

Articles

Nonnative Smallmouth Bass in the Snake River, Idaho: Population Dynamics, Demographics, and Management Options

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Abstract

The Snake River in Idaho, USA, supports a popular sport fishery for nonnative Smallmouth Bass *Micropterus dolomieu*, but there are limited studies on the population dynamics of this introduced species in Idaho and other water systems in the western United States. The purpose of this study was to describe the population dynamics and demographics of Smallmouth Bass in the Snake River, Idaho. In total, we sampled 4,929 Smallmouth Bass during electrofishing surveys on the Snake River (separated into nine segments) and three major tributaries (Boise, Payette, and Weiser rivers). We estimated age for 1,869 Smallmouth Bass sampled from the Snake River ($n = 1,433$) and three tributaries ($n = 436$). Catch-per-unit-effort for all nine segments combined on the Snake River was 36.6 fish/h (± 4.4 SE). In the tributaries, catch-per-unit-effort varied from 43.6 to 125.0 fish/h. Relative weight of all Smallmouth Bass varied from 86 to 107, indicating that fish were in relatively good body condition. Fish in the system grew fast, with relative growth index values often near or exceeding 100 for all age classes. Total annual mortality for the Snake River was $45.1 \pm 0.7\%$, and it was 36.8–40.5% in the tributaries. Furthermore, we estimated exploitation to be 5.3% (90% CI; $\pm 2.2\%$) for the Snake River and tributaries combined. We used a yield-per-recruit population model to evaluate the effects of varying minimum length limits on the fishery. With the observed population demographics and exploitation rates, increasing the current minimum length limit from 305 mm to 356 or 406 mm would probably have little influence on the number of Smallmouth Bass available to anglers. However, increasing the length limit would result in reduced biomass available for harvest. The potential for recruitment overfishing was minimal for all minimum length limits and levels of exploitation. As such, changes to current harvest regulations do not appear warranted. Our findings provide important information on the population dynamics of Smallmouth Bass that can be useful in evaluating their management across Idaho and in similar systems in western North America.

Keywords: demographics; management; *Micropterus dolomieu*; population dynamics; Smallmouth Bass

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Introduction

Black basses *Micropterus* spp. are popular sport fishes worldwide largely due to their aggressive nature, ability to grow to trophy sizes, and capacity to thrive in a diversity of habitats (Coble 1975; Brewer and Orth 2015). They occur across North America and have been widely introduced to systems in Asia, Africa, Europe, and South America (Robbins and MacCrimmon 1974; Brewer and Orth 2015). Black basses are regularly ranked as the most popular group of freshwater sport fishes in the United States (U.S. Fish and Wildlife Service [USFWS] 2011). In particular, the Smallmouth Bass *Micropterus dolomieu* is one of the most socially, economically, and ecologically important species in North America. It is present in systems across the United States and is found in a variety of habitats (e.g., lakes, rivers, and streams) across various latitudes (Coble 1975). Its native distribution includes portions of several major rivers in the central and eastern United States, including the Ohio, Tennessee, and Mississippi rivers, as well as the Saint Lawrence–Great Lakes system (Scott and Crossman 1973). There also has been an expansion of the distribution of this species because of shifts in climate and intentional and unintentional introductions (Schade and Bonar 2005; Stepien et al. 2007; Carey et al. 2011).

The transfer of Smallmouth Bass outside its native distribution to the western United States began in the 1800s. One of the first recorded introductions of Smallmouth Bass west of its native distribution took place in California, USA, in 1874 (Lampman 1946). Following the introduction in California, introductions in Oregon and Washington, USA, occurred in the 1920s (LaVigne et al. 2008). In addition to these early introductions, Munther (1970) reported on the introduction of Smallmouth Bass to the Snake River, Idaho–Washington, in the late 1800s, but provided no evidence as to the specific location. Keating (1970) reported that the Idaho Department of Fish and Game (IDFG) facilitated the first introduction of Smallmouth Bass to the Snake River, Idaho, in 1942. Smallmouth Bass dispersed after introduction and became established in the mainstem of the Snake River downstream of Swan Falls Dam and in the lower reaches of the Boise, Payette, and Weiser rivers. Following the completion of the Hells Canyon Hydroelectric Project (i.e., Brownlee, Oxbow, and Hells Canyon dams) in the 1950s and 1960s, the Smallmouth Bass population(s) in the portion of the Snake River between Swan Falls Dam and Brownlee Reservoir increased dramatically (Kozfkay et al. 2006). Impoundment of the Snake River made the system more suitable for Smallmouth Bass by increasing water temperatures and stabilizing flows in the river upstream of Brownlee Dam. As a result, the Snake River now supports a highly popular Smallmouth Bass sport fishery.

Currently, a daily bag limit of six fish (Smallmouth Bass and Largemouth Bass *Micropterus salmoides* in aggregate), each with a minimum length limit of 305 mm, is used to manage black basses in the Snake River and its major tributaries (Boise, Payette, and Weiser rivers) between Swan Falls Dam and Brownlee Dam. During the past 5 decades, IDFG has collected minimal information on Smallmouth Bass, only sampling the Snake River in 1972 and 2006 (Kozfkay et al. 2006). Importantly, local anglers and IDFG

staff have recently expressed concern about the harvest of Smallmouth Bass during seasonal congregations in and around the lower reaches of the Weiser and Payette rivers. Despite the popularity of the fishery, there is a lack of information on population dynamics of Smallmouth Bass in the Snake River for management purposes.

Numerous studies exist on Smallmouth Bass populations within their native distribution (Paragamian and Coble 1975; Marinac-Sanders and Coble 1981; Paragamian 1984a; Raffetto et al. 1990; Jansen et al. 2008), but little research exists on Smallmouth Bass in areas where they are nonnative, particularly in western North America. Of the research conducted, the vast majority focused on distribution and movement (LaVigne et al. 2008; Rubenson and Olden 2016; McClure et al. 2020) or the predatory effects of Smallmouth Bass on native fishes (Poe et al. 1991; Naughton et al. 2004; Carey et al. 2011).

Given the paucity of information on nonnative Smallmouth Bass populations in western North America, we conducted this study to describe patterns in relative abundance, length and age structure, growth, and mortality of Smallmouth Bass in the Snake River, Idaho. Using information on population dynamics and demographics, we conducted a yield-per-recruit analysis to evaluate different management scenarios (e.g., changes to the minimum length limit). The information presented in this study provides a comprehensive overview of the population dynamics and ecology of an introduced population of Smallmouth Bass. In particular, our work provides insight for managing Smallmouth Bass in systems where they pose a threat to the conservation and management of native fishes.

Study Area

The Snake River has a drainage area of 282,000 km² and originates in northwestern Wyoming, USA. It flows through western Wyoming before turning west and entering Idaho. The study area included the portion of the Snake River downstream of Swan Falls Dam (~32 km south of Boise, Idaho) to Brownlee Dam (Figure 1). However, the primary focus of this study was the segment of the Snake River from Swan Falls Dam to Farewell Bend (i.e., upstream termination of Brownlee Reservoir), a distance of approximately 200 river kilometer (rkm), and included the lower portion (20 rkm upstream from the mouth) of the Boise, Payette, and Weiser rivers. Swan Falls Dam, constructed by the Trade Dollar Mining Company in 1901, is the oldest hydroelectric dam on the Snake River. The Idaho Power Company, who currently owns and operates the dam, acquired the dam in 1916. In 1958, the Idaho Power Company finished construction of Brownlee Dam, the first and most upstream of three dams built between 1958 and 1967 that make up the Hells Canyon Hydroelectric Project. The dams and reservoirs serve functions in flood control, recreation, and power generation.

The Boise, Payette, and Weiser rivers are large tributaries in Idaho that join with the Snake River between Swan Falls Dam and Farewell Bend (Figure 1). The Weiser River is the northernmost major tributary; it drains 2,672 km² and has an average annual discharge of 0.9×10^9 m³. The Payette River drains approximately 5,214 km² and discharges an



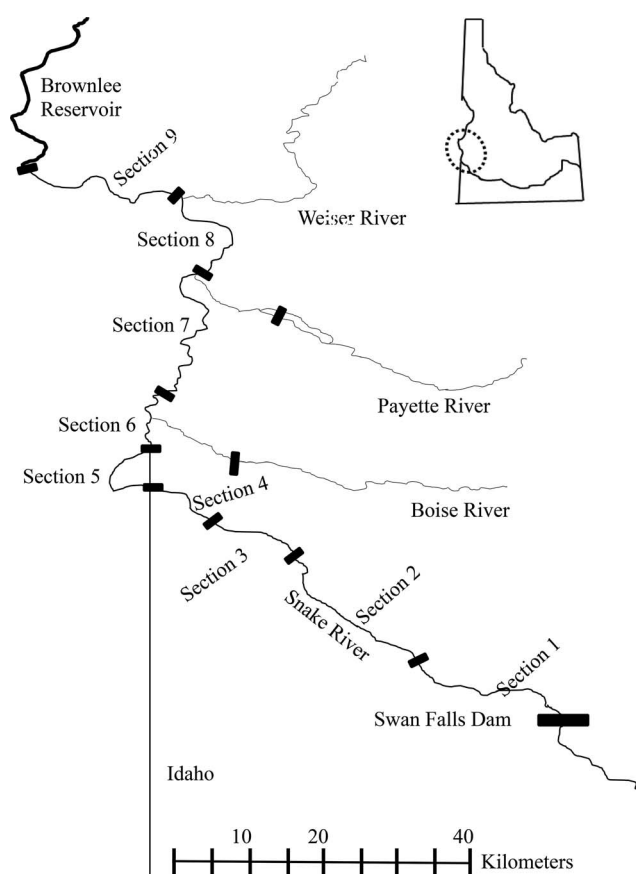


Figure 1. Map of the study area sampled in 2016 between Swan Falls Dam and Brownlee Dam, Idaho, USA. The river flows from south to north. The small black bars indicate segment breaks.

average of $2.7 \times 10^9 \text{ m}^3$ of water/y. The Boise River is the most southern major tributary in the study area; it drains an area of $6,598 \text{ km}^2$ and contributes an annual average discharge of $2.4 \times 10^9 \text{ m}^3$ of water to the system.

Methods

Sampling

We used a stratified random sampling design to sample the Snake River and three major tributaries. In 2006, IDFG divided the Snake River from Swan Falls Dam to Farewell Bend into nine segments (11.3–32.2 rkm long; Figure 1) based on potential management boundaries. We randomly selected 40 sampling reaches, approximately 2 rkm long, from the nine segments. We allocated the number of reaches sampled per segment in proportion to segment length (Scheaffer et al. 2006), with more sampled reaches in longer segments than shorter segments. In addition, we selected three 2-rkm-long reaches from the lower segments of the Boise and Payette rivers. Because of low flows and access restrictions, we sampled three 500-m-long reaches on the Weiser River.

Fish collection. We used jet-powered boats outfitted with electrofishing equipment (Midwest Lake Electro-fishing Systems [MLES], Polo, MO; Infinity Control Box; Smith-Root, Vancouver, WA; AUA-6 Anode Array) to sample

fish from the Snake River. For the Boise and Payette rivers, we used two rafts outfitted with the same electrofishing equipment used on the jet-powered boats to sample fish. We used a canoe outfitted with an MLES Infinity control box, a transfer box, and two handheld anodes to sample fish on the Weiser River. We used pulsed direct current at 60 Hz and 25% duty cycle to sample fish. We standardized power output to 2,750–3,250 W (Miranda 2009). We netted Smallmouth Bass by using 6.3-mm delta-style, knotless mesh dipnets. Sampling on the Snake and Weiser rivers occurred in a downstream direction moving back and forth across the river channel. On the Boise and Payette rivers, one raft floated downstream near each riverbank. We divided each 2 rkm reach into four 500-m subunits to minimize stress on captured fish. We recorded electrofishing time (i.e., “current on” effort) for each 500-m subunit except for two of the Payette River reaches when the timer on the electrofishing box malfunctioned.

Field processing. We measured all Smallmouth Bass to the nearest millimeter (total length; Data S1, *Supplemental Material*). We measured weight (grams) and collected dorsal spines from 10 fish per cm length group (Quist et al. 2012). We removed the first and second dorsal spines near the base of the spine, placed them in a coin envelope, allowed them to dry, and later processed and aged spines in the laboratory following Koch and Quist (2007). In an effort to estimate angler exploitation, we tagged 826 Smallmouth Bass in the Snake River and major tributaries greater than 260 mm with T-bar anchor tags between the pterygiophores of the second and third dorsal spines (Dell 1968; Guy et al. 1996). Each tag had a unique identification number on one side and a phone number on the other side that allowed anglers to report the capture and/or harvest of fish to IDFG. We tagged an additional 305 Smallmouth Bass captured during angling events (i.e., tournaments) in Brownlee Reservoir. We returned fish captured in the Snake River and tributaries alive to the water near the point of capture. We released all fish captured in Brownlee Reservoir alive at three central locations in the reservoir. In addition, we used data from mark-recapture electrofishing surveys to correct for size selectivity of electrofishing gear (Beamesderfer and Riemann 1988). We completed three mark-recapture surveys on the Snake River, one on the Payette River, and one on the Boise River, for a total of five mark-recapture surveys. During the mark-recapture surveys, we marked ($n = 1,113$) and later recaptured ($n = 125$) as many fish as possible. A majority of the sampling occurred from May to September 2016; however, one of the Snake River mark-recapture events and the tributary mark-recapture events occurred during July–August 2017.

Data summarization

Catch rates, length structure, and body condition. We estimated catch-per-unit-effort (CPUE) for each reach as the number of Smallmouth Bass captured per hour of electrofishing (Data S2, *Supplemental Material*). We estimated mean CPUE for each of the nine river segments and the three tributaries as the mean of the reaches. We used proportional size distribution (PSD) to characterize length structure as

$$\text{PSD} = \frac{\text{no. of fish} \geq Q}{\text{no. of fish} \geq S},$$

where stock length (S) is 180 mm and quality length (Q) is 280 mm (Gablehouse 1984; Neumann et al. 2012). We also estimated PSD of preferred (PSD-P; 350 mm) and memorable (PSD-M; 430 mm)-length Smallmouth Bass. We estimated the mean PSD for each of the nine river segments and the three tributaries as the mean of reaches reach to provide insight on how length structure varied in the system. We used relative weight (W_r) to provide insight on how body condition varied spatially and by length of Smallmouth Bass as

$$W_r = \left(\frac{W}{W_s} \right) \times 100,$$

where W is the weight of the fish and W_s is the length-specific standard weight of the fish (Wege and Anderson 1978; Kolander et al. 1993; Neumann et al. 2012). We only calculated W_r for fish greater than 150 mm (Neumann et al. 2012). Unfortunately, weight data were unavailable for the Weiser River, one reach on the Payette River, and four reaches on the Snake River due to a malfunctioning scale. We summarized relative weight by standard length category (i.e., substock [150–179 mm], stock – quality [180–279 mm], quality – preferred [280–349 mm], preferred – memorable [350–429 mm], memorable – trophy [430–509 mm], and trophy [≥ 510 mm]; Neumann et al. 2012). We estimated the mean W_r for each of the nine river segments and the three tributaries as the mean of reaches.

Growth. We used the Dahl–Lea method to estimate backcalculated lengths-at-age as

$$L_i = \left(\frac{S_i}{S_c} \right) \times L_c,$$

where L_i is the backcalculated length of the fish when the i th increment was formed, L_c is the length of the fish at the time of capture, S_c is the radius of the spine at the time of capture, and S_i is the radius of the spine at the i th increment (Francis 1990; Quist et al. 2012). We reported mean backcalculated lengths-at-ages (MBCLAs) by year class and summarized MBCLAs by segment and tributary. We further evaluated growth by using relative growth index (RGI) as

$$\text{RGI} = \left(\frac{L_t}{L_s} \right) \times 100,$$

where L_t is the observed length at age (t) and L_s is the predicted age-specific length (Quist et al. 2003; Jackson et al. 2008). We obtained predicted age-specific lengths from standard equations summarizing growth of Smallmouth Bass across their distribution (Jackson et al. 2008). We summarized RGI values by age for each segment and tributary. Last, we fit a von Bertalanffy growth model for Smallmouth Bass for the Snake River and three major tributaries combined as

$$L_t = L_\infty \times (1 - e^{-K(t-t_0)}),$$

where L_t is the length of the fish at time t , L_∞ is the mean asymptotic length, K is the growth coefficient, and t_0 is the

time when the length of the fish would theoretically equal 0 mm (Quist et al. 2012). We used mean backcalculated length at age data to fit the von Bertalanffy growth model. Given concerns with independence between individual observations, we used a hierarchical model with individual fish as a random effect to obtain parameter estimates (Ogle et al. 2017).

Mortality. We estimated total annual mortality (A) by using weighted catch curves for age-2 and older fish (Ricker 1975; Smith et al. 2012). We estimated and summarized annual angler exploitation (μ) for the Snake River and tributaries by using information from IDFG's tag reporting system (Meyer et al. 2012). We estimated annual exploitation as

$$\mu = \frac{\left(\frac{N_r}{\tau} \right)}{N_0 \times \gamma \times \theta},$$

where N_r is the number of tags returned from harvested fish, τ is the reporting rate, N_0 is the number of fish tagged, γ is tag retention, and θ is survival of tagged fish. We obtained estimates of tag retention ($\gamma = 0.85$), survival of tagged fish ($\theta = 0.99$), and reporting rate ($\tau = 0.54$) from Meyer and Schill (2014) for Smallmouth Bass in Idaho. We combined data from the Snake River and tributaries because too few fish were in the tributaries to provide a reliable estimate of exploitation. We also calculated exploitation for Brownlee Reservoir to provide additional insight on the system.

Harvest simulations. Fisheries managers were interested in the potential effects of changing harvest restrictions on the Smallmouth Bass fishery. As such, we used a Beverton–Holt yield-per-recruit model to evaluate changes in length structure, yield, and the potential for recruitment overfishing with varying minimum length limits on Smallmouth Bass. We estimated yield per recruit (Y) as

$$Y = \frac{(F \times N_t \times e^{Z(t-t_0)} \times W_\infty)}{K} \times [\beta(X, P, Q)] - [\beta(X_1, P, Q)],$$

where F is the instantaneous rate of fishing mortality; $N_t = N_0 \times e^{-M(t-t_0)}$, the number of recruits entering the fishery at some minimum length of time t ; N_0 is the initial population size; M is the instantaneous rate of natural mortality; t_r is the age of recruitment to the fishery; t_0 is the age when length would theoretically be 0 mm from the von Bertalanffy growth model; Z is the instantaneous rate of total mortality; W_∞ is the asymptotic weight, derived from the length-weight relationship and L_∞ from the von Bertalanffy growth model; β is the incomplete beta function, $X = e^{-K(t_r-t_0)}$; K is the growth coefficient from the von Bertalanffy growth model; $X_1 = e^{-K(\text{age}_{\max}-t_0)}$; $\text{age}_{\max}$ is the maximum age from the sample; $P = \frac{Z}{K}$; and Q is $1 + \text{slope of the length-weight relationship}$ (Loftus 2015). Table 1 shows the parameter estimates used in the model. In addition to information on growth, maximum age, and the length-weight relationship, we specified the rates of conditional natural mortality (cm ; i.e., mortality that would occur in the absence of fishing mortality) and conditional fishing

Table 1. Parameter estimates used in the population model of Smallmouth Bass *Micropterus dolomieu* sampled in 2016 from the Snake, Boise, Payette, and Weiser rivers, Idaho, USA, combined. The numbers in parentheses are 1 SE.

Value	Description	Estimate
N_0	Number of recruits per year	1,000
b	The y-intercept of the regression line of weight on length	-4.612
m	Slope of the regression line of weight on length	2.893
L_∞	Theoretical maximum mean length (mm)	570 (13.28)
K	Growth coefficient (rate at which fish approaches L_∞)	0.187 (0.00)
t_0	Time when length theoretically equals 0 (y)	-0.542 (0.02)
age_{max}	Maximum age of fish in the sample (y)	9
$\log F$	Fecundity-length (L) relationship	$1.77 \log L - 0.7285$

mortality (cf ; i.e., mortality attributable to fishing in the absence of natural mortality) in the models. We estimated that cm was approximately 40% given estimates of A from the age-structure data and F from estimates of μ . Because exploitation is more intuitive and applicable to management agencies than cf , we varied cf such that the resulting exploitation rates varied from 0 to 100%. We conducted simulations using Fisheries Analysis and Modeling Simulator (Loftus Consulting, Annapolis, MD) and assumed that natural and fishing mortality occurred simultaneously (i.e., type II fishery; Ricker 1975; Loftus 2015). We used the current minimum length limit of 305 mm as a baseline for comparison against two other potential increases in the minimum length limit (i.e., 356 and 406 mm). We selected the 356-mm minimum length limit because the Smallmouth Bass fishery in a section of the Snake River just upstream of the study area is managed with a 356-mm minimum length limit. We also considered a more restrictive minimum length limit (406 mm) that has been discussed among managers in Idaho. The model assumes knife-edge selectivity where fish are fully susceptible to harvest once they reach the minimum length limit (Ricker 1975; Loftus 2015). We evaluated the abundance of fish in the population at 356, 406, and 456 mm under varying exploitation to provide insight on potential changes in length structure. We plotted total yield (kilograms) against exploitation to evaluate the likelihood of growth overfishing. Growth overfishing occurs when yield decreases with increasing levels of exploitation because harvest of fish occurs before they are able to realize their full growth potential (Ricker 1975; Loftus 2015).

We also examined the potential for recruitment overfishing by using the same yield-per-recruit model. Recruitment overfishing occurs when harvest of fish occurs from a population at a rate such that they are unable to replace themselves (Ricker 1975). Recruitment overfishing is typically examined by assessing the reproductive potential of an exploited population relative to an unexploited population (Goodyear 1993; Mace and Sissenwine 1993). The spawning potential ratio (SPR) represents the proportion of lifetime egg production of an exploited

population relative to that of an unexploited population. We calculated SPR as

$$\text{SPR} = 100 \times \left(\frac{P_{\text{exploited}}}{P_{\text{unexploited}}} \right),$$

where the lifetime egg production (P) of a cohort of recruits is calculated from the formula

$$P = \sum_{i=1}^n E_i \prod_{j=0}^{t-1} S_{ij},$$

where n is the number of ages in an unfished population; E_i is the mean fecundity of females of age i ; $S_{ij} = e^{-(F_{ij} + M_{ij})}$, the mean density-dependent annual survival probabilities of females of age i when age j ; F_{ij} is the instantaneous rate fishing mortality of females of age i when age j ; and M is the instantaneous rate of natural mortality of females of age i when age j . An unexploited population has an SPR of 100; SPR decreases with exploitation. We examined SPRs at different levels of exploitation in response to the aforementioned minimum length limits. Previous research suggests that SPR for a population should be maintained above 20% to avoid recruitment overfishing (Goodyear 1993; Slipke et al. 2002). As such, we considered 20% as the minimum SPR to prevent recruitment overfishing of Smallmouth Bass. For the SPR analysis, we obtained a fecundity-length relationship from the literature (Kilambi et al. 1977). We assumed that all age-3 and older Smallmouth Bass were mature based on field observations, 50% of the population was female, and 100% of females reproduced every year.

Results

In total, we sampled 4,929 Smallmouth Bass during electrofishing surveys on the Snake River and three major tributaries. In the Snake River, CPUE varied from 15.3 to 83.1 fish/h among segments and was highest in segment 1 and lowest in segment 5 (Figure 2). When we combined all segments on the Snake River, CPUE was 36.6 fish/h (± 4.4 SE). On the tributaries, CPUE varied from 43.6 to 125.0 fish/h and was the highest in the Weiser River (mean $\pm$ SE, 125.0 $\pm$ 40.1 fish/h). The Weiser River also had the highest CPUE of substock-length fish. For preferred-length fish, CPUE was less than 4.0 fish/h among all segments and major tributaries. Catch-per-unit-effort of memorable-length fish was also low at less than 2.0 fish/h among segments and tributaries. We encountered no trophy-length fish during sampling.

Proportional size distribution of Smallmouth Bass varied from 25 to 77 among segments (Figure 3). Segments 8 and 9 near Brownlee Reservoir and segment 1, just downstream of Swan Falls Dam, generally had the lowest PSD values. Length structure in the tributaries was similar to that in the mainstem Snake River (PSD = 46). In the tributaries, PSD was highest in the Boise River (52), followed by the Payette (44) and Weiser (42) rivers. Proportional size distribution for memorable-length fish was highest in segment 9 (9) and the Payette River (11).



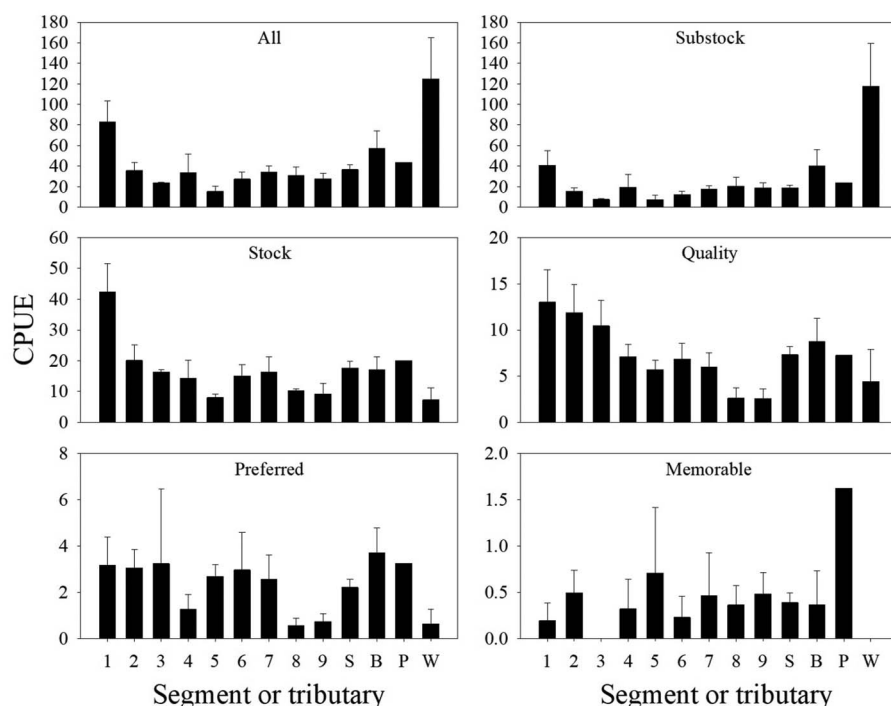


Figure 2. Catch-per-unit-effort (CPUE, number of fish/hour of electrofishing) of Smallmouth Bass *Micropterus dolomieu* sampled in 2016 from nine segments in the Snake River, Idaho, USA, all nine segments combined (S), and three tributaries (i.e., Boise [B], Payette [P], and Weiser [W] rivers, Idaho). Catch rates are provided for all fish, substock (<180 mm), stock- (≥ 180 mm), quality- (≥ 280 mm), preferred- (≥ 350 mm), and memorable (≥ 430)-length fish. Error bars represent 1 SE.

Relative weight of Smallmouth Bass in the Snake River and tributaries varied from 86 to 107, indicating that fish were in relatively good body condition (Figure 4). In general, body condition appeared to decline from upstream (near Swan Falls Dam) to downstream (near Brownlee Reservoir). In addition, longer fish tended to be in poorer condition than shorter fish. In the tributaries, average W_r for all fish was near 100 and most similar to the upper and middle segments (i.e., segments 1–7) of the Snake River. Similar to the mainstem Snake River, body condition of Smallmouth Bass in tributaries declined with increasing length, but the pattern was not consistent.

We estimated age for 1,869 fish sampled from the Snake River ($n = 1,433$) and three major tributaries ($n = 436$). Smallmouth Bass varied in age from age-1 to age-9, and most fish (87.9%) were age-3 or younger. Growth was similar among segments in the Snake River (Table 2). In all nine segments, RGI was greater than 100 for age-1, age-2, and age-3 fish, indicating fast growth. For the remaining age classes, (i.e., ages 4–9) RGI was greater than 100 in eight of nine segments and was never less than 89 for any age class. When all nine segments in the Snake River were combined, RGI was greater than or equal to 106 for all ages. Growth rates were similar among the tributaries, but were slower than for the Snake River. Relative growth index values were typically near or greater than 100 for all three tributaries and never below 94 for any age.

Estimates of A varied from 37.3 to 60.2% among the nine segments of the Snake River (Figure 5). Segment 5 had the lowest estimate of A ($37.3 \pm 2.8\%$) and segment 8 had the highest ($60.2 \pm 4.5\%$). When we combined data

from all nine segments, mortality was $44.5 \pm 0.7\%$. In general, A was lower in the tributaries than in the Snake River and varied from 36.8 to 40.5%. The Boise River had the lowest estimate of mortality ($36.8 \pm 2.2\%$) and the Weiser River had the highest ($40.5 \pm 5.3\%$). Estimated exploitation was 5.3% (90% CI; $\pm 2.2\%$) for the Snake River and its tributaries, and estimated use (i.e., caught, but not harvested) was 14.9% (4.3%). In Brownlee Reservoir, estimated exploitation was 16.2% (6.3%) and estimated use was 39.2% (10.9%).

The number of simulated fish available at the different lengths of interest (i.e., 356, 406, and 456 mm) varied depending on the minimum length limit and exploitation rate. Among all three lengths of interest, the number of fish in the population decreased as exploitation increased (Figure 6). At low rates of exploitation (i.e., 4%), the difference in the number of fish available at different lengths was negligible ($\pm 5.7\%$). However, when we increased exploitation to 20% and the minimum length limit from 305 to 356 mm, the result was a 40% increase in the number of fish available at both 356 and 406 mm. A lower minimum length limit (e.g., 305 vs. 356 mm) resulted in higher yield per recruit at all levels of exploitation (Figure 7). For example, at a low rate of exploitation (i.e., 4%), an increased minimum length limit from 305 to 356 mm resulted in 29.8% reduction in the biomass of fish available for harvest. At the same level of exploitation, increasing the minimum length limit from 305 to 406 mm resulted in a 60.8% decrease in the biomass of fish available for harvest. Spawning potential ratio never fell below 20% with any of the three lengths limits (Figure 8). Even at a high rate of exploitation

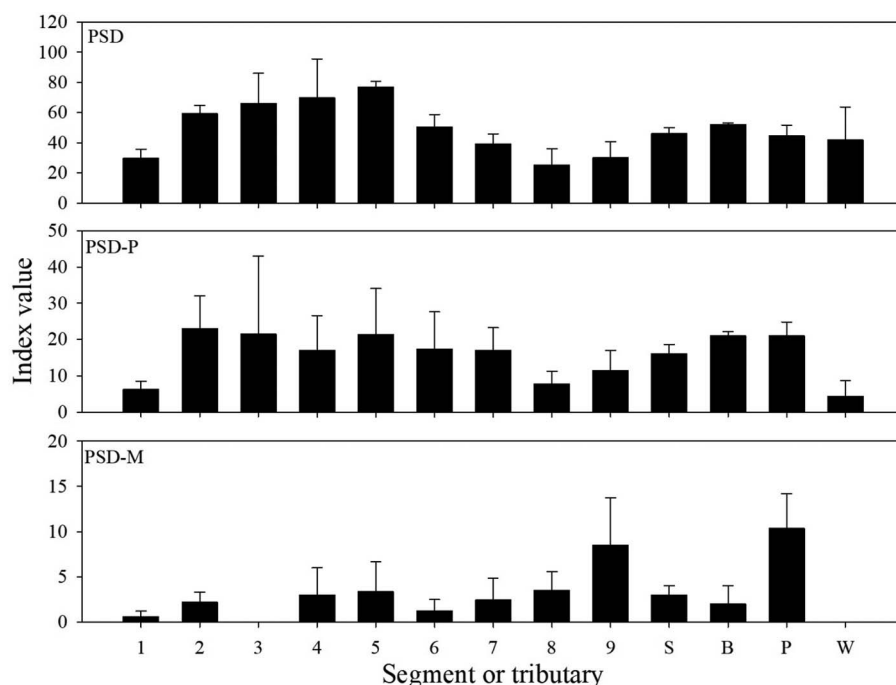


Figure 3. Proportional size distribution (PSD) index values of Smallmouth Bass *Micropterus dolomieu* sampled in 2016 from nine segments in the Snake River, Idaho, USA, all nine segments combined (S), and the tributaries (i.e., Boise [B], Payette [P], and Weiser [W] rivers, Idaho). In addition, preferred (PSD-P, ≥ 350 mm) and memorable (PSD-M, ≥ 430 mm) values are provided as well. Error bars represent 1 SE.

(i.e., 53%), SPR was 49.1% for the current 305-mm minimum length limit, suggesting recruitment overfishing is likely not a concern with the current or alternative minimum length limits.

Discussion

Results of this study provide a comprehensive overview of the population dynamics and demographics of a nonnative Smallmouth Bass population in a large western river system. As might be expected from a study encompassing nearly 200 rkm, we observed high variability in population metrics across the study area. Nevertheless, several interesting patterns emerged that provide insight into the population dynamics and demographics of Smallmouth Bass in the Snake River system. Among the most apparent patterns was that catch rates and length structure varied among reaches in the Snake River and tributaries. Catch-per-unit-effort was typically highest in the upper section (i.e., segment 1), where most Smallmouth Bass were less than 180 mm. The uppermost segment in our study area was in the tailwaters of Swan Falls Dam, characterized by clear water, large rocky substrate and abundant deep pool habitat. Although Smallmouth Bass inhabit a variety of habitats across their native distribution, they prefer deep habitats with rocky substrate (Coble 1975; Hubert and Lackey 1980; Probst et al. 1984; Dauwalter et al. 2007). In addition, Smallmouth Bass use rocky substrate for spawning (Coble 1975; Hubert and Lackey 1980; Dauwalter and Fisher 2007). The mechanism(s) responsible for spatial structuring in abundance and length structure observed in

our study is unknown, but high densities of small fish could be a reflection of habitat quality and density-dependent processes. For example, Ridgway et al. (2002) reported that juvenile Smallmouth Bass in Lake Opeongo, Ontario, Canada, remained near their nest of origin for up to a year after hatching. The authors proposed that movement of age-2 and older Smallmouth Bass away from rearing habitat was a response to a density-dependent process. As such, high densities of small Smallmouth Bass in the uppermost segment of our study area may suggest that a portion of the Snake River is important spawning and juvenile rearing habitat. At some point, Smallmouth Bass likely leave the uppermost segment for other portions of the system. The observation that downstream reaches and tributaries tended to have fewer Smallmouth Bass supports this contention, but fish were typically larger than those in upstream reaches. Unlike the uppermost segment, deep pools and rocky substrate were uncommon in other areas of the study area. Instead, habitat in other segments of the Snake River and lower portion of tributaries featured shallow runs with fine substrate (e.g., sand, silt). Consequently, lower catch rates may be due to the relatively poor spawning and rearing habitat and/or the inability of the habitat to support high densities of large Smallmouth Bass. Jansen et al. (2008) found similar patterns in six large Iowa, USA, rivers where catch rates of Smallmouth Bass were lowest in the upper Iowa and Wapsipinicon rivers. These rivers, particularly the Wapsipinicon River, contained finer substrate and were much shallower than the other study rivers. The authors also found that length structure varied among populations, but the largest fish were in systems with lower catch rates

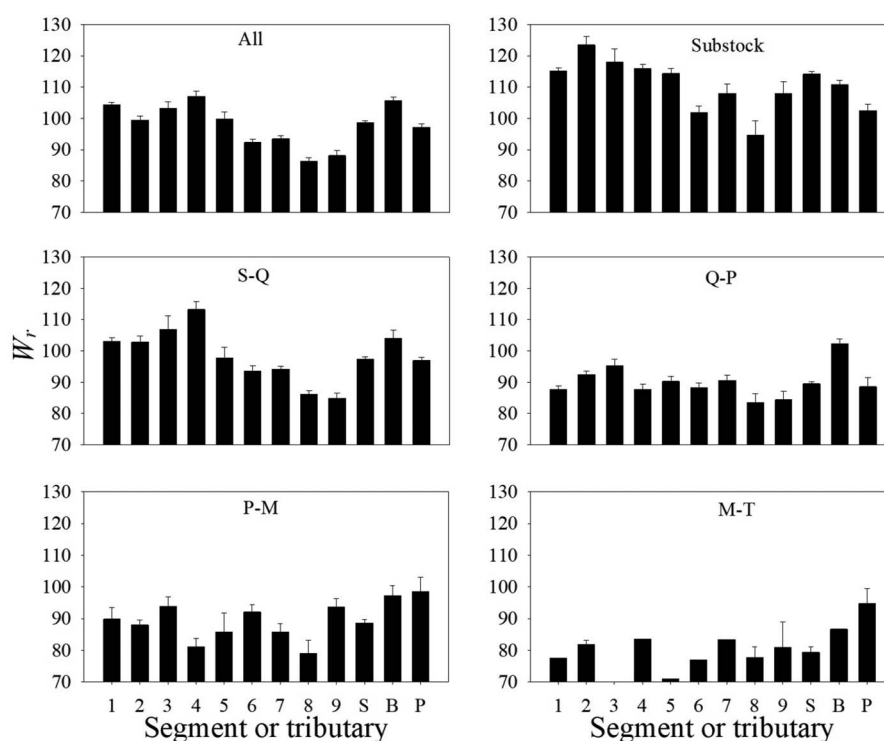


Figure 4. Relative weight (W_r) index values of Smallmouth Bass *Micropterus dolomieu* sampled in 2016 from nine segments in the Snake River, Idaho, USA, all nine segments combined (S), and the tributaries (i.e., Boise [B], Payette [P], and Weiser [W] rivers, Idaho). Index values are provided for all fish, substock (<180 mm), stock-quality (S-Q; 180–279 mm), quality-preferred (Q-P; 280–349 mm), preferred-memorable (P-M; 350–429 mm), and memorable-trophy (M-T; 430–509 mm)-length fish. Error bars represent 1 SE.

and complex habitat characteristics (e.g., Des Moines and Iowa rivers). Compared with systems within the native distribution of Smallmouth Bass, average catch rates in the Snake River (15–125 fish/h) were generally high. Jansen et al. (2008) reported catch rates from approximately 40 to 180 fish/h in Iowa rivers; most reaches had catch rates less than 70 fish/h. Paragamian and Coble (1975) reported catch rates of 5–17 Smallmouth Bass/h in the Red Cedar River, Wisconsin, USA. Weathers and Bain (1992) reported catch rates of 7 fish/h in the Tennessee River, Alabama, USA.

Body condition of Smallmouth Bass in the Snake River system was generally good, with W_r values at or above 100. As might be expected, W_r values for Smallmouth Bass in other systems are highly variable. In Iowa rivers, Jansen et al. (2008) reported that W_r values were typically less than 100. Similarly, Austen and Orth (1988) reported that W_r values were less than 85 for Smallmouth Bass in the New River, Virginia, USA. Reed and Rabeni (1989) found that W_r varied from 59 to 103 for Smallmouth Bass in Big Buffalo Creek, Missouri. Weathers and Bain (1992) found that W_r increased with length, with Smallmouth Bass greater than 400 mm having W_r values in excess of 120. We observed the opposite pattern: W_r declined slightly with length. The specific mechanism for this pattern is unknown, but may be due to prey densities or the ability of Smallmouth Bass to effectively forage. Savino and Stein (1982) showed that the ability of Largemouth Bass to capture prey declined as the structural complexity of the environment increased. Eurasian Watermilfoil *Myriophyllum spicatum* is an invasive aquatic macrophyte that forms thick

stands in the Snake River, particularly in segments 2–7 of our study area. High densities of aquatic vegetation may limit the efficiency of Smallmouth Bass to capture prey. In addition, the fish assemblage in these same segments seems to lack abundant small-bodied fishes and large invertebrates (i.e., crayfishes) that could serve as a prey resource.

Information on growth is important for understanding fish population dynamics because it provides an integrated measure of environmental conditions. In addition, growth has direct and indirect effects on intra- and interspecific interactions, recruitment dynamics, and mortality (e.g., Winemiller 2005; Quist et al. 2012). A variety of environmental and biotic factors influence growth of Smallmouth Bass in lotic systems. For example, Putnam et al. (1995) found an inverse relationship of growth of Smallmouth Bass greater than 200 mm to the amount of cobble substrate in Illinois, USA, streams. The authors suggested that large Smallmouth Bass selected for cobble substrate, which influenced their growth via density-dependent interactions. Paragamian and Wiley (1987) found a relationship of growth of age-1 Smallmouth Bass to discharge in Iowa streams; growth of age-2 and older was not associated with discharge. Beamesderfer and North (1995) summarized information on 409 Smallmouth Bass populations in North America and found a positive relationship of growth of Smallmouth Bass to the number of days with air temperatures greater than 10°C. King et al. (1991) reported that growth of Smallmouth Bass in two New York, USA, streams was fastest in the system with warm water temperature. In our study, Smallmouth Bass exhibited moderate-to-fast

Table 2. Mean back-calculated length at age (mm) for Smallmouth Bass *Micropterus dolomieu* sampled in 2016 from nine segments in the Snake River (S), Idaho, USA, and the tributaries (i.e., Boise [B], Payette [P], and Weiser [W] rivers, Idaho). The first number in parentheses represents 1 SE, and the second number represents the relative growth index. The asterisk (*) indicates that there was one fish in the sample.

River segment	n	1	2	3	4	5	6	7	8	9
1	317	109.3 (1.3, 129)	186.2 (2.4, 115)	252.0 (2.8, 107)	297.8 (6.1, 124)	321.6 (9.9, 99)	350.6 (11.9, 97)	381.0 (28.8, 103)	370.1*	
2	243	118.1 (1.5, 136)	202.8 (2.9, 119)	274.4 (3.0, 117)	316.4 (5.0, 108)	362.1 (7.5, 111)	397.7 (6.7, 106)	443.9 (13.0, 112)	474*	
3	38	114.1 (3.3, 140)	203.7 (5.7, 129)	281.7 (5.8, 121)	332.0 (11.7, 117)	369.2 (11.8, 114)	425.0*			
4	80	114.6 (2.2, 135)	210.9 (5.4, 126)	281.9 (5.1, 120)	325.9 (7.3, 111)	364.3 (12.3, 113)	379.9 (29.9, 95)	431.0*		
5	46	106.7 (2.5, 121)	198.8 (6.8, 103)	284.1 (4.1, 120)	331.0 (9.3, 116)	363.1 (11.9, 115)	381.4 (15.4, 105)	398.1*		
6	122	109.5 (2.0, 129)	205.3 (3.4, 121)	276.8 (4.4, 117)	324.7 (6.9, 110)	370.6 (9.7, 111)	400.5 (13.9, 115)	399.6 (3.6, 100)	421*	
7	273	107.2 (1.1, 121)	201.2 (1.8, 119)	259.0 (3.2, 108)	315.9 (4.3, 106)	364.0 (7.7, 109)	401.5 (13.3)	433.0 (22.9, 110)		
8	141	103.6 (2.1, 112)	197.2 (3.7, 116)	263.1 (5.5, 110)	324.5 (10.2, 113)	403.3 (25.8, 115)	453.8 (23.2, 111)	456.8*	478*	
9	180	101.0 (1.6, 112)	184.9 (4.2, 112)	238.3 (6.8, 102)	284.3 (13.8, 95)	345.9 (20.7, 109)	382.5 (16.4, 99)	430.8 (14.6)	458.9 (11.1, 113)	478.1*
S	1,440	109.2 (0.6, 125)	197.2 (1.2, 117)	264.3 (1.5, 112)	313.5 (2.6, 122)	359.9 (4.0, 109)	392.5 (5.4, 109)	422.1 (8.9, 107)	443.5 (17.1, 106)	478*
B	161	93.6 (2.1, 98)	184.8 (5.8, 102)	252.2 (7.7, 99)	317.4 (11.2, 105)	360.4 (15.3, 107)	396.0 (20.9, 109)	412.5 (23.4)	438.2 (26.2, 99)	481.9*
P	159	89.5 (1.8, 97)	179.7 (4.3, 105)	247.6 (7.1, 106)	301.7 (11.8, 94)	336.9 (12.8, 116)	406.2 (11.6, 111)	425.7 (13.8)	446.4 (9.9)	465.7 (7.4, 108)
W	71	91.3 (2.8, 98)	183.7 (11.0, 123)	240.3 (11.7, 102)	292.2 (29.4, 100)	324.7 (49.5, 97)				

growth. Specifically, RGI values varied from 89 to 140 across ages and locations, and nearly all values exceeded 100, suggesting fast growth relative to other populations across North America. Beamesderfer and North (1995) estimated

age at quality length (A_q) for Smallmouth Bass across North America. Age at quality length varied from 1.8 to 8.9 y, with a mean A_q of 4.0 y. In the Snake River and its tributaries, Smallmouth Bass reached quality length in approximately

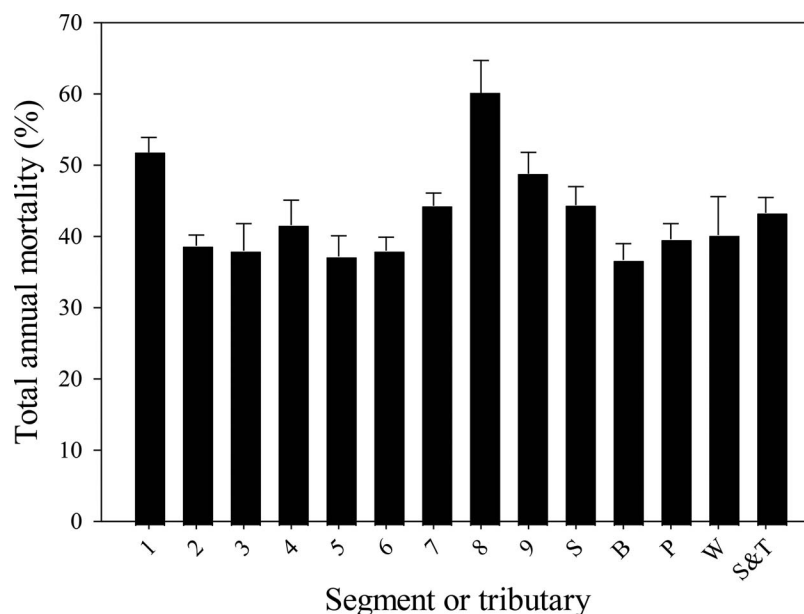


Figure 5. Total annual mortality (A) estimates for Smallmouth Bass *Micropterus dolomieu* sampled in 2016 from the nine segments in the Snake River, Idaho, USA, all nine segments combined (S), and the tributaries (T; Boise [B], Payette [P], and Weiser [W] rivers, Idaho). Numbers in parentheses are 1 SE.

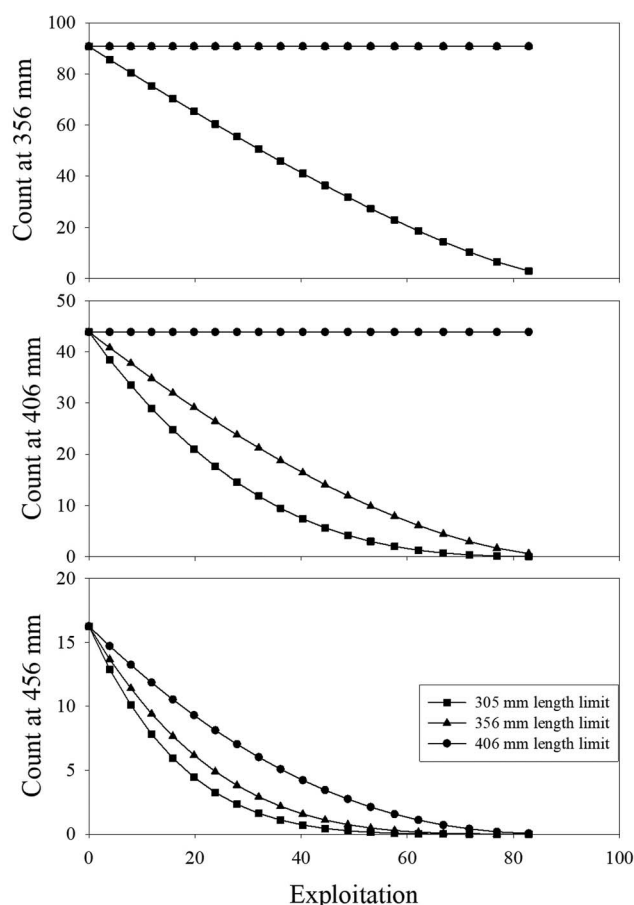


Figure 6. Simulated response to the number of Smallmouth Bass *Micropterus dolomieu* available at three minimum length limits (305, 356, and 406 mm) sampled in 2016 from the Snake, Boise, Payette, and Weiser rivers, Idaho, USA. Conditional natural mortality (cm) was set at 0.40.

3.4 y, which would place them in the upper 75th percentile of A_q values provided by Beamesderfer and North (1995). The specific factors promoting fast growth of Smallmouth Bass in our study system are not clear; however, fast growth is likely a combination of an abundance of suitable prey and temperatures conducive for rapid growth. Unfortunately, we lack information on prey availability, but the observation that fish were in relatively good body condition suggests that prey is sufficient to support fast growth. With regard to thermal characteristics, the optimal water temperature for growth of large juvenile (>50 g) and adult Smallmouth Bass is 22°C (Whitledge et al. 2002, 2006). Once temperatures exceed 22°C, growth of Smallmouth Bass declines, particularly once temperatures exceed 26°C (Whitledge et al. 2002). Mean monthly water temperatures in the Snake River and tributaries evaluated in our study typically vary between 12 and 23°C during April–September (U.S. Geological Survey gaging stations: 13211210 [Snake River], 1326900 [Snake River], 13213100 [Boise River], 13251000 [Payette River], 13266000 [Weiser River]). During June–August, mean monthly water temperature is typically 20–22°C and rarely exceeds 23°C, thereby providing optimal temperatures for growth of Smallmouth

Bass. Future research focused on prey availability and the trophic ecology of Smallmouth Bass in the system would be valuable.

Mortality of Smallmouth Bass in the Snake River and its tributaries was relatively high. Total annual mortality of Smallmouth in the Snake River and its tributaries varied from 37 to 60% and averaged 43%. Although estimates of mortality were relatively high, they are similar to those of other Smallmouth Bass populations across North America. Jansen et al. (2008) reported that A was greater than 40% for four of six Smallmouth Bass populations in Iowa. Coble (1975) reported that 11 of 12 Smallmouth Bass populations in the midwestern and northeastern United States had A rates greater than 50%. Similar results have been reported for populations throughout the native distribution of Smallmouth Bass (e.g., Fajen 1975; Paragamian and Coble 1975; Paragamian 1984a). In the western United States, patterns in A seem to be more variable. For example, Smallmouth Bass in John Day Reservoir, Washington–Oregon, experienced A rates between 48 and 55% (Bennett et al. 1991). In reservoirs of the Snake River, Idaho–Washington–Oregon (downstream of our study area), Bennett et al. (1991) reported that A was 28% in Little Goose Reservoir, 27% in Brownlee Reservoir, and 19% in Lower Granite Reservoir. High exploitation may partially explain high A in some populations. Weathers and Bain (1992) reported that A varied from 50 to 57% for Smallmouth Bass in the Tennessee River, Alabama, but angler exploitation was approximately 50%. Paragamian (1984a) reported that A was 62–84% and exploitation was 34% for age-2 and older Smallmouth Bass in the Maquoketa River, Iowa. In our study, exploitation was approximately 5%, suggesting that Smallmouth Bass in the system experience high natural mortality. As such, abundance is likely maintained by consistently high recruitment and length structure is maintained by fast growth.

A concern expressed by anglers and IDFG staff was the potential effect of angler harvest of seasonal aggregations of prespawning and spawning Smallmouth Bass in the system, particularly in the lower reaches of the Payette and Weiser rivers; thus, it became a major impetus for this research. Although harvest of some Smallmouth Bass occurs, the proportion of the population harvested (~5%) is very low. Nevertheless, we examined the potential influence of altering the minimum length limit. Minimum length limits have been in use to adjust fishing mortality of Smallmouth Bass across their distribution, with variable success. In some systems with high exploitation, minimum length limits often result in desired changes to the population. For example, Paragamian (1984b) found that μ decreased by 45%, A declined by 27%, and PSD increased from 14 to 35 after implementation of a 305-mm minimum length limit (no prior minimum length limit) on Smallmouth Bass in the Maquoketa River, Iowa. Lyons et al. (1996) reported increased relative abundance and length structure following implementation of a 356-mm minimum length limit on Smallmouth Bass in Wisconsin streams. Similarly, Newman and Hoff (2000) reported that management goals were met in Pallette Lake, Wisconsin, following implementation of a 406-mm minimum length limit. Before the regulation change, μ was 53% and A was 79%. Following the new regulation, μ declined to 10% and A to 40%. Slipke

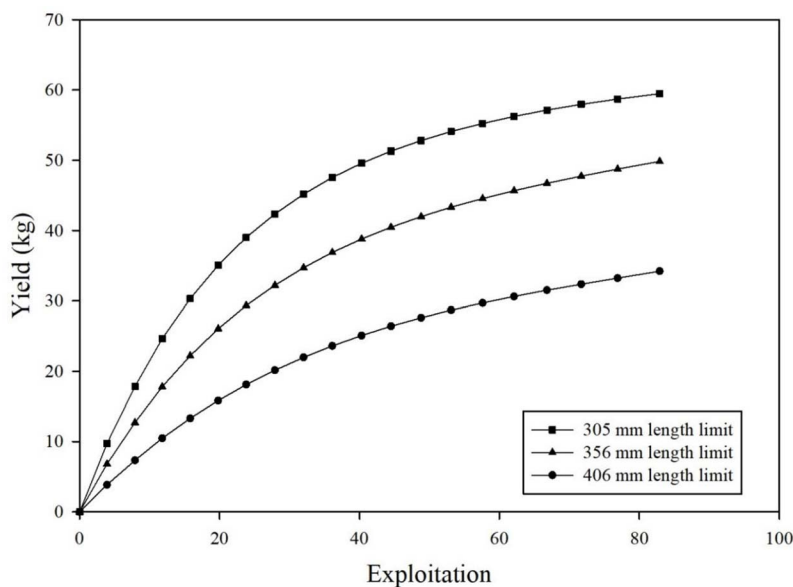


Figure 7. Simulated yield for Smallmouth Bass *Micropterus dolomieu* sampled in 2016 from the Snake, Boise, Payette, and Weiser rivers, Idaho, USA, with conditional natural mortality (c_m) set at 40%. We conducted the simulations for three minimum length limits (305, 356, and 406 mm).

et al. (1998) reported similar results for Smallmouth Bass in the Tennessee River, Alabama. In the New River, Virginia, Austen and Orth (1988) found that implementing a 305-mm minimum length limit (no prior length limit) resulted in slow growth, low W_r , and no changes in length structure. As a result of their research, the authors recommended removal of the minimum length limit. Buynak and Mitchell (2002) reported that a 305-mm minimum length limit on Smallmouth Bass in Elkhorn Creek, Kentucky, USA, resulted in high densities of small, slow-growing fish. Like all regulations, the success of minimum length limits is

dependent on complex interactions between population rate functions and dynamics of the fishery. In our study, altering the minimum length limit would likely have little influence on the number of large (e.g., >356 mm) Smallmouth Bass available to anglers or on yield. Similarly, Smallmouth Bass are highly unlikely to be in danger of recruitment overfishing. An SPR of 20% is generally considered a threshold for recruitment overfishing (Goodyear 1993). Even if exploitation increased to 80% with the current regulation (305-mm minimum length limit), the SPR would not fall below 20%.

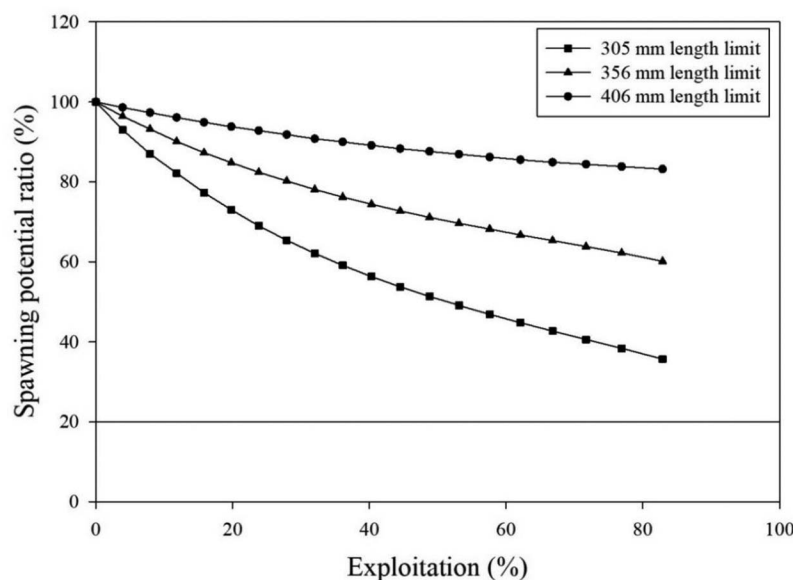


Figure 8. Simulated spawning potential ratio for Smallmouth Bass *Micropterus dolomieu* sampled in 2016 from the Snake, Boise, Payette, and Weiser rivers, Idaho, USA, with conditional natural mortality (c_m) set at 40%. We conducted the simulations for three minimum length limits (305, 356, and 406 mm). The line at 20% represents the threshold for recruitment overfishing.

This research provides one of the most comprehensive summaries of Smallmouth Bass population dynamics in the western United States. In the Snake River system and its tributaries, Smallmouth Bass exhibited high relative abundance, fast growth, moderate-to-high mortality, and low exploitation. Based on the yield-per-recruit model, changes in harvest regulations do not appear to be warranted given current management objectives. Similar studies in western North America would be useful to identify factors associated with variability in population demographics and dynamics of Smallmouth Bass. Such information would be particularly useful for guiding strategies associated with managing Smallmouth Bass fisheries or programs aimed at reducing the influence of nonnative Smallmouth Bass on native fishes.

Supplemental Material

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Data S1. Datafile titled “McClure_et_al_Data_S1” including sampling date, sampling reach, total length (TL; mm), weight (W; g), distance from the center of the dorsal spine to each annulus (A1–A10), and distance from the center of the dorsal spine to the edge (Edge) for Smallmouth Bass *Micropterus dolomieu* sampled from the Snake, Boise, Weiser, and Payette rivers in Idaho, 2016–2017.

Data S2. Datafile titled “McClure_et_al_Data_S2” including sampling reach, catch (C), and effort (E; hr:min:sec) for Smallmouth Bass *Micropterus dolomieu* sampled from the Snake, Boise, Weiser, and Payette rivers in Idaho, 2016–2017.

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