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Estimated Loss of Juvenile Salmonids to Predation by Northern Squawfish, Walleyes, and Smallmouth Bass in John Day Reservoir, Columbia River

BRUCE E. RIEMAN[1] AND RAYMOND C. BEAMESDERFER

Oregon Department of Fish and Wildlife
17330 Southeast Evelyn Street, Clackamas, Oregon 97015, USA

STEVEN VIGG[2] AND THOMAS P. POE

U.S. Fish and Wildlife Service, National Fishery Research Center–Seattle
Columbia River Field Station, Cook, Washington 98605, USA

Abstract.—We estimated the loss of juvenile salmonids *Oncorhynchus* spp. to predation by northern squawfish *Ptychocheilus oregonensis*, walleyes *Stizostedion vitreum*, and smallmouth bass *Micropterus dolomieu* in John Day Reservoir during 1983–1986. Our estimates were based on measures of daily prey consumption, predator numbers, and numbers of juvenile salmonids entering the reservoir during the April–August period of migration. We estimated the mean annual loss was 2.7 million juvenile salmonids (95% confidence interval, 1.9–3.3 million). Northern squawfish were responsible for 78% of the total loss; walleyes accounted for 13% and smallmouth bass for 9%. Twenty-one percent of the loss occurred in a small area immediately below McNary Dam at the head of John Day Reservoir. We estimated that the three predator species consumed 14% (95% confidence interval, 9–19%) of all juvenile salmonids that entered the reservoir. Mortality changed by month and increased late in the migration season. Monthly mortality estimates ranged from 7% in June to 61% in August. Mortality from predation was highest for chinook salmon *O. tshawytscha*, which migrated in July and August. Despite uncertainties in the estimates, it is clear that predation by resident fish predators can easily account for previously unexplained mortality of out-migrating juvenile salmonids. Alteration of the Columbia River by dams and a decline in the number of salmonids could have increased the fraction of mortality caused by predation over what it was in the past.

Adult runs of Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss* in the Columbia River have declined dramatically from historic levels. The apparent survival of chinook salmon *O. tshawytscha* leaving the upper drainage as juveniles and returning as adults dropped from about 4% in 1964–1968 to less than 0.8% in 1972 (Ebel 1977). The decline in other species was similar. The declines have been attributed primarily to the development of the Columbia River basin for hydroelectric power (Ebel 1977; Northwest Power Planning Council 1987a). As many as nine run-of-the-river dams and reservoirs must be now negotiated by juvenile chinook salmon, coho salmon *O. kisutch*, sockeye salmon *O. nerka*, and steelhead emigrating from hatcheries and natural production areas. It is estimated that 10–45% of the juvenile salmonids that pass an individual dam and reservoir are lost (Sims and Ossiander 1981; McKenzie et al. 1983; Sims et al. 1984, Fish Passage Center 1987).

Some fish die from physical injury during passage of the dams (Schoeneman et al. 1961), but such losses represent only part of the total mortality, leaving a large part unexplained. Substantial mortality occurs within the reservoirs (McKenzie et al. 1983; Northwest Power Planning Council 1986). Causes of this reservoir mortality include nitrogen supersaturation, disease, and predation by resident fish and birds (Long et al. 1968; Raymond 1969, 1979; Ebel 1977; Leong and Barila 1983; Northwest Power Planning Council 1987b). Previously available data suggested that predation was important in local areas (Thompson 1959; Long et al. 1968; Uremovich et al. 1980; Bennett et al. 1983); however, evidence was circumstantial.

Our objective was to estimate the number of juvenile salmon and steelhead lost to resident fish predators in an entire Columbia River reservoir. We drew on the results presented in three preceding papers in this issue that characterize the diets (Poe et al. 1991), prey consumption rates (Vigg et

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[1] Present address: Idaho Department of Fish and Game, 1798 Trout Road, Eagle, Idaho 83616, USA.

[2] Present address: U.S. Department of Energy, Bonneville Power Administration, Post Office Box 3621, Portland, Oregon 97208-3621, USA.

al. 1991), and abundance of predators (Beamesderfer and Rieman 1991) in John Day Reservoir, Columbia River. In this paper, we relate predation to the numbers of fish that entered the reservoir to estimate mortality and determine whether predation can account for the "unexplained" loss. We also compare predation mortality immediately below the dam with estimates of passage mortality at the dam to determine if many fish apparently lost to predators might actually have been killed during passage of the dam.

The resident fish community in John Day Reservoir contains at least 34 species. Although many of these may be nominally piscivorous, four species—northern squawfish *Ptychocheilus oregonensis*, walleye *Stizostedion vitreum*, smallmouth bass *Micropterus dolomieu*, and channel catfish *Ictalurus punctatus*—are particularly effective predators on salmonids (Gray and Rondorf 1986; Poe et al. 1991). Our analysis of predation was restricted to the first three species because data suitable for population estimates were not available for channel catfish (Beamesderfer and Rieman 1991).

Methods

John Day Reservoir is one of four "run-of-the-river" impoundments operated for hydroelectric power generation and navigation on the lower Columbia River between Oregon and Washington. A map and description of the study area are given by Poe et al. (1991).

Predation loss and mortality.—To estimate the mean monthly and total seasonal loss of juvenile salmonids to three predators—northern squawfish, walleye, and smallmouth bass—in John Day Reservoir for the period 1983–1986, we multiplied estimates of mean daily consumption (Vigg et al. 1991) by predator number (Beamesderfer and Rieman 1991) for each species of predator. We restricted the analysis to the period from April to August, the period when most salmonids migrate through the system (Poe et al. 1991). Estimates were stratified by month. For northern squawfish, we calculated consumption for two areas in the reservoir. We pooled data for northern squawfish from the McNary Dam boat-restricted zone (an area immediately below the dam) and from all other areas downstream. We used two areas because estimates of consumption by northern squawfish and density of northern squawfish near the dam were consistently and substantially higher than those in other areas (Beamesderfer and Rieman 1991; Vigg et al. 1991). For walleyes and smallmouth bass, we pooled data for estimates in the entire reservoir because consumption data did not show large or consistent differences among sampling areas (Vigg et al. 1991). We estimated the total loss of all salmonids and partitioned monthly estimates by the predator diet composition of salmon and steelhead (Poe et al. 1991) to examine differences in mortality among stocks.

Estimates were extrapolated to a full month by multiplying daily consumption by the number of days in a month and to full season by summing the estimates for each month. To represent each month, we pooled data for all 4 years of the study because sampling for consumption estimates was limited to only a portion of a month or was omitted in some months of individual years (Vigg et al. 1991). Our estimates represent predators larger than 250 mm long (northern squawfish and walleyes; all measurements are fork lengths) or 200 mm long (smallmouth bass) because consumption of juvenile salmonids by smaller predators was negligible (Poe et al. 1991; Vigg et al. 1991) and because the effectiveness of the sampling gear limited population estimates to fish of those sizes (Beamesderfer and Rieman 1991).

We estimated mean monthly and seasonal (April–August) mortality by dividing our loss estimates by the estimated numbers of salmon and steelhead passing the dam plus the numbers released into the reservoir from hatcheries.

The total number of salmonids eaten was estimated as

$$L_{hijk} = P_i R_{jk} C_{ijk} D_j G_{hij} ;$$

L_{hijk} is the number of salmonid species h lost to predator i in month j and area k, P_i is the number of predator species i in the reservoir, R_{jk} is the proportion of predators in area k during month j (see the following equations for northern squawfish); C_{ijk} is the number of all salmonids consumed daily by predator i in month j and reservoir area k, D_j is the number of days in month j, and G_{hij} is the proportion of salmonid h in the diet of predator species i in month j. The reservoir area k ($k = 1, 2$) applies only to northern squawfish. The proportion R_{jk} was estimated for each month, based on relative catch per unit of sampling effort (CPUE) in each area weighted by the relative size of each area, as

$$R_{j1} = 0.03U_{j1}/(0.03U_{j1} + 0.97U_{j2})$$

and

$$R_{j2} = 1 - (R_{j1});$$

U_{j1} or U_{j2} is the CPUE for squawfish in month j and area 1 (the restricted zone) or 2 (the remaining reservoir), 0.03 is the proportion of reservoir area contained within the restricted zone, and 0.97 the proportion of the remaining reservoir.

The mortality estimates were

$$A_{hj} = \sum_{ik} [L_{hijk}/(m_{hj} + H_{hj})]$$

and

$$A = \sum_{hijk} L_{hijk} \Big/ \sum_{hj} (m_{hj} + H_{hj});$$

A_{hj} is the proportion lost to predators for salmonid species h in month j, A is the proportion of all salmonids lost through the whole season, m_{hj} is the estimated passage at McNary Dam for salmonid h in month j, and H_{hj} is the number of hatchery-produced salmonids h released directly in the reservoir during month j.

We used a Monte Carlo simulation to approximate the standard deviation of the number and proportion of salmonids consumed (Caputi 1988). Our calculation was programmed as a Fortran algorithm that randomly selected values for each variable in the estimator from hypothetical distributions of each variable. We assumed normal distributions, described by the mean and variance of the mean from all observations or estimates of each variable. We ran 500 iterations of the program and calculated the mean and standard deviation for total and monthly estimates. The confidence limits were described as the range of estimates encompassing 95% of the simulations. Because we pooled data among years, our estimates represented the mean loss and mortality over the period of study and not a mean for individual years.

Estimates of prey consumption and composition.—We used monthly mean consumption estimates (number of prey fish consumed by an individual predator per day) after Swenson (1972) and Swenson and Smith (1973). In this method, an average diel feeding pattern was reconstructed from pooled stomach contents of a sample of predators collected in the field by back-calculating the original weight, percent digestion, and time of ingestion of each prey fish. Consumption estimates were detailed by Vigg et al. (1991). For our purposes, we stratified estimates by two reservoir areas and by months but pooled over years.

Because the consumption estimates were based on pooled stomach contents and consumption per predator, we were unable to calculate a variance directly. We used a second method based on consumption rates for individual predators to approximate a variance for the "Swenson" estimates. We calculated the mean and variance of the mean consumption rate from all observations by our second estimates for individual predators. For each predator in a given sample we estimated the number of salmonids eaten per day as

$$C = \sum_{n=1}^{z} 1/\mathrm{D90}_n;$$

C is the number of salmonids consumed by a predator per day, and $\mathrm{D90}_n$ is the number of days to 90% digestion for salmonid prey item n of z. The criterion for turnover time was 90% digestion because this represents the stage beyond which a prey fish could no longer be identified in the stomach contents, and because the digestion rate was assumed to change after 90% digestion is reached (the rest is largely undigestible).

Time for 90% digestion for each prey item was estimated from algorithms presented by Vigg et al. (1991). The estimators incorporated individual predator weight, temperature, and meal size as dependent variables. The meal-size term was calculated from the sum of three values: (1) the original weight of the specified salmonid prey back-calculated from body or bone measurements (Vigg et al. 1991), (2) the original weights of any prey that were within 10% of the original weight of the specified salmonid prey and 20% of the percent digestion of the specified salmonid prey, and (3) the digested weight of all other food items in the stomach. We assumed that the variance in our second method was representative of the variance in the consumption estimates from the Swenson technique. We approximated a variance of the monthly means for Swenson estimates (Table 1) by assuming an equal coefficient of variation between methods.

We estimated the relative proportions of salmon and steelhead from the remains of all salmonids in stomach samples for each predator (Table 2). Salmonid remains were classified based on bone morphology according to methods detailed in Hansel et al. (1988) and stomach analyses detailed in Poe et al. (1991). Variances for the proportions (P) were estimated as

$$\hat{V}(P) = [P(1 - P)]/N;$$

N equals the total number of salmonids identified in all stomachs (Zar 1984).

TABLE 1.—Estimated consumption rates of juvenile salmonids by predator fish in John Day Reservoir by month, 1983–1986. Consumption rates are mean number of smolts eaten per day per individual predator (from Vigg et al. 1991). The restricted zone is that portion of the tailrace immediately below McNary Dam from which boats are excluded.

Area[a] and month	Sample size	Consumption rate	Variance
Northern squawfish			
Restricted zone			
Apr	242	0.14	2.3×10^{-4}
May	424	0.49	11.4×10^{-4}
Jun	614	0.36	14.3×10^{-4}
Jul	589	2.03	102.6×10^{-4}
Aug	502	0.40	25.2×10^{-4}
Below restricted zone			
Apr	264	0.04	1.2×10^{-4}
May	586	0.25	6.1×10^{-4}
Jun	469	0.09	3.2×10^{-4}
Jul	243	0.15	12.4×10^{-4}
Aug	434	0.09	4.5×10^{-4}
Walleye			
Below restricted zone			
Apr	231	0.02	0.9×10^{-4}
May	384	0.11	10.2×10^{-4}
Jun	297	0.12	11.4×10^{-4}
Jul	70	0.41	197.4×10^{-4}
Aug	77	0.21	83.9×10^{-4}
Smallmouth bass			
Below restricted zone			
Apr	293	<0.01	0.1×10^{-4}
May	673	0.01	0.3×10^{-4}
Jun	793	0.02	0.5×10^{-4}
Jul	608	0.12	2.2×10^{-4}
Aug	489	0.07	7.2×10^{-4}

[a] Estimates for walleyes and smallmouth bass do not include the boat-restricted zone because few fish of these species were collected there.

TABLE 2.—Estimated proportions of salmon prey identified from all salmonids (salmon plus steelhead) found in predator fish from John Day Reservoir by month, 1983–1986 (from Poe et al. 1991).

Month	Sample size[a]	Proportion	Variance
Northern squawfish			
Apr	131	0.88	9.0×10^{-4}
May	567	0.85	2.3×10^{-4}
Jun	272	0.91	2.9×10^{-4}
Jul	837	1.00	[b]
Aug	132	1.00	[b]
Walleye			
Apr	12	1.00	
May	45	0.91	18.5×10^{-4}
Jun	27	0.96	14.4×10^{-4}
Jul	3	1.00	[b]
Aug	7	1.00	[b]
Smallmouth bass			
Apr		1.00	
May	7	1.00	
Jun	22	0.96	18.5×10^{-4}
Jul	28	1.00	[b]
Aug	13	1.00	[b]

[a] Total prey identified as salmonids.

[b] Variance assumed to be nil because few steelhead were in the reservoir.

Estimates of predator number.—The numbers of northern squawfish and walleyes longer than 250 mm and the number of smallmouth bass longer than 200 mm in the reservoir were estimated with mark–recapture data (Beamesderfer and Rieman 1991). We used population estimates made each year from 1984 to 1986 for northern squawfish, and in 1985 and 1986 for smallmouth bass, with Overton's (1965) modification of the "Schnabel" estimator for marking and recovery within a year. Because recovery rates for walleyes were low within the year of marking, we used the estimates for 1983 to 1986, made with the modified Petersen method (Ricker 1975) based on marking in one year and recovery in the following year. The walleye data were corrected for mortality in the year of tagging and for growth in both years of sampling. We used the means and variances of the available population estimates (Table 3) as the predator numbers in our loss estimator. We assumed those means to be representative of predator numbers for 1983–1986 even when estimates were limited to only 2 or 3 years in the 4-year period. We note that even though we used a mean for northern squawfish, a significant increase in the abundance of this species occurred during the study period.

We used the catch rate data from Beamesderfer and Rieman (1991) to describe the catch per unit of effort of northern squawfish inside the restricted zone and throughout the remaining reservoir. We

TABLE 3.—Estimated number of three species of predator fishes present in John Day Reservoir. The means represent 1984–1986 for northern squawfish, 1982–1986 for walleyes, and 1982–1986 for smallmouth bass (from Beamesderfer and Rieman 1991).

Predator	Sample size (years)	Mean number	Variance
Northern squawfish	3	85,000	96.4×10^{6}
Walleye	4	10,000	2.1×10^{6}
Smallmouth bass	2	35,000	9.0×10^{6}

TABLE 4.—Estimated catch per unit of effort (CPUE) for northern squawfish in two areas of John Day Reservoir by month, 1984–1986. The unit of effort was 15 min of electrofishing current-on time (from Beamesderfer and Rieman 1991).

Month	Number of samples	Mean CPUE	Variance
	Restricted zone		
Apr	33	6.03	1.562
May	26	8.81	4.880
Jun	31	10.81	4.753
Jul	35	8.63	2.130
Aug	32	9.94	2.921
	Below restricted zone		
Apr	498	0.35	0.002
May	586	0.54	0.003
Jun	635	0.51	0.004
Jul	554	0.43	0.003
Aug	501	0.28	0.009

TABLE 5.—Estimated number of juvenile salmon and steelhead that entered John Day Reservoir by month, 1983–1986. The estimates are the means of all four years.[a]

Month	Number	Variance
	Salmon[b]	
Apr	1,567,000	1.37×10^{11}
May	5,894,000	1.81×10^{11}
Jun	4,465,000	1.33×10^{12}
Jul	5,246,000	1.28×10^{12}
Aug	801,000	1.64×10^{11}
	Steelhead	
Apr	129,000	1.14×10^{9}
May	955,000	3.94×10^{10}
Jun	210,000	4.11×10^{9}
Jul	3,000	7.56×10^{5}
Aug	<1,000	6.00×10^{3}

[a] Estimates are the sum of fish entering the reservoir by passing McNary Dam and fish released directly into the reservoir from hatcheries.

[b] Salmon include yearling chinook and subyearling chinook, coho, and sockeye salmon. Yearling chinook salmon were about 80% of all salmon in April and May. Subyearling chinook salmon were about 95% of all salmon in June, July, and August

pooled samples as before to calculate a mean and variance for the mean catch rate (Table 4).

Estimates of salmonid smolt numbers.—We approximated the daily passage of all juvenile salmon and steelhead at McNary Dam from 1983 to 1986 after Giorgi and Sims (1987). The estimator, derived only for yearling chinook salmon and for steelhead, relies on relations between sampling efficiency and powerhouse flow. We assumed that the relation for yearling chinook salmon was also representative of those for subyearling chinook salmon, coho salmon, and sockeye salmon. Unpublished work indicates that subyearling chinook salmon may be guided to the turbine bypass at lower rates than yearlings (A. Giorgi, National Marine Fisheries Service, personal communication). We recognize a possibility of bias for this segment of our estimates, and consider this in the discussion.

To approximate the number of fish entering the reservoir and available to predators (Table 5), we subtracted numbers of fish removed at the collection facility (and later transported downstream by barge or truck) and added the number of fish released directly into the reservoir from hatcheries. Daily estimates were summed over each month. The mean prey number and variance of the mean were calculated from the four yearly estimates in each month. We obtained all data on the number of salmonids collected at the dam and later transported, powerhouse flow, and hatchery releases, from records of the Fish Passage Center of the Columbia Basin Fish and Wildlife Authority, Portland, Oregon.

Dam-related mortality.—Our predation estimates did not differentiate between healthy prey fish and moribund or dead fish killed in passage because the condition of prey in gut samples was not distinguishable. To consider the potential bias in our loss estimates, we estimated daily mortality attributed only to northern squawfish predation in the restricted zone sampling area and we then compared those estimates with estimates of mortality from dam passage on the same days. A predation mortality estimate substantially larger than a dam mortality estimate was assumed to be evidence that predators were taking live juvenile salmonids in addition to those damaged during passage. We made daily predation loss and mortality estimates in the same fashion as described earlier, but did not extrapolate beyond the days when sampling for consumption estimates was done.

We projected daily mortality expected from passage at McNary Dam from 1984 through 1986 by weighting mortality for each passage route under the assumptions of FISHPASS, a model developed by the U.S. Army Corps of Engineers (unpublished report). Passage mortality was estimated as

$$A_p = T\,[(FB_1) + (1 - F)B_2] + (1 - T_1)B_3;$$

A_p is the expected proportion of fish lost on day 1, T is the proportion of total flow and fish passing through the turbines and turbine bypass, F is the

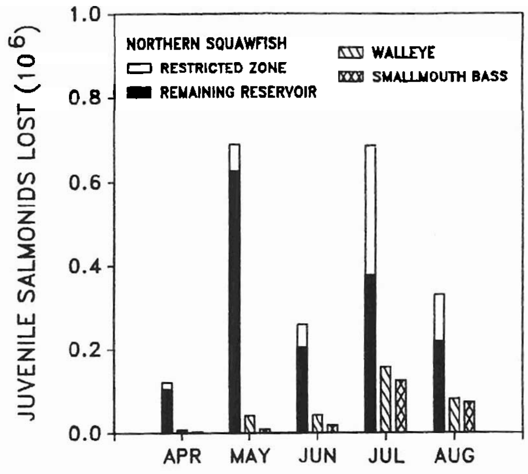

FIGURE 1.—Estimated mean monthly number of juvenile salmonids lost to predation by northern squawfish, walleye, and smallmouth bass in John Day Reservoir, 1983–1986. Estimates for northern squawfish are shown separately for the restricted zone and the rest of the reservoir.

TABLE 6.—Estimated loss to and mortality[a] from predation of juvenile salmon and steelhead in John Day Reservoir by month, 1983–1986.

	Number lost		Mortality[a]	
Month	Mean	SD	Mean	SD
		Salmon		
Apr	118,000	28,000	0.08	0.034
May	633,000	85,300	0.11	0.017
Jun	297,000	40,200	0.07	0.025
Jul	968,000	164,200	0.19	0.062
Aug	468,000	107,900	0.61	0.298
		Steelhead[b]		
Apr	15,000	4,900	0.12	0.061
May	107,000	17,100	0.11	0.031
Jun	26,000	6,300	0.13	0.089

[a] Proportion of fish entering the reservoir, calculated as (number of prey eaten)/(number passing McNary Dam plus hatchery releases to the reservoir).

[b] Estimates were not made for steelhead in July and August because of low numbers in the reservoir.

proportion of salmonids successfully guided through the turbine bypass, B_1 (0.02) is the mortality of fish passing through the turbine bypass, B_2 (0.15) is the mortality of fish passing through the turbines, and B_3 (0.02) is the mortality of fish passing over the spillway. We assumed $F = 0.75$ for steelhead and $F = 0.40$ for all salmon, which approximate values projected from the models of Giorgi and Sims (1987), as described earlier. We obtained data on daily flow and the proportion of flow through the turbines from records of the Fish Passage Center.

Results

Predation Loss and Mortality

We estimated a mean seasonal loss of 2.7 million (SD = 338,000) juvenile salmon and steelhead to fish predators in John Day Reservoir. Our simulated 95% confidence interval was 1.9 to 3.3 million.

Northern squawfish was by far the dominant predator, accounting for 78% of the total salmonid loss to the three principal predators; walleyes accounted for 13% and smallmouth bass for 9% (Figure 1). Of the three predators, only northern squawfish were abundant in the McNary Dam restricted zone. We estimate that 26% of the losses to northern squawfish and 21% of total losses (to all predators, and in all areas) were in the restricted zone. Thus, most of the total loss of salmonids to the three predators was in the main body of the reservoir. The relative importance of northern squawfish was highest in April and May (92% of total), although the importance of walleyes and smallmouth bass increased in July and August. Northern squawfish accounted for about 75% of the total loss in July and 67% in August (Figure 1).

The total loss was lowest in April and highest in July (Table 6). Peak losses in May and July coincided with peaks in salmonid numbers. Salmon were the most important (94%) salmonids consumed by predators in all months. No steelhead were found in predator stomachs during July and August. The loss of steelhead was highest in May.

Our estimate of total loss was 14% for salmon and steelhead that entered John Day Reservoir. The simulated confidence limits ranged from 9 to 19%. Total mortality rate (all fish) was higher in July and August than earlier in the season (Table 6). The increase was due to mortality of salmon. We did not estimate mortality for steelhead in July and August because numbers passing into the reservoir were low and because no steelhead were identified in predator stomachs.

Dam-Related Mortality

Predicted mortality from passage at the dam was greater than, or of similar magnitude to, predation by northern squawfish immediately below the dam in the restricted zone from April to July. Passage mortality was less than half the estimated loss to predation in August; estimates of mortality

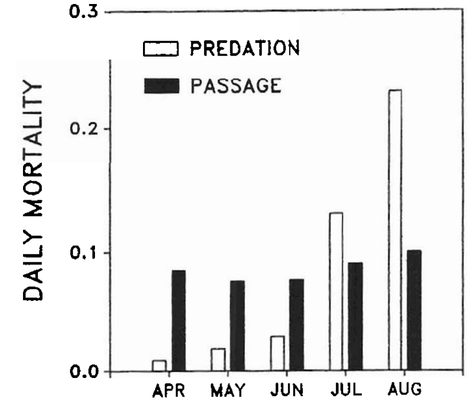

FIGURE 2.—Comparison of estimated mortality (proportion of daily passage) of juvenile salmonids lost to predation immediately below McNary Dam and to injury during passage of McNary Dam. The data represent the means of daily estimates pooled by month, 1984–1986.

from both causes increased from April to August (Figure 2).

Discussion

Our estimates support the hypothesis that predation accounts for the unexplained loss of juvenile salmonids in the Columbia River. The estimated 9–19% loss to predators in John Day Reservoir was obviously important compared with other known mortalities. Existing estimates of all mortality at individual dam and reservoir projects in the Columbia River system range from 10 to 45% (Sims and Ossiander 1981; McKenzie et al. 1983; Sims et al. 1984). Schoeneman et al. (1961) estimated that 2% of the fish passing over the spillway at a Columbia River dam and 11% of the fish passing through turbines were killed. Using the present assumptions about passage and model FISHPASS, we approximated a combined spillway, turbine bypass, and turbine mortality of 4–10% at McNary Dam. Other causes of mortality are known in the Columbia River reservoirs. Ruggerone (1986) estimated that gulls ate 2% of the salmon and steelhead passing Wanapum Dam. Loss to infectious disease may also be an important cause of mortality, particularly among hatchery fish (Leong and Barila 1983; Northwest Power Planning Council 1987a) but it has not been quantified. Predation appeared to be at least equivalent to mortality at the dam, and could easily represent the single most important loss.

We believe that predation is the major component of the unexplained mortality throughout the river. Because our estimates of predation are the first for a Columbia River reservoir, we cannot determine whether the magnitude of predation and numbers of predators are similar in other reservoirs or have changed in the river over time. Predators are common in other Columbia River reservoirs, however, and we believe it is reasonable to assume that their densities are not substantially less than those in John Day.

We also believe that predation is more important now than before the dams were built, and that it has contributed to the decline of salmon and steelhead runs. The number of predator species has increased with the introductions of exotics, including walleye, smallmouth bass, and channel catfish. Dams disrupt smolt migrations and undoubtedly stress and disorient juvenile salmonids, potentially making them more vulnerable to predators. Dams also delay smolt migrations, increasing travel time through the reservoir (Raymond 1979) and exposing juvenile salmonids to predation for longer periods and later in the season (when we found that consumption rates are high). Smolt numbers are lower than those of historic runs. Theory suggests that predators can also impose a depensatory mortality (Ricker 1950; Peterman 1977; Larkin 1979) and accelerate a decline started by some other stress (Coutant et al. 1979).

Northern squawfish was the major predator and alone caused substantial mortality of juvenile salmon and steelhead. Similar conclusions have been reached elsewhere, as evidenced by the many attempts to control populations of this and other *Ptychocheilus* species (Brown and Moyle 1981).

The universal importance of squawfish predation on salmonids is debated, although such predation has been documented in the Columbia River (Thompson 1959; Uremovich et al. 1980) and other systems (Foerster and Ricker 1941; Hartman and Burgner 1972; Steigenberger and Larkin 1974; Brown and Moyle 1981; Buchanan et al. 1981). Foerster and Ricker (1941) demonstrated that a reduction in northern squawfish predation increased the production of sockeye salmon smolts in Cultus Lake, British Columbia. Others have concluded from food studies, however, that squawfish predation in large rivers may be important only in unusual or artificial conditions. Unusual conditions might include localized hatchery releases or major habitat alterations (such as dams) that increase vulnerability or availability of salmonids as prey (Thompson 1959; Brown and Moyle 1981; Buchanan et al. 1981). We found pronounced northern squawfish predation associated with McNary Dam. The estimated loss, if considered on a linear basis (i.e., per kilometer) was more than 50 times greater immediately below the dam than that in the remaining reservoir.

Predation outside the restricted zone, however, represented the largest part (79%) of the total loss. The consumption of salmonids by individual northern squawfish away from the dam was relatively low, averaging only about 0.14 fish/day (Vigg et al. 1991) and might, by the standards of other studies, be considered unimportant. Obviously we must consider the predator population size. In a system supporting a population of 100,000 or more predators, even a low consumption rate becomes important. Predation associated with the unusual conditions at the dam is not the only important predation in John Day Reservoir. Similar conclusions might be reached in other studies if the size of predator populations were considered.

The predation process can be dynamic, and we believe that changes in the environment or characteristics of the prey can strongly influence the loss (Peterman 1977; Coutant et al. 1979; Vigg 1988). We found, for example, that our loss and mortality estimates varied from month to month. We observed a nearly eightfold variation in estimates of total loss and salmon mortality for all months. Vigg (1988) found that prey consumption by northern squawfish varied as a function of prey number, and considered the relation to be indicative of a functional response (Peterman and Gatto 1978). The form of the relation may vary with season and in response to changes in the prey composition (Vigg 1988). Temperature also has an influence on predator metabolic demands and was directly related to consumption rates for northern squawfish (Beyer et al. 1988). Because of the variation in predation, mortality of fish of different stocks of salmonids migrating through the system will be different. Mortality from predation is lower for yearling chinook salmon and steelhead that migrate primarily in April and May than it is for subyearling chinook salmon, which migrate primarily during summer. Subyearling chinook salmon may also be more vulnerable to predators because they move more slowly through the reservoir (Miller and Sims 1984) and are smaller than yearling chinook salmon or steelhead (Poe et al. 1991).

The dynamics of predation on salmonids should be an important consideration in Columbia River management. The timing of migration for salmon and steelhead is influenced by the timing of hatchery releases and water flow manipulations throughout the Columbia River hydropower system. The number and composition of prey, water flow, and water temperature vary markedly from year to year. Numbers of migrants are influenced by hatchery releases and by transportation programs that carry fish entirely past dams and reservoirs. Predator abundance and population structure also vary with recruitment and the presence of strong or weak age-classes. Sport fisheries and fishing regulations can influence predator population size and structure. As a result, we believe that conditions may change and that mortality from predation could differ substantially from that estimated here. Managers of Columbia basin salmon and steelhead stocks should consider that predator-related mortality will vary both naturally and in response to manipulation of the system.

Our estimates incorporated some of the natural variation. Because of the need to pool data and the short duration of study, however, we could not partition sampling error and the inherent variation in our estimates. The source and magnitude of expected variation might be better detailed by dynamic simulation. Present studies provide additional data on the functional and physiological responses of predators, prey selection, and predator population dynamics. Simulations incorporating this information can provide a more detailed description of changes expected in predation. Changes in predation with normal variation, and manipulation of the reservoir environment, smolt abundance, and predator populations, are considered in other work (Beamesderfer et al. 1990; Rieman and Beamesderfer 1990).

Although losses of salmon and steelhead to predation appear substantial, we recognize important uncertainties. We cannot strictly partition mortality from predation and mortality from other sources, because the causes probably are not independent. Predators attack the most vulnerable or obvious prey (Coutant et al. 1979). Except for August, our estimates of predation immediately below McNary dam were less than, or similar to, our projections of the direct loss at the dam. We conclude that predators in the restricted zone are taking live smolts late in the season, but we cannot show that they eat live smolts exclusively during any period. Better information on the consumption of healthy and moribund prey immediately below the dam will be needed to precisely partition all components of mortality.

Our range of simulated estimates incorporates sampling error and seasonal variation, but does not account for the potential bias in each component of the estimator. Sampling in large systems such as John Day Reservoir is always difficult (Campbell 1979), and the probability of bias in population estimates may be particularly large. Beamesderfer and Rieman (1991) concluded that the potential bias in the population estimates used here could be severalfold. The bias is probably negative, however, which means that our predation estimates are probably conservative.

We did not account for loss to all predators, again making our estimates conservative. Channel catfish and white sturgeon *Acipenser transmontana* are in the reservoir, and are known to eat salmonids. White sturgeon probably eat only moribund or injured juvenile salmonids, but channel catfish sometimes eat considerable numbers of healthy salmonids (Bennett et al. 1983; Poe et al. 1991; Vigg et al. 1991). We developed no useful estimates of channel catfish numbers. The species is common in the reservoir (Poe et al. 1991), however, and must cause additional mortality.

Our estimates of mortality depended on estimates of salmonid numbers that are also subject to errors of uncertain magnitude. The passage estimator was based on relations between sampling efficiency and powerhouse discharge developed for yearling chinook salmon and steelhead and for intermediate flows (Giorgi and Sims 1987). Because these fishes and flows predominate during April and May, the method should provide "reasonably accurate" estimates of passage (and thus mortality) during that period (Giorgi and Sims 1987). Recent work, however, suggests that the method of Giorgi and Sims (1987) may overestimate yearling chinook and steelhead passage at the dam by as much as 20–90% (A. Giorgi, National Marine Fisheries Service, personal communication). Errors in the passage estimate of that magnitude would mean that our April and May mortality estimates are biased low by a similar magnitude.

Our extrapolation of passage estimates for other stocks and for periods of higher powerhouse flow later in the year could also be biased. Collection efficiency of subyearling chinook salmon, which represented more than 80% of the salmonids passing the dam in late June, July, and August, may be lower than that assumed in the estimator. Estimates of collection efficiency for subyearling chinook salmon are limited and highly variable but averaged about 30% during July and August 1986 (Swan and Norman 1987) compared with about 40% assumed in the passage estimator. An error of that magnitude would mean that our June-to-August estimates of salmon mortality were overestimated by 25%. The apparent increase in mortality in July and August, relative to earlier months, could be partly due to error in the passage estimator with changing salmonid stocks. More reliable estimates of passage for subyearling chinook salmon would be useful. Even with some bias in the estimates of passage, however, mortality of salmon would still be higher late in the season than early in the season, and could be higher overall than estimated here.

We conclude that predation was an important cause of mortality of juvenile salmonids migrating through John Day Reservoir in 1983–1986. Our work has important limitations, but we believe we have made conservative estimates of loss. Predation probably causes mortality equal to or higher than that caused by passage at the dams. Predation must be considered an important factor in the management of depressed Columbia River stocks of salmon and steelhead, particularly if similar losses occur in other reservoirs. Efforts to reduce predation could produce substantial benefits in salmon and steelhead production. Alternatives for management of predation are considered in other work (Beamesderfer et al. 1990; Rieman and Beamesderfer 1990).

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