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Response of Smallmouth Bass to Sustained Removals of Northern Pikeminnow in the Lower Columbia and Snake Rivers

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Abstract.—We describe the response of smallmouth bass *Micropterus dolomieu* density, year-class strength, consumption of juvenile salmonids *Oncorhynchus* spp., mortality, relative weight, and growth to sustained removals of northern pikeminnow *Ptychocheilus oregonensis* in the lower Columbia and Snake rivers. Although fishery exploitation of northern pikeminnow (250 mm fork length and larger) averaged 12.1% annually from 1991 to 1996, we detected no response by smallmouth bass. Density of smallmouth bass varied among years, but we found no evidence of increased density concurrent with removals of northern pikeminnow. Year-class strength of smallmouth bass also varied, and variations were similar among areas; however, we found no trend of increasing year-class strength. Consumption of juvenile salmonids by smallmouth bass was zero for 74 of our 104 estimates and did not appear to increase over time. Estimates of mortality varied among areas, but we found no differences among years for any area. Relative weight and growth also varied among years, but we found no increases corresponding to removals of northern pikeminnow. Our estimates of density, consumption, mortality, and growth were similar to estimates made prior to northern pikeminnow removals. Spatial separation of smallmouth bass and most juvenile salmonids may limit increases in predation, even if exploitation of northern pikeminnow increases. The lack of response by smallmouth bass increased confidence in the hypothesis that sustained removal of northern pikeminnow increases survival of juvenile salmonids.

A large-scale management program for northern pikeminnow *Ptychocheilus oregonensis* was begun in 1990 to increase survival of juvenile salmonids *Oncorhynchus* spp. in the Columbia River basin (Parker et al. 1995; Beamesderfer et al. 1996). The program consists of both sport and agency-operated fisheries that target northern pikeminnow (minimum length, 250 mm fork length—approximately the size northern pikeminnow become important predators on juvenile salmonids: Poe et al. 1991). The goal of the program is to sustain annual exploitation of northern pikeminnow 250 mm and larger at 10–20%, which may reduce losses of juvenile salmonids by as much as 50% (Rieman and Beamesderfer 1990). Over 1.1 million northern pikeminnow were removed by this program from 1990 to 1996, and estimates of annual exploitation in the lower Columbia and Snake rivers have averaged 12.1% (range, 8.1–15.5%; Friesen and Ward 1999).

Although predation on juvenile salmonids by native northern pikeminnow has been well documented throughout the lower Columbia River basin (Rieman et al. 1991; Ward et al. 1995), other predators such as introduced smallmouth bass *Micropterus dolomieu* are also present. Zimmerman and Parker (1995) found that smallmouth bass are distributed throughout the lower Columbia and Snake rivers with densities highest in Snake River reservoirs. Beamesderfer and Rieman (1991) estimated the number of smallmouth bass of 200 mm fork length and larger in John Day Reservoir, Columbia River, to be approximately 38,000 (1.8/ha) compared with approximately 103,000 northern pikeminnow of 250 mm and larger. Curet (1993) estimated the number of smallmouth bass age 1 or older in Lower Granite Reservoir, Snake River, to be approximately 47,000 (13.0/ha), the number of 250+-mm smallmouth bass to be approximately 8,000, and the number of 250+-mm northern pikeminnow to be approximately 16,000. Densities of smallmouth bass are lower than the minimum of 16 fish/ha reported by Carlander (1977). Rieman et al. (1991) estimated that smallmouth bass were responsible for only 7% of the total predation on juvenile salmonids in John Day Reservoir; however, Tabor et al. (1993) found that smallmouth bass may become more important predators when wild subyearling chinook salmon *Oncorhynchus tshawytscha* are abundant, usually in late spring and summer. These salmon are of suitable forage size and their habitat often overlaps with that of smallmouth bass.

The effects of large-scale removals of northern pikeminnow on smallmouth bass are unknown and

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difficult to predict. If mortality of juvenile salmonids is significantly reduced by sustained removals of northern pikeminnow, predation by smallmouth bass may be enhanced due to increased availability of juvenile salmonid prey. A change in growth rate might accompany increased consumption of juvenile salmonids, altering size distributions and abundance. Johnson (1977) and Hayes et al. (1992) found that populations of yellow perch *Perca flavescens* were enhanced by intensive removals of white sucker *Catostomus commersoni*; however, removals were far more intensive (80–85% of adult white suckers), and competition between yellow perch and white sucker was strongly indicated. Diets of smallmouth bass and northern pikeminnow overlap (Poe et al. 1991; Zimmerman 1999, this issue), but differences in distribution and temperature preferences between the two species may limit potential competition. Although both species use littoral areas extensively, densities of smallmouth bass are generally highest in forebays immediately upstream from dams and in midreservoir areas (Zimmerman and Parker 1995), whereas northern pikeminnow densities are generally highest in tailraces immediately downstream from dams and lowest in midreservoir areas (Ward et al. 1995). Smallmouth bass prefer temperatures of 21–27°C (Wydoski and Whitney 1979) and northern pikeminnow prefer 16–22°C (Brown and Moyle 1981). Digestion rates increase with increasing water temperature for both species; however, digestion rates are slower for smallmouth bass than for northern pikeminnow under comparable conditions (Rogers and Burley 1991).

Our objective was to determine if smallmouth bass populations responded to sustained removals of northern pikeminnow. We examined smallmouth bass density, year-class strength, consumption of juvenile salmonids, mortality, relative weight, and growth over a period of years coinciding with the management program. Although northern pikeminnow removals began concurrently with our data collection, few, if any northern pikeminnow were removed from most areas until after our data collection had begun (Parker et al. 1995; Knutsen and Ward 1999, this issue). Information comparing smallmouth bass populations before and after sustained removals of northern pikeminnow will help assess the effectiveness of the removal program in reducing predation on juvenile salmonids.

Methods

Data collection and laboratory analysis.—We used boat electrofishing from 1990 through 1996 to collect smallmouth bass in four areas in the lower Columbia and Snake rivers: the unimpounded Columbia River downstream from Bonneville Dam, Bonneville Reservoir, John Day Reservoir, and Lower Granite Reservoir (for a map and description of the study area see Zimmerman and Ward (1999, this issue). Because the large size of each area precluded complete sampling, we partitioned each area into sampling reaches. The area downstream from Bonneville Dam was subdivided into three sampling reaches: river kilometer (Rkm) 115–121, Rkm 172–178, and Rkm 190–197. We sampled in three 6-km long reaches in Bonneville and John Day reservoirs corresponding to forebay (immediately upstream from the dam), midreservoir, and tailrace (immediately downstream from The Dalles Dam [Bonneville Reservoir] or McNary Dam [John Day Reservoir]). In Lower Granite Reservoir, we sampled the transition zone (Rkm 222–228) between the uppermost portion of the reservoir and the free-flowing reach of the Snake River downstream from Hells Canyon Dam. Sampling effort was divided equally between spring (April–June) and summer (July–August). Details of electrofishing methods and gear specifications are given by Zimmerman and Ward (1999).

We measured fork length (mm) and weight (g) of and collected scales from all smallmouth bass captured. Stomach contents from smallmouth bass 200 mm fork length and longer were pumped with a modified Seaburg stomach sampler (Seaburg 1957). All stomach samples were kept on ice and later frozen until subsequent laboratory analysis.

We used standard methods to determine ages of smallmouth bass from scales (Jearld 1983). Data were pooled so that for each reservoir and the Columbia River downstream from Bonneville Dam, fish were grouped by 25-mm fork length intervals, and scales from 20 individuals were selected randomly from each group to be aged.

In the laboratory, stomach contents were thawed and weighed to the nearest 0.01 g. To speed processing of samples, we first digested them with a solution of lukewarm tap water, 2% (wet weight) pancreatin (8× porcine digestive enzyme), and 1% (wet weight) sodium sulfide. The solution was poured into sample bags until contents were submersed; then the bags were sealed and contents were mixed to ensure that all food was in contact with the solution. Samples were placed in a desiccating oven at 40°C for 24 h. Digested samples were poured through a 425-μm sieve and rinsed with tap water. Diagnostic bones of prey fish were examined under a dissecting microscope and iden-

TABLE 1.—Mean catches of smallmouth bass 200 mm fork length and larger during 15-min electrofishing runs in the Columbia and Snake rivers, transformed by $\log_{10}$(catch + 1). Values of $P \leq 0.05$ indicate significant differences between spring and summer catch rates, all years combined; RKm is river kilometer.

Area, reach	Years sampled	Mean catch (SD) Spring	Mean catch (SD) Summer	P
Downstream from Bonneville Dam				
Rkm 115–121	1992, 1994–1996	0.01 (0.05)	0.04 (0.10)	0.01
Rkm 172–178	1992, 1994–1996	0.29 (0.36)	0.12 (0.19)	<0.01
Rkm 190–197	1992, 1994–1996	0.18 (0.27)	0.11 (0.18)	0.03
Bonneville Dam tailrace	1992, 1994–1996	0.15 (0.27)	0.14 (0.22)	0.84
Bonneville Reservoir				
Forebay	1990–1992, 1994–1996	0.06 (0.15)	0.06 (0.14)	0.97
Midreservoir	1990–1992, 1994–1996	0.21 (0.28)	0.13 (0.21)	<0.01
The Dalles Dam tailrace	1990–1992, 1994–1996	0.45 (0.39)	0.34 (0.29)	<0.01
John Day Reservoir				
Forebay	1990–1996	0.33 (0.31)	0.38 (0.31)	0.12
Midreservoir	1990–1996	0.45 (0.36)	0.35 (0.32)	<0.01
McNary Dam tailrace	1990–1996	0.09 (0.17)	0.11 (0.21)	0.26
Lower Granite Reservoir				
Rkm 222–228	1991, 1994–1996	0.45 (0.40)	0.29 (0.30)	<0.01

tified to the lowest possible taxon (Hansel et al. 1988). We enumerated prey fish consumed by adding the number of diagnostic bone pairs to remaining unpaired bones.

Catch rates.—We used catch per 15-min electrofishing run as an index of smallmouth bass density for each reach. Beamesderfer and Rieman (1988) found that electrofishing captured a wider size range of smallmouth bass than other gears, and Zimmerman and Parker (1995) concluded that electrofishing catch rates were higher than those of other gears. Because analysis of variance (ANOVA; $\alpha = 0.05$) of data transformed to $\log_{10}$(catch + 1) indicated that catch rates differed between spring and summer for many reaches (Table 1), we calculated mean catch rates and 95% confidence intervals separately for each season, then used ANOVA to compare mean transformed catch rates among years. We then used least-squares means analyses to determine where differences existed with $\alpha = 0.01$ to control possible increases in type I error associated with multiple testing (Neter et al. 1990).

Variation among years in physical conditions such as water depth and flow may influence electrofishing efficiency and therefore bias comparisons of density. To reduce potential bias, sampling was always concentrated in nearshore areas with depths less than 3 m. To evaluate effects of flow, we used correlation analysis to determine the relationship between flow and mean catch rate for spring and summer in the tailrace downstream from Bonneville Dam, the forebay and tailrace in Bonneville Reservoir, and the forebay and tailrace in John Day Reservoir (reaches near dams where daily flow information was available). We used mean flow for dates sampled at Bonneville Dam for the tailrace downstream from Bonneville Dam and in Bonneville Reservoir forebay, The Dalles Dam for Bonneville Reservoir tailrace, John Day Dam for John Day Reservoir forebay, and McNary Dam for John Day Reservoir tailrace (U.S. Army Corps of Engineers, unpublished data).

Year-class strength.—We used the method of El-Zarka (1959), described in detail by Knutsen and Ward (1999), to index relative year-class strength for cohorts of smallmouth bass. The index was developed by comparing the relative abundance of each year-class in catches from standardized sampling over a number of years. We examined the correlations of year-class strength with area and with years since implementation of northern pikeminnow removals (1990).

Consumption of juvenile salmonids.—Because direct estimates of consumption for multiple reaches and years would be prohibitive in time and cost, we developed an index to compare consumption of juvenile salmonids by smallmouth bass among years. Our consumption index is analogous to the consumption index for northern pikeminnow developed by Ward et al. (1995), which was highly correlated with direct estimates of consumption, and it is easily obtained so that laboratory effort is minimized. To validate our consumption index, we computed both the index and a direct estimate of consumption rate for reaches sampled in 1995 and 1996, and we used linear regression to examine the relationship between the index and consumption rate. We limited the regression to reaches where we found evidence of consumption, because inclusion of the many reaches with no evidence of consumption may have resulted in an overestimate of the correlation.

Rogers and Burley (1991) estimated the days to 90% digestion ($D90_i$) for smallmouth bass as

$$D90_i = 24.542 \cdot M_i^{0.29} \cdot e^{-0.15T} \cdot W^{-0.23}; \quad (1)$$

M_i = meal size (g) at time of ingestion of salmonid prey item i;
T = water temperature (°C);
W = predator weight (g).

The daily consumption rate (C) of juvenile salmonids by smallmouth bass could then be expressed as

$$C = 0.0407 \cdot e^{0.15T} \cdot W^{0.23} \cdot \sum_{i=1}^{n} M_i^{-0.29}. \quad (2)$$

However, this requires measurement of meal size M_i, which is time-consuming and difficult to quantify. Ward et al. (1995) found that substituting the product of the mean number of salmonids per gut (S) and the mean total gut weight (GW) for meal size resulted in a consumption index (CI) that was highly correlated with direct estimates of consumption. Therefore, a potential index of juvenile salmonid consumption by smallmouth bass would be

$$\mathrm{CI} = 0.0407 \cdot e^{0.15T} \cdot W^{0.23} \cdot (S \cdot \mathrm{GW}^{-0.29}). \quad (3)$$

To validate our index, we used a meal turnover-time method (Diana 1979) to directly estimate consumption rate at reaches sampled in 1995 and 1996:

$$C = (R \cdot p \cdot W)/\mathrm{SW}; \quad (4)$$

R = daily ration (% body weight/d);
p = proportion of diet (by weight) that is salmonid prey;
SW = mean salmonid prey weight (g) before digestion.

Daily ration (R) was estimated as

$$R = (M \cdot n)/(D90_i \cdot N); \quad (5)$$

M = average size of ingested meal (% body weight);
n = number of fish that contain food in the stomach;
N = total number of fish examined.

An estimate of original meal weight of fishes was based on lengths of prey fishes. Identity and original fork lengths of prey fishes were determined from diagnostic bones (Hansel et al. 1988); then original weights were estimated from length–weight regressions (Vigg et al. 1991). Original weights of other prey items were estimated by adjusting the observed nonfish weight with the same ratio used for fish weight (Tabor et al. 1993). Consumption rates were adjusted for diel feeding periodicity by assuming that smallmouth bass consumed 32% of their daily ration during the hours we sampled (Vigg et al. 1991).

Mortality.—To estimate mortality rates, we used age-specific catch of smallmouth bass from 1990 to 1996 to produce year-class-specific catch curves. However, age-specific catches for each year-class were biased by differences in sampling effort among years. To correct for these differences we (1) determined sampling effort (number of electrofishing runs) during each year that fish from a given year-class were collected, (2) left the age-specific catch for the year with highest effort unchanged, (3) determined the relative differences in effort between each of the other years and the year with the highest effort, and (4) increased age-specific catches by the same relative differences (Rieman and Beamesderfer 1990). We used analysis of covariance (ANCOVA; $\alpha = 0.05$) with year-class as the covariate to compare total instantaneous mortality, and we used least-squares-means analyses to test for differences among individual year-classes ($\alpha = 0.01$).

Relative weight.—We used mean relative weight (W_r) to compare fish condition among years: $W_r = 100(\text{observed weight})/W_s$, W_s being the length-specific standard weight of smallmouth bass. The standard weight equation defined by Kolander et al. (1993) for smallmouth bass at least 150 mm total length is

$$\log_{10}(W_s) = -5.239 + 3.200 \cdot \log_{10}(\text{total length}). \quad (6)$$

We computed 95% confidence intervals for each estimate of mean W_r, and used ANOVA ($\alpha = 0.05$) to compare differences in W_r among years for each reach. We used least-squares-means analyses to test for differences among individual years ($\alpha = 0.01$).

Growth.—We used scales collected from 1990 to 1996 to calculate annual growth increments of smallmouth bass from 1989 to 1995. We then used ANOVA ($\alpha = 0.05$) to compare mean growth increments of like-aged fish among years, and we used least-squares-means analyses to test for differences among individual years ($\alpha = 0.01$). We limited our analysis to ages 2 through 5 because these were the ages for which sample sizes were most complete.

Results

Catch Rates

Catch rates of smallmouth bass differed between spring and summer ($P \leq 0.05$) for 7 of 11 reaches sampled (Table 1). Catch was highest in spring at 6 of the 7 reaches. Because of these differences, we compared catch rates among years separately for each season.

Catch rates varied among years for 6 of 11 reaches in both spring (Figure 1), and summer (Figure 2). We found no evidence of increased catch of smallmouth bass at any reach in spring. Catch rate appeared to increase in the tailrace of Bonneville Reservoir, but catch from 1993 to 1996 did not differ from that in 1990. Differences among years downstream from Bonneville Dam were the result of high catches in one year. In summer, catch rate appeared to increase in the midreach of John Day Reservoir, but only the 1995 catch differed from that in 1990. Catch in Lower Granite Reservoir decreased after 1991.

Catch rates differed among years for both spring and summer in 4 of 11 reaches. In the tailrace of Bonneville Reservoir, the apparent increase in spring catches was not observed in summer. In the midreach of John Day Reservoir, the apparent increase in summer catches was not observed in spring. In Lower Granite Reservoir, an apparent trend of decreased catch rates was observed in both spring and summer.

We found no consistent relationship between catch rate and river flow (Table 2). In spring, catch rate increased with increased flow in three of five 5 reaches and decreased in the other two. In summer, catch rate increased with increased flow at one of five reaches and decreased at the other four. The relationship was significant ($P \leq 0.05$) for only one of five reaches in spring and for no reaches in summer.

Year-Class Strength

Year-class strengths of smallmouth bass were highly variable (Figure 3). Variations in year-class strength were all positively correlated among areas (Table 3) although only the correlation between Bonneville and John Day reservoirs was significant ($P \leq 0.05$). In most areas, strong year-classes from 1990 to 1992 were followed by a relatively weak year-class in 1993. We found no trend of increased year-class strength since implementation of northern pikeminnow removals in 1990 (Table 3).

Consumption of Juvenile Salmonids

Our proposed consumption index (CI) for smallmouth bass (equation 4) was linearly related to and highly correlated with direct estimates of consumption rate (CR):

$$\mathrm{CR} = -0.003 + 1.969(\mathrm{CI});$$

$r = 0.97$; $P \leq 0.01$. Ten reaches with evidence of consumption in 1995 and 1996 (Figures 4, 5) were included in the regression, incorporating a wide range of consumption indices (0.02–0.80) and consumption rates (0.03–1.65). We therefore used our index to evaluate consumption of juvenile salmonids by smallmouth bass from 1990 to 1996.

Consumption of juvenile salmonids was highly variable among reaches and seasons but was generally low (Figures 4, 5), even though sampling was scheduled to coincide with peak abundance of juvenile salmonids. The CI was zero for 74 of 104 estimates, including 22 of 39 with relatively large sample sizes (at least 30 smallmouth bass examined). Although spring consumption indices were especially low, we found consistent evidence of predation on juvenile salmonids in Lower Granite Reservoir and, to a lesser extent, in the forebay of John Day Reservoir. In summer, consumption was usually highest in the forebay of John Day Reservoir, and was also evident in the Rkm 190–197 reach downstream from Bonneville Dam. Most juvenile salmonids had migrated from Lower Granite Reservoir prior to our summer sampling. Although use of the consumption index precluded statistical analyses, we found no indication that consumption by smallmouth bass increased over time.

Mortality

Estimates of total instantaneous mortality were high but varied among areas (range, 0.61–1.63; Table 4). We found no significant differences in mortality among year-classes for any area, indicating that mortality did not decrease concurrently with removals of northern pikeminnow.

Relative Weight

Mean W_r of smallmouth bass varied among years for all areas (Figure 6); however, we found no evidence that condition of smallmouth bass has improved concurrently with removals of northern pikeminnow. In John Day Reservoir and downstream from Bonneville Dam, mean W_r was sig-

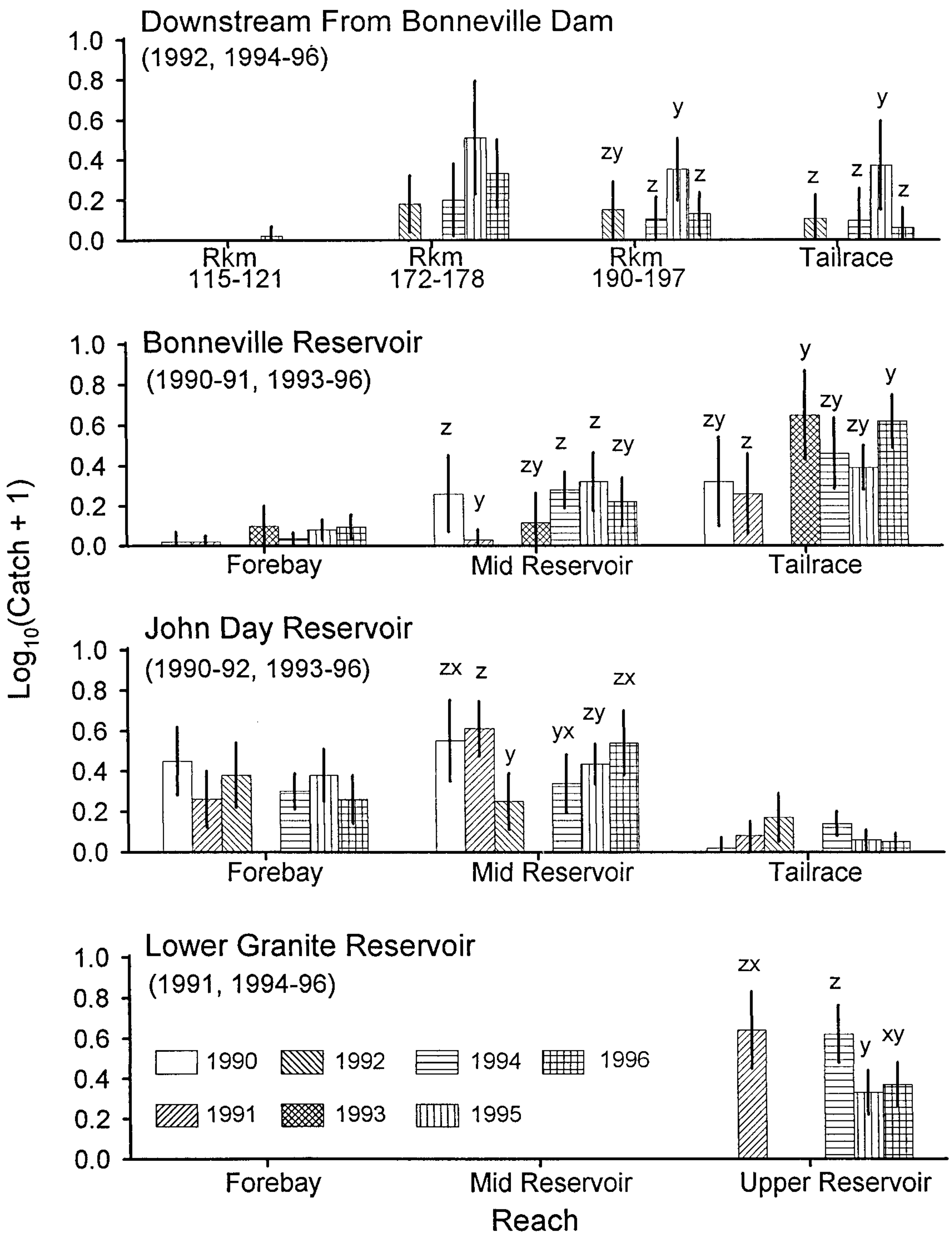

FIGURE 1.—Mean spring catches of smallmouth bass 200 mm fork length and larger in the lower Columbia and Snake rivers during 15-min electrofishing runs, transformed to $\log_{10}$(catch + 1). Data groups with letters contain significant differences in catch among years (ANOVA; $P \leq 0.05$); within these groups, catches without a letter in common differ ($P \leq 0.01$). Years sampled are indicated in parentheses. Vertical bars represent 95% confidence intervals; Rkm = river kilometer.

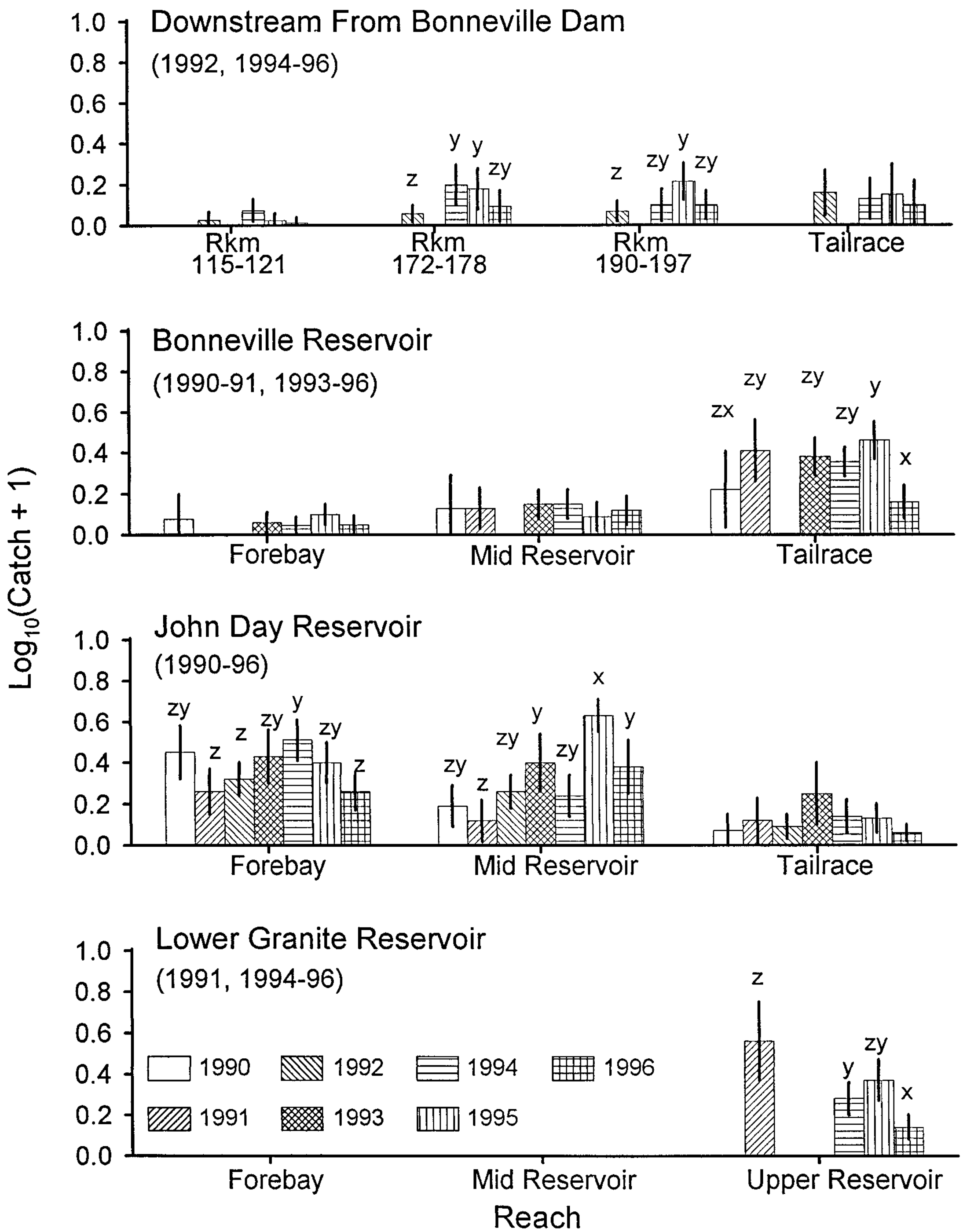

FIGURE 2.—Mean summer electrofishing catches of smallmouth bass in the lower Columbia and Snake rivers. Conventions are those of Figure 1.

TABLE 2.—Correlations (r) between mean catch rate of smallmouth bass 200 mm fork length and larger during 15-min electrofishing runs in the lower Columbia River, transformed by $\log_{10}$(catch + 1), and mean river flow (m^3/s) on dates sampled.

Area, reach	Spring		Summer	
	r	P	r	P
Downstream from Bonneville Dam				
Bonneville Dam tailrace	0.03	0.92	−0.81	0.19
Bonneville Reservoir				
Forebay	0.62	0.19	0.50	0.31
The Dalles Dam tailrace	0.54	0.27	−0.54	0.27
John Day Reservoir				
Forebay	−0.35	0.49	−0.52	0.23
McNary Dam tailrace	−0.85	0.03	−0.39	0.39

nificantly lower in 1995 and 1996 than in previous years. In Lower Granite Reservoir, mean W_r decreased each year sampled, so that mean W_r was significantly lower in 1996 than in 1991 and 1994. In Bonneville Reservoir, differences among years were due to a high mean W_r in 1994.

Growth

Annual growth of smallmouth bass varied among years for all ages in most areas (Figure 7); however, no temporal trends were evident. Growth in 1993 and 1995 was significantly less ($P \leq 0.01$) than growth in 1994 for all ages downstream from Bonneville Dam and in John Day and Lower Granite reservoirs. In Bonneville Reservoir, growth in 1993 and 1995 was less than growth in 1994 for ages 3 and 4. Growth in 1994 was similar to, and growth in 1995 was less than, growth during the first year sampled for all areas other than John Day Reservoir.

Discussion

We found no evidence of smallmouth bass response to sustained removals of northern pikeminnow. No increases in smallmouth bass density, year-class strength, consumption of juvenile salmonids, relative weight, or growth, or decreases in mortality have been realized concurrently with northern pikeminnow removals. An ideal study would have included comparisons to an area not subject to removals of northern pikeminnow or smallmouth bass; however, northern pikeminnow management included the entire lower Columbia and Snake rivers (Friesen and Ward 1999), precluding the possibility of an appropriate control area. Confidence in our results is enhanced by several years of data available for most areas and by comparison of our results with those from previous studies in the lower Columbia River basin.

Our catch rates of smallmouth bass were similar

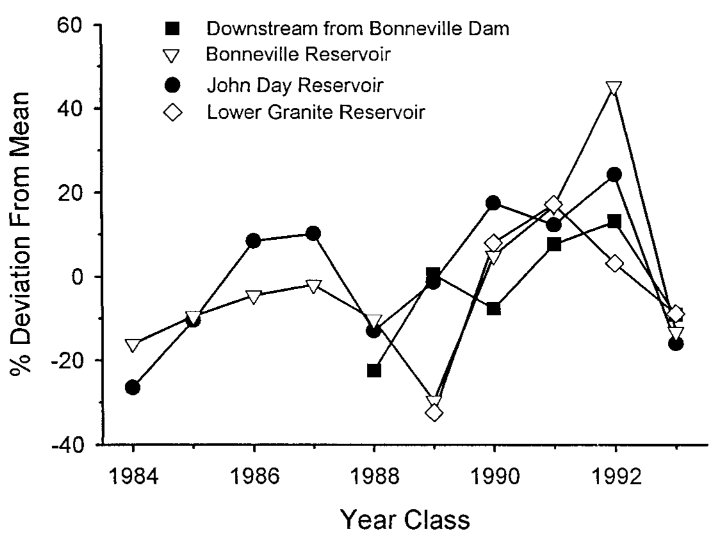

FIGURE 3.—Indexes of relative year-class strength for smallmouth bass in the lower Columbia and Snake rivers.

TABLE 3.—Correlations (r) of smallmouth bass year-class strength between sample areas and among years since implementation of northern pikeminnow removal began (1990). Correlation probabilities (P) are in parentheses.

Correlate	Year-class strength versus area: Bonneville Reservoir	John Day Reservoir	Lower Granite Reservoir	Year-class strength versus years of pikeminnow exploitation
Downstream from Bonneville Dam	0.60 (0.21)	0.47 (0.29)	0.40 (0.44)	0.44 (0.46)
Bonneville Reservoir		0.74 (0.02)	0.77 (0.13)	−0.13 (0.83)
John Day Reservoir			0.39 (0.45)	−0.71 (0.18)
Lower Granite Reservoir				−0.27 (0.66)

to those reported prior to removals of northern pikeminnow. Mean transformed catch per 15-min electrofishing run in John Day Reservoir from 1984 to 1986 (spring and summer combined) ranged from 0.35 to 0.40 in the forebay, from 0.31 to 0.44 in the midreservoir, and from 0.03 to 0.27 in the tailrace (Beamesderfer and Rieman 1991; Beamesderfer and Ward 1994), compared to our ranges (1990–1996, spring and summer combined) of 0.26–0.45 in the forebay, 0.29–0.58 in the midreservoir, and 0.05–0.25 in the tailrace. Our catch rates in Lower Granite Reservoir were lower than those reported by Bennett et al. (1983), who included fish smaller than 200 mm fork length.

The first evidence of any response by smallmouth bass would likely be changes in diet, which could then lead to changes in growth (Johnson 1977; Hayes et al. 1992). Although the exploitation rate of northern pikeminnow in John Day Reservoir averaged about 12% annually from 1990 to 1993 (Friesen and Ward 1999), Zimmerman (1999) found that the general diet of smallmouth bass has not changed concurrently with northern pikeminnow removals (Poe et al. 1991). Sculpins *Cottus* spp. remained the most common fish in the diet of smallmouth bass in lower Columbia River reservoirs, and crayfish (Decapoda) remained the most common nonfish prey item.

Our findings agree with those of Vigg et al. (1991), who found that in John Day Reservoir, consumption of juvenile salmonids by smallmouth bass was highest in the forebay. Information from Vigg et al. (1991) indicates that smallmouth bass consumption may have averaged 0.2–0.3 juvenile salmonids per day in the forebay during July, whereas we found consumption rates of 0.3–0.5 juvenile salmonids per day during summer in the forebay in 1995 and 1996. Our sampling was timed to coincide with peak abundance of juvenile salmonids (Zimmerman and Ward 1999), which probably explains the higher consumption rates. Conversely, consumption in the midreservoir and tailrace was lower than reported by Vigg et al. (1991).

Friesen and Ward (1999) estimated that potential predation by northern pikeminnow may have been reduced by 25% (range, 14–38%) since implementation of northern pikeminnow removals, which would presumably increase the number of juvenile salmonids potentially available to smallmouth bass. The apparent lack of increase in the consumption of juvenile salmonids by smallmouth bass in most reaches may be a result of spatial separation between predator and prey. Gray and Rondorf (1986) suggested that the potential for predation is high when juvenile salmonids occur in littoral areas that overlap with the preferred habitat of smallmouth bass, and Tabor et al. (1993) reported that high levels of predation in one area of the lower Columbia River were due to the overlap in habitat between smallmouth bass and subyearling chinook salmon of suitable forage size. Curet (1993) noted that subyearling chinook salmon move offshore between late May and late June in Lower Granite Reservoir and may become spatially separated from smallmouth bass. In general, subyearling chinook salmon increase in size and travel further from shore as they migrate downstream, and other juvenile salmonids are larger and travel further from shore than subyearling salmon (Johnsen and Simms 1973). Therefore, even if exploitation of northern pikeminnow increases, substantial increases in predation by smallmouth bass may be precluded by the behavior of most juvenile salmonids.

Our consumption index proved an efficient method of evaluating the temporal and spatial dynamics of predation on juvenile salmonids. Simpler measures, such as the frequency of occurrence of juvenile salmonids in smallmouth bass stomachs, are useful for comparisons of diet (Zimmerman 1999), but are not appropriate for evaluations

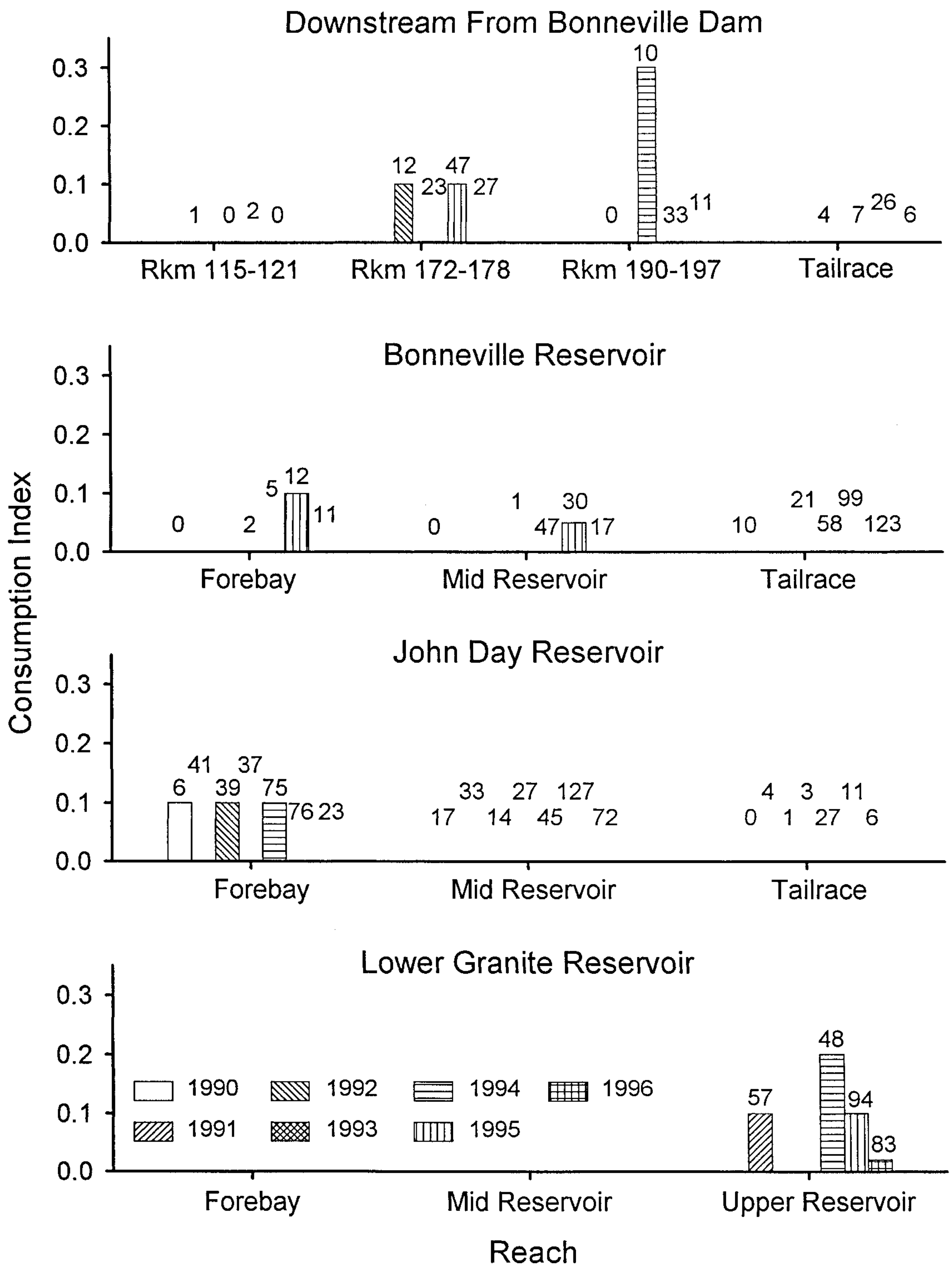

FIGURE 4.—Spring consumption indexes for smallmouth bass in the lower Columbia and Snake rivers.. Number of fish examined is shown above each bar. Years sampled are the same as shown in Figure 1; Rkm = river kilometer.

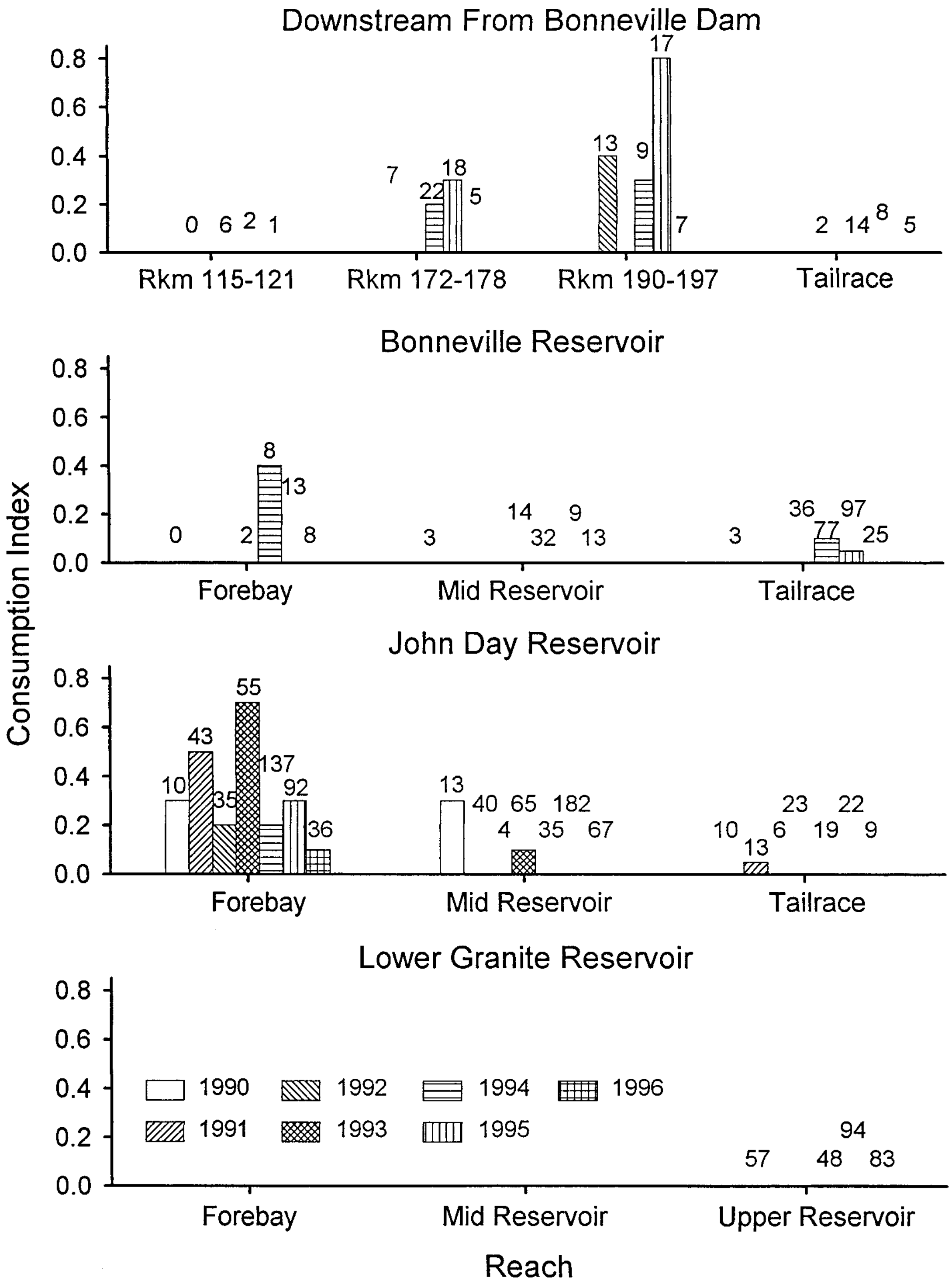

FIGURE 5.—Summer consumption indexes for smallmouth bass in the lower Columbia and Snake rivers. Conventions are those of Figure 4.

TABLE 4.—Age-specific catches (numbers of fish, corrected for effort) and estimates of total instantaneous mortality (Z) for year-classes of smallmouth bass in the lower Columbia and Snake rivers. We found no significant differences in mortality rate among year-classes for any area ($P > 0.01$).

Area, year-class	Catch at age 3	4	5	6	Z
Downstream from Bonneville Dam					
1989	61		10	7	0.75
1990		26	15	1	1.63
1991	52	43	5		1.17
Bonneville Reservoir					
1987	60	26		5	0.83
1988	83		25	9	0.72
1989		87	23	10	1.08
1990	208	74	25	10	1.02
1991	118	88	35		0.61
John Day Reservoir					
1986		63	31	9	0.97
1987	136	67	26	13	0.80
1988	144	138	49	13	0.82
1989	333	155	51	22	0.93
1990	225	160	69	19	0.83
1991	280	188	56		0.80
Lower Granite Reservoir					
1990		153	36	10	1.36
1991	272	91	23		1.24

of consumption because they do not account for differences in predator weight, prey weight, or water temperature, all of which affect digestion rates. Conversely, estimates of absolute predation are prohibitive in time and cost, especially when data are collected for multiple years and sampling areas. The high degree of correlation between the consumption index and direct estimates of consumption rate verifies the usefulness of the index.

Mortality estimates from standard catch curves are subject to uncertainty because of variations in year-class strength; however, reliability of our mortality estimates is enhanced because we used catch curves constructed from the catch of individual year-classes over a number of years. Our estimates of mortality are similar to estimates made prior to removals of northern pikeminnow. Connolly and Rieman (1988) estimated mean mortality (total instantaneous) for the 1977–1981 year-classes to be 0.75 (range, 0.40–0.92) in lower John Day Reservoir, a little lower than our mean of 0.86 (range, 0.80–0.97) for the 1986–1991 year-classes.

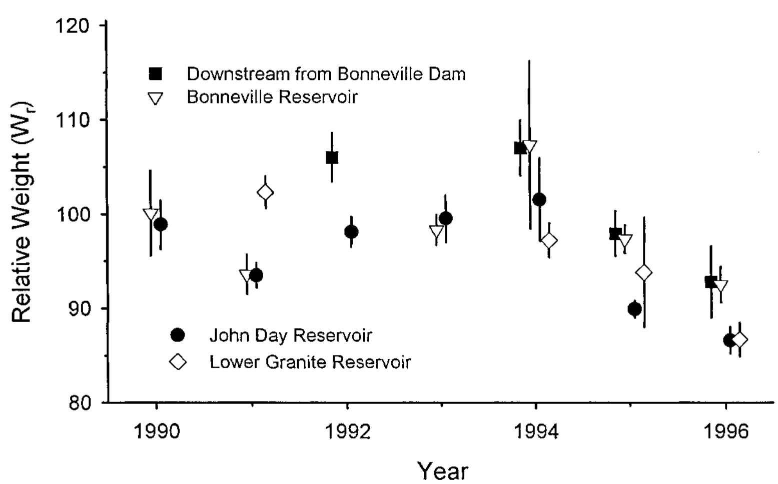

FIGURE 6.—Mean relative weight (W_r) of smallmouth bass in the lower Columbia and Snake rivers. Vertical bars represent 95% confidence intervals. Differences among years are significant ($P \leq 0.05$) for all areas.

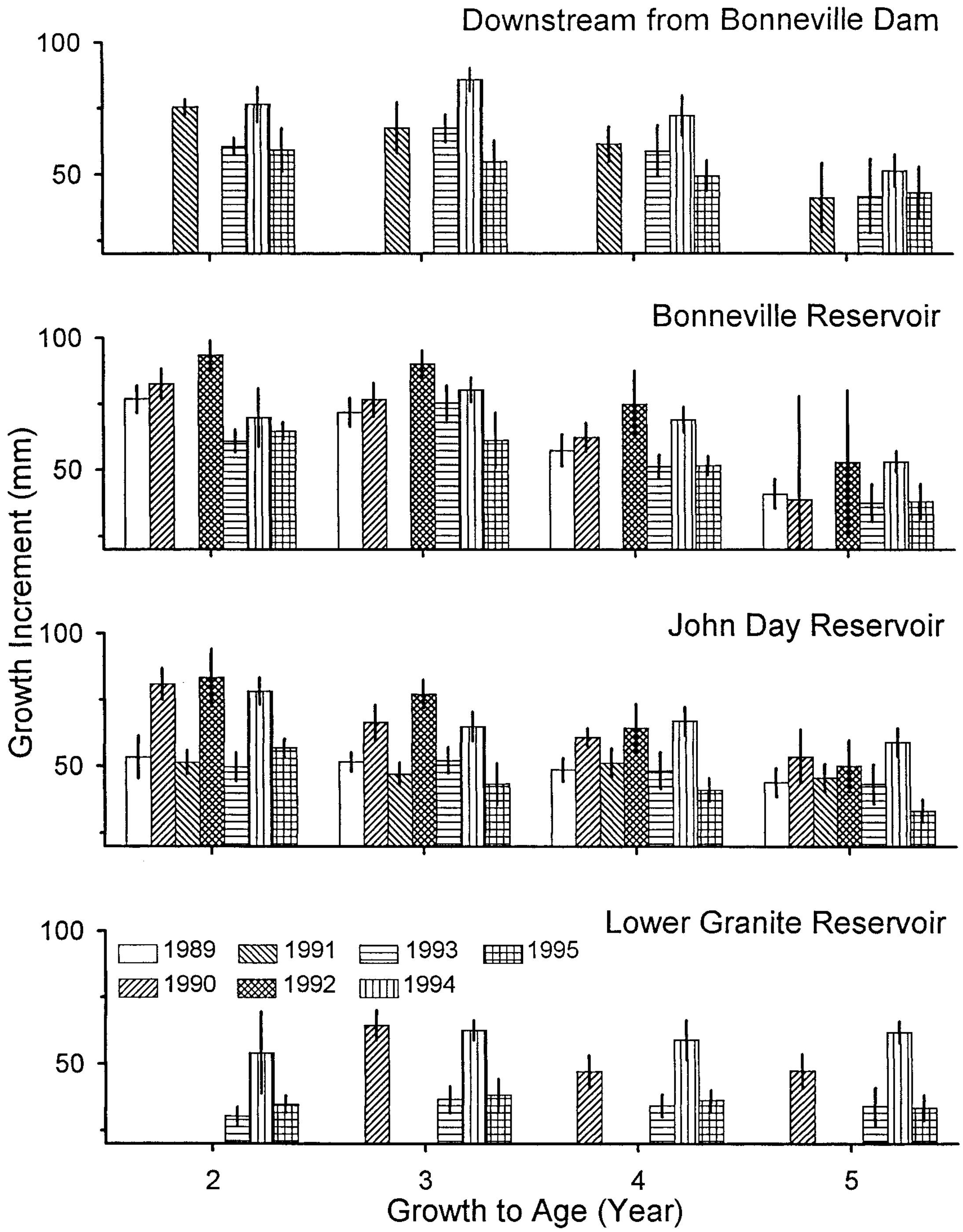

FIGURE 7.—Mean annual growth increments for smallmouth bass aged 2–5 in the lower Columbia and Snake rivers. Vertical bars represent 95% confidence intervals. Differences among years are significant ($P \leq 0.05$) for all ages except age 5 downstream from Bonneville Dam.

Bennett et al. (1983) estimated mortality in Little Goose Reservoir, Snake River, to be 1.27, between our estimates of 1.24 and 1.36 for the adjacent Lower Granite Reservoir.

Higher mortality in the Snake River may be due to higher exploitation. Although Lower Granite Reservoir has about 50% the surface area of Bonneville Reservoir and about 20% that of John Day Reservoir, information from Bennett et al. (1983) suggests that in 1980, angler effort for smallmouth bass in Lower Granite Reservoir was approximately double that expended annually in Bonneville Reservoir and 50% that expended annually in John Day Reservoir from 1993 to 1995 (Washington Department of Fish and Wildlife, unpublished data).

Although we found no evidence of changes in the total mortality rate of smallmouth bass, we did not calculate separate estimates for fishing mortality and natural mortality. Increases in growth and condition might result in decreases in natural mortality; however, decreases in natural mortality may be masked by increases in fishing mortality. Sizable increases in fishing mortality from 1993 to 1995 were unlikely, however, because changes in annual effort by smallmouth bass anglers in Columbia River reservoirs were minimal (Washington Department of Fish and Wildlife, unpublished data).

Sizeable increases in fishing mortality due to incidental catch by anglers targeting northern pikeminnow were also unlikely. Harvest of incidentally caught smallmouth bass throughout the lower Columbia and Snake rivers was 2,700 in 1994 and 4,400 in 1995 (Washington Department of Fish and Wildlife, unpublished data). In 1994, harvest by anglers targeting smallmouth bass was approximately 20,000 in just Bonneville, The Dalles, John Day, and McNary reservoirs, Columbia River. Harvest throughout the lower Columbia and Snake rivers was probably much greater, because harvest in just Little Goose Reservoir, Snake River, has been estimated at over 13,000 (Bennett et al. 1983), and abundance of smallmouth bass in the lower Snake River is approximately double that in the lower Columbia River (Zimmerman and Parker 1995).

Limitations of our sampling methods precluded us from directly estimating mortality of smallmouth bass younger than age 3; however, variations in year-class strength may reflect variations in natural mortality of fish during the first year of life. Connolly and Rieman (1988) found that year-class strength of smallmouth bass in John Day Reservoir was influenced by first-year growth, and larger age-0 smallmouth bass can experience significantly higher survival over the winter than smaller fish (Shuter et al. 1980). Some combination of physical influences (flow, temperature, reservoir fluctuations, etc.) probably influence survival as well (Henderson and Foster 1957; Montgomery et al. 1980). Positive correlations among year-class strengths from areas we sampled support the theory that year-class strengths are influenced by physical conditions. The lack of increase in year-class strengths since implementation of northern pikeminnow removals indicates that mortality of young smallmouth bass has not changed in response to those removals.

Although W_r decreased downstream from Bonneville Dam and in John Day and Lower Granite reservoirs after 1994, we found no indication of relationships between W_r and other population characteristics. We found no trends in density, as measured by catch rate, or in growth, concurrent with the decrease in W_r. Densities of smallmouth bass and other predators are relatively low (Rieman and Beamesderfer 1990; Curet 1993), making density-dependent relationships unlikely. Low values for mean W_r, such as those in 1995 and 1996, were observed prior to removals of northern pikeminnow (Mesa et al. 1990).

Although our estimates of growth varied annually, they were similar to estimates made prior to northern pikeminnow removals. Connolly and Rieman (1988) estimated mean growth from age 1 to age 2 in John Day Reservoir to be 69 mm, well within our range of 50–89 mm. Estimates for growth to ages 3–5 were all near the middle of our estimated ranges. Bennett et al. (1983) estimated mean growth from age 1 to age 2 in Lower Granite Reservoir to be 53 mm, just within our range of 34–54 mm. Estimates for growth to ages 3–5 (60 mm, 51 mm, and 48 mm) were well within our estimated ranges (36–64 mm, 36–60 mm, and 33–62 mm). We confirmed the finding of Bennett et al. (1983) that growth to age 3 was greater than growth to age 2 in Lower Granite Reservoir. We also confirmed that mean length at age was usually greater in John Day Reservoir than in Lower Granite Reservoir. The agreement of our age determinations and growth increments with those from previous studies is important, because evaluations of mortality and growth rely on accurate age determinations from scale analyses.

Effectiveness of northern pikeminnow management relies partially on the lack of response by smallmouth bass to sustained removals of northern pikeminnow. Smallmouth bass are the most abundant and widespread predator other than northern pikeminnow in the lower Columbia and Snake rivers, and therefore they have high potential for reducing benefits of the management program. The lack of response by smallmouth bass increases confidence in the hypothesis that sustained removals of northern pikeminnow increases survival of juvenile salmonids.

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References

Beamesderfer, R. C., and B. E. Rieman. 1988. Size selectivity and bias in estimates of population statistics of smallmouth bass, walleye, and northern squawfish in a Columbia River reservoir. North American Journal of Fisheries Management 8:505–510.

Beamesderfer, R. C., and B. E. Rieman. 1991. Abundance and distribution of northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:439–447.

Beamesderfer, R. C., and D. L. Ward. 1994. Review of the status, biology, and alternatives for management of smallmouth bass in John Day Reservoir. Oregon Department of Fish and Wildlife, Information Report 94-4, Clackamas.

Beamesderfer, R. C. P., D. L. Ward, and A. A. Nigro. 1996. Evaluation of the biological basis for a predator control program on northern squawfish (*Ptychocheilus oregonensis*) in the Columbia and Snake rivers. Canadian Journal of Fisheries and Aquatic Sciences 53:2898–2908.

Bennett, D. H., P. M. Bratovich, W. Knox, D. Palmer, and H. Hansel. 1983. Status of the warmwater fishery and the potential of improving warmwater fish habitat in the lower Snake reservoirs. Final Report (Contract DACW68-79-C0057) to U.S. Army Corps of Engineers, Walla Walla, Washington.

Brown, L. R., and P. B. Moyle. 1981. The impact of squawfish on salmonid populations: a review. North American Journal of Fisheries Management 1:104–111.

Carlander, K. D. 1977. Handbook of freshwater fishery biology, volume 2. Iowa State University Press, Ames.

Connolly, P. J., and B. E. Rieman. 1988. Population dynamics of walleye and smallmouth bass and potential predation on juvenile salmonids in a mainstem Columbia River reservoir. Pages 307–348 *in* T. P. Poe and B. E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983–86. Final Report (contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.

Curet, T. S. 1993. Habitat use, food habits and the influence of predation on subyearling chinook salmon in Lower Granite and Little Goose reservoirs, Washington. Master's thesis. University of Idaho, Moscow.

Diana, J. S. 1979. The feeding pattern and daily ration of a top carnivore, the northern pike (*Esox lucius*). Canadian Journal of Zoology 57:2121–2127.

El-Zarka, S. E. 1959. Fluctuations in the population of yellow perch, *Perca flavescens* (Mitchill) in Saginaw Bay Lake Huron. U.S. Fish and Wildlife Service Fishery Bulletin 151:365–415.

Friesen, T. A., and D. L. Ward. 1999. Management of northern pikeminnow and implications for juvenile salmonid survival in the lower Columbia and Snake rivers. North American Journal of Fisheries Management 19:406–420.

Gray, G. A., and D. W. Rondorf. 1986. Predation on juvenile salmonids in Columbia Basin reservoirs. Pages 178–185 in G. E. Hall and M. J. Van Den Avyle, editors. Reservoir fisheries management: strategies for the 80's. American Fisheries Society, Southern Division, Reservoir Committee, Bethesda, Maryland.

Hansel, H. C., S. D. Duke, P. T. Lofy, and G. A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of prey species. Transactions of the American Fisheries Society 117:55–62.

Hayes, D. B., W. W. Taylor, and J. C. Schneider. 1992. Response of yellow perch and the benthic invertebrate community to a reduction in the abundance of white suckers. Transactions of the American Fisheries Society 121:36–53.

Henderson, C., and R. F. Foster. 1957. Studies of smallmouth black bass (*Micropterus dolomieui*) in the Columbia River near Richland, Washington. Transactions of the American Fisheries Society 86:112–127.

Jearld, W. E. 1983. Age determination. Pages 301–323 in L. A. Nielsen and D. L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Johnsen, R. C., and C. W. Simms. 1973. purse seining for juvenile salmon and trout in the Columbia River estuary. Transactions of the American Fisheries Society 102:341–345.

Johnson, F. H. 1977. Responses of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) to removal of white sucker (*Catostomus commersoni*) from a Minnesota Lake, 1966. Journal of the Fisheries Research Board of Canada 34:1633–1642.

Knutsen, C. J., and D. L. Ward. 1999. Biological characteristics of northern pikeminnow in the lower Columbia and Snake rivers before and after sustained exploitation. Transactions of the American Fisheries Society 128:1008–1119.

Kolander, T. D., D. W. Willis, and B. R. Murphy. 1993. Proposed revision of the standard weight (Ws) equation for smallmouth bass. North American Journal of Fisheries Management 13:398–400.

Mesa, M. G., S. D. Duke, and D. L. Ward. 1990. Spatial and temporal variation in proportional stock density and relative weight of smallmouth bass in a reservoir. Journal of Freshwater Ecology 5:323–339.

Montgomery, J. C., D. H. Fickeisen, and C. D. Becker. 1980. Factors influencing smallmouth bass production in the Hanford area, Columbia River. Northwest Science 54:296–305.

Neter, J., W. Wasserman, and M. H. Kutner. 1990. Applied linear statistical models. Irwin Press, Homewood, Illinois.

Parker, R. M., M. P. Zimmerman, and D. L. Ward. 1995. Variability in biological characteristics of northern squawfish in the lower Columbia and Snake rivers. Transactions of the American Fisheries Society 124: 335–346.

Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Prendergast. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:405–420.

Rieman, B. E., and R. C. Beamesderfer. 1990. Dynamics of a northern squawfish population and the potential to reduce predation on juvenile salmonids in a Columbia River reservoir. North American Journal of Fisheries Management 10:228–241.

Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:448–458.

Rogers, J. B., and C. C. Burley. 1991. A sigmoid model to predict gastric evacuation rates of smallmouth bass (*Micropterus dolomieui*) fed juvenile salmon. Canadian Journal of Fisheries and Aquatic Sciences 48:933–937.

Seaburg, K. G. 1957. A stomach sampler for live fish. Progressive Fish-Culturist 19:137–139.

Shuter, B. J., J. A. Maclean, F. E. J. Fry, and A. A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Transactions of the American Fisheries Society 109: 1–34.

Tabor, R. A., R. S. Shively, and T. P. Poe. 1993. Predation on juvenile salmonids by smallmouth bass and northern squawfish in the Columbia River near Richland, Washington. North American Journal of Fisheries Management 13:831–838.

Vigg, S., T. P. Poe, L. A. Prendergast, and H. C. Hansel. 1991. Rates of consumption of juvenile salmonids and alternative prey fish by northern squawfish, walleyes, smallmouth bass, and channel catfish in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:421–438.

Ward, D. L., J. H. Petersen, and J. J. Loch. 1995. Index of predation on juvenile salmonids by northern squawfish in the lower and middle Columbia River and in the lower Snake River. Transactions of the American Fisheries Society 124:321–334.

Wydoski, R. S., and R. R. Whitney. 1979. Inland fishes of Washington. University of Washington Press, Seattle.

Zimmerman, M. P. 1999. Food habits of smallmouth bass, walleyes, and northern pikeminnow in the lower Columbia River basin during outmigration of juvenile anadromous salmonids. Transactions of the American Fisheries Society 128:1036–1054.

Zimmerman, M. P., and R. M. Parker. 1995. Relative density and distribution of smallmouth bass, channel catfish, and walleye in the lower Columbia and Snake rivers. Northwest Science 69:19–28.

Zimmerman, M. P., and D. L. Ward. 1999. Index of predation on juvenile salmonids by northern pikeminnow in the lower Columbia River basin, 1994–1996. Transactions of the American Fisheries Society 128:995–1007.