

ARTICLE

Juvenile Chinook Salmon Mortality in a Snake River Reservoir: Smallmouth Bass Predation Revisited

John M. Erhardt and Kenneth F. Tiffan*

U.S. Geological Survey, Western Fisheries Research Center, 5501A Cook-Underwood Road, Cook, Washington 98605, USA

William P. Connor

U.S. Fish and Wildlife Service, Idaho Fishery Resource Office, 276 Dworshak Complex Drive, Orofino, Idaho 83544, USA

Abstract

Predation by nonnative fishes has been identified as a contributing factor in the decline of juvenile salmonids in the Columbia River basin. We examined the diet composition of Smallmouth Bass *Micropterus dolomieu* and estimated the consumption and predation loss of juvenile Chinook Salmon *Oncorhynchus tshawytscha* in Lower Granite Reservoir on the Snake River. We examined 4,852 Smallmouth Bass stomachs collected from shoreline habitats during April–September 2013–2015. Chinook Salmon were the second most commonly consumed fish by all size-classes of Smallmouth Bass (≥ 150 mm TL) throughout the study. Over the 3 years studied, we estimated that a total of 300,373 Chinook Salmon were consumed by Smallmouth Bass in our 22-km study area, of which 97% (291,884) were subyearlings (age 0) based on length frequency data. A majority of the loss (61%) occurred during June, which coincided with the timing of hatchery releases of subyearling fall Chinook Salmon. Compared to an earlier study, mean annual predation loss increased more than 15-fold from 2,670 Chinook Salmon during 1996–1997 to 41,145 Chinook Salmon during 2013–2015 (in reaches that could be compared), despite lower contemporary Smallmouth Bass abundances. This increase can be explained in part by increases in Smallmouth Bass consumption rates, which paralleled increases in subyearling Chinook Salmon densities—an expected functional response by an opportunistic consumer. Smallmouth Bass are currently significant predators of subyearling Chinook Salmon in Lower Granite Reservoir and could potentially be a large source of unexplained mortality.

Predation by native and nonnative fishes is one factor that has been implicated in the decline of juvenile salmonids in the Pacific Northwest. Impoundment of much of the Snake and Columbia rivers has altered food webs and created habitat favorable for species such as the Smallmouth Bass *Micropterus dolomieu*. Smallmouth Bass are common throughout the Columbia River basin and have become the most abundant predators in lower Snake River reservoirs (Zimmerman and Parker 1995). This is a concern for subyearling Snake River fall Chinook Salmon *Oncorhynchus tshawytscha* (hereafter, subyearlings), as they may be particularly vulnerable to predation because

of their relatively small size and because their rearing habitats often overlap with or are in close proximity to habitats used by Smallmouth Bass (Curet 1993; Tabor et al. 1993).

Concern over juvenile salmon predation precipitated a number of large-scale studies to quantify its effect in the late 1980s, 1990s, and early 2000s (Poe et al. 1991; Rieman et al. 1991; Vigg et al. 1991; Fritts and Pearsons 2004; Naughton et al. 2004). Smallmouth Bass predation represented 9% of all salmon consumed by predatory fishes in John Day Reservoir, Columbia River, during 1983–1986 (Rieman et al. 1991). In transitional habitat

*Corresponding author: ktiffan@usgs.gov
Received September 13, 2017; accepted December 12, 2017

between the Hanford Reach of the Columbia River and McNary Reservoir, juvenile salmon (presumably subyearlings) were found in 65% of Smallmouth Bass (>200 mm FL) stomachs and composed 59% of the diet by weight (Tabor et al. 1993). In Lower Granite Reservoir on the Snake River, Anglea (1997) reported that Chinook Salmon composed 3.45% of Smallmouth Bass (175–249 mm TL) diets, and Naughton et al. (2004) found that salmonids (Chinook Salmon and steelhead *Oncorhynchus mykiss*) composed 5–11% of Smallmouth Bass diets (all sizes) depending on reservoir location. However, these studies in the Snake River were conducted soon after the Endangered Species Act listing of Snake River fall Chinook Salmon (NMFS 1992). During that time, fall Chinook Salmon abundance was at an historic low, which may explain why consumption rates were relatively low compared to those from studies conducted in the Columbia and Yakima rivers, where abundance was higher (Tabor et al. 1993; Fritts and Pearsons 2004).

Although previous predation studies focused on juvenile steelhead and yearling and subyearling Chinook Salmon, we believe that subyearling fall Chinook Salmon may be particularly vulnerable to Smallmouth Bass predation in Lower Granite Reservoir due to their small size, extended reservoir rearing, and seaward migration timing that occurs when Smallmouth Bass abundance and metabolic rates are high. In contrast, yearling Chinook Salmon and steelhead emigrate seaward earlier in the spring, when temperatures are relatively cool, and they do not spend extended time in the reservoir that would increase their vulnerability to Smallmouth Bass predation. The study by Naughton et al. (2004) provides an important baseline for evaluating changes in predation on subyearlings in Lower Granite Reservoir. The Clearwater River and Snake River arms of the upper end of the reservoir studied by Naughton et al. (2004) are particularly important for subyearlings originating upstream because passage from riverine into impounded habitats can result in behavioral changes that may increase predation vulnerability. Tiffan et al. (2009) showed that subyearlings delay downstream movement in these transitional habitats of Lower Granite Reservoir, which may increase the duration of their exposure to predators. Naughton et al. (2004) showed that fish constituted a large portion of Smallmouth Bass diets in Lower Granite Reservoir. Considering that subyearlings probably now make up a larger proportion of the forage fish population due to their increase resulting from recovery measures (Connor et al. 2013), it is plausible that they should make up a larger portion of Smallmouth Bass diets. We speculate that predation on subyearlings by Smallmouth Bass in the Snake River may have increased in recent years for these reasons. We initiated a study in 2013 to re-examine Smallmouth Bass predation on subyearlings in Lower Granite Reservoir. Our objectives were

to (1) estimate the abundance of Smallmouth Bass, (2) describe the seasonal variation in Smallmouth Bass diets during the subyearling Chinook Salmon rearing and out-migration period, (3) quantify the consumption and loss of subyearlings to Smallmouth Bass predation, and (4) compare these contemporary metrics to those reported by Naughton et al. (2004).

METHODS

Study area.—We conducted our study from April to September of 2013–2015 within the upper portion of Lower Granite Reservoir on the Snake River (Figure 1). This portion of the reservoir was chosen because subyearlings delay their seaward migration and rear in this area, potentially increasing their vulnerability to predation (Tiffan et al. 2009). Additionally, this area comprised two reaches where Smallmouth Bass predation was studied during 1996–1997 by Naughton et al. (2004). The first reach included 10 river kilometers (rkm) of the Snake River from its confluence with the Clearwater River (rkm 224, as measured from the mouth of the Snake River) to Asotin, Washington (rkm 234). We refer to this reach as the Snake River transition zone (SRTZ) because the river transitions from free-flowing at Asotin to being impounded at the confluence. The SRTZ reach is analogous to the “Snake River Arm” reach studied by Naughton et al. (2004). The second reach included the Clearwater River from its mouth (rkm 0) to the Clearwater Paper Mill (rkm 4.6). We refer to this reach as the Clearwater River transition zone (CRTZ) because the river transitions from free-flowing at the mill to being impounded at its mouth. The CRTZ reach is analogous to the “Clearwater River Arm” reach studied by Naughton et al. (2004). In addition to the reaches studied by Naughton et al. (2004), we added a 7-km reach of the Snake River from the Port of Wilma (rkm 217) to the confluence of the Snake and Clearwater rivers (rkm 224). We refer to this impounded reach as the confluence (CON), where fish migration rates are slow and predation vulnerability is likely to be high (Tiffan et al. 2010).

Sampling frequency.—The duration of sampling in each reach coincided with the presence of subyearlings rearing along reservoir shorelines. Subyearlings disperse from upstream spawning areas and hatchery release sites into the SRTZ during April through late June (Connor et al. 2002). By July, water temperatures typically exceed 20°C and subyearlings have usually migrated downstream into the reservoir below the confluence of the Snake and Clearwater rivers. The Clearwater River is cooler than the Snake River during egg incubation, and fry emergence is later in the Clearwater River than in the Snake River (Connor et al. 2003). Because of later emergence, subyearlings produced in the Clearwater River are migrating

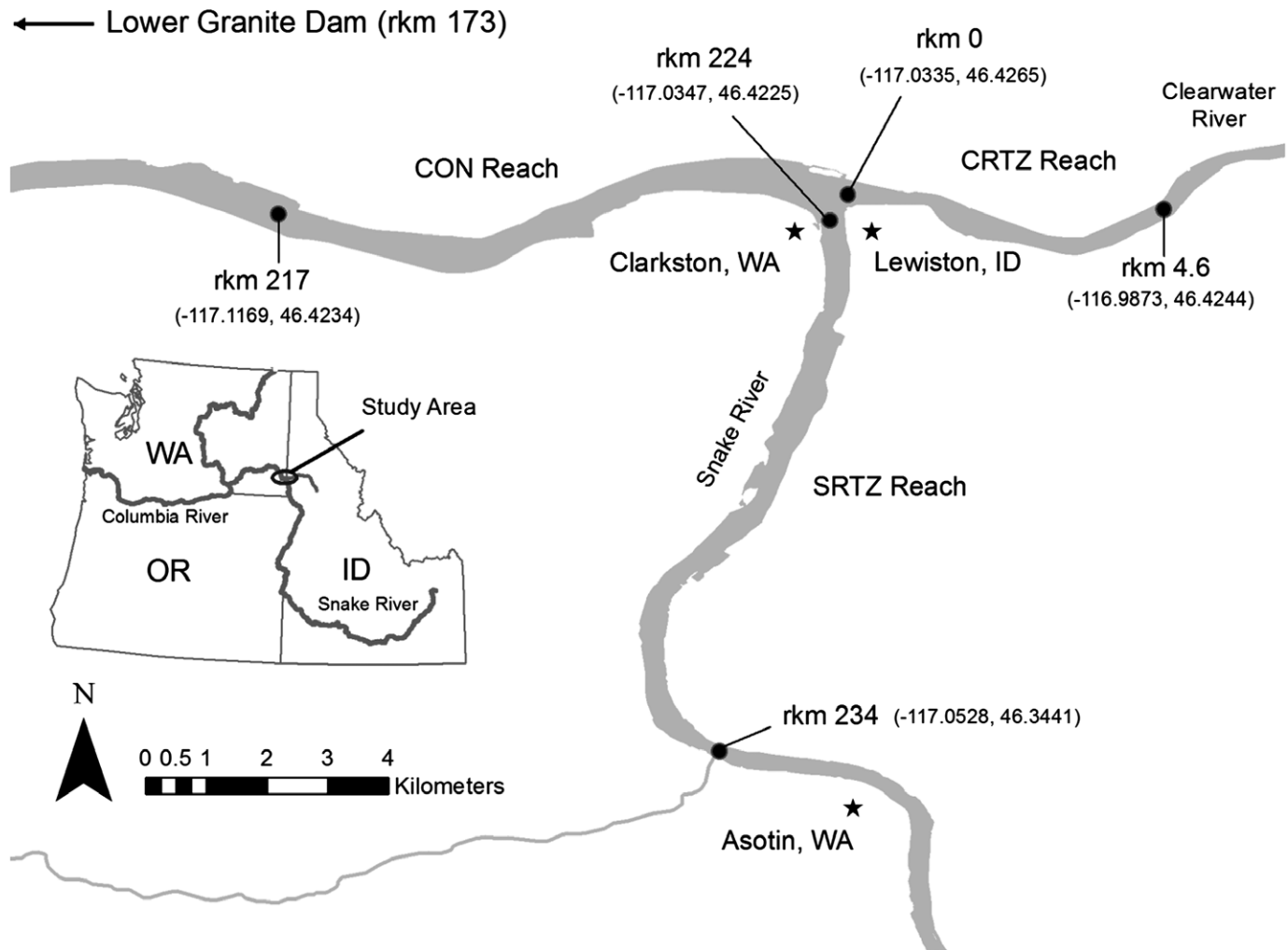


FIGURE 1. Sampling reaches in the upper end of Lower Granite Reservoir on the Snake River, where Smallmouth Bass were collected to estimate predation loss of juvenile Chinook Salmon during 2013–2015 (SRTZ = Snake River transition zone; CRTZ = Clearwater River transition zone; CON = confluence). The locations of reach boundaries are given in river kilometers (rkm) and latitude, longitude (decimal degrees).

through the CRTZ and CON reaches from late May through early September (Tiffan et al. 2010). Subyearlings originating from the Snake and Clearwater rivers are present in the CON reach from April through early September (Tiffan et al. 2010).

Smallmouth Bass collections.—During 2013–2015, Smallmouth Bass (≥ 150 mm TL) were collected biweekly in 1–2-d sampling intervals within the SRTZ and CON reaches from April to the end of June and then were collected triweekly in the CON reach from July to mid-September. The SRTZ reach was not sampled after the end of June because of high water temperatures. The CRTZ reach was sampled triweekly from June to August 2014–2015. Each reach was stratified by two shoreline habitat types: riprap and natural (i.e., non-riprap). We then randomly selected two 500–800-m sites representing

each habitat type in both the CON and SRTZ reaches. These sites remained fixed and were sampled during every interval. Additional random sites of varying habitat and length were also occasionally sampled to increase sample sizes of collected Smallmouth Bass. The shoreline of the CRTZ reach consisted solely of riprap, and the entire reach was sampled during each sampling interval.

Sites were sampled by boat electrofishing between sunset and midnight using one dipnetter and an electrical output of 400-V DC with 60 pulses/s at 2–4 A. Endangered Species Act permit restrictions precluded electrofishing when water temperatures exceeded 18°C (typically July), so angling was used thereafter. Summer angling in the CON reach consisted of trolling with three or four rods to sample the entirety of each habitat in the reach. A variety of artificial lures was used to represent different prey types

(mainly plugs and soft plastic baits). Angling was not conducted in the SRTZ reach because sampling had finished by that time each year. Cool water temperatures in the Clearwater River allowed us to electrofish the CRTZ reach all summer.

All collected Smallmouth Bass with a TL of at least 150 mm were measured and tagged with a unique spaghetti tag. During 2013, five Smallmouth Bass per site were weighed to the nearest 10 g. These weights were used to develop a regression ($\text{weight} = 0.000007 \cdot \text{TL}^{3.09}$; $n = 3,350$, $r^2 = 0.93$) to estimate weights for fish that were only measured. At each sampling site, we collected stomach contents from Smallmouth Bass by using a nonlethal lavage technique modified from Seaburg (1957) that removed 99.8% of diet items (Erhardt et al. 2014). The lavage instrument consisted of a 6-mm-diameter tube connected to a common garden spray nozzle that supplied filtered river water via a wash-down pump installed on the boat. Stomach contents were collected in a 42- μm sieve and were preserved in a 90% solution of ethanol.

Absolute abundance.—Abundance of 150-mm and larger Smallmouth Bass was estimated using catchability models derived from relationships between electrofishing CPUE (Smallmouth Bass per m of shoreline) and mark-recapture estimates for each habitat type (riprap and natural). This approach was used because we were logistically unable to conduct an adequate number of recapture events to estimate absolute abundance in all habitats during every sampling interval. In addition, CPUE data existed for all sampling intervals and were derived from a larger spatial area that allowed for better characterization of the Smallmouth Bass population. Absolute abundance was estimated 1–2 times at each fixed site in the CON and SRTZ reaches during all years from tagged fish recaptured 2–3 d after marking (described above). Abundance for each mark-recapture event was calculated with the Chapman estimator of the Petersen index (Seber 1982) and was converted to absolute density (fish/m) based on the shoreline distance of the fixed site. We assumed no differences in catchability between reaches or years, and we pooled data by reach and year within each habitat to develop our models.

Catchability models for each habitat type were derived by regressing absolute density on CPUE (Hansen et al. 2000; Rogers et al. 2003). Because the absolute density data had associated error, it was necessary to account for this in order to derive 95% confidence intervals (CIs). To do this, we calculated the slope and intercept for each model by using Monte Carlo simulations (Hansen et al. 2000; Rogers et al. 2003). We first used the absolute abundance estimates and SDs from the mark-recapture models to simulate 1,000 normally distributed random values of possible abundances for each event. These random variables were then used with the corresponding CPUE data

to generate 1,000 ordinary least-squares regressions to derive slopes and intercepts. Next, we empirically determined the median and 95% CIs of the parameter estimates by examining the distribution of the estimates. Finally, the derived regressions were used to estimate Smallmouth Bass abundance and 95% CIs for each habitat, reach, and sampling interval from mean electrofishing CPUE during 2013–2015. We expanded the estimates by the total distance of riprap (SRTZ: 6,535 m; CON: 6,790 m; CRTZ: 9,216 m) and natural (SRTZ: 12,244 m; CON: 7,925 m) shorelines in each reach to estimate total abundance as well as the number of Smallmouth Bass per river kilometer. These methods were only used to derive abundance estimates from spring electrofishing data, which were typically collected through June. Thereafter, when angling was used (only in the CON reach), we assumed a constant abundance based on the last electrofishing sampling interval estimate.

Dietary analysis.—Smallmouth Bass diet items were identified to the lowest practical taxon, counted, blotted for 30 s, and weighed (± 0.001 g wet weight). Ingested fish were usually identified to species by using diagnostic bones (i.e., dentary, cleithrum, and opercle; Parrish et al. 2006). Bones were measured with an ocular micrometer mounted in a dissecting scope and used to back-calculate FL or SL at ingestion based on species-specific bone-length regressions from the literature (Hansel et al. 1988) or from regressions we developed (Erhardt et al. 2014). We used additional regressions to calculate FL from SL, nape-to-tail, or dorsal standard lengths when necessary (Vigg et al. 1991; Parrish et al. 2006). Fish remains that did not contain diagnostic bones were classified as “unidentified” and were weighed. When a sample only contained unidentifiable fish parts along with a diagnostic bone, we associated all weight to the species identified. In the few instances when consumed salmonids could not be identified to species, they were assigned to the species of similar-sized salmonids that were consumed during the same sampling interval.

We summarized the predominant diet items (proportion by weight) of Smallmouth Bass by sampling interval and for Smallmouth Bass size groups, similar to Naughton et al. (2004). We also reported proportion of diet by weight to the same taxonomic levels as Naughton et al. (2004). For the sake of brevity, we combined diet results by habitats, reaches, and years because preliminary analysis suggested that trends varied more temporally than spatially and that these trends were similar each year. We also pooled our data by sampling interval in the SRTZ and CRTZ reaches to make them comparable to those of Naughton et al. (2004). For comparison, data from Naughton et al. (2004; their Table 3), which did not incorporate temporal trends, were pooled by reach (by weighting by the sample sizes) and years (by taking the mean);

we did not include fish larger than 389 mm from the Naughton et al. (2004) study because of low sample sizes. We also estimated the maximum FLs of Chinook Salmon consumed by Smallmouth Bass using least absolute value regression (Scharf et al. 1998; Cade et al. 1999). This was done by fitting a 95% quantile regression of the back-calculated FLs of ingested Chinook Salmon on Smallmouth Bass TL by using the Blossom package of R version 3.2.4 (R Development Core Team 2016; Talbert et al. 2016).

Numerical consumption and loss.—We calculated the consumption rate C (number of Chinook Salmon consumed per Smallmouth Bass per day) in a series of steps similar to those described by Fritts and Pearsons (2004). First, we calculated the original weight of each prey fish at ingestion for each Smallmouth Bass by using length–weight regressions (Vigg et al. 1991; Parrish et al. 2006) with the back-calculated length at ingestion described above. These were summed with other diet items (if present) to derive a meal weight (MW) for each individual Smallmouth Bass (Vigg et al. 1991). We accounted for a 21.3% weight loss (Shields and Carlson 1996) associated with preservation in 90% ethanol for all diet items used in the calculation. Next, we input MW into an evacuation rate model of Smallmouth Bass digestion of salmonids, as developed by Rogers and Burley (1991) and modified by Fritts and Pearsons (2004). The model predicts time (h) to 90% evacuation (ET_{90}),

$$ET_{90} = (24.542)(MW^{0.29}e^{-0.15T}W^{-0.23})(24), \quad (1)$$

where W is Smallmouth Bass weight (g; measured or estimated) and T is temperature. Finally, we calculated C for each individual Smallmouth Bass via the equation presented by Ward et al. (1995),

$$C = n(24/ET_{90}), \quad (2)$$

where n is the number of Chinook Salmon found in the Smallmouth Bass gut. Mean C was calculated for each habitat, reach, and sampling interval and included all Smallmouth Bass examined with both full and empty stomachs. We also calculated mean C after pooling all fish from both habitats during each month. However, these monthly estimates were only used to make direct comparisons to the Naughton et al. (2004) study, where monthly estimates of C were reported as salmonids per Smallmouth Bass per day. We compared the two studies by calculating the means (among years) of the monthly consumption estimates.

The total loss of juvenile salmonids to Smallmouth Bass predation was estimated by multiplying C by the corresponding Smallmouth Bass abundance estimate for each

habitat within each reach. Daily loss estimates were then expanded by the number of days between sampling events (typically 14 or 21 d). We estimated the percentage of Chinook Salmon consumed that were yearlings (age 1) or sub-yearlings (age 0) by examining monthly length frequency distributions of estimated FL at ingestion along with the timing of presence of each age-class. We assumed that all Chinook Salmon consumed after May were sub-yearlings because yearlings typically migrate through the study area before June. We calculated the total loss of Chinook Salmon in the SRTZ and CRTZ reaches during 1996–1997 from data reported by Naughton et al. (2004; their Table 5). We assumed that the percentage of salmonid loss represented by Chinook Salmon was constant across reaches during July 1997 in order to derive a comparable estimate.

RESULTS

Absolute Abundance

Abundance of 150-mm and larger Smallmouth Bass increased throughout the spring during 2013–2015 (Figure 2). The catchability models showed linear increases in absolute density (Smallmouth Bass/m) with increasing electrofishing CPUE (range = 0.027–0.513 Smallmouth Bass/m) for both natural (absolute density = $6.46 \cdot \text{CPUE} + 0.07$, $R^2 = 0.91$) and riprap habitats (absolute density = $5.01 \cdot \text{CPUE} + 0.03$, $R^2 = 0.87$). Abundance derived from these models was generally higher in the CON reach than in the SRTZ reach despite the greater size of the SRTZ reach. Total abundances in the SRTZ reach (habitats and years combined) were lowest in late April (mean = 2,052 Smallmouth Bass [205 fish/rkm]), peaked in early June (mean = 9,360 [936 fish/rkm]), and then decreased slightly in late June (mean = 8,275 [828 fish/rkm]). Abundance estimates for the SRTZ reach were slightly higher in natural habitat than in riprap habitat during most occasions; however, the 95% CIs always overlapped (Figure 2). These were lower than the single abundance estimate of 11,877 Smallmouth Bass (990 fish/rkm) larger than 174 mm reported by Naughton et al. (2004) for this reach (Figure 2). Total abundances in the CON reach (habitats and years combined) were lowest in late April (mean = 2,328 Smallmouth Bass [333 fish/rkm]) and peaked in late June (mean = 12,327 [1,761 fish/rkm]). Abundance estimates for the CON reach were generally higher in riprap habitats than in natural habitats, although CIs overlapped for all but one occasion. There was a marked increase in abundance in riprap habitat within the CON reach during late June 2014 (estimate = 16,110 Smallmouth Bass [2,301 fish/rkm]; Figure 2). Total Smallmouth Bass abundance in the CRTZ was low during all years (Table 1). Abundance was generally higher in 2014 (range = 564–

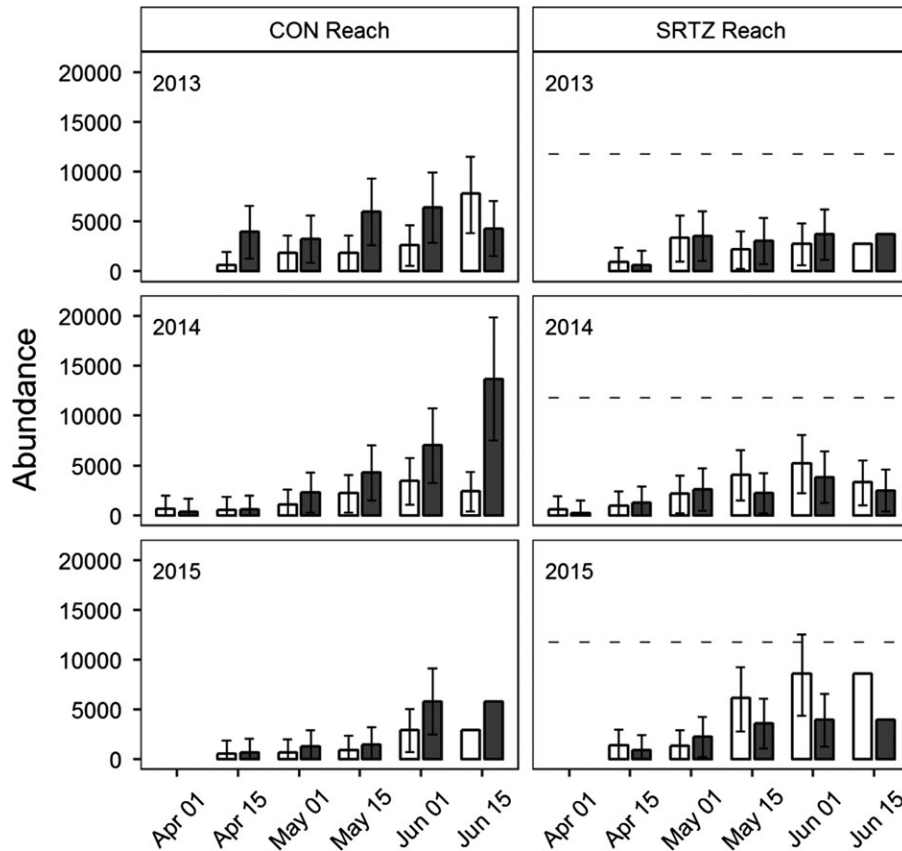


FIGURE 2. Absolute abundance ($\pm 95\%$ confidence interval [CI]) of 150-mm TL and larger Smallmouth Bass along natural (open bars) and riprap (solid bars) shorelines in the confluence (CON) and Snake River transition zone (SRTZ) reaches of Lower Granite Reservoir, 2013–2015. Abundance was derived from linear catchability models (mark–recapture estimates regressed on electrofishing CPUE), and CIs were derived from Monte Carlo simulations. The horizontal dashed lines in the SRTZ panels represent the single population estimate generated for that reach by Naughton et al. (2004).

972 Smallmouth Bass [123–211 fish/rkm]) than in 2015 (range = 399–752 [87–163 fish/rkm]). These were also lower than the single abundance estimate of 3,820 Smallmouth Bass (637 fish/rkm) larger than 174 mm reported by Naughton et al. (2004). The size distribution of Smallmouth Bass was skewed to the left during the spring months, and most of the fish captured ($\sim 63\%$) were between 150 and 200 mm; fish in this size range dropped to about 40% of the captures during summer months. Larger fish (>400 mm), although few, were also more frequently captured during spring ($\sim 0.6\%$) than during summer months ($\sim 0.1\%$). The 17 largest individuals (443–535 mm) were captured during April–June.

Dietary Analysis

We performed gastric lavage on 4,852 Smallmouth Bass captured from April through September during 2013–2015. Prey items were present in the stomachs of 3,937 (81%) of Smallmouth Bass ranging in size from 150 to 526 mm. Fish and crustaceans were the predominant prey

for all three size-classes during all sampling intervals (Figure 3). The predominant nonsalmonid fishes consumed by Smallmouth Bass were Sand Rollers *Percopsis transmontana* ($n = 1,571$), sculpins ($n = 135$), and suckers ($n = 58$). We also identified 31 Mountain Whitefish *Prosopium williamsoni*, which we grouped with nonsalmonids for calculating prey percentages by weight. Nonsalmonids (mainly Sand Rollers) comprised the highest proportion of diets (by weight) during the spring and early summer, which ranged from about 0.70 to 0.80 for most Smallmouth Bass size-classes (Figure 3). There was a major dietary shift toward crustaceans (mainly crayfish) during summer, with diet proportions reaching 0.74 for the largest (>249 -mm) size-class of Smallmouth Bass (Figure 3). Crustaceans were a predominant prey item (0.88) during April for 150–174-mm fish, but this diet proportion mainly comprised the nonnative opossum shrimp *Neomysis mercedis* (99% of crustacean weight). Pooling our sampling intervals for the SRTZ and CRTZ reaches indicated that for all three size-classes of Smallmouth Bass, diets contained

TABLE 1. Seasonal abundance (95% confidence interval in parentheses) and consumption rate (mean \pm SD; Chinook Salmon-Smallmouth Bass⁻¹·d⁻¹) of 150-mm TL and larger Smallmouth Bass in the Clearwater River transition zone (i.e., CRTZ reach) of Lower Granite Reservoir on the Snake River during 2014–2015. Abundance (a single estimate) and consumption data for 175-mm TL and larger Smallmouth Bass collected by Naughton et al. (2004) during 1996–1997 are shown for comparison.

Date	Abundance	Number of stomachs examined	Consumption rate
2014			
Jun 15	972 (0–2,922)	116	0.169 \pm 0.342
Jul 1	615 (0–2,433)	36	0.150 \pm 0.340
Jul 15	564 (0–2,363)	41	0.031 \pm 0.140
Aug 1			
Aug 15	907 (0–2,834)	54	0.011 \pm 0.079
2015			
Jun 15	752 (0–2,621)	66	0.623 \pm 0.784
Jul 1	621 (0–2,422)	71	0.196 \pm 0.368
Jul 15	501 (0–2,278)	47	0.168 \pm 0.319
Aug 1	450 (0–2,208)	38	0.080 \pm 0.260
Aug 15	399 (0–2,139)	25	0.021 \pm 0.106
1996			
Apr–May	3,820 (2,328–6,283)	294	0.000 ^a
1997			
Apr–May	3,820 (2,328–6,283)	97 ^b	0.000 ^a
Jun	3,820 (2,328–6,283)		0.016 ^a
Jul–Aug	3,820 (2,328–6,283)		0.000 ^a

^aConsumption rates from Naughton et al. (2004) are reported as salmonids per Smallmouth Bass per day (i.e., includes steelhead and Chinook Salmon).

^bSample size applies to the entire April–August time period.

higher proportions of nonsalmonids than were observed during the 1996–1997 study (Figure 3; Naughton et al. 2004).

Of the salmonids consumed by Smallmouth Bass, we identified 434 Chinook Salmon and 6 steelhead. Chinook Salmon were consumed by Smallmouth Bass in all three size-classes from early April to early August and were often the second or third most abundant prey based on proportion by weight (Figure 3). The proportion of salmonids in Smallmouth Bass diets generally increased through spring and early summer and then decreased in mid-summer (late July). For Smallmouth Bass exceeding 249 mm, salmonids were the predominant prey item by weight (0.61) during April; we assumed that these were yearling Chinook Salmon based on their estimated sizes (Figure 4). The next peak in salmonid diet proportion for

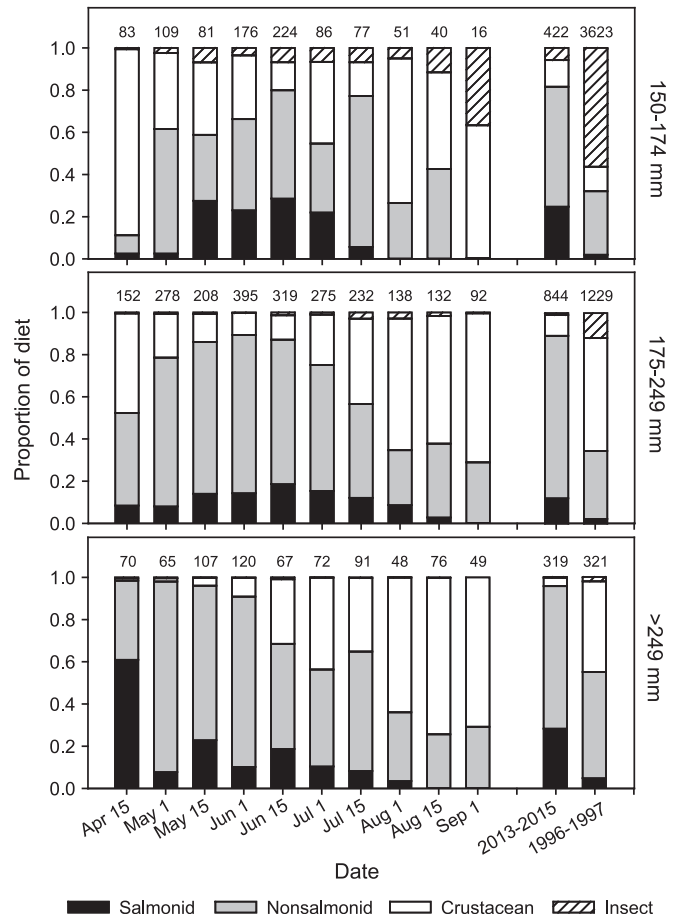


FIGURE 3. Proportion (by weight) of different prey types in the diets of Smallmouth Bass collected from Lower Granite Reservoir on the Snake River, 2013–2015. Data were pooled by reach (Snake River transition zone, Clearwater River transition zone, and confluence) and habitat and are shown in biweekly intervals (first 10 bars). The two bars at the right show overall diet proportions for the combined Snake River and Clearwater River transition zones for this study and the Naughton et al. (2004) study. The size-classes of Smallmouth Bass examined are shown on the right y-axes and were the same as those of Naughton et al. (2004) except that Naughton’s smallest size-class included fish as small as 70 mm. Numbers above bars represent sample sizes of Smallmouth Bass examined.

Smallmouth Bass larger than 249 mm occurred during mid-May (0.23), and we assumed that these salmonids were subyearlings based on their estimated sizes. Salmonids comprised the highest proportion by weight of the diets for 175–249-mm Smallmouth Bass during mid-June (0.19). The 150–174-mm size-class generally had higher proportions of salmonids in their diet than the other size-classes beginning in mid-May (peak proportion = 0.29). Pooling our sampling intervals for the SRTZ and CRTZ reaches for comparison with the results of Naughton et al. (2004) showed that proportions of salmonids in Smallmouth Bass diets are higher today than they were during the mid-1990s. Between 1996–1997 and 2013–2015,

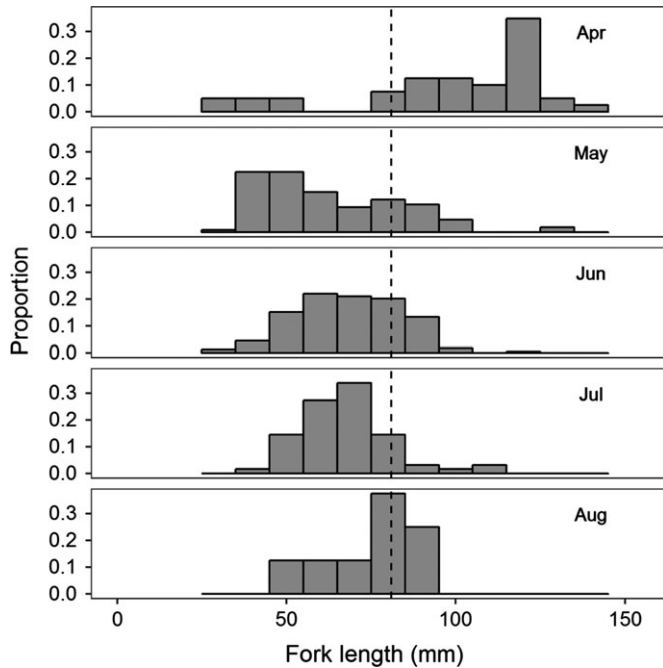


FIGURE 4. Monthly relative length frequency distributions of Chinook Salmon (10-mm bins) consumed by Smallmouth Bass in Lower Granite Reservoir on the Snake River, 2013–2015. Chinook Salmon sizes to the left of the vertical line represent those vulnerable to predation by 150-mm TL Smallmouth Bass.

salmonid proportions in diets increased about 13-fold for 150–174-mm Smallmouth Bass (from 0.02 to 0.25), sixfold for 175–249-mm fish (from 0.02 to 0.12), and sixfold for fish larger than 249 mm (from 0.05 to 0.28; Figure 3). However, direct comparisons between the studies should be interpreted with caution because the smallest size-class studied by Naughton et al. (2004) included Smallmouth Bass down to 70 mm and sampling in the SRTZ extended into August.

Quantile regression indicated that the size of Chinook Salmon consumed increased with increasing Smallmouth Bass size ($FL_{\text{Chinook Salmon}} = 57.59 + 0.16 \cdot TL_{\text{Smallmouth Bass}}$) and showed that a 150-mm Smallmouth Bass frequently consumed salmon up to 81 mm FL—or 54% of predator body length. The maximum length of salmonids relative to Smallmouth Bass length was 55% but decreased with increasing Smallmouth Bass size.

Numerical Consumption of Chinook Salmon

Rates of Chinook Salmon consumption by Smallmouth Bass (C ; Chinook Salmon·Smallmouth Bass⁻¹·d⁻¹) generally agreed with seasonal dietary proportions but were variable between years, between reaches, and between habitats (Figure 5). During 2013, peak consumption in the SRTZ reach was much higher in natural habitat ($C_{\text{SRTZ,natural}} = 0.273$) than in riprap ($C_{\text{SRTZ,riprap}} = 0.102$)

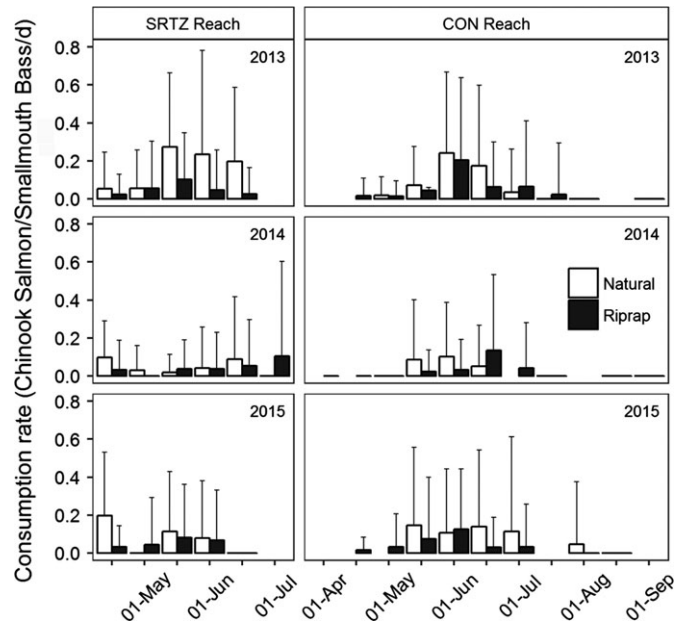


FIGURE 5. Mean (+SD) rates of Chinook Salmon consumption by 150-mm TL and larger Smallmouth Bass in the Snake River transition zone (SRTZ) and confluence (CON) reaches of Lower Granite Reservoir, 2013–2015. Consumption rates are shown for Smallmouth Bass collected in natural (open bars) and riprap (solid bars) habitats.

and remained relatively high into June (Figure 5). For loss estimates, we assumed that consumption in the SRTZ reach dropped to zero by early July in 2013 and 2015 (late July in 2014), as water temperatures exceeded 20°C and subyearling Chinook Salmon were no longer present in that reach. Consumption in the CON reach during 2013 was more similar between habitats. Estimates were only slightly higher in natural habitat than in riprap and reached zero by early August. For the CON and SRTZ reaches, consumption in 2014 was much lower than that in 2013 and never exceeded 0.134 (late June, riprap) in the CON reach or 0.104 (early July, riprap) in the SRTZ reach (Figure 5). Consumption estimates were also low in 2015 and never exceeded 0.145 (late May, natural) in the CON reach or 0.197 (late April, natural) in the SRTZ reach (Figure 5). Mean monthly consumption estimates for the SRTZ reach were always higher during 2013–2015 than during 1996–1997, but our estimates did not include data from August because we did not sample that month. Between studies, there was about a tenfold increase in consumption within the SRTZ reach during May (from 0.006 in 1996–1997 to 0.062 in 2013–2015) and an approximately 13-fold increase in consumption during June (from 0.006 in 1996–1997 to 0.075 in 2013–2015).

Consumption rates in the CRTZ reach decreased through time during the summers of 2014 and 2015

(Table 1). In 2014, consumption decreased from a high of 0.169 in late June to 0.011 in late August. In 2015, consumption decreased from a high of 0.623 in late June to 0.011 in late August. For the period 1996–1997 (Naughton et al. 2004), consumption was only observed during June 1997 (0.016 salmonids·Smallmouth Bass⁻¹·d⁻¹) and was zero for all other months (Table 1). Pooling the June CRTZ reach data from the present study and calculating the mean (of the years) showed an approximately 50-fold increase from 0.008 during 1996–1997 to 0.396 during 2014–2015.

Estimated Loss

We estimated that 300,373 Chinook Salmon were consumed by 150-mm and larger Smallmouth Bass in our study area from April through September in 2013–2015 (Table 2). Across years, 61% of the loss occurred during June, and 20% occurred during May. Chinook Salmon losses were highest in 2015 (112,856 fish; 95% CI = 33,869–216,100 fish) and lowest in 2014 (76,566 fish; 95% CI = 29,551–131,083 fish). Estimated Chinook Salmon loss in 2013 was 110,951 fish (95% CI = 37,686–183,043 fish), but this estimate did not include any losses in the CRTZ reach, which was not sampled during that year. Across years, the total loss of Chinook Salmon was higher in the CON reach (58.9%; ~177,000 fish) than in the SRTZ reach (35.1%; ~105,000 fish) and the CRTZ reach (6.0%; ~18,000 fish; Table 2). By comparison, estimated Chinook Salmon losses in the SRTZ reach were 552 fish in 1996 and 2,953 fish in 1997, and losses in the CRTZ reach were 0 fish in 1996 and 1,834 fish in 1997 (Naughton et al. 2004). Averaging losses in Table 2 across years for comparable reaches (SRTZ and CRTZ) showed that mean annual loss increased more than 15-fold from 2,670 Chinook Salmon during 1996–1997 to 41,145 Chinook Salmon during 2013–2015. In 2013–2015, Chinook Salmon losses were similar across habitats, with about

145,000 (48%) fish being consumed in natural habitat and approximately 155,000 (52%) fish being consumed in riprap habitat.

The size distribution of Chinook Salmon consumed (based on estimated FL at ingestion) showed multiple modes that shifted to the right through time (Figure 4). In April, two size-classes of Chinook Salmon were apparent: fish smaller than 60 mm, which were presumably subyearlings (15.0%); and fish mainly larger than 80 mm, which were presumably yearlings (85.0%). By May, the larger size-class had almost disappeared (2.7%), but a new 80–90-mm size-class appeared that likely comprised hatchery subyearlings, as hatchery releases began during this month. Based on these results, we estimate that of the 300,373 Chinook Salmon consumed by Smallmouth Bass during our study, 291,884 (97%) were subyearlings and 8,489 were yearlings.

DISCUSSION

Total loss of juvenile Chinook Salmon to Smallmouth Bass predation in Lower Granite Reservoir has increased substantially since the mid-1990s, when the last predation study (Naughton et al. 2004) was conducted. The increase in predation could be explained by an increase in the abundance of Smallmouth Bass over time, but this does not appear to be the case. Our estimates of Smallmouth Bass abundance (fish/rkm) in the SRTZ and CRTZ reaches were lower than those reported by Naughton et al. (2004) for these same reaches. However, comparisons of Smallmouth Bass abundance between the Naughton et al. (2004) study and our study are difficult to interpret because of the different estimation methods used and the large CIs in both studies. We believe that accounting for seasonal variability in abundance by making estimates at biweekly intervals increased the precision of our loss estimates and represented an improvement over assuming

TABLE 2. Annual loss (95% confidence interval in parentheses) of Chinook Salmon to Smallmouth Bass predation in the Snake River transition zone (SRTZ reach), confluence (CON reach), and Clearwater River transition zone (CRTZ reach) of Lower Granite Reservoir on the Snake River. Estimates for 2013–2015 are for 150-mm TL and larger Smallmouth Bass. Estimates for 1996 and 1997 were obtained from Naughton et al. (2004) for 175-mm TL and larger Smallmouth Bass. The CRTZ reach was not sampled in 2013.

Reach	Habitat	2013	2014	2015	1996	1997
SRTZ	Natural	28,398 (5,732–50,649)	10,402 (3,015–18,220)	32,549 (13,861–50,948)	No data	No data
	Riprap	11,219 (3,127–19,556)	9,269 (1,653–17,017)	13,516 (3,891–23,378)	No data	No data
	Both	39,617 (8,859–70,205)	19,671 (4,668–35,237)	46,065 (17,752–74,326)	552	2,953 ^a
CON	Natural	36,159 (14,339–56,934)	10,133 (2,350–17,627)	27,846 (6,385–50,139)	No data	No data
	Riprap	35,175 (14,488–55,904)	42,013 (22,533–61,643)	25,611 (9,732–42,198)	No data	No data
	Both	71,334 (28,827–112,838)	52,146 (24,883–79,270)	53,457 (16,117–92,337)	No data	No data
CRTZ	Riprap	No data	4,749 (0–16,576)	13,334 (0–49,437)	0	1,834
Total		110,951 (37,686–183,043)	76,566 (29,551–131,083)	112,856 (33,869–216,100)	552	4,787

^aEstimate based on Chinook Salmon representing 19% of the total salmonids consumed (see Table 5 in Naughton et al. 2004).

constant abundance estimated one time, which would have dramatically inflated our loss estimates. In a similar predation study, Fritts and Pearsons (2004) also found increasing Smallmouth Bass abundance during spring in the Yakima River, Washington. Although we did assume constant abundance in the CON reach during summer, this assumption probably had minimal impact on our loss estimates because consumption rates on Chinook Salmon were very low after June. In contrast, Naughton et al. (2004) reported that the highest consumption occurred from June to August, which may have been due to later out-migration timing of juvenile fall Chinook Salmon in the 1990s (Connor et al. 2013). The lower Smallmouth Bass abundance we observed in the CRTZ reach may have been influenced by the cooler temperatures in the Clearwater River resulting from coldwater releases during summer from Dworshak Reservoir located upstream (Columbia Basin Research 2017; Supplemental Figure S.1).

The high predation on Chinook Salmon we observed was more likely due to an increase in Smallmouth Bass consumption rates rather than an increase in abundance. The consumption rates we calculated were at least an order of magnitude higher than those calculated by Naughton et al. (2004). Our consumption rates compare favorably with those we calculated from Smallmouth Bass studied in the Yakima River, where Smallmouth Bass are abundant (Fritts and Pearsons 2004). From that study, we used a mean Smallmouth Bass abundance of 11,392 fish and a study period of 90 d (March 21–June 20) to estimate consumption rates of subyearlings ranging from 0.12 to 0.33 Chinook Salmon–Smallmouth Bass⁻¹·d⁻¹. By comparison, the consumption rates we estimated during May and early June 2013 in our study ranged from 0.05 to 0.27 Chinook Salmon–Smallmouth Bass⁻¹·d⁻¹ in natural habitats. In John Day Reservoir on the Columbia River, individual Smallmouth Bass sampled in July consumed 0.12 fish/d (Vigg et al. 1991). Consumption estimates for our study are conservative, however, because some Chinook Salmon might not have been identified as such if their diagnostic bones were missing from the stomach samples, and we often witnessed Smallmouth Bass regurgitating meals during sampling before their stomach contents could be collected.

We believe that the increase through time in the number of juvenile Chinook Salmon out-migrating from the Snake River is an important factor explaining the increased Smallmouth Bass consumption and Chinook Salmon loss we observed. Comparatively, there was a 16-fold increase in mean annual subyearling Chinook Salmon passage at Lower Granite Dam between 1996–1997 (mean = 58,542) and 2013–2015 (mean = 956,371; Columbia Basin Research 2017). This was due to increases in both natural and hatchery production of juvenile fish (Connor et al.

2013). In addition, the timing of the juvenile out-migration has shifted to earlier in the season compared to the 1990s, resulting in smaller migrants that may be more vulnerable to predation (Connor et al. 2013). Furthermore, the peak consumption during our study coincided with the timing of hatchery subyearling releases within the basin. The appearance of the mode during May in the length frequency distribution of consumed Chinook Salmon (Figure 4) suggested that these were hatchery subyearlings. Hatchery fish are known to be more naïve of predators than wild fish (e.g., Berejikian 1995; Álvarez and Nieceza 2003) and may have contributed to the increase in consumption rates relative to those observed in the 1990s.

The small size of subyearling Chinook Salmon makes them particularly susceptible to Smallmouth Bass predation. We showed that Smallmouth Bass as small as 150 mm frequently consumed Chinook Salmon up to about 54% of predator body size, or about an 81-mm fish, which is slightly lower than the 60% body size limit reported by Zimmerman (1999) for the lower Columbia River and the 57% body size limit reported by Fritts and Pearsons (2006) for the Yakima River. Although we did not examine consumption by Smallmouth Bass smaller than 150 mm, they have the potential to contribute substantially to predation losses of subyearling Chinook Salmon in Lower Granite Reservoir, particularly since much of the Smallmouth Bass population is skewed toward smaller sizes, and fish as small as 85 mm TL can consume subyearlings (Bennett et al. 1999). Many of the hatchery subyearlings that are released during May are vulnerable to predation by 150-mm Smallmouth Bass because of their small size (Figure 4), while a majority of subyearlings are vulnerable to 250-mm Smallmouth Bass. Yearling Chinook Salmon, which typically migrate in early spring, are mainly vulnerable to predation by Smallmouth Bass larger than 300 mm, but predators of that size were rarely captured in our study.

The greater number of juvenile Chinook Salmon available to Smallmouth Bass as prey in recent years may also be an artifact of reduced predation by Northern Pikeminnow *Ptychocheilus oregonensis*. In 1990, a sport-reward harvest program was implemented to reduce predation on juvenile salmon by Northern Pikeminnow (Beamesderfer et al. 1996; Friesen and Ward 1999). Since that time, indices of Northern Pikeminnow abundance, salmonid consumption, and predation have declined in Lower Granite Reservoir, whereas Smallmouth Bass abundance and predation indices have generally increased (Storch et al. 2014). Storch et al. (2014) also showed that in 2013, Smallmouth Bass predation indices for salmonids in Little Goose and Lower Monumental reservoirs (the next two reservoirs downstream from Lower Granite Reservoir) were the highest recorded since indexing began in 1991. Although many factors could contribute to increases

in Smallmouth Bass predation on juvenile Chinook Salmon, a compensatory response by Smallmouth Bass to reductions in the Northern Pikeminnow population remains a possibility (Beamesderfer et al. 1996).

The loss of juvenile Chinook Salmon to Smallmouth Bass predation in Lower Granite Reservoir will likely fluctuate with annual variability in prey type and availability. Recent changes to the food web since the Naughton et al. (2004) study may have altered the prey base and affected Smallmouth Bass demographics and feeding ecology. The endemic Sand Roller and the nonnative *N. mercedis*—the two main nonsalmonid prey types consumed by Smallmouth Bass in our study—either were not present or were present at such low densities that they were not consumed during the mid-1990s (Tiffan et al. 2017a, 2017b). In 2014, we observed the lowest consumption and loss of Chinook Salmon but the highest consumption of Sand Rollers. The Sand Roller along with other prey fishes or crayfish may serve as a predation buffer for juvenile Chinook Salmon; however, *N. mercedis* may provide an important energy source for juvenile Smallmouth Bass that may lead to increased growth and survival, thus indirectly increasing predation. Chinook Salmon predation loss is also affected by annual variation in Smallmouth Bass abundance and their distributional overlap with their prey. We generally collected more Smallmouth Bass in riprap habitat of the CON reach, which provided more cover (Munther 1970; Todd and Rabeni 1989), but this type of habitat is not preferred by juvenile Chinook Salmon (Garland et al. 2002). In contrast, we often observed higher Smallmouth Bass abundance in sandy natural habitat in the SRTZ reach that was likely used by Smallmouth Bass for spawning. The preference of juvenile Chinook Salmon for this type of habitat (Tiffan et al. 2016) may have provided Smallmouth Bass with better foraging opportunities that contributed to the often-higher consumption rates in natural habitat.

Annual fluctuations in environmental conditions also affect predation losses of Chinook Salmon. Annual variation in river flows can influence water temperature and turbidity, thereby potentially modifying Smallmouth Bass foraging success (Sweka and Hartman 2003; Carter et al. 2010) and predator avoidance by Chinook Salmon (Gregory 1993). Peak turbidities were higher in 2014 (~26 NTU) than in 2013 (~18 NTU) or 2015 (~15 NTU), as were flows (Figure 6), which may explain the lower Chinook Salmon loss in 2014. Water temperatures were also warmer in 2013 and 2015, which may have resulted in higher losses in those years by increasing predator metabolism and predation rates (Figure 6; Petersen and Kitchell 2001). River flow could also explain some of the differences in results between our study and the Naughton et al. (2004) study because flows were substantially higher in 1996 and 1997 (Figure 6).

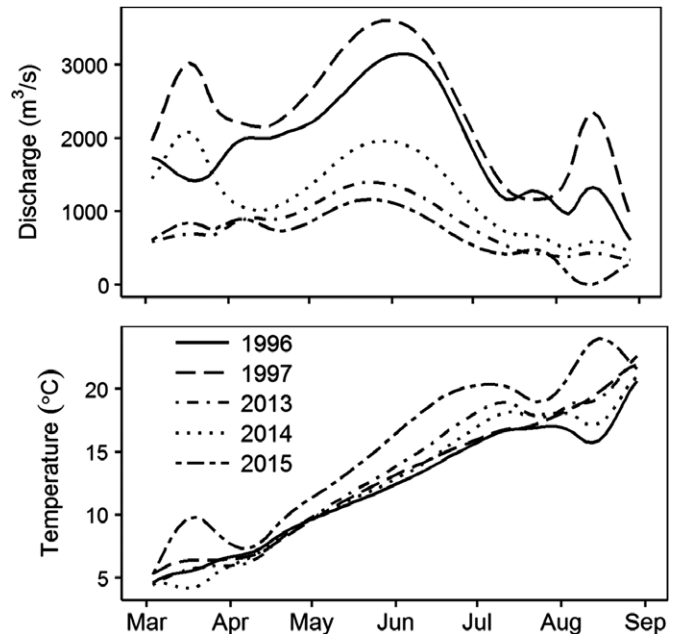


FIGURE 6. Loess-smoothed mean daily discharge (top panel) and temperature (bottom panel) in the Snake River. Data were obtained from U.S. Geological Survey gauge 13334300 near Anatone, Washington.

The large increase in loss of subyearling fall Chinook Salmon to Smallmouth Bass predation paralleled subyearling increases in density and suggests a functional feeding response by Smallmouth Bass that one would expect for an opportunistic feeder. Our results indicate that subyearlings are especially vulnerable to predation within the transitional reservoir areas we studied. These are important rearing areas for subyearlings (Tiffan et al. 2016) and for active migrants that delay or slow their downstream movements through these habitats (Tiffan et al. 2009). A better understanding of subyearling losses to predation throughout the drainage and reservoir will equip managers with necessary information to assess recovery efforts and identify areas of high mortality. Although we suspect that our study area may be a predation bottleneck for subyearlings, this hypothesis needs to be confirmed by examining Smallmouth Bass predation in other areas of the reservoir and river.

ACKNOWLEDGMENTS

We thank our U.S. Geological Survey colleagues, particularly Scott St. John, Brad Bickford, Tobyn Rhodes, R. J. Hemingway, and Amanda Schmidt, whose efforts contributed to this study. This study was funded by Bonneville Power Administration Project 200203200, administered by D. Docherty. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Data are

publicly available from StreamNet at <http://www.streamnet.org/files/642/642.zip> and <http://www.streamnet.org/files/643/643.zip>. There is no conflict of interest declared in this article.

REFERENCES

- Álvarez, D., and A. G. Nicieza. 2003. Predator avoidance behaviour in wild and hatchery-reared Brown Trout: the role of experience and domestication. *Journal of Fish Biology* 63:1565–1577.
- Anglea, S. A. 1997. Abundance and food habits of Smallmouth Bass and distribution of crayfish in Lower Granite Reservoir, Idaho–Washington. Master's thesis. University of Idaho, Moscow.
- Beamesderfer, R. C., D. L. Ward, and A. A. Nigro. 1996. Evaluation of the biological basis for a predator control program on Northern Squawfish (*Ptychocheilus oregonensis*) in the Columbia and Snake rivers. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2898–2908.
- Bennett, D. H., M. A. Madsen, S. M. Anglea, T. Cichosz, T. J. Dresser Jr., M. Davis, and S. R. Chipps. 1999. Fish interactions in Lower Granite Reservoir, Idaho–Washington. Department of Fish and Wildlife Resources, College of Forestry, Wildlife, and Range Sciences, University of Idaho, Moscow.
- Berejikian, B. A. 1995. The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator. *Canadian Journal of Fisheries and Aquatic Sciences* 52:2476–2482.
- Cade, B. S., J. W. Terrell, and R. L. Schroeder. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology* 80:311–323.
- Carter, M. W., D. E. Shoup, J. M. Deters, and D. H. Wahl. 2010. Effects of turbidity and cover on prey selectivity of adult Smallmouth Bass. *Transactions of the American Fisheries Society* 139:353–361.
- Columbia Basin Research. 2017. Columbia River DART (Data Access in Real Time). Columbia Basin Research, School of Aquatic and Fishery Sciences, University of Washington, Seattle. Available at <http://www.cbr.washington.edu/dart>. (February 2018).
- Connor, W. P., H. L. Burge, R. Waitt, and T. C. Bjornn. 2002. Juvenile life history of wild fall Chinook Salmon in the Snake and Clearwater rivers. *North American Journal of Fisheries Management* 22:703–712.
- Connor, W. P., K. F. Tiffan, J. M. Plumb, and C. M. Moffitt. 2013. Evidence for density-dependent changes in growth, downstream movement, and size of Chinook Salmon subyearlings in a large-river landscape. *Transactions of the American Fisheries Society* 142:1453–1468.
- Connor, W. P., C. E. Piston, and A. P. Garcia. 2003. Temperature during incubation as one factor affecting the distribution of Snake River fall Chinook Salmon spawning areas. *Transactions of the American Fisheries Society* 132:1236–1243.
- Curet, T. S. 1993. Habitat use, food habits, and the influence of predation on subyearling Chinook Salmon in Lower Granite and Little Goose reservoirs, Washington. Master's thesis. University of Idaho, Moscow.
- Erhardt, J. M., S. J. St. John, B. K. Bickford, T. N. Rhodes, and K. F. Tiffan. 2014. Smallmouth Bass predation on juvenile fall Chinook Salmon in Lower Granite Reservoir on the Snake River. Pages 27–60 in K. F. Tiffan, W. P. Connor, B. J. Bellgraph, and P. M. Chittaro, editors. Snake River fall Chinook Salmon life history investigations. Annual Report to the Bonneville Power Administration, Project 200203200, Portland, Oregon.
- Friesen, T. A., and D. L. Ward. 1999. Management of Northern Pike-minnow and implications for juvenile salmonid survival in the lower Columbia and Snake rivers. *North American Journal of Fisheries Management* 19:406–420.
- Fritts, A. L., and T. N. Pearsons. 2004. Smallmouth Bass predation on hatchery and wild salmonids in the Yakima River, Washington. *Transactions of the American Fisheries Society* 133:880–895.
- Fritts, A. L., and T. N. Pearsons. 2006. Effects of predation by nonnative Smallmouth Bass on native salmonid prey: the role of predator and prey size. *Transactions of the American Fisheries Society* 135:853–860.
- Garland, R. D., K. F. Tiffan, D. W. Rondorf, and L. O. Clark. 2002. Comparison of subyearling fall Chinook Salmon's use of riprap revetments and unaltered habitats in Lake Wallula of the Columbia River. *North American Journal of Fisheries Management* 22:583–589.
- Gregory, R. S. 1993. Effect of turbidity on the predator avoidance behaviour of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 50:241–246.
- Hansel, H. C., S. D. Duke, P. T. Lofy, and G. A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. *Transactions of the American Fisheries Society* 117:55–62.
- Hansen, M. J., T. D. Beard Jr., and S. W. Hewett. 2000. Catch rates and catchability of Walleyes in angling and spearing fisheries in northern Wisconsin lakes. *North American Journal of Fisheries Management* 20:109–118.
- Munther, G. L. 1970. Movement and distribution of Smallmouth Bass in the middle Snake River. *Transactions of the American Fisheries Society* 99:44–53.
- Naughton, G. P., D. H. Bennett, and K. B. Newman. 2004. Predation on juvenile salmonids by Smallmouth Bass in the Lower Granite Reservoir system, Snake River. *North American Journal of Fisheries Management* 24:534–544.
- NMFS (National Marine Fisheries Service). 1992. Threatened status for Snake River spring/summer Chinook Salmon, threatened status for Snake River fall Chinook Salmon. *Federal Register* 57:78(22 April 1992):14653–14663.
- Parrish, J. K., K. Haapa-aho, W. Walker, M. Stratton, J. Walsh, and H. Ziel. 2006. Small-bodied and juvenile fishes of the mid-Columbia region including keys to diagnostic otoliths and cranial bones. University of Washington, Seattle.
- Petersen, J. H., and J. F. Kitchell. 2001. Climate regimes and water temperature changes in the Columbia River: bioenergetic implications for predators of juvenile salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1831–1841.
- Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Prendergast. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:405–420.
- R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by Northern Squawfish, Walleyes, and Smallmouth Bass in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:448–458.
- Rogers, J. B., and C. C. Burley. 1991. A sigmoid model to predict gastric evacuation rates of Smallmouth Bass (*Micropterus dolomieu*) fed juvenile salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 48:933–937.
- Rogers, M. W., M. J. Hansen, and T. D. Jr Beard. 2003. Catchability of Walleye to fyke netting and electrofishing in northern Wisconsin lakes. *North American Journal of Fisheries Management* 23:1193–1206.
- Scharf, F. S., F. Juanes, and M. Sutherland. 1998. Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. *Ecology* 79:448–460.

- Seaburg, K. G. 1957. A stomach sampler for live fish. *Progressive Fish-Culturist* 19:137–139.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Edward Arnold, London.
- Shields, P. A., and S. R. Carlson. 1996. Effects of formalin and alcohol preservation on lengths and weights of juvenile Sockeye Salmon. *Alaska Fishery Research Bulletin* 3:81–93.
- Storch, A. J., C. Mallette, and S. Williams. 2014. Evaluate predator control fisheries and establish an index of predation by Northern Pike-minnow and other piscivorous fishes on juvenile salmonids in the lower Columbia and Snake rivers. Annual Report to the Bonneville Power Administration, Project 199007700, Portland, Oregon.
- Sweka, J. A., and K. J. Hartman. 2003. Reduction of reactive distance and foraging success in Smallmouth Bass, *Micropterus dolomieu*, exposed to elevated turbidity levels. *Environmental Biology of Fishes* 67:341–347.
- Tabor, R. A., R. S. Shively, and T. P. Poe. 1993. Predation on juvenile salmonids by Smallmouth Bass and Northern Squawfish in the Columbia River near Richland, Washington. *North American Journal of Fisheries Management* 13:831–838.
- Talbert, M., J. Richards, P. Mielke, and B. Cade. 2016. Blossom: statistical comparisons with distance-function based permutation tests. Available: <http://CRAN.Rproject.org/package=Blossom>. (February 2018).
- Tiffan, K. F., W. P. Connor, B. J. Bellgraph, and R. A. Buchanan. 2010. Snake River fall Chinook Salmon life history investigations. Annual Report to the Bonneville Power Administration, Project 200203200, Portland, Oregon.
- Tiffan, K. F., J. M. Erhardt, and B. K. Bickford. 2017a. Ecology of the opossum shrimp (*Neomysis mercedis*) in a lower Snake River reservoir, Washington. *Northwest Science* 91:124–139.
- Tiffan, K. F., J. M. Erhardt, T. N. Rhodes, and R. J. Hemingway. 2017b. Ecology of the Sand Roller (*Percopsis transmontana*) in a lower Snake River reservoir, Washington. *Northwestern Naturalist* 98:203–214.
- Tiffan, K. F., J. R. Hatten, and D. A. Trachtenberg. 2016. Assessing juvenile salmon rearing habitat and associated predation risk in a lower Snake River reservoir. *River Research and Applications* 32:1030–1038.
- Tiffan, K. F., T. J. Kock, C. A. Haskell, W. P. Connor, and R. K. Steinhorst. 2009. Water velocity, turbulence, and migration rate of sub-yearling fall Chinook Salmon in the free-flowing and impounded Snake River. *Transactions of the American Fisheries Society* 138:373–384.
- Todd, B. L., and C. F. Rabeni. 1989. Movement and habitat use by stream-dwelling Smallmouth Bass. *Transactions of the American Fisheries Society* 118:229–242.
- Vigg, S., T. P. Poe, L. A. Prendergast, and H. C. Hansel. 1991. Rates of consumption of juvenile salmonids and alternate prey fish by Northern Squawfish, Walleyes, Smallmouth Bass, and Channel Catfish in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:421–438.
- Ward, D. L., J. H. Petersen, and J. J. Loch. 1995. Index of predation on juvenile salmonids by Northern Squawfish in the lower and middle Columbia River and in the lower Snake River. *Transactions of the American Fisheries Society* 124:321–334.
- Zimmerman, M. P. 1999. Food habits of Smallmouth Bass, Walleyes, and Northern Pikeminnow in the lower Columbia River basin during outmigration of juvenile anadromous salmonids. *Transactions of the American Fisheries Society* 128:1036–1054.
- Zimmerman, M. P., and R. M. Parker. 1995. Relative density and distribution of Smallmouth Bass, Channel Catfish and Walleye in the lower Columbia and Snake rivers. *Northwest Science* 69:19–28.

SUPPORTING INFORMATION

Additional supplemental material may be found online in the supporting information tab for this article.