-N; Panels B, E) and a previously invaded site (AI-P; Panels C, F). Niche areas are defined using ellipses based on the KUD method. Creek chub, stonecat, and white sucker are shown because they exhibited varying levels of support for evidence of niche compression (Table 2)

Table 2 Mean isotopic niche areas (standard deviation [SD]; number of years) for eight species captured at two or more sampling sites in multiple years based on smallmouth bass invasion status (stars, Fig. 1)

Species	Uninvaded (AC)	Newly (AI-N)	Previously (AI-P)
Common carp	–	5.9 (3.2, 3)	13.5 (7.2, 2)
Creek chub	14.5 (1.1, 2)	8.0 (3.4, 3)	1.1 (0, 1)
Longnose sucker	1.4 (0.4, 2)	–	1.4 (1.2, 2)
Sand shiner	–	4.4 (5.3, 2)	2.9 (1.0, 2)
Shorthead redhorse	–	2.1 (1.7, 2)	1.9 (1.0, 2)
Smallmouth bass	–	16.9 (5.4, 3)	21.8 (1.7, 2)
Stonecat	4.9 (2.0, 2)	2.3 (0.3, 2)	–
White sucker	20.8 (2.4, 2)	4.3 (2.2, 3)	25.3 (0.3, 2)

Bolded species differ across sites based on non-overlapping mean values ± SD

the Laramie River, likely due to the high flow conditions of 2010–2011. However, they did not overcome an anthropogenic barrier on the North Laramie River, which currently prevents expansion in that system (barriers identified from the national barrier dataset of Ostroff et al. 2013). Barriers have been shown to be effective in limiting upstream

expansions of smallmouth bass in South African streams (Van der Walt et al. 2016).

Third, the expansion may have been prompted by rising reservoir levels which increased recruitment and survival leading to density-dependent movement. Creel surveys indicated that smallmouth bass angler catch rates were high in 2012, suggesting the

population increase may have extended beyond 2011 (Gale 2015). Increased reservoir levels from the extreme high flow conditions likely created more shoreline habitat for adult smallmouth bass to occupy that could have increased catch rates (Wyoming Game and Fish Department 2011). However, average length data of smallmouth bass collected from Grayrocks Reservoir did not indicate major shifts in size structure for 2010–2012 to suggest young-of-year recruitment drove CPUE increases (Table S4). The magnitude of the upstream expansion (83 rkm) also suggests that the climatic conditions causing the expansion were acting on adult, large-bodied smallmouth bass given their high vagility (Rubenson and Olden 2017).

Another potential mechanism for the range expansion unrelated to flow and precipitation could be warming temperatures, which relaxes growth limitation and over-wintering survival at upstream limits (e.g., Lawrence et al. 2015; Rubenson and Olden 2017). However, temperature was not found to be significant in the models and growth estimates derived from scale data and bioenergetics models (Shuter et al. 1980; Francis 1990) for water temperature data are similar between a newly invaded site and previously invaded site (see Table S5). Furthermore, smallmouth bass have become locally abundant with active reproduction resulting in an average of 15.2 individuals per 100 m (SD = 16.3) during the 19 sampling events at newly invaded sites (blue symbols; Fig. 1). However, growth is likely to limit the expansion at sites farther upstream, which have cold in-stream temperatures that drop growth rate potential (AC site; Table S5). Despite the speculative nature of the causal mechanism, our evidence suggests that extreme climatic events (high precipitation) likely had a role in eliciting the expansion.

While climate-induced temperature and hydrologic changes have been predicted to cause range expansions of black bass species (Chiu et al. 2005; Sharma et al. 2009; Bae et al. 2018), our results reveal these expansions may not be gradual in nature. Smallmouth bass were largely confined to Grayrocks Reservoir and downstream reaches from 1980 to 2009 (Quist et al. 2005), implying that an abrupt environmental change drove the recent expansion. Extreme precipitation and warming events have been well-documented as inducing extreme changes in community structure (Boucek and Rehage 2014; Marques et al. 2014) and while climatic extremes have been hypothesized to facilitate

biological invasions (Smith 2011), there are relatively few documented examples (but see Winder et al. 2011). Our results provide new evidence to support this hypothesis, with the highest precipitation events since reservoir construction and the highest discharge events since 1983–1984 both coinciding with the upstream expansion of smallmouth bass. Flooding events, in particular, are hypothesized to increase dispersal opportunities for non-native species (Diez et al. 2012), especially those in reservoirs (Schultz et al. 2003; Sun et al. 2020). With projected increases in climatic extremes, the potential for explosive expansions of invasive species is concerning given the unpredictable nature of extreme events (Smith 2011).

Community- and species-level impacts

Contrary to predictions, smallmouth bass did not cause a decline in native fish richness, but did induce changes in the relative abundance of certain fish species. Predation susceptibility is closely linked to habitat use and body size (Scholosser 1987; Kirk et al. 2017), and our results support that paradigm. The four species indicative of pre-expansion communities (creek chub, fathead minnow, johnny darter, longnose dace) were all small-bodied minnows or darters. Despite the Laramie River and other regional systems having high non-native species richness (Kirk et al. 2020), smallmouth bass are more piscivorous and have greater effects on native fishes compared with other non-native predators (Johnson et al. 2008; Hickerson et al. 2019). A similar subset of congenerics and conspecifics were the most likely to be extirpated from Ontario lakes invaded by *Centrarchidae* species (bass and sunfish; Alofs and Jackson 2015). The four susceptible species are also largely lotic (riverine) species that dominate upstream assemblages, and may be more naïve to the presence of reservoir predators at their downstream limits. A complementary study documented declines of another minnow (hornyhead chub [*Nocomis biguttatus*]) in response to smallmouth bass presence within our study system, and suggested competition or predation as a mechanism for decline (Hickerson et al. 2019).

In contrast, the five indicator species that characterized post-expansion communities attain large body sizes (common carp, *Catostomidae spp.*) or occupy microhabitats (e.g., stonecats in riffle habitats) that

provide a size or habitat refugia from predation (Van der Walt et al. 2016; Kirk et al. 2017). The only species to not follow habitat-body size patterns is the common shiner, which has contradictory responses in the literature. While common shiner has been found to be sensitive to non-native predators in field studies (Alofs and Jackson 2015; Kirk et al. 2017), it also demonstrated no responses to non-native black bass in experimental studies (Knight and Gido 2005). Furthermore, one species (red shiner [*Cyprinella lutrensis*]) identified as highly susceptible to *Centrarchidae* predators in Great Plains systems did not exhibit abundance declines in our study (Knight and Gido 2005; Marsh-Matthews et al. 2013). Overall, smallmouth bass have caused some shifts in community composition, but have not resulted in extirpations within the first decade of invasion. However, continued monitoring is critical because impacts may increase with future environmental change. For example, predation rates of smallmouth bass are predicted to increase with climate warming due to rising metabolic rates (Pease and Paukert 2014).

Isotopic niches provided compelling evidence to support the top-down effects of smallmouth bass observed in the community analyses. For example, three of the species that had isotopic niches unaffected by smallmouth bass (common carp, longnose sucker, shorthead redhorse) were positively associated with the post-expansion period from the indicator species analysis. Our invader-induced patterns are similar to a recent study by Rogosch and Olden (2020), with community-level isotopic niche area decreasing, carbon range decreasing, and nitrogen range increasing for sites with high abundances of non-native fishes. In our study, these effects appeared most pronounced for the newly invaded site versus the previously invaded site close to Grayrocks Reservoir, possibly because trophic interactions become stronger in lotic habitats versus reservoir habitats (Mercado-Silva et al. 2009). Such compressions of isotopic niche space and carbon range are indicative of non-consumptive effects (e.g., competition), whereby the presence of a non-native species shifts the resource use of other species (e.g., Vander Zanden et al. 2004; Marks et al. 2010). This community-level inference is supported by the compression of isotopic niche area and decline in trophic position of creek chub, which was likely the historic top predator in this system (Baxter and Simon 1995).

While we attempted to standardize sampling data, there was still evidence that our inferences about community change may be confounded by sampling differences across data sources. For example, sites with smallmouth bass present before (BI) and after (AI-P) the expansion differed in community structure for NMDS axis two. These are downstream sites (gold symbols; Fig. 1) that should theoretically be unchanged between time periods based on our hypothesis, although variation in sampling month or annual flow could also explain some of those differences (Weaver and Kwak 2003). Changes induced by smallmouth bass along NMDS axis two should thus be interpreted with caution. In contrast, the first NMDS axis was unlikely confounded by methodological differences because significant differences were only observed for previously uninvaded (BC) and newly invaded sites (AI-N); the specific comparison that we expected would show a difference in fish community composition.

Conclusions

In conclusion, our study builds on the growing body of literature documenting the spread and impacts of recent black bass invasions. Smallmouth bass exhibited a rapid and unanticipated expansion as a result of climatically extreme conditions (e.g., high precipitation and high river flows), which affected the relative abundance and trophic niches of small-bodied fish species. Evaluating rapid and unanticipated biological invasions will require developing long-term monitoring programs for areas identified as high expansion risk and then quickly assembling research efforts to monitor these chance events (Blossey 1999; Freeman et al. 2007; Ibáñez et a. 2014). While non-native impacts can be inferred from a spatial context, such as control-impact evaluations, these designs are problematic because environmental variation can also confound differences between control and impact groups. In contrast, BACI designs provide greater inferential strength when inferring biotic changes compared with these simpler designs (Ballew et al. 2016; Christie et al. 2019). Unfortunately, BACI evaluations often require a priori study designs with protocols for sampling replication and data standardization. Given the unpredictable nature of biological invasions (Ricciardi et al. 2011), the use of BACI

designs may be largely opportunistic, as in our study. Even though our modified, five category BACI analysis was different from traditional designs, it controlled for environmental variation among sites and provided confidence that observed community changes were induced by smallmouth bass. As global change accelerates, so too will biological invasions, and we should be prepared to rapidly assess those invasions when they occur.

Data Availability

Data used for analyzing climate relationships with smallmouth bass abundance (objective 1), community-level changes before and after the smallmouth bass expansion (objective 2), and community isotopic niche data (objective 3) are available online at the Dryad Digital Repository, https://doi.org/10.5061/dryad.c2fqz619n.

Declarations

Conflict of interest There is no conflict of interest declared in this article.

Ethics approval Data collection for this article was approved via permits through the Wyoming Game and Fish Department and through the University of Wyoming Institutional Animal Care and Use committee.

Consent to publication We consent to the publication of this manuscript dependent upon peer review and article acceptance.

References

Alofs KM, Jackson DA (2015) The vulnerability of species to range expansions by predators can be predicted using historical species associations and body size. Proc R Soc B 282:20151211

Alofs KM, Jackson DA, Lester NP (2014) Ontario freshwater fishes demonstrate differing range-boundary shifts in a warming climate. Divers Dist 20:123–136

Bae M, Murphy CA, García-Berthou E (2018) Temperature and hydrologic alteration predict the spread of invasive largemouth bass (Micropterus salmoides). Sci Total Environ 639:58–66

Ballew NG, Bacheler NM, Kellison GT, Schueller AM (2016) Invasive lionfish reduce native fish abundance on a regional scale. Sci Rep 6:32169

Baxter GT, Simon JR (1995) Fishes of Wyoming. Wyoming Game and Fish Department, Cheyenne, Wyoming

Blossey B (1999) Before, during and after: the need for long-term monitoring in invasive plant species management. Biol Invas 1:301–311

Boucek RE, Rehage JS (2014) Climate extremes drive changes in functional community structure. Glob Chang Biol 20:1821–1831

Buckwalter JD, Frimpong EA, Angermeier PL, Barney JN (2020) Species traits predict stream-fish invaders in an Appalachian (USA) river basin. Freshw Biol 65:552–564

Chick JH, Gibson-Reinemer DK, Soeken-Gittinger L, Casper AF (2020) Invasive silver carp is empirically linked to declines of native sport fish in the upper Mississippi river system. Biol Invas 22:723–734

Chiu C, Mandrak NE, Minns CK (2005) Potential impacts of climate change on the distributions of several common and rare freshwater fishes in Canada. Diver Dist 11:299–310

Christie AP, Amano T, Martin PA, Shackelford GE, Simmons BI, Sutherland WJ (2019) Simply study designs in ecology produce inaccurate estimates of biodiversity responses. Jour Appl Ecol 56:2742–2754

Comte L, Buisson L, Daufresne M, Grenouillet G (2013) Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. Freshw Biol 58:625–639

Craig LS, Olden JD, Arthington AJ, Entrekin S, Hawkins CP, Kelly JJ, Wooten MS (2017) Meeting the challenge of interacting threats in freshwater ecosystems: a call to scientists and managers. Elem Sci Anth 5:72

Cucherousset J, Olden JD (2011) Ecological impacts of non-native freshwater fishes. Fisheries 36:215–230

Diez JM, D'Antonio CM, Dukes JS, Groshol ED, Olden JD, Sorte CJB, Miller LP (2012) Will extreme climatic events facilitate biological invasions? Fron Ecol Environ 10:249–257

Eckrich CA, Albeke SE, Flaherty EA, Bowyer RT, Ben-David M (2019) rKIN: Kernel-based method for estimating isotopic niche size and overlap. J Anim Ecol 89:1–15

Falke JA, Gido KB (2006) Spatial effects of reservoirs on fish assemblages in Great Plains streams in Kansas, USA. River Res Applic 22:55–68

Francis RICC (1990) Back-calculation of fish length: a critical review. J Fish Biol 36:883–902

Freeman JP, Stohlgren TJ, Hunter ME, Omi PN, Martinson EJ, Chong GW, Brown CS (2007) Rapid assessment of postfire plant invasions in coniferous forests of the western United States. Ecol Appl 17:1656–1665

Gale SB (2015) Grayrocks reservoir programmed creel survey, 2015. Wyoming Game and Fish Department, Fish Division, Administrative Report, Cheyenne, WY, USA.

U.S. Geological Survey, 2020, Data inventory page for site 06670500—Laramie River, near Fort Laramie, Wyoming: U.S. Geological Survey web page, accessed March 26, 2020, at https://waterdata.usgs.gov/nwis/inventory/?site_no=06670500.

Gibson-Reinemer DK, Rahel FJ, Albeke SE, Fitzpatrick RM (2017) Natural and anthropogenic barriers to climate tracking in river fishes along a mountain-plains transition zone. Divers Distr 23(761–770):8

Gido KB, Propst DL, Olden JD, Bestgen KR (2013) Multidecadal responses of native and introduced fishes to natural and altered flow regimes in the American Southwest. Can J Fish Aquat Sci 70:554–564

Gido KB, Schaefer JF, Falke JA (2009) Convergence of fish communities from the littoral zone of reservoirs. Freshw Biol 54:1163–1177

Gido KB, Schaefer JF, Pigg J (2006) Patterns of fish invasions in the Great Plains of North America. Biol Cons 118:121–131

Gozlan RE, Britton JR, Cowx I, Copp GH (2010) Current knowledge on non-native freshwater fish introductions. Jour Fish Biol 76:751–786

Graham RJ, Orth DJ (1986) Effects of temperature and streamflow on time and duration of spawning by smallmouth bass. Trans Ameri Fish Soc 115:693–702

Hickerson BT, Maitland BM, Walters AW (2019) Effects of multiple nonnative fish on an imperiled cyprinid, Hornyhead Chub. Trans Am Fish Soc 148:1132–1145

Ibáñez I, Diez JM, Miller LP, Olden JD, SorteBlumenthal CJBDM, Lawler JJ (2014) Integrated assessment of biological invasions. Ecol Appl 24:25–37

Jackson DA, Mandrak NE (2002) Changing fish biodiversity: predicting the loss of cyprinid biodiversity due to global climate change. Am Fish Soc Symp 32:89–98

Johnson BM, Martinez PJ, Hawkins JA, Bestgen KR (2008) Ranking predatory threats by nonnative fishes in the Yampa River, Colorado, via bioenergetics modeling. North Ameri Journa Fish Managem 28:1941–1953

Kirk MA, Maitland BM, Rahel FJ (2020) Spatial scale, reservoirs and nonnative species influence the homogenization and differentiation of Great Plains—Rocky Mountain fish faunas. Hydrobiologia 847:3743–3757

Kirk MA, Wissinger SA, Goeller BC, Rieck LO (2017) Co-varying impacts of land use and non-native brown trout on fish communities in small streams. Freshw Biol 62:600–614

Knight LG, Gido KB (2005) Habitat use and susceptibility to predation of four prairie stream fishes: implications for conservation of the endangered Topeka shiner. Copeia 1:38–47

Kuczynski L, Legendre P, Grenouillet G (2018) Concomitant impacts of climate change, fragmentation and non-native species have led to reorganization of fish communities since the 1980s. Global Ecol Biogeogr 27:213–222

Lawrence DJ, Beauchamp DA, Olden JD (2015) Life-stage-specific physiology defines invasion extent of a river fish. Journ Anim Ecol 84:879–888

Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42–48

Loppnow GL, Vascotto K, Venturelli PA (2013) Invasive smallmouth bass (Micropterus dolomieu): history, impacts, and controls. Manag Biol Invas 4:191–206

Lowe S, Browne M, Boudjelas S, Dee Poorter M (2000) 100 of the world's worst invasive alien species. A selection from the Global Invasive Species database. The invasive species specialist group (ISSG), a specialist group on the species survival commission (SSC) of the World Conservation Union (IUCN). IUCN-2000-126.

Maitland BM (2020) Isotopic ecology of aquatic communities along the Rocky Mountains—Great Plains ecotone. PhD Dissertation. University of Wyoming, Laramie, WY, USA.

Marchetti MP, Moyle PB, Levine R (2004) Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. Fresh Biol 49:646–661

Marks JC, Haden GA, O'Neill M, Pace C (2010) Effects of flow restoration and exotic species removal on recovery of native fish: lessons from a dam decommissioning. Restor Ecol 18:934–943

Marques SC, Primo AL, Martinho F, Azeiteiro UM, Pardal MA (2014) Shifts in estuarine variability following extreme climatic events: a comparison between drought and regular years. Mar Ecol Prog Ser 499:65–76

Marsh-Matthews E, Thompson J, Matthews WJ, Geheber A, Franssen NR, Barstedt J (2013) Differential survival of two minnow species under experimental sunfish predation: implications for re-invasion of a species into its native range. Freshw Biol 58:1745–1754

Mercado-Silva N, Helmus MR, Vander-Zanden MJ (2008) The effects of impoundment and non-native species on a river food web in Mexico's central plateau. Riv Res Appl. https://doi.org/10.1002/rra.1205

Mitchell AL, Knouft HG (2009) Non-native fishes and native species diversity in freshwater fish assemblages across the United States. Biol Invasions 11:1441–1450

Ostroff A, Wieferich D, Cooper AA, Infante D (2013) 2012 National anthropogenic barrier dataset (NABD). U.S. Geological Survey, Aquatic GAP Program, Denver, CO, U.S.A.

Patton TM, Hubert WA (1996) Water temperature affects smallmouth bass and channel catfish in a tailwater stream on the Great Plains. North Am J Fish Manag 16:124–131

Pease AA, Paukert CP (2014) Potential impacts of climate change on growth and prey consumption of stream-dwelling smallmouth bass in the central United States. Ecol Freshw Fish 23:336–346

Pereira FW, Vitule JRS (2019) The largemouth bass Micropterus salmoides (Lacepede, 1802): impacts of a powerful freshwater fish predator outside its native range. Rev Fish Bio Fisheries 29:639–652

Perkin JS, Gido KB, Cooper AR, Turner TF, Osborne MJ, Johnson ER, Mayes KB (2015) Fragmentation and dewatering transform Great Plains stream fish communities. Ecol Mono 85:73–92

Peterson MI, Kitano S, Ida H (2020) Spawning season and nesting habitat of invasive smallmouth bass *Micropterus dolomieu* in the Chikuma River, Japan. Icthyological Research 67:1–6

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718

Quezada-Romegialli C, Jackson AL, Hayden B, Kahilainen KK, Lopes C, Harrod C (2018) tRophicPosition, an r package for the Bayesian estimation of trophic position from consumer stable isotope ratios. Methods Ecol Evol 9:1592–1599

Quist MC, Hubert WA, Rahel FJ (2004) Relations among habitat characteristics, exotic species, and turbid-river cyprinids in the Missouri River drainage of Wyoming. Trans Ameri Fish Soc 133:727–742

Quist MC, Hubert WA, Rahel FJ (2005) Fish assemblage structure following impoundment of a Great Plains river. West North Ameri Natur 65:53–65

R Development Core Team (2017) R: a language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria

Ricciardi A, Palmer ME, Yan ND (2011) Should biological invasions be managed as natural disasters? Bioscience 61:312–317

Rogosch JS, Olden JD (2020) Invaders induce coordinated isotopic niche shifts in native fish species. Can J Fish Aquat Sci 77:1348–1358

Rubenson ES, Olden JD (2017) Dynamism in the upstream invasion edge of a freshwater fish exposes range boundary constraints. Oecologia 184:453–467

Rubenson ES, Olden JD (2020) An invader in salmonid rearing habitat: current and future distributions of smallmouth bass (Micropterus dolomieu) in the Columbia River basin. Can J Fish Aquat Sci 77:314–325

Schlosser IJ (1987) The role of predation in age- and size-related habitat use by stream fishes. Ecology 68:651–659

Schultz AA, Maughan OE, Bonar SA, Matter WJ (2003) Effects of flooding on abundance of native and nonnative fishes downstream from a small impoundment. N Ameri Journ Fish Manag 23:503–511

Sharma S, Herborg L, Therriault TW (2009) Predicting introduction, establishment and potential impacts of smallmouth bass. Diver Distr 15:831–840

Shuter BJ, MacLean JA, Fry FEJ, Regier HA (1980) Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Trans Am Fish Soc 109:1–34

Smith MD (2011) An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. Journ Ecol 99:656–633

Stewart DR, Walters AW, Rahel FJ (2016) Landscape-scale determinants of native and non-native Great Plains fish distributions. Divers Distrib 22:225–238

Sun H, He D, Sui X, Chen Y (2020) Predicting impacts of future climate change and hydropower development towards habitats of natives and non-native fishes. Sci Total Environ 707:135419

Thornton PE, Thornton MV, Mayer BW, Wei Y, Devarakonda R, Vose RS et al (2007) Dayment: daily surface weather data on a 1-km grid for North America, Version 3. https://doi.org/10.3334/ORNLDAAC/1328. ORNL DAAC, Oak Ridge, Tennessee, USA.

Van der Walt JA, Weyl OL, Woodford DJ, Radloff FG (2016) Spatial extent and consequences of black bass (Micropterus spp.) invasion in a Cape Floristic Region river basin. Aquatic Conserv Mar Freshw Ecosyst 26:736–748

Vander Zanden MJ, Olden JD, Thorne JH, Mandrak NE (2004) Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. Ecol Appl 14:132–148

Weaver DM, Kwak TJ (2013) Assessing effects of stocked trout on nongame fish assemblages in southern Appalachian mountain streams. Trans Am Fish Soc 142:1495–1507

Winder M, Jassby AD, Mac Nally R (2011) Synergies between climate anomalies and hydrological modifications facilitate estuarine biotic invasions. Ecol Letters 14:749–757

Wyoming Game and Fish Department. 2011. Annual fisheries progress report on the 2011 work schedule. Wyoming Game and Fish Department, Cheyenne, WY, USA.

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Meth Ecol Evol 1:3–14