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Food Habits of Smallmouth Bass, Walleyes, and Northern Pikeminnow in the Lower Columbia River Basin during Outmigration of Juvenile Anadromous Salmonids

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Abstract.—I compared the diets of adult smallmouth bass *Micropterus dolomieu*, walleyes *Stizostedion vitreum*, and northern pikeminnow *Ptychocheilus oregonensis* collected in impounded and unimpounded reaches of the lower Columbia and lower Snake rivers during the outmigration of juvenile anadromous salmonids *Oncorhynchus* spp. from 1990 to 1996. Gravimetric proportions of fish, crayfish, and other prey consumed by each predator in spring and summer differed among the three river reaches for each predator species. Fish prey were generally the largest dietary component for all three predator species, although crayfish were also prevalent in the diets of smallmouth bass and, to a lesser extent, northern pikeminnow. Numerical proportions of salmonids, cottids, and other fish prey differed among predator species and among study reaches. Juvenile salmonids formed the majority of fish prey consumed by northern pikeminnow, whereas cottids, cyprinids, catostomids, and percopsids were more commonly consumed by smallmouth bass and walleyes. Weight of juvenile salmonids consumed by smallmouth bass and northern pikeminnow varied among years, but did not increase from 1990 to 1996. Back-calculated lengths of consumed prey fish often differed among predator species, and maximum length of consumed salmonids and sculpins was linearly related to smallmouth bass and northern pikeminnow length. Daily rations and numerical salmonid consumption rates differed among river reaches, and consumption of nonsalmonids by smallmouth bass was much greater than that of northern pikeminnow. This study clarified predator–prey relationships between indigenous and introduced predator and prey species in the lower Columbia and lower Snake rivers.

Introductions of nonnative fish species have contributed to declines and local extinctions of indigenous fish populations throughout the western United States (Wydoski and Bennett 1981; Moyle et al. 1986; Miller et al. 1989). The mechanisms by which introduced fishes interact with, reduce, or eliminate native species are frequently unknown, although they may include competition, predation, habitat alteration, genetic effects, or disease transmission (Moyle et al. 1986; Allendorf 1991). The consequences of introductions are particularly unpredictable where many native species appear to be persisting alongside many introduced species. Such is the case in the lower Columbia River basin, which supports a diverse assemblage of native and nonnative warm-, cool-, and cold-water species (Wydoski and Whitney 1979; Farr and Ward 1993; Table 1).

Efforts to study fish communities of the main-stem lower Columbia and Snake rivers have been hindered by logistical constraints associated with sampling large rivers (Campbell 1979). The studies have been largely motivated by a regional priority of understanding and ameliorating the effects of impoundments on anadromous salmonids (Bentley and Raymond 1976; Ebel and Raymond 1976; Raymond 1979; Zaugg et al. 1985; Berggren and Filardo 1993). Studies have been limited in geographic scope to a single reservoir (Hjort et al. 1981; Beamesderfer and Rieman, 1991; Vigg et al. 1991) or reach (Tabor et al. 1993), and with the exception of Poe et al. (1991), have mainly addressed predation on juvenile salmonids. Nevertheless, these studies contributed much of what is known about potential interactions between native and nonnative species in main-stem habitats in the basin.

Previous studies elevated regional awareness of the magnitude of juvenile salmonid predation by resident predators and provided a biological foundation for a predator control program targeting indigenous northern pikeminnow (Rieman and Beamesderfer 1990; Beamesderfer et al. 1996). The Northern Pikeminnow Management Program was implemented in 1990 to enhance survival of outmigrating juvenile salmonids through managed harvest of northern pikeminnow in the lower Columbia River basin. Approximately 1.1 million northern pikeminnow have been harvested since

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TABLE 1.—A partial list of native and nonindigenous species of the main-stem lower Columbia and Snake rivers.

Native species	Introduced species
Pacific lamprey *Lampetra tridentata*	American shad *Alosa sapidissima*
White sturgeon *Acipenser transmontanus*	Rainbow trout *Oncorhynchus mykiss*
Coho salmon *Oncorhynchus kisutch*	Brown trout *Salmo trutta*
Chinook salmon *O. tshawytscha*	Common carp *Cyprinus carpio*
Steelhead *O. mykiss*	Goldfish *Carassius auratus*
Cutthroat trout *O. clarki*	Yellow bullhead *Amerius natalis*
Bull trout *Salvelinus confluentus*	Brown bullhead *A. nebulosus*
Mountain whitefish *Prosopium williamsoni*	Channel catfish *Ictalurus punctatus*
Northern pikeminnow *Ptychocheilus oregonensis*	Striped bass *Morone saxatilis*
Peamouth *Mylocheilus caurinus*	White crappie *Pomoxis annularis*
Chiselmouth *Acrocheilus alutaceus*	Black crappie *P. nigromaculatus*
Redside shiner *Richardsonius balteatus*	Smallmouth bass *Micropterus dolomieu*
Largescale sucker *Catostomus macrocheilus*	Largemouth bass *M. salmoides*
Bridgelip sucker *C. columbianus*	Bluegill *Lepomis macrochirus*
Threespine stickleback *Gasterosteus aculeatus*	Pumpkinseed *L. gibbosus*
Sand roller *Percopsis transmontana*	Walleye *Stizostedion vitreum*
Sculpins *Cottus* spp.	Yellow perch *Perca flavescens*

1990 (Friesen and Ward 1999). The potential impacts of predator control efforts on predator–prey relationships are uncertain. However, program benefits in terms of enhanced juvenile salmonid survival would be lessened if surviving northern pikeminnow and nonnative predators exerted compensatory predation on juvenile salmonids (Beamesderfer et al. 1996).

Poe et al. (1994) hypothesized that the proliferation of nonnative predators has exacerbated northern pikeminnow predation on juvenile salmonids in the Columbia River basin. Predator distributions are not uniform throughout the basin (Zimmerman and Parker 1995), so an examination of predators' diets throughout much of the lower basin could increase understanding of the relative impacts of introduced predator species. Evaluating predators' diets from 1990 to 1996 should also reveal any gross, compensatory changes in piscivory associated with the Northern Pikeminnow Management Program.

In this study, I compared general food habits and piscivory of smallmouth bass, walleyes, and northern pikeminnow collected from 1990 to 1996 from three large river reaches: the unimpounded Columbia River downstream from Bonneville Dam, the impounded Columbia River from Bonneville Dam to McNary Dam, and the Snake River from Little Goose Dam to the upstream extent of Lower Granite Reservoir. Analyses were restricted to adult predators (smallmouth bass and walleye at least 200 mm fork length and northern pikeminnow at least 250 mm fork length) collected during periods when spring- and summer-migrating anadromous juvenile salmonids were available. My specific objectives address (1) variation in predators' diets between seasons and among river reaches, (2) annual variation in piscivory on juvenile salmonids, (3) sizes of consumed fish prey, and (4) daily ration of salmonid and nonsalmonid fish prey for smallmouth bass and northern pikeminnow.

Methods

Field sampling.—Predators were sampled at fixed sites established throughout three reaches of the lower Columbia River basin from 1990 to 1996 (Figure 1). Sites in the unimpounded lower Columbia River were river kilometer (RKm) 114–121, RKm 172–178, RKm 190–197, and in Bonneville Dam tailrace. Sites in lower Columbia River reservoirs included near-dam areas (forebay and tailrace zones within Bonneville, The Dalles, and John Day reservoirs), and midreservoir areas away from dams (RKm 275–281 in Bonneville Reservoir and RKm 390–396 in John Day Reservoir). Snake River sampling sites included two impounded sites (tailraces of Little Goose and Lower Granite dams), and the transition zone (RKm 222–228) between the uppermost portion of Lower Granite Reservoir and the free-flowing reach of the Snake River downstream from Hell's Canyon Dam. Sites in John Day Reservoir were sampled each year (Table 2). All sites were sampled annually from 1994 to 1996, whereas sampling differed among sites and years in other reservoirs and reaches from 1990 to 1993.

Each sampling site was subdivided into 24 nearshore transects approximately 500 m long. Predators were captured by electrofishing a minimum of six randomly selected transects per day within each site. Standardized effort in each transect was

FIGURE 1.—Sampling sites in the lower Columbia River basin, 1990–1996. Sites in the unimpounded lower Columbia River are (U1) river kilometer (RKm) 115–121, (U2) RKm 172–178, (U3) RKm 190–197, and (U4) Bonneville Dam tailrace. Sites in the impounded lower Columbia River are (I1) Bonneville Reservoir forebay, midreservoir, and (The Dalles Dam) tailrace, (I2) The Dalles Reservoir forebay and (John Day Dam) tailrace, and (I3) John Day Reservoir forebay, midreservoir, and (McNary Dam) tailrace. Sites in the lower Snake River are (S1) Little Goose Dam tailrace, (S2) Lower Granite Dam tailrace, and (S3) RKm 222–228.

15 min of continuous output at 4–5 A. A minimum of eight boat-days of effort was allocated annually to each site, effort being divided between spring (April–June) and summer (July–September). Exceptions to seasonal stratification are noted in Table 2. Fish were collected between 0300 and 1200 hours, which encompassed peaks in diel consumption rates (Vigg et al. 1991). Smallmouth bass and northern pikeminnow were collected every year, whereas walleye were collected only in 1990–1993 and 1996.

Smallmouth bass, walleye, and northern pikeminnow were measured (fork length in mm) and weighed (g). Stomachs of smallmouth bass and walleye 200 mm and larger were pumped with a modified Seaburg sampler (Seaburg 1957). Northern pikeminnow 250 mm and larger were sacrificed and the entire digestive tracts were removed. All samples were placed in labeled Whirl-Pak bags on ice and later stored in freezers.

Laboratory analysis.—Gut contents were thawed in the laboratory, blotted dry, and sorted into three prey categories: fish, crayfish, and other prey (molluscs, aquatic and terrestrial insects, plant matter). Prey types were weighed to the nearest 0.01 g and returned to the original Whirl-Pak bags for digestion and subsequent prey fish identification. A solution of lukewarm tap water, 2% (wet weight) pancreatin (8× porcine digestive enzyme), and 1% (wet weight) sodium sulfide was poured into each bag and mixed with the gut contents to speed sample processing time (Ward et al. 1995). The bags were sealed and 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 (dentaries, cleithra, pharyngeal arches) were examined under a dissecting microscope and identified to the lowest possible taxon (Hansel et al. 1988). Consumed prey fish were counted by adding the number of paired diagnostic

TABLE 2.—Sampling sites in the unimpounded Columbia River downstream from Bonneville Dam, in lower Columbia River reservoirs, and in lower Snake River reservoirs, and years that sites were sampled (×). All sites were sampled during spring (April–June) and summer (July–September) except where indicated; RKm is river kilometers.

Sampling site	1990	1991	1992	1993	1994–1996
Unimpounded Columbia River					
RKm 115–121			×		×
RKm 172–178			×		×
RKm 190–197			×		×
Bonneville Dam tailrace	×		×	×	×
Columbia River reservoirs					
Bonneville					
Forebay	×			×	×
Midreservoir	×			×	×
The Dalles Dam tailrace	×			×	×
The Dalles					
Forebay	×			×	×
John Day Dam tailrace	×			×	×[a]
John Day					
Forebay	×	×	×	×	×
Midreservoir	×	×	×	×	×
McNary Dam tailrace	×	×	×	×	×
Snake River reservoirs					
Lower Monumental Dam tailrace		×			×
Little Goose Dam tailrace		×			×
Lower Granite					
RKm 222–228		×			×

[a] Sampled in summer only.

bones to remaining unpaired bones. In 1995 and 1996, intact diagnostic bones of prey fishes were measured to the nearest 0.05 mm with hand calipers.

Spatial and seasonal variation in diets.—Seasonal diet data were pooled across sites and years within each large sampling reach and season. We calculated an index of feeding (IF) as a measure of stomach fullness (McCabe et al. 1993). The IF is the relative weight of stomach or gut contents:

$$\mathrm{IF} = 100(W_s/W_f), \qquad (1)$$

where W_s = weight (g) of gut or stomach contents, and W_f = weight (g) of predator. Analyses of variance and least square means (SAS Institute 1990) were used to compare arcsine-transformed IFs for main effects (reaches, seasons) and interaction (reach × season). Analyses of variance and least squares means were also used to compare the weight of fish prey among reaches, between seasons, and among reach × season combinations. The mean proportions by weight of each prey type (fish, crayfish, and other prey) and prey fish taxa (salmonids, sculpins, and other prey fishes) were compared among reaches with contingency tables and the chi-square statistic for each predator species and season. In some cases, two prey types or prey fish types were pooled due to small proportional weight of a particular category. Finally, I tabulated the numerical frequency of all prey fishes found in predators' stomach and gut contents.

Annual variation in piscivory on juvenile salmonids.—I compared arcsine-transformed relative prey weight (g salmonids/g predator weight) among years for smallmouth bass in Snake River reservoirs (spring) and Columbia River reservoirs (summer) and northern pikeminnow in all reaches and seasons except Snake River reservoirs in summer. Annual samples of smallmouth bass, northern pikeminnow, and walleye were too small in other reach–season combinations to compare annual variation in piscivory in other reaches and season.

Prey size.—Linear regression equations of Hansel et al. (1988) were used to estimate original fork lengths of prey fishes from measurements of diagnostic bones (dentaries, cleithra, pharyngeal arches) found in predators' guts in 1995 and 1996. For prey taxa with a sample size of four or more individuals, lengths of consumed prey were compared between or among predator species by analyses of variance if samples were normally distributed with equal variance or Mann–Whitney or Kruskal–Wallace tests if samples failed tests of normality and equal variance. Dunn's (nonparametric) or least square means (parametric) was used to test for differences in prey size among three predator species. Relationships between predator length (25-mm fork length intervals) and the maximum size of prey fish consumed were analyzed by linear regression.

Daily fish ration.—For each river reach and season, I estimated total daily ration of smallmouth bass and northern pikeminnow collected in 1995 and 1996 with the equation

$$R = M \cdot n/\mathrm{ET90} \cdot N, \qquad (2)$$

where R = total daily ration as a percent of predator weight, M = mean original meal size (% body weight) among fish that contained food, n = number of predators that contained food, ET90 = 90% emptying time (d) of digestive tract contents, and N = total number of predators (Diana 1979; Tabor et al. 1993). Sample sizes of walleyes were deemed insufficient to estimate walleye fish consumption rates.

Original weights of ingested prey fishes were estimated from length–weight regressions for common forage fishes (Vigg et al. 1991). Original weights of nonfish prey items were estimated by adjusting observed nonfish weights by the same ratio of original to digested fish prey weight (Tabor et al. 1993). I estimated values for ET90 by using digestion rate equations for smallmouth bass (Rogers and Burley 1991),

$$\mathrm{ET90} = 24.542 S^{0.29} e^{-0.15T} W^{-0.23}, \qquad (3)$$

and for northern pikeminnow (Beyer et al. 1988),

$$\mathrm{ET90} = 47.792 S^{0.61} T^{-1.60} W^{-0.27}, \qquad (4)$$

where S = meal weight (g), T = temperature (°C), and W = predator weight (g). Rations were estimated for a sample of predators and therefore do not have an observed variance. To express some measure of variability in R, I calculated a low and high estimate using ±2 SD of mean original meal size (M).

Daily ration for individual prey fish taxa was calculated as

$$R_i = \frac{R \cdot p_i \cdot 1{,}000}{\text{mean predator weight (g)}}, \qquad (5)$$

where R_i = daily ration of prey type i (mg prey/g predator) and p_i = the proportion (by weight) of prey type i in the diet. Average numerical consumption rates of smallmouth bass and northern pikeminnow on various prey fishes were calculated as

$$C = \frac{R \cdot p_i \cdot \text{mean predator weight (g)}}{\text{mean original weight of prey type } i}, \qquad (6)$$

where C = daily consumption (prey/predator), R = total daily ration (% predator weight), and p_i = proportion (by weight) of prey type i in the diet. Rations and consumption rates were adjusted for diel feeding periodicity by assuming that smallmouth bass consumed 32.0% and northern pikeminnow consumed 40.5% of their daily ration between 0300 and 1200 hours (Vigg et al. 1991).

Results

Spatial and Seasonal Variation in Diets

Predator sample sizes totaled 4,248 smallmouth bass, 178 walleyes, and 5,404 northern pikeminnow from 1990 to 1996. No walleyes were sampled in the Snake River, and only 38 were sampled downstream from Bonneville Dam. Percentages of fish containing food ranged from 65 to 78% for smallmouth bass, from 40 to 63% for walleyes, and from 65 to 78% for northern pikeminnow (Table 3). Ranges of mean weight among predators that contained food were 209–452 g for smallmouth bass, 1,446–1,930 g for walleyes, and 622–894 g for northern pikeminnow. Exclusive of fish with empty stomachs, the IF of smallmouth bass was greater in summer than spring (F = 10.34; df = 1, 1; $P < 0.001$), and greater in the Snake River than both Columbia River reaches (F = 10.31; df = 1, 2; P = 0.001). The IF of walleye did not differ between reaches or seasons (F = 1.09; df = 1, 1; P = 0.358). Northern pikeminnow in the Snake River had higher IFs than northern pikeminnow in the Columbia River (F = 65.03; df = 1, 2; $P < 0.001$). Stomach fullness was significantly greater in summer than spring in the unimpounded lower Columbia River (F = 5.72; df = 1, 2; P = 0.003), but did not differ between seasons in the impounded reaches of the Columbia and Snake rivers.

Combined weight of fish and crayfish contributed at least 97% of stomach contents among smallmouth bass in all reaches and seasons (Figure 2). In spring, fish were the largest prey component for smallmouth bass downstream from Bonneville Dam (74%) and in the Snake River (70%), whereas crayfish were the largest component (48%) for smallmouth bass in Columbia River reservoirs (χ^2 = 14.472; df = 2; $P < 0.001$). In summer, fish contributed most (83%) to smallmouth bass stom-

TABLE 3.—Numbers of gut samples examined (*N*), frequencies of occurrence of samples containing food (FO_{food}), mean predator weights, and mean indexes of feeding (IF) for smallmouth bass, walleyes, and northern pikeminnow from the lower Columbia River basin, 1990–1996.

	Lower Columbia River					
	Unimpounded		Impounded		Lower Snake River	
Species, variable	Spring	Summer	Spring	Summer	Spring	Summer
Smallmouth bass						
N	231	156	1,672	1,384	582	223
FO_{food} (%)	73.2	68.0	67.6	78.1	65.1	75.3
Mean weight[a] (g)	369	452	356	341	360	209
Mean IF[a] (%)	0.8	1.2	1.0	1.2	1.3	1.6
Walleye						
N	25	8	74	71	0	0
FO_{food} (%)	40.0	62.5	48.7	59.2		
Mean weight[a] (g)	1,930	1,447	1,446	1,692		
Mean IF[a] (%)	0.9	2.0	0.7	0.8		
Northern pikeminnow						
N	912	800	1,242	1,626	716	108
FO_{food} (%)	73.2	68.0	67.6	78.1	65.1	75.3
Mean weight[a] (g)	862	622	894	690	746	697
Mean IF[a] (%)	1.7	2.0	1.5	1.3	2.3	2.4

[a] Excludes fish with empty stomachs.

ach contents downstream from Bonneville Dam, whereas the proportional weight of crayfish was greatest in the impounded reaches of the Columbia (50%) and Snake (52%) rivers ($\chi^2 = 35.006$; df $= 2$; $P < 0.001$). Walleye stomachs contained over 99% fish prey regardless of reach or season. Fish prey were the largest component of northern pikeminnow gut contents in all three reaches in spring (70–86%) and summer (48–84%). The proportional weight of crayfish was greater for northern pikeminnow in Columbia River reservoirs than in other reaches ($\chi^2 = 34.481$; df $= 4$; $P < 0.001$). Prey other than fish and crayfish (mostly amphipods and aquatic and terrestrial insects) were more prevalent among northern pikeminnow than among smallmouth bass and walleye.

In spring, sculpins were the predominant prey (% by weight) of smallmouth bass in the unimpounded and impounded Columbia River, whereas salmonids accounted for 66% of consumed fish mass in the Snake River ($\chi^2 = 99.34$; df $= 4$; $P < 0.001$; Figure 3). In summer, the proportion of prey fish other than salmonids and sculpins was greatest in the unimpounded Columbia River and the Snake River ($\chi^2 = 41.27$; df $= 2$; $P < 0.001$). In spring, prey other than salmonids and sculpins contributed the greatest proportional weight of fish prey for walleyes downstream from Bonneville Dam, whereas salmonids were the largest component in Columbia River impoundments ($\chi^2 = 55.43$; df $= 2$; $P < 0.001$). The proportional weight of sculpins was greater in summer than spring, and the proportion of prey other than salmonids and sculpins was greatest among walleyes in Columbia River impoundments in summer ($\chi^2 = 13.20$; df $= 2$; $P = 0.001$). Fish consumed by northern pikeminnow were overwhelmingly juvenile salmonids (>84% by weight) regardless of river reach and season. The proportion of salmonids was greatest in the Snake River in spring ($\chi^2 = 8.68$; df $= 2$; $P = 0.013$) but did not differ among reaches in summer ($\chi^2 = 1.67$; df $= 2$; $P = 0.435$).

The numerical frequency of chinook salmon greatly exceeded that of steelhead among identified salmonid prey consumed by all predator species. Steelhead exceeded 3% of prey only for northern pikeminnow in the Snake River (21%; Table 4). Native cyprinids, catostomids, sand rollers (percopsids), and cottids were much more common in smallmouth bass and walleye stomachs than in northern pikeminnow stomachs. Peamouth, northern pikeminnow, and redside shiners were the most commonly consumed cyprinids. The frequency of native fishes consumed by smallmouth bass and northern pikeminnow was greatest downstream from Bonneville Dam. The ingestion frequencies of introduced fishes (ictalurids, centrarchids, and yellow perch [percids]) were greatest for smallmouth bass (24.8%) and northern pikeminnow (4.5%) in the Snake River.

Annual Variation in Piscivory on Juvenile Salmonids

Relative weight of juvenile salmonids consumed by smallmouth bass in Columbia River reservoirs was greater in the summer of 1992 and 1994 than

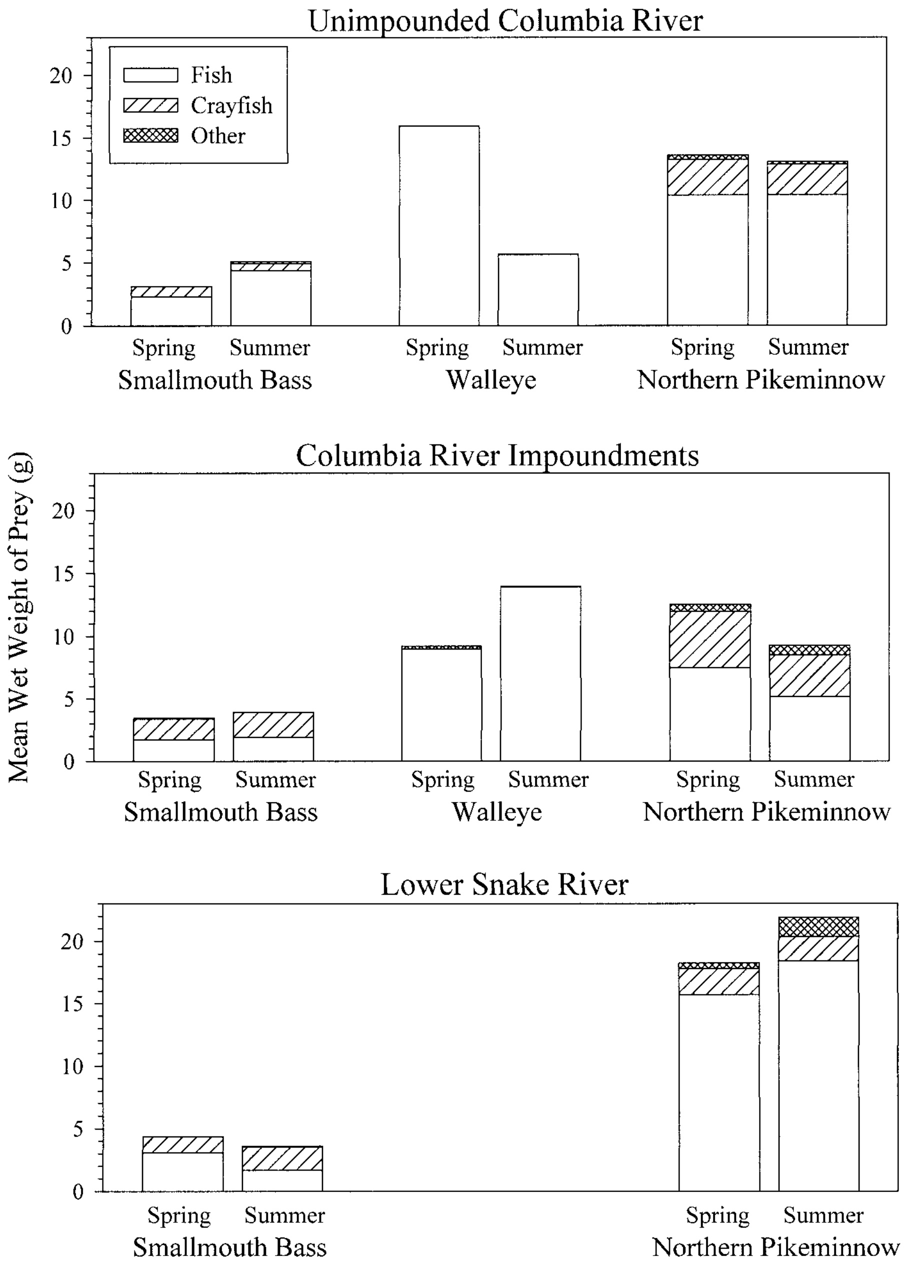

FIGURE 2.—Mean weights (g) of fish, crayfish, and other prey in smallmouth bass, walleye, and northern pikeminnow stomachs that contained food in three areas of the lower Columbia basin during spring and summer 1990–1996.

in all other summers studied (F = 7.49; df =1, 47; P < 0.001 but was similar among years for smallmouth bass in Snake River reservoirs in spring (F = 2.12; df = 1, 39; P = 0.115; Figure 4). Relative weight of salmonids consumed by northern pikeminnow differed among years downstream from Bonneville Dam in spring (F = 5.28; df = 1, 292; P < 0.001) and summer (F = 3.16; df = 1, 238; P = 0.009) and in Columbia River impoundments in spring (F = 8.92; df = 1,325; P < 0.001) and summer (F = 16.94; df = 1, 273; P < 0.001); however, there was no directional trend over time. Relative weight of salmonids consumed in spring by northern pikeminnow in the

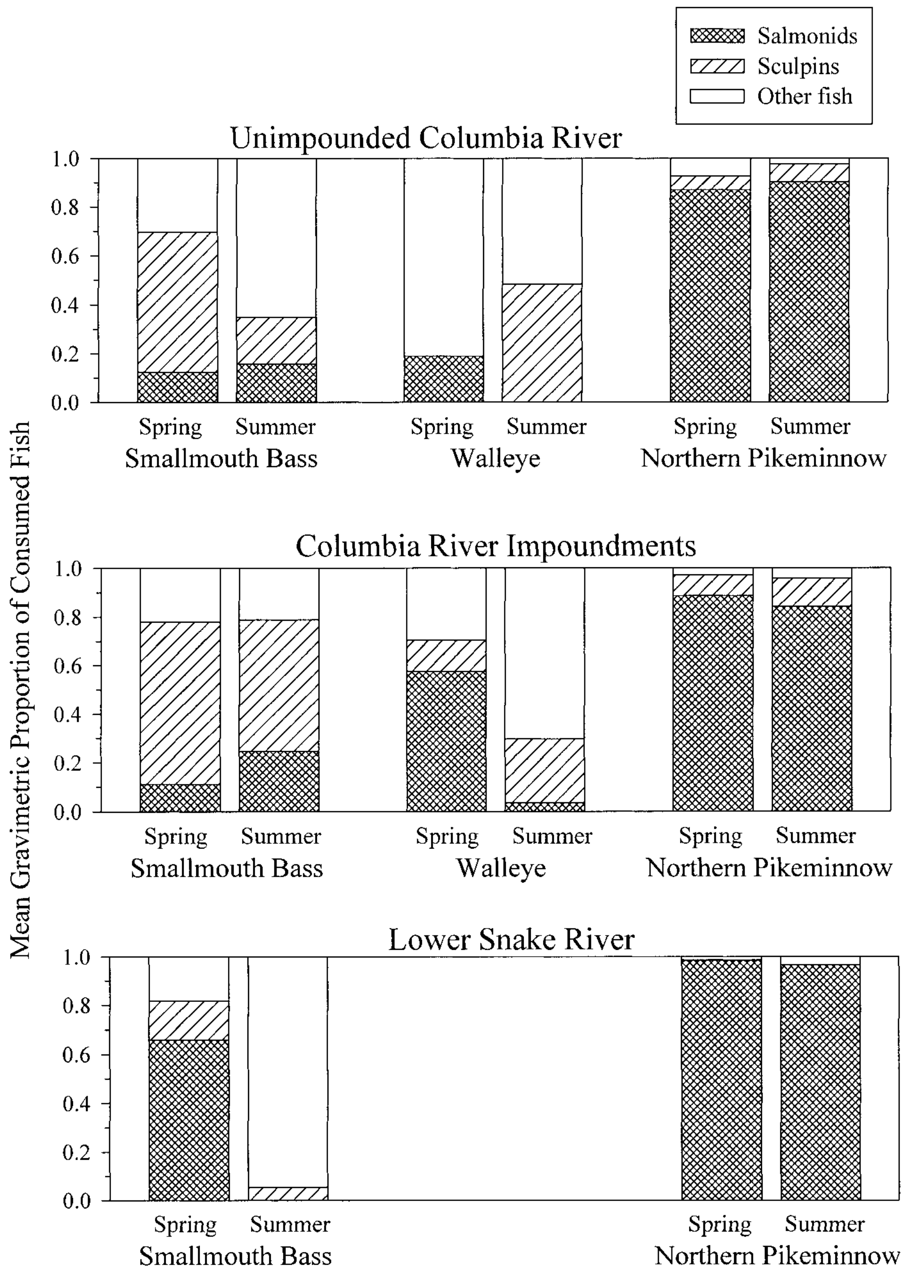

FIGURE 3.—Proportions (by weight) of juvenile salmonids, sculpins, and other fishes in smallmouth bass, walleye, and northern pikeminnow stomachs that contained food in three areas of the lower Columbia basin during spring and summer 1990–1996.

Snake River was similar among years ($F = 0.41$; df = 1, 327; $P = 0.743$).

Prey Size

Back-calculated lengths of prey consumed by all predator species in 1995 and 1996 ranged from a 23-mm sculpin to a 284-mm largescale sucker (Figure 5). Chinook salmon consumed in summer were smaller than those consumed in spring by smallmouth bass ($F = 35.89$; df = 1, 33; $P < 0.001$) and northern pikeminnow ($T = 1{,}629$; $N_1 = 127$; $N_2 = 42$; $P < 0.001$). The three predator

TABLE 4.—Total number of fish (*N* [total]), numbers of identifiable fish (*N* [identified]), and numerical frequencies (%) of fish identified at least to family consumed by smallmouth bass, walleyes, and northern pikeminnow in the Columbia River downstream from Bonneville Dam (DBD), lower Columbia River reservoirs (COL), and lower Snake River (SNK), 1990–1996.

	Smallmouth bass			Walleye		Northern pikeminnow		
Sample size	DBD	COL	SNK	DBD	COL	DBD	COL	SNK
N (total)	198	983	299	14	117	1,619	1,372	378
N (identified)	153	703	198	8	87	1,555	1,261	353
Frequency (%)								
Petromyzonidae	0	0.3	0	0	0	0.3	0.8	9.3
Salmonidae	12.4	14.2	25.8	12.5	13.8	92.4	82.5	85.3
Chinook salmon	9.8	7.7	12.6	0	5.7	64.2	29.3	49.3
Steelhead	0	0	2.5	0	0	2.3	2.5	21.2
Unidentified species	2.6	6.5	10.7	12.5	8.1	25.9	50.5	14.7
Cyprinidae	19.0	11.8	14.1	50.0	13.8	0.8	1.0	0.3
Common carp	0.7	0	0	0	0	0.1	0	0
Chiselmouth	1.3	0.3	3.5	0	0	0	0	0.3
Peamouth	7.2	5.5	3.0	0	6.9	0.4	0.6	0
Northern pikeminnow	6.5	4.3	3.5	12.5	4.6	0.2	0	0
Redside shiner	2.6	0.4	0	25.0	2.3	0.1	0.1	0
Unidentified species	0.7	1.3	4.0	12.5	0	0	0.2	0
Catostomidae	16.3	3.3	8.6	0	5.7	0.1	0.2	0.3
Ictaluridae	0	1.6	15.2	0	0	0	0	1.4
Percopsidae	3.3	1.4	0	25.0	13.8	0.3	0.1	0
Gasterosteidae	2.6	0.4	0	0	0	0.7	0.2	0
Cottidae	45.8	64.0	36.9	12.5	51.7	5.3	16.4	0.8
Centrarchidae	0	2.1	9.6	0	1.1	0.1	0.2	3.1
Smallmouth bass		1.7	3.0		0	0.1	0.1	0.8
Crappie species		0.1	4.0		1.1	0	0	1.7
Sunfish species		0.1	1.5		0	0	0.1	0
Unidentified species		0.1	1.0		0	0	0	0.6
Percidae	0.7	0.4	0	0	0	0	0	0

species consumed similar-sized chinook salmon in spring ($H = 0.84$; df = 2; $P = 0.656$), whereas chinook salmon consumed by smallmouth bass in summer were smaller than those consumed by northern pikeminnow ($T = 476$; $N_1 = 21$; $N_2 = 42$; $P = 0.004$). Northern pikeminnow were the only species that contained diagnostic steelhead bones in spring, and mean length of ingested steelhead was larger than that of chinook salmon ($T = 3,321$; $N_1 = 26$; $N_2 = 127$; $P < 0.001$). Smallmouth bass consumed smaller sculpins than northern pikeminnow, whereas sculpins consumed by walleye were similar in length to those consumed by smallmouth bass and northern pikeminnow ($H = 34.17$; df = 2; $P < 0.001$). Walleye consumed larger cyprinids than smallmouth bass ($H = 8.86$; df = 2; $P = 0.012$). Only four cyprinids were found in northern pikeminnow digestive tracts. Sand roller lengths were similar among predator species ($F = 0.26$; df = 2, 28; $P = 0.777$).

The maximum size of juvenile salmonid prey increased with predator length for smallmouth bass ($P = 0.004$; df = 8; $r^2 = 0.73$) and northern pikeminnow ($P < 0.001$; df = 11; $r^2 = 0.73$; Figure 6). Size of cottid prey increased with length of smallmouth bass ($P = 0.008$; df = 9; $r^2 = 0.61$) and northern pikeminnow ($P = 0.002$; df = 8; $r^2 = 0.75$), but not walleye ($P = 0.136$; df = 5; $r^2 = 0.46$). Maximum size of consumed cyprinids increased with length of smallmouth bass ($P = 0.002$; df = 9; $r^2 = 0.72$) and walleye ($P = 0.013$; df = 7; $r^2 = 0.67$).

Based on the regression equations in Figure 6, the mean maximum salmonid length was 119 mm (40% of predator length) for smallmouth bass and 167 mm (43% of predator length) for northern pikeminnow. Mean maximum sculpin length consumed by smallmouth bass and northern pikeminnow was 140 mm (45% of smallmouth bass length and 39% of northern pikeminnow length). Mean maximum cyprinid length was 167 mm (51% of predator length) for smallmouth bass and 169 mm (34% of body length) for walleye. Mean maximum prey lengths exceeded mean prey lengths in Figure 6 for summer chinook salmon, sculpins, and cyprinids consumed by smallmouth bass and chinook salmon (spring and summer) and for sculpins consumed by northern pikeminnow.

Daily Fish Ration

In 1995 and 1996, the total mass of food consumed per smallmouth bass per day averaged 5.5 g (spring) and 27.5 g (summer) downstream from Bonneville Dam, 2.9 g (spring) and 16.7 g (summer) in Columbia River reservoirs, and 2.8 g (spring) and 11.7 g (summer) in Snake River reservoirs. Daily ration per northern pikeminnow averaged 15.9 g (spring) and 17.4 g (summer) downstream from Bonneville Dam, 13.6 g (spring) and 14.7 g (summer) in Columbia River reservoirs, and 24.0 g (spring) and 14.4 g (summer) in Snake River reservoirs.

Smallmouth bass ingested higher rations of sculpins and cyprinids than of other prey taxa except in the Snake River, where consumption of salmonids in spring exceeded that of other prey (Figure 7). Smallmouth bass rations of most prey types were greater in summer than spring. Summer consumption of cyprinids by smallmouth bass downstream from Bonneville Dam and in the Snake River exceeded that of all other prey types. The majority of northern pikeminnow rations comprised juvenile salmonids and sculpins. Overall rations were greater in summer than spring, except in the Snake River. Snake River sampling in summer occurred after the period of juvenile salmonid outmigration, whereas sampling coincided with availability of summer migrants throughout the Columbia River. Consequently, salmonid consumption was greatly underestimated for northern pikeminnow and missed altogether for smallmouth bass.

Mean spring daily consumption of juvenile salmonids by individual smallmouth bass ranged from 0.01 prey in Columbia River reservoirs to 0.10 prey in the Snake River (Figure 8). In summer, smallmouth bass consumption exceeded 1.0 juvenile salmonid per predator in impounded and unimpounded reaches of the Columbia River. Daily consumption of nonsalmonids by smallmouth bass was generally greatest downstream from Bonneville Dam, particularly in summer, when daily consumption of sculpins and cyprinids equaled 1.60 prey/predator. Maximum daily rates of juvenile salmonid consumption by northern pikeminnow occurred in the unimpounded Columbia River in summer (1.65 prey per predator) and in the Snake River in spring (1.80 prey/predator). Daily consumption of juvenile salmonids in Columbia River reaches was greater in summer (0.84–1.65 prey/northern pikeminnow) than spring (0.40–0.80). Northern pikeminnow consumed more salmonids than any nonsalmonid taxon on a daily basis in all reaches and seasons.

Discussion

Proportions of fish and nonfish prey, composition and sizes of fish prey, and rates of consumption of salmonid and nonsalmonid fishes differed among predator species and river reaches, and provided strong evidence for distinct impacts of introduced predator species in different areas of the lower Columbia basin. In some cases, differences in abundance or availability of various prey types or habitats among reaches contributed to spatial variation in the diets of introduced smallmouth bass and walleye and native northern pikeminnow.

For example, the proportional weight of crayfish in smallmouth bass stomachs was greater in the impounded reaches of the lower Columbia and Snake rivers than the unimpounded lower Columbia River. Rocky substrates are an important habitat feature for both smallmouth bass and crayfish wherever they cooccur (Edwards et al. 1993), and areas of gravel, cobble, and boulders were much greater in Columbia River reservoirs than the unimpounded river (Parsley and Beckman 1994). Zimmerman and Parker (1995) reported that ictalurids and centrarchids were far more abundant in the Snake River than the lower Columbia River. I found the frequency of ictalurid and centrarchid prey in smallmouth bass and northern pikeminnow stomachs was greatest in the Snake River. Daily consumption of native sculpins and cyprinids by smallmouth bass was greater in the unimpounded lower Columbia River than the upriver impoundments, particularly in summer. Native cyprinids used riverine habitats in dam tailraces of Columbia River impoundments, whereas centrarchids were most abundant in backwaters and more lentic habitats downstream from dam tailraces (Hjort et al. 1981; Beamesderfer and Rieman 1991; Zimmerman and Parker 1995). Consequently, spatial segregation may have reduced encounters between smallmouth bass and native cyprinids in Columbia River impoundments relative to the more lotic conditions downstream from Bonneville Dam.

Smallmouth bass and walleyes preyed upon sculpins, cyprinids, suckers, and sand rollers to a much greater extent than did northern pikeminnow in this study, consistent with the findings of Poe et al. (1991) and Vigg et al. (1991) for predators in John Day Reservoir. Daily consumption rates of smallmouth bass on sculpins, cyprinids, and suckers exceeded rates of northern pikeminnow in all reaches and seasons except Columbia River im-

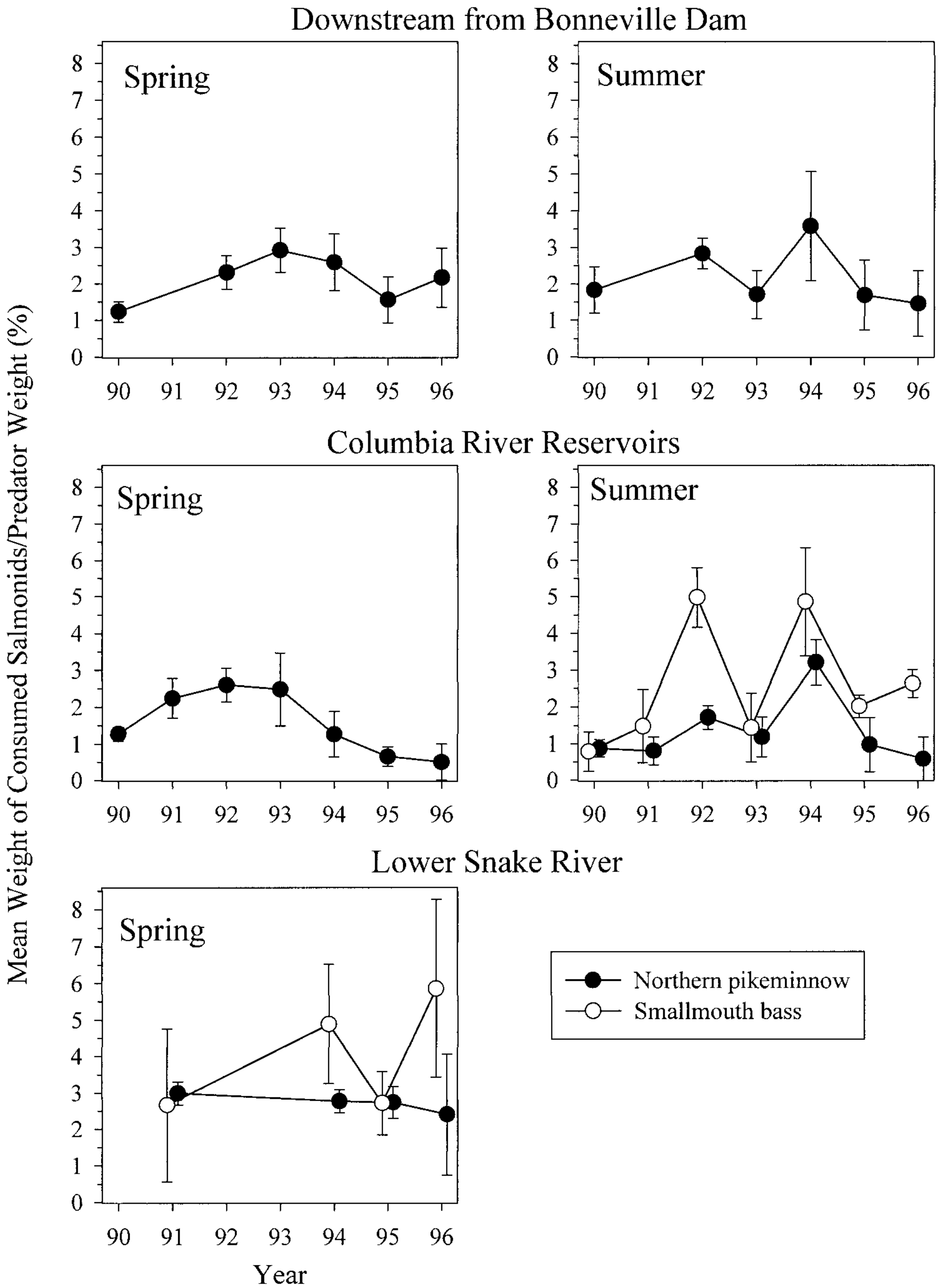

FIGURE 4.—Annual variation in seasonal mean relative weights (100·prey weight/predator weight) of juvenile salmonids consumed by northern pikeminnow and smallmouth bass in two to three areas of the lower Columbia basin, 1990–1996. Error bars are ±2 SE.

poundments in summer. Smallmouth bass abundance increased dramatically from the unimpounded lower Columbia River to the Snake River reservoirs (Zimmerman and Parker 1995). Therefore, the probability that smallmouth bass have affected predator–prey dynamics is greater in the Snake River than the unimpounded Columbia River.

Walleye populations have thus far been restrict-

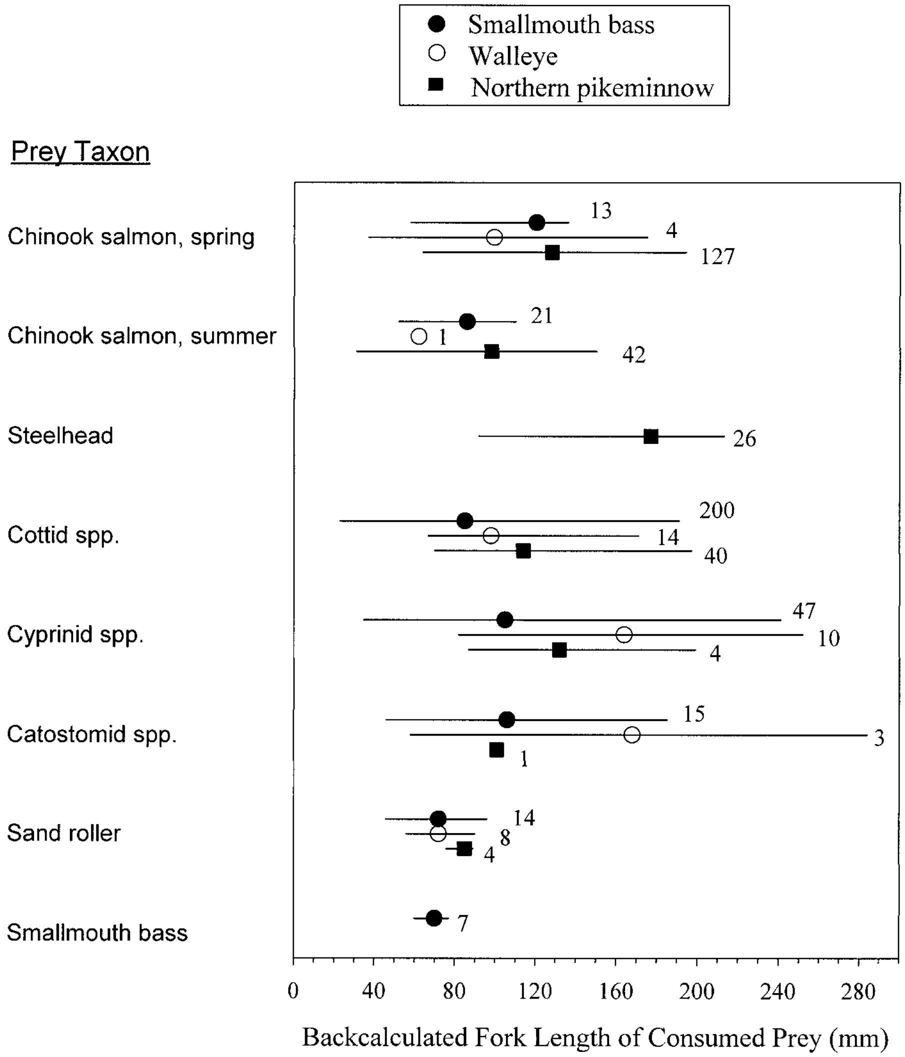

FIGURE 5.—Mean back-calculated fork lengths of prey fishes consumed by smallmouth bass, walleyes, and northern pikeminnow throughout the lower Columbia and lower Snake rivers in 1995 and 1996. Ranges of prey lengths are depicted as horizontal bars. Symbols (circles or squares) are placed at the means of prey lengths, and numbers of prey are given at the right.

ed to the Columbia River, and the impact of their predation on native fishes has been related to wide fluctuations in year-class strength and abundance (Beamesderfer and Rieman 1991; Friesen and Ward 1997). I did not estimate walleye consumption rates due to small sample sizes, but Vigg et al. (1991) estimated that nonsalmonid consumption rates of walleye 200–400 mm in length were similar to those of smallmouth bass and exceeded those of northern pikeminnow in John Day Reservoir.

It seems unlikely that smallmouth bass and walleye have affected prey populations such as largescale suckers and peamouth, which were apparently quite abundant throughout the lower basin. Conversely, the impact of predation on indigenous sand roller populations may be significant. Predation on sand rollers was restricted to the Columbia River in this study, and was also documented by Poe et al. (1991) for John Day Reservoir. The current status of sand roller populations in the Snake River is unknown, although they were considered particularly uncommon in the upper portions of the basin 20 years ago (Gray and Dauble

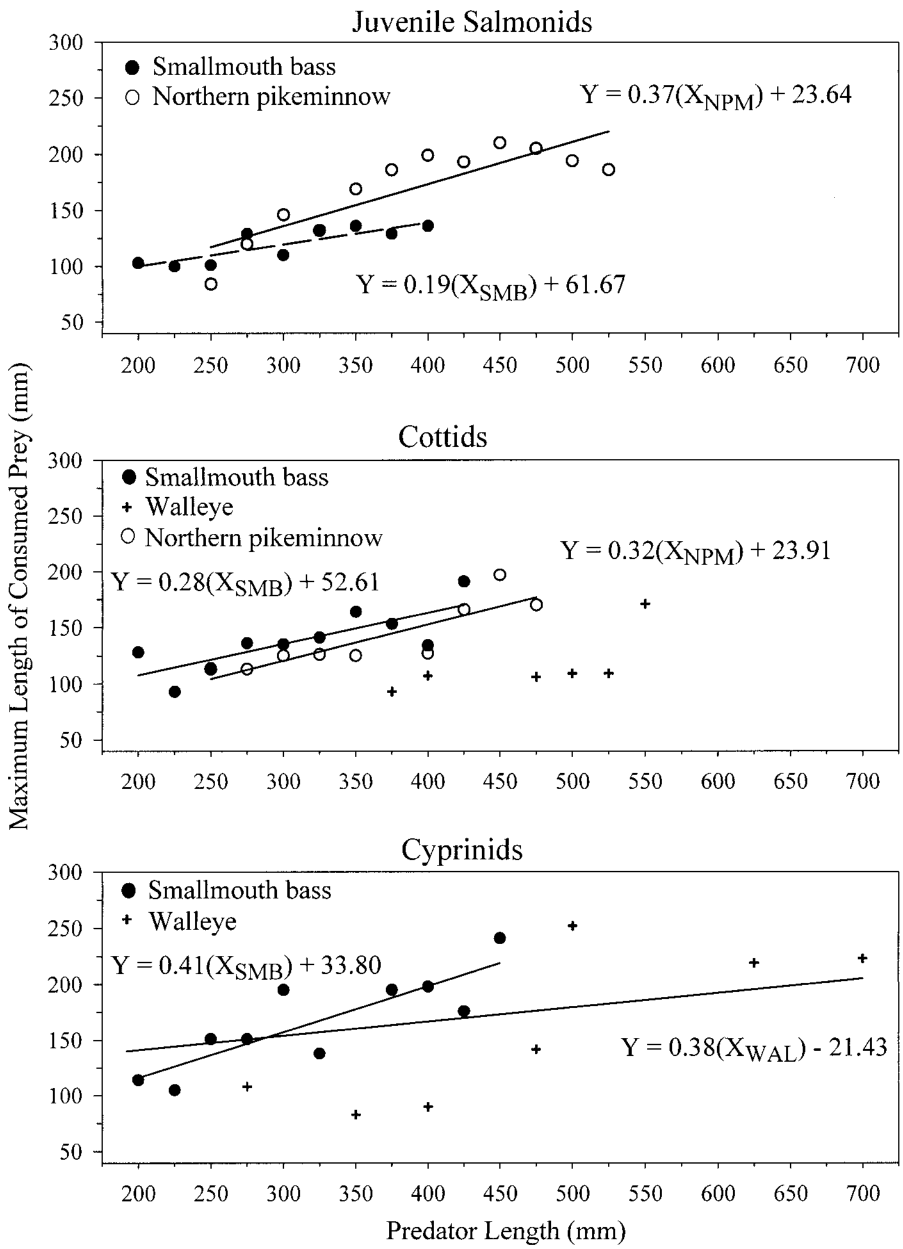

FIGURE 6.—Linear regressions of maximum length of prey consumed (*Y*) on predator fork length (*X*) for juvenile salmonids, cottids, and cyprinids variously consumed by smallmouth bass (SMB), northern pikeminnow (SQF), and walleyes (WAL) in the lower Columbia and lower Snake rivers in 1995 and 1996.

1979; Wydoski and Whitney 1979). Sand rollers use dense, bankside cover during daytime, and became active in more open water at night (Gray and Dauble 1979), which would make them particularly vulnerable to nocturnal predators.

Regional attention on predator–prey relationships in the Columbia Basin has largely been concerned with the impacts of predation by northern pikeminnow and introduced predators on juvenile anadromous salmonids. Benefits to salmonid survival associated with sustained harvest of northern pikeminnow would be compromised if salmonid

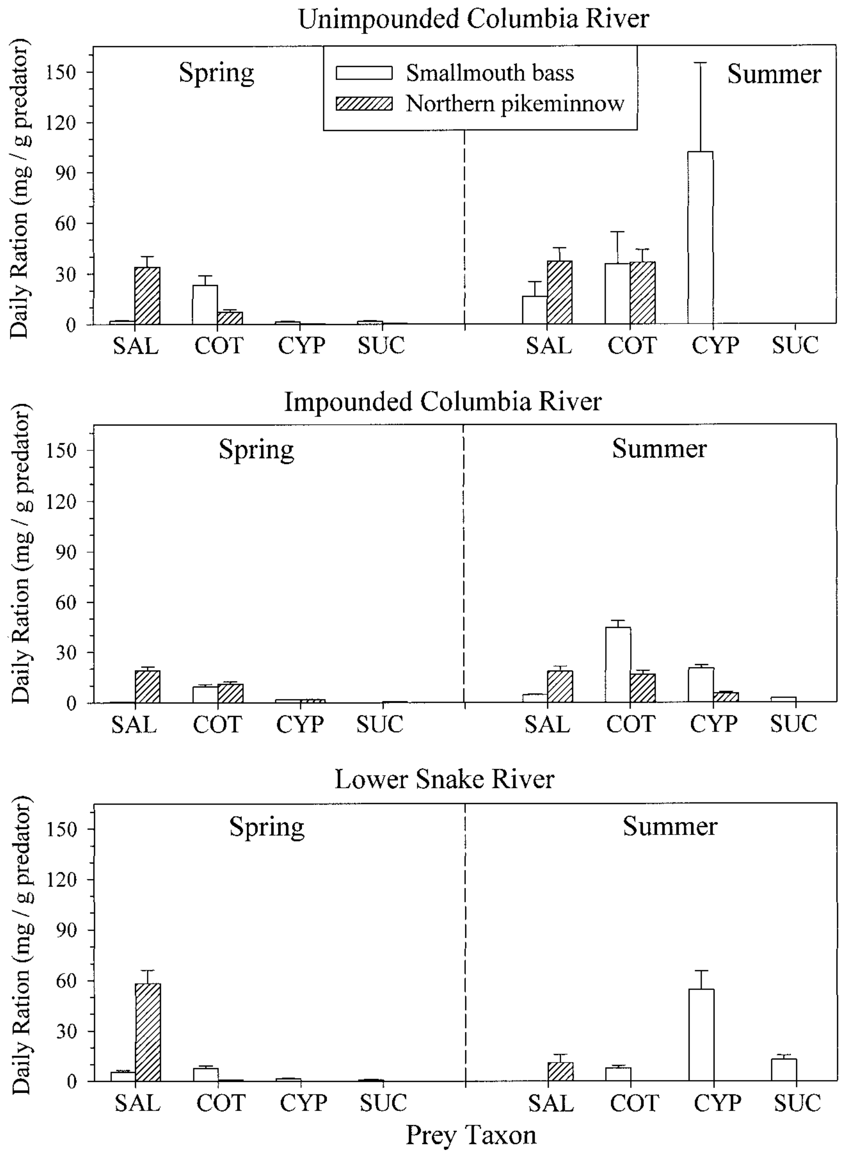

FIGURE 7.—Daily rations (mg prey/g predator) of juvenile salmonids (SAL), sculpins (COT), cyprinids (CYP), and catostomids (SUC) consumed by smallmouth bass and northern pikeminnow in three areas of the lower Columbia basin during spring and summer 1995–1996. Bars are daily rations calculated from ± SE of mean meal size.

consumption by surviving pikeminnow or other predators were exacerbated as a consequence of the Northern Pikeminnow Management Program. Changes in food habits have been documented following removal of another species (e.g., Johnson 1977; Hayes et al. 1992). In my study, the weight of juvenile salmonids ingested by smallmouth bass and northern pikeminnow exhibited annual variation; however, the pattern of variation appeared random and there was no evidence of a compensatory feeding response. Beamesderfer et al. (1996) argued that compensation by surviving northern pikeminnow was unlikely because exploitation of the species has been relatively low (<20%). Declining numbers of large, more predaceous individuals and reduced indices of salmonid consumption by northern pikeminnow have been attributed to predator removals (Friesen and

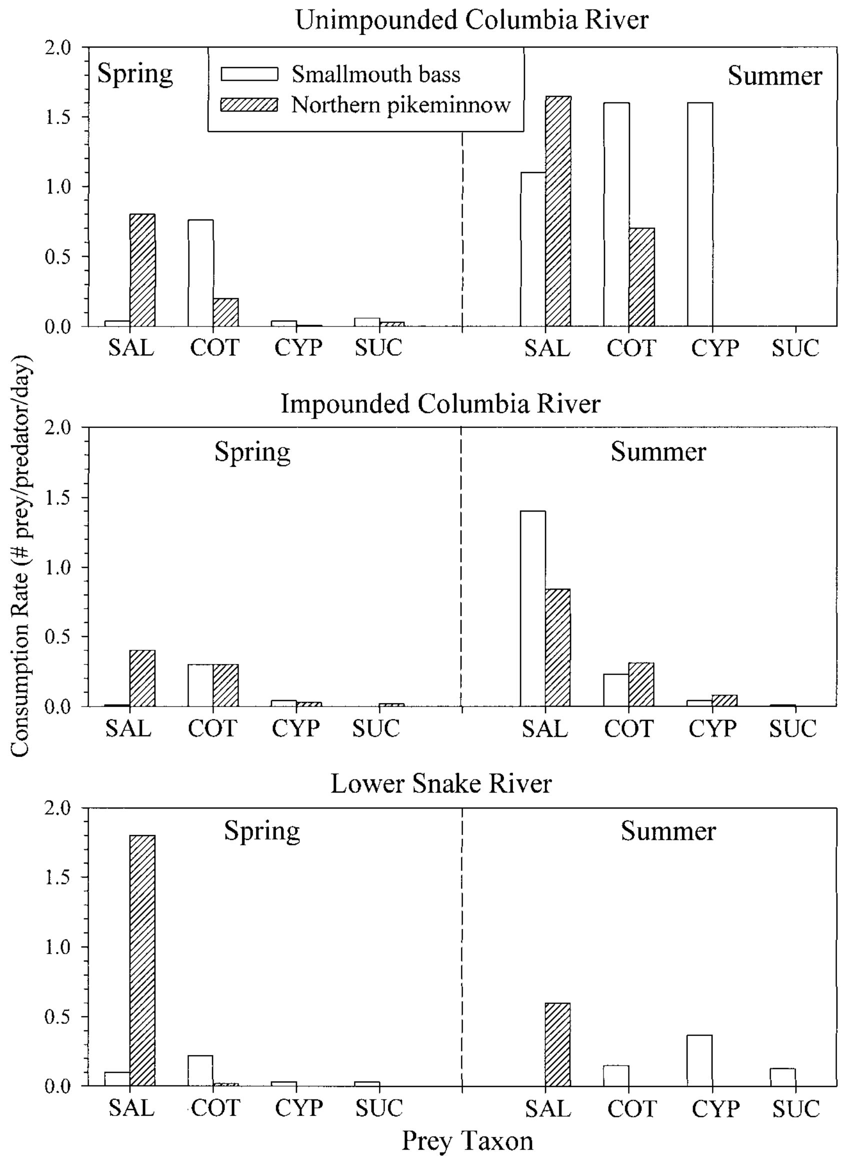

FIGURE 8.—Daily numerical consumption (prey/predator) of juvenile salmonids (SAL), sculpins (COT), cyprinids (CYP), and catostomids (SUC) by smallmouth bass and northern pikeminnow in three areas of the lower Columbia basin during spring and summer 1995–1996.

Ward 1999; Zimmerman and Ward 1999, this issue).

Incidence of juvenile salmonid predation, as indicated by prey weight and numerical frequency, was much greater for northern pikeminnow than for smallmouth bass and walleyes throughout the lower basin, as was the case in John Day Reservoir (Poe et al. 1991; Vigg et al. 1991). Although daily northern pikeminnow rations (mg salmonids/g) exceeded smallmouth bass rations in all reaches and seasons in this study, daily numerical consumption by smallmouth bass during summer was 1.1 salmonids/predator downstream from Bonneville Dam and 1.4 salmonids/predator in Columbia River reservoirs. Daily consumption by northern pikeminnow during summer in those two reaches was 1.6 and 0.8 salmonids/predator, respectively. The size difference between the two predator species, and the smaller size of juvenile salmonids consumed by smallmouth bass than by northern pikeminnow contributed to relatively high rates of juvenile salmonid consumption by smallmouth bass during summer in the impounded and unimpounded lower Columbia River.

My results paralleled other studies that compared juvenile salmonid predation between smallmouth bass and northern pikeminnow. Tabor et al. (1993) estimated that daily juvenile salmonid consumption was 1.0–1.4 salmonids per smallmouth bass and 0.3–0.6 salmonids per northern pikeminnow during May and June in the Columbia River upstream from McNary Reservoir. Curet (1993) estimated that smallmouth bass predation on wild, subyearling chinook salmon from April through June exceeded that of northern pikeminnow in Lower Granite Reservoir in the Snake River. I was unable to compare juvenile salmonid predation between smallmouth bass and northern pikeminnow in the Snake River during the same time period (subyearling chinook salmon were no longer available when sampling was conducted in late summer), but Curet's (1993) findings were consistent with results from the lower Columbia River (Tabor et al. 1993; this study). Tabor et al. (1993) and Curet (1993) attributed high levels of smallmouth bass predation to habitat overlap between subyearling chinook salmon of wild origin and smallmouth bass in low-velocity, nearshore areas.

Smallmouth bass preyed on relatively small juvenile salmonids. They consumed few steelhead, preyed on smaller chinook salmon in spring than northern pikeminnow, and consumed far more subyearling chinook salmon in summer than yearling chinook salmon in spring. Smallmouth bass were capable of ingesting much larger prey (including a 241-mm cyprinid), and their feeding activity was similar between spring and summer, based upon the frequencies of prey occurrence in stomachs. An important consequence of size-selective predation would be increased vulnerability of wild juvenile salmonids, which are typically smaller than those reared in hatcheries (Zimmerman et al. 1994). Size-selective salmonid predation by smallmouth bass likely reflected the size-related vulnerability of salmonid prey in all seasons (Poe et al. 1991) and the overlap of subyearling chinook salmon rearing habitat with preferred habitats of smallmouth bass in summer.

The relative contributions of salmonid and nonsalmonid prey to predators' diets was undoubtedly influenced by the sampling scheme used in this study. In spring, predators were collected during the outmigration of yearling chinook salmon and steelhead along with lesser numbers of coho salmon and sockeye salmon *Oncorhynchus nerka*, whereas summer sampling roughly coincided with outmigration of smaller, subyearling chinook salmon (Fish Passage Center, Columbia Basin Fish and Wildlife Authority, unpublished data). Resident nonsalmonid prey were also available but were likely underrepresented in predators' diets, particularly that of northern pikeminnow. Other migratory fishes such as juvenile American shad and Pacific lamprey may be seasonally important prey for resident predators, but they were largely absent from predator diets in my study, presumably due to the sampling schedule.

My results are generally consistent with other dietary studies within and outside the lower Columbia basin. This is important because I have described predators' food habits only during peaks in seasonal availability of migrating juvenile salmonids. The primary prey of adult smallmouth bass throughout that species' range are crayfish and fish (Scott and Crossman 1973; Carlander 1977; Edwards et al. 1983, Austen and Orth 1987; Roell and Orth 1993). Smallmouth bass preyed on crayfish, sculpins, suckers, cyprinids, and sand rollers to a greater extent (by weight and % frequency of occurrence) than did northern pikeminnow in John Day Reservoir (Poe et al. 1991). Walleye diets in that study overwhelmingly comprised fish prey by weight. Cyprinids, catostomids, sand rollers, and cottids made up 84% by weight of the total diet of walleyes in John Day Reservoir (Poe et al. 1991). Nevertheless, the incidence of predation on salmonids was undoubtedly inflated by the sample timing used in my study.

Alternatively, fish predation by smallmouth bass and walleye has been underestimated by limiting diet analyses to adult individuals. Poe et al. (1991) found that fish were important prey for smallmouth bass and walleyes smaller than 200 mm in John Day Reservoir, whereas fish formed a relatively small portion of the diets of northern pikeminnow smaller than 250 mm. Smallmouth bass and walleye less than 200 mm were excluded from my study. Other important levels of piscivory, such as predation by smaller individuals on fish eggs and early life stages, were not considered. Additionally, fish can affect community structure and function through indirect mechanisms that might cascade to lower trophic levels (McQueen et al. 1986; Carpenter et al. 1987; Northcote 1988).

Poe et al. (1994) contended that exotic predators ''outcompete'' northern pikeminnow for crayfish, sculpins, and other nonsalmonid prey and that juvenile salmonid predation by northern pikeminnow has increased since the introduction of exotic predators. Results of this study yielded some indirect evidence for competition among predator species. Both smallmouth bass and northern pikeminnow consumed crayfish, sculpins, and summer-migrating chinook salmon. Northern pikeminnow consumed fewer cyprinids, catostomids, and cottids in the Snake River, where smallmouth bass greatly outnumbered northern pikeminnow and preyed on nonsalmonids extensively. Conversely, northern pikeminnow consumption rates on juvenile salmonids were high in the unimpounded lower Columbia River (Ward et al. 1995; Zimmerman and Ward 1999), where smallmouth bass were least abundant (Zimmerman and Parker 1995).

The aquatic ecosystem in the lower Columbia River basin has undoubtedly undergone profound biotic and abiotic change since the late 1800s. Many introduced species have expanded in abundance and distribution as a consequence of habitat changes associated with hydropower development (Li et al. 1987). The results presented here shed light on predator–prey interactions in the lower Columbia and lower Snake rivers and establish a reference point from which to evaluate long-term community-level changes in response to northern pikeminnow removals.

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