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Perspective

Assessing the potential for Smallmouth Bass population establishment in Grand Canyon

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ABSTRACT

Objective: The expansion of nonnative Smallmouth Bass *Micropterus dolomieu* into the Grand Canyon ecosystem downstream of Glen Canyon Dam is widely seen as a potential threat to native fishes, particularly the Humpback Chub *Gila cypha*, which is listed as threatened under the Endangered Species Act. This concern stems from observations in the Green and upper Colorado rivers, where dam-modified habitats and reservoir introductions have allowed Smallmouth Bass to become established and impact native fish species. Our objective was to compare habitat conditions between a Smallmouth Bass population center in the Green River—where Humpback Chub are rare—and two major Humpback Chub population centers in the Colorado River in Grand Canyon, where Smallmouth Bass invasion is a conservation concern, to help assess invasion risk and inform management actions downstream of Glen Canyon Dam.

Methods: We developed a conceptual model of Smallmouth Bass recruitment potential emphasizing the roles of temperature, turbidity, and the timing of these conditions, based on literature for Smallmouth Bass and Largemouth Bass *Micropterus nigricans*. Using U.S. Geological Survey gauge station data, we summarized daily temperature and turbidity patterns near a known Smallmouth Bass population center in the middle Green River (near Jensen, Utah) and compared those with conditions in the Colorado River in Glen Canyon and Grand Canyon downstream from Glen Canyon Dam. We then used our conceptual model of Smallmouth Bass early life history, along with observed turbidity and temperature patterns, to explore how irregular recruitment could affect Smallmouth Bass population dynamics and individual growth potential using an age-structured population model and a bioenergetics model.

Results: Although warm reservoir releases due to low water storage in Lake Powell has made temperature regimes in Glen and Grand canyons more similar to those of the middle Green River, the Colorado River ecosystem in Grand Canyon has a very different turbidity regime from that of the middle Green River. The Colorado River in Grand Canyon becomes very turbid during late summer and fall, when tributaries experience flash floods during the North American monsoon season. These periods of high turbidity coincide with critical early life stages of Smallmouth Bass, likely limiting foraging efficiency, growth, and overwinter survival. Our population model indicates that rapidly growing and sustained Smallmouth Bass populations require successful recruitment at least once every 2 years, but empirical data suggest that these conditions occur only every 5–7 years in Grand Canyon. This would make long-term establishment of self-sustaining Smallmouth Bass populations in Grand Canyon unlikely or at least highly uncertain.

Conclusions: Despite the presence of nonnative predators, Humpback Chub populations in Grand Canyon have expanded during the past 10–15 years, very likely due to favorably warm river temperature. While Smallmouth Bass in Glen or Marble canyons (between Glen Canyon Dam and the Little Colorado River) may pose a downstream dispersal risk (and potentially a threat to Humpback Chub populations), high turbidity conditions downstream of the Little Colorado River reduce the likelihood of persistent local Smallmouth Bass recruitment. These results suggest that Smallmouth Bass invasion risk to Humpback Chub is not uniform across the Colorado River basin and should be evaluated in the context of the different site-specific water quality and flow regime conditions, other known risks to Humpback Chub, and Humpback Chub population size in different parts of the basin.

KEYWORDS: Colorado River, Grand Canyon, nonindigenous species, population dynamics, recruitment

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LAY SUMMARY

Smallmouth Bass pose a potential but context-dependent threat to Humpback Chub in the Grand Canyon ecosystem. High turbidity in Grand Canyon downstream of the Little Colorado River may act as a natural barrier to sustained Smallmouth Bass recruitment, suggesting that risk assessments and management actions should be location-specific, include multiple abiotic and biotic factors, and be informed by long-term environmental conditions and time horizons.

INTRODUCTION

The threat of Smallmouth Bass invasion

Nonnative warmwater fish are considered a significant threat to native fish in the Colorado River. Native and nonnative species groups have been described as immiscible (Marsh & Pacey, 2005), and there is a widespread view that new invasions of competitive and predatory nonnative species should be aggressively controlled. Predatory nonnative warmwater sport fish—including Largemouth Bass *Micropterus nigricans*, Smallmouth Bass *Micropterus dolomieu*, Flathead Catfish *Pylodictis olivaris*, Channel Catfish *Ictalurus punctatus*, Striped Bass *Morone saxatilis*, Green Sunfish *Lepomis cyanellus*, and Walleye *Sander vitreus*—are often the species of greatest management concern because these species could have direct impact on native fish populations through predation (Mueller, 2005; Tyus & Saunders, 2000).

Debates about the decline of native fish and the success of nonnative fish in the Colorado River system often focus on two main factors: habitat changes from dam construction and operation (e.g., fragmentation, altered flow, temperature, and sediment supply regimes) and the introduction of nonnative fish for sport fishing. As Johnson et al. (2008) note for the upper Colorado River region (Figure 1), these factors typically act together—and often synergistically—making it difficult to isolate their effects or to design targeted management actions. Management strategies in the region to support native fish include nonnative fish removal, designer flows, and flow regime releases that simulate more natural flow and temperature regimes (Bestgen & Hill, 2016; Coggins et al., 2011; Melis et al., 2015; Salter et al., in review). However, these efforts occur within a system increasingly stressed by reduced water storage, driven by declining natural runoff in a warming regional climate (Schmidt et al., 2023; Udall & Overpeck, 2017; Wheeler et al., 2022).

Smallmouth Bass invasion is generally believed to have negatively impacted native fish species in the Colorado River system, including the Endangered Species Act threatened Humpback Chub *Gila cypha* (Table 1) and Endangered Species Act endangered Colorado Pikeminnow *Ptychocheilus lucius* (Francis et al., 2022; Johnson et al., 2008; U.S. Fish and Wildlife Service [USFWS], 2018, 2025). Smallmouth Bass were first introduced into the upper Colorado River basin, defined as the watershed upstream from Lake Powell, in 1967 at Flaming Gorge Reservoir (Green River; Figure 1), with stockings into at least six other reservoirs in the same region from 1967 to 1992. Repeated escapement from reservoirs allowed Smallmouth Bass to spread into tributaries with favorable conditions. Flaming Gorge is the largest reservoir in the Colorado River system upstream from Lake Powell and is located on the upper Green River, the longest of the headwater branches of the Colorado River.

The middle Green River begins at the confluence of the upper Green and Yampa rivers (Figure 1). Flaming Gorge Dam, located at approximately 65 mi (the standard unit of measure by convention in the Colorado River; see Methods; Table 2), fully regulates flows from the upper Green and partially influences the middle Green River. While the Yampa River remains largely unregulated, its downstream base flows are significantly reduced.

The history of escapement and establishment of Smallmouth Bass in the Yampa River (Figure 1) and the status of native fish in that river are an influential case study that drives current management strategies of aggressive Smallmouth Bass control elsewhere in the watershed. Smallmouth Bass were not detected in the Yampa River prior to their stocking in Elkhead Reservoir (Figure 1) in 1978, based on surveys from 1951 to 1977 (Bailey & Alberti, 1952; Carlson et al., 1979; Holden & Stalnaker, 1975), and remained rare through the 1980s (Hawkins et al., 2009; McAda et al., 1994; Wick et al., 1983). Dam modifications at Elkhead Reservoir in 1992 and 2005 allowed fish to escape downstream, increasing Smallmouth Bass numbers in the Yampa River (Breton et al., 2013). Native fish declined during the 1990s to 2000s, and predation by nonnative species, especially Smallmouth Bass, was identified as the probable driver, though reduced flow and habitat change may have also contributed to these reductions (Johnson et al., 2008), and many of these changes occurred prior to the observed increases in Smallmouth Bass catch.

Smallmouth Bass now occur throughout the upper Colorado River basin (Burdick, 2008; Valdez et al., 1982). By 2003, the Upper Colorado River Endangered Fish Recovery Program identified the species as the greatest threat to native and endangered fish recovery (Upper Colorado River Recovery Program, 2024), prompting a basinwide removal effort. Between 2003 and 2023, more than US$11.6 million was spent on nonnative fish control, primarily targeting Smallmouth Bass. Although catch rates declined temporarily following removal efforts, populations often rebounded under favorable recruitment conditions, such as low flow, warm temperatures, and low turbidity. Despite two decades of removals, Smallmouth Bass remain established in the Green and upper Colorado watersheds, where habitat changes and nonnative predators continue to complicate native fish recovery.

Further south, downstream from Glen Canyon Dam, Smallmouth Bass catches in the Grand Canyon ecosystem have historically been very rare despite established populations in Lake Powell and Lake Mead that are immediately upstream and downstream, respectively. The "Glen Canyon Dam Long-Term Experimental and Management Plan Final Supplemental Environmental Impact Statement" identifies recent detections of large numbers of young-of-year Smallmouth Bass below Glen Canyon Dam and that establishment of Smallmouth Bass could threaten populations of the threatened Humpback Chub below the dam (Bureau of Reclamation, 2024). This increase may reflect entrainment from Lake Powell through Glen Canyon

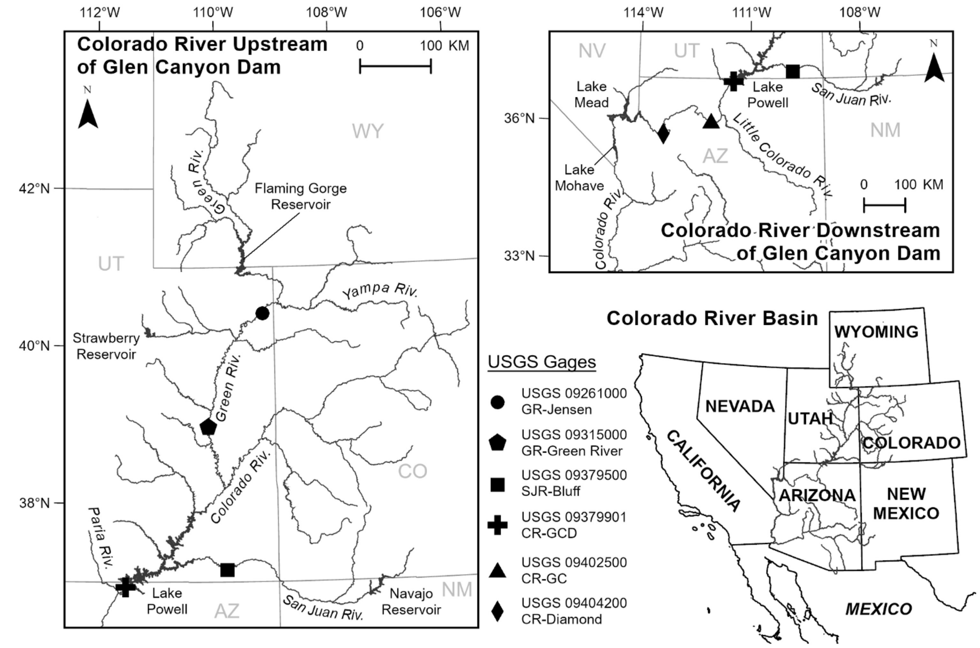

Figure 1. Map of the Colorado River system area of interest with key features, including Flaming Gorge and Glen Canyon dams, the U.S. Geological Survey (USGS) gauges where temperature and turbidity information were obtained (see legend), and the key tributaries of interest (Green, San Juan, and Little Colorado rivers). Map by K. Wilkinson.

Table 1. Humpback Chub status in the Colorado River basin. River mile [RM] 0 is Lees Ferry.

Category	Details
Conservation status	Threatened under Endangered Species Act; one of 14 native fish species in the Colorado River basin
Historical range	Formerly widespread throughout the Colorado River basin
Upper Colorado River basin adult Humpback Chub populations	• Black Rocks ~400 (USFWS, 2018) • Westwater Canyon ~2,000 (USFWS, 2018) • Cataract Canyon ~300 (USFWS, 2018) • Desolation and Gray canyons ~1,700 (USFWS, 2018) • Extirpated from Dinosaur National Monument (Yampa River and Whirlpool Canyon) due to low flows and predation, including by Smallmouth Bass (Valdez et al., 2021) Population trends stable or declining
Lower Colorado River basin adult Humpback Chub populations	• Grand Canyon, near Little Colorado River (downstream RM 61–66): ~10,000 adults (Van Haverbeke et al., 2020) • Western Grand Canyon (RM 157–281): several thousand fish per mile of sampling (Dzul et al., 2023; Van Haverbeke et al., 2017) • Current Grand Canyon population is larger than in the early 2000s (Coggins et al., 2006; Van Haverbeke et al., 2017, 2023; Yackulic et al., 2018) • Small population in Marble Canyon near Fence Fault (Andersen et al., 2010; Valdez and Masslich, 1999)
Key dam construction	Flaming Gorge Dam completed in 1962, Glen Canyon Dam completed in 1963
Management program	Upper Colorado River Endangered Fish Recovery Program, 1988; Glen Canyon Dam Adaptive Management Program, 1990s (Gloss et al., 2005)
Example experimental actions	• Smallmouth Bass removal efforts (Bestgen & Hill, 2016) • Fluctuating flows to suppress Smallmouth Bass (Bestgen, 2018) • Rainbow Trout removal near Little Colorado River (Coggins et al., 2011) • Fluctuating flows to suppress trout (Korman et al., 2011, 2012) • Stable flows to enhance Humpback Chub recruitment (Dodrill et al., 2015; Finch et al., 2016) • Cool mix releases from Lake Powell (Eppehimer et al., 2024)

Dam's penstocks at a time of exceptionally low reservoir levels, local reproduction in the tailwater immediately downstream from the dam, or both (Trammell et al., 2024). Low reservoir levels likely elevated both risks by shifting water releases to the epilimnion of the reservoir, potentially entraining Smallmouth Bass and warming downstream temperatures to levels suitable for Smallmouth Bass spawning (Eppehimer et al., 2024).

The recent increase in Smallmouth Bass catches downstream from Glen Canyon Dam has triggered a major management response to limit the species' establishment and potential downstream spread (Trammell et al., 2024). This management response has been controversial since the response includes implementation of the "cool mix" operational strategy wherein cool water is released from Lake Powell using the river outlets

Table 2. Geographic and physiographic descriptions and locations of key locations (river mile [RM] 0 is Lees Ferry). Abbreviation: USGS = U.S. Geological Survey.

Site name/alias	Purpose	RM	USGS gauge ID	Latitude	Longitude	Notes
GR-Jensen	Water quality station: Green River near Jensen, Utah	~317, measured from confluence of Green and Yampa rivers	GCMRC-GR10/9261000	40.3833° N	109.3500° W	Two gauges combined; near Smallmouth Bass population center
CR-GCD	Colorado River below Glen Canyon Dam, upstream Lees Ferry	−15.7	09379901	36.9369° N	111.4831° W	Just below Glen Canyon Dam
CR-GC	Colorado River near Grand Canyon	87	09402500	36.1525° N	112.0961° W	~26 mi below Little Colorado River confluence
CR-Diamond	Colorado River near Peach Springs (near Diamond Creek)	226	09404200	35.7547° N	113.5319° W	~15 mi above full Lake Mead pool
Glen Canyon	From Glen Canyon Dam to Lees Ferry	−15.7 to 0	–	–	–	Characterized by cold, clear water from Glen Canyon Dam releases
Marble Canyon	From Lees Ferry to Little Colorado River	1 to 61	–	–	–	Influenced by canyon morphology and tributary inflows from Paria River
Grand Canyon	From Little Colorado River to Pearce Ferry Rapid	62 to 280	–	–	–	Includes western Grand Canyon and terminates at Pearce Ferry Rapid
Little Colorado River	Major tributary; ecological and geomorphic transition point	61 to 66	–	–	–	Major tributary, often native fish study site. Confluence reach RM 61–66 native fish population center
Western Grand Canyon	Reach between Havasu Creek and Pearce Ferry Rapid	157 to 280	–	–	–	Broadly represents western reaches of Colorado River in Grand Canyon

that withdraw hypolimnetic reservoir water approximately 37 m deeper in the reservoir. The river outlets bypass the penstocks and turbines, where hydropower is produced, and hence lead to higher costs for some hydropower users. A resident Smallmouth Bass population immediately downstream from Glen Canyon Dam poses a conservation concern because such a population could become a source of dispersal into downstream parts of the Colorado River in Grand Canyon (river mile [RM; the standard unit of measure by convention in the Colorado River] 62 and downstream reaches; RM 0 = Lees Ferry) occupied by Humpback Chub. The presence of predatory nonnative fish near native fish populations is particularly problematic due to the potential for predation and competition, which could reverse Humpback Chub population gains seen during the past two decades (Table 1; Coggins et al., 2011; Van Haverbeke et al., 2017; Yard et al., 2011; Yackulic et al., 2014, 2018).

This study evaluated whether the prevailing understanding of Smallmouth Bass invasion and predation risk in the upper Colorado River basin is applicable to the Grand Canyon ecosystem downstream from Glen Canyon Dam, where climate, temperature, and native fish populations are different. We first developed a conceptual model of early life stage survival based on data on Smallmouth Bass and Largemouth Bass. We compared this model with environmental conditions in the middle Green River, where Smallmouth Bass are abundant but native species like Colorado Pikeminnow and Humpback Chub are rare, and with conditions in the Grand Canyon ecosystem, which downstream of the Little Colorado River support the largest Humpback Chub populations (Table 1; Table 2). We used an age-structured population model and a general bioenergetics model to explore how recruitment frequency and growth affect the potential persistence of a hypothetical Smallmouth Bass population in Grand Canyon (Table 2) under current temperature and turbidity regimes. This paper does not assess the impacts on Smallmouth Bass and native fish by specific management actions; instead, we aim to clarify invasion dynamics and inform future experimental and adaptive strategies to reduce risks to native fish.

Study area

The Colorado River originates in the middle and southern Rocky Mountains, with three major subbasins: the Green, upper Colorado, and San Juan rivers. The Green and upper Colorado rivers converge in Canyonlands National Park, and the San Juan joins the main stem approximately 140 mi downstream, within Lake Powell (Figure 1; Table 2).

A standardized RM system is used to reference locations along the Colorado River downstream of Glen Canyon Dam, with distances measured downstream from Lees Ferry as positive values. The U.S. Geological Survey (USGS) gauge at Lees Ferry is at RM 0, and the gauge near Peach Springs, Arizona, just upstream of Diamond Creek, is near RM 225.

The Colorado River system is divided at Lees Ferry, 1 mi downstream of the Colorado–Paria confluence, as defined by the Colorado River Compact (https://www.usbr.gov/lc/region/pao/lawofrvr.html).

Managers typically refer to the entire stretch from Glen Canyon Dam through Marble and Grand canyons to the head of Lake Mead as the "Grand Canyon ecosystem." We use this same term. This river corridor includes the 15-mi tailwater upstream from Lees Ferry, 61-mi Marble Canyon, and 179 mi of Grand Canyon upstream of Lake Mead. However, only the tailwater and the first mile of Marble Canyon fall within the upper basin; the rest lies in the lower basin under the Colorado River Compact. In this paper, we refer to Grand Canyon as the geomorphic reach that is found from about RM 62 to RM 280 (Pearce Ferry Rapid) that critically includes inputs from the Little Colorado River (Figure 1; Table 2).

The Green River is informally divided into lower, middle, and upper sections. The middle Green River begins at the confluence of the upper Green and Yampa rivers in Dinosaur National Monument. Flaming Gorge Dam, located about 67 mi upstream from this confluence, fully regulates the upper Green River and partially influences the flow of the middle Green River. However, this influence is moderated by inflows from the Yampa River, which remains largely unregulated.

We also analyzed data from the San Juan River collected at the USGS gauging station near Bluff, Utah (Figure 1). Streamflow at this station is partially regulated by Navajo Reservoir.

Fish communities and environmental effects

Endemic fish in the Colorado River evolved under highly variable seasonal and monthly patterns of streamflow, temperature, sediment supply, sediment transport, and turbidity (Moran et al., 2018). These conditions were significantly altered by large dams and consumptive water use (Miller, 1961; Schmidt et al., 2023). For example, Glen Canyon Dam reduced variability in annual and monthly Colorado River flows downstream while increasing daily and hourly fluctuations to support hydropower production. Base flows have also increased (Topping et al., 2003). When Lake Powell was relatively full, cool water was released from the hypolimnion. However, recent reservoir declines have shifted releases to the warmer epilimnion (Eppehimer et al., 2024). Water temperatures in Grand Canyon ecosystem rise seasonally due to downstream warming depending on discharge magnitude (Wright et al., 2009).

Suspended sediment supply has also changed significantly. Grams et al. (2005) estimated a 59% reduction in annual suspended sediment load in the middle Green River near Jensen following construction of Flaming Gorge Dam, primarily due to fine sediment trapping in the reservoir. Downstream from Glen Canyon Dam, sediment supply to the tailwater has declined by more than 99% because all upstream sediment is trapped in Lake Powell (Topping et al., 2000). Today, fine sediment enters the Colorado River below Glen Canyon from the Paria and Little Colorado rivers and smaller ephemeral streams. Turbidity remains low in the Glen Canyon Dam tailwater (median < 2 formazin nephelometric units [FNU]) but rises downstream of the Paria River and increases sharply downstream from the Little Colorado River (about RM 62), where monsoon floods, which occur more commonly in the lower Colorado River basin (Appendix A), can increase turbidity into the hundreds or thousands of FNU (Stone, 2010; Voichick & Topping, 2014). These tributary inputs of fine sediment remain a defining feature of the Grand Canyon ecosystem downstream of the Little Colorado River.

Fine sediment and turbidity levels are of relevance to native and nonnative fish populations in the Grand Canyon ecosystem because most centrarchids and salmonids, including Smallmouth Bass and Rainbow Trout *Oncorhynchus mykiss*, evolved in systems where turbidity rarely exceeds 50 FNU (Moran et al., 2018; Trebitz et al., 2007). Estimates of Smallmouth Bass and Rainbow Trout visual reactive distances to turbidity show significant impairment at turbidity levels ≥ 50 nephelometric turbidity units (NTU) (Heimstra et al., 1969; Sweka & Hartman, 2003).

Environmental factors affecting native and nonnative fish in Grand Canyon have been studied since the 1990s. During the 1980s, high reservoir levels in Lake Powell led to cool hypolimnetic releases into the Grand Canyon ecosystem, supporting a high-quality recreational trout fishery in the tailwater. As Lake Powell storage declined, summer and fall releases became warmer in 2004, 2005, and again after 2020 (Figures S1–S2 [see online Supplementary Material]). These warmer releases have likely driven major ecological shifts in Grand Canyon, including growth and expansion of native fish populations (Coggins et al., 2011; Van Haverbeke et al., 2017; Yackulic et al., 2018) and increased potential for nonnative warmwater species to expand (Dibble et al., 2021; Hedden et al., 2024).

During the past decade, Rainbow Trout populations have declined in the Grand Canyon ecosystem, largely due to reduced growth rates influenced by changes in flow, temperature, prey availability, turbidity-related declines in foraging efficiency, and competition (Korman et al., 2021, 2022; McKinney et al., 2001). Korman et al. (2021) found spatial variation in Rainbow Trout growth across five reaches, with turbidity low in Glen Canyon and higher in Marble Canyon, where episodic turbidity likely reduced growth and contributed to population declines. Laboratory studies show that turbidity as low as 25 FNU can reduce predation risk for native fish from Rainbow Trout and Brown Trout *Salmo trutta* and warmwater predators like Smallmouth Bass (Ward et al., 2016; Ward & Vaage, 2019). However, Yard et al. (2011) observed increased trout piscivory in Grand Canyon during turbid conditions, likely due to prey fish transported from the Little Colorado River during monsoon events and aggregating along shorelines. Together, these findings underscore turbidity as a key but complicated factor shaping predator growth, survival, and native–nonnative fish interactions in the Colorado River ecosystem.

Basis for conceptual model of Smallmouth Bass recruitment

We hypothesize that a key bottleneck for Smallmouth Bass population establishment and growth within Grand Canyon occurs during late summer and fall, leading into the first winter of life, when environmental conditions, particularly temperature and turbidity, can limit feeding, growth, and overwinter survival. This hypothesis is informed by bass, primarily Smallmouth Bass and Largemouth Bass, recruitment research (Appendix B), including by Ludsin & DeVries (1997), who identified seasonal bottlenecks in Largemouth Bass recruitment related to hatch date, growth, and lipid accumulation, and related studies showing how abiotic factors, such as temperature, turbidity, and flow, along with biotic factors, like prey availability and competition, influence year-class strength.

These studies emphasize that growth during one life stage affects survival in the next, ultimately shaping recruitment success. Smallmouth Bass have persisted for decades in the Colorado Plateau part of the Colorado River system, demonstrating their ability to overcome life stage bottlenecks under existing environmental conditions. For similar success in the Grand Canyon, environmental conditions must also support survival through the critical late summer, fall, and early winter.

We identified water temperature and turbidity as two interdependent factors influencing Smallmouth Bass recruitment for comparing environmental conditions in the middle Green River and the Grand Canyon ecosystems. These variables are known to influence *Micropterus* spp. recruitment and are critical for shaping native and nonnative fish populations in Grand Canyon. Both can be influenced by management actions (on temperature management, see Glen Canyon Dam Adaptive Management Program, 2024; on turbidity management, see Randle et al., 2007).

METHODS

Water temperature and turbidity data

We summarized water temperature and turbidity data from key locations to represent environmental conditions at different locations in the middle and lower Green River, the San Juan River, and the Grand Canyon ecosystem (Figure 1; Table 2). The middle Green River gauge is near Jensen, Utah, close to a known Smallmouth Bass population center (T. Jones, U.S, Fish and Wildlife Service, personal communication). Data from two USGS gauges at this site, gauge numbers GCMRC-GR1/09261000 (abbreviated GR-Jensen, Table 2), were combined to produce the most complete record, spanning different periods and sensor types. We also examined data from the Green River near Green River, Utah, which is about 197 mi downstream of Jensen, and the San Juan River near Bluff, Utah (Table 2), which is about 43 mi upstream from Lake Powell when the lake is full.

For the Grand Canyon ecosystem, we analyzed data collected at three gauging stations (Figure 1, Table 2): Colorado River below Glen Canyon Dam (USGS gauge 09379901, abbreviated CR-GCD; RM −15.7) and two stations downstream of the Little Colorado River, Colorado River near Grand Canyon (USGS gauge 09402500, abbreviated CR-GC; RM 87) and Colorado River above Diamond Creek near Peach Springs (USGS 09404200, abbreviated CR-Diamond, RM 224). The two locations in Grand Canyon are near the largest Humpback Chub population centers (Table 1).

We summarized available temperature and turbidity data and considered the timing, magnitude, and duration of turbidity events to key age-0 Smallmouth Bass recruitment periods, including spawning, early life, and growth to first winter. While we included data from all available years and months at each monitoring station, we focused on the 2017–2022 period, when comparable upper and lower basin data were available. Data from other stations, including those on the Yampa River, had short time series, uncertain data quality, or incomplete data records and were not suitable for use.

We summarized water temperature and turbidity data (either directly measured or interpreted from acoustic sediment sensors) because both variables influence fish growth and survival (Appendix B). Because optical turbidity sensors often fail in rivers with high suspended sediment transport like the Colorado, we also used sediment concentrations (mg/L silt + clay) from acoustic Doppler profilers as a proxy for turbidity (Voichick & Topping, 2014). We summarized turbidity from both sensors to assess the magnitude, timing, and duration of turbidity events at each location. For acoustic Doppler profiler data, we used a threshold of 200 mg/L silt + clay, which is approximately equivalent to 50 NTU (Topping et al., 2000; Voichick & Topping, 2014; J. C. Schmidt, Utah State University, personal communication). The NTU and FNU values were treated as equivalent for this analysis. Sensor data were collected at varying intervals depending on the parameter, year, and instrument. For consistency, we calculated mean daily values to assess daily patterns, reducing the influence of subdaily sensor anomalies. Data cleaning is described in Appendix C.

A water temperature of 16°C is considered the threshold for Smallmouth Bass spawning in the upper Colorado River basin (Bestgen, 2018) and is assumed to apply throughout the Grand Canyon ecosystem (Eppehimer et al., 2024). Visual reactive distances for Smallmouth Bass are significantly reduced at turbidity levels ≥50 NTU (Heimstra et al., 1969; Sweka & Hartman, 2003). We used graphical analysis to identify when these temperature and turbidity thresholds were met.

Age-structured population model

We used an age-structured population model to simulate invasion dynamics by a hypothetical Smallmouth Bass population under different recruitment scenarios. The model estimated the time required for a population to reach carrying capacity, assuming a small number of initial individuals introduced from Glen Canyon Dam. We evaluated how different intervals between successful spawning years (ranging from 1 to 7 years) affected population growth and persistence. We also evaluated a scenario of adding a small "constant" recruitment each year that would mimic immigration from upstream in a source–sink framework. Standard fisheries population dynamics equations were used to model survival, survivorship, length, weight, and fecundity at age (Appendix D, Box 1; Walters & Martell, 2004). Expected recruitment ($N_{a,t}$) was estimated using a Beverton–Holt stock–recruit relationship, parameterized using Botsford incidence functions evaluated at an unfished equilibrium to estimate eggs per recruit in an unfished population (epro) as a function of survivorship (L_a), fecundity (fec_a), length (L_a), and weight (W_a) at age (see Appendix 4 as well as Box 3.2 in Walters & Martell, 2004). The inverse of epro provided an estimate of the unfished equilibrium egg-to-age-1 survival rate. Annual deviations from expected recruitment (ε_t) were normally distributed with SD = 0.8 for favorable years, ones with low turbidity during

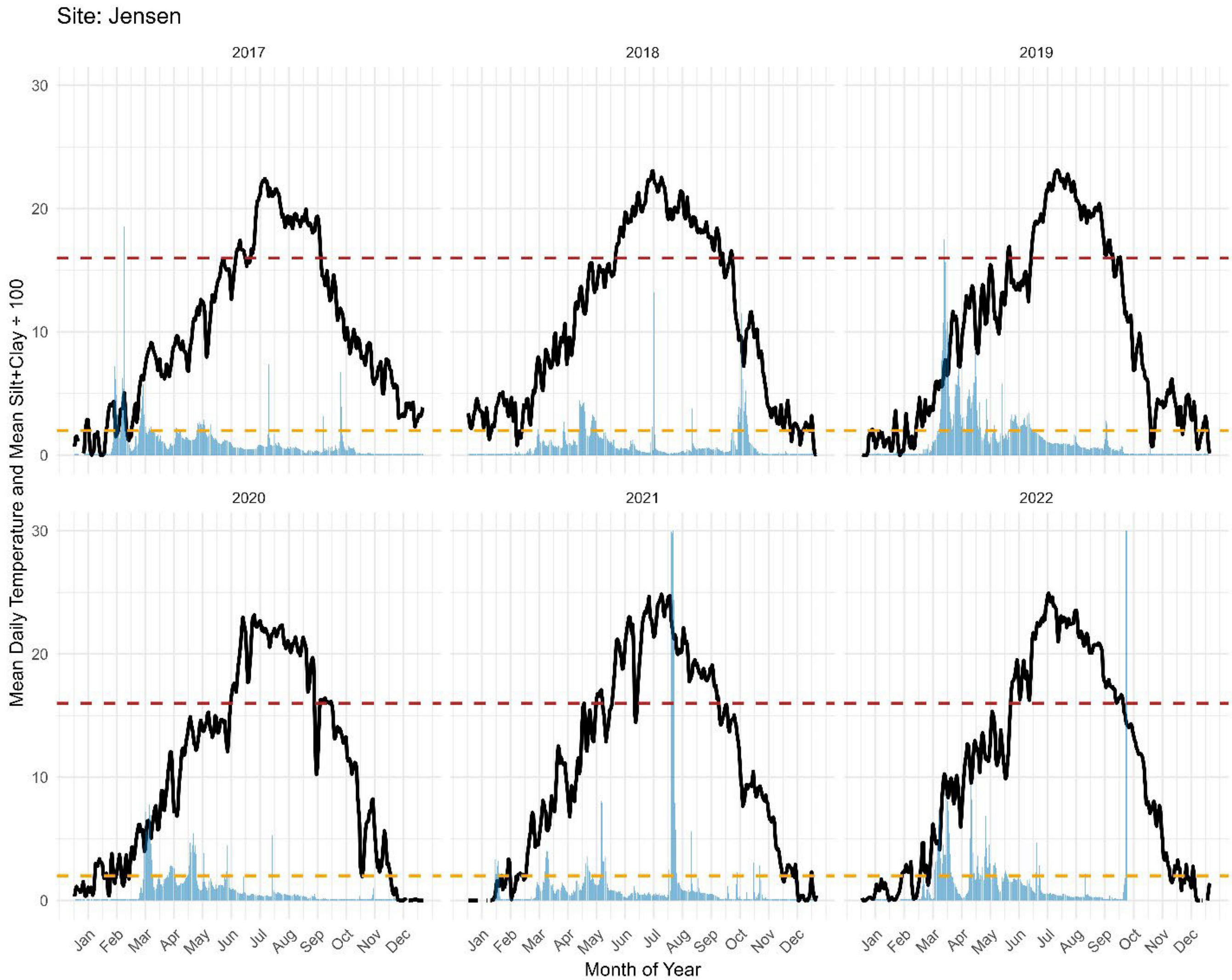

Figure 2. Mean daily Green River water temperature (black line) and scaled values (blue bars, scaled by dividing by 100) of mean daily silt + clay concentration (mg/L; *y*-axis) and month of year (*x*-axis) using data from acoustic sensors from near Jensen, Utah. This site is located upstream of Glen Canyon Dam at U.S. Geological Survey gauge GCMRC-GR1/09261000 Green River. The *y*-axis is limited to a maximum value of 3,000 mg/L silt + clay. Jensen data are missing after September 2022. Each value of turbidity on the graph has been divided by 100 to scale the data for plotting. The dashed brown line is a reference line for 16°C and the dashed orange line for 200 mg/L silt + clay scaled to a value of 2.

summer and fall that may allow age-0 bass to feed, grow, and survive their first winter. Recruitment was zero in unfavorable years. Based on observed patterns in turbidity near Diamond Creek, recruitment was only allowed to occur every 1 to 7 years. Life history parameters were based on a review of Smallmouth Bass (Beamesderfer & North, 1995; Appendix D).

Temperature- and turbidity-dependent Smallmouth Bass growth model

We applied the general bioenergetics model described by Walters & Essington (2010) (also Essington et al., 2001; van Poorten & Walters, 2016) to simulate first-year weight and length growth of postlarval Smallmouth Bass (Appendix D). This model, previously used in studies of Grand Canyon fish growth (Coggins & Pine, 2010; Walters et al., 2012), was run daily from 2003 through 2024 using predicted food consumption and metabolic rates based on observed temperatures and turbidities at the two Grand Canyon sites. The objective was to estimate the frequency of conditions favorable for strong juvenile growth and survival, rather than to predict absolute age-1 sizes. These outputs informed the age-structured model by characterizing intervals between potential strong year-classes.

RESULTS

Water temperature

Water temperatures of the GR-Jensen and CR-Diamond sites exceeded the 16°C Smallmouth Bass spawning threshold for 4 to 6 months each year when Lake Powell release temperature at Glen Canyon Dam was at its very warmest and Lake Powell was at very low levels (Figures 2–4; Figures S1, S2). Water temperatures at CR-GCD and CR-GC sites have reached 16°C typically later in the calendar year than at GR-Jensen or at CR-Diamond (Figures S1, S2).

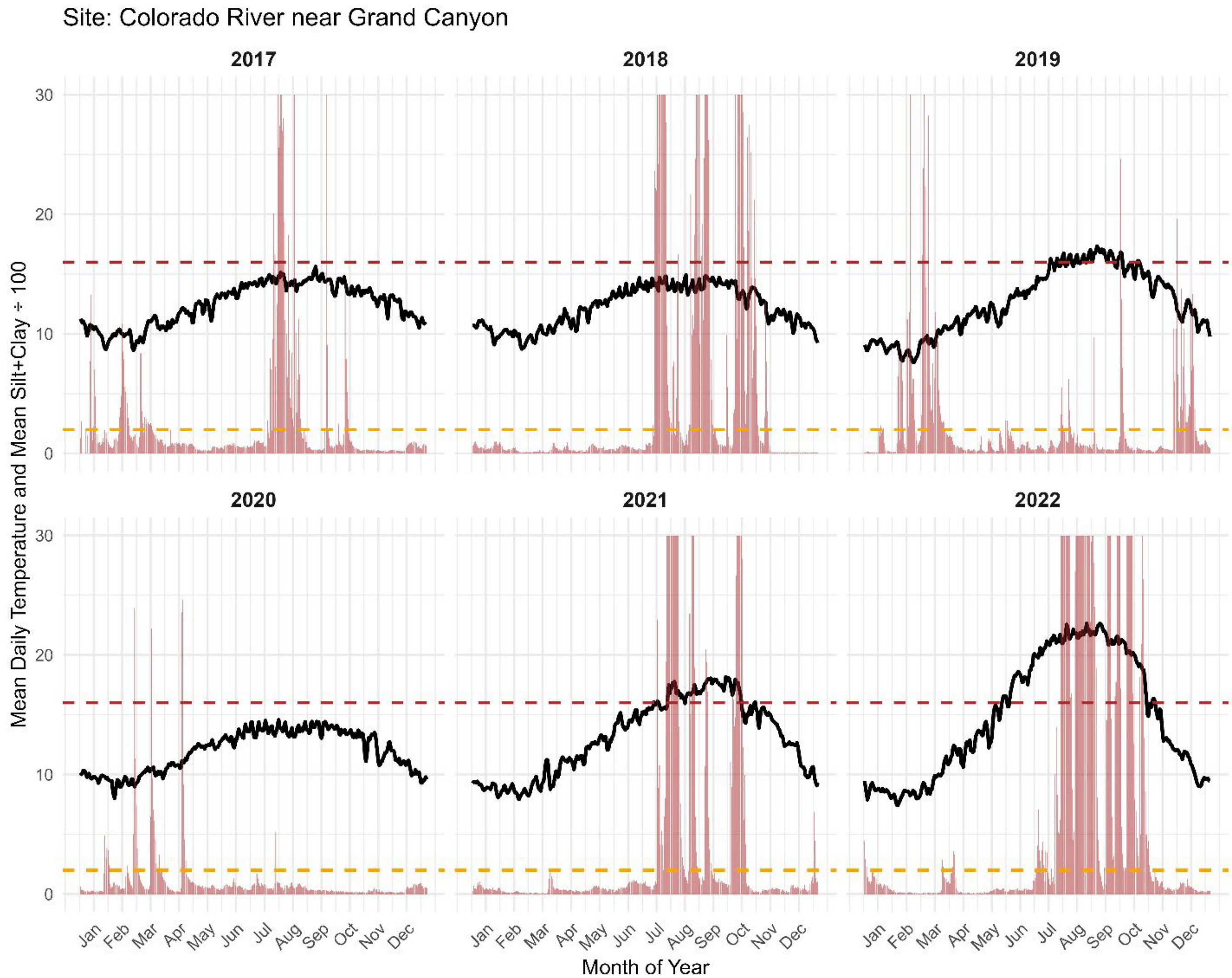

Figure 3. Mean daily Colorado River water temperature (black line) and scaled values (brown bars, scaled by dividing by 100) of mean daily silt + clay concentration (mg/L; *y*-axis) and month of year (*x*-axis) using data from acoustic sensors from the Colorado River near Grand Canyon U.S. Geological Survey gauge 09402500 at river mile 87. The *y*-axis is limited to a maximum value of 3,000 mg/L silt + clay. Each value of turbidity on the graph has been divided by 100 to scale the data for plotting. The dashed brown line is a reference line for 16°C and the dashed orange line for 200 mg/L silt + clay scaled to a value of 2.

Turbidity

Turbidity in the Grand Canyon ecosystem increases substantially from Glen Canyon Dam (where FNU values are near zero) to Diamond Creek, due to the delivery of silt and clay from tributaries Paria and Little Colorado rivers and from smaller tributaries (Figures 2–4; Figure S3). For example, from July 2017 to June 2023 silt and clay transport in Marble Canyon averaged about 1.1×10^6 mg/year, while downstream of the Little Colorado River at the CR-GC site, the average was 5.4×10^6 mg/year over the same period (Grand Canyon Monitoring Research Center, 2025; Topping et al., 2021; J. Schmidt, Utah State University, personal communication). These periods of sediment transport result in turbidity levels well above 50 FNU, the levels at which Smallmouth Bass reactive distance to prey is reduced downstream of the Little Colorado River (Sweka & Hartman, 2003). Critically, these threshold levels are exceeded at CR-GC and CR-Diamond during both during the spring runoff and late summer during the monsoon season (Figures S3, S4).

Turbidity inferred from silt + clay concentrations (acoustic sediment sensors; mg/L) was lower in magnitude and frequency at GR-Jensen (Figure 2) than at the two Grand Canyon gauges (CR-GC and CR-Diamond; Figures 3–4). During years when these gauges had silt + clay data, GR-Jensen consistently experienced fewer days with turbidity ≥200 mg/L (Figure S4). In 4 of 5 years, the CR-GC gauge had more high-turbidity days than GR-Jensen, and CR-Diamond had more in all 5 years (Figure S4). From 2013 to 2024, seasonal turbidity patterns differed between GR-Jensen and CR-GC (Figures S3–S7). At GR-Jensen, high turbidity occurred primarily in spring, reflecting snowmelt-driven runoff (Figure S6). In contrast, CR-GC and CR-Diamond downstream from the Little Colorado River experienced both larger and more frequent turbidity events in spring, as well as significant summer turbidity during the July–October monsoon season (Figures S5–S7).

Monthly summaries of turbidity events ≥200 mg/L show differences between the GR-Jensen and CR-GC and

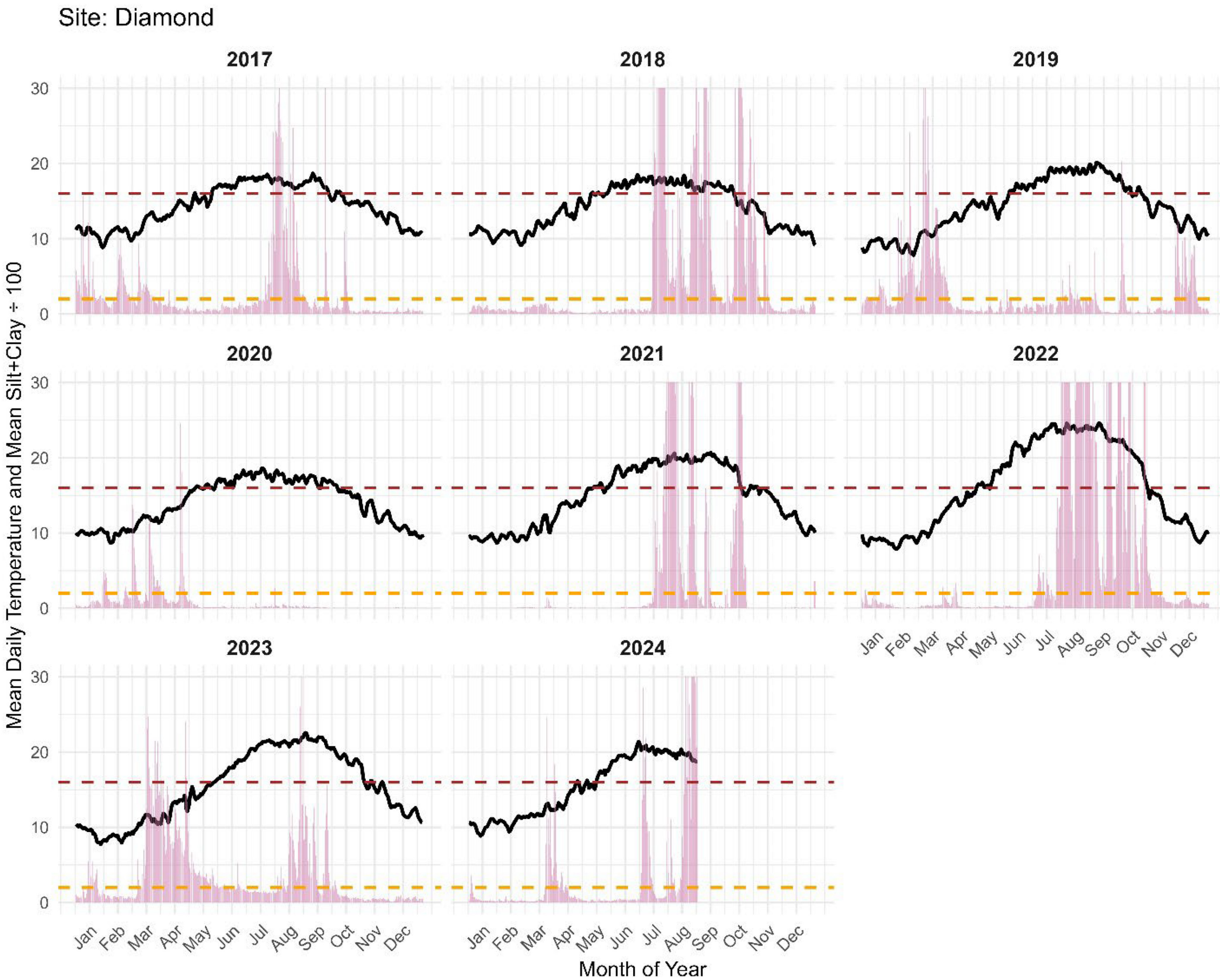

Figure 4. Mean daily Colorado River water temperature (black line) and scaled values (magenta bars, scaled by dividing by 100) of mean daily silt + clay concentration (mg/L; *y*-axis) and month of year (*x*-axis) using data from acoustic sensors from Diamond Creek. Diamond Creek is on the Colorado River near Peach Springs U.S. Geological Survey gauge 09404200 at river mile 226. The *y*-axis is limited to a maximum value of 3,000 mg/L silt + clay. Each value of turbidity on the graph has been divided by 100 to scale the data for plotting. The dashed brown line is a reference line for 16°C and the dashed orange line for 200 mg/L silt + clay scaled to a value of 2.

CR-Diamond (Figure S6), with GR-Jensen having fewer days each year when these turbidity conditions are met. Figures S6 and S7 demonstrate that both warmwater and high-turbidity conditions occur less frequently at GR-Jensen than they do at CR-GC or CR-Diamond downstream from the Little Colorado River. Grand Canyon monsoonal events in summer and fall produce turbidity events that are typically greater in magnitude, duration, and frequency than those observed in the GR-Jensen at any time of year (Figures S3–S7). Periods of exceptionally low silt + clay levels resulting in very low turbidity at GC-Diamond do occur, such as 2020–2021, when the North American monsoon failed to occur. Those events are irregular over the past two decades of available data.

Age-structured population model

Based on existing data, we estimate that conditions suitable for Smallmouth Bass spawning and survival through the first winter—with summer temperatures exceeding 16°C and turbidity <50 NTU through the late summer and fall (e.g., 2020)—occur only once every 5 to 7 years near CR-Diamond, and as water temperatures are higher during persistent low levels in Lake Powell, a similar interval is likely near CR-GC (Figure S8). If recruitment occurs on this interval, our model predicts that Smallmouth Bass may persist at low and variable abundance but would be unlikely to achieve rapid and sustained population growth, which would require recruitment at least once every 2 years (Figure S10). When simulations were initiated at low abundance to reflect early invasion stages and minimize density-dependent effects, intrinsic population growth rates (r) declined sharply as the interval between successful age-0 cohorts increased. Recruitment occurring only once every 5 years led to substantially reduced population growth rates and hence a low probability of population establishment. When recruitment was limited to once every 7 years, r was negative in most scenarios, suggesting that population persistence would be unlikely without additional immigration or environmental change (Figure S10).

Source–sink dynamics and the role of Glen Canyon

We examined an alternative invasion pathway, where Smallmouth Bass establish in Glen Canyon and provide annual low recruitment as emigrants to the simulated population further downstream. These results suggest that low annual recruitment from emigrants does not result in large changes in the predicted Smallmouth Bass *r*. Large numbers of emigrants would be similar to more frequent recruitment.

The age-structured population is dependent on assumptions about the maximum survival rate of eggs to age 1 (s_{max}). These assumptions were based on plausible values for the steepness of the recruitment curve (compensation ratio [CR]), which is the ratio of maximum to equilibrium age-0 survival (Figure S10). The CR only affects the speed of the early invasion, not the predicted long-term abundance, because of the way the recruitment *b* parameter is scaled. Thus, while the model is sensitive to the CR parameter, the overall predictions are similar across a range of CR values. Model assumptions and details are discussed in Appendix D, and a simple spreadsheet version of the model itself can be used to evaluate sensitivity to parameter estimates via download from the supplemental files.

Temperature- and turbidity-dependent age-0 growth model

The bioenergetics model predicted that 2023 was the only year at CR-GC in which age-1 Smallmouth Bass reached sizes (~8–10 cm; Figure S9), comparable to those reported by Beamesderfer & North (1995). The model did not predict exceptional growth during the extended low-turbidity periods of 2018 and 2020–2021. This is because even during these periods of low suspended sediment, on an annual basis there are still periods during the critical Smallmouth Bass recruitment and growth periods that are not favorable. Moderate to large juvenile sizes were projected for earlier cohorts (2005, 2011, 2017–2021) but only under conditions where juvenile bass were assumed to spend more time foraging to offset turbidity-related feeding limitations, a behavior that may increase predation risk (Ahrens et al., 2012). Long-term trends in predicted growth reflect climate-driven warming, overlaid with a weak signal of favorable warm and low-turbidity conditions approximately every 6 years (Figure S8). At CR-Diamond, similar temporal patterns were observed, although higher ambient temperatures and metabolic costs resulted in predictions of larger but more variable age-1 body sizes compared with those at CR-GC.

Similar temporal patterns in Smallmouth Bass growth and foraging time were predicted at both Grand Canyon locations, with more extreme variation, including larger maximum body sizes, at CR-Diamond. This was attributed to higher temperatures at CR-Diamond, which elevated both feeding and metabolic loss rates, despite slightly higher turbidity that reduced food intake. The temporal pattern of growth variation was largely insensitive to changes in key bioenergetics parameters, including the consumption and metabolic rate scaling constants (*H, m*) and Q10 coefficients for temperature effects on consumption and metabolism. This model can be examined efficiently for sensitivity to parameter estimates by modifying the inputs to the spreadsheet version of the model, which can be downloaded from the supplemental files.

DISCUSSION

The establishment of Smallmouth Bass in Glen Canyon poses a legitimate management concern due to the potential for dispersal of individuals to downstream locations, including Humpback Chub population centers in Grand Canyon near RM 62 and in western Grand Canyon downstream from about RM 157. However, our results show that while temperature regimes in the upper and lower Colorado River are becoming more similar, the establishment of self-sustaining Smallmouth Bass populations in Grand Canyon is unlikely, or at least highly uncertain, given other environmental differences in the upper Colorado River and Grand Canyon. High turbidity, especially during early life history critical periods, may significantly reduce Smallmouth Bass feeding efficiency and recruitment, limiting their establishment potential in Grand Canyon. This suggests that models focused solely on temperature may overestimate the risk of Smallmouth Bass invasion and therefore impacts to native fish.

Despite the presence of other nonnative predators of management concern—such as Rainbow Trout, Brown Trout, Common Carp *Cyprinus carpio*, Green Sunfish, and Channel Catfish—in Glen and Grand canyons, Humpback Chub populations have expanded substantially in the past 10–15 years in both major population centers in Grand Canyon. Therefore, while some risk will always remain, the long-term threat of Smallmouth Bass to Humpback Chub may be moderated by environmental conditions in Grand Canyon. In addition, the two Humpback Chub populations in Grand Canyon are significantly more abundant than the very small populations in the upper basin (Table 1), making the populations more resilient to episodic periods of higher predation from Smallmouth Bass or other nonnative predators. Decision makers should consider this broader ecological context in making management decisions related to Smallmouth Bass. The Colorado River faces basinwide challenges such as climate change, altered hydrology, and habitat fragmentation. But local conditions within Grand Canyon that are strongly influenced by sediment input from the Little Colorado River and other tributaries, longitudinal temperature changes, and distance from Glen Canyon Dam will likely continue to create a critical refuge for native fish.

Turbidity could reduce invasion risk

Smallmouth Bass invasion in Grand Canyon poses a potential risk to native species, but our findings suggest that persistent recruitment of Smallmouth Bass may be limited by environmental conditions, particularly turbidity, and complex interactions among climate, Grand Canyon geomorphology, and Smallmouth Bass early life history.

We hypothesized that Smallmouth Bass invasion success, defined as the persistence of a population with age structure and biomass capable of significantly impacting Humpback Chub, depends at least on the interaction of temperature, turbidity, and fish growth and survival. Turbidity in particular influences foraging efficiency, growth, and ultimately recruitment as shown in Smallmouth Bass and Largemouth Bass and Rainbow Trout. In Glen Canyon, warming temperatures and low turbidity may promote favorable conditions for Smallmouth Bass persistence via entrainment through Glen Canyon Dam, local reproduction, or both. However, such conditions sharply contrast with the highly turbid environment found downstream from the Little Colorado River, especially during the North American monsoon season (Appendix A), which coincides with a likely critical period for Smallmouth Bass recruitment.

Irregular recruitment reduces risk of population establishment

Our conceptual and age-structured population models show that episodic local recruitment, driven by relatively rare combinations of long late summer and fall periods of warm temperatures and low turbidity, would likely constrain Smallmouth Bass abundance and reduce long-term risks to native fish. In Grand Canyon, turbidity events occur frequently after Smallmouth Bass spawning temperatures exceed 16°C (Figures 3–4), coinciding with critical early life stages for bass. These events would very likely reduce foraging success, growth, and overwinter survival of age-0 bass. We estimate that conditions suitable for successful Smallmouth Bass spawning and overwinter survival may occur only once every 5 to 7 years under the present climate, making sustained population growth unlikely.

We predict that Smallmouth Bass intrinsic population growth rates decline sharply as the interval between successful spawning years increases (Figure S10). Our model predicts that Smallmouth Bass invasions (starting at low population sizes) from local recruitment are unlikely even with spawning every 5 years across a range of CRs. Longer spawning intervals or lower CRs reduce the likelihood of successful invasion. These results echo observations from field and lab studies in this and other systems where turbidity constrains visual predator behaviors or populations (Korman et al., 2021; Surber, 1939; Sweka & Hartman, 2003; Ward et al., 2016; Ward & Vaage, 2019).

Alternative recruitment scenarios based on upstream emigrants from Glen or Marble canyons require different assumptions related to emigration rates, growth, and survival, which have previously been explored for Brown Trout (Runge et al., 2018) in the Colorado River ecosystem. Korman et al. (2016) demonstrate that the abundance of Rainbow Trout near the Little Colorado River in Grand Canyon is primarily influenced by limited downstream dispersal from Glen Canyon, where trout densities were 30–50 times higher. Despite low overall Rainbow Trout movement rates, immigration from upstream populations explained a threefold increase in trout abundance near the Little Colorado River. However, Korman et al. (2016) and Korman et al. (2021) demonstrate that apparent survival of Rainbow Trout was low due to complicated interactions between phosphorous-driven declines in prey availability, negative effects on feeding efficiency from increasing turbidity, and warmer temperatures, with the greatest effects downstream of the Little Colorado River. If Smallmouth Bass do become established in the clear-water reach above Lees Ferry, downstream dispersers may then encounter the same turbidity conditions that have limited Rainbow Trout survival in Marble Canyon to the Little Colorado River, where Humpback Chub first become abundant. Turbidity patterns in Marble Canyon are influenced by the Paria River, and these inputs have been shown to influence Rainbow Trout survival (Korman et al., 2021). While warming water temperatures with distance from Glen Canyon Dam would be deleterious to Rainbow Trout, turbidity is likely a key limiting factor for both Rainbow Trout and Smallmouth Bass.

Smallmouth Bass that emigrate from Glen or Marble canyons downstream would be entering a landscape in Grand Canyon where Humpback Chub populations have been expanding for a decade and now occupy over 100 mi or more between the Little Colorado River and Lake Mead. It is uncertain whether low Smallmouth Bass density from occasional local reproduction, small numbers of emigrants, or both would be capable of reversing the Humpback Chub population gains observed in the past decade in Grand Canyon (Table 2) across timescales of management concern (e.g., 10–100 years). Detailed assessments of Smallmouth Bass recruitment dynamics related to environmental variables and movement patterns related to dispersal, growth, and survival from Colorado River basin reaches near Smallmouth Bass population centers, combined with population modeling work similar to efforts in the lower basin related to Brown Trout invasion, could provide information that helps to resolve some of this uncertainty (Runge, 2011; Runge et al., 2015, 2018).

Our bioenergetics model predicts poor Smallmouth Bass growth near Diamond Creek during periods of high turbidity, similar to past years 2007–2011 and 2013–2017, aligning with periods of reduced Rainbow Trout growth in Marble and Grand canyons (Korman et al., 2021). This suggests shared environmental drivers, reinforcing the role of broadscale processes like sediment dynamics and temperature in structuring fish populations.

Turbidity patterns differ across upper Colorado River and Grand Canyon ecosystem

We found distinct seasonal patterns in temperature and turbidity between the middle Green River and Grand Canyon. In the Green River Smallmouth Bass population center near Jensen, spring turbidity subsides before peak summer temperatures, aligning with spawning windows similar to the native range of Smallmouth Bass. Late summer turbidity peaks do occur in some years near Jensen (Figure S5), and assessing whether Smallmouth Bass year-class strength is lower in these years is important. In contrast, Grand Canyon experiences both spring turbidity peaks prior to suitable Smallmouth Bass spawning temperatures and monsoon-driven summer and fall turbidity peaks after Smallmouth Bass spawning temperatures are reached, likely impairing early life stage growth and survival (Table 2). This is a key difference—The middle Green River experiences frequent years with turbidity conditions that would be suitable for Smallmouth Bass recruitment, whereas Grand Canyon experiences such conditions irregularly. The difference between the two reaches is the timing and frequency of monsoon-driven turbidity events, which are centered over the southern portion of the basin.

Turbidity may already be limiting Smallmouth Bass expansion in Grand Canyon. Smallmouth Bass have been detected in western Grand Canyon downstream of Diamond Creek, with Lake Mead as a possible source population (see Figure 4 in Trammell et al., 2024). Yet, despite favorable temperatures, no sustained populations have been documented (Rosen et al., 2012; Valdez, 1994). The formation of Pearce Ferry rapid around 2010 may have reduced upstream fish movement from

Lake Mead, but 2000–2010 had suitable thermal conditions and a source population, and upstream invasion of Smallmouth Bass is documented (Kirk et al., 2022). The lack of establishment suggests that other limiting factors, likely turbidity, may have played a role.

Humpback Chub populations in western Grand Canyon have increased significantly during the past decade (Rogowski et al., 2018; Van Haverbeke et al., 2017), despite co-occurrence with nonnative predators downstream of Pearce Ferry rapid (Albrecht et al., 2018). This supports the idea that environmental conditions may suppress Smallmouth Bass populations and could be a factor contributing to observed increases in Humpback Chub.

This spatial variability underscores the importance of location-specific risk assessments for guiding fish management in the southwestern USA (Gido et al., 2013). Similar dynamics may explain why Smallmouth Bass and Largemouth Bass remain scarce in tributaries like the San Juan River despite upstream reservoirs acting as potential source populations (Gido & Propst, 2012; Pennock et al., 2022; Pilger et al., 2008). Data from the San Juan River gauge near Bluff, Utah (Figure S11), show frequent high-turbidity events that coincide with periods critical to the growth of young bass, possibly explaining their limited success.

In the Green River, Smallmouth Bass abundance trends may decline with increasing distance south from Flaming Gorge Dam (Lawry et al., 2023). Although turbidity data are limited, it also appears that the timing and duration of turbidity events increases at more southerly latitudes in the Green River basin, likely because of increased influence of the North American monsoon and changes in geomorphology. For example, turbidity data from the Green River near Green River, Utah (USGS site 09315000), approximately 197 mi downstream of the Green River near Jensen, show summer peaks (Figure S11) exceeding 50 FNU—the threshold that impairs Smallmouth Bass feeding—in an area where Smallmouth Bass catch rates are lower than at upstream locations, including near Jensen, Utah (Lawry et al., 2023).

Implications for Humpback Chub populations in Marble and Grand canyons

Predation by Smallmouth Bass on native fish recruits, including Humpback Chub, is a management concern due to the potential for reduced recruitment, subsequent declines in adult population size, and increased extinction risk. Coggins et al. (2006) estimated that Humpback Chub recruitment in the Little Colorado River population declined substantially in the 1980s, likely contributing to a 40–60% reduction in the adult population during the 1990s and early 2000s. Although the population remained above the recovery target of 2,100 adults (age 4 and older) and the extinction risk for a population of that size was very low (Pine et al., 2013), the declining adult trend and persistently low age-3 recruitment indicated that USFWS (2002) recovery goals at that time were not being met for this population (Coggins et al., 2006).

During the past two decades, this trend reversed, and Humpback Chub populations in the Grand Canyon ecosystem are many-fold larger than observed since monitoring began in the 1990s. Contributing factors include higher juvenile survival in a warming Colorado River, reduced predation by Rainbow Trout, and more favorable hydrology in the Little Colorado River (Van Haverbeke et al., 2013; Yackulic et al., 2014, 2018). Humpback Chub were downlisted from endangered to threatened in 2021 (Endangered and Threatened Wildlife and Plants, 2021), and recovery goals and actions for the population continue to evolve (Young et al., 2016)

If Smallmouth Bass establishment in the Grand Canyon ecosystem increases natural mortality of Humpback Chub through predation, resulting in lower recruitment, then such effects on adult populations are likely to manifest over decadal timescales. This is because there is currently a large Humpback Chub population in western Grand Canyon of a larger body size than what would be nominally preyed upon by adult Smallmouth Bass (see example Fritts & Pearsons, 2006). Our results highlight critical uncertainties regarding the potential for local recruitment of Smallmouth Bass in the Grand Canyon ecosystem, with this uncertainty being greatest near the largest Humpback Chub population center in western Grand Canyon and likely lowest for a small Humpback Chub aggregation in Marble Canyon near Fence Fault (RM 30).

The current Humpback Chub Recovery Plan treats the Grand Canyon ecosystem as a single management unit with respect to genetic diversity (Endangered and Threatened Wildlife and Plants, 2021). We recommend that the risk of Smallmouth Bass establishment—and any resulting recruitment impacts on Humpback Chub viability—be considered in the context of other known population risks, the current Humpback Chub population size at different locations in the upper and lower Colorado River, and the timescales of these effects. The risks posed by Smallmouth Bass to Humpback Chub and other native fishes are unlikely to be uniform across the Colorado River system; thus, decisions related to the best management actions to take may differ depending on the location within the Colorado River basin.

While our analysis suggests that the risk of Smallmouth Bass establishing in Grand Canyon at levels that could reverse native fish recovery is lower than expected based on upper basin experience, management decisions must reflect the risk tolerance of Colorado River stakeholders.

Conclusions

The threat of Smallmouth Bass to Humpback Chub is likely highly site dependent, shaped by temperature, turbidity, geomorphology, hydrologic regimes, and adult population size and likely other factors, including prey availability and juvenile habitat. While warming may promote favorable Smallmouth Bass spawning conditions across the lower basin, high summer turbidity in Grand Canyon—driven by the North American monsoon and sediment inputs from tributaries, including the Paria and Little Colorado rivers—is likely to limit Smallmouth Bass recruitment and population growth. These conditions contrast sharply with the upper Colorado River (e.g., Green River near Jensen, Utah), where fewer and shorter-duration turbidity events mostly in spring prior to Smallmouth Bass spawning align more closely with native Smallmouth Bass habitat conditions. In this way, the two factors of habitat modification and nonnative fish predation (Johnson et al., 2008) may not be operating concurrently in Grand Canyon downstream of the Little Colorado River because the habitat effects of turbidity persist due to fine sediment inputs from tributaries and washes during monsoon season.

Our analyses and modeling suggest that the alignment of suitable temperature, high turbidity, and key Smallmouth Bass life history phases likely impedes reproduction, growth, and recruitment in Grand Canyon. In contrast, the absence of frequent late-summer turbidity events has allowed the species to establish populations in parts of the upper basin where these conditions, especially low turbidity, are more common. This hypothesis warrants further investigation, particularly given the attention focused on Smallmouth Bass invasion in the Grand Canyon ecosystem and the efforts underway to reduce this risk, including large-scale dam management and cool mix releases from Lake Powell (Eppehimer et al., 2024). Assessing the relationships between Smallmouth Bass catch and environmental conditions in the upper Colorado River remains a key area for future research. Our findings support incorporating turbidity and other important factors from the bass early life history literature into predictive models of native and nonnative fish dynamics (Dibble et al., 2021; Gido & Propst, 2012). This approach will improve understanding of invasion risk and help guide management decisions.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Transactions of the American Fisheries Society* online.

DATA AVAILABILITY

A public repository contains spreadsheet versions of models used in this paper (available at https://github.com/billpine/SMB_Grand_Canyon). All water temperature and turbidity data are publicly available on USGS data servers referenced in the paper.

ETHICS STATEMENT

No live animals were used as part of this paper. The paper only used computer simulations or water quality data.

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CONFLICTS OF INTEREST

There are no conflicts of interest associated with this research.

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APPENDIX A: NORTH AMERICAN MONSOON AND RIVERBED SEDIMENT

The North American monsoon is a seasonal weather pattern marked by a sharp increase in summer rainfall across northwestern Mexico and the southwestern United States (Adams &

Comrie, 1997). It exhibits substantial spatial and temporal variability, including within the Colorado River basin. The monsoon's core influence lies in northwestern Mexico, where up to 70% of annual precipitation occurs from July to September. The monsoon impact diminishes northward but still affects southern and eastern Arizona, New Mexico, and south-central Colorado. In the Colorado River basin, monsoon rainfall patterns are shaped by large-scale atmospheric circulation interacting with regional topography and low-level moisture inputs from the Gulf of California. Climate projections suggest medium confidence in monsoon intensification under warming scenarios, low agreement on potential precipitation declines, and high confidence in a delayed monsoon onset (Szopa et al., 2021). Monsoon-driven precipitation contributes to bimodal runoff patterns (spring snowmelt and summer rain) and localized sediment delivery, which can be substantial in tributaries like the Little Colorado River (Stone, 2010; Stone et al., 2018; Topping et al., 2000). These inputs influence water quality and fish communities. For example, Gido & Propst (2012) suggest that in New Mexico, reduced monsoon activity may limit sediment transport, potentially favoring nonnative fish recruitment by maintaining clean spawning substrates and enhancing food availability. Because the monsoon is centered over Mexico, its effects on the Colorado River basin, especially frequency, intensity, and duration, decline with increasing latitude (Adams & Comrie, 1997).

The sand-bed channels of the Green and Colorado rivers have changed significantly over the past century due to altered flow regimes, reduced sediment supply, and changes in riparian vegetation. In the Green River, two major periods of channel narrowing were observed. The first began in the 1930s, driven by declining flood magnitudes and the spread of nonnative tamarisk *Tamarix* spp. The second followed the construction of Flaming Gorge Dam in the 1960s, which reduced snowmelt floods and promoted vertical buildup of fine sediment in inset floodplains (Allred & Schmidt, 1999; Walker et al., 2020). Downstream, similar narrowing and floodplain development occurred along the Colorado River, even as sediment supply declined—indicating that flood duration and bed grain size strongly influence sediment transport (Dean et al., 2020).

Over time, both rivers have experienced a decrease in suspended sand concentrations, reflecting lower discharge and coarsening of the riverbed, which reduces the availability of transportable sediment (Dean et al., 2020; Topping et al., 2018). Sand transport in these rivers is often out of equilibrium, driven by sporadic sediment inputs and the movement of sand waves. These sand waves can have greater long-term effects on grain size and sediment dynamics than dams (Topping et al., 2018). Partitioned sediment budgets also show that rivers can absorb changes—like floodplain erosion or bed coarsening—without major shifts in channel form, meaning that sand loss does not always cause instability (Leonard & Schmidt, 2024). Critically these sediment inputs continue from the Little Colorado River, so while the overall Colorado River suspended sediment concentrations have declined, the Colorado River downstream of the Little Colorado River tributary still experiences spring snowmelt and summer monsoon-driven sediment input.

APPENDIX B: LITERATURE REVIEW

Table B1. Literature review of Smallmouth Bass and Largemouth Bass recruitment dynamics that informed the conceptual model of Smallmouth Bass recruitment in Grand Canyon.

Reference	Key information
Beeman (1924)	Observed that Smallmouth Bass fry experienced severely limited growth and survival under food scarcity conditions.
Surber (1939)	Found that high turbidity during spawning often destroyed most Smallmouth Bass fry in Virginia streams. However, later-season spawning often compensated as turbidity declined.
Wallen (1951, 1955, as cited in Bulkley, 1975)	Found juvenile Largemouth Bass suffered mortality at turbidity levels averaging 101,000 ppm. Even lower turbidity (100–388 ppm) reduced survival and growth due to diminished plankton availability. These ppm values likely reflect suspended sediment concentrations.
Cleary (1956)	Found that postnest swim-up survival of Smallmouth Bass in Iowa streams was reduced by high water levels, increased turbidity, and low temperatures. Prolonged turbidity from watershed erosion reduced fingerling production and fishing quality by impairing sight-dependent feeding.
Buck (1956)	Lower turbidity levels impaired survival and growth of juvenile Largemouth Bass by limiting plankton production and food availability.
Hastings & Cross (1962)	Found that turbidity levels between 100–388 ppm negatively affected juvenile black bass *Micropterus* spp. growth and survival by reducing primary productivity and prey abundance.
Heimstra et al. (1969, as cited in Bulkley, 1975)	Reported similar negative foraging responses to turbidity in Largemouth Bass, including reduced prey detection rates.
Stroud & Clepper (1975)	Proceedings compiling decades of lab and field studies on early life history requirements for species of black bass.
Eipper (1975)	Identified starvation and meteorological conditions as critical drivers of embryo and larval mortality in black bass.
Bulkley (1975)	Reported that turbidity causes mechanical injury and reduces light penetration, which limits prey availability. Found that slow growth in turbid environments inhibited reproductive capacity in black bass.
Pflieger (1975)	In Missouri, found that rapid river discharge changes during fry emergence harmed Smallmouth Bass recruitment. Smaller fluctuations before nesting or after larval emergence improved outcomes by enhancing food availability and lowering predation.
Larimore (1975, 2002)	Showed that spring floods could raise turbidity to 2,000 Jackson turbidity units, causing Smallmouth Bass fry up to 25 mm TL to lose vertical orientation, reducing survival.

Reference	Key information
Shuter et al. (1989)	Found that smaller Smallmouth Bass lost energy faster under starvation with temperature-dependent survival times: at 17°C, a 14-mm bass survived 8 d under starvation while a 62-mm bass survived 45 d.
Ludsin & DeVries (1997)	Identified four early life bottlenecks for Largemouth Bass: (1) hatching date, (2) diet shift to piscivory, (3) fall lipid accumulation, and (4) winter survival. Early spawning allowed time for growth and triglyceride storage, improving overwinter success.
Post et al. (1998)	Found that overwinter mortality in small Largemouth Bass (<50–60 mm TL) was linked to starvation, influenced by predator abundance, adult competition, and size-selective mortality.
Peterson & Kwak (1999)	Smallmouth Bass recruitment in Illinois' Kankakee River impacted by high streamflows during spawning leading to increased egg and fry mortality. Warm temperatures improved feeding and growth, while fluctuating winter flows elevated stress and juvenile mortality.
Pine et al. (2000)	Early-hatched Largemouth Bass cohorts had higher first-summer survival than later-hatched cohorts, primarily due to a foraging and growth advantage.
Fullerton et al. (2000)	Showed Largemouth Bass winter survival was determined by winter severity, food availability, and fish size. Noted that low-latitude populations had lower cold tolerance.
Garvey et al. (2002)	In the second black bass symposium, showed how abiotic factors (temperature, oxygen, flow variability, productivity) and biotic factors (prey availability, predator density, intraspecific competition) interact across environmental gradients to drive Largemouth Bass recruitment variability.
Sweka & Hartman (2003)	Demonstrated that reactive distance to prey declined exponentially with increasing turbidity, reducing prey detection but not capture efficiency. At turbidity >40 NTU, prey consumption and growth declined significantly for Smallmouth Bass.
Phelps et al. (2008)	Found that daily growth rate, not hatch date, determined age-0 Smallmouth Bass size in South Dakota lakes. Growth was driven by temperature and food availability.

APPENDIX C: DATA CLEANING AND SUMMARIZATION

Invalid values for temperature, turbidity, and silt + clay were set to "not available". Thresholds for removal included temperature <0°C or >30°C, turbidity <0 or = −999, and silt + clay <0 or = −999. Daily means were calculated from subdaily data to standardize across sites.

For each site, year, and month, we calculated the number of days with mean daily temperature ≥16°C and, separately, days with turbidity ≥50 FNU or ≥200 mg/L silt + clay (depending on available data). Data availability varied by site but represent the most complete records for comparison.

APPENDIX D

Box 1. Predicting maximum first-year survival rates and population growth rates for invading Smallmouth Bass

Most fish have high enough fecundity (in the thousands at least) to potentially produce many age-1 recruits for each spawner under ideal conditions. But natural mortality rates of eggs, larvae, and small juveniles are almost always very high, so very few fish survive to their first birthday even under ideal conditions. A basic issue in fish population dynamics is how much that first-year survival rate can increase when an unharvested population is reduced through factors like fishing, or conversely, how high that survival rate can be when a fish stock is introduced at low densities into an environment. Fortunately, we have many observations of how much first-year survival rate has improved in populations that have been reduced through fishing, and an elegant way to describe that improvement is with the "Goodyear compensation ratio," or just CR, introduced by Phil Goodyear. The CR is just the ratio of first-year survival when abundance is very low ($s_{\max}$) to first year survival in the natural unharvested population before it is fished or after it stops growing (s_o), i.e., $\mathrm{CR}=s_{\max}/s_o$.

In terms of stock–recruitment theory, we typically predict recruitment using a function of the form

$$R = s_{\max} f(E), \tag{DB1.1}$$

where $f(E)$ is a decreasing function of total egg deposition; e.g., $1/(1+bE)$ is called the Beverton–Holt function and $\exp^{(-bE)}$ is called the Ricker function. At an unfished natural equilibrium with average recruitment R_o, unfished egg production is given by $E_o = R_o \times \mathrm{epro}$, where epro is the average egg production per age-1 recruit. In an age-structured model, epro is given the sum over ages of fecundities f_a times age-specific survivorships L_a, i.e., the Botsford incidence function for egg production, as

$$\mathrm{epro} = \sum_{a=1}^{a=a_{\max}} f_a L_a \tag{DB1.2}$$

where survivorships $L_1 = 1$ and $L_a = L_{a-1} S_a$ for age $a > 1$. In this equation, S_a is the annual survival rate from age a to age $a+1$.

An important observation about the epro unfished egg production per recruit is that 1/epro is the unfished recruitment per egg, i.e., $s_o = 1/\mathrm{epro}$, where s_o is again the average unfished age-0 survival rate. What has been found in meta-analysis of stock recruitment data for many fish species is that the compensation ratio CR leading to prediction of the $s_{\max} = \mathrm{CR} \times s_o$ maximum survival rate needed to predict age-0 survival rate following new introductions is relatively predictable (Hilborn & Walters, 2021). When we express s_o and s_{max} as instantaneous mortality rates M_o and M_{min} [in the model $s = \exp(-M)$], the difference $(M_o - M_{min})$ is a predictable fraction, typically near 0.2, of M_o, i.e., $M_{min} = 0.8 \times M_o$. The change in M, $M_o - M_{min}$, is the natural logarithm of the compensation ratio, i.e., $\ln(\mathrm{CR}) = 0.2 \times M_o$. More simply, for an age-structured model used to predict invasions or responses to fishing using predictions of egg production and first-year survival rates from a basic stock–recruitment model of Equation (DB1.1) form, s_{max} is given by just

$$s_{max} = \mathrm{CR}/\mathrm{epro}, \quad \text{(DB1.3)}$$

In this equation, epro is easily estimated given age schedules of fecundity and annual survival rates of 1-year-old and older fish, and CR can be predicted from meta-analysis results for many, many fish species. Using typical Smallmouth Bass survivorship and fecundity schedules from the literature and from observations in the upper basin, we estimate that CR is most likely around 6.0 but could be as high as 15 if we have underestimated maximum fecundity and if the ratio $(M_o - M_{min})/M_o$ is as high as 0.3, the maximum seen over species by Hilborn & Walters (2021).

We developed a basic age-structured population model to predict invasion dynamics using Equation (DB1.1) to predict recruitment in conjunction with alternative assumptions about frequency of successful year-class production. The age dynamics $N_{a,t}$ (a = age, t = year) are given in this model by

$$E_t = \sum f_a N_{a,t} \text{ egg production year t,} \quad \text{(DB1.4)}$$

$$N_{1,t} = s_{max} E_t / (1\text{-b} \times E_t) \times R_t \text{ Beverton-Holt recruitment,} \quad \text{(DB1.5)}$$

$$N_{a,t} = N_{a\text{-}1,t\text{-}1} S_{a\text{-}1,t\text{-}1} \text{ for a>1, survival of older fish over time.} \quad \text{(DB1.6)}$$

Here, the scaling parameter b for maximum recruitment is set to give average recruitment near 1.0 after invasion. The $S_{a,t}$ can be varied to represent effects of culling on survival rate. The annual recruitment rate multipliers R_t are set to e^{wt} every nth year representing successful recruitment, 0 for other years, with w_t being a normally distributed recruitment anomaly for successful spawning years (we used $\sigma_w = 0.4$ to give considerable variation in recruitment for strong cohorts). For the age accounting, we assumed a maximum age of 20 years absent mortality due to harvest or mechanical removal.

We calculated f_a using growth and maturity schedules assuming von Bertalanffy growth with $K = 0.2$ and mean age at maturity of 3.5. Annual survival rates S_a were assumed to vary according to a Lorenzen (Lorenzen, 1996, 2022; Lorenzen et al., 2022) model for size-dependent survival rate, with survival varying as a −0.29 power of relative body weight so as to correspond with age variation in survival rates seen in Lorenzen's meta-analysis of a variety of fish species. The resulting age schedules are given in Table D1.

Note that the model defined by Equations DB1.4–1.6 exhibits maximum population growth rate for very low numbers at age; i.e., it does not assume any questionable "Allee effects" in the invasion dynamics. By simply setting the initial numbers at age very low, e.g., 10^{-6}, we can easily simulate the intrinsic population growth rate "r" or annual growth rate $\lambda = e^r$ over the first 30 or so years of any simulation test, allowing simple evaluation of the effects of various parameter values on predicted invasion rates and success.

We simulated two alternative invasion patterns. For the first pattern, we simply initialized the model age structure with a low number of age-1 recruits from "upstream" sources, with no later invasion events. For the second, we assumed a low annual addition of age-1 recruits from some upstream source, like an established population in Glen Canyon. Initial sensitivity tests indicated that adding low immigrant juvenile numbers every year did not substantially affect long-term population growth patterns but did affect calculations of population growth rates r over the first 2–30 years after invasion.

The calculations above are implemented in a relatively simple Excel spreadsheet (available at https://github.com/billpine/SMB_Grand_Canyon/upload). We chose this (rather than code-based methods) in order to make them as transparent and understandable as possible to model users interested in evaluating sensitivity of the predictions to various parameters and harvest culling scenarios.

Table D1. Assumed baseline Smallmouth Bass mean age-specific fecundities (f_a) and survival rates (S_a) used in estimating recruitment compensation ratios and in age-structured simulations of invasion dynamics.

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
f_a	8.21	111	555	1,572	2,970	4,333	5,475	6,394	7,130	7,722	8,198	8,578	8,881	9,121	9,311	9,460	9,578	9,670	9,743	9,799
S_a	0.31	0.49	0.58	0.63	0.66	0.68	0.69	0.7	0.71	0.71	0.72	0.72	0.72	0.72	0.73	0.73	0.73	0.73	0.73	0.73

Box 2. Temperature- and turbidity-dependent growth model for Smallmouth Bass

We used the general bioenergetics model described in Walters & Essington (2010) (see also Essington et al., 2001; van Poorten & Walters, 2016) to model first-year weight growth of postlarval Smallmouth Bass for the 2002–2023 period, using daily water temperature and silt–clay concentration data at Bright Angel Creek, locations representative of the river reach just below the Little Colorado River, where native fish impacts are first expected if Smallmouth Bass can successfully colonize that reach. The basic model growth rate equation for a fish of body weight W is

$$dW/dt = f_t(S) f_s(S) f_c(T) H W^{2/3} - f_m(T) m W. \quad \text{(DB2.1)}$$

In this model, the annual average consumption and metabolism parameters H and m are modified for each day by three multiplicative functions of temperature T and turbidity S as

$$f_s(S) = \exp(-S/S_h) \text{ turbidity effect on feeding,} \quad \text{(DB2.2)}$$

$$f_c(T) = Q10_c^{(T-T_{\text{bar}})/10} \text{ temperature effect on feeding,} \quad \text{(DB2.3)}$$

$$f_m(T) = Q10_m^{(T-T_{\text{bar}})/10} \text{ temperature effect on metabolism.} \quad \text{(DB2.4)}$$

The parameters of this model (H, m, S_h, $Q10_c$, $Q10_m$, and mean temperature T_{bar}) were estimated from various data sources as described below with the exception of T_{bar}, which was obtained directly from the temperature time series data recorded at Diamond Creek.

Laboratory experiments have shown that reduced prey availability due to turbidity (Equation DB2.2) do not necessarily lead to reduced growth, presumably because at least small juvenile fish increase their foraging time to try to maintain growth rates needed for survival (Gregory & Northcote, 1993; Sweka & Hartman, 2003). We have examined the effect of such responses by including foraging time multiplier on the feeding rate term of Equation (DB2.1):

$$f_t(S) = \min\{T_{\max}, 1/f_s(S)\}. \quad \text{(DB2.5)}$$

Here, $T_{\max}$ is a maximum relative time spent foraging, and the $1/f_s$ term inflates feeding rate in inverse proportion to reduction in reactive distance. Reasonable values of $T_{\max}$ are likely to be in the range of 3 to 5; i.e., juvenile fish are likely to be able to spend as much as 3–5 times their normal daily foraging times when apparent prey densities as impacted by turbidity are lower. Note that such increases in foraging time at low apparent prey densities are also likely to lead to increased mortality rates, and in fact, one way to derive the well-known Beverton–Holt stock–recruitment model is to assume that foraging times increase when competition reduces prey density so as to maintain constant growth rates (Walters & Korman, 1999).

Estimates of H and m were obtained by fitting length-at-age data for upper basin Smallmouth Bass in Breton et al. (2015) to the von Bertalanffy growth curve while noting that the general structure A1 without T,S forcing is the defining relationship for the von Bertalanffy growth curve. For this curve, there is a simple transformation between the H, m, and the von Bertalanffy parameters K, L_∞ ($m=3K$, $H=mL_\infty a^{1/3}$, where a is the intercept parameter of the length–weight equation $W=aL^3$). The H, m estimates obtained this way are near the lower end of the set of H, m estimates reported in Fishbase for locations around North America (see "strawberry utah SMB growth.xlsx" at https://github.com/billpine/SMB_Grand_Canyon); i.e., Smallmouth Bass growth in the upper Colorado River basin is a bit slower than expected from Smallmouth Bass on average.

Estimates of the turbidity S_h needed to reduce feeding rate by about two-thirds (to $1/e$ of maximum rate) were obtained from a general relationship assembled for visual feeding salmonids by Rosenfeld & Taylor (2003).

The $Q10_m$ parameter for variation in metabolic rate with temperature can be reasonably estimated from laboratory data and is likely in the range of 2.0–3.5 (Shuter et al., 1980; Tetzlaff et al., 2010; Whitledge et al., 2002; reviews of Wisconsin bioenergetics model typical parameter values). Unfortunately, the $Q10_c$ parameter is a function of feeding conditions (e.g., prey density and size) as well as basic physiology, so only a minimum value for it can be obtained from laboratory studies. Estimates for it from field growth data (references for $Q10_m$ above, also Coutant & DeAngelis, 1983) imply that it is considerably higher than $Q10_m$, most likely on order 4.0. Fortunately, simulated growth patterns using Equation (DB2.1) are quite similar for a substantial range of values of both $Q10$ parameters since the annual temperature range in Grand Canyon is relatively narrow and much larger effects on growth variation are predicted to occur because of turbidity variation.

The basic model structure and parameter values described above predict low but positive growth rates on order 0.1 mm/d for age-0 bass during their first winter, given Colorado River temperatures that drop to around 8°C for. Even these low growth rates may result in overestimation of spring body sizes (and hence Smallmouth Bass invasion risk), so the basic model is conservative in that regard. Smallmouth Bass are observed to become torpid (stop moving and feeding, seek refuge cover) at temperatures much below 14°C. So we examined this possibility by including a "torpid multiplier" that reduces both feeding and metabolic rates for every simulation day with temperature $T<T_{\text{torpid}}$. Sensitivity tests with alternative values for T_{torpid} and with multiplier values like 0, 0.5 for lower temperatures showed that including the torpid period did indeed reduce predicted spring body sizes but did not change the basic interannual patterns of growth variation; i.e., growth is simply rescaled in ways that could be easily corrected to fit field data by increasing the H parameter.

For many fish species, juvenile length growth over the growing season is close to linear. This has led to development of so-called "biphasic growth" models (Lester et al., 2004; Quince et al., 2008), where the metabolic rate term of Equation (DB2.1) is replaced with the same power of weight as for the consumption term, i.e., with $-f_m(T)mW^{2/3}$. For this model, the exponent for both consumption and metabolism can be replaced with a higher power than ⅔; e.g., Quince et al. (2008) suggest values between 0.69 and 0.75 based on powers summarized from various studies for users of the Wisconsin bioenergetics model. We set up a version of the model with this structure and found that using single powers between 0.67 and 0.75 had only very minor effects on the predicted growth patterns, with larger powers leading to slightly larger sizes in years more favorable for growth.