Transactions of the American Fisheries Society 135:853–860, 2006
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DOI: 10.1577/T05-014.1

[Note]

Effects of Predation by Nonnative Smallmouth Bass on Native Salmonid Prey: the Role of Predator and Prey Size

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Abstract.—The size of predators that consume the most fish and the size of prey fish that are the most vulnerable to predation are important factors to consider when assessing the predation risks to valued prey fish such as Chinook salmon *Oncorhynchus tshawytscha* in the Pacific Northwest. We found that native salmonids' risk of predation by nonnative smallmouth bass *Micropterus dolomieu* in the lower Yakima River, Washington, generally decreased with increasing predator and prey size. Among smallmouth bass, those with fork lengths (FLs) ranging from 150 to 199 mm consumed 42.9% of the salmonids consumed. Overall, most of the salmonids were consumed by smallmouth bass smaller than 250 mm (69.6%), and the vast majority were consumed by smallmouth bass smaller than 300 mm (83.6%). Small smallmouth bass were much more abundant than large smallmouth bass, and the proportion of smallmouth bass that contained salmonid prey items in the gut decreased with increasing predator size. Salmonids that were 100 mm or larger were rarely consumed by smallmouth bass. We found that the maximum relative length of salmonids ([prey length/predator length] × 100) consumed by smallmouth bass was 56.6%. In addition, the relative length of salmonid prey decreased with increasing smallmouth bass size. Smallmouth bass generally ate salmonids at lengths that were less than 50% of predator capacity and that averaged 25% of predator length. The introduction of smallmouth bass to the Yakima River appears to have changed the size-based predation risk dynamics in the lower river, which were historically dominated by northern pikeminnow *Ptychocheilus oregonensis*.

The size and abundance of both predators and prey are important factors that can be used to assess predation risk. For example, determination of the minimum and maximum fish sizes that predators consume can be used to set the size bounds of the prey that are vulnerable to predators (Pearsons and Fritts 1999). There is generally a positive relationship between the size of a predator and the maximum prey size that can be consumed (Hoyle and Keast 1987; Hambright 1991) and/or the optimal size of fish that it will eat (Hoyle and Keast 1987). Mouth size physically limits a predator's ability to consume large fish (Hambright 1991). Predators may not eat small prey because the energetic cost of searching for and capturing small prey may not be profitable (Werner and Hall 1974). Furthermore, determining which predator sizes eat the most fish can be used to assess and contain risks to prey. Larger predators may have the ability to eat more fish per capita (Rogers and Burley 1991), but smaller predators may be much more numerous and thus may be able to eat far more fish. In this scenario, reducing predation by smaller fish may be the best approach for reducing impacts on salmonids.

Northern pikeminnow *Ptychocheilus oregonensis* were historically one of the main fish piscivores on salmonids in the Columbia River (Li et al. 1987) and in tributaries to the Columbia River, such as the John Day River (Pearsons 1994) and the lower Yakima River (Patten et al. 1970). Although northern pikeminnow are still considered to be the dominant fish piscivore in the Columbia River (Poe et al. 1991; Rieman et al. 1991), northern pikeminnow are now rarely captured in the lower Yakima River (Washington Department of Fish and Wildlife, unpublished data), and smallmouth bass *Micropterus dolomieu* are now the dominant piscine predators of salmonids in the lower Yakima River (Fritts and Pearsons 2004). Smallmouth bass are also apparently more numerous than northern pikeminnow in the John Day River (Shrader and Gray 1999). Northern pikeminnow and smallmouth bass differ in biology, such as the age at which they become piscivorous and their body shape (i.e., mouth gape), and may pose different predation risks to native salmonids (Li et al. 1987).

In this paper, we provide detailed information about the minimum, average, and maximum sizes of prey fish consumed by smallmouth bass and the per capita and population consumption of salmonids by different sizes of smallmouth bass in the lower Yakima River. We discuss the potential predation risks to salmonids posed by nonnative smallmouth bass and compare these risks to those posed by northern pikeminnow.

Study Area

The Yakima River is a Columbia River tributary located in south-central Washington State and has a drainage area of approximately 15,900 km^2. Chinook

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Received January 14, 2005; accepted February 11, 2006
Published online June 26, 2006

salmon *Oncorhynchus tshawytscha* are the most numerous salmonid found within our study area during the spring and early summer; coho salmon *O. kisutch* and steelhead *O. mykiss* are also present in lower numbers. Two life history types of Chinook salmon were present during sampling: stream type and ocean type (Healey 1983). Stream-type (spring) Chinook salmon rear in the upper portions of the Yakima River drainage for a full year before migrating downstream through our study area towards the Pacific Ocean as yearling smolts. The majority of ocean-type Chinook salmon migrate seaward out of the Yakima River as subyearlings by late June; these Chinook salmon reared in our study area throughout the duration of sampling. Hatchery releases of fall and spring Chinook salmon and coho salmon also occur during the spring. Approximately 2 million fall Chinook salmon, 800,000 spring Chinook salmon, and 1 million coho salmon are released annually. During our electrofishing surveys in the lower Yakima River, we collected potential prey fish for size data. The mean length of spring Chinook salmon was 128 mm fork length (FL; range, 70–192 mm); fall Chinook salmon averaged 77 mm (range, 32–117 mm), coho salmon averaged 150 mm (range, 97–219 mm), and steelhead averaged 174 mm (range, 105–288 mm).

We selected two sample sections of approximately 8 km (river kilometer [rkm] 13–21) and 7.8 km (approximately rkm 49–57) in length, which were representative of the lower 68 km of the Yakima River (Fritts and Pearsons 2004). The criteria for selecting these sections were (1) that they were located near the center of the reaches that they represented, (2) that they had access to launch and retrieval of the boat, and (3) that they contained habitats similar to those in the surrounding reaches. The lower section is referred to as the "Vangie" section, and the upper is referred to as the "Benton" section. Each section was chosen to represent the available habitat in a larger reach: the Vangie reach was 28.1 km in length, and the Benton reach was 39.9 km in length. These reaches were separated by a low-head diversion dam located at rkm 28.1.

Methods

We used a drift-boat electrofisher (McMichael et al. 1998) to sample along the left bank of each section three times during the spring of 1998 and weekly or every other week during the spring of 1999–2002. We attempted to net all 100-mm and larger smallmouth bass to gather information on length, weight, age, growth, and diet and to calculate catch per unit effort (CPUE; fish/min) for 150-mm and larger smallmouth bass. To determine the abundance of smallmouth bass in the lower Yakima River, we conducted mark–recapture estimates of 150-mm and larger smallmouth bass once or twice each year by electrofishing both banks of the river concurrently with two drift-boat electrofishers (Fritts and Pearsons 2004). All 150-mm and larger smallmouth bass were marked with a fin clip, and all 200-mm and larger smallmouth bass were tagged with a numbered Floy anchor tag. All fish were weighed (g), measured (mm FL), and then released. Recapture runs occurred 1 d after the marking runs to ensure that there was little or no movement into or out of our sample sections. All captured 150-mm and larger smallmouth bass were examined for marks during the recapture sampling. Abundance estimates for 150-mm and larger smallmouth bass were generated with Chapman's modification of the Petersen method (Seber 1973) for each year except 2001, when we were unable to obtain enough recaptures to generate valid estimates. We generated a relationship between the mark–recapture abundance estimates and the CPUE calculated for the left bank during the mark sampling in the same manner as in Fritts and Pearsons (2004) but with the addition of the 2002 data, that is,

$$\text{Abundance} = 4{,}785 \times \text{CPUE}.$$

This relationship was applied to the calculated CPUE of 150-mm and larger smallmouth bass in each section during the weekly diet sampling in which no mark–recapture estimates were performed and was also used for all weeks during 2001. This resulted in separate abundance estimates for each section for 3 weeks in 1998, 12 weeks in 1999, 14 weeks in 2000, 12 weeks in 2001, and 13 weeks in 2002.

To partition the weekly smallmouth bass abundance estimates into abundance estimates by size-class (E_{SZ}), we first applied the method described by Seber (1973) to the mark–recapture data for each size-class, namely,

$$E_{\text{SZ}} = \frac{m_x + c_x - r_x}{m + c - r} \cdot N,$$

where m_x = the number of individuals within a size-class that were marked during the marking run, c_x = the number of individuals within a size-class that were captured in the recapture run, r_x = the number of marked individuals within a size-class that were captured in the recapture run, m = the total number of individuals that were marked in the mark run, c = the total number of individuals that were captured in the recapture run, r = the total number of marked individuals that were captured in the recapture run, and N = the total abundance estimate. This method assumes equal capture vulnerability between the size-classes. Inspection of the mean recapture rates indicated that capture vulnerability was sufficiently similar to meet this assumption. We then calculated the mean proportion of the total estimated abundance for each size-class in the Benton and Vangie sections for each year. These proportions were then used to partition the weekly CPUE calculated abundance estimates for each section into weekly abundance estimates by size-class (PE_{SC}). Mean proportions for 1998–2000 and 2002 combined were used to partition the CPUE estimates for 2001 since no mark–recapture estimates were performed. We assumed that the proportion of fish by size-class remained the same throughout the spring.

We collected scales to determine the length at age of smallmouth bass in our study area. This was done to discover the age at which smallmouth bass become predaceous and the age at which they are the most predaceous. During spring 1999–2001, we collected scale samples from 123, 73, and 100 smallmouth bass, respectively. Scales were later magnified with a microfiche reader, aged by counting annuli, and measured to the nearest millimeter from the focus to the anterior edge of each annulus and the focus to the anterior edge of the scale along the longest axis (Jearld 1983). To back-calculate length at age, we used the Fraser–Lee model with a standard intercept of 35 mm, as supported by Klumb et al. (1999).

From 1998 to 2002, we collected diet data by employing pulsed gastric lavage (Light et al. 1983) on a systematic subsample of 150-mm and larger smallmouth bass (Table 1), for a total sample of 4,135 predators. The systematic subsample consisted of lavaging every other fish or every third fish, depending on the expected number of fish captured, to examine a minimum of 20 fish a day throughout each section. Diet samples were placed in Whirl-Pak bags with 10 mL of a saturated sodium bicarbonate solution and were frozen on dry ice. Samples remained frozen in a laboratory freezer until ready for examination within 1–3 months.

Stomach samples were thawed, weighed to the nearest 0.1 g wet weight, immersed in a porcine pancreatin solution, and placed in a drying oven at 40°C for 2–24 h depending on the size and condition of the sample. We used a key of diagnostic bones for accurate identification of prey species (Frost 2000). When prey fish were too digested for direct measurements of FL, we back-calculated their lengths based on measurements of the appropriate diagnostic bones and the equations found in Hansel et al. (1988), as well as some equations presented here (Table 2), to identify the minimum, maximum, and mean sizes of fish consumed by smallmouth bass. Our equations (Table 2) were developed to increase our ability to calculate prey lengths by use of the otolith, lingual plate, maxillary, and parasphenoid bones (Norden 1961) when other diagnostic bones were not present. All measurements for our equations were taken along the longest axis of each bone. We also calculated the relative lengths of prey fish (%) by dividing each prey length by the predator length and multiplying this value by 100.

TABLE 1.—Number of Yakima River smallmouth bass examined for stomach contents in each size-group collected from 1998 to 2002.

Size-group (mm FL)	1998	1999	2000	2001	2002
150–199	65	313	473	149	315
200–249	135	447	189	193	217
250–299	88	165	137	39	158
300–349	71	129	80	19	180
350–399	57	106	69	13	51
400–449	14	62	43	9	35
450–549	8	30	35	12	29

To estimate smallmouth bass consumption of salmonids, we used the same meal turnover method presented in Fritts and Pearsons (2004), calculated separately for each 50-mm size-group of smallmouth bass. The number of hours to 90% evacuation from the stomach (ET_{90}) for all food items combined was calculated based on the following equation from Rogers and Burley (1991):

$$\mathrm{ET}_{90} = 24.542 \cdot (S^{0.29} e^{-0.15T_2} W^{-0.23}) \cdot 24,$$

where S = meal weight (g), T_2 = mean temperature (°C) of the 24-h period starting at 1100 hours on the previous day (Fritts and Pearsons 2004), and W = predator weight (g). This was calculated for each day during the spring by use of daily water temperatures, the meal weight, and the weight of each predator collected during that week. This evacuation time was used in the equation presented by Ward et al. (1995) to estimate the consumption rate, C (salmonids·predator^{-1}·d^{-1}):

$$C = n(24/\mathrm{ET}_{90}),$$

where n = the number of salmonids observed in each predator gut sample. This was calculated daily for each predator collected during the week of interest. The mean consumption rate for each size-group of smallmouth bass during each week was then extrapolated by the estimated weekly abundance of each smallmouth bass size-group in each study section (PE_{SC}) and the fraction (F) of those predators that contained a salmonid in the gut. This resulted in an estimate of total salmonid consumption per day by each predator size-group in each section (SE), namely,

$$\mathrm{SE} = \mathrm{PE}_{\mathrm{SC}} \cdot F \cdot C.$$

TABLE 2.—Parameters of regressions ($y = a + bx$) between diagnostic bone measurements (mm) and fork length (FL; mm) of Chinook salmon prey found in smallmouth bass stomachs and the ranges of prey lengths used in the regressions. All bone measurements were taken along the longest axis.

Diagnostic bone	N	a	b	FL	R^2
Lingual plate	13	−7.2456	21.544	30–124	0.93
Maxillary	15	−0.2085	9.2615	30–138	0.96
Otolith	30	−4.6229	38.913	30–138	0.93
Parasphenoid	10	−3.5422	6.8755	30–82	0.94

These estimates were further extrapolated to obtain an estimate of consumption for each study reach (S_{tot}), namely,

$$S_{\text{tot}} = (\text{SE}/\text{SL}) \cdot \text{RL},$$

where SL = the length of the study section (km) and RL = the length of the respective reach (km). The two reach estimates were summed to obtain the estimated daily consumption of salmonids in the lower 68 km of the Yakima River.

Linear regression was used to determine the relationships between (1) the mean estimated predator abundance and predator size-group, (2) the percent occurrence of salmonids in the gut samples over the 5-year period and predator size-group, (3) the relative prey length and predator length, and (4) the consumption of salmonids for each year and predator size-group. Predator size was the independent variable in all of the linear regressions. All statistical tests were considered significant at P-values less than 0.05. All data tested with linear regression met the assumption of normality based on the Kolmogorov–Smirnov goodness of fit of the residuals to a normal distribution ($P > 0.05$). The salmonid consumption data were log transformed ($\log[y + 1]$) prior to regression analysis to meet the assumption of normality. We were unable to transform the prey length data to meet the assumption of normality, so we did not test for a relationship between smallmouth bass length and salmonid prey length.

Results

Consumption of salmonids by smallmouth bass was inversely related to smallmouth bass length ($F_{1,33} = 33.82$, $P < 0.001$; Table 3). The 150–199-mm smallmouth bass consumed the highest proportion of salmonids in 4 of the 5 years studied (Table 3). Smallmouth bass of the 150–199-mm size-group consumed an average of 42.9% of the salmonids consumed by this species from 1998 to 2002; the 200–249-mm size-group consumed 26.7%. Overall, most of the salmonids were consumed by smallmouth bass smaller than 250 mm, and the vast majority was consumed by smallmouth bass smaller than 300 mm (mean of 83.6% over the 5-year period) (Table 3).

The inverse relationship between the number of salmonids consumed and the size of smallmouth bass was related to the abundance and diet composition of different smallmouth bass size-classes. The mean abundance of smallmouth bass from 1998 to 2002 decreased with increasing size ($F_{1,5} = 15.66$, $P = 0.01$; Table 4). Salmonids were less common in the guts of larger smallmouth bass than in the guts of smaller individuals ($F_{1,5} = 18.99$, $P = 0.007$), and larger smallmouth bass were less likely to contain food items than were smaller smallmouth bass (Table 5). We found that smallmouth bass collected in the Yakima River attained mean FLs of 90 mm at age 1, 148 mm at age 2, 207 mm at age 3, 254 mm at age 4, and 301 mm at age 5.

The relative length of salmonids consumed by smallmouth bass decreased with increasing predator

TABLE 3.—Estimated consumption of salmonids by smallmouth bass for each predator size-group collected from 1998 to 2002 in the lower 68 km of the Yakima River. The mean cumulative percent consumption is also included.

Size-group (FL; mm)	1998	1999	2000	2001	2002	Cumulative percent consumption
150–199	159,386	17,232	51,209	39,581	45,186	42.9
200–249	65,310	31,368	30,174	31,776	35,715	69.6
250–299	34,183	14,364	9,443	27,787	16,037	83.6
300–349	2,328	17,526	8,552	11,726	18,101	91.6
350–399	10,812	5,675	7,348	7,511	6,259	96.8
400–449	1,161	10,786	0	0	493	98.5
450–549	0	0	634	10,254	244	100.0

TABLE 4.—Mean estimated abundance and mean percent abundance for each size-group of smallmouth bass in two sections of the Yakima River sampled during 1998–2002.

Size-group (FL; mm)	Mean estimated abundance	Mean percent abundance
150–199	1,586	42.2
200–249	748	19.9
250–299	410	10.9
300–349	459	12.2
350–399	298	7.9
400–449	157	4.2
450–549	99	2.6

length ($F_{1,\ 471} = 97.57$, $P < 0.001$) and varied from a minimum of 7.3% to a maximum of 56.6% (Figure 1). The mean relative length of salmonids consumed by smallmouth bass was 25.0%. Only 3.6% of the smallmouth bass that contained fish prey consumed a salmonid larger than or equal to 100 mm (Figure 1), which is the smallest-sized fish we would classify as a spring Chinook salmon in the lower Yakima River (Fritts and Pearsons 2004). The size range of salmonids consumed by smallmouth bass was 22–153 mm, and the mean size consumed was 59 mm (Figure 1).

Discussion

We were surprised that the smallest size-class of smallmouth bass that we studied was the greatest consumer of salmonids. We expected that the abundance of small smallmouth bass would be much higher than that of large individuals, but we did not expect the rate of salmonid consumption to be so much higher in smaller individuals than in larger individuals. Knowledge of both abundance and consumption rate is necessary to provide a compelling assessment of predation risk. Unfortunately, relatively few studies have assessed size-based predation risks, particularly those posed by nonnative predators. This shortcoming is probably caused more by the difficulty of estimating abundance rather than by the difficulty of collecting diet information. For example, many studies have reported the diet composition of nonnative smallmouth bass (Poe et al. 1991; Vigg el al. 1991; Tabor et al. 1993; Zimmerman 1999), but few have incorporated abundance estimates (Rieman et al. 1991). Fortunately, there is a vast amount of literature on predation by northern pikeminnow in the Columbia River basin (Rieman and Beamesderfer 1990; Poe et al. 1991; Vigg et al. 1991), which allowed us to compare the relative risks to salmonids posed by native and nonnative predators.

The introduction of smallmouth bass to the Yakima River appears to have changed the size-based predation risk dynamics that were historically present in the lower part of the basin. In contrast to northern pikeminnow, one of the predominant native predators in the Columbia River basin, in smallmouth bass the consumption of salmonids was negatively related to predator length. Most of the salmonids were consumed by smallmouth bass smaller than 250 mm, which were more likely to contain salmonid prey in their diet and were by far the most abundant in the Yakima River. Northern pikeminnow in the Columbia River are not highly predaceous on salmonids until they attain a length of 250 mm, and the incidence of salmonids in the diet is positively correlated with northern pikeminnow size (Poe et al. 1991; Vigg et al. 1991). Rieman and Beamesderfer (1990) modeled potential predation by northern pikeminnow age-classes and concluded that intermediate and older age-classes contributed most (>50%) to the simulated predation in an unexploited population. These age-classes corresponded to fish larger than 400 mm. The Rieman and Beamesderfer (1990) model's conclusions are contrary to our findings for smallmouth bass in the lower Yakima River. Historically, the greatest predation threat to juvenile salmonids in the lower Yakima River was from northern pikeminnow larger than 400 mm, but now smallmouth bass less than 250 mm pose the greatest threat. It is unknown whether salmonids have rapidly adapted to recognize the change in predation risk associated with predators of different sizes, but a lack of adaptation could influence survival.

TABLE 5.—Mean percent occurrence of prey items in the guts of smallmouth bass collected in the Yakima River from 1998 to 2002. The invertebrate column does not include crayfish.

Size-group (FL; mm)	Prey type				Empty stomachs (%)
	Salmonid	Nonsalmonid	Crayfish	Invertebrate	
150–199	11.9	7.8	6.7	53.9	26.5
200–249	15.3	14.8	14.8	37.1	27.8
250–299	13.7	17.9	18.3	27.3	35.1
300–349	10.0	14.1	16.7	21.4	45.0
350–399	8.1	8.1	8.8	20.3	53.9
400–449	7.4	11.1	14.2	17.3	50.6
450–549	3.6	15.2	7.1	15.2	60.7

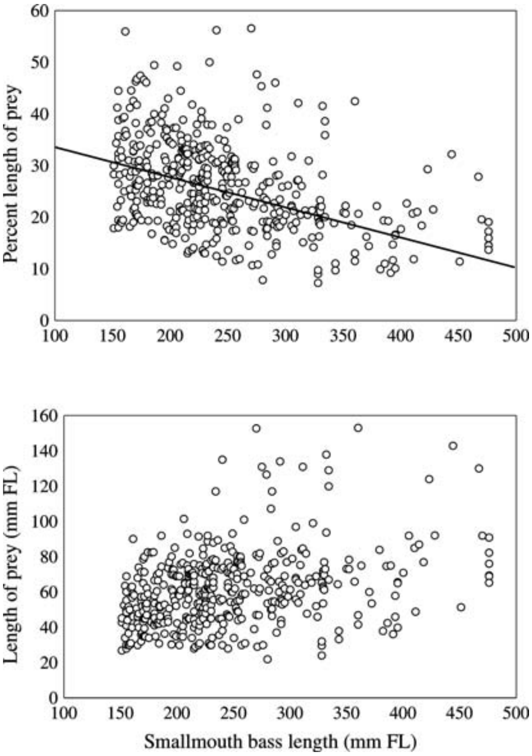

FIGURE 1.—The relative percent length ([prey length/predator length] × 100) of salmonid prey versus smallmouth bass predator length (upper panel) and salmonid prey fork length versus predator length (lower panel) from samples collected in the lower Yakima River from 1998 to 2002. The simple linear regression line is included in the upper panel ($F_{1,\,471} = 97.57$, $P < 0.001$, $R^2 = 0.17$) but is absent from the lower panel because the data were nonnormally distributed.

The introduction of smallmouth bass may have also changed the predation risk to different sizes of salmonids. Smallmouth bass have the ability to consume salmonids that are up to 56.6% of predator FL; if that proportion also applies to larger smallmouth bass, then a 400-mm smallmouth bass could consume salmonids larger than 225 mm. Although smallmouth bass have the ability to consume large juvenile salmonids, we found that few large smallmouth bass consumed salmonids. The majority of salmonids were consumed by smallmouth bass that were smaller than 250 mm, and smallmouth bass of this size could only consume salmonids smaller than approximately 140 mm. Northern pikeminnow in the Columbia River were found to consume larger salmonids as they increased in size, and many prey were yearling salmonids (Poe et al. 1991; Zimmerman 1999). Poe et al. (1991) found that 400-mm northern pikeminnow could consume salmonids with FLs up to 202 mm. Because there is also a positive relationship between northern pikeminnow size and salmonid consumption and because northern pikeminnow larger than 400 mm consume the majority of salmonids, larger juvenile salmonids are at a greater risk of predation from northern pikeminnow than from smallmouth bass. We speculate that in the past, larger salmonids such as spring Chinook salmon, coho salmon, and steelhead were at a greater risk of predation in the lower Yakima River than presently, whereas ocean-type Chinook salmon are now at the greatest risk.

The age at which smallmouth bass become piscivorous is also considerably earlier than that of northern pikeminnow. Smallmouth bass become piscivorous at about 100–150 mm, whereas northern pikeminnow become piscivorous at about 200–250 mm (Poe et al. 1991; Vigg et al. 1991). Smallmouth bass in the adjacent Hanford Reach of the Columbia River can attain a length of 300 mm during their third year of life (Henderson and Foster 1956). Our analysis of back-calculated length at age based on scales collected during March–June in the Yakima River indicate that smallmouth bass reach mean FLs of 149 mm at age 2 and 311 mm at age 5. Analyses of northern pikeminnow scales from the Columbia River indicate that these predators reach 250 mm at the age of 4 or 5 (Rieman and Beamesderfer 1990; Parker et al. 1995). In short, smallmouth bass become piscivorous approximately 2 or 3 years earlier than do northern pikeminnow.

It would have been advantageous for us to examine a representative sample of gut contents from smallmouth bass smaller than 150 mm so that we could determine the minimum size at which they become predaceous on salmonids in the lower Yakima River. Poe et al. (1991) found that fish were not an important prey category for smallmouth bass in the Columbia River until the smallmouth bass reached 100 mm. Using the mean relative length of salmonids ingested by 150–159-mm smallmouth bass (25%), we estimate that a 100-mm smallmouth bass could, if given the opportunity, easily consume a fish in the 30–35-mm size range, which is the size of newly emerged fall Chinook salmon.

It is clear from this study that introduction of nonnative piscivores can have unanticipated negative consequences. The size dynamics of predation risk have been altered relative to the historic dynamics that were present when native northern pikeminnow were the key predators. Smallmouth bass become piscivorous 2–3 years earlier than northern pikeminnow. Salmonid consumption is negatively related to smallmouth bass size, and this relationship is opposite that of northern pikeminnow; the risk to different salmonid life history types has therefore changed due to the establishment of smallmouth bass.

Acknowledgments

We owe thanks to a number of people who have assisted in the collection of this data over the years. Those individuals include Jason Allen, Eric Bartrand, Vernon Bogar, Kenneth Ham, Jeff Jackson, Brenda Ben James, Christopher Johnson, Geoff McMichael, Michael Schmuck, Phillip Smith, and Gabriel Temple. Geoff McMichael was also instrumental in the initial design and refinement of this study, and Kenneth Ham provided assistance in mathematics and modeling. Conrad Frost and James Petersen of the U.S. Geological Survey's Columbia River Research Laboratory provided valuable bone keys and training that made this work possible. Comments from Charity Davidson, Daniel Hayes, Christopher Johnson, Gabriel Temple, and three anonymous reviewers greatly improved the quality of this manuscript. We owe special thanks to David Byrnes of the Bonneville Power Administration (BPA) for helping to secure funding for this project. This work was funded by the BPA as part of the Yakima Klickitat Fisheries Project through a contract to the Washington Department of Fish and Wildlife's Yakima Species Interactions Studies.

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