Snake River Fall Chinook Salmon Life History Investigations

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Abstract

Smallmouth bass predation on subyearling fall Chinook salmon was examined in the upper portion of Lower Granite Reservoir during 2013. During the time subyearlings were present in the reservoir, smallmouth bass were collected, their stomach contents removed for diet analysis, and their abundance estimated with mark-recapture techniques. In 2013, the greatest consumption of subyearlings by smallmouth bass occurred in late May and early June—as much as 50% of their diet by weight. Sand rollers were the most common non-salmonid fish consumed by smallmouth bass. In the section of the reservoir above the confluence with the Clearwater River, the abundance of bass was higher in non-riprap habitat than in riprap, but the opposite was true in the section below the confluence. We estimated that over 168,000 subyearlings were lost to smallmouth bass predation in 2013. Given the predominance of sand rollers in the diet of smallmouth bass, we believe this species reduces predation on subyearling fall Chinook salmon. A complete report of our findings is provided in the Appendix.

Introduction

Predation by nonnative fishes is one factor that has been implicated in the decline of juvenile salmonids Oncorhynchus spp. in the Pacific Northwest. The only evaluation of predation on subyearling Snake River fall Chinook salmon in the upper portion of Lower Granite Reservoir was conducted by Naughton et al. (2004). However, this study in the Snake River was conducted soon after Endangered Species Act (ESA) listing of Snake River fall Chinook salmon (NMFS 1992). During this time, fall Chinook salmon abundance was at an historic low and 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). We speculate that predation on subyearlings by smallmouth bass in the Snake River may have increased in recent years for several reasons. Since their ESA listing, recovery measures implemented for Snake River fall Chinook salmon have resulted in a large increase in the juvenile population (Connor et al. 2013). For example, the annual subyearling passage index for fall Chinook salmon at Lower Granite Dam, the first dam encountered during downstream migration, was 18,533 in 1996 when the Naughton study was conducted but was 749,074 in 2013 (DART 2014). Both Zimmerman (1999) and Naughton et al. (2004) showed that fish can comprise a large portion of smallmouth bass diets. Considering that subyearlings probably now make up a larger portion of the forage fish population, it is plausible they should make up a large portion of smallmouth bass diets. Here we report on findings from work conducted 2013. The objective of the RM&E research project was to describe the seasonal variation in smallmouth bass diets and estimate consumption of subyearlings during their rearing and outmigration period in Lower Granite Reservoir. This work is important to understand the effect of predation on juvenile salmon now that many of the populations are healthier than they were prior to ESA listing.
Methods

Estimate subyearling loss to smallmouth bass predation in the Snake River
(MonitoringMethods.org Protocol 272, published)

We conducted our study in the upper portion of Lower Granite Reservoir in the section from Asotin, WA to the confluence of the Clearwater River (Snake River transition zone [SRTZ]), the section from the confluence to Port of Wilma (confluence zone [CON]), and the lower 4 km of the Clearwater River (Clearwater River transition zone [CRTZ]; Figure 1). These sections of the reservoir were selected so our results would be comparable to Naughton et al. (2004) to document changes in predation since the mid-1990s—a period of low fall Chinook salmon abundance.

Sampling was conducted either biweekly or triweekly from late April through mid-September, 2013. This frequency of sampling was used to document the seasonal changes in smallmouth bass abundance, diet, and consumption of subyearlings. Fixed sampling sites were established in both riprap and non-riprap habitats and then sampled through time to make recapturing tagged smallmouth bass more effective.

Collected smallmouth bass >150 mm TL had their stomach contents removed by non-lethal lavage, were measured, Floy tagged, and released. Subsequent recapture information was used to estimate absolute abundance. Catch per unit effort (# bass/m shoreline) was also calculated. Abundance estimates were ultimately used to expand consumption estimates to generate a loss estimate of subyearlings to predation.

Smallmouth bass stomach contents were identified to major taxonomic group: insects, crustaceans, fish, and other. Fish species and length at ingestion were identified from diagnostic bones and associated regressions (Hansel et al. 1988; Rogers and Burley 1991; Rieman et al. 1991; Vigg et al. 1991; Parrish et al. 2006). Consumption of different prey taxa was expressed as percent frequency of occurrence and percent weight on a seasonal basis.

The consumption of subyearling fall Chinook salmon was estimated following established, peer-reviewed methods (Rogers and Burley 1991; Rieman et al. 1991; Vigg et al. 1991; Naughton et al. 2004; Parrish et al. 2006). In brief, we first estimated the fresh weight of subyearlings at ingestion. Next, we estimated the meal weight of all prey. Then we input this into an evacuation rate model to determine if the subyearlings were ingested within 24 h of when the bass was collected. Finally, we estimated total loss as the sum of the number of subyearlings eaten per bass over all sampling intervals multiplied by the abundance of bass in our study area. The same procedure was used for estimating the loss of sand rollers—another important prey fish of smallmouth bass.
**Results**

Smallmouth bass abundance varied seasonally by study section and habitat type (i.e., riprap or non-riprap). Smallmouth bass abundance in shoreline areas during triweekly sampling intervals ranged from 3,292 to 8,796 (mean, 6,422) in the SRTZ, and from 4,043 to 11,321 (mean, 7,376) in the CON. More bass were collected in non-riprap habitat in the SRTZ than in riprap, but the opposite was true in the CON. However, there were 997 bass/km of shoreline in the CON compared to 612 bass/km of shoreline in the SRTZ.

We captured 1,782 smallmouth bass for dietary analysis and prey items were present in the stomachs of 1,522 fish. Weekly mean sizes were between 184 and 256 mm TL. In both

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*Figure 1. Map of the two study sections of Lower Granite Reservoir that were sampled for smallmouth bass diet and salmonid consumption in 2013 (CON, confluence; SRTZ, Snake River Transition Zone; rkm, river kilometer).*
habitats of the SRTZ, non-salmonid fishes were the dominant prey item in all weeks except during the week of 24 June when salmonids predominated in non-riprap and during the week of 29 April when crustaceans predominated in riprap (Figure 2). Non-salmonid fishes were also the most predominant prey by weight in all but the week of 19 August when crustaceans were the main prey item in non-riprap habitat of the CON section (Figure 3). The diet of bass collected in riprap habitat of the CON reach was predominated by crustaceans for all but May and mid-June, when non-salmonid fish were predominant. During this time, salmonids composed up to 47% diet by weight in the SRTZ non-riprap and up to 32% by weight in the CON non-riprap. No salmonids were consumed in the SRTZ after 24 June and none were consumed in the CON after 29 July. Sand rollers were the predominant non-salmonid consumed by smallmouth bass.

Total loss of salmonids to smallmouth bass predation within our study area in 2013 was estimated to be 168,380 individuals, of which 154,952 were Chinook salmon (Table 1). Of the Chinook salmon consumed, we estimate that 150,823 (97%) were subyearlings based on length-frequency distributions. The total annual loss was higher in the SRTZ section (90,318 fish) than in the CON section (78,062 fish) in spite of the CON section being sampled for a longer duration (into early September; Table 1). In the SRTZ, 82% of the total loss occurred in non-riprap habitat whereas in the CON only 59% of the loss occurred in non-riprap. This is because bass densities and consumption rates (Table 1) were higher in non-riprap habitats in the SRTZ section than in the CON section.

Discussion/Conclusion

During 2013 smallmouth bass consumption of subyearling fall Chinook salmon was greatest during late May through mid-June, the time of peak abundance of subyearlings in shoreline habitats. Subyearlings prefer non-riprap habitats (Garland et al. 2002; Tiffan et al. 2006), whereas smallmouth bass have a greater affinity for riprap (Munther 1970; Todd and Rabeni 1989). We probably saw higher consumption of subyearlings by smallmouth bass in non-riprap habitats in the SRTZ because that habitat comprises the majority of habitat in that section. Furthermore, the substrate in non-riprap habitat in this section is composed of cobbles and there is more overhanging vegetation, both of which may attract bass. In contrast, there is more riprap in the CON section and the non-riprap habitat in this section is characterized by shallow depths and silty substrate that bass don’t prefer, which may explain the contrasting habitat use of smallmouth bass between the two sections. Thus, subyearlings may incur more predation risk in the SRTZ due to smallmouth bass use of the more prevalent non-riprap habitat in that section.
Figure 2. Seasonal variation in diet composition (percent weight based on non-empty stomachs) of smallmouth bass in the Snake River Transition Zone section in non-riprap (top panel) and riprap (bottom panel) habitats in 2013.
Figure 3. Seasonal variation in diet composition (percent weight based on non-empty stomachs) of smallmouth bass in the Confluence section in non-riprap (top panel) and riprap (bottom panel) habitats in 2013.
Table 1. Estimated losses of juvenile salmonids and consumption rates (C: salmonids eaten/bass/day) by smallmouth bass in two sections of Lower Granite Reservoir during 2013.

<table>
<thead>
<tr>
<th>Week</th>
<th>Snake River Transition Zone</th>
<th></th>
<th>Confluence</th>
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<tr>
<td></td>
<td>Non-riprap</td>
<td>Riprap</td>
<td>Combined</td>
<td>Non-riprap</td>
<td>Riprap</td>
<td>Combined</td>
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<tr>
<td></td>
<td>Loss</td>
<td>C</td>
<td>Loss</td>
<td>C</td>
<td>Total Loss</td>
<td>Loss</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>29 Apr</td>
<td>4,724</td>
<td>0.143</td>
<td>685</td>
<td>0.053</td>
<td>5,409</td>
<td>29 Apr</td>
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<tr>
<td>13 May</td>
<td>7,753</td>
<td>0.091</td>
<td>4,684</td>
<td>0.124</td>
<td>12,437</td>
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</tr>
<tr>
<td>27 May</td>
<td>32,286</td>
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<td>8,581</td>
<td>0.217</td>
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</tr>
<tr>
<td>10 Jun</td>
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<td>0.033</td>
<td>10,886</td>
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</tr>
<tr>
<td>08 Jul</td>
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<td>0.000</td>
<td>0</td>
<td>08 Jul</td>
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<tr>
<td>All weeks</td>
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<td>17,092</td>
<td>0.000</td>
<td>90,318</td>
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<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>29 Apr</td>
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<tr>
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<tr>
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<td>0</td>
<td>0.000</td>
<td>0</td>
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<tr>
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<td>78,062</td>
<td>All weeks</td>
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</table>

To put our results in perspective, we estimated a mean abundance of smallmouth bass in the SRTZ of 6,422 fish in 2013 whereas Naughton et al. (2004) estimated 11,877 bass in 1996. They also estimated a total loss of juvenile Chinook salmon of 1,200 fish in 1996 and 6,343 in 1997. Although smallmouth bass abundance in this section today is almost half of that estimated in the mid-1990s, we estimated a loss of juvenile Chinook salmon over 10-fold higher than that estimated by Naughton et al. (2004). Our estimated loss was even higher in the CON section. The reason for this may be that subyearlings are far more abundant today than they were 20 years ago and they could comprise a larger portion of the prey fish population. Naughton et al. (2004) found that fish composed about 50% of smallmouth bass diets in the SRTZ. Our results were similar in that prey fish constituted a large fraction of the diet in most sampling weeks. Interestingly, sand rollers, which were absent during Naughton’s study, are now very abundant and probably reduce predation pressure on subyearlings by serving as alternate prey for smallmouth bass.
This study only examined smallmouth bass predation over a relatively small spatial scale and found the loss of subyearlings to be high. One factor that has a large effect on loss estimates is the quality of the abundance estimate, which is heavily dependent on obtaining sufficient recaptures of marked fish. One of the limitations of this study was we were not allowed to electrofish once water temperatures exceeded 18°C. This meant we had to rely on angling for marking and recapturing fish, which is not as effective as electrofishing and resulted in wide confidence intervals on abundance estimates. Future studies should consider how to effectively sample at high temperatures to achieve accurate abundance estimates.

**Adaptive Management & Lessons Learned**

Predation likely occurs to varying extents throughout freshwater habitats in which subyearlings rear and migrate. Our estimates of loss demonstrate that predation is a significant mortality source for subyearling Snake River fall Chinook salmon in the Snake River. Their small size and use of shoreline habitats during rearing makes them particularly vulnerable to predation until they become larger and move off shore out of the habitats of predators. Our results could inform predator control decisions and hatchery release strategies to reduce predation. Although we studied smallmouth bass predation in a localized area of one reservoir, our results should be generally applicable throughout the hydrosystem at locations where subyearling and smallmouth bass habitats overlap. At the end of our study, we will disseminate our findings in peer-reviewed journal articles and at professional and management meetings.
References


Appendix

Smallmouth Bass Predation on Juvenile Fall Chinook Salmon in Lower Granite Reservoir, Snake River

John M. Erhardt, Scott J. St. John, Tobyn N. Rhodes, Brad K. Bickford, and Kenneth F. Tiffan
U.S. Geological Survey
Western Fisheries Research Center
5501A Cook-Underwood Rd.
Cook, WA 98605
INTRODUCTION

Predation by both native and nonnative fishes is one factor that has been implicated in the historical 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 smallmouth bass *Micropterus dolomieu*. Smallmouth bass are common throughout the Columbia River basin and have become the most abundant predator of juvenile salmon in lower Snake River reservoirs (Zimmerman and Parker 1995). This is a concern for Snake River fall Chinook salmon *Oncorhynchus tshawytscha* subyearlings that may be particularly vulnerable because of their relatively small size and because their main-stem rearing habitats often overlap or are in close proximity to habitats used by smallmouth bass (Curet 1993; Tabor et al. 1993).

Concern over juvenile salmon predation spawned 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, from 1983 through 1986 (Rieman et al. 1991). Where the Columbia River changes from free-flowing to impounded between the Hanford Reach and McNary Reservoir, juvenile salmon (presumably subyearlings) were found in 65% of smallmouth bass (>200 mm) stomachs and composed 59% of the diet by weight (Tabor et al. 1993). Within Lower Granite Reservoir on the Snake River, Anglea (1997) reported that subyearlings made up 7% of smallmouth bass diets, and Naughton et al. (2004) showed that monthly consumption (based on weight) ranged from 5% in the upper areas of the reservoir to 11% in the forebay. However, these studies in the Snake River were conducted soon after Endangered Species Act (ESA) listing of Snake River fall Chinook salmon (NMFS 1992). During this 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).

We speculate that predation on subyearlings by smallmouth bass in the Snake River may have increased in recent years for several reasons. Since their ESA (Endangered Species Act) listing in 1992, recovery measures implemented for Snake River fall Chinook salmon have resulted in a large increase in the juvenile population (Connor et al. 2013), although current populations are far below historical levels. In Lower Granite Reservoir, both Zimmerman (1999) and Naughton et al. (2004) showed that fish can comprise a large portion of smallmouth bass diets. Considering that subyearlings probably now make up a larger portion of the forage fish population, it is plausible they should make up a large portion of smallmouth diets. Second, migrating subyearlings delay downstream movement in the transition zones of the Clearwater River and Snake River for varying lengths of time (Tiffan et al. 2010) which increases their exposure and vulnerability to predators. Spatial overlap in locations of smallmouth bass and
subyearlings that died during migration provides support for this (Tiffan et al. 2010). Finally, the later outmigration of subyearlings from the Clearwater River results in their presence in Lower Granite Reservoir during the warmest summer months when predation rates of smallmouth bass should be highest. We initiated a study in 2012 to re-examine smallmouth predation on subyearlings in Lower Granite Reservoir. Our objectives were to 1) describe the seasonal variation in smallmouth bass diets during the subyearling rearing and outmigration period, and 2) estimate the abundance of smallmouth and quantify their consumption of subyearlings. This report primarily summarizes findings from 2013 although some data from 2014 was included to establish a relationship between electrofishing catch-per-unit-effort and smallmouth bass abundance.

STUDY AREA

We conducted our study from April to September, 2013, in the upper portion of Lower Granite Reservoir on the Snake River (Figure 1). We chose this portion of the reservoir because subyearling rearing is common there and it is also an area where some fish delay their seaward migration, potentially increasing their vulnerability to predation (Tiffan et al. 2010; Tiffan and Connor 2012). We divided the study area into two sections. The first included the Snake River from its confluence with the Clearwater River upriver 10.5 km to Asotin, Washington (river kilometer [rkm] 224 to 234). We refer to this section as the Snake River transition zone (SRTZ) because the river transitions from free-flowing at Asotin to being impounded at the confluence. The SRTZ section is analogous to the Snake River Arm section in Naughton et al. (2004). The second section included the Snake River from the Port of Wilma (rkm 217) upstream to the confluence of the Snake and Clearwater rivers (rkm 224). We refer to this section as the confluence (CON).

We varied the duration of our sampling in each river section to coincide with the presence of subyearlings. Subyearlings disperse into the SRTZ from upstream spawning areas and hatchery release sites and are present in this area from April through late June (Connor et al. 2002). By July, water temperatures exceed 20°C and subyearlings have emigrated downstream below the Clearwater River. Because of later emergence, subyearlings produced in the Clearwater River are migrating through the CON section from late May through early September (Tiffan et al. 2010). Summer releases of cool water from Dworshak Reservoir maintain water temperatures in the Clearwater River around 12°C. Subyearlings originating from the Snake and Clearwater rivers are present in the CON from April through early September (Tiffan et al. 2010; Tiffan and Connor 2012).
Figure 1. Map of the two study sections of Lower Granite Reservoir that were sampled for smallmouth bass diet and salmonid consumption in 2013 (CON, confluence; SRTZ, Snake River Transition Zone; rkm, river kilometer).
METHODS

Smallmouth bass collections

We collected smallmouth bass in each section using boat electrofishing and angling. We began sampling with electrofishing in the spring until water temperatures exceeded our ESA permit restriction of 18°C. Once this temperature was met we switched to angling.

Both study sections were stratified into two habitat types: riprap and non-riprap. We electrofished two randomly chosen sites (around 500-800 m in length) per habitat type in each section biweekly from 29 April to 24 June. Sites were randomly chosen for the population of starting locations (i.e., 0.1 km intervals). These sites were fixed for the duration of electrofishing. On some occasions, additional randomly chosen sites were electrofished in each habitat to increase our sample size. Once water temperatures exceeded 18°C we sampled each habitat triweekly by angling from 8 July to 9 September. Angling was only conducted once in the SRTZ during the week of 8 July because we assumed water temperatures were too warm for the presence of juvenile salmonids.

All electrofishing transects were sampled from sunset to midnight except in some instances when recapture sampling was conducted (see below). Electrofishing output was 400 V DC with 60 pulses per second at 2-4 amps. Smallmouth bass were collected by one to two dipnetters. The time and distance sampled was recorded for each transect. Angling was conducted during daytime hours by 2-4 people on 1-2 boats. During each sampling week, the shorelines of the entire section were trolled with 3 to 4 rods. Additional random locations were angled for about 20 minutes each.

All captured smallmouth bass were placed in an aerated live well supplied with recirculating water and held no longer than 60 minutes. All fish >150 mm TL were measured and then tagged with a unique Floy tag. Five bass per site were weighed (W, to nearest 10 g) and pooled with data collected from 2012 to develop a regression (Wt = 0.000008TL^{3.09}) to estimate the remaining bass weights from TL.

At each sampling site, we collected stomach contents from up to 30 randomly selected smallmouth bass using a modified non-lethal lavage (Seaburg 1957). The lavage instrument consisted of a ¼” 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 425µm sieve and preserved in 90% ethanol.
Smallmouth bass abundance

We calculated catch-per-unit-effort (CPUE) for each individual site electrofished and angled by dividing the total number of bass captured by the number of minutes sampled. We also computed a distance-based CPUE by dividing total bass captured by shoreline distance sampled (m) for sites that were electrofished in both 2013 and 2014. These CPUEs were used to develop a relationship (a catchability coefficient) between CPUE and abundance estimates derived from mark-recapture models for each habitat type (riprap and non-riprap). The relationship was used to derive weekly abundance estimates from electrofishing CPUE. This was necessary as many of our tagged fish were removed from our study area during sampling by another agency which precluded absolute abundance estimation in some sampling weeks.

Recapture sampling was conducted throughout the season 1-2 times at each fixed site. Recapture sampling occurred at night 2-3 days after initial tagging and stomach collection sampling. We calculated the Chapman estimator of the Petersen index (Seber 1982):

\[
\hat{N} = \frac{(n_1+1)(n_2+1)}{(R+1)} - 1,
\]

where \(n_1\) = number of bass caught and marked in the first sampling period, \(n_2\) = number of bass caught in the second sampling period, and \(R\) = the number of recaptured bass in the second sampling period. The abundance estimates for each event were then divided by the length of the site (m) to determine absolute density of bass (fish/m) because sample sites were of unequal length. A significant relationship between CPUE (based on distance) and absolute abundance (fish/m) was observed for both habitats (riprap: \(P = 0.002\); non-riprap: \(P = 0.017\); Figure 2). We applied this regression to all individual electrofishing transects in 2013. We calculated the mean abundance (fish/m) for each habitat type and week and multiplied it by the total distance of riprap (SRTZ: 6,535 m; CON: 6,790 m) and non-riprap (SRTZ: 12,244 m; CON: 7,925 m) shorelines in each section to derive a total abundance estimate. These methods were only used to derive abundance estimates until mid-June when electrofishing was ended due to high water temperatures.

Diet analysis

Smallmouth bass diet items were identified to the lowest practical taxon in the laboratory and were placed into four groups: insects, crustaceans, fish, and other. All diet items were then enumerated, blotted for 30 s, and weighed (± 0.001 g). All insects were identified to order and unidentifiable insect parts were not enumerated, but were weighed together as a group. Crustaceans were generally identified to order and where possible to species. Prey that could not
Figure 2. Relationship between electrofishing catch per unit effort (CPUE) and absolute abundance estimated from mark-recapture of smallmouth bass for two habitat types (riprap and non-riprap) in the SRTZ and CON sections of the Snake River.

be assigned to a group were classified as “other” and often consisted of vegetation, rocks, and worms. Ingested fish were identified to the lowest possible taxon (usually species) using diagnostic bones (i.e., dentary, cleithrum, opercle; Parrish 2006). Fish remains were soaked in warm water to soften muscle tissue which was then scraped from the bones. Bones were measured with an ocular micrometer mounted in a dissecting scope. We back-calculated fork length at ingestion for individual salmonid and other prey fish consumed using species-specific bone-length regressions from the literature (Hansel et al. 1988) or to standard length (SL) with regressions developed by this study (Table 1). We used additional regressions to calculate FL from SL, nape to tail lengths, 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.
Table 1. Linear regressions for predicting various measures of juvenile Chinook salmon length based on measurements of diagnostic bones. Regression model take the form of $y=a+bx$, where $y$ is the fish length (mm) to be estimated, $a$ is the intercept, $b$ is the slope, and $x$ is the measure of the diagnostic bone (mm).

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<th>$a$</th>
<th>$b$</th>
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<td>6.984</td>
<td>0.95</td>
</tr>
<tr>
<td>Dentary</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fork length</td>
<td>30</td>
<td>14.823</td>
<td>7.819</td>
<td>0.83</td>
</tr>
<tr>
<td>Standard length</td>
<td>96</td>
<td>13.291</td>
<td>7.499</td>
<td>0.80</td>
</tr>
<tr>
<td>Opercle</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fork length</td>
<td>12</td>
<td>9.844</td>
<td>10.888</td>
<td>0.89</td>
</tr>
<tr>
<td>Standard length</td>
<td>29</td>
<td>10.485</td>
<td>9.884</td>
<td>0.80</td>
</tr>
</tbody>
</table>

The diet composition of smallmouth bass was examined in each habitat of each section on a weekly basis. We determined the frequency of occurrence (number of samples with specific prey/number of stomachs examined) and percent diet composition of different prey based on non-empty stomachs only. We also calculated the maximum relative length of prey fish consumed by smallmouth bass (prey fish FL/bass TL * 100) as a measure of prey vulnerability.

Consumption

We used a series of regressions to estimate the daily consumption of juvenile salmonids by smallmouth bass (≥150 mm) for each habitat in each river section. Consumption rate ($C$; number of salmonids consumed/bass/day) was calculated as:

$$C = n/N,$$  \hspace{1cm} (2)

where $n$ is the number of salmonids consumed within 24 hours of capture, and $N$ is the total number of bass stomachs examined (including stomachs that were empty; Naughton et al. 2004). First, we calculated the original weight of each prey fish at ingestion ($WI$) for each bass stomach sample that contained at least one salmonid by using length-weight regressions (Vigg et al. 1991; Parrish et al. 2006) with the back-calculated length at ingestion (described above). Next, we
calculated meal weight \( MW \) using an equation similar to Vigg et al. (1991) for individual bass that had prey fish in their stomach where the digested weight was within 90% of \( WI (WI_{90}) \):

\[
MW = \sum_{i=1}^{np} WI_{90} + O ,
\]

where \( np \) = the number of prey fish in the stomach of an individual bass (that were <90% digested) and \( O \) is the digested weight of all other prey items (mainly insects and crustaceans) in the sample. We also included all digested weights of prey fish that were not within 90% of original weight in the calculation of \( E \) because meal weight has an impact on evacuation rates (Rogers and Burley 1991). We used 90% digestion (after Rogers and Burley 1991) because indigestible parts could remain in the gut of fish for a long time. Next, we input \( MW \) into an evacuation model developed for smallmouth bass digestion rates of salmonids by Rogers and Burley (1991):

\[
E = MW[1 - \exp(-0.005tMW^{-0.29}e^{0.15T_0^{0.23}})]^{1.95} ,
\]

where \( T \) is temperature (°C; measured at time of sample collection), \( W \) is bass weight (g; also taken at time of sample collection), and \( t \) is hours (set to 24). If the amount evacuated \( (E) \) was less than the total digested weight of the meal then the salmonids were included in the calculation of daily consumption rate \((n \) in equation 2).

We estimated the total loss of juvenile salmonids to predation by smallmouth bass using an equation similar to Rieman et al. (1991):

\[
L_{ths} = \tilde{N}_{ths}C_{ths}D_t
\]

where \( L_{ths} \) is the loss of salmonids during sampling interval \( i \) in habitat \( h \) and in study section \( s \), \( \tilde{N}_{ths} \) is the biweekly (or triweekly) abundance estimate of smallmouth bass (from equation 1) for each habitat \( h \) and section \( s \), \( C_{ths} \) is the consumption rate during sampling interval \( i \) in habitat \( h \) for section \( s \) (equation 2), and \( D_t \) is the number of days in sampling interval \( i \) (14 or 21). Since we only derived estimates of abundance for the first five sampling intervals, we assumed constant abundance (using the last estimate) for the remainder of the triweekly samplings through the summer. This only impacted loss estimates for the CON section during the weeks of 8 July and 29 July and the SRTZ section during the week of 8 July because consumption rates were zero during the weeks of 19 August and 9 September.
RESULTS

Abundance

Relative abundance.—We sampled a total of 114 sites, of which 47 were sampled with electrofishing and 67 were angled (Tables 2 and 3). A total of 1,194 minutes were expended electrofishing to collect 1,827 bass and 2,117 minutes were expended angling to collect 715 bass. Only minimal effort was expended angling during early spring when electrofishing was used because angling CPUE’s were very low. Angling CPUE increased into the summer in the CON section. Overall, both angling and electrofishing CPUE’s were higher for both habitats in the CON section than in the SRTZ section.

Absolute abundance.—Abundance estimates of smallmouth bass ≥150mm TL, predicted from CPUE relationships, showed an increasing trend through spring for both habitats in each river section (Table 4). Abundances in the SRTZ ranged from 3,292 (314 fish/km) to 8,796 (838 fish/m), and in the CON from 4,043 (546 fish/km) to 11,321 (1,530 fish/km). Densities (fish/m) of bass in the SRTZ were very similar between non-riprap and riprap habitat for most weeks; however, total abundances were higher in the non-riprap because of the greater amount of that habitat. In the CON section, abundance and densities were higher in riprap habitat for all weeks except 24 June.

Diet

We captured 1,782 smallmouth bass for dietary analysis from April through September. Prey items were present in the stomachs of 1,522 fish. Smallmouth bass were similar in size between habitats and study sections. Weekly mean sizes were between 184 and 256 mm TL (Table 5). Over all sections and weeks, bass averaged 204 mm and ranged from 150 to 526 mm TL. Common prey in smallmouth bass stomachs (based on frequency of occurrence) varied seasonally. In both habitats of the SRTZ, crustaceans were the most frequent prey in late April to mid-May, followed by non-salmonid fishes in late May to mid-June, and insects in late June (Table 6). In both habitats of the CON, crustaceans were the most frequent diet item in all weeks with the following exceptions. During the week of 13 May, non-salmonid fishes were most frequent in the diet in non-riprap, and during the week of 8 July insects were predominant. In riprap habitat, insects were most commonly consumed during the week of 24 June (Table 7).

The frequency of occurrence of salmonids in smallmouth bass diets peaked in late May in the SRTZ and in mid-June in the CON. In both sections, salmonids occurred in a higher percentage of stomachs in the non-riprap habitat (up to 47% in SRTZ and 32% in CON). Salmonids were found in stomachs during all weeks in the SRTZ and we assumed by 8 July most migratory salmonids moved downriver to cooler water temperatures. In the CON section, we did not find any salmonids in smallmouth bass diets after the week of 29 July.
Table 2. Seasonal catch-per-unit-effort of smallmouth bass ≥150mm TL collected by boat electrofishing and angling in riprap and non-riprap habitats of the Snake River Transition Zone in Lower Granite Reservoir during 2013.

<table>
<thead>
<tr>
<th>Week beginning</th>
<th>Method</th>
<th>Number of sites</th>
<th>Effort (minutes)</th>
<th>Number captured</th>
<th>Number per minute</th>
</tr>
</thead>
<tbody>
<tr>
<td>29 Apr</td>
<td>Electrofishing</td>
<td>3</td>
<td>43</td>
<td>13</td>
<td>0.30</td>
</tr>
<tr>
<td>29 Apr</td>
<td>Angling</td>
<td>1</td>
<td>30</td>
<td>1</td>
<td>0.03</td>
</tr>
<tr>
<td>13 May</td>
<td>Electrofishing</td>
<td>2</td>
<td>42</td>
<td>66</td>
<td>1.57</td>
</tr>
<tr>
<td>13 May</td>
<td>Angling</td>
<td>1</td>
<td>22</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>27 May</td>
<td>Electrofishing</td>
<td>3</td>
<td>95</td>
<td>61</td>
<td>0.64</td>
</tr>
<tr>
<td>10 Jun</td>
<td>Electrofishing</td>
<td>2</td>
<td>60</td>
<td>52</td>
<td>0.87</td>
</tr>
<tr>
<td>10 Jun</td>
<td>Angling</td>
<td>2</td>
<td>102</td>
<td>7</td>
<td>0.07</td>
</tr>
<tr>
<td>24 Jun</td>
<td>Electrofishing</td>
<td>1</td>
<td>39</td>
<td>17</td>
<td>0.44</td>
</tr>
<tr>
<td>24 Jun</td>
<td>Angling</td>
<td>2</td>
<td>126</td>
<td>2</td>
<td>0.02</td>
</tr>
<tr>
<td>8 Jul</td>
<td>Angling</td>
<td>3</td>
<td>133</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>All</td>
<td>Electrofishing</td>
<td>11</td>
<td>279</td>
<td>209</td>
<td>0.75</td>
</tr>
<tr>
<td>All</td>
<td>Angling</td>
<td>9</td>
<td>413</td>
<td>11</td>
<td>0.03</td>
</tr>
</tbody>
</table>

**Riprap**

<table>
<thead>
<tr>
<th>Week beginning</th>
<th>Method</th>
<th>Number of sites</th>
<th>Effort (minutes)</th>
<th>Number captured</th>
<th>Number per minute</th>
</tr>
</thead>
<tbody>
<tr>
<td>29 Apr</td>
<td>Electrofishing</td>
<td>2</td>
<td>28</td>
<td>19</td>
<td>0.68</td>
</tr>
<tr>
<td>29 Apr</td>
<td>Angling</td>
<td>1</td>
<td>33</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>13 May</td>
<td>Electrofishing</td>
<td>3</td>
<td>45</td>
<td>151</td>
<td>3.36</td>
</tr>
<tr>
<td>13 May</td>
<td>Angling</td>
<td>1</td>
<td>25</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>27 May</td>
<td>Electrofishing</td>
<td>3</td>
<td>82</td>
<td>167</td>
<td>2.04</td>
</tr>
<tr>
<td>10 Jun</td>
<td>Electrofishing</td>
<td>2</td>
<td>65</td>
<td>146</td>
<td>2.25</td>
</tr>
<tr>
<td>10 Jun</td>
<td>Angling</td>
<td>2</td>
<td>116</td>
<td>23</td>
<td>0.20</td>
</tr>
<tr>
<td>24 Jun</td>
<td>Electrofishing</td>
<td>1</td>
<td>30</td>
<td>30</td>
<td>1.00</td>
</tr>
<tr>
<td>24 Jun</td>
<td>Angling</td>
<td>3</td>
<td>179</td>
<td>10</td>
<td>0.06</td>
</tr>
<tr>
<td>8 Jul</td>
<td>Angling</td>
<td>2</td>
<td>79</td>
<td>10</td>
<td>0.13</td>
</tr>
<tr>
<td>All</td>
<td>Electrofishing</td>
<td>11</td>
<td>250</td>
<td>513</td>
<td>2.05</td>
</tr>
<tr>
<td>All</td>
<td>Angling</td>
<td>9</td>
<td>432</td>
<td>43</td>
<td>0.10</td>
</tr>
</tbody>
</table>
Table 3. Seasonal catch-per-unit-effort of smallmouth bass ≥150mm TL collected by boat electrofishing and angling in riprap and non-riprap habitats of the Confluence section in Lower Granite Reservoir during 2013.

<table>
<thead>
<tr>
<th>Week beginning</th>
<th>Method</th>
<th>Number of sites</th>
<th>Effort (minutes)</th>
<th>Number captured</th>
<th>Number per minute</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-riprap</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>29 Apr</td>
<td>Electrofishing</td>
<td>2</td>
<td>29</td>
<td>2</td>
<td>0.07</td>
</tr>
<tr>
<td>29 Apr</td>
<td>Angling</td>
<td>1</td>
<td>26</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>13 May</td>
<td>Electrofishing</td>
<td>2</td>
<td>32</td>
<td>27</td>
<td>0.84</td>
</tr>
<tr>
<td>27 May</td>
<td>Electrofishing</td>
<td>2</td>
<td>45</td>
<td>27</td>
<td>0.60</td>
</tr>
<tr>
<td>27 May</td>
<td>Angling</td>
<td>1</td>
<td>26</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>10 Jun</td>
<td>Electrofishing</td>
<td>4</td>
<td>112</td>
<td>83</td>
<td>0.74</td>
</tr>
<tr>
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<td>Electrofishing</td>
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<td>37</td>
<td>73</td>
<td>1.97</td>
</tr>
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<td>Angling</td>
<td>1</td>
<td>32</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>8 Jul</td>
<td>Angling</td>
<td>8</td>
<td>330</td>
<td>84</td>
<td>0.25</td>
</tr>
<tr>
<td>29 Jul</td>
<td>Angling</td>
<td>3</td>
<td>229</td>
<td>71</td>
<td>0.31</td>
</tr>
<tr>
<td>19 Aug</td>
<td>Angling</td>
<td>3</td>
<td>243</td>
<td>66</td>
<td>0.27</td>
</tr>
<tr>
<td>9 Sep</td>
<td>Angling</td>
<td>3</td>
<td>250</td>
<td>62</td>
<td>0.25</td>
</tr>
<tr>
<td>All</td>
<td>Electrofishing</td>
<td>11</td>
<td>255</td>
<td>212</td>
<td>0.83</td>
</tr>
<tr>
<td>All</td>
<td>Angling</td>
<td>20</td>
<td>1136</td>
<td>283</td>
<td>0.25</td>
</tr>
<tr>
<td>Riprap</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>29 Apr</td>
<td>Electrofishing</td>
<td>4</td>
<td>93</td>
<td>163</td>
<td>1.75</td>
</tr>
<tr>
<td>29 Apr</td>
<td>Angling</td>
<td>1</td>
<td>18</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>13 May</td>
<td>Electrofishing</td>
<td>3</td>
<td>75</td>
<td>162</td>
<td>2.16</td>
</tr>
<tr>
<td>13 May</td>
<td>Angling</td>
<td>1</td>
<td>23</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>27 May</td>
<td>Electrofishing</td>
<td>3</td>
<td>112</td>
<td>259</td>
<td>2.32</td>
</tr>
<tr>
<td>27 May</td>
<td>Angling</td>
<td>1</td>
<td>29</td>
<td>1</td>
<td>0.03</td>
</tr>
<tr>
<td>10 Jun</td>
<td>Electrofishing</td>
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<td>101</td>
<td>248</td>
<td>2.46</td>
</tr>
<tr>
<td>24 Jun</td>
<td>Electrofishing</td>
<td>1</td>
<td>28</td>
<td>61</td>
<td>2.18</td>
</tr>
<tr>
<td>24 Jun</td>
<td>Angling</td>
<td>2</td>
<td>127</td>
<td>28</td>
<td>0.22</td>
</tr>
<tr>
<td>8 Jul</td>
<td>Angling</td>
<td>11</td>
<td>473</td>
<td>88</td>
<td>0.19</td>
</tr>
<tr>
<td>29 Jul</td>
<td>Angling</td>
<td>7</td>
<td>567</td>
<td>161</td>
<td>0.28</td>
</tr>
<tr>
<td>19 Aug</td>
<td>Angling</td>
<td>3</td>
<td>244</td>
<td>50</td>
<td>0.20</td>
</tr>
<tr>
<td>9 Sep</td>
<td>Angling</td>
<td>3</td>
<td>204</td>
<td>50</td>
<td>0.25</td>
</tr>
<tr>
<td>All</td>
<td>Electrofishing</td>
<td>14</td>
<td>410</td>
<td>893</td>
<td>2.18</td>
</tr>
<tr>
<td>All</td>
<td>Angling</td>
<td>29</td>
<td>1685</td>
<td>378</td>
<td>0.22</td>
</tr>
</tbody>
</table>
Table 4. Abundance estimates of smallmouth bass ≥150 mm TL in riprap and non-riprap habitat in the Snake River transition zone (SRTZ) and confluence (CON) study sections in Lower Granite Reservoir in 2013.

<table>
<thead>
<tr>
<th>Section</th>
<th>Week</th>
<th>Riprap abundance (fish/m of shoreline)</th>
<th>Non-riprap abundance (fish/m of shoreline)</th>
<th>Total abundance (fish/river km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SRTZ</td>
<td>30-April</td>
<td>930 (0.142)</td>
<td>2,362 (0.193)</td>
<td>3,292 (314)</td>
</tr>
<tr>
<td>SRTZ</td>
<td>13-May</td>
<td>2,704 (0.414)</td>
<td>6,091 (0.497)</td>
<td>8,796 (838)</td>
</tr>
<tr>
<td>SRTZ</td>
<td>28-May</td>
<td>2,820 (0.431)</td>
<td>4,063 (0.332)</td>
<td>6,883 (656)</td>
</tr>
<tr>
<td>SRTZ</td>
<td>10-June</td>
<td>3,501 (0.536)</td>
<td>4,697 (0.384)</td>
<td>8,199 (781)</td>
</tr>
<tr>
<td>SRTZ</td>
<td>24-June</td>
<td>1,481 (0.227)</td>
<td>3,459 (0.283)</td>
<td>4,940 (471)</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td></td>
<td><strong>2,287 (0.350)</strong></td>
<td><strong>4,134 (0.338)</strong></td>
<td><strong>6,422 (612)</strong></td>
</tr>
<tr>
<td>CON</td>
<td>30-April</td>
<td>2,787 (0.410)</td>
<td>1,256 (0.158)</td>
<td>4,043 (546)</td>
</tr>
<tr>
<td>CON</td>
<td>13-May</td>
<td>3,299 (0.486)</td>
<td>2,274 (0.287)</td>
<td>5,573 (753)</td>
</tr>
<tr>
<td>CON</td>
<td>28-May</td>
<td>5,229 (0.770)</td>
<td>2,293 (0.289)</td>
<td>7,522 (1,017)</td>
</tr>
<tr>
<td>CON</td>
<td>10-June</td>
<td>5,430 (0.800)</td>
<td>2,289 (0.377)</td>
<td>8,419 (1,138)</td>
</tr>
<tr>
<td>CON</td>
<td>24-June</td>
<td>3,948 (0.581)</td>
<td>7,373 (0.930)</td>
<td>11,321 (1,530)</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td></td>
<td><strong>4,139 (0.609)</strong></td>
<td><strong>3,097 (0.388)</strong></td>
<td><strong>7,376 (997)</strong></td>
</tr>
</tbody>
</table>
Table 5. Seasonal lengths of smallmouth bass collected in non-riprap and rip rap habitat for diet analysis from study sections in Lower Granite Reservoir in 2013.

<table>
<thead>
<tr>
<th>Week Beginning</th>
<th>SRTZ</th>
<th>CON</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>Mean</td>
</tr>
<tr>
<td>Non-riprap</td>
<td></td>
<td></td>
</tr>
<tr>
<td>29 Apr</td>
<td>14</td>
<td>218</td>
</tr>
<tr>
<td>13 May</td>
<td>66</td>
<td>220</td>
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<tr>
<td>27 May</td>
<td>58</td>
<td>256</td>
</tr>
<tr>
<td>10 Jun</td>
<td>59</td>
<td>248</td>
</tr>
<tr>
<td>24 Jun</td>
<td>19</td>
<td>203</td>
</tr>
<tr>
<td>08 Jul</td>
<td>1</td>
<td>162</td>
</tr>
<tr>
<td>29 Jul</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>19 Aug</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>09 Sep</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>All</td>
<td>217</td>
<td>235</td>
</tr>
<tr>
<td>Riprap</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All</td>
<td>19</td>
<td>224</td>
</tr>
<tr>
<td>29 Apr</td>
<td>151</td>
<td>204</td>
</tr>
<tr>
<td>13 May</td>
<td>166</td>
<td>197</td>
</tr>
<tr>
<td>27 May</td>
<td>169</td>
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<tr>
<td>10 Jun</td>
<td>40</td>
<td>196</td>
</tr>
<tr>
<td>08 Jul</td>
<td>2</td>
<td>194</td>
</tr>
<tr>
<td>29 Jul</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>19 Aug</td>
<td>--</td>
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Table 6. Seasonal variation in diet composition (percent frequency of occurrence of non-empty stomachs) of smallmouth bass in the SRTZ section of Lower Granite Reservoir in 2013. Ns indicate the number of smallmouth bass with empty and non-empty stomachs.

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<th>Salmonid</th>
<th>Other fishes</th>
<th>Sand roller&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Neomysis mercedis&lt;sup&gt;b&lt;/sup&gt;</th>
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<sup>a</sup>Also represented in Other fishes  
<sup>b</sup>Also represented in Crustaceans
Table 7. Seasonal variation in diet composition (percent frequency of occurrence of non-empty stomachs) of smallmouth bass in the CON section of Lower Granite Reservoir in 2013. Ns indicate the number of smallmouth bass with empty and non-empty stomachs.

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<th>N (empty)</th>
<th>N (non-empty)</th>
<th>Insects</th>
<th>Crustaceans</th>
<th>Salmonid</th>
<th>Other fishes</th>
<th>Sand roller&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Neomysis mercedis&lt;sup&gt;b&lt;/sup&gt;</th>
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<sup>a</sup>Also represented in Other fishes
<sup>b</sup>Also represented in Crustaceans
Diet composition based on percent weight showed a different outcome than the frequency of occurrence data (Figures 3 and 4). In both habitats of the SRTZ, non-salmonid fishes were the predominant prey item in all weeks except during the week of 24 June when salmonids predominated in non-riprap and during the week of 29 April when crustaceans predominated in riprap (Table 8). Non-salmonid fishes were also the most predominant prey by weight in all but the week of 19 August when crustaceans were the main prey item in non-riprap habitat of the CON section (Table 9). The diet of smallmouth bass collected in riprap habitat of the CON was predominated by crustaceans for all but May and mid-June, when non-salmonid fish were predominant. Salmonids composed up to 50% diet by weight in the SRTZ non-riprap and up to 43% by weight in the CON non-riprap.

Most of the salmonids consumed were Chinook salmon (83% by count, 93-95% by weight) and only a small percent (7% by count, and <2% by weight) were mountain whitefish Prosopium williamsoni (Table 10). The predicted lengths of the Chinook salmon ranged in size from 32 to 123 mm FL. The remaining 16% (by count) were unidentifiable salmonid species because some diagnostic bones were not present, damaged, or difficult to identify. Mountain whitefish were only found in stomachs from mid-May to mid-June and ranged in size from 35-64 mm FL. After apportioning the unidentifiable salmonids to Chinook or mountain whitefish based on weekly percentages, we estimate that 92% (by count) were Chinook salmon. From length frequency distributions of the predicted lengths at ingestion of the Chinook salmon, we determined that 97% were subyearlings, with only a few yearlings being consumed in late April (Figure 5). We assumed the Chinook salmon that represented the left-skewed modes in the size distributions in early and late May were probably hatchery fish based on their size.

Smallmouth bass consumed a total of 12 different non-salmonid fish species, but the most predominant fish (by weight and count) was sand rollers Percopsis transmontana (Table 10). Sand rollers were the most predominant prey item for most weeks in both habitats of the SRTZ and the most predominant prey in both CON habitats until mid-July. The size distribution of sand rollers ranged from 20-110 mm FL (Figure 6). The smallest bass that contained a salmonid was 150 mm. The maximum size of vulnerability (in FL) of prey fish during 2013 was 56% (mean= 29%) of the total length of bass. We calculated the size of vulnerability of prey fish for 25-mm bass size groups and found a decreasing trend with increasing bass size (Figure 7).

Consumption and loss

Total loss of salmonids to smallmouth bass predation within our study area in 2013 was estimated to be 168,380 individuals, of which 154,952 were Chinook salmon (Table 11). Of the Chinook salmon consumed, we estimate that 150,823 (97%) were subyearlings based on length-
Figure 3. Seasonal variation in diet composition (percent weight based on non-empty stomachs) of smallmouth bass in the Snake River Transition Zone section in non-riprap (top panel) and riprap (bottom panel) habitats in 2013.
Figure 4. Seasonal variation in diet composition (percent weight based on non-empty stomachs) of smallmouth bass in the Confluence section in non-riprap (top panel) and riprap (bottom panel) habitats in 2013.
Table 8. Seasonal variation in diet composition (percent weight based on non-empty stomachs) of smallmouth bass in non-riprap and riprap habitats of the SRTZ section in the Snake River during 2013. Ns indicate the number of smallmouth bass with empty and non-empty stomachs.

<table>
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<th>Week beginning</th>
<th>N (empty)</th>
<th>N (non-empty)</th>
<th>Insects</th>
<th>Crustaceans</th>
<th>Salmonid</th>
<th>Other fish</th>
<th>Unidentified fish</th>
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Table 9. Seasonal variation in diet composition (percent weight based on non-empty stomachs) of smallmouth bass in non-riprap and riprap habitats of the CON section in the Snake River during 2013. Ns indicate the number of smallmouth bass with empty and non-empty stomachs.

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<th>Other fish</th>
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Table 10. Summary of prey items obtained from all smallmouth bass stomachs sampled in riprap and non-riprap habitat of Lower Granite Reservoir in 2013.

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<th>Total mass (g) Non-riprap</th>
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<td>3</td>
<td>0.5</td>
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<td>Crayfish</td>
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<td>76</td>
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<td>Copepoda</td>
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<td>Unknown</td>
<td>8.9</td>
<td>7</td>
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<td>Other fish</td>
<td>Sand roller</td>
<td>398.7</td>
<td>87</td>
<td>351.1</td>
<td>90</td>
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<td>Sculpin spp.</td>
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<td>5.8</td>
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<tr>
<td></td>
<td>Sucker spp.</td>
<td>20.4</td>
<td>4</td>
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<td>Chiselmouth</td>
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<td>Northern pikeminnow</td>
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<td>&lt;1</td>
<td>1.7</td>
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<td>Black crappie</td>
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<tr>
<td></td>
<td>Peamouth</td>
<td>--</td>
<td>--</td>
<td>4.8</td>
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<tr>
<td>Unidentifiable fish</td>
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<td>25.8</td>
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<td>Eggs</td>
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<td>Bivalvia &lt;0.1</td>
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<td>12</td>
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<td>Unknown</td>
<td>1.9</td>
<td>69</td>
<td>0.6</td>
<td>43</td>
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Figure 5. Size distribution (relative percent) of Chinook salmon consumed by smallmouth bass in Lower Granite Reservoir, 2013.
Figure 6. Size distribution (relative percent) of sand rollers consumed by smallmouth bass in Lower Granite Reservoir, April-September 2013.
Figure 7. Maximum and mean relative length of prey fish (prey fish length/bass length*100) for 25 mm size groups of smallmouth bass sampled in Lower Granite Reservoir, 2013.
Table 11. Estimated losses of juvenile salmonids and smallmouth bass consumption rates (C: salmonids eaten/bass/day) in two sections of Lower Granite Reservoir during 2013.

<table>
<thead>
<tr>
<th>Week</th>
<th>Non-riprap Loss</th>
<th>C</th>
<th>Riprap Loss</th>
<th>C</th>
<th>Combined Total Loss</th>
</tr>
</thead>
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<td><strong>Snake River Transition Zone</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>29 Apr</td>
<td>4,724</td>
<td>0.143</td>
<td>685</td>
<td>0.053</td>
<td>5,409</td>
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<tr>
<td>13 May</td>
<td>7,753</td>
<td>0.091</td>
<td>4,684</td>
<td>0.124</td>
<td>12,437</td>
</tr>
<tr>
<td>27 May</td>
<td>32,286</td>
<td>0.568</td>
<td>8,581</td>
<td>0.217</td>
<td>40,867</td>
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<td>10 Jun</td>
<td>18,268</td>
<td>0.278</td>
<td>2,451</td>
<td>0.050</td>
<td>20,719</td>
</tr>
<tr>
<td>24 Jun</td>
<td>10,195</td>
<td>0.211</td>
<td>691</td>
<td>0.033</td>
<td>10,886</td>
</tr>
<tr>
<td>08 Jul</td>
<td>0</td>
<td>0.000</td>
<td>0</td>
<td>0.000</td>
<td>0</td>
</tr>
<tr>
<td>All weeks</td>
<td>73,226</td>
<td></td>
<td>17,092</td>
<td></td>
<td>90,318</td>
</tr>
<tr>
<td><strong>Confluence</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>29 Apr</td>
<td>0</td>
<td>0.000</td>
<td>1,197</td>
<td>0.031</td>
<td>1,197</td>
</tr>
<tr>
<td>13 May</td>
<td>3,538</td>
<td>0.111</td>
<td>1,082</td>
<td>0.023</td>
<td>4,620</td>
</tr>
<tr>
<td>27 May</td>
<td>3,567</td>
<td>0.111</td>
<td>5,904</td>
<td>0.081</td>
<td>9,471</td>
</tr>
<tr>
<td>10 Jun</td>
<td>14,531</td>
<td>0.347</td>
<td>16,289</td>
<td>0.214</td>
<td>30,820</td>
</tr>
<tr>
<td>24 Jun</td>
<td>20,644</td>
<td>0.200</td>
<td>3,747</td>
<td>0.068</td>
<td>24,391</td>
</tr>
<tr>
<td>08 Jul</td>
<td>3,601</td>
<td>0.023</td>
<td>2,926</td>
<td>0.035</td>
<td>6,527</td>
</tr>
<tr>
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<td>1,036</td>
<td>0.013</td>
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<td>19 Aug</td>
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<td>0.000</td>
<td>0</td>
<td>0.000</td>
<td>0</td>
</tr>
<tr>
<td>09 Sep</td>
<td>0</td>
<td>0.000</td>
<td>0</td>
<td>0.000</td>
<td>0</td>
</tr>
<tr>
<td>All weeks</td>
<td>45,881</td>
<td></td>
<td>32,181</td>
<td></td>
<td>78,062</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>119,107</td>
<td></td>
<td>49,273</td>
<td></td>
<td>168,380</td>
</tr>
</tbody>
</table>
frequency distributions. The total annual loss was higher in the SRTZ section (90,318 fish) than in the CON section (78,062 fish) in spite of the CON section being sampled longer (into early September; Table 11). In the SRTZ, 82% of the total loss occurred in non-riprap habitat whereas in the CON only 59% of the loss occurred in non-riprap. This is because bass densities (Table 4) and consumption rates (Table 11) were higher in non-riprap habitats in the SRTZ section than in the CON section.

DISCUSSION

Juvenile salmonids were a major component of smallmouth bass diets at times in 2013, with the majority being subyearling fall Chinook salmon. Most consumption in the SRTZ occurred in late May and early June whereas most consumption in the CON section occurred in early to late June. Substantially more subyearlings were consumed in non-riprap habitats in both sections, which they prefer over riprap (Garland et al. 2002). Salmonids composed up to 43% of the diet by weight in the CON (non-riprap) and 48% in the SRTZ (non-riprap) when peak consumption occurred. Frequencies of occurrence were also high, with up to 47% of the bass sampled in June containing salmonids in the SRTZ. The highest consumption rate (0.57 salmonids/bass/day) occurred in the non-riprap habitat in the SRTZ during the week of 27 May.

Our estimates of salmonid consumption are much higher than those reported by Naughton et al. (2004), who estimated that only 10% of smallmouth bass diets were composed of salmonids in the Snake River arm in 1997. Our estimates are more consistent with Tabor et al. (1993) who found that salmonids composed up to 59% of the diet of smallmouth bass in the upper end of McNary Reservoir in the Columbia River. In 2013, we estimated 168,380 salmon were consumed within our study area, of which 154,952 were Chinook salmon. In the SRTZ alone, we estimated that 90,318 salmonids were consumed, a 13-fold increase from that estimated in 1997 by Naughton et al. (2004). Conversely, the highest weekly abundance estimates of smallmouth bass (≥150 mm) in the SRTZ (838 fish/rkm) were slightly lower than reported by Naughton et al. (2004), who reported 11,877 bass (≥175mm) in the SRTZ (990 fish/rkm). About 20% of our catch throughout the study was composed of bass between 150 to 175 mm which would make our estimates much lower in comparison. The increase in total salmonid loss, but decrease in bass abundance, indicates the increase in salmonid consumption is due to a large increase in daily bass consumption rates (prey/bass/day).

There are several reasons for this increase in daily consumption rates of salmonid by smallmouth bass. First, the run size of subyearlings has increased dramatically since 1996. Hatchery supplementation has directly increased the population via annual releases of juveniles and indirectly as a result of increased production from natural spawners (Connor et al. 2013). Naughton et al. (2004) concluded that the increase in consumption from 1996 to 1997 was due, in part, to the increase in the number of subyearlings that passed Lower Granite Dam during outmigration (1 April to 1 October; 18,066 fish in 1996, 97,985 fish in 1997). In 2013, 749,074
subyearlings were estimated to have passed the dam (DART 2014). Second, river flows were lower in 2013 than in 1996-1997, especially in June when peak consumption occurred (Figure 9). Mean daily discharge in June 2013 was 367.4 kcfs, less than one-half of that in June 1997 (117.8 kcfs). The lower river flows, and less turbid water usually associated with low flows, may provide higher foraging efficiency for smallmouth bass (Sweka and Hartman 2003) and also affect prey selectivity (Carter et al. 2010). Lower velocities in the transitional area between the free-flowing river and reservoir of the Snake River have also been linked to decreased migratory cues for subyearlings, which delay migration and increase predation within these areas (Tiffan et al. 2009). Higher water temperatures, which are usually associated with lower river flows, can increase evacuation rates of smallmouth bass and subsequently increase consumption (Rogers and Burley 1991).

![Snake River flows measured at the Anatone gage for 1996, 1997, and 2013.](image)

Figure 8. Snake River flows measured at the Anatone gage for 1996, 1997, and 2013.
Variation in smallmouth bass abundance and consumption between study sections was influenced by subyearling presence and habitat differences. Subyearlings first encounter the SRTZ as they disperse downstream from upstream production areas. By the end of June, most subyearlings have already left this section because water temperatures typically exceed 22°C (DART 2014). However, the concentration of subyearlings in this section in May and early June increased their vulnerability to predation in spite of smallmouth bass abundance being lower in this section than the CON section. This was due to higher water velocities in the SRTZ (Tiffan et al. 2009). By July and August, consumption of subyearlings in the CON was low because there are fewer subyearlings in the system as many fish from the Snake River have emigrated seaward. Most subyearlings in this section during summer originate from the Clearwater River, where emergence is later than in the Snake River. The CON had a higher bass abundance but lower total salmonid loss. A main difference between the sections was the difference in abundance of bass between the habitat types. The CON had much higher densities of bass in riprap habitat (0.77 fish/m) than in non-riprap habitat (0.29 fish/m) during peak consumption (late May). In contrast, in the SRTZ bass densities were similar between habitats (riprap: 0.414 fish/m, non-riprap: 0.497) during mid-May. The different habitat preferences of subyearlings and smallmouth bass ultimately affect predation loss estimates. Although smallmouth bass densities in riprap habitat were much higher in the CON, subyearlings do not prefer this habitat (Garland et al. 2002). This is supported by higher salmonid loss estimates in non-riprap habitat. It should be noted that bass densities in non-riprap habitat in the CON did spike during the final week (24 June) of sampling with electrofishing while densities dropped in riprap. This may be related to bass moving into non-riprap habitat for spawning, or the high abundance of males guarding nests. We acknowledge that our abundance estimates may have been affected by differential survival between fish that were only Floy tagged and those that were stomach pumped and then Floy tagged.

We found that subyearlings comprised the majority (97%) of the Chinook salmon consumed by smallmouth bass. This equates to a total loss 150,303 subyearlings in 2013. Subyearlings may be more vulnerable to predation in transitional and reservoir habitats because of their small size. We found that smallmouth bass as small as 150 mm contained subyearlings, which suggests that even small bass may pose a predation threat. Fritts and Pearsons (2006) found that 150-199 mm smallmouth bass accounted for 42.9% of the salmonid consumption in the Yakima River and that larger bass could consume a wider size range of salmon. In our study, the maximum relative length of salmonids (salmonid FL/bass TL * 100) consumed by 150-199 mm smallmouth bass was 47.2%. This suggests that subyearling susceptibility to predation based on size alone is very high because of the high abundance of small-sized (<200 mm) bass in Lower Granite Reservoir. Conversely, Anglea (1997) found that smallmouth bass ranging in size from 250-389 mm had the highest salmonid consumption in Lower Granite Reservoir in 1994-1995. Although we did not estimate consumption rates of individual bass size groups (because this decreases sample sizes dramatically), we found that the highest percent frequency
of occurrence of salmonids in bass diets was in the 325-mm bass size group (Figure 9). An accurate estimation of the size distribution of the population would be needed to derive size-specific abundances. Size specific consumption rates could then be used to derive size-specific total loss estimates. Theoretically, there should be more smaller-sized fish unless there was a very poor recruitment year, so impacts from smaller size groups may still be greater regardless of frequencies of occurrence being lower.

Estimates of smallmouth bass abundance had the greatest influence on our total salmonid loss estimates. We believe that our estimates are conservative because studies conducted in the Columbia River have shown that smallmouth bass abundance estimates are negatively biased (Beamesderfer and Rieman 1998). Additionally, CPUE trends from ODFW electrofishing indexing surveys have shown large increases since 1997 (Williams 2014). We initially used an open population Jolly-Seber model to estimate weekly abundances, but found highly significant relationships between closed model mark-recapture events and electrofishing CPUE allowing us to use catch equations. These estimates were less affected by other electrofishing projects conducted by other agencies within the study area. Further effort, however, should be directed towards strengthening the relationships between CPUE and absolute abundance, especially at higher densities. Our weekly abundance estimates were an improvement over single, season-wide estimates because bass abundance changes seasonally due to increasing temperatures and spawning activity. Other factors such as river flows, recruitment, and mortality also affect estimates seasonally. Smallmouth bass abundance in shoreline areas increased seasonally as expected and is consistent with other studies within the Columbia River basin (Zimmerman and Parker 1995; Fritts and Pearsons 2004).

Laboratory factors may also have influenced our estimates of consumption. First, all samples were stored in 90% ethanol which may have affected the length and weight measurements of digested fish. Sockeye salmon *O. nerka* fry preserved in 95% ethanol lost 19.7% of mean fresh weight after 16 days (Shields and Carlson 1996). Weight loss due to ethanol preservation would increase the percent digested calculation and lead to underestimates of consumption because fish would not be included if they were now more than 90% digested. Second, the presence of unidentifiable fish parts in samples presented an analytical complication. They often comprised a large portion of percent diet by weight at times, and may have increased estimates of consumption. Many of the unidentifiable parts that we encountered were digested fish without heads. This limited our ability to identify diet items because the diagnostic bones are located in the fish’s head. In samples containing fish without heads or only bones, the main diagnostic bone present was usually a sculpin cleithrum. There were only a few instances where unidentifiable bones from salmonids were present under these circumstances. This would imply that a greater portion of the unidentifiable fish parts were likely salmonids, or at the least not from sculpin.
In conclusion, smallmouth bass predation on salmonids during our study was highest during June when conditions were conducive for efficient feeding and temporal and spatial overlap of bass and salmonids occurred. Fall Chinook salmon may be particularly vulnerable to predation due to their small size, extended reservoir rearing, and migrating at times when bass abundance and metabolic rates are high. We believe our estimates of consumption and abundance are conservative and further research should be directed towards determining salmonid loss across a range of river flows and water temperatures. In 2013, June flows were lower than they were in 1996 and 1997, when the last predation study was conducted in this area. The increase in subyearling abundance since ESA listing has been identified as a factor contributing to density-dependent changes in growth and timing of reservoir entry (Connor et al. 2013). Early reservoir entry and smaller size may put subyearlings at a higher risk if smallmouth bass abundance and consumption are higher in the reservoir than in the river. Further research is needed to estimate consumption in the riverine sections as well as further downstream in Lower Granite Reservoir where Naughton et al. (2004) found their highest consumption.
REFERENCES


