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Predation on Juvenile Salmonids by Smallmouth Bass in the Lower Granite Reservoir System, Snake River

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Abstract.—We estimated the consumption of juvenile salmon *Oncorhynchus* spp. and steelhead *O. mykiss* by smallmouth bass *Micropterus dolomieu* in the tailrace and forebay of the Lower Granite Dam and compared this consumption with that in the two major river arms of the upper Lower Granite Reservoir, Snake River, Idaho–Washington. We examined over 9,700 smallmouth bass stomachs from April through August during 1996 and 1997. Juvenile salmonids were not a major component of smallmouth bass diets by weight and number at any location in either 1996 or 1997. Of the approximately 8,600 stomach samples containing food items, only 67 had juvenile salmonid remains. Juvenile salmonids accounted for approximately 11% of smallmouth bass diets by weight in the forebay in 1996 and 5% in the Snake and Clearwater river arms in 1997, with smaller proportions at other locations. Crustaceans and nonsalmonid fishes were the dominant prey items by weight at all locations in 1996 and 1997 except for the Snake River arm in 1996, where macroinvertebrates were dominant. Monthly consumption rates (smolts/bass/d) of juvenile salmonids by smallmouth bass were highest in the forebay (0.02) in April 1996 and in the restricted zone of the forebay (0.05) in July 1997. We estimated that approximately 17,500 (1996: 6,728; 1997: 10,809) juvenile salmonids were consumed by smallmouth bass from April through August in 1996 and 1997. High flows and resulting lower water temperatures and higher turbidity in the Lower Granite Reservoir during our study probably affected salmonid predation rates by smallmouth bass. Management efforts directed at enhancing migratory conditions for juvenile salmonids (e.g., higher flows, lower water temperatures, and higher turbidity) will probably also reduce predation from smallmouth bass.

Hydroelectric development of the Columbia River basin has converted much of the lower Columbia River and nearly all of the lower Snake River to a series of reservoirs extending from one dam to the next. These types of habitat modifications have been implicated in a basinwide decline of wild anadromous salmonids *Oncorhynchus* spp. during the latter 20th century (NPPC 1987). Snake River stocks of juvenile anadromous salmonids pass as many as eight mainstream dams during their seaward migration. As a result, the mortality rates of juvenile salmonids have increased because of passage through turbines, increased migration times and asynchronous smoltification, and gas bubble disease from nitrogen saturation (Raymond 1968; Bently and Raymond 1976; Ebel and Raymond 1976; Rosentreter 1977; Weitkamp and Katz 1980; Zaugg et al. 1985; Budy et al. 2002; Smith et al. 2002). Predation also has been implicated as a major source of mortality of juvenile salmonids in the Columbia River (Rieman et al. 1991; Tabor et al. 1993). Although northern pikeminnow *Ptychocheilus oregonensis* are the major smolt predator in Columbia River reservoirs (Rieman et al. 1991; Ward et al. 1995), smallmouth bass *Micropterus dolomieu* are the most abundant predator in the lower Snake River reservoirs (Zimmerman and Parker 1995).

Predatory interactions between smallmouth bass and juvenile Pacific salmonids in the Columbia Basin have been examined by several authors (Rieman et al. 1991; Tabor et al. 1993). Smallmouth bass reportedly consumed 9% of an estimated 2.7 million juvenile salmonids annually consumed by predatory fishes in the John Day Reservoir, Columbia River, from 1983 through 1986 (Rieman et al. 1991). In the middle Columbia River, Tabor et al. (1993) reported a high incidence of predation by smallmouth bass, although their estimates followed hatchery releases of juvenile salmonids and

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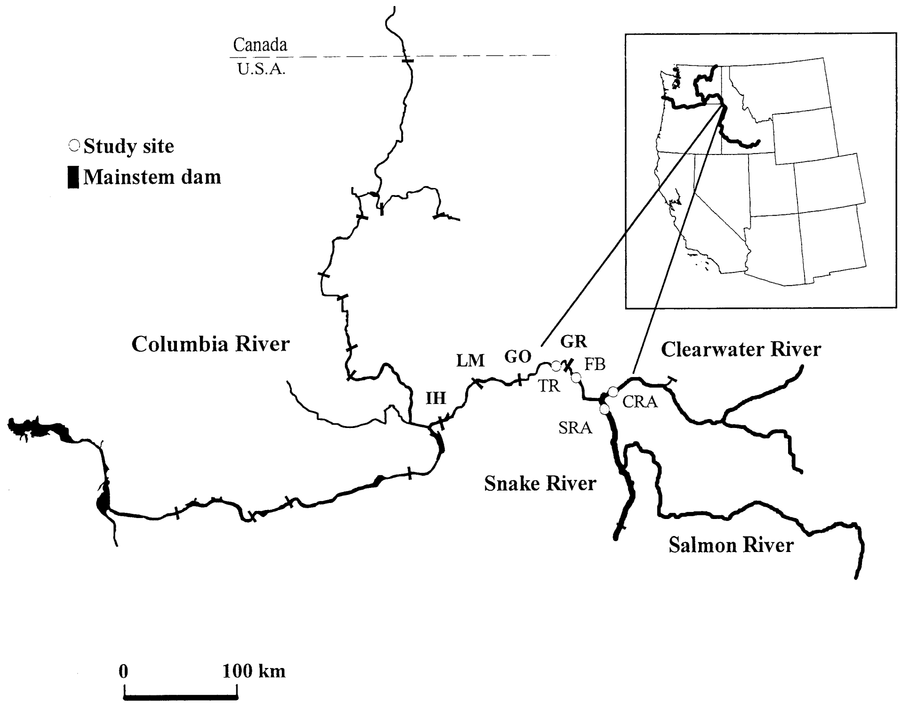

FIGURE 1.—Map of the Columbia River basin and study area in the Lower Granite Reservoir system. The lower Snake River dams are Ice Harbor (IH), Lower Monumental (LM), Little Goose (GO), and Lower Granite (GR). Study sites are the Lower Granite Dam tailrace (TR), Lower Granite Dam forebay (FB), Clearwater River arm (CRA), and Snake River arm (SRA).

were based on a limited number (n = 93) of samples. Anglea (1997) reported consumption rates up to 7% of subyearling fall Chinook salmon *O. tshawytscha* in the Lower Granite Reservoir, Snake River. The commonality of the Columbia River and Snake River reservoir studies is that the highest incidences of predation occurred when smallmouth bass and juvenile Pacific salmonids coexist in littoral areas. During peak migration times and lower water temperatures, smallmouth bass predation was minimal in the Columbia River. Little is known about predation in the Snake River system. The Lower Granite Reservoir, the first in a series of impoundments on the lower Snake River, is the hub where fish transportation or bypass is initiated. Thus, juvenile salmon and steelhead *O. mykiss* must pass through this reservoir before encountering the Lower Granite Dam. Additionally, the importance of reservoir location in affecting predation rates was identified in the John Day Reservoir (Vigg et al. 1991) and superficially by predator indexing over a broader geographic scale (Ward et al. 1995). The objectives of this study were to estimate the number of smallmouth bass and quantify their consumption of juvenile salmon and steelhead in the tailrace and forebay of the Lower Granite Dam, and to compare these results with those for the free-flowing to impounded transitional areas in the Snake and Clearwater river arms of the upper Lower Granite Reservoir.

Study Area

The Lower Granite Reservoir, Snake River, is in southeastern Washington and west-central Idaho near the cities of Clarkston, Washington, and Lewiston, Idaho (Figure 1). The Lower Granite Dam was completed in 1975 to provide hydroelectric power, barge navigation, recreation, and flood control. The Lower Granite Reservoir has a total surface area of 3,602 ha at full pool, a mean depth of 16.6 m, and a maximum depth of 42.1 m (Curet 1994). Surface water temperatures typically range from less than 7°C in March (U.S. Army Corps of Engineers, unpublished data) to 25°C in late summer (Funk et al. 1985). Shoreline habitat consists of riprap, cobble, talus, sand–silt beaches, and embayments. Our study area included four locations: the Lower Granite Dam tailrace (river kilometer [Rkm] 167–173), the Lower Granite Dam forebay (Rkm 173–179), the Snake River arm (Rkm 225–

237), and the Clearwater River arm (Rkm 0–6). Locations in the forebay and tailrace included the boat restriction zones (RZ) immediately upstream and downstream of the Lower Granite Dam that were treated as separate areas.

Three species of juvenile anadromous salmonids migrate through the Lower Granite Reservoir: Chinook salmon, steelhead, and sockeye salmon *O. nerka*. Spring and summer Chinook salmon, steelhead, and sockeye salmon juveniles migrate seaward in April, May, and June as yearlings or older. Fall Chinook salmon migrate seaward in June, July, and August mostly as subyearlings (Connor et al. 2001). In 1996, nearly eight million juvenile salmonids were collected at the Lower Granite Dam, and nearly seven million were collected in 1997. Juvenile migrations at the Lower Granite Dam in 1996 and 1997 consisted of approximately 90% steelhead, 9% spring or summer Chinook salmon, and less than 1% sockeye and fall Chinook salmon (Fish Passage Center 1997 and 1998; www.fpc.org).

Methods

Smallmouth bass collections.—We collected smallmouth bass near and parallel to the shoreline in the four sampling locations (tailrace, forebay, and Snake and Clearwater river arms) by nighttime electrofishing with an output of 400 V at 3–5 amps. We used proportional allocation methods (Scheaffer et al. 1990) to determine the number of sites of each habitat to sample within each reservoir location. Sites were randomly selected from the four locations then fixed for the duration of the study. We sampled weekly at least eight 400-m sites from April–August 1996 and 1997 in the tailrace and forebay, 16 sites from May–August in 1996 and eight sites from April–August in 1997 in the Snake River arm, and eight sites from May–August in the Clearwater River arm in both years. All captured smallmouth bass were immediately placed in a live well and measured (total length [TL], mm). Smallmouth bass at least 175 mm TL were marked with a numbered Floy tag and released. All fish were examined for injuries and scars from missing tags, but we did not assess tag loss rates. Weights of captured fish were estimated using weight–length regressions developed for the lower Snake River reservoirs (D. H. Bennett, unpublished data).

Smallmouth bass abundance.—The program MARK (White and Burnham 1999) was used to estimate the population abundance of smallmouth bass 175 mm TL or larger during 1996 in each of the four regions. We chose an open population model over a closed population model in each region because of some evidence of movement, and sampling extended over a 4–5-month period during which some mortality, both natural and fishing, and recruitment (fish growing into the 175-mm-TL size-class) undoubtedly occurred. The Jolly–Seber-Lambda model also includes parameters for survival probabilities (phi), capture probabilities (p), and initial population size (N). The parameters lambda, phi, and p are allowed to be time period specific, and the program MARK calculated profile likelihood confidence intervals for each parameter.

Relative abundance and density of smallmouth bass.—Because we did not estimate population abundance in 1997, we used catch per unit effort (CPUE) to determine if the relative abundance of smallmouth bass at least 175 mm TL was different at each of the sampling sites between 1996 and 1997. We used an aligned ranks procedure (Lehman and D'Abrera 1983) and analysis of variance (ANOVA; $P = 0.05$) to compare CPUE statistically in the tailrace, forebay, Snake River arm, and Clearwater River arm. We used months as blocking variables, reservoir locations as treatments, and the ranks of CPUEs of smallmouth bass at least 175 mm TL were dependent variables. We then subjected the ranks of CPUEs to ANOVA (Conover and Iman 1981) for a randomized block design. We also determined the population density of smallmouth bass at least 175 mm TL by dividing population abundance estimates by the surface areas of the tailrace (199 ha), forebay (478 ha), Clearwater River arm (154 ha), and Snake River Arm (359 ha).

Dietary analysis.—The stomachs of smallmouth bass at least 70 mm TL were pumped using a modified gastric lavage technique (Seaburg 1957) which has been shown to be an extremely efficient method for collecting the stomach contents of fish (Bromley 1988). All collections were preserved in a 10% buffered formalin solution. Prey items were identified in the laboratory to the lowest practical taxon with the aid of a dissecting microscope. The number of items and digested weights of the items were recorded. Digested weights were obtained by blotting prey items dry and weighing them to the nearest 0.001 g. Macroinvertebrates were identified to order or family, crustaceans to family or genus, and fish to genus or species. Partially digested, unidentifiable macroinvertebrates were weighed as a group.

When prey fish were too digested to measure fork length (FL) or total length, diagnostic bone lengths (Hansel et al. 1988) and nape to tail lengths (Vigg et al. 1991) were used to estimate the fork length using regression equations. Diagnostic bone lengths were taken from cleithra, opercles, pharyngeal teeth, and dentaries found in the stomachs of smallmouth bass. Due to the possibility of length-related differences in diet composition, we conducted the dietary analysis on four length-classes of smallmouth bass (70–174 mm, 175–249 mm, 250–389 mm, and >389 mm TL).

Numerical consumption.—We used a simple meal turnover time adapted from Adams et al. (1982) to estimate the daily consumption rate (by weight) of juvenile salmonids by smallmouth bass 175 mm TL or larger (R. Tabor, U.S. Fish and Wildlife Service, personal communication):

$$C = n/N, \tag{1}$$

where C is the consumption rate of juvenile salmonids (number consumed/predator/d), n is the number of salmonids consumed within 24 h of capture, and N is the total number of smallmouth bass sampled, including those with empty stomachs.

The weights of digested juvenile salmonids at collection were compared with the estimated liveweights of juvenile salmonids derived from regression equations (Vigg et al. 1991) after a 24-h digestion period. Prey weights heavier than the estimated liveweights after a 24-h digestion period were included in the calculation of the daily consumption rate. Prey weights lighter than the calculated liveweight after a 24-h digestion period were not used in the calculation of daily consumption rates because we assumed that those prey fish were consumed during a period longer than 24 h. To estimate the portion (g) of meal evacuated from the stomach of smallmouth bass (E), we used the algorithm from Rogers and Burley (1991):

$$E = S[1 - \exp(-0.005tS^{-0.29}e^{0.15T}W^{0.23})]^{1.95}, \tag{2}$$

where E represents grams evacuated, S is the meal weight (g), t is time (h), T is temperature (°C) at capture, and W is smallmouth bass weight (g).

Meal weight was calculated by the method of Vigg et al. (1991):

$$S = O_i + O_j + D_k, \tag{3}$$

where S is meal weight (g), O_i is the calculated original weight of juvenile salmonids at injestion, O_j is the calculated original weight of any other prey fish that was digested within 10% of the original weight, and D_k is the digested weight of other prey items in the sample. An advantage of this model is that predation rates are based on the digestion of salmonids and are not significantly influenced by differential digestion rates among prey types. Hard-bodied prey (such as crayfish) can have a significantly different digestion rate than prey fish (Bromley 1994). Other models that incorporate all prey types in calculations can have large errors if crayfish or other hard-bodied prey make up a large portion of the diet and if the digestion equation was developed for salmonids (Rogers and Burley 1991).

Estimated loss of juvenile salmonids.—We used the equation presented by Rieman et al. (1991) to estimate total loss of juvenile salmonids in the tailrace and forebay of the Lower Granite Dam and the Clearwater and Snake river arms of the Lower Granite Reservoir:

$$L_{ij} = PS_iC_{ij}D_jG_{ji}, \tag{4}$$

where L_{ij} is the loss of salmonid to size-group i during month j, P represents the number of predators at least 175 mm TL, S_i is the proportion of each predator within size-group i, C_{ij} is the consumption of predator size-group i during month j, D_j is the number of days in month j, and G_{ji} is the proportion of juvenile salmonids in predator size-group i during month j.

TABLE 1.—Estimates of initial population abundance of smallmouth bass at least 175 mm total length (TL) in 1996 (N) per region, along with 95% profile likelihood confidence intervals. Abbreviations are as follows: CRA = Clearwater River arm; SRA = Snake River arm.

Location	Sample periods	Unique marks	N	95% profile likelihood confidence interval
Tailrace	18	323	1,743	1,089–2,793
Forebay	13	519	1,294	839–1,997
CRA	12	255	3,820	2,328–6,283
SRA	15	969	11,877	8,818–16,002

Results

Smallmouth Bass Abundance

Our abundance estimate of smallmouth bass at least 175 mm TL was highest in the Snake River arm, followed by the Clearwater River arm, the Lower Granite Dam tailrace, and the Lower Granite Dam forebay (Table 1). The confidence intervals are 95% profile likelihoods and were largely within ±50% of the estimate (ranging from +64% to −34%). We did not conduct population estimates in 1997, although catch per unit effort was not significantly different ($P > 0.05$) between 1996 and 1997 at each of the sampling sites. The population density of smallmouth bass greater than or

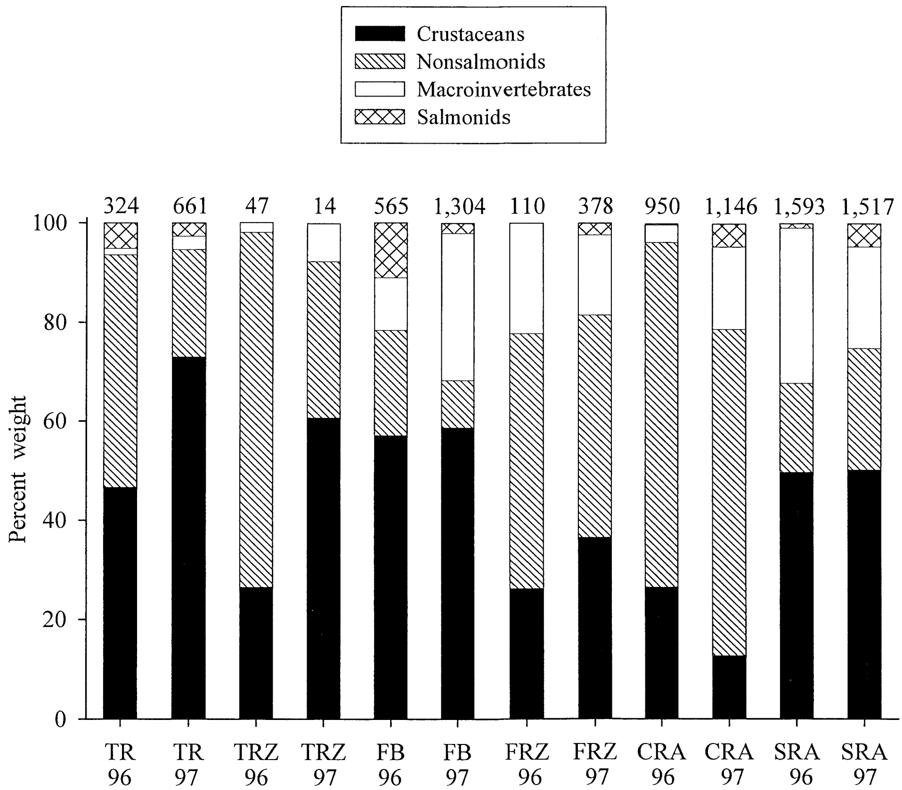

FIGURE 2.—Spatial variation in diet composition (percent weight) by location of smallmouth bass 70 mm in total length or larger (n = 8,609) collected in the Lower Granite Reservoir and tailrace in 1996 and 1997. Locations are as follows: Lower Granite Dam tailrace (TR), tailrace restricted zone (TRZ), forebay (FB), forebay restricted zone (FRZ), Clearwater River arm (CRA), and Snake River arm (SRA).

equal to 175 mm TL was highest in the Snake River arm (33.1 fish/ha), followed by the Clearwater River arm (24.8 fish/ha), the tailrace (8.8 fish/ha), and the forebay (2.7 fish/ha).

Dietary Analysis

We examined 3,589 (1996) and 5,020 (1997) stomach samples from smallmouth bass sampled April through August. In 1996, 89% (n = 3,181) of the samples were from smallmouth bass 70–249 mm TL compared with 91% (n = 4,571) in 1997. The diets of smallmouth bass differed among reservoir locations during both years (Figure 2). During 1996, the proportional contribution of juvenile salmonids in the diet was highest (11%) in the forebay, whereas in 1997 juvenile salmonids made up the highest percentage (5.0%) in the Snake and Clearwater river arms. Juvenile Chinook salmon comprised 16% (1996) and 59% (1997) of all salmonids ingested. Juvenile salmonids were absent from the stomach samples of smallmouth bass collected in the tailrace-RZ during 1996 and 1997 and in the forebay-RZ during 1996. Crustaceans and nonsalmonid fishes dominated diets in the various sections.

Although predation on juvenile salmonids by smallmouth bass at least 70 mm TL occurred from April through August, we found high variability in spatial and temporal intensity. In 1996, juvenile salmonids were abundant (by weight) in the stomach contents of smallmouth bass in the tailrace in May (23%) and in the forebay in April (13%), May (31%), and August (14%; Table 2). In 1997, the presence of juvenile salmonids in smallmouth bass diets was highest in the Snake River arm during August, accounting for about 11% of the diet.

The diet composition of smallmouth bass within a particular length-class was consistent between years and among sampling locations (Table 3). Salmonids were consumed by all length-classes of smallmouth bass during both years except those greater than 389 mm TL in 1997. Macroinvertebrates or crustaceans were the primary prey items (by weight) of 70–74-mm-TL smallmouth bass at all locations except the Clearwater River arm,

TABLE 2.—Monthly variation in diet composition (percent weight) of smallmouth bass at six sampling locations in the Lower Granite Reservoir system, April through August 1996 and 1997 (RZ = boat restriction zone; other abbreviations are defined in Table 1).

Location	Prey item and sample size	1996					1997				
		Apr	May	Jun	Jul	Aug	Apr	May	Jun	Jul	Aug
Tailrace	Salmonids	0.0	22.7	0.3	0.0	0.0	0.0	4.1	0.0	3.8	0.0
	Nonsalmonids	81.6	23.9	44.1	49.2	53.3	99.6	6.2	11.4	25.0	31.1
	Crustaceans	18.4	53.0	54.1	49.0	44.4	0.4	89.3	87.9	67.7	62.5
	Macroinvertebrates	0.1	0.4	1.5	1.8	2.3	0.0	0.4	0.8	3.4	6.4
	Sample size	38	87	70	76	53	3	54	206	362	36
Tailrace–RZ	Salmonids				64.1	85.0			1.7	41.2	71.7
	Nonsalmonids				34.6	12.1			97.2	55.7	1.1
	Crustaceans				1.3	2.9			1.1	3.1	27.1
	Macroinvertebrates				0.0	0.0			0.0	0.0	0.0
	Sample size				29	18			5	5	4
Forebay	Salmonids	13.3	31.3	0.0	0.0	14.5	0.0	0.0	0.0	2.7	0.2
	Nonsalmonids	23.4	22.4	34.3	17.2	4.1	15.2	82.1	72.8	55.5	65.3
	Crustaceans	61.6	44.5	63.4	64.9	52.6	84.7	10.4	23.6	6.6	1.3
	Macroinvertebrates	1.7	1.7	2.4	17.9	28.9	0.1	7.5	3.7	35.2	33.3
	Sample size	48	98	116	170	133	15	76	252	764	197
Forebay–RZ	Salmonids	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.0
	Nonsalmonids	0.0	18.7	93.7	7.5	43.3	100.0	70.7	14.9	52.0	7.7
	Crustaceans	100.0	74.4	5.1	71.2	22.5	0.0	15.8	79.2	29.5	68.9
	Macroinvertebrates	0.0	6.9	1.2	21.3	34.2	0.0	13.5	5.9	15.7	23.4
	Sample size	1	9	11	32	57	1	19	67	229	62
CRA	Salmonids		0.0	0.3	0.2	0.0		0.0	4.3	3.1	9.7
	Nonsalmonids		85.2	73.8	60.6	84.4		40.3	70.8	56.8	63.1
	Crustaceans		11.8	23.1	35.6	4.6		42.2	9.1	23.5	6.6
	Macroinvertebrates		3.0	2.8	3.6	11.0		17.5	15.8	16.5	20.7
	Sample size		111	348	363	128		86	731	220	109
SRA	Salmonids		0.3	0.2	3.6			1.2	0.1	6.9	10.3
	Nonsalmonids		14.2	4.7	32.5	56.3	93.8	19.6	15.5	30.9	23.6
	Crustaceans		77.5	19.1	42.5	32.8	0.5	57.0	63.3	43.2	41.1
	Macroinvertebrates		8.1	76.1	21.4	10.8	5.7	22.2	21.2	19.1	25.0
	Sample size		373	251	698	271	9	257	487	544	220

where nonsalmonid fishes were dominant. Crustaceans comprised the greatest percent of the diet (by weight) of 175–249-mm-TL smallmouth bass at all locations in 1996 and 1997 except the Clearwater River arm, where nonsalmonid fishes were the primary prey item. Nonsalmonid fishes dominated the diet of 250–389-mm-TL smallmouth bass at all locations in 1996 except the Snake River arm, where crustaceans made up the highest percent of the diet weight. In 1997, crustaceans were the primary prey item at all locations except the Clearwater River arm, where nonsalmonid fishes were most the most abundant prey item by weight. Crustaceans or nonsalmonid fishes dominated the highest percent of the diet weight of smallmouth bass greater than 389 mm TL at all locations in 1996 and 1997 except the forebay in 1996, where one steelhead comprised about 99% of the diet weight.

Numerical Consumption

Consumption rates of juvenile salmonids by smallmouth bass were low and highly variable among months and reservoir locations in 1996 and 1997 (Table 4). In 1996, our estimated highest monthly consumption rates (smolts/bass/d) of juvenile salmonids by smallmouth bass were in the forebay in April (0.02) and generally low at other locations and in other months. In 1997, monthly consumption rates were highest in the forebay-RZ in July (0.05), with consumption rates generally low (<0.02) at other locations and in other months.

Estimated Loss of Juvenile Salmonids

We estimated approximately 17,500 juvenile salmonids were consumed by smallmouth bass from April through August during both years (Table 5). Overall, smolt losses were highest in the Snake River arm followed by the tailrace of the Lower Granite Dam. Smolt losses were highest in June 1996 and August 1997. All smolt losses in the forebay of the Lower Granite Dam in 1997 occurred in July.

Discussion

Juvenile salmonids were not a major prey of smallmouth bass at any location in either 1996 or

TABLE 3.—Variation in diet composition (percent weight) of four length-classes (TL) of smallmouth bass at six sampling locations in the Lower Granite Reservoir system, April through August 1996 and 1997. Abbreviations are defined in Tables 1 and 2.

Location	Prey item and sample size	1996 Length-class (mm)				1997 Length-class (mm)			
		70–174	175–249	250–389	>389	70–174	175–249	250–389	>389
Tailrace	Salmonids	3.1	0.0	7.5	0.0	0.0	1.6	3.4	0.0
	Nonsalmonids	10.1	30.9	55.3	0.7	5.0	12.2	27.9	8.7
	Crustaceans	57.6	67.1	36.9	99.2	86.5	82.3	67.2	91.3
	Macroinvertebrates	29.2	2.1	0.3	0.1	8.5	3.9	1.5	0.0
	Sample size	70	149	102	3	193	248	218	2
Tailrace–RZ	Salmonids	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
	Nonsalmonids	0.0	18.7	90.9	0.0	0.0	30.6	33.3	
	Crustaceans	4.9	77.1	8.2	100.0	44.0	68.8	49.4	
	Macroinvertebrates	95.1	4.2	0.8	0.0	56.0	0.6	17.3	
	Sample size	2	28	16	1	1	6	7	
Forebay	Salmonids	0.0	3.5	3.2	98.8	1.8	1.0	5.0	
	Nonsalmonids	3.2	8.0	57.6	0.0	4.1	4.8	29.2	
	Crustaceans	51.8	75.2	35.6	0.0	38.0	66.0	54.5	
	Macroinvertebrates	45.0	13.3	3.6	1.2	56.1	28.2	11.3	
	Sample size	110	399	53	3	554	658	92	
Forebay–RZ	Salmonids	0.0	0.0	0.0	0.0	0.8	5.7	0.0	0.0
	Nonsalmonids	16.9	5.4	91.3	99.3	8.1	4.0	26.9	99.9
	Crustaceans	32.8	52.1	6.4	0.0	44.9	69.8	46.3	<0.1
	Macroinvertebrates	50.3	42.5	2.3	0.7	46.2	20.6	26.8	0.0
	Sample size	35	66	7	2	246	114	15	3
CRA	Salmonids	0.7	0.2	0.0		6.0	0.0	7.6	
	Nonsalmonids	69.1	60.0	91.3		45.5	66.6	86.0	
	Crustaceans	11.3	38.7	8.4		4.8	31.3	3.3	
	Macroinvertebrates	18.8	1.1	0.4		43.7	2.1	3.1	
	Sample size	692	206	52		1,066	51	29	
SRA	Salmonids	0.3	3.5	0.0	0.0	0.6	2.8	9.9	0.0
	Nonsalmonids	3.9	18.3	41.8	94.9	10.4	29.1	32.4	0.0
	Crustaceans	6.0	71.0	55.6	4.6	27.6	48.1	56.0	99.9
	Macroinvertebrates	89.9	7.2	2.6	0.5	61.4	20.0	1.7	<0.1
	Sample size	1,010	414	162	7	875	558	78	8

1997. The highest percentage of juvenile salmonids observed in smallmouth bass diets during both years was less than 11% compared with estimates by Anglea (1997) of 72% and 34% for 1994 and 1995, respectively. Tabor et al. (1993) reported that juvenile salmonids composed 59% of the diet of smallmouth bass at the upstream end of the McNary Reservoir. In contrast, Poe et al. (1991) reported that juvenile salmonids comprised only 4% of the diet of smallmouth bass in the John Day Reservoir. High variation in juvenile salmonid consumption by smallmouth bass is common within the basin and is probably related to variations in biotic and abiotic conditions.

Although salmonid consumption was low during both years, consumption was nearly six times higher in 1997 than in 1996. Differences in flow, temperature, and run sizes between years were substantial; on August 1, the approximate date when 75% of the age-0 Chinook salmon passed the Lower Gran-

TABLE 4.—Consumption rates of juvenile salmonids by smallmouth bass at least 175 mm TL at six locations in the Lower Granite Reservoir system, April through August 1996 and 1997. Abbreviations are defined in Tables 1 and 2.

Location	Sample size	Salmonids consumed per smallmouth bass per day: 1996 Samples					Sample size	1997 Samples				
		Apr	May	Jun	Jul	Aug		Apr	May	Jun	Jul	Aug
Tailrace	290	0.000	0.012	0.000	0.000	0.000	491	0.000	0.026	0.000	0.008	0.000
Tailrace–RZ	132		0.000	0.000	0.000	0.000	13	0.000		0.000	0.000	0.000
Forebay	559	0.020	0.007	0.000	0.000	0.000	844	0.000	0.000	0.000	0.008	0.000
Forebay–RZ	96	0.000	0.000	0.000	0.000	0.000	136	0.000	0.000	0.000	0.048	0.000
CRA	294	0.000	0.000	0.000	0.000	0.000	97	0.000	0.000	0.016	0.000	0.000
SRA	747	0.000	0.000	0.011	0.003	0.000	715	0.000	0.011	0.000	0.004	0.015

TABLE 5.—Estimated loss of juvenile Chinook salmon and steelhead to predation by smallmouth bass 175 mm or longer at four areas of the Lower Granite Reservoir and tailrace, April–August 1996 and 1997. Estimated losses in the tailrace and forebay include restricted zones. Abbreviations are defined in Table 1.

Location and species	Estimated loss									
	1996 Samples[a]					1997 Samples[b]				
	Apr	May	Jun	Jul	Aug	Apr	May	Jun	Jul	Aug
Tailrace	0	648	0	0	0	0	1,405	0	432	0
Forebay	776	281	0	0	0	0	0	0	321	0
CRA	0	0	0	0	0	0	0	1,834	0	0
SRA	0	0	3,919	1,104	0	0	0	0	1,479	5,344
Total monthly loss	776	929	3,919	1,104	0	0	1,405	1,834	2,226	5,344
Chinook salmon	0	648	0	552	0	0	1,405	1,834	432	2,672
Percent of monthly total	0	70	0	50	0	0	100	100	19	50
Steelhead	776	281	3,919	552	0	0	0	0	1,794	2,672
Percent of monthly total	100	30	100	50	0	0	0	0	81	50

[a] The total number of fish lost in 1996 was 6,728, consisting of 1,200 Chinook salmon (18%) and 5,528 steelhead (82%).

[b] The total number of fish lost in 1997 was 10,809, consisting of 6,343 Chinook salmon (59%) and 4,466 steelhead (41%).

ite Dam during both years, water temperatures were similar although flows were up to 566 m^3/s higher in 1997 (Figure 3; http://www.cqs.washington.edu/dart/dart.html). Approximately 90% of the entire downstream migration of age-0 Chinook salmon passed the Lower Granite Dam by the end of August of both years. Although flows remained about 198 m^3/s higher in August 1997, water temperatures were about 4°C warmer in 1997 than in 1996 (20.6°C versus 16.7°C). Also, numbers passed over the Lower Granite Dam were considerably higher in 1997 (97,985) than in 1996 (18,066). We conclude that the five times higher loss of juvenile Chinook salmon in 1997 than in 1996 was apparently related to the higher water temperatures and higher abundance of age-0 Chinook salmon.

We believe that low water temperatures and high turbidity associated with comparatively high flows were probably the principal abiotic factors influencing smallmouth bass predation of juvenile salmonids in 1996 and 1997. Similar to other studies (Vigg et al. 1991; Cada et al. 1997; Gregory and Levings 1998), our study suggests that increased turbidities and decreased temperatures accompanying high flows may improve the survival of juvenile salmonids by reducing predation. Therefore, factors that appear to affect water temperature, turbidity, and flow probably are related to the year-to-year and spatial variation in smallmouth bass predation on juvenile salmonids. We hypothesize that higher flow years create conditions less favorable for predation on juvenile salmonids and low flow years create conditions for higher predation. Since discharge during the spring is inversely related to water temperatures and directly related to turbidity (Connor et al. 1998), we anticipate that the relative magnitude of predation by smallmouth bass is predictably related to flows in the Snake River. The higher flows (Figure 3) and higher turbidities (Figure 4) that occurred in 1996 and 1997 compared with other years seem strongly linked to reduced predation rates by smallmouth bass. In fact, reduced PIT tag detection rates of subyearling Chinook salmon in low flow years (i.e., 1994) probably reflect decreases in survival (Connor et al. 1998). Recently, Connor et al. (2003) demonstrated that the survival of subyearling Chinook salmon was positively related to flow and negatively related to water temperature (r^2 = 0.92). We believe annual differences in survival is largely a function of more intense predation under

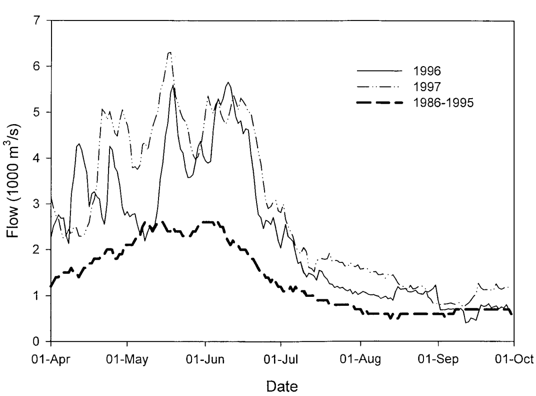

FIGURE 3.—Daily mean discharge from the Lower Granite Dam, Snake River, during 1996 and 1997 and 1986–1995 average.

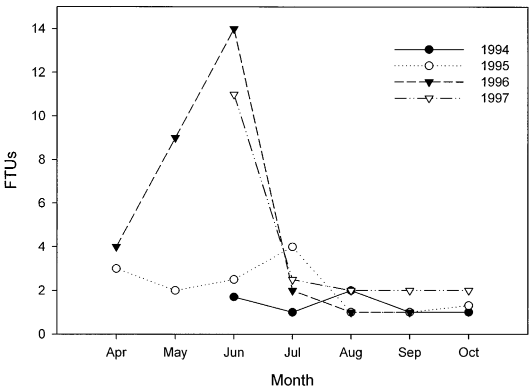

FIGURE 4.—Mean monthly turbidity (Formazin turbidity unit [FTU]) at 1-m depth in the Lower Granite Reservoir, Snake River, near river kilometer 200 during 1994–1997 (S. Juul, U.S. Army Corps of Engineers, unpublished data).

lower flow and higher temperatures. Thus, higher flows during spring runoff in the Snake River probably affect the physical characteristics in the Lower Granite Reservoir that can directly affect juvenile salmonid predation by smallmouth bass.

Our hypothesis that predation levels are closely linked to discharge is supported by literature from other systems. For example, Coble (1975) found that lower water temperatures reduce feeding activity in smallmouth bass. Because smallmouth bass are generally considered visual predators (Carlander 1977), increased turbidity should reduce the detection of smolts. Cada et al. (1997) provided evidence that reduced turbidity associated with impoundment-related reductions in water velocity was correlated with lower survival of juvenile Pacific salmon. Gregory and Levings (1998) found that age-0 Pacific salmon were less likely to encounter and be consumed by predators in turbid than in clear water. They found that predation of age-0 Chinook salmon was significantly higher in a clear-water tributary (0–6 NTU) of the Fraser River than in the turbid (27–108 NTU) main stem.

The higher predation rates observed for smallmouth bass in the Columbia (Vigg et al. 1991) and Snake rivers (Ward et al. 1995) during summer may be attributed to the increased metabolic demands that accompany higher water temperatures (Cech et al. 1994). Optimal water temperature for smallmouth bass can range from 12–31°C depending on the age of the fish (Ferguson 1958; Barans and Tubb 1973), although 29°C (Coble 1975) is more commonly accepted. Smallmouth bass begin actively feeding when water temperatures are 15°C (Carlander 1977). Water temperatures in the Lower Granite Reservoir were approximately 8°C at the beginning of April 1996 and 1997 and reached a maximum of 23°C in August. Thus, the highest water temperatures in the Lower Granite Reservoir are at or below the optimum temperature for consumption and growth of smallmouth bass.

The precision of total loss estimates is related to the quality of the population estimate. We feel confident in our population estimates at the various locations in the Lower Granite Reservoir and Dam. Although we used population estimates conducted in 1996 to estimate predation in 1997, the lack of significant differences in catch per unit effort in 1997 support our use of the 1996 estimates. Our use of 1996 data as an estimate of the 1997 population is also supported by results of about 10 years of sampling in the Lower Granite Reservoir with suggested population structures similar to that estimated in 1996 (D. H. Bennett, unpublished data). We found the formulation of the Jolly–Seber-Lambda programmed into MARK extremely flexible and used a relatively simple model for each of the four regions. The model included only five parameters: one for the survival rate (phi), one for the trend parameter (lambda), two to model capture rate (p), and one for the initial population abundance (N). The classic open population model, the Jolly–Seber model (Jolly 1965; Seber 1965), which estimates ‘‘births’’ (recruitment in this case) and deaths was not used because of the sparseness of the recapture history (over 90% of the recaptured fish were recaptured just once). Using the implementation of the Jolly–Seber model within POPAN (Arnason et al. 1995), for example, resulted in negative estimates of births in all four regions for several time periods. Instead of the Jolly–Seber model, a less data-demanding open population procedure, labeled Jolly–Seber-Lambda in the program MARK (White and Burnham 1999) was chosen. Rather than explicitly estimating births and deaths, the Jolly–Seber-Lambda model includes a parameter lambda, which is a multiplier of abundance in a previous time period that reflects positive or negative changes in abundance in the next time period, implicitly allowing for births and deaths. Although we did not directly quantify tag loss, our close examination of each fish suggested tag loss was minimal. Beamesderfer and Rieman (1991) estimated a 3% tag loss for smallmouth bass in the John Day Reservoir. For example, using a 3% tag loss (p = 3%), estimates of N are biased high (1/0.97 = 1.0309) by 3.1%. Therefore, we believe our loss estimates based on very large sample sizes of stomachs and reliable population estimates are representative of juvenile salmonid losses in the four locations of the Lower Granite Reservoir system during 1996 and 1997.

Fisheries managers in the Northwest are faced with difficult decisions on whether intervention is necessary to minimize predation on juvenile salmonids (Beamesderfer 2000). Although any mortality of a species on the endangered list from predation is not good, alternative species that utilize the smallmouth bass feeding niche may ultimately have a greater predatory impact (Stewart et al. 1981) than smallmouth bass. Some preliminary observations suggest northern pikeminnow populations are depressed in the presence of smallmouth bass in southern Idaho impoundments (H. Pollard, NOAA Fisheries, Portland, Oregon, personal communication). Regardless of the size of smallmouth bass, predation is most intense on subyearling Chinook salmon. Although predation can vary dramatically by flow year, the manipulation of smallmouth bass population structure by management intervention does not seem warranted. Ways to minimize predation and ultimately increase survival (Connor et al. 1998) seem related to decreasing the suitability of the foraging environment. We believe results from our 2-year study of predation support the proposal by Gray and Rondorf (1986) and Connor et al. (2003) that summer flow augmentation is a beneficial interim recovery measure for fall Chinook salmon. Our data suggest that improving conditions in the downstream migration corridor for juvenile salmonids through enhanced cooler flows would decrease predation and increase survival.

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