

Estimating drivers and identifying uncertainties in smallmouth bass population dynamics in an invaded river network

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Abstract

Smallmouth bass (*Micropterus dolomieu*) is an important recreational sportfish and destructive non-native species when introduced into freshwater habitats. There is therefore a need to understand the drivers of, and uncertainties in, smallmouth bass population dynamics for various management objectives. We combined long-term smallmouth bass catch-effort and early life history data from a non-native population in the Green River sub-basin of the upper Colorado River to develop a demographic model that links interannual variability in environmental conditions to recruitment in three river reaches. We used the model to quantify how hydrology, river temperature, and exploitation drive smallmouth bass population dynamics. Early life stages were influenced by timing of hatching and discharge. Dispersal of age-0 fish and density-dependent dynamics were identified as primary sources of uncertainty. Determining the true nature of density-dependent dynamics is important, as the impact of exploitation-based management actions is dependent on the strengths of any density-dependent feedbacks. Our model provides a framework to predict smallmouth bass population responses to future climate conditions, reservoir operations, and exploitation levels.

Key words: population dynamics, non-native removal, recruitment, flow-ecology, simulation model

Introduction

Quantifying the strength of drivers of population and ecosystem dynamics is critical for identifying cost-effective management strategies, but system complexity makes this challenging (Bond et al. 2015). This is especially true in river ecosystems modified by stressors including non-native species, climate change, and river regulation, which alters thermal and hydrologic regimes, modifies physical habitat, and fragments river networks (Reid et al. 2019). Evaluating management actions can be difficult in the context of multiple stressors because stressor effects vary at different temporal and spatial scales, and there is uncertainty regarding the effectiveness of management actions in influencing system dynamics (e.g., Yackulic et al. 2022). Thus, models and experiments that estimate population or ecosystem responses to stressors are essential to quantifying drivers and forecasting system response to different management actions. These, in turn, help managers make proactive decisions instead of relying on reactive responses after substantial damage has occurred (Pimentel et al. 2005).

Understanding drivers of smallmouth bass *Micropterus dolomieu* population dynamics is a management priority because they are recreationally important (Schramm Jr. et al. 1991; Carey et al. 2011) and are also an invasive species that negatively impacts native fish populations (Loppnow et al. 2013). Smallmouth bass have been stocked in over 20 countries (Carey et al. 2011) and are widespread and expanding outside their native range (Loppnow et al. 2013; Brewer and Orth 2014). Invasive populations are linked to reduced growth and abundance as well as extirpations of small prey fishes and large native predators (Loppnow et al. 2013). With increasing water temperatures associated with climate change, more habitats outside their native range will likely be suitable for smallmouth bass, potentially leading to further range expansion (Sharma and Jackson 2008; Lawrence et al. 2015; Rubenson and Olden 2020; Voss et al. 2022). Conversely, some native smallmouth bass are of conservation concern due to stocking of non-native congeners (Taylor et al. 2019) and warming river temperatures at the southern extent of their range (Middaugh et al. 2018).

Several factors have been linked to fluctuations in smallmouth bass populations including density dependence in recruitment success, variation in the timing and duration of spring flooding that drive hatch dates and nest success, variation in summer temperatures that influence age-0 growth, overwinter survival, and removal via angling or mechanical removal (Brewer and Orth 2014). However, the relative importance of these different drivers is not well understood. Smallmouth bass recruitment in lakes often fits a Ricker-style model which allows for strong density dependence and the potential for over-compensatory dynamics (Zipkin et al. 2008; Loppnow and Venturelli 2014). Over-compensation or the “hydra effect” is characterized by an increased average population size in response to increased extrinsic (density-independent) mortality (Abrams and Matsuda 2005; Sieber and Hilker 2012; Grosholz et al. 2021) and may allow populations to recover quickly from low adult abundances. Over-compensation makes suppressing non-native smallmouth bass populations to low abundances through removal of adults challenging (Loppnow and Venturelli 2014). Survival of age-0 smallmouth bass is influenced by nesting conditions, including fungus (Knotek and Orth 1998), predation (Dauwalter and Fisher 2007), water temperature (Shuter et al. 1980; Peterson and Kwak 1999), and flow (Lukas and Orth 1995; Smith et al. 2005), and overwinter survival varies as a function of total length and overwinter conditions (Shuter and Post 1990; Lawrence et al. 2015; Voss et al. 2022). Forecasting smallmouth bass population responses to global change or management actions therefore requires accounting for a broad set of population drivers.

Smallmouth bass have been introduced into, and spread through many dryland rivers across the western United States (USA; Brewer and Orth 2014) and are considered a major threat to native fish conservation (Minckley and Deacon 1991; Johnson et al. 2008). Drought has persisted across most of the western USA for the past two decades and is characterized by declines in watershed runoff associated with warming air temperatures (Udall and Overpeck 2017). The range and relative abundance of smallmouth bass is predicted to increase in response to drought as historically cold river temperatures begin to warm and flow magnitude and variability decline (Rogoshch et al. 2019). In the Colorado River basin, invasive smallmouth bass are widely established and are a management priority due to their high piscivory rates of native fishes, including federally protected species (Minckley and Deacon 1991; Johnson et al. 2008). Intensive efforts to mechanically remove non-native fishes across the Colorado River basin, while effective at driving short-term reductions in density and shifts in size structure, have not led to long-term declines in abundance in large river reaches (Mueller 2005; Coggins Jr. et al. 2011; Breton et al. 2014; Franssen et al. 2014; Zelasko et al. 2016; Pennock et al. 2018), and some endangered fishes continue to decline (Bestgen et al. 2018). Managers are concerned about range expansion into other portions of the basin as reservoirs with declining elevations release warmer water from fixed outflow structures, creating suitable temperatures for smallmouth bass (Dibble et al. 2021; Bruckerhoff et al. 2022; Eppehimer et al. 2024). For example, warm water releases from Glen Canyon Dam in 2022

created suitable temperatures for smallmouth bass spawning in the Grand Canyon segment for the first time in over 50 years and corresponded with the first observations of smallmouth bass reproduction in this segment (Eppehimer et al. 2024). There is an urgent need to understand the relative importance of drivers of smallmouth bass population dynamics to inform ongoing management decisions, ranging from mechanical removal efforts to designer flows (Yarnell et al. 2015; Poff and Schmidt 2016) to ongoing negotiations regarding large-scale reservoir management in the Colorado River basin (Dibble et al. 2021; Bruckerhoff et al. 2022).

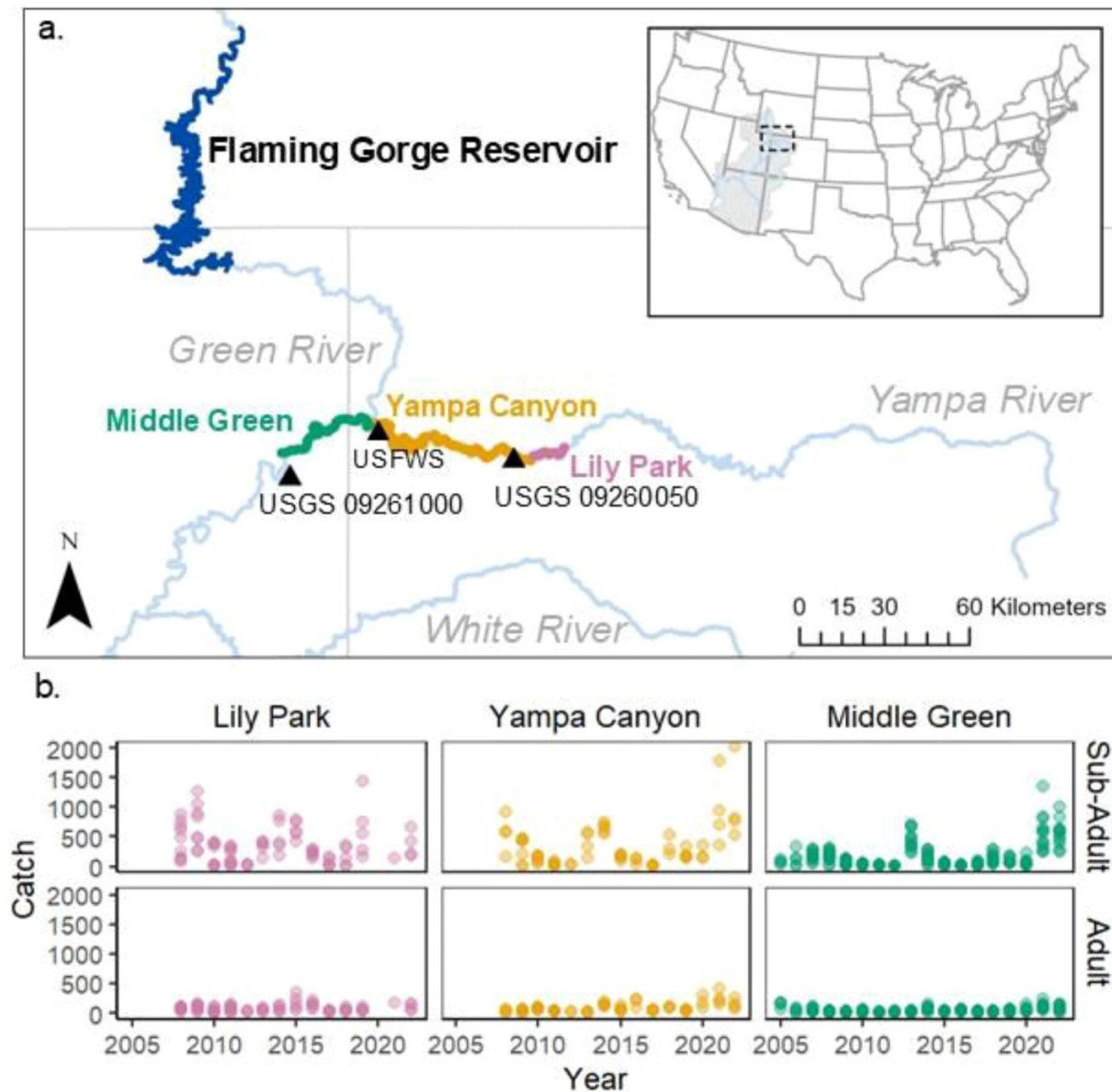
Here, we link long-term smallmouth bass removal and early life history data to observed environmental conditions across three river segments in the Colorado River basin in an age-structured demographic model. Our objective is to develop a demographic model that estimates the strength of different hypothesized drivers of smallmouth bass population change, including density dependence, hydrology, river temperature, exploitation, and dispersal. The model was developed to represent dynamics in a sub-basin of the Colorado River, the Green River, that has experienced declines in watershed runoff but is also managed through reservoir operations and mechanical removal of smallmouth bass. We expanded existing smallmouth bass demographic models that include impacts of density dependence and exploitation (Zipkin et al. 2008; Loppnow et al. 2013; Breton et al. 2015) by including environmental drivers (river temperature and hydrology) and fitting the model to observed data. Our goal was to not only identify drivers of smallmouth bass population change, but to build a simulation model to explore smallmouth bass responses to management actions and future hydrologic conditions. We highlight the utility of this model by retrospectively analyzing responses of smallmouth bass to simulated changes in exploitation effort while incorporating observed variation in environmental conditions.

Materials and methods

Study area

The Green River subbasin of the upper Colorado River drains parts of Wyoming, Colorado, and Utah and upper reaches of the mainstem Green River are regulated by releases from Flaming Gorge Dam. The Green River subbasin is ecologically important because segments of this subbasin are designated as critical habitat by the U.S. Fish and Wildlife Service (US Fish and Wildlife Service 1994) for several endangered or threatened fishes, including razorback sucker *Xyrauchen texanus*, humpback chub *Gila cypha*, Colorado pikeminnow *Ptychocheilus lucius*, and bonytail *Gila elegans*. The establishment of non-native fishes, especially piscivores like smallmouth bass, has contributed to declines in abundance and distribution of these fishes of conservation concern. Due to this threat, the Upper Colorado River Endangered Fish Recovery Program (hereafter Recovery Program) began mechanically removing smallmouth bass in portions of the Green River sub-basin in 2003 (Fuller 2004; Christopherson et al. 2005).

Fig. 1. The Green River watershed is in the upper Colorado River basin (a, inset). We modeled smallmouth bass dynamics in the Lily Park (pink) and Yampa Canyon (yellow) reaches of the Yampa River and the Middle Green (green) reach of the Green River (a). State boundary geospatial data was obtained from the [National Weather Service \(1999\)](#) and stream and waterbody lines were obtained from the National Hydrography Dataset ([USGS 2019](#)). Datum is NAD83 and coordinate system is WGS1984. The Middle Green is the only study reach that is directly influenced by releases from Flaming Gorge Reservoir. We used hydrology and temperature data from the USGS stream gage at Jensen on the Green River ([USGS 2023a](#)) and at Deerlodge Park on the Yampa River ([USGS 2023b](#)). Temperature data on the Yampa River were primarily obtained from a US Fish and Wildlife Service logger at Echo Park (USFWS) and was supplemented when daily temperatures were missing with temperature data from the Deerlodge Park gage. We fit the model to catch data of adult (>200 mm) and sub-adult smallmouth bass (100–200 mm) in each reach during each raft or boat mounted electrofishing trip (b).



The mainstem Yampa River is a co-equal tributary (in discharge) to the Green River and is largely free flowing since the minimal water development is in small, higher elevation tributary reaches. The Yampa River provides important spawning habitat for endangered Colorado pikeminnow and was also historically considered the epicenter of the smallmouth bass invasion in the Green River. Smallmouth bass catch increased in the Yampa River after drawdowns of a

tributary reservoir, Elkhead Reservoir on Elkhead Creek, in 1992 and 2005 that allowed bass escapement into the river ([Breton et al. 2014](#)). Smallmouth bass have since established self-sustaining populations across the Yampa River and downstream into the Green River ([Breton et al. 2014](#)). We focused on the two lower reaches of the Yampa River, Lily Park (8 km) and Yampa Canyon (74 km; [Fig. 1](#)) because these reaches contain a known spawning area for Colorado pikeminnow ([Tyus](#)

and McAda 1984; Tyus 1985) and likely interact with populations in downstream reaches of the Green River through dispersal. Smallmouth bass are also established and abundant in reaches upstream of Lily Park, and fish from these reaches likely move downstream into Lily Park, which is a relatively short reach (approximately 8 km). We acknowledge our representation of dynamics and estimates of abundance in the Lily Park reach are likely influenced by smallmouth bass upstream from Lily Park. We therefore predict our estimates of abundance and densities in the Lily Park reach will be biased high relative to estimates in other studies (e.g., Breton et al. 2014).

We focused on the middle section of the Green River downstream of Flaming Gorge Reservoir beginning at the Yampa River confluence at Echo Park and ending at Split Mountain (hereafter, Middle Green reach; Fig. 1). This section is partially regulated by releases from Flaming Gorge Dam but is also influenced by the mostly unregulated Yampa River. We focused on this reach because it provides rearing habitat for Colorado pikeminnow and has a continuous long-term record of intensive smallmouth bass removal.

Input data

We compiled catch-effort data collected by boat electrofishing during non-native removal efforts in the Yampa and Green rivers in 2005 through 2022 (Fig. 1). We used catch data from reaches of interest described above including Lily Park, Yampa Canyon, and Middle Green River. Each spring and summer, multiple sampling trips were conducted in each reach. We defined a trip as a full sampling occasion comprised of multiple electrofishing passes from the top of the reach to the bottom. Sampling trips typically lasted 2–4 days. On most trips, counts of removed fish were summarized by three size classes (<100 mm, 100–200 mm, and >200 mm), however in some reaches and years individual fish were measured. Catch-effort data for each study reach were extracted from annual reports which have sampling details (Lily Park: Project #125/98c, Yampa Canyon: Project #110, Middle Green: Project #123a) and are publicly available on the Upper Colorado River Endangered Fish Recovery Program website (UCREFR 2024).

In addition to catch data for each removal reach, we also used observations of recaptured tagged smallmouth bass to estimate movement rates among our reaches of interest. Smallmouth bass were sometimes tagged with individual Floy tags during early removal trips to estimate abundance each year. The Recovery Program compiled encounter locations for marked and recaptured Floy-tagged fish across the reaches of interest using the Species, Tagging, Research and Monitoring System (STReaMs 2018) database.

We calculated hydrologic metrics based on conditions in the Green River at the U.S. Geological Survey (hereafter USGS) gage at Jensen (#09261000; USGS 2023a) and in the Yampa River from the USGS gage at Deerlodge Park (#09260050; USGS 2023b; Fig. 1). Temperature metrics for the Green River were also obtained from the Jensen gage, while temperature data from the Yampa River were collected at Echo Park by USFWS (Fig. 1). The temperature logger at Echo Park was period-

ically out of service, in those cases we used daily mean temperature from Deerlodge Park to fill in any data gaps. Mean daily discharge and temperature for each river was summarized as metrics used to predict smallmouth bass hatch dates based on equations from Bestgen and Hill (2016) or as other predictors included in the model. Calculation of each flow metric is described below in description of the model.

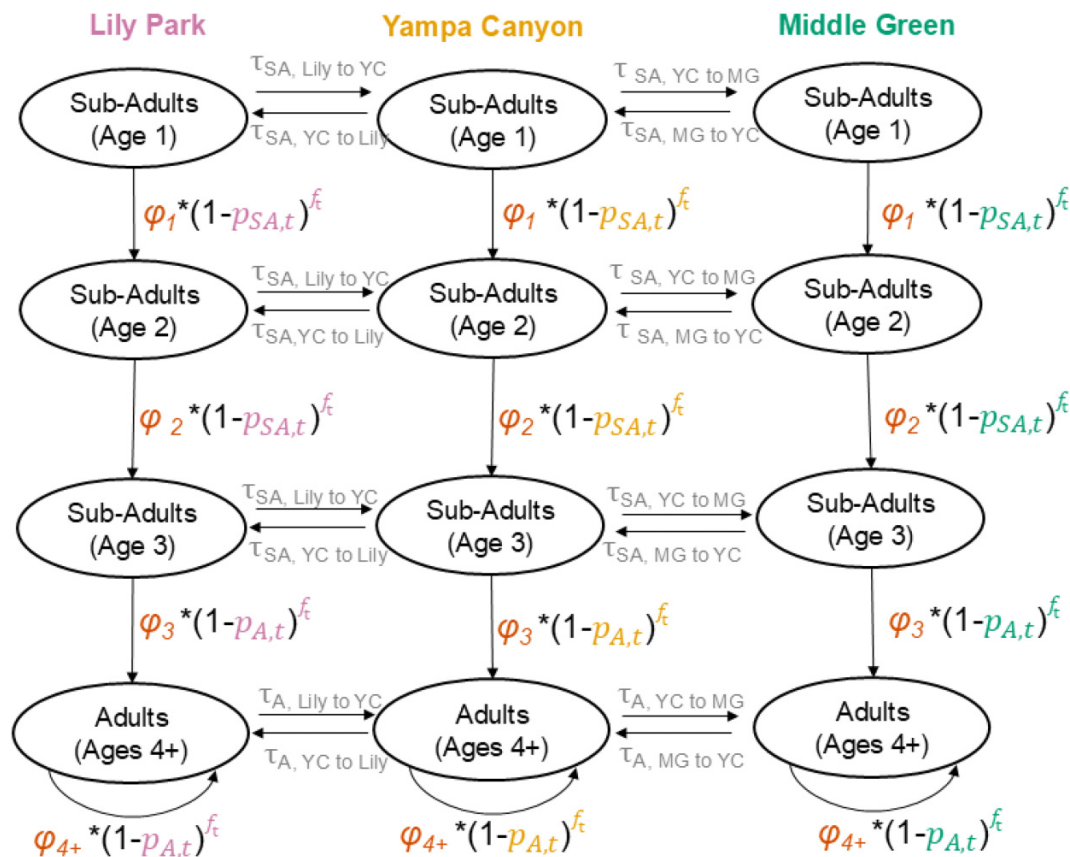
Model structure

We developed a custom age-structured model (Caswell 1996) based on Breton et al. (2015) that included five age classes (ages 0–4+), with ages-1 and 2 (100–200 mm TL) as non-reproductive sub-adults and ages-3+ (greater than 200 mm TL) as reproductive adults. We used an age-structured population instead of a size or stage-structured model as we did not have length or growth data for most years in our system and so we could build on the existing smallmouth bass population model in the system (Breton et al. 2015). Abundance estimates of smallmouth bass represented the number of fish in the spring (April) before reproduction and removal trips began, and transitions among age classes occurred at an annual timestep and included impacts of exploitation from mechanical removal, dispersal among reaches, and natural mortality (Fig. 2). The model was a post-breeding model in that we predicted age-0 abundance, but because catch data were collected both before, during, and after age-0 fish entered the system, we explicitly modeled the availability of age-0 fish to exploitation (see next section). Age-0 modeling therefore included intra-annual dynamics to incorporate the influence of density-dependent production, discharge variability during hatch, daily vulnerability to exploitation, growth, and dispersal (Fig. 3). Parameters associated with transitions among age classes estimated by our model are shown in Figs. 2 and 3 and parameters are described in Table 1. We estimated smallmouth bass abundance for each age class (age-0 through 4+) in each year and linked these abundances to observed catch by predicting catch rates based on exploitation effort.

Production, survival, dispersal, and exploitation of age-0 fish

Production of age-0 fish and recruitment to age-1 was a function of spawner abundance, total abundance of all age classes of fish, predicted hatch dates (which were a function of flow and thermal regimes), flow conditions during hatch, exploitation due to mechanical removal, and overwinter survival (which was a function of hatch dates and summer temperatures; Fig. 3). We first calculated the number of spawners by assuming 75% of all reproductive fish participated in spawning each year (Breton et al. 2015). Although observed proportions of adults spawning within a season are variable and lower than 75% across published studies (17–55%, Raffetto et al. 1990; Baylis et al. 1991, 1993), we used 75% to assume potentially higher levels of reproduction in this non-native population following Breton et al. (2015). Because age-3 smallmouth bass can also reach the reproductive threshold of 200 mm TL, we estimated the percentage of age-3 fish over 200 mm TL by assuming a normal distribution

Fig. 2. Conceptual model of smallmouth bass dynamics for three reaches in the Green River watershed. Smallmouth bass transitioned into the next age class before exploitation and reproduction began in the early spring (April). Main processes modeled included reproduction, exploitation, movement among adjacent study area reaches, and overwinter survival. Parameters may be constant (orange) or vary by a combination of reach (pink, yellow, green), age classes (first subscript), and year (t). Annual survival is represented by φ and descriptions of other parameters are described in the main text and Table 1. Parameters not estimated in the model are light grey. Movement rates (τ) were estimated by a separate movement model (see the main text).



of lengths with a mean of 208.5 mm and standard deviation of 12.5 based on aged fish collected from the Yampa River (Breton et al. 2015). We therefore assumed 63% of age-3 fish were over the 200 mm TL threshold. The number of spawning females (S) in each reach (r) each year (t) was therefore calculated as

$$(1) \quad S_{r,t} = (0.5)(0.75)(0.63N_{3,r,t} + N_{4+,r,t})$$

where $N_{4+,r,t}$ is the abundance of age-4 and older smallmouth bass in each reach (r) and year (t). Because a balanced sex ratio was assumed, we multiplied the summed abundance of reproductive fish by 0.5 in eq. 1. Note this equation is calculated based on age-3 and age-4+ abundances before exploitation or natural mortality occurs and likely overestimates the number of available spawners each year.

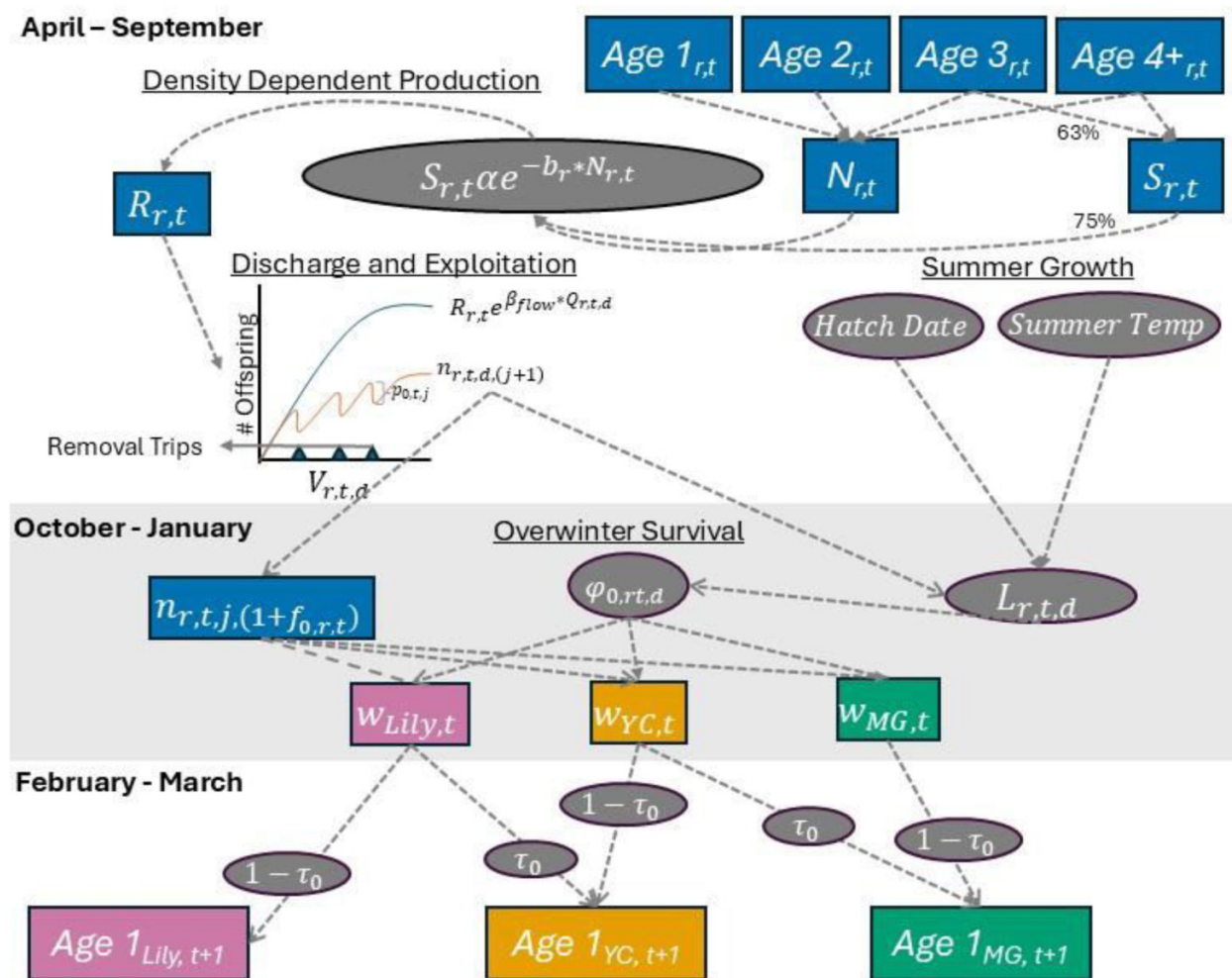
To estimate the number of offspring produced each year and account for uncertainty in the density-dependent production process, we fit the model using a modified version of the Shepard stock recruitment model (Shepard 1982). The Shepard model allows for the degree of compensation to be predicted as either non-asymptotic (Cushing 1973), asymptotic (Beverton and Holt 1957) or domed-shaped (Ricker 1954) forms. The recruitment model was modified to include

density-dependent impacts of all smallmouth bass age-1 and older ($N_{\text{Total},r,t}$), not just spawners. Young (ages 1–3) smallmouth bass typically reach sizes large enough to consume larvae, and cannibalism is predicted to be an important mechanism of density-dependent responses in smallmouth bass (Dong and Deangelis 1998). To control for different lengths of each reach and improve model convergence, we predicted the number of offspring produced per river mile ($R_{r,t}$) as

$$(2) \quad R_{r,t} = \left(\frac{S_{r,t}}{k_r} \alpha \right) / \left(1 + \left(b_r * \frac{N_{\text{Total},r,t}}{k_r} \right)^c \right)$$

where k_r is the length of each reach, α is maximum number off offspring produced per female per river mile at low stock densities, b_r is the strength of the negative effect of density on recruitment, c is a parameter controlling the shape of the curve where $c < 1$ mimics a Cushing (1973) style curve with no asymptote, $c = 1$ mimics a Beverton-Holt (1957) curve with an asymptote, and $c > 1$ mimics an overcompensatory Ricker (1954) curve. Estimates of b_r varied by reach (r) to account for potential differences in carrying capacity due to differences in habitat quality among reaches but were held constant over time.

Fig. 3. Conceptual model representing age-0 dynamics (spawning through transition to age-1) driven by density-dependent production, discharge during the hatch, exploitation, summer growth, overwinter survival, and downstream movement. Offspring ($R_{r,t}$) were produced as a function of the number of spawners ($S_{r,t}$) and the total number of age-1 and older fish ($N_{r,t}$) present in the system in April before any removal trips (Density Dependent Production). Offspring available for exploitation ($n_{r,t,d,j}$) for each electrofishing trip j was a function of days past $V_{r,t,d}$ (the day in which offspring produced on hatch date d grow to 50 mm and are vulnerable to electrofishing), discharge during the hatch, and the capture probability p during each electrofishing trip (discharge and exploitation). Overwinter survival ($\varphi_{0,r,t,d}$) of fish produced on each day of the hatch was a function of length at the end of the growing season ($L_{r,t,d}$). Fish transitioning to the age-1 class in February and March the following year was based on the number of age-0 fish surviving the winter ($w_{r,t}$) and downstream movement among reaches. Age-0 movement (τ_0) was an unknown parameter and was set at 5% in the baseline model. Blue squares represent life stages across all reaches while pink, yellow and green squares represent life stages for specific reaches. Grey circles represent parameters and environmental drivers of transitions among life stages.



Survival of offspring to age-1 varied in response to conditions during hatch, exploitation, and summer growth. We used coefficients derived by Bestgen and Hill (2016) that linked observed hatch dates determined using age-0 otolith daily growth increments (Hill and Bestgen 2014) to flow and temperature metrics and hatch date. Based on this regression, initial hatch date (h) in terms of days after January 1 was calculated each year at each reach as

$$(3) \quad h_{r,t} = 149.68 + (0.013 \text{volume}_{r,t}) + (72.57 \text{hf_days}_{r,t}) + (0.574 \text{date}_{r,t})$$

where $\text{volume}_{r,t}$ is the total spring volume of flows between April and July in 1000 acre feet, $\text{hf_days}_{r,t}$ is the number of high flow days in each reach, calculated as the number of days in March, April, May, and June in which flows were over $348 \text{ m}^3 \cdot \text{s}^{-1}$ in the Middle Green reach and over $227 \text{ m}^3 \cdot \text{s}^{-1}$ in the Yampa Canyon reach and $\text{date}_{r,t}$ is the first day of the year in which water temperatures in each river reach 16°C .

We assumed individuals hatched over a 31-day period starting on the initial date, $h_{r,t}$, and the proportion of individuals hatching on each day was described by a truncated normal distribution centered on 15 days after $h_{r,t}$ with standard deviation of 6 (to distribute hatching across the entire 31-day

Table 1. Parameter symbols, descriptions, and priors used in the smallmouth bass population model.

Parameter	Description	Input value, prior, or hyperprior	Source or rationale, if applicable
$\tau_{SA, Lily \text{ to } YC}$	Sub-adult annual movement rate downstream from Lily Park to Yampa Canyon	0.32	Dispersal model fit to recaptures of tagged fish in the system.
$\tau_{SA, YC \text{ to } Lily}$	Sub-adult annual movement rate upstream from Yampa Canyon to Lily Park	0.03	Dispersal model fit to recaptures of tagged fish in the system.
$\tau_{SA, YC \text{ to } MG}$	Sub-adult annual movement rate downstream from Yampa Canyon to the Middle Green	0.07	Dispersal model fit to recaptures of tagged fish in the system.
$\tau_{SA, MG \text{ to } YC}$	Sub-adult annual movement rate upstream from the Middle Green to Yampa Canyon	0.10	Dispersal model fit to recaptures of tagged fish in the system.
$\tau_A, Lily \text{ to } YC$	Adult annual movement rate downstream from Lily Park to Yampa Canyon	0.28	Dispersal model fit to recaptures of tagged fish in the system.
$\tau_A, YC \text{ to } Lily$	Adult annual movement rate upstream from Yampa Canyon to Lily Park	0.05	Dispersal model fit to recaptures of tagged fish in the system.
$\tau_A, YC \text{ to } MG$	Adult annual movement rate downstream from Yampa Canyon to the Middle Green	0.07	Dispersal model fit to recaptures of tagged fish in the system.
$\tau_A, MG \text{ to } YC$	Adult annual movement rate upstream from the Middle Green to Yampa Canyon	0.19	Dispersal model fit to recaptures of tagged fish in the system.
τ_0	Age-0 downstream movement rate	0.05	Humston et al. (2010) assessed in sensitivity analysis
$p_{r, l, t}$	Time t and life stage l (sub-adult, adult) varying capture probability in each reach r .	$\text{logit}(p_{r, l, t}) \sim \text{Normal}(\mu_{l, r}, \sigma_{l, r})$	
$p_{0, j, t}$	Age-0 capture probability in each year t in the Middle Green reach	$\text{logit}(p_{0, j, t}) \sim \text{Normal}(\mu_0, \sigma)$	
$\mu_{l, r}$	Mean capture probability for life stage l in each reach r on logit scale	$\mu_{SA, Lily} \sim \text{Normal}(-1.3, 0.3)$ $\mu_{SA, YC} \sim \text{Normal}(-1.3, 0.3)$ $\mu_{SA, MG} \sim \text{Normal}(-3, 0.3)$ $\mu_A, Lily \sim \text{Normal}(-0.8, 0.3)$ $\mu_A, YC \sim \text{Normal}(-0.8, 0.3)$ $\mu_A, MG \sim \text{Normal}(-2.7, 0.3)$	Based on mean estimates of capture probabilities for electrofishing trips in 2004 through 2011 in Breton et al. (2014)
μ_0	Mean capture probability for age-0 fish in the Middle Green reach on logit scale	$\sim \text{Uniform}(-5, -1)$	We assumed age-0 capture probabilities were not higher than 0.27 given electrofishing selects for larger individuals (Dolan and Miranda 2003) and based on estimated capture probability of smallmouth bass ~ 100 mm in Breton et al. (2014). Note input priors were transformed on the logit scale.
$\sigma_{l, r}$	Standard deviation of capture probabilities for life stage l in each reach r	$\sim \text{Uniform}(0.5)$	
σ_0	Standard deviation of capture probabilities for age-0 fish.	$\sim \text{Uniform}(0.5)$	
α	Maximum age-0 production per spawner	$\sim \text{Uniform}(0, 1500)$	Since age-0 production was unknown, we assumed production could be any value between 0 and 1500. Previous studies estimated α to be just under 1000 (Peterson and Kwak 1999).
b_r	Magnitude of density dependence in each reach.	$\log(b_r) \sim \text{Uniform}(-12, -1)$	Previous estimates of b for smallmouth bass ranged from 2.25×10^{-4} to 2.23×10^{-28} (Peterson and Kwak 1999; Zipkin et al. 2008). Because the magnitude of density dependence was unknown, we allowed b to range from 4.2×10^{-5} to 0.36 (-12 to -1 on the log scale).

Table 1. (concluded).

Parameter	Description	Input value, prior, or hyperprior	Source or rationale, if applicable
c	Shape parameter of density-dependent age-0 production where $c < 1$ mimics a Cushing (1973) style curve with no asymptote, $c = 1$ mimics a Beverton-Holt (1957) curve with an asymptote, and $c > 1$ mimics an overcompensatory Ricker (1954) curve	$\sim \text{Uniform} (0,3)$	
β_{flow}	Slope for effect of mean 7-day discharge for each day of the hatch period on age-0 survival, logit scale	$\sim \text{Uniform} (-5,5)$	
β_0	Intercept for age-0 survival model, logit scale	$\sim \text{Normal} (-1.9, 0.8)$	Based on average survival rate of age-0 smallmouth bass in Curry et al. (2005) .
β_1	Slope for effect of end autumn length, based on hatch dates, on age-0 survival, logit scale	$\sim \text{Uniform} (-2,5)$	Predicted effect of summer length to be positive based on observation that smallmouth bass that reach longer lengths are more likely to survive the winter (Shuter et al. 1980; Shuter and Post 1990)
φ_1	Survival of age-1 smallmouth bass	$\sim \text{Normal} (0.37, 0.12)$	Based on range of survival values predicted based on the parameters estimated in Lorenzen (1996) that lead to mean adult survival rates similar to observations in Paragamian and Coble (1975) . See Methods for full description.
φ_2	Survival of age-2 smallmouth bass	$\sim \text{Normal} (0.49, 0.08)$	Same as φ_1
φ_3	Survival of age-3 smallmouth bass	$\sim \text{Normal} (0.58, 0.05)$	Same as φ_1
φ_{4+}	Survival of age-4 and older smallmouth bass	$\sim \text{Normal} (0.70, 0.03)$	Same as φ_1
Φ_r	Size parameter for negative binomial distribution used to fit predicted sub-adult and adult catch to observed catch in each reach r .	$\sim \text{Uniform} (0.01, \infty)$	
Φ_0	Size parameter for negative binomial distribution used to fit age-0 catch to observed catch in each reach r .	$\sim \text{Uniform} (0.01, \infty)$	
$N_{r,a,\text{Initial}}$	Initial abundance of smallmouth bass in each reach r and age class a .	$\log (N_{r,a,\text{Initial}}) \sim \text{Uniform} (5,15)$	

period) and was normalized to sum to 1. Individuals hatching on each of the d days in the 31-day period also differed in their exposure to flow disruptions (**Fig. 4**), and we also incorporated this in the equation describing realized production (production corrected for flow conditions) $n_{r,t,d,1}$, derived from each hatch date, d , in reach, r , and year, t :

$$(4) \quad n_{r,t,d,1} = R_{r,t} k_r \left(\frac{e^{-\frac{(d-16)^2}{2 \times 36}}}{\sum_{i=1}^{31} e^{-\frac{(i-16)^2}{2 \times 36}}} \right) e^{\beta_{\text{flow}} Q_{r,t,d}} e^{\beta_{\text{flow}} Q_{r,t,d}}$$

where $Q_{r,t,d}$ is the 7-day average scaled (z-scored) discharge for each day of hatch and β_{flow} is the estimated impact of $Q_{r,t,d}$.

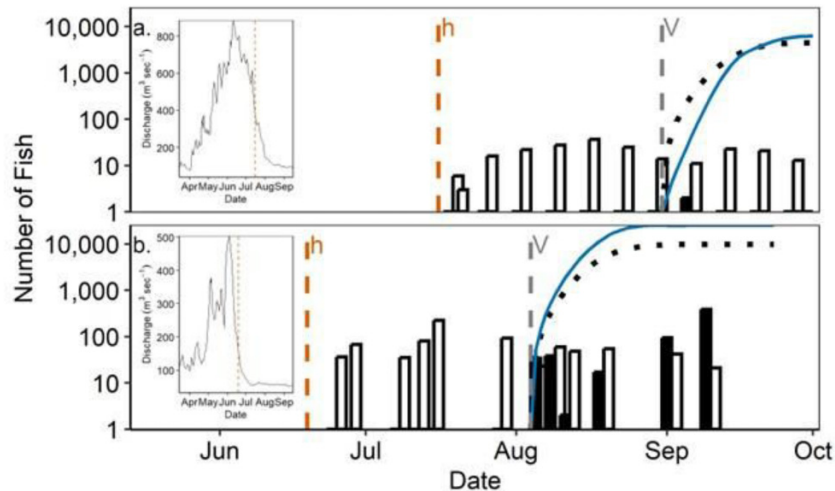
Available length frequency histograms (**Fig. A1**) from a sample of removal trips suggested smallmouth bass were not consistently vulnerable to electrofishing until they grew larger than 50 mm (**Appendix A**). Since electrofishing trips occur throughout the late spring, summer and early fall and age-0 smallmouth bass grow to a size greater than 50 mm over the course of the growing season, some trips occurred before any age-0 smallmouth bass were vulnerable to capture, some trips occurred when only a portion of the year's

cohort was vulnerable, and some trips occurred when the whole cohort was vulnerable. To determine whether individuals hatched on a particular day were vulnerable to a given electrofishing trip, we calculated the date, $V_{r,t,d}$, at which an individual born on d th day of the hatch (equivalent to the $h_{r,t} + d - 1$ day of the year) would become vulnerable to electrofishing according to:

$$(5) \quad V_{r,t,d} = h_{r,t} + j - 1 + \frac{(51 - 5.5)}{g_r}$$

where g_r is the mean age-0 growth rate for a given reach (1.1 mm/day for the Yampa River, 1.0 mm/day for the Middle Green River based on **Bestgen and Hill 2016**), and larvae are assumed to hatch at 5.5 mm based on laboratory observations (**Bestgen and Hill 2016**). Trips occurring before $V_{r,t,1}$ were assumed to only remove age-1 or older smallmouth bass and were ignored in calculating age-0 abundances (**Fig. 4**). All fish less than 100 mm observed in the Yampa River reaches were reclassified as sub-adults because all trips occurred before $V_{r,t,1}$ so that removals of age-0 fish only occurred in the Middle Green reach. The effects of trips that occurred on, or

Fig. 4. Smallmouth bass < 100 mm TL (white bars) were assumed to be age-1 fish if captured before V (grey dashed vertical line), the date in which individual born on 1st day of the hatch (h , orange dashed vertical line) would become vulnerable to electrofishing. Smallmouth bass under 100 mm captured after V (black bars) were assumed to be age-0 fish. We calculated V as the date in which fish grew to 51 mm based on observed age-0 growth rates in the study system. The total number of fish available to electrofishing varied each year on each trip based on total reproductive output based on the spawner recruit relationship (dotted line), corrected for flow conditions during the hatch (blue solid line). In the Middle Green reach in 2011 (a), sustained high flows (see inset) and low temperatures led to a late hatch and fewer age-0 fish than predicted by the Shepard model alone during the beginning of the hatch. In 2020 (b), a rapid drop in discharge before the hatch (see inset) led to more age-0 fish than predicted by the Shepard model. Note that the y-axes are log₁₀ transformed.



after, $V_{r,t,1}$ on the abundance of age-0 individuals were estimated by iterating through each trip, j , from the first trip on, or after, $V_{r,t,1}$ through the total numbers of trips, $f_{0,r,t}$ that occurred on, or after, $V_{r,t,1}$ and using the following equation:

$$(6) \quad n_{r,t,d,(j+1)} = n_{r,t,d,j} (1 - p_{0,t} p_{0,t} x_{r,t,d,j})$$

where $n_{r,t,d,(j+1)}$ represents the number of age-0 fish in reach r in year t originating from hatch date d remaining after removal trip j , $n_{r,t,d,j}$ represents the number of age-0 fish just prior to removal trip j , $p_{0,t}$ represents the capture probability of age-0 fish each year, and $x_{r,t,d,j}$ is an indicator variable taking a value of 0 if trip j occurred before the date at which fish from hatch date d became vulnerable (i.e., $V_{r,t,d}$) and 1 if trip j occurred on, or after, $V_{r,t,d}$. Note that $p_{0,t}$ was only estimated for trips occurring in the Middle Green reach since all trips occurring in reaches of the Yampa River occurred before $V_{r,t,1}$. Values of $p_{0,t}$ varied randomly across years and were modelled as

$$(7) \quad \text{logit}(p_{0,t}) \sim \text{Normal}(\mu_0, \sigma_0)$$

where μ_0 and σ_0 were estimated by the model (Tables 1 and 2).

Age-0 smallmouth bass remaining after the final electrofishing trip were subjected to overwinter survival, which also differed by hatch date since individuals hatched earlier are expected to be larger and experience less overwinter mortality (Shuter and Post 1990). Specifically, overwinter survival

(φ_0) was modelled as

$$(8) \quad \text{logit}(\varphi_{0,r,t,d}) = \beta_0 + \beta_1 L_{r,t,d}$$

where $L_{r,t,d}$ is the predicted autumn length (mm) of an individual born of the d th hatch date and β_0 and β_1 are estimated parameters. We calculated $L_{r,t,d}$ using growth equations presented in Bestgen and Hill (2016), adjusted for the 31-day hatching period:

$$(9) \quad \text{length}_{r,t,d} = 134.1 + (-0.66 \times h_{r,t}) + (2.82 \text{summer_temp}_{r,t}) - (1.6 \times d)$$

where $\text{summer_temp}_{r,t}$ is the mean summer (1 July to 15 August) temperature. The number of age-0 individuals surviving after removals that originated from each hatch date were multiplied by their hatch-date-specific overwinter survival to estimate the overall number of age-0 bass surviving through the winter, $w_{r,t}$, according to the following equation:

$$(10) \quad w_{r,t} = \sum_{j=1}^{31} (\varphi_{0,r,t,d} n_{r,t,(1+f_{0,r,t})j})$$

Age-0 smallmouth bass were assumed to only disperse downstream based on a priori hypotheses about the study system and estimates in other systems (Humston et al. 2010). This parameter was unidentifiable given the data available. We therefore assumed a constant rate of downstream dispersal. Because this parameter was not estimated by our model and there was limited information in the literature regarding age-0 dispersal, we tested model sensitivity to varying values

Table 2. Parameter estimates (95% credible intervals) assuming 5% of age-0 smallmouth bass disperse downstream.

Parameter	Mean estimate (95% credible interval)	Parameter	Mean estimate (95% credible interval)
μ_0^*	-3.38 (-4.19, -2.48)	φ_1	0.63 (0.48, 0.79)
$\mu_{SA, Lily}^*$	-1.95 (-2.52, -1.34)	φ_2	0.76 (0.64, 0.89)
$\mu_{SA, YC}^*$	-1.76 (-2.35, -1.17)	φ_3	0.72 (0.63, 0.81)
$\mu_{SA, MG}^*$	-3.33 (-3.79, -2.81)	φ_{4+}	0.79 (0.73, 0.86)
$\mu_A, Lily^*$	-1.37 (-1.83, -0.88)	Φ_{Lily}	1.39 (1.10, 1.72)
μ_A, YC^*	-1.29 (-1.88, -0.67)	Φ_{YC}	1.94 (1.42, 2.53)
μ_A, MG^*	-3.03 (-3.38, -2.67)	Φ_{MG}	2.40 (1.95, 2.84)
$\sigma_{Lily, SA}$	1.45 (0.77, 2.35)	Φ_0	0.34 (0.25, 0.45)
$\sigma_{YC, SA}$	2.23 (1.52, 3.47)	$N_{Lily, 1, Initial}^*$	9.57 (5.34, 14.08)
$\sigma_{MG, SA}$	1.11 (0.72, 1.69)	$N_{Lily, 2, Initial}^*$	9.67 (5.22, 14.22)
$\sigma_{Lily, A}$	0.96 (0.47, 1.71)	$N_{Lily, 3, Initial}^*$	9.95 (5.27, 14.09)
$\sigma_{YC, A}$	2.79 (1.82, 4.13)	$N_{Lily, 4+, Initial}^*$	9.99 (5.31, 14.14)
$\sigma_{MG, A}$	0.69 (0.42, 1.09)	$N_{YC, 1, Initial}^*$	9.11 (5.15, 14.27)
σ_0	0.75 (0.18, 1.34)	$N_{YC, 2, Initial}^*$	8.84 (5.17, 14.22)
α	29.27 (8.21, 106.21)	$N_{YC, 3, Initial}^*$	8.47 (5.13, 13.73)
cc	1.12 (0.20, 2.86)	$N_{YC, 4+, Initial}^*$	8.18 (5.15, 13.57)
b_{Lily}^*	-10.75 (-13.85, -5.24)	$N_{Lily, 1, Initial}^*$	9.57 (5.34, 14.08)
b_{YC}^*	-4.10 (-6.12, -0.34)	$N_{MG, 1, Initial}^*$	6.66 (5.07, 8.34)
b_{MG}^*	-7.04 (-13.51, -1.24)	$N_{MG, 2, Initial}^*$	6.35 (5.07, 8.03)
β_{flow}	-1.58 (-2.10, -1.11)	$N_{MG, 3, Initial}^*$	5.95 (5.04, 7.35)
β_0	-1.16 (-2.31, 0.04)	$N_{MG, 4+, Initial}^*$	7.32 (6.64, 8.09)
β_1	0.82 (0.06, 1.77)		

Note: Descriptions of parameters and transformations (marked with *) are provided in Table 1.

of age-0 downstream dispersal (τ_0 , Appendix B). We tested sensitivity assuming 0%–50% dispersal based on previously reported values (Humston et al. 2010). For baseline models presented in the main text, τ_0 was assumed to be 5% because standard errors of many parameter estimates were the lowest at either 0% or 5% movement (Appendix B).

The number of age-0 fish recruiting to age-1 (number of fish in April the following calendar year) in each reach was calculated as

$$(11) \quad N_{Lily, 1, (t+1)} = w_{Lily, t} (1 - \tau_0)$$

$$(12) \quad N_{YC, 1, (t+1)} = w_{YC, t} (1 - \tau_0) + (w_{Lily, t} \tau_0)$$

$$(13) \quad N_{MG, 1, (t+1)} = w_{MG, t} (1 - \tau_0) + (w_{YC, t} \tau_0)$$

No downstream movement of age-0 bass into the Lily Park reach from upstream reaches was included. Because smallmouth bass reproduction is known to occur upstream of Lily Park, $N_{Lily, a=1}$ is assumed to represent fish in the Lily Park reach and above.

Annual exploitation, dispersal, and survival (age-1 and older)

We assumed annual survival rates of fish age-1 and older were constant across space and years but varied with age. We estimated annual survival for age-1 through age-4+ smallmouth bass using priors informed by the mass mortality re-

lationships estimated by Lorenzen (1996) and empirical estimates of natural mortality in Paragamian and Coble (1975). We first calculated all possible age specific mortality rates for smallmouth bass based on the mean and 90% confidence intervals for the mortality–weight relationship derived for riverine fishes (Lorenzen 1996) based on age–weight relationships using the standard weight equation for smallmouth bass (Kolander et al. 1993). We then removed estimates from any combination of parameters in the mortality–weight model that produced estimates of adult mortality outside the range of estimates observed in Paragamian and Coble (1975). Finally, we used the range of potential age-specific mortality rates estimated using the remaining combination of parameters in the Lorenzen equation to derive means and standard deviations to use as priors on age-specific survival in our model (Table 1).

We estimated capture probability for an electrofishing trip ($p_{r, l, t}$) for each reach (r), life stage (l ; sub-adult vs. adult), and year (t) as random effects:

$$(14) \quad \text{logit}(p_{r, l, t}) \sim \text{Normal}(\mu_{r, l}, \sigma_{r, l})$$

where $\mu_{r, l}$ is the mean capture probability for either sub-adults or adults in each reach on a logit scale and $\sigma_{r, l}$ is the standard deviation for each life stage in each reach. Although $p_{r, l, t}$ represents the capture probability of an individual trip, our model assumed capture probabilities only varied among years and rivers, not across trips within a year. We allowed capture probabilities to vary among years to account for changing personnel and average conditions among years.

We recognize within year variation in discharge and temperature likely influences capture probabilities; however, our attempts to model that variation led to model convergence issues, likely due to data limitations.

To incorporate exchange of adult (>200 mm) and sub-adult (100–200 mm) bass among our study reaches we analyzed individual movements of marked smallmouth bass within the system outside of our population model, scaled individual movements to predict reach-scale rates of exchange, and inputted reach scale estimates as data into our population model. Specifically, we assumed a Cauchy distribution to describe movement (see Korman et al. 2016 and Dzul et al. 2018 for other examples of applying this distribution to describe fish movement) and estimated location and scale parameters based on the observed movement of individuals between marking and recapture events where downriver movements are defined as negative and upriver movements as positive. Location and scale parameters were estimated separately for sub-adult and adult fish and were based only on movements observed over approximately 1-year intervals (i.e., where recaptures occurred one calendar year after marking). To scale individual rates of movement to reach-scale movement rates, $\tau_{l, D-R}$, for a given life stage, l , we assumed individuals were evenly distributed in a donor (starting) reach, D , and used the following equation to estimate flux to a receiving (ending) reach, R :

$$(15) \quad \tau_{l, D-R} = \sum_{x=X_{D,down}+0.5}^{X_{D,up}-0.5} \int_{Y_{R,down}}^{Y_{D,down}} \text{Cauchy}(x-y, \chi_l, \gamma_l) dy / N_D$$

where $X_{D,down}$ and $X_{D,up}$ are the river miles corresponding to the bottom and top of the donor reach, $Y_{D,down}$ and $Y_{D,up}$ are the river miles corresponding to the bottom and top of the receiving reach, χ_l and γ_l are the estimated location and scale parameters for life stage, l , and N_D is the total number of river miles in the donor reach. Values of $\tau_{l, D-R}$ were generated for each pair of neighboring reaches and each life stage and used as constant parameters in the population model. We only included movement among the three study reaches; we did not include movement from adjacent reaches into or out of the Lily Park or Middle Green reaches. Including dynamics from adjacent reaches would require estimating abundances in those reaches. Smallmouth bass are well established upstream of Lily Park; given this knowledge and the small size of the Lily Park reach (approximately 8 km), we expect our estimates of recruitment and abundance will be inflated and influenced by dynamics in the upstream adjacent reach. Impacts of movement into the most downstream reach in our study, the Middle Green, are assumed to be weaker because this reach is larger (approximately 42 km).

The abundance of fish in each age class (ages 1 through 4+) transitioning to the next stage each year ($N_{r,(a+1),(t+1)}$) was influenced by exploitation, dispersal, and age-specific survival (in that order). We therefore made the simplifying assumption that all natural mortality occurred over the fall and winter after reproduction and exploitation, which may lead to higher predicted catch than observed. We believed this was a reasonable assumption given the post-reproductive and winter periods are likely primary sources of natural mortality.

We calculated abundance as

$$(16) \quad N_{Lily,(a+1),(t+1)} = \left[N_{Lily,a,t} (1 - p_{Lily,a,t})^{f_{Lily,t}} (1 - \tau_{a, Lily \text{ to } YC}) + N_{YC,a,t} (1 - p_{YC,a,t})^{f_{YC,t}} \tau_{a, YC \text{ to } Lily} \right] \varphi_a$$

$$(17) \quad N_{YC,(a+1),(t+1)} = \left[N_{YC,a,t} * (1 - p_{YC,a,t})^{f_{YC,t}} * (1 - \tau_{a, YC \text{ to } Lily} - \tau_{a, YC \text{ to } MG}) + N_{Lily,a,t} (1 - p_{Lily,a,t})^{f_{Lily,t}} \tau_{a, Lily \text{ to } YC} + N_{MG,a,t} (1 - p_{MG,a,t})^{f_{MG,t}} \tau_{a, MG \text{ to } YC} \right] \varphi_a$$

$$(18) \quad N_{MG,(a+1),(t+1)} = \left[N_{MG,a,t} * (1 - p_{MG,a,t})^{f_{MG,t}} * (1 - \tau_{a, MG \text{ to } YC}) + N_{YC,a,t} (1 - p_{YC,a,t})^{f_{YC,t}} \tau_{a, YC \text{ to } MG} \right] \varphi_a$$

where $p_{r,a,t}$ is the capture probability by age class (ages-1 through 3 grouped as sub-adults and age-4+ as adults) of being captured on a trip and $f_{r,t}$ is the number of trips completed in each reach and year.

Fitting the model

Predicted catch (C) of age-1 through age-4+ fish (a) for each electrofishing trip (j) in each reach (r) each year (t) was calculated as

$$(19) \quad C_{r,a,t,j} = N_{r,a,t} p_{r,a,t} (1 - p_{r,a,t})^{(j-1)}$$

Predicted catch, $C_{r,a,t,j}$ was aggregated by life stage (l) so it could be linked to observed catch data that was pooled as sub-adults (100–200 mm TL) and adults (over 200 mm TL). Predicted catch of sub-adults ($C_{r,SA,t,j}$) and adults ($C_{r,A,t,j}$) were fit to observed catch ($Y_{r,l,t,j}$) data (see *Input Data*) using a negative binomial distribution on a log scale:

$$(20) \quad Y_{r,l,t,j} \sim \text{NB}(C_{r,a,t,j}, \Phi_r)$$

where Φ_r is the overdispersion parameter which varied by river to account for unexplained variation in catch rates due to hypothesized differences in capture probabilities among trips that vary by river. Observed catch was available for 2008–2022 in the Lily Park and Yampa Canyon reaches and from 2005 to 2022 in the Middle Green reach.

Catch of age-0 fish was fit to observed catch of fish under 100 mm TL captured during electrofishing trips that occurred after $V_{r,t,j}$. Any fish under 100 mm TL captured before $V_{r,t,j}$ were assumed to be age-1 fish and were included in the sub-adult class (Fig. 4). We verified our classification of fish as age-1 versus age-0 by visually analyzing length frequency histograms for years and reaches in which individual length data were available (SI 1). All fish under 100 mm TL in the Lily Park and Yampa Canyon were considered age-1 under these criteria, therefore we calculated the predicted catch of age-0 fish in the Middle Green reach as: $C_{0,1,t,j} = n_{3,t,j,i} - n_{3,t,j,(i+1)}$. We then compared $C_{0,1,t,j}$ to observed age-0 catch in the Middle Green reach (Y_0) according to

$$(21) \quad Y_{0,t,j} \sim \text{NB}(C_{0,1,t,j}, \Phi_0)$$

where Φ_0 is the overdispersion parameter.

The model was fit in the program *Stan* (Stan Development Team 2013) and included three chains, each with 1500 burn-in and 1000 sampling iterations for a total of 3000 posterior

draws for all model parameters. All environmental covariates were standardized and centered around means. Priors and hyperpriors on all parameters are reported in Table 1. Chains were checked for approximate convergence through visual examination and by ensuring all values of $\hat{R} < 1.1$. We compared observed and predicted catch, assessed distributions of and correlations among parameter posteriors, and developed observed quantile versus expected quantile plots using a negative binomial distribution as forms of posterior predictive checks.

Simulation case study: retrospective analysis of mechanical removal effort

To highlight the utility of the model as a tool for assessing population responses to alternative management actions or changing environmental conditions, we predicted potential differences from observed smallmouth bass abundances in response to two management endpoints: no mechanical removal and sustained maximum effort each year. Observed discharge and temperature in each reach from 2005 to 2022 were used as input into the simulation. We accounted for uncertainty in our parameter estimates by using the 3000 draws from the posterior distributions.

In the first scenario, we assumed there was no effort to remove smallmouth bass from any of the three reaches by setting the number of trips ($f_{r,t}$) to zero each year. For the maximum effort scenario, we assumed the maximum number of trips logistically possible in each river was the maximum $f_{r,t}$ observed in each reach. Because fish are mechanically removed using raft or boat mounted electrofishing, low flow conditions can limit the timing and number of trips, especially in the Yampa River. We therefore randomly sampled maximum $f_{r,t}$ (9, 7, and 16) sample dates that fell between the earliest (13 April, 8 April, and 3 June) and latest (1 October, 10 August, and 8 October) observed sampling dates for Lily Park, Yampa Canyon, and Middle Green reaches, respectively. The timing of the simulated trips was important, as the number of age-0 fish available for capture is zero before $V_{r,t,d}$ and increases throughout the summer.

We calculated the percent change from the baseline model estimates of sub-adult and adult abundances of smallmouth bass based on observed exploitation effort (N_{baseline}) to estimates produced in the two simulation scenarios (N_{scenario}) for each independent draw from the posterior distribution. Percent change from baseline was therefore calculated as

$$(22) \quad \frac{(N_{\text{scenario}} - N_{\text{baseline}})}{N_{\text{baseline}}} * 100$$

We ran simulations assuming either 5% or 50% of age-0 fish disperse downstream to assess how sensitive results were to this parameter.

Results

Total mean catch summed across electrofishing trips within a year (and therefore the number removed) of sub-adult smallmouth bass was 1941 (range = 77–5533) in Lily Park, 1463 (range = 54–4121) in Yampa Canyon, and 1890 (range = 56–7381) in the Middle Green reach. Total mean

catch of adults was 447 (range = 90–868), 382 (range = 63–1012), and 569 (range = 125–1796) for the Lily Park, Yampa Canyon, and Middle Green reaches, respectively. Maximum annual catch was observed in 2009 for the Lily Park Reach and 2021 for the Yampa Canyon and Middle Green reaches (Fig. 1b). Mean catch of age-0 fish per year in the Middle Green was 898 but was highly variable among years (0–8033), with maximum catch observed in 2007.

Dispersal

Thirty-six percent of sub-adult and 48% of adult smallmouth bass moved less than 10 km from the initial tagging location. Movement of sub-adult smallmouth bass in the Green River subbasin was skewed downstream with a location parameter (peak of distribution) of -0.87 (SE: 0.51) km and scale parameter (half of the width of the distribution at half the maximum height) of 15.81 (SE:1.87) km, while adult movement was biased upstream with a location parameter of 1.66 (SE:0.13) km and scale parameter of 10.46 (SE:1.07) km. Based on these distributions of distances moved and the total length of each focal reach, we estimated 32% and 28% of sub-adults and adults, respectively, in Lily Park moved downstream to Yampa Canyon, 2.8% and 4.6% moved upstream from Yampa Canyon to Lily Park, 6.5% and 7.4% moved downstream to the Middle Green from Yampa Canyon, and 9.6% and 18.5% moved upstream to Yampa Canyon from the Middle Green reach. Note the distributions of distances moved by individual fish in each life stage were constant among reaches and differences in percentages of fish moving among reaches are largely driven by the length of the reach.

Demographic model

Correlations among observed and predicted catch were lowest for age-0 fish (Pearson's $r = 0.3636$) and the Lily Park reach for adults (Figs. 5a–5c). Our model using negative binomial distributions generally fit the data well, as indicated by only minor deviations in observed quantiles from expected quantiles (Fig. 5d–5f). Sensitivity analysis of parameter estimates revealed shifts in estimates (interpreted by credible intervals not overlapping mean estimate of baseline model, Fig. B1) of the slope coefficients describing age-0 survival, with higher levels of dispersal corresponding with steeper slopes for the effect of end of summer length (Appendix B). Higher dispersal values were also associated with weaker effects of discharge on age-0 production (Appendix B). Uncertainty (range of 95% credible intervals) in some parameters, especially those associated with the stock-recruit relationship (α , c , and b_r), varied with increased levels of downstream movement (Appendix B).

Estimated capture probabilities for a single electrofishing trip varied asynchronously among years across the three reaches (Fig. 6), likely driven by varying geomorphology among reaches influencing electrofishing efficiency and variation in crews and average sampling conditions among years. For example, capture probabilities in Lily Park had higher uncertainty and more variability than Yampa Canyon or the Middle Green (Fig. 6). Mean estimates of capture probabilities were higher for adults than sub-adults and higher in both

Fig. 5. Goodness-of-fit metrics comparing observed catch to predicted catch in each reach for each age class, including Pearson correlation coefficients (r) among observed and mean predicted counts and mean for age-0 fish in the Middle Green (a) and sub-adults (b) and adults (c) across all three reaches and expected versus observed quantiles of each life stage based on a negative binomial distribution (d–f). Dashed line is the 1:1 line.

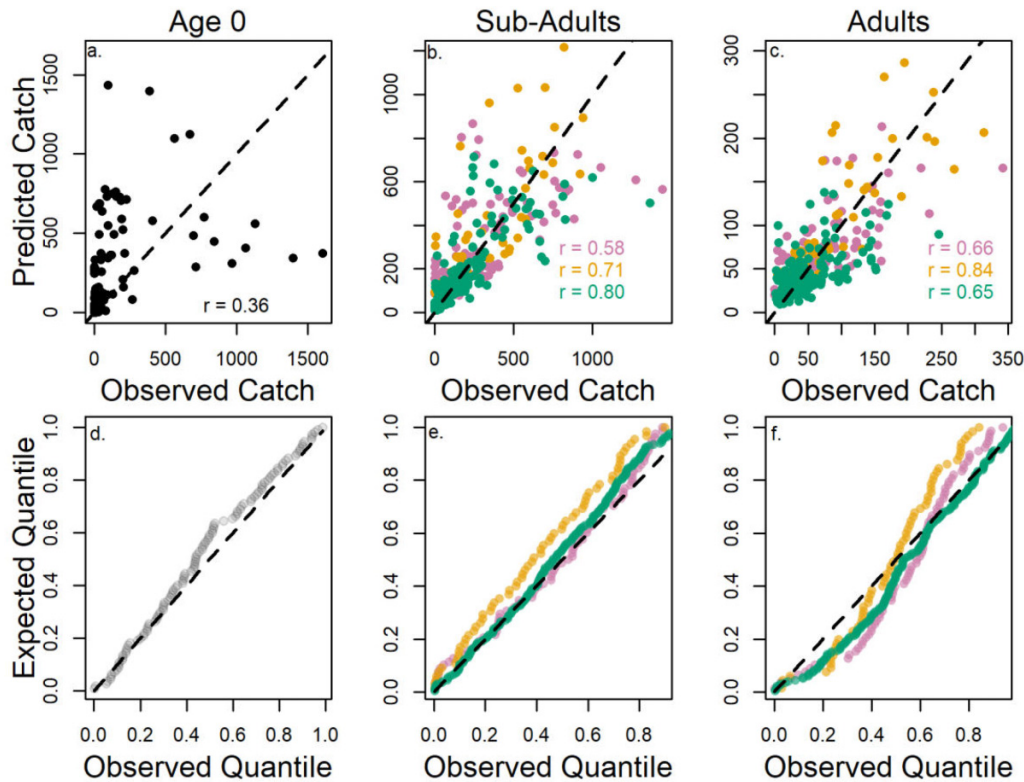
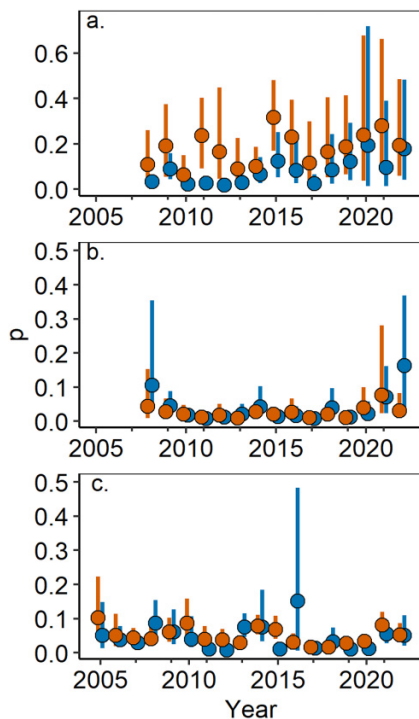


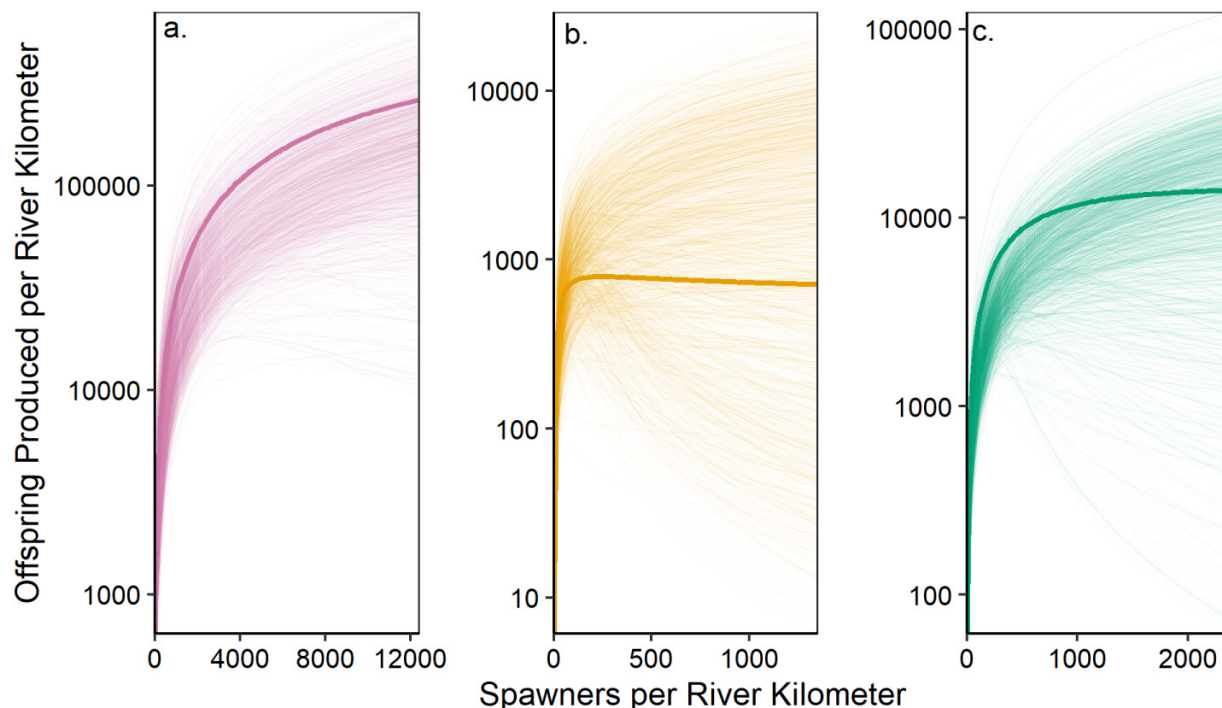
Fig. 6. Mean and 95% credible intervals for estimated capture probabilities for adults (orange) and sub-adults (blue) in the Lily Park (a), Yampa Canyon (b), and Middle Green (c) reaches. Note different y axes among reaches.



Yampa River reaches than in the Middle Green (Table 2, Fig. C1, Appendix C). Age-0 capture probabilities were generally low across years (mean = 0.03, range = 0.02–0.077, Fig. C2, Appendix C).

Recruitment of fish to age-1 varied across time and reaches in response to density-dependent production of offspring, hatch date (as a function of flow and thermal regimes pre-hatch), flow conditions during hatching, exploitation, and growth during the summer (as a function of hatch date and summer temperature). Parameters associated with density-dependent production of age-0 fish had relatively high uncertainty. Mean maximum production of offspring (α) was estimated to be 29, but 95% credible intervals ranged from 8 to 106. Similarly, 95% credible intervals of the stock-recruitment shape parameter (c) ranged from 0.2 to 2.9, capturing the full range of possible curve types (Cushing, Beverton-Holt, and Ricker). The strength of density dependence was the weakest in the Lily Park reach and strongest in Yampa Canyon (Table 2). Uncertainty in parameter estimates associated with the Shepard density-dependent model are highlighted in Fig. 7 which shows the density of offspring produced per kilometer across varying spawner densities in each reach. Daily discharge during the hatching period had a negative effect on the number of age-0 fish produced ($\beta_{\text{flow}} = -1.60$, $\text{SE} < 0.01$), and age-0 length in autumn had a strong positive effect on overwinter survival ($\beta_1 = 0.81$, $\text{SE} = 0.09$; Table 2). The total number of recruits (number of age-0 fish that survived the

Fig. 7. The predicted relationship between the density of offspring produced and the density of spawners varied among the Lily Park (a), Yampa Canyon (b), and Middle Green reaches. Plots are drawn using estimates of α (max production), b_r (strength of density dependence in each reach), and c (shape parameter) across 1000 random draws from the posterior distribution. Bold lines represent the shape of the relationship based on mean parameter estimates.



winter and were available as age-1 fish before spring and summer sampling) was highly variable each year, with the largest recruitment years occurring in Lily Park and Yampa Canyon (Fig. 8). Relatively large numbers of age-0 fish were predicted to transition to age-1 in relatively warm, dry years (e.g., 2012 and 2018) in all reaches; however, 2020 and 2021 were the largest recruitment years in the Middle Green reach, but not in the Yampa River reaches (Fig. 8). Recruitment was low in years with later hatching periods, cooler water temperatures, and higher flows during the hatch (e.g., 2011 and 2019).

Densities of sub-adult smallmouth bass were typically higher and more variable in the Lily Park and Yampa Canyon reaches relative to the Middle Green. Sub-adults were more abundant than adults in all reaches (Fig. 9). Our density estimates were similar to or lower than previous estimates (Breton et al. 2014) in the Middle Green reach (Figs. 9c and 9f). As expected, our model predicted higher densities than previous estimates in Lily Park (Figs. 9a and 9d). Our densities estimates were also higher in Yampa Canyon than previous estimates (Fuller 2009; Breton et al. 2014; Figs. 9b and 9e).

Simulation case study: retrospective analysis of mechanical removal effort

Simulations assuming either 5% or 50% age-0 downstream dispersal yielded similar trends in simulation results (although different absolute values), so only results from the 5% dispersal scenario are presented here. Results assuming 50% dispersal are presented in Appendix D. If no past effort was made to remove smallmouth bass, our simulation predicted abundance of adults and sub-adults would have increased in

Fig. 8. Mean and 95% credible intervals for the estimated total number of recruits in the Lily Park (a), Yampa Canyon (b), and Middle Green (c) reaches each year. A recruit is defined as the number of age-0 fish transitioning to the age-1 class after accounting for density-dependent production, hatch date, flow conditions during hatching, and summer growth.

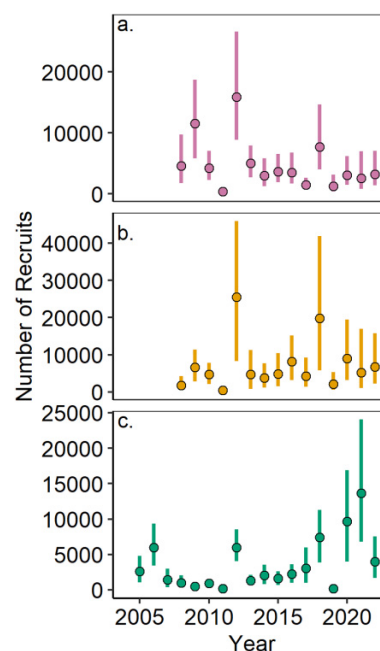
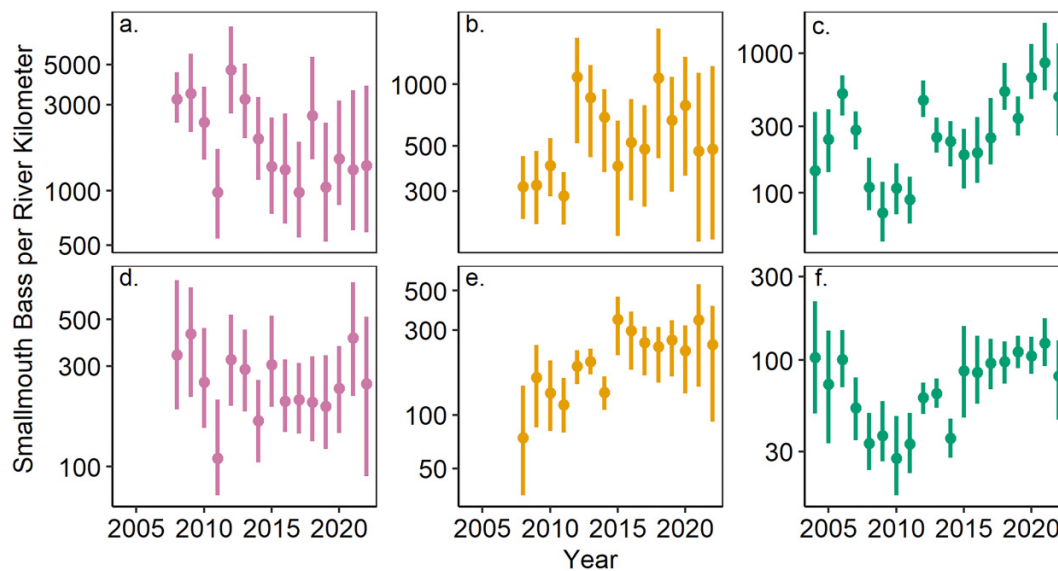


Fig. 9. Estimated density with 95% credible intervals of sub-adult (a–c; 100–200 mm) and adult (d–f; >200 mm) smallmouth bass each year in the Lily Park (pink), Yampa Canyon (yellow), and Middle Green (green) reaches. Densities were calculated by dividing the estimated abundances by the total length of each reach (km). Y-axes are on the logarithmic scale and limits differ among reaches.



all three reaches (Figs. 10a–10f). Across years of the simulation, the largest predicted median (across iterations) increase in abundance of adults in the absence of exploitation was in Lily Park, with a peak of 8338% ($PI_{95\%} = 1367\% - 64\,160\%$) relative to observed levels of exploitation (hereafter baseline, Fig. 10d.). Predicted change in abundance of sub-adults was also highest in the Lily Park reach with a peak median % change across years of 4839% ($PI_{95\%} = 645\% - 38\,849\%$) relative to baseline (Fig. 10d).

Simulated maximum effort every year generally led to declines relative to baseline across reaches for both adults and sub-adults (Figs. 10g–10i). Maximum (across years) median (across iterations) % change from baseline in Lily Park was -88% ($PI_{95\%} = -96\% \text{ to } -75\%$) for both sub-adults and adults. Maximum median % changes from baseline in Yampa Canyon and Middle Green were -74% ($PI_{95\%} = -88\% \text{ to } -57\%$) and -52% ($PI_{95\%} = -77\% \text{ to } 17\%$), and -74% ($PI_{95\%} = -89\% \text{ to } -55\%$) and -68% ($PI_{95\%} = -89\% \text{ to } -38\%$) and for sub-adults and adults, respectively.

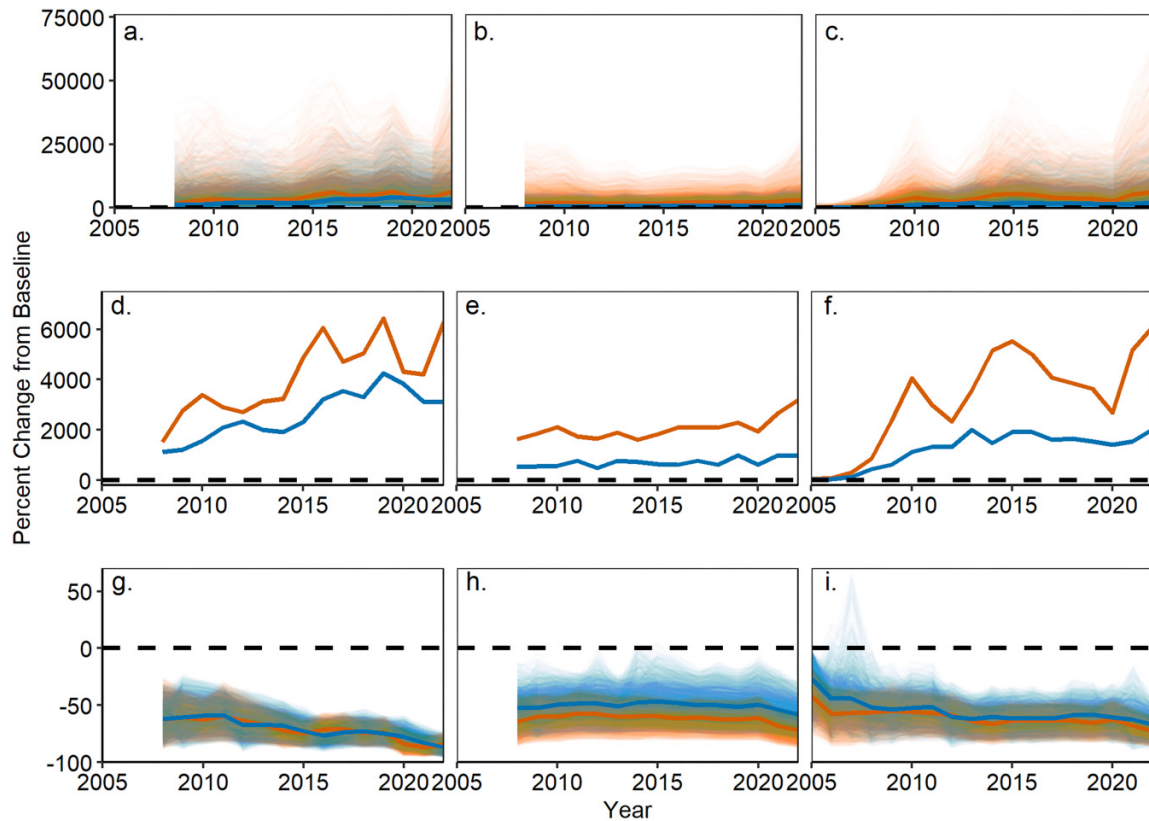
Discussion

Our model successfully captured fluctuations in observed catch of smallmouth bass based on hypothesized and estimated dynamics of dispersal, recruitment, survival, and exploitation. We made many assumptions about the biological and observational processes driving smallmouth bass population dynamics and capture efficiencies through the model structure, use of informative priors, and use of literature derived estimates of some parameters. These assumptions were necessary given the lack of system-specific estimates of many demographic parameters and likely bias some of our results, especially estimates of abundance and density. For example, we predicted our estimates of densities in the Lily Park reach would be higher than true densities, due to the lack

of inclusion of downstream dispersal from upper reaches in our model. Despite these limitations, our model provided several useful observations that warrant further exploration. Smallmouth bass dispersal was biased downstream and facilitated exchange of fish among reaches with different environmental conditions. The timing of hatch and conditions during hatch were important drivers of age-0 recruitment to age-1, but there was relatively high uncertainty in parameters describing the shape and strength of density-dependent production, highlighting the challenge of differentiating density-dependent dynamics in exploited populations that never approach carrying capacity because of removal efforts. Our retrospective analysis suggested sustained maximum effort could have led to up to 89% lower densities than under observed exploitation levels. Despite not reaching that potential, our analysis also revealed the success of removal efforts at keeping abundances of smallmouth bass much lower than predicted if no exploitation had occurred. However, uncertainty in density dependent parameters led to likely unreasonably high % change in abundance in no-removal scenarios (Fig. 10). The models presented in this study can be used to further investigate smallmouth bass responses to exploitation efforts, including targeting different age classes, timing of exploitation, and levels of effort, as well as responses to future environmental conditions resulting from climate variability, water use, and reservoir management.

The distribution of movement distances observed in the Green River basin support previous observations of variable and potentially context-dependent movement and dispersal patterns (Ridgway et al. 2002; Westhoff et al. 2016; Miller and Brewer 2022). Our analysis of reencountered fish suggested 36% of sub-adult and 48% of adult smallmouth bass moved less than 10 km in a year. This result is consistent with other studies reporting the proportion of sedentary smallmouth bass varies between 37% and 69% (Funk 1955; VanArnum et al.

Fig. 10. Simulated % change in abundance of smallmouth bass sub-adults (orange, 100–200 mm) and adults (blue, over 200 mm) from observed exploitation effort (baseline) for two exploitation scenarios in the Lily Park (left column), Yampa Canyon (middle column), and Middle Green (right column) reaches. Percent change from baseline was calculated as the difference between the scenario and baseline abundance divided by the baseline abundance and multiplied by 100. The no effort scenario (a–f) assumed no fish were removed and the max effort scenario (g–i) assumed the maximum number of observed electrofishing trips was completed every year. Parameters used in simulations of max and no effort scenarios were drawn from the 3000 posterior draws from the model fit to observed data and both simulations included effects of observed environmental variation (flow and temperature) on recruitment. Bold lines represent median estimates across simulations and thin lines are drawn for simulations between the 2.5th and 97.5th percentiles. Median lines for the no removal scenario are shown in the middle panels (d–f) to highlight general trends.



2004; Westhoff et al. 2016). Although most individuals moved short distances, some fish moved up to 150 km from tagging locations. These long-distance movements (over 100 km) have been observed in other large river systems (Rubenson and Olden 2017; McClure et al. 2020). We also observed an upstream bias in dispersal of adult fish. Adult smallmouth bass sometimes have high nesting site fidelity (Ridgway et al. 1991) and the Yampa River, especially Lily Park and upstream reaches, are hypothesized to be high quality nesting habitats relative to downstream reaches; therefore, upstream bias in dispersal may be due to reproductive adults moving back to nesting sites. Although adult bass often go back to the same nesting areas, offspring typically nest away from natal sites (Humston et al. 2021). Density-dependent movement of sub-adults can lead to net displacement away from nesting areas. Our observation of biased downstream movement by age-1 and 2 bass may support this “juvenile transition hypothesis” (Ridgway et al. 2002). However, our estimates of dispersal in the system were based on recaptures of tagged individuals, not a study designed explicitly to assess movement and dispersal. Because dispersal plays an important role in smallmouth bass invasion dynamics (Rubenson and Olden 2017) as

well as population stability and synchrony over time (Hanski 2001), targeted studies of adult and sub-adult movement are needed to more accurately assess the role of dispersal in population dynamics, especially across riverscapes with variable environmental conditions such as the Green River sub-basin.

Dispersal of age-0 smallmouth bass was a primary source of uncertainty in our model due to the scarcity of information from other systems to inform model structure and our inability to estimate this parameter directly. We assumed age-0 smallmouth bass only dispersed downstream based on expert opinion in the study system and observations in other systems (Humston et al. 2010). Our sensitivity analysis indicated mean estimates and uncertainty in parameters associated with density-dependent production and age-0 survival changed in response to increases in the assumed proportion of age-0 fish moving downstream (Appendix B), while other parameters were less sensitive. Sensitivity in these parameters in response to changing assumptions about age-0 dispersal is not surprising given that less movement out of a reach would lead to estimates of age-0 production to be lower. We did not assess model fit or sensitivity to other dispersal patterns of age-0 fish, such as net non-directional movement,

as evidenced by frequent movements between upstream and downstream in some systems (Humston et al. 2017). Studies in lakes suggest age-0 fish remain within approximately 200 m of the nesting habitats (Ridgway et al. 2002); however, it is difficult to compare observations in lakes to rivers with unidirectional flow. Conflicting observations in the literature regarding age-0 behavior and dispersal suggest more work is needed to address this source of uncertainty in smallmouth bass population dynamics.

As predicted, we estimated a strong effect of age-0 autumn length on survival. Fish that hatch earlier and grow larger are known to have higher overwinter survival (Shuter et al. 1980) due to larger lipid reserves (Ludsin and DeVries 1997) and lower susceptibility to displacement and predation (Rice et al. 1993). While summer growth was an important driver of age-0 overwinter survival, we were unable to assess the impact of winter severity as another source of overwinter mortality. Cold water temperatures limit growth and can directly cause mortality due to low dissolved oxygen levels (if there is ice cover), physiological stress, starvation (Shuter et al. 1980, 1989; Shuter and Post 1990) and decreased swimming ability (Suski and Ridgway 2009). Our attempts to include effects of winter conditions (number of starvation days) in the model led to identifiability issues unless highly informative priors were used. Because warm winters could also lead to increased size-dependent mortality if food availability does not meet bioenergetic demands (Curry et al. 2005), future work is needed to understand the importance of winter water temperatures to age-0 survival.

Density-dependent processes are difficult to quantify, but are predicted to be important drivers of smallmouth bass in many systems and are hypothesized to play an important role in the effectiveness of removal efforts of non-native fish generally (Klein et al. 2023). We observed uncertainty in the shape of the density dependent parameter, with 95% credible intervals spanning values producing non-asymptotic (Cushing 1973), compensatory (Beverton and Holt 1957) and over-compensatory (Ricker 1954) forms. Uncertainty in the shape of density-dependent relationships may have resulted from these populations being exploited if densities in the study area were below levels in which the true shape of the relationship can be revealed. Other studies highlight the challenge of differentiating between compensatory and over-compensatory dynamics, even when using simulated data with known properties (de Valpine and Hastings 2002). Understanding the true density-dependent dynamics of invasive populations is important, as over-compensatory dynamics can drive outcomes of exploitation efforts for smallmouth bass (Zipkin et al. 2008; Loppnow and Venturelli 2014) and other species (Abrams 2009; Grosholz et al. 2021). Over-compensatory dynamics, characterized by stronger increases in population growth rate at low abundances, can lead to higher abundances of young fish in exploited populations relative to unexploited populations (Ridgway et al. 2002; Zipkin et al. 2008). We observed some evidence of this in our retrospective analysis of sub-adults in the Middle Green River, where maximum exploitation effort led to increases in abundance in a few iterations (Fig. 10). More empirical studies focused on linking early life stages to spawner abundance of

smallmouth bass or adaptive management may help disentangle the true nature of density-dependent dynamics in the Green River sub-basin and in other riverine systems.

In addition to the shape or nature of density dependence (compensatory vs. overcompensatory), the strength of density dependence in riverine smallmouth bass populations is unknown, especially relative to lake populations. Strong density-dependent processes, including cannibalism and inter- and intra-class competition are hypothesized to regulate northern lake populations of smallmouth bass (DeAngelis et al. 1991; Dong and DeAngelis 1998; Ridgway et al. 2002; Zipkin et al. 2008). However, the parameter capturing the strength of density dependence is directly related to carrying capacity, the uncertainty in this parameter in this study is highlighted in the no-removal simulation scenario, in which some iterations led to likely unreasonable high percent increases in smallmouth bass. The importance of inter- and intraspecific interactions that lead to density-dependent population regulation in riverine systems is debated (Grossman et al. 1998; Jackson et al. 2001) due to strong disturbance regimes associated with flow and temperature variation. Alternatively, density dependence may be important for some populations, but disturbance regimes keep populations well below levels in which negative effects of density can be observed (see discussion in Jackson et al. 2001). We hypothesized a combination of environmental and biotic factors drove smallmouth bass populations in the Green River and estimated relatively weak effects of density dependence. This study is the first we know of to simultaneously assess the role of density dependence and environmental heterogeneity on smallmouth bass populations in a lotic system.

Our model estimated a negative effect of high flow events on smallmouth bass spawning and nest success that can be used to inform management of invasive smallmouth bass in regulated rivers. High-velocity flows and accompanying low water temperatures and increased turbidity are known to negatively impact smallmouth bass nest success (Lukas and Orth 1995; Peterson and Kwak 1999; Dauwalter and Fisher 2007). Elevated discharge during the hatching period led to lower predicted production of smallmouth bass in 2011, while in 2020 a quick drop in discharge following the hatch led to higher production of smallmouth bass relative to average conditions (Fig. 3). Conditions in 2011 were characterized by a slow decline in discharge to summer base flow conditions and lower temperatures. High water velocities associated with high discharge and low water temperatures are predicted to negatively influence nest success and have been suggested as a potential management option in regulated reaches of the Green River, and field studies are underway to assess the impact of short-duration releases from Flaming Gorge Dam on nest success (Bestgen 2018). Results from field observations can be used to adapt the model presented here to incorporate pulse flows to predict smallmouth bass population responses to different magnitudes and frequencies of high-flow releases to inform future management in the Green River and other regulated rivers.

Predicting smallmouth bass responses to management actions and future climate conditions is a priority across the Colorado River basin and elsewhere. In reaches with estab-

lished populations of smallmouth bass, such as the Green River, projecting population responses to future management actions and conditions is a management priority to mitigate impacts of smallmouth bass on native fish populations, especially declining Colorado pikeminnow (Bestgen et al. 2018). The model presented here can be used to test the outcomes of combinations of different actions and climate scenarios to prioritize smallmouth bass management. Management scenarios may include spatial variation in effort of adult mechanical removal (prioritizing effort in different reaches), timing of removal trips, and timing/frequency of nest disrupting flow releases from Flaming Gorge Dam. These management actions can be tested under the context of future watershed runoff and water storage decisions (Bruckerhoff et al. 2022). The current mega-drought influencing the western US has led to declines in runoff across the Colorado River basin (Udall and Overpeck 2017). In river reaches without established or with newly introduced smallmouth bass populations, this model can also be used to assess the risk of establishment (Eppehimer et al. 2024). This is a priority across the Colorado River basin because warmer reservoir releases associated with lower reservoir levels are leading to increased risk of establishment of invasive smallmouth bass in tailwaters (Dibble et al. 2021).

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Data availability

Raw catch data are publicly available on the Upper Colorado River Endangered Fish Recovery Program website (<https://coloradoriverrecovery.org/uc/documents/work-plan-documents/annual-reports/>) and temperature and discharge data are available through the US Geological Survey Current Water Data for the Nation website (USGS 2023a, 2023b). Summarized catch and environmental data and model code are available at <https://doi.org/10.5061/dryad.76hdr7t5z>.

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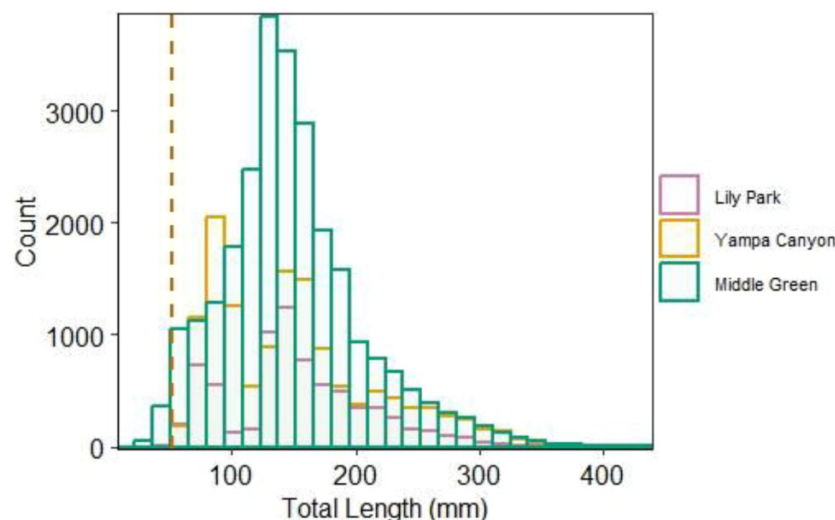
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Appendix A: Length frequency histogram of smallmouth bass used to inform length threshold for recruitment to gear

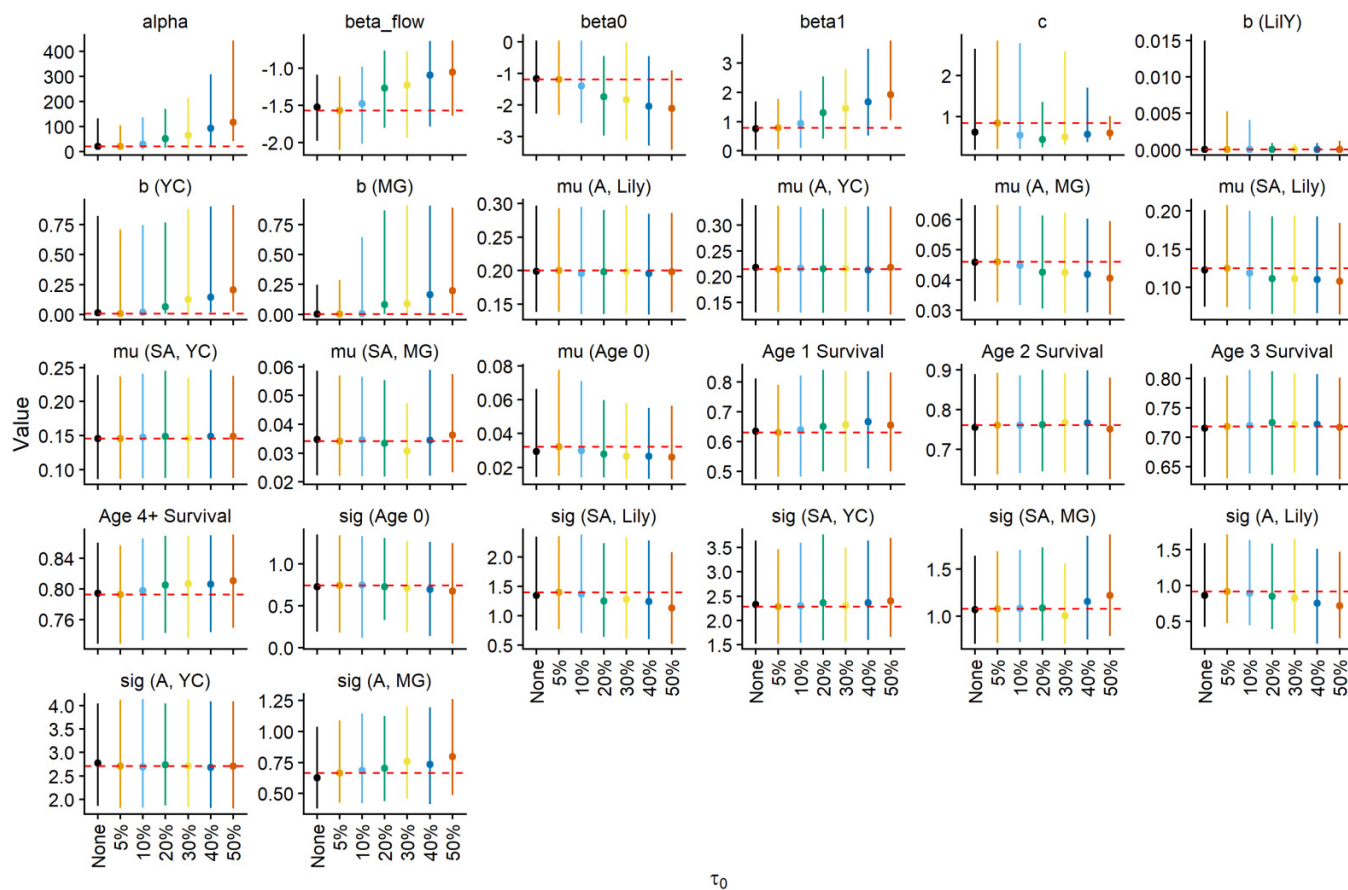
Fig. A1. Length frequency histogram of smallmouth bass captured by boat mounted electrofishing in the Lily Park and Yampa Canyon reaches of the Yampa River and Middle Green reach of the Green River between 2014 and 2022. Dashed vertical line indicates assumed threshold of 50 mm when age-0 fish recruit to gear and are vulnerable to exploitation.



Appendix B: Sensitivity of model parameter estimates to different levels of downstream age-0 dispersal

We assessed the sensitivity of parameter estimates to varying levels of age-0 downstream dispersal (τ_0). Model structure and all priors and hyperpriors were unchanged from baseline model that assumed $\tau_0 = 5\%$.

Fig. B1. Median and 95% credible intervals around parameters for different values of τ_0 . Dashed red lines highlight median parameter estimates when $\tau_0 = 5\%$.



Appendix C: Capture probabilities of smallmouth bass in the Green River subbasin

We estimated time (year, t) varying, life stage (l) specific capture probabilities ($p_{r,l,t}$) for smallmouth bass in each river reach (r), including the Lily Park, Yampa Canyon, and Middle Green reaches of the upper Green River subbasin. Capture probabilities were estimated as random effects each year with fixed means for each life stage in each reach (see Table 1 in main text for mean estimates).

Fig. C1. Prior (blue) and posterior (orange) distribution for mean capture probabilities across reaches and life stages.

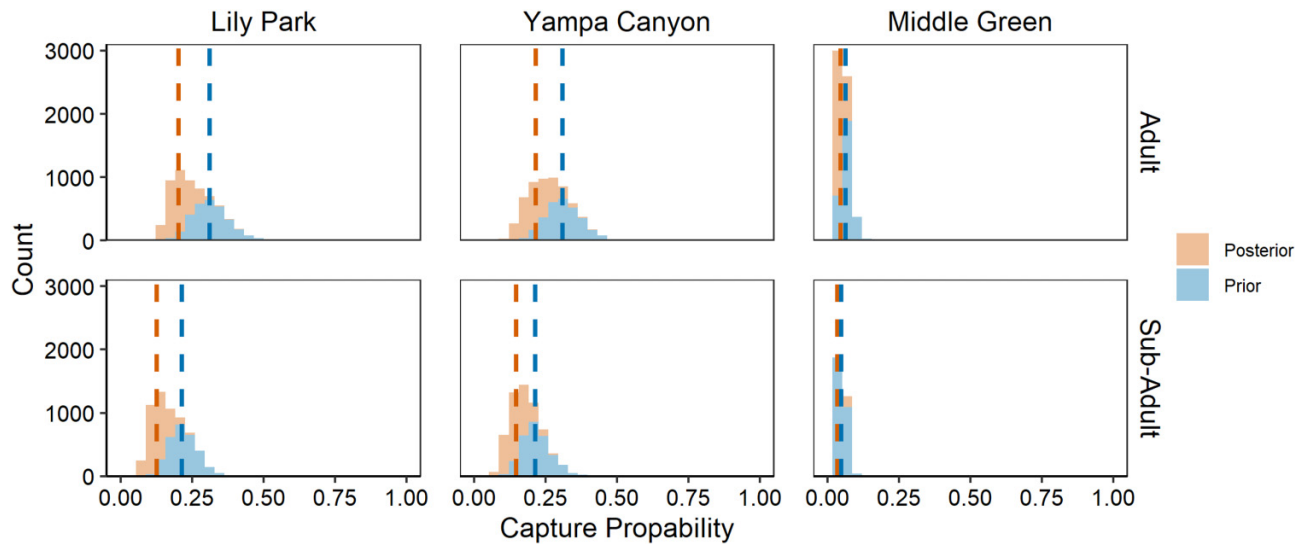
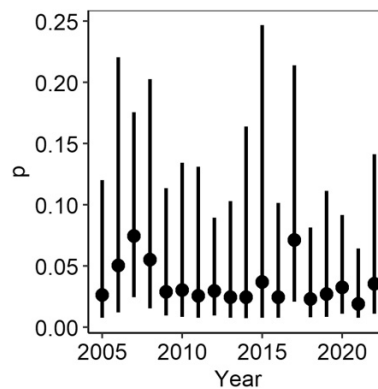


Fig. C2. Estimated capture probabilities each year for age-0 smallmouth bass in the Middle Green reach.



Appendix D: Simulated smallmouth bass population responses to exploitation scenarios assuming 50% of age-0 smallmouth bass disperse downstream

Fig. D1. Simulated percent change in abundance of smallmouth bass sub-adults (orange, 100–200 mm) and adults (blue, over 200 mm) from observed exploitation effort (baseline) for two exploitation scenarios in the Lily Park (left column), Yampa Canyon (middle column), and Middle Green (right column) reaches assuming 50% of age-0 smallmouth bass disperse downstream. The no effort scenario (a–f) assumed no fish were removed and the max effort scenario (g–i) assumed the maximum number of observed electrofishing trips was completed every year. Parameters used in simulations of max and no effort scenarios were drawn from the 300 posterior draws from the model fit to observed data and both simulations included density-independent effects of observed environmental variation (flow and temperature) on recruitment. Bold lines represent median estimates across simulations and thin lines are drawn for simulations between the 2.5th and 97.5th percentiles. Median lines for the no removal scenario are shown in the middle panels (d–f) to highlight general trends.

