

and

Robert M. Parker, 1617 College Drive, Apt. #2, Baton Rouge, Louisiana 70808

Relative Density and Distribution of Smallmouth Bass, Channel Catfish, and Walleye in the Lower Columbia and Snake Rivers

Abstract

We used two indices derived from catch and effort to compare density and relative abundance of smallmouth bass *Micropterus dolomieu*, channel catfish *Ictalurus punctatus*, and walleye *Stizostedion vitreum vitreum* among reaches (forebays, mid-reservoirs, tailraces) and reservoirs of the lower Columbia and Snake Rivers, and among unimpounded sampling zones in the Columbia River downstream from Bonneville Dam. Smallmouth bass density was highest in forebay and mid-reservoir reaches of Snake River reservoirs. Density was greatest in lower Snake River reservoirs, intermediate in Columbia River reservoirs, and lowest in the Columbia River downstream from Bonneville Dam. Smallmouth bass were most abundant in Lower Granite Reservoir. Channel catfish were distributed throughout all reaches within reservoirs. Density was far greater in the Snake River than in the Columbia River. Walleye density was low throughout the lower Columbia River, and walleye were absent in the Snake River upstream from Ice Harbor Dam. Distribution and relative abundance of introduced piscivorous fishes indicate that predator-prey relationships differ among reservoirs, between impounded and unimpounded reaches, and between the lower Snake and Columbia rivers. Differences in the relative abundance of introduced predators should contribute to variation in losses of juvenile salmonids to resident predators.

Introduction

Fish communities in the Columbia River basin have been shaped by a combination of numerous species introductions and extensive habitat alterations following impoundment. Slower water velocities and warmer temperatures in impoundments have increased the habitat available to populations of exotic warm and cool water species, most notably smallmouth bass *Micropterus dolomieu*, channel catfish *Ictalurus punctatus*, and walleye *Stizostedion vitreum vitreum* (Poe *et al.* 1991). Their growing populations are supporting new sport fisheries of increasing recreational and economic importance, particularly in light of the dwindling stocks of Columbia River salmon *Oncorhynchus* spp. and steelhead *O. mykiss*. Region-wide interest in smallmouth bass, channel catfish, and walleye stems not only from their potential to enhance sport fishing opportunities, but from justifiable concern regarding the impacts of introduced predators on fishes native to the Columbia and Snake Rivers.

The annual downstream migration of juvenile anadromous salmonids through the Columbia and Snake Rivers represents a potential seasonal food resource for piscivorous fishes. Impoundments prolong migration rates of juvenile salmon and steelhead, concentrate them at dams, and increase their susceptibility to predation (Ebel 1977, Raymond 1979, 1988). The magnitude of predation losses

relative to other sources of mortality can be significant (Rieman *et al.* 1991). Although northern squawfish *Ptychocheilus oregonensis* accounted for most of the predation-related mortality in John Day Reservoir from 1983 to 1986 (Rieman *et al.* 1991), smallmouth bass, channel catfish, and walleye also consumed juvenile salmonids (Vigg *et al.* 1991). Introduced predators undoubtedly interact with and prey on resident native species including northern squawfish, although the impact of these interactions has not been extensively studied.

Determining predator distributions in the lower Columbia River basin is a first step towards increasing our understanding of the impacts of introduced predators. Unfortunately, most of the pertinent information on Columbia River basin fish communities resides in institutional documents of limited circulation, with the exception of Beamesderfer and Rieman (1991). Additionally, logistical problems associated with sampling large river systems have limited the geographical scope of individual research efforts in the Columbia River basin. We gathered standardized catch and effort data for smallmouth bass, channel catfish, and walleye throughout the lower Columbia and Snake Rivers from 1990 to 1992. In this paper, we compare density and relative abundance of each species among reservoirs in the lower Snake and Columbia Rivers, and in the unimpounded Columbia River downstream from Bonneville Dam. We also

examine distributional differences among reaches (forebay, mid-reservoir, and tailrace) within reservoirs.

Methods

Field Sampling

We sampled from 1990 through 1992 to collect information on resident piscivorous fishes throughout the lower Columbia and lower Snake Rivers. Because the large size of the area precluded our sampling all reservoirs in the same year, we sam-

pled fish in Columbia River reservoirs (Bonneville, The Dalles, John Day, and McNary) in 1990, Snake River reservoirs (Ice Harbor, Lower Monumental, Little Goose, and Lower Granite) in 1991, and the Columbia River downstream from Bonneville Dam in 1992 (Figure 1). We sampled John Day Reservoir in 1990, 1991 and 1992 in order to examine annual variability.

We usually sampled three, 6-kilometer long reaches in each reservoir: forebay (immediately upstream from the dam), mid-reservoir, and tailrace (immediately downstream from the next dam). Two

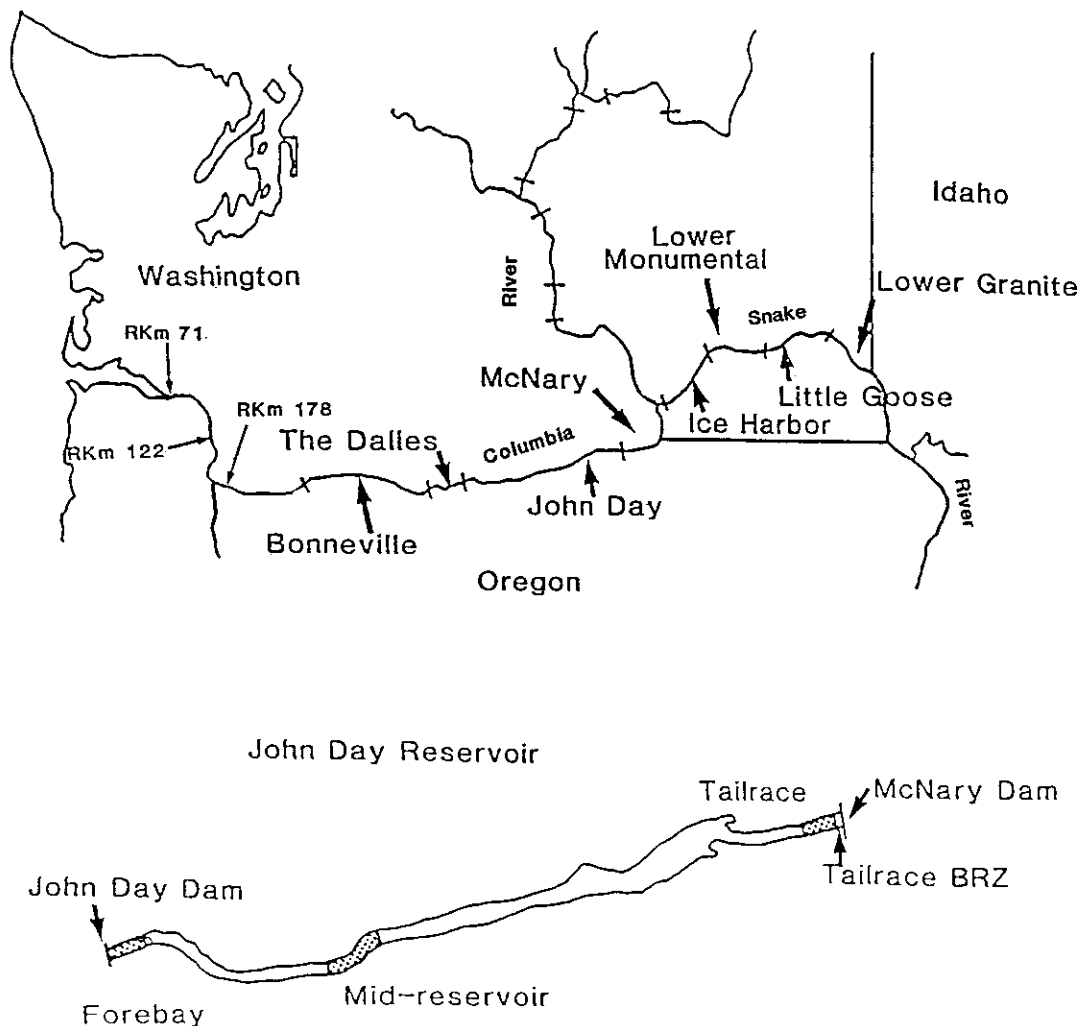


Figure 1. Sampling areas in the lower Columbia River basin. Small arrows indicate boundaries between sampling zones downstream from Bonneville Dam sampled in 1992. Large arrows indicate Columbia River reservoirs sampled in 1990, and Snake River reservoirs sampled in 1991. Map of John Day Reservoir illustrates reaches sampled within reservoirs.

exceptions were (1) the upper reach of Lower Granite reservoir was not in the tailrace of a dam, and (2) we sampled four reaches in McNary Reservoir: forebay, mid-reservoir, tailrace of Ice Harbor Dam, and the upper reservoir immediately upstream from the confluence of the Columbia and Snake Rivers. Because of its size, we partitioned the Columbia River downstream from Bonneville Dam into three zones: River kilometer (Rkm) 71-121, Rkm 122-177, and Rkm 178-234. The upper zone included Bonneville Dam tailrace. Sampling in each zone was stratified by lower, middle, and upper reaches (analogous to forebay, mid-reservoir, and tailrace reaches within reservoirs). All reaches were subdivided into 24 nearshore sampling sites of equal length.

We sampled fish with three gears: an electrofishing boat, bottom gill nets, and surface gill nets. We electrofished parallel to shore, with current of approximately 4 amperes. Bottom and surface gill nets were fished perpendicular to shore, and measured 46-m long by 2.4-m deep, with alternating panels of 3.2, 4.4, and 5.1-cm bar mesh. Sites within each reach were sampled from 0300 to 1200 hours in the order in which they were randomly selected on a daily basis from the numbers set of 1-24. We completed a minimum of 24, 15-minute power-on electrofishing runs, 24, 1-h bottom gill-net sets, and 24, 1-h surface gill-net sets in each reach. Total effort in each reach is

summarized in Table 1. Smallmouth bass, channel catfish, and walleye were counted and measured (fork length in mm).

Gear Selectivity

We compared mean catch per unit of effort (CPUE) for fish of all fork lengths to evaluate selectivity among gears for each species. We selected the most effective gear to calculate density indices for each species based on CPUE.

Density

We used CPUE as an index of density of each species in each sampling area. We also calculated a second index of density derived from frequency distributions of CPUE. Although CPUE is a commonly used index of fish density (or abundance when population size is known), Bannerot and Austin (1983) recommended the use of the square root of the relative frequency of zero-fish catches. The zero-catch index is inversely related to density such that low values correspond to high fish densities. Therefore, we used the reciprocal (1/square root of the proportion of zero catches) so the index would be directly proportional to density. This adjustment created a problem in the mid-reservoir of Lower Granite Reservoir, where at least one smallmouth bass was captured in every electrofishing run, and the proportion of zero catches equaled

TABLE 1. Total effort (spring and summer) by sampling gear and reach in zones downstream from Bonneville Dam (1992), Columbia River reservoirs (1990), and Snake River reservoirs (1991). Units of effort are number of 15' electrofishing runs, and 1-h bottom and surface gill-net sets. Reaches are FB (forebay), MR (mid-reservoir), TR (tailrace), and UR (upper reservoir).

Reservoir or zone	Effort by Sampling Gear and Reach											
	Electrofishing				Bottom gillnet				Surface gillnet			
	FB	MR	TR	UR	FB	MR	TR	UR	FB	MR	TR	UR
Rkm 71-121	-	130	-	-	-	157	-	-	-	158	-	-
Rkm 122-177	-	128	-	-	-	79	-	-	-	81	-	-
Rkm 178-234	-	126	37	-	-	70	31	-	-	67	32	-
Bonneville	23	27	27	-	26	21	24	-	16	23	29	-
The Dalles	38	12	30	-	26	23	24	-	27	21	24	-
John Day	35	37	31	-	18	30	30	-	26	34	29	-
McNary	34	37	31	30	30	28	27	32	28	27	25	34
Ice Harbor	33	33	43	-	43	37	37	-	43	38	37	-
Lower Monumental	42	37	33	-	40	43	41	-	40	40	43	-
Little Goose	37	31	33	-	40	36	38	-	40	37	38	-
Lower Granite	35	34	-	33	43	44	-	50	42	47	-	46

TABLE 2. Surface areas (hectares) of zones downstream from Bonneville Dam and reaches within Columbia and Snake River reservoirs. Near-shore areas are the total mid-reservoir areas minus those areas greater than 12.2 m deep and greater than 46 m from shore.

Reservoir or reach	Surface area (hectares)					
	Total	Forebay	Mid-reservoir			
			Total	Near-shore	Tailrace	Upper
RKm 71-121	7,604	—	—	6,421	—	—
RKm 122-177	6,072	—	—	5,080	—	—
RKm 178-234	6,123	—	5,715	5,119	408	—
Bonneville	7,632	390	6,866	2,919	376	—
The Dalles	3,639	526	2,631	1,604	479	—
John Day	19,781	792	18,171	7,933	810	—
McNary	12,218	863	10,508	5,579	206	641
Ice Harbor	3,285	578	2,420	1,452	287	—
Lower Monumental	2,425	421	1,639	620	365	—
Little Goose	3,888	599	3,086	1,492	203	—
Lower Granite	3,240	594	2,306	1,236	—	340

zero. We therefore assigned a zero-fish catch index value to that reach based on the proportional difference in CPUE between the mid-reservoir reaches in Little Goose and Lower Granite reservoirs.

We pooled data from lower, middle, and upper reaches to compare mean CPUE and zero-catch indices among the three zones of the Columbia River downstream of Bonneville Dam. We pooled data from Columbia River reservoirs and Snake River reservoirs to compare mean CPUE and zero-catch indices among forebay, mid-reservoir, and tailrace reaches within each river. We described 95% confidence intervals for CPUE indices as plus and minus two standard errors of mean CPUE.

We calculated reservoir-wide CPUE and zero-catch indices by taking the product of each reach-specific index and the proportion of total reservoir surface in that reach (Table 2), and summing the products across reaches. Each reservoir-wide density index was therefore a weighted mean, where the relative surface area of the forebay, mid-reservoir, and tailrace was used as a weighting factor for the corresponding reach-specific index values. Standard errors for reservoir-wide CPUE indices were estimated using a BASIC program that generated a random, normal distribution of 500 reservoir-wide CPUE indices based on the mean and standard error of CPUE in each reach (forebay, mid-reservoir, and tailrace) within each reservoir. We described 95% confidence intervals as

plus and minus two standard errors. Our approach was similar to Rieman *et al.* (1991), who used a Monte Carlo simulation to estimate standard deviation of the number of salmonids consumed by predators.

Our sampling sites were limited to nearshore areas throughout the lower Columbia and Snake Rivers. Therefore, we estimated the surface area in mid-reservoirs and the three zones downstream from Bonneville Dam that was both less than 12.2 m and within 46 m of shore (Table 2). We used these near-shore surface areas as the weighting factor for the corresponding reach-specific density indices when calculating reservoir-wide indices for each species.

Relative Abundance

We calculated an index of relative abundance as the product of each reservoir-wide CPUE density index (or zone-specific CPUE downstream from Bonneville Dam) and corresponding reservoir surface area (Table 2). We expressed relative abundance in each reservoir and zone as a proportion of the reservoir or zone with the highest observed index value.

Results

Smallmouth Bass

Electroshocking accounted for approximately 91% of the total catch of 7,227 smallmouth bass.

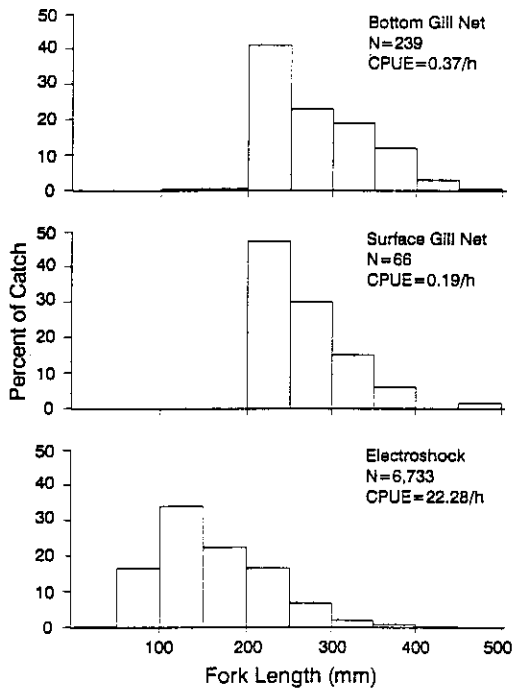


Figure 2. Size composition and catch per unit effort (CPUE) of smallmouth bass by gear type. N = number of fish measured.

Electroshocking CPUE was 60 times greater than bottom gill-net CPUE, and 117 times greater than surface gill-net CPUE (Figure 2). Fish from 100 to 149 mm fork length represented the largest proportion of the electrofishing catch, whereas nearly all fish captured in gill nets were greater than 200 mm. We used electrofishing catch and effort data to calculate density indices.

Density of smallmouth bass downstream from Bonneville Dam was highest in the two up-river zones and lowest from Rkm 71-121 (Figure 3). Density was similar among forebay, mid-reservoir, and tailrace reaches of Columbia River impoundments, but was higher in forebay and mid-reservoirs than tailraces of Snake river impoundments. The CPUE and zero-catch indices yielded similar differences in density among reaches and zones. Density was greatest in Snake River reservoirs, intermediate in Columbia River reservoirs, and lowest downstream from Bonneville Dam for both indices (Figure 4). Relative abundance of smallmouth bass was greatest in Lower Granite Reservoir and lowest in the unimpounded Columbia River

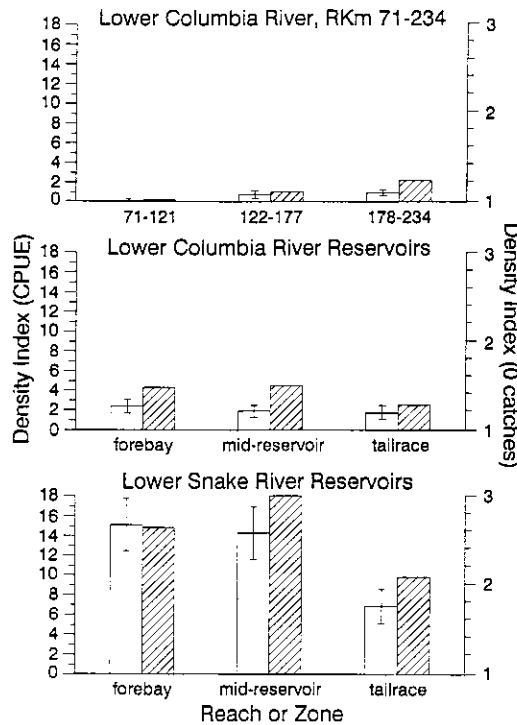


Figure 3. Indices of smallmouth bass density in sampling zones of the lower Columbia River downstream from Bonneville Dam, in reaches of Columbia River reservoirs (Bonneville, The Dalles, John Day, McNary), and in reaches of Snake River reservoirs (Ice Harbor, Lower Monumental, Little Goose, Lower Granite). Indices are electrofishing CPUE (open bars) and the relative frequency of zero catches for electrofishing (hatched bars). Error bars indicate 95% confidence intervals around mean CPUE.

from Rkm 71 to 121. Relative abundance in Snake River reservoirs was high, considering their small size relative to Columbia River reservoirs.

Electrofishing catch rates of smallmouth bass in John Day Reservoir were very similar from 1990 through 1992. Reservoir-wide density indices were 3.01 in 1990, 3.46 in 1991, and 4.47 in 1992. Density in the tailrace was less than in the forebay and mid-reservoir each year. In any year, density of smallmouth bass in John Day Reservoir was less than in Snake River reservoirs sampled in 1991, and an order of magnitude greater than Columbia River zones downstream from Bonneville Dam sampled in 1992.

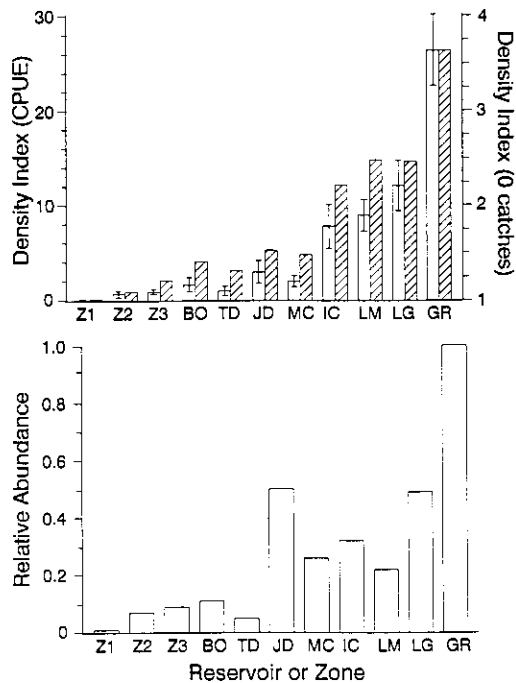


Figure 4. Indices of smallmouth bass density and relative abundance in sampling zones in the Columbia River downstream from Bonneville Dam, and in Columbia and Snake River reservoirs. Error bars indicate 95% confidence intervals around mean CPUE. Density indices are as described for Figure 3. Relative abundance is the product of reservoir-wide CPUE density indices and the corresponding surface areas. Lower Columbia River sampling zones are RKM 71-121 (Z1), RKM 122-177 (Z2), and RKM 178-234 (Z3). Reservoirs are Bonneville (BO), The Dalles (TD), John Day (JD), McNary (MC), Ice Harbor (IH), Lower Monumental (LM), Little Goose (LG), and Lower Granite (GR).

Channel catfish

We sampled 2,392 channel catfish with all gears. Bottom gill nets accounted for 78% of the total catch (Figure 5). Bottom gill nets selectively sampled fish greater than 200 mm fork length. Electroshocking was more effective at sampling both very small (<100 mm) and very large (>600 mm) fish when compared to bottom gill nets; however, very few small and large fish were captured by electrofishing because overall CPUE was one sixth that of bottom gill nets. We used catch and effort data from bottom gill-net sampling to calculate indices of channel catfish density.

No channel catfish were captured downstream from Bonneville Dam. Both CPUE and zero-catch

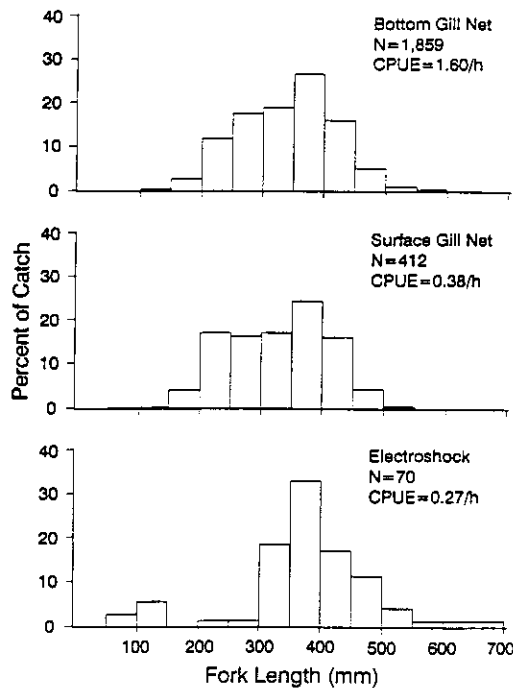


Figure 5. Size composition and catch per unit effort (CPUE) of channel catfish by gear type. N=number of fish measured.

indices for channel catfish were highest in tailtraces of Columbia River reservoirs (Figure 6). Catch per unit effort among reaches within Snake River reservoirs was higher in mid-reservoirs and tailtraces than forebays, whereas the zero-catch index was lower in forebays and mid-reservoirs than tailtraces (Figure 6). We captured channel catfish in each Columbia River reservoir; however, catches were extremely low except in McNary Reservoir. We therefore restricted our reservoir-wide comparisons of density and relative abundance to McNary Reservoir and the four Snake River reservoirs. Density of channel catfish was highest in Ice Harbor Reservoir and lowest in McNary and Lower Granite reservoirs (Figure 7). Differences in reservoir-wide density were similar between the CPUE and zero-catch indices. Relative abundance was more than twice as great in Ice Harbor Reservoir than in any of the other reservoirs (Figure 7).

Bottom gill-net catch rates of channel catfish in John Day Reservoir were variable from 1990 through 1992, primarily because catches in all three years were very low. Only 4 were sampled in 1990, 16 in 1991, and 15 in 1992. Catch rates

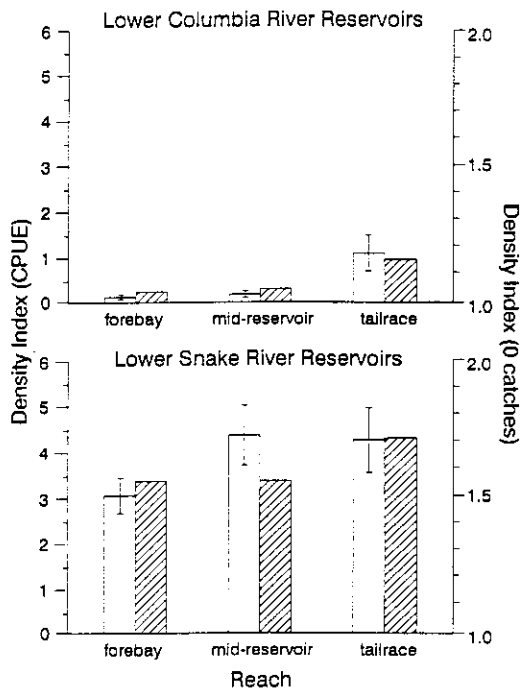


Figure 6. Indices of channel catfish density in reaches of Columbia River reservoirs (Bonneville, The Dalles, John Day, McNary) and Snake River reservoirs (Ice Harbor, Lower Monumental, Little Goose, Lower Granite). Indices are bottom gill-net CPUE (open bars) and the relative frequency of zero catches for bottom gill nets (hatched bars). Error bars indicate 95% confidence intervals around mean CPUE.

were greatest in the tailrace reach of John Day Reservoir in each year. In any year, density of channel catfish in John Day Reservoir was at least an order of magnitude less than density in Snake River reservoirs sampled in 1991.

Walleye

Only 88 walleye were captured during the study. Catch per hour was 0.16 for electroshocking, 0.03 for bottom gill nets, and <0.01 for surface gill nets. Walleye captured by electroshocking ranged from 150 to 750 mm fork length, whereas those captured in bottom gill nets ranged from 350 to 600 mm. Only 3 walleye were captured in surface gill nets.

Because of the small sample size for all gears, we did not calculate density indices for walleye. We can offer the following observations on walleye distribution. We captured walleye throughout

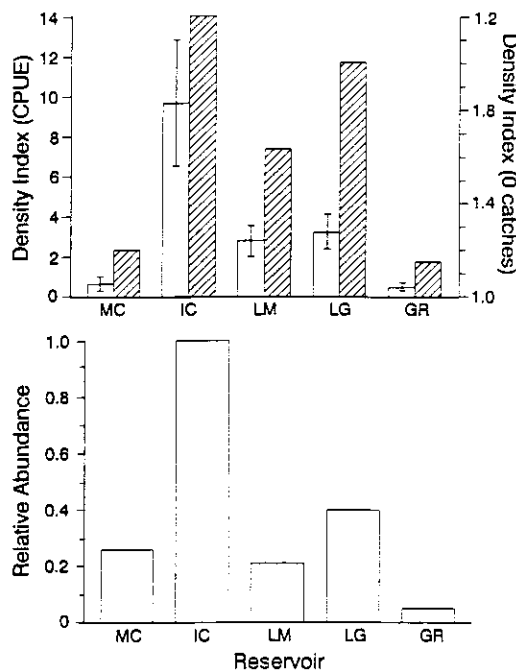


Figure 7. Indices of channel catfish density and relative abundance in McNary (MC), Ice Harbor (IC), Lower Monumental (LM), Little Goose (LG), and Lower Granite (GR) reservoirs. Error bars indicate 95% confidence intervals around mean CPUE. Density indices are as described for Figure 6. Relative abundance is the product of reservoir-wide CPUE density indices and the corresponding surface areas.

much of the lower Columbia River, from Rkm 137 to upper McNary Reservoir, and in the Snake River from the mouth to Ice Harbor Dam tailrace. No walleye were captured in the Snake River reservoirs. Catch rates were highest in tailraces, intermediate in mid-reservoirs, and very low in forebays. Downstream from Bonneville Dam, catch rates were highest from Rkm 178 to 234. Among Columbia River reservoirs, catch rates were highest in The Dalles Reservoir, followed in order by Bonneville, John Day, and McNary reservoirs.

Discussion

Differences in the density and relative abundance of introduced predators within and among reservoirs were striking, particularly when compared with density and relative abundance of northern squawfish (Ward *et al.* in press). Density of smallmouth bass was generally greatest in forebays and mid-reservoirs, whereas density of northern squawfish was greatest in tailraces. Smallmouth bass densities were greatest upstream from John

Day Dam, particularly in the Snake River, whereas northern squawfish density is greatest in the lower Columbia River downstream from John Day Dam. Density of channel catfish was highest in Snake River reservoirs, particularly in tailrace restricted zones. Walleye distribution was limited to the Columbia River and the Snake River downstream from Ice Harbor Dam. Our catch rates of walleye in reservoirs were low but consistent with recent sport angling success (Tinus and Beamesderfer 1994). Recreational fishery surveys conducted in lower Columbia River reservoirs showed CPUE was greatest in The Dalles Reservoir, followed in order by Bonneville and John Day reservoirs (Tinus and Beamesderfer 1994).

In general, impoundments contained higher densities of introduced predators than the unimpounded Columbia River downstream from Bonneville Dam. Ward *et al.* (in press) reported that density and abundance of northern squawfish was relatively high in the unimpounded Columbia River. The high density of northern squawfish downstream from Bonneville Dam is noteworthy because some authors have suggested that impoundments have enhanced northern squawfish populations (Poe *et al.* 1991). Northern squawfish occurred in the diets of smallmouth bass and walleye in John Day Reservoir (Poe *et al.* 1991). Other native species commonly eaten by introduced predators include cottids and catostomids. Our results indicate that predation by introduced species on juvenile northern squawfish and other native species may be greater in reservoirs than unimpounded reaches.

Many differences exist between lower Columbia River and lower Snake River reservoirs that might contribute to higher densities of smallmouth bass and channel catfish in the Snake River. Water temperatures during summer are higher in the lower Snake River than in the lower Columbia River, sometimes creating a thermal barrier to adult salmonids returning to the Snake River (Trefethen 1972). Snake River reservoirs are generally smaller, have greater mean depths, and are more isolated and less accessible to anglers than Columbia River reservoirs. The effect of these factors, and undoubtedly many other habitat features, on the proliferation of smallmouth bass and channel catfish has not been studied. In the course of our sampling, we observed that densities of other introduced warm water species such as white crappie *Pomoxis annularis*, black crappie *P.*

nigromaculatus, and pumpkinseed *Lepomis gibbosus* are also much greater in the lower Snake River than the lower Columbia River.

Our findings suggest that the magnitude and dynamics of predation by resident fishes on juvenile salmonids are quite different in the lower Snake River than the lower Columbia River. Losses of juvenile salmonids to predation by northern squawfish are greater in the lower Columbia River than the lower Snake River (Ward *et al.* in press). Our study has shown that relative abundance of smallmouth bass and channel catfish was much greater in the Snake River than the Columbia River. Diet and consumption rates of channel catfish in John Day Reservoir (Poe *et al.* 1991, Vigg *et al.* 1991) indicated that they may be important predators on juvenile salmonids, particularly in tail-races. Daily consumption rates of juvenile salmonids by smallmouth bass exceeded those by northern squawfish in the Columbia River near Richland, Washington (Tabor *et al.* 1993).

Introduced predators might be expected to consume greater numbers of juvenile salmonids in the Snake River than in the Columbia River; however, several factors may limit predation by smallmouth bass and channel catfish. Peak migration of juvenile salmonids past Snake River dams occurs in spring, when cool water temperatures would lower consumption rates of predators. Many juvenile salmonids are collected at Lower Granite and Little Goose dams and transported to the Columbia River downstream from Bonneville Dam, reducing their availability to resident predators in impoundments, particularly in Ice Harbor and Lower Monumental reservoirs.

Populations of all predator species could be affected by a predator control program begun in 1990 to reduce northern squawfish predation on juvenile salmonids. If mortality of juvenile salmonids is significantly reduced by sustained harvest of northern squawfish, predation by other species may be enhanced due to increased availability of juvenile salmonid prey. A change in growth rate might accompany dietary shifts, altering size distributions, fecundity, or abundance, as was shown for yellow perch *Perca flavescens* following removal of white suckers *Catostomus commersoni* (Hayes *et al.* 1992). Conversely, both smallmouth bass and walleye are harvested incidentally by anglers fishing for northern squawfish. Angling for walleye has increased throughout the lower Columbia River (Tinus and Beamesderfer 1994), but exploitation

rates have not been determined. Additional harvest of smallmouth bass and walleye could be significant, particularly in areas where abundance appears low.

Several uncertainties limited our comparison of relative density and abundance among reservoirs. We excluded deep (> 12.2 m), mid-channel (> 46 m from shore) areas when calculating reservoir-wide indices of density and abundance because our sampling was limited to near-shore areas. If smallmouth bass or channel catfish utilize mid-channel areas to a significant extent, we would have underestimated their density and abundance, particularly in large reservoirs where mid-reservoir reaches are proportionally large.

We recognize that comparing Columbia River reservoirs, Snake River reservoirs, and the unimpounded lower Columbia River may be uncertain because sampling in each area was conducted in different years. This uncertainty was at least partly ameliorated by sampling John Day Reservoir each year. The rank order of the density index for smallmouth bass in John Day Reservoir among the 11 sampling areas (8 reservoirs and 3 unimpounded zones) was the same in any year.

Any index of fish density or abundance has shortcomings. The relationship of CPUE to abundance is not always one of strict proportionality (Richards and Schnute 1986). Bannercot and Austin (1983) evaluated statistical bias in CPUE relative to several other indices that are based on frequency distributions of catch. They showed the square root of the relative frequency of zero catches to be an unbiased index of density, and recommended its use over CPUE. Our results based on the zero-catch index were generally similar to those based on CPUE.

Although both indices yielded similar results, the index based on the proportion of zero catches had several limitations. It is inversely related to

density such that low index values corresponded to high fish densities, although this was easily overcome by using the reciprocal. This adjustment created a problem when the proportion of zero catches equaled zero, suggesting that the utility of the index may be limited to areas with low to moderate densities of fish. Additionally, frequency distributions of catch and effort yield a single index value without variance. Nevertheless, we believe the validity of our findings was reinforced by the fact that both indices yielded similar patterns of density differences among areas and reservoirs, although we acknowledge that indices are practical surrogates for more robust approaches to population estimation, such as mark-recapture methodologies.

Our results present a picture of the current distribution and relative abundance of introduced piscivorous fishes in the lower Columbia River basin. Despite uncertainties, we believe that predator distributions provide strong evidence that important differences exist in predator-prey relations among reservoirs, between impounded and unimpounded reaches, and between the lower Columbia and Snake rivers.

Acknowledgements

This project was funded by the Bonneville Power Administration (contract DE-BI79-90BP07084) and administered by William Maslen. Administration and contracting was facilitated by Tony Nigro and Ray Beamesderfer of the Oregon Department of Fish and Wildlife, and Charles Willis of Cramer and Associates. We thank David Ward and Ray Beamesderfer for their thoughtful comments on the manuscript. The manuscript would not have been possible without the hard work of many Oregon Department of Fish and Wildlife seasonal employees who worked on this study. We thank them for their dedication during field sampling.

Literature Cited

- Bannercot, S. P., and C. B. Austin. 1983. Using frequency distributions of catch per unit effort to measure fish-stock abundance. *Transactions of the American Fisheries Society* 112:608-617.
- 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.
- Ebel, W. J. 1977. Panel 2: Fish passage problems and solutions—major passage problems. *In* E. Schwiebert (ed.), *Columbia River Salmon and Steelhead*. American Fisheries Society, Special Publication No. 10, Washington, D.C. Pp. 33-39.
- 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.

- Poc, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Predergast. 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.
- Raymond, H. L. 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. *Transactions of the American Fisheries Society* 108:505-529.
- Raymond, H. L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer chinook salmon and steelhead in the Columbia River basin. *North American Journal of Fisheries Management* 8:1-24.
- Richards, L. J. and J. T. Schnute. 1986. An experimental and statistical approach to the question: Is CPUE an index of abundance? *Canadian Journal of Fisheries and Aquatic Sciences* 43:1214-1227.
- Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poc. 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.
- Tabor, R. A., R. S. Shively, and T. P. Poc. 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.
- Tinus, E. S., and R. C. Beamesderfer. 1994. An update on the distribution, fisheries, and biology of walleye in the lower Columbia River. Information Report Number 94-3. Oregon Department of Fish and Wildlife, Portland.
- Trefethen, P. 1972. Man's impact on the Columbia River. In R. T. Oglesby (ed.), *River Ecology and Man*. Academic Press, New York. Pp. 77-98.
- Vigg, S., T. P. Poc, L. A. Predergast, 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. Peterson, and J. Loch. In Press. Index of predation on juvenile salmonids by northern squawfish in the lower and middle Columbia River and the lower Snake River. *Transactions of the American Fisheries Society*.

Received 1 June 1993

Accepted for publication 12 September 1994