EVALUATION OF THE NORTHERN SQUAWFISH MANAGEMENT PROGRAM

Final Report of Research, 1990-96

Edited by

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ABSTRACT

Development of the hydropower system in the lower Columbia and Snake rivers has resulted in increased losses of juvenile salmonids to resident fish predators. The native northern squawfish *Ptychocheilus oregonensis* is the dominant predator of juvenile salmonids, but introduced smallmouth bass *Micropterus dolomieu* and walleye *Stizostedion vitreum* are also abundant. A large-scale management program for northern squawfish was begun in 1990 to increase survival of juvenile salmonids in the Columbia and Snake rivers. The Northern Squawfish Management Program (NSMP) consists of a public sport-reward fishery, and agency-operated dam-angling and gillnet fisheries that target northern squawfish ≥250 mm fork length, approximately the size at which northern squawfish become important predators on juvenile salmonids. The goal of the program is to sustain annual exploitation of 'predator-size' northern squawfish at 10-20%, which may reduce losses of juvenile salmonids by as much as 50%. We evaluated the management program to determine if annual exploitation of northern squawfish was maintained in the target range. We also monitored predator populations to describe the response of northern squawfish, smallmouth bass, and walleye to the management program. From 1990-96, over 1.1 million northern squawfish ≥250 mm fork length were removed from the lower Columbia and Snake rivers. Annual exploitation averaged 12.0%, and ranged from 8.1% to 15.5%. The sport-reward fishery accounted for 86.5% of the harvest. All fisheries targeted large, piscivorous, northern squawfish (96.1-99.5% of reported catch). We found no evidence that surviving northern squawfish compensated for sustained removals. Indices of northern squawfish abundance and consumption of juvenile salmonids were consistently lower from 1994-96 than 1990-93. Size structure of northern squawfish populations appeared to decrease in response to removals of large fish; however, we found no trend of increased growth, fecundity, or year-class strengths. We found no evidence of smallmouth bass or walleye response to sustained removals of northern squawfish. No trends in smallmouth bass density, consumption of juvenile salmonids, population structure, growth, mortality, or year-class strength have been realized concurrent with the NSMP. Variations in walleye density and population structure appear to be driven by variations in year-class strength, not by response to removals of northern squawfish. We found no trends in growth or mortality of walleye. We found no evidence that diets of northern squawfish, smallmouth bass, or walleye changed in response to sustained removals of northern squawfish. Piscivory and salmonid predation varied annually for smallmouth bass and walleye, but did not increase coincident with removals of northern squawfish. Piscivory by northern squawfish declined over time from 1990-96 Losses of juvenile salmonids to predation have probably decreased since implementation of the NSMP. Results indicate that if all variables other than exploitation of northern squawfish were held constant, predation by northern squawfish on juvenile salmonids has decreased to 62% (range 45-75%) of pre-program levels. Lack of response by surviving northern squawfish and other predators, and lack of changes in diet of these fish increases confidence in the hypothesis that sustained removals of northern squawfish increases survival of juvenile salmonids.

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PREFACE

This document is the final report of research conducted from 1990-96 by the Oregon Department of Fish and Wildlife (ODFW) to evaluate Bonneville Power Administration (BPA) project 90-077, the Northern Squawfish Management Program (NSMP). The Summary of Project summarizes and integrates the results, conclusions, and recommendations of the evaluation. The report contains research papers that describe how we addressed project objectives, how we reached our conclusions, and why we made our recommendations. The papers are listed and numbered consecutively in the Table of Contents and the numbers are used to reference each paper in the Summary of Project. It is the integration of these individual papers that provides the best picture of the current status of the NSMP.

SUMMARY OF PROJECT

Introduction

Development of the hydropower system in the lower Columbia and Snake rivers has resulted in increased losses of juvenile salmonids to resident fish predators. Impoundments delay the downstream migration of juveniles, increasing their exposure to predators and high water temperatures. Migrating fish are concentrated and endure stress as they pass dams, increasing their vulnerability to predation. The native northern squawfish *Ptychocheilus oregonensis* is the dominant predator of juvenile salmonids, but introduced smallmouth bass *Micropterus dolomieu* and walleye *Stizostedion vitreum* are also abundant.

A large-scale management program for northern squawfish was begun in 1990 to increase survival of juvenile salmonids in the Columbia and Snake rivers. The Northern Squawfish Management Program (NSMP) consists of a public sport-reward fishery, and agency-operated dam-angling and gillnet fisheries that target northern squawfish ≥250 mm fork length, approximately the size at which northern squawfish become important predators on juvenile salmonids. Because consumption of juvenile salmonids generally increases with size of northern squawfish, low exploitation rates may result in relatively large reductions in predation. The goal of the program is to sustain annual exploitation of "predator-size" northern squawfish at 10-20%, which may reduce losses of juvenile salmonids by as much as 50%.

We evaluated the management program to determine if annual exploitation of northern squawfish was maintained in the target range. We also monitored predator populations to describe the response of northern squawfish, smallmouth bass, and walleye to the management program. Benefits of the management program could be less than expected if surviving northern squawfish or other predators increase their rates of predation, growth, or reproduction. We used our findings to estimate the benefits of the management program in terms of reduced predation on juvenile salmonids. Study objectives included:

(1)   Determine the exploitation rate and size of northern squawfish harvested annually for each fishery;

(2)   Index abundance and consumption of juvenile salmonids by northern squawfish annually;

(3)   Describe the response of northern squawfish population structure, growth, mortality, fecundity, and year-class strength to sustained removals;

(4)   Describe the response of smallmouth bass and walleye density, consumption of juvenile salmonids, population structure, growth, mortality, and year-class strength to sustained removals of northern squawfish;

(5)   Examine annual and spatial variation in diets of northern squawfish, smallmouth bass, and walleye;

(6)   Integrate data on northern squawfish harvest, and response of northern squawfish, smallmouth bass, and walleye to northern squawfish removals to estimate effects of the NSMP on losses of juvenile salmonids to predation.

Conclusions

We believe there are several important findings of our study. These include:

(1) **Management fisheries in the Columbia and Snake rivers are effective at removing large northern squawfish.** From 1990-96, over 1.1 million northern squawfish ≥250 mm fork length were removed from the lower Columbia and Snake rivers (Paper 1). Annual exploitation averaged 12.0%, and ranged from 8.1% to 15.5%. Exploitation was greater than 10% all years except 1993. The sport-reward fishery accounted for 86.5% of the harvest. All fisheries targeted large, piscivorous, northern squawfish (96.1-99.5% of reported catch); however, mean fork length was higher in the gillnet (409 mm) and dam-angling (401 mm) fisheries than in the sport-reward fishery (346 mm).

(2) **We found no evidence that surviving northern squawfish compensated for sustained removals.** Indices of northern squawfish abundance and consumption of juvenile salmonids were consistently lower from 1994-96 than 1990-93 (Paper 2). We found no single environmental or salmonid passage variable to be consistently related to consumption of juvenile salmonids by northern squawfish. Size structure of northern squawfish populations appeared to decrease in response to removals of large fish (Paper 3); however, we found no trend of increased growth, fecundity, or year-class strengths.

(3) **We found no evidence of smallmouth bass or walleye response to sustained removals of northern squawfish.** No trends in smallmouth bass density, consumption of juvenile salmonids, population structure, growth, mortality, or year-class strength have been realized concurrent with the NSMP (Paper 4). Variations in walleye density and population structure appear to be driven by variations in year-class strength, not by response to removals of northern squawfish. We found no trends in growth or mortality of walleye (Paper 5).

(4) **We found no evidence that diets of northern squawfish, smallmouth bass, or walleye changed in response to sustained removals of northern squawfish.** Piscivory and salmonid predation varied annually for smallmouth bass and walleye, but did not increase coincident with removals of northern squawfish (Paper 6). Piscivory by northern squawfish declined over time from 1990-96 (Papers 2 and 6). Consumption rates of non-salmonid prey fishes by smallmouth bass exceeded consumption rates by northern squawfish (Paper 6).

(5) **Losses of juvenile salmonids to predation have probably decreased since implementation of the NSMP**. Modeling results indicate that if all variables other than exploitation of northern squawfish were held constant, predation by northern squawfish on juvenile salmonids has decreased to 62% (range 45-75%) of pre-program levels (Paper 1). Estimates of predation by northern squawfish (Paper 2) support results from modeling. Lack of response by surviving northern squawfish and other predators (Papers 3, 4, and 5), and lack of changes in diet of these fish (Papers 2 and 6) increases confidence in the hypothesis that sustained removals of northern squawfish increases survival of juvenile salmonids.

Limitations

Some of our results are uncertain because of important limitations. Limitations were generally the product of working in a large and complex system. In addition, limitations existed because of the difficulty of controlling conditions during sampling periods. Several important limitations were:

(1) **Benefits of the NSMP could only be measured indirectly**. Our estimate of reductions in predation were based on changes in northern squawfish size structure in response to removals (Papers 1 and 3), combined with lack of compensation by surviving northern squawfish and other predators (Papers 2, 3, 4, 5, and 6). Direct measurement of survival of migrating juvenile salmonids to the Columbia River estuary were not possible. Numbers of returning adult salmonids are affected by too many additional variables (ocean conditions, harvest, etc.) to be used to measure success of the program.

(2) **Estimates of predation are indices, not absolute**. Estimates of absolute predation for the entire lower Columbia and Snake rivers would be prohibitive in time and cost. Managers need a quick, efficient method to determine the spatial and temporal dynamics of predation on juvenile salmonids.

(3) **Actual predation on juvenile salmonids is influenced by variables we were unable to control**. Environmental variables including river flow, spill at dams, and water temperature vary annually. Numbers of migrating juvenile salmonids and passage timing also vary annually. Although these variables undoubtedly influence predation, we were unable to identify any consistent relationships between predation and environmental or passage variables (Paper 2).

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Recommendations

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Based on our findings, we have several recommendations concerning the NSMP:

(1) **Management of northern squawfish should continue to be used as a method to increase survival of juvenile salmonids.** The program is successful at removing large numbers of northern squawfish ≥250 mm fork length, and this exploitation translates to a considerable reduction in predation on juvenile salmonids. The program is an effective tool for improving salmonid survival in the Columbia and Snake rivers.

(2) **Total catch and exploitation rates of the fisheries should continue to be monitored annually**. Annual exploitation rates must be sustained at 10-20% to meet program goals. Information on exploitation rates will be needed as a basis for continuing or discontinuing the program or individual fisheries, or for implementing changes to fisheries (incentives to increase effort, adjustments to season length to increase or decrease catch, etc.).

(3) **Response of northern squawfish and other predators should be evaluated every 3-5 years**. We have found no evidence of compensation to date by surviving northern squawfish, smallmouth bass, or walleye. Although compensation is unlikely, it remains possible, particularly if removals are sustained over a number of years. Periodic sampling to monitor predation and biological characteristics of predaceous fish species would be prudent.

Management of Northern Squawfish and Implications for Juvenile Salmonid Survival in the
Lower Columbia and Snake Rivers

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INTRODUCTION

The construction of eight hydroelectric dams on the lower Columbia and Snake rivers between 1933 and 1975 transformed these rivers into a series of long, slow-moving reservoirs that reduce the survival of outmigrating juvenile salmonids. The impoundments delay the downstream migration of juveniles and concentrate them at dams, causing prolonged exposure to predators and other sources of mortality (Schoeneman et al. 1961; Raymond 1968; Bentley and Raymond 1976; Ebel 1977; Raymond 1979; Weitzkamp and Katz 1980).

The effects of the hydropower system on losses of juvenile salmonids to resident fish predators have been well-documented in the Columbia and Snake rivers (Rieman et al. 1991; Petersen 1994; Petersen and Gadomski 1994; Ward et al. 1995). The native northern squawfish *Ptychocheilus oregonensis* is clearly the dominant predator of juvenile salmonids (Poe et al. 1991; Vigg et al. 1991; Ward and Zimmerman 1997; Zimmerman 1997). Rieman et al. (1991) estimated the annual loss of juvenile salmonids to predation by northern squawfish in John Day Reservoir, Columbia River, to be 2.1 million; Petersen (1994) revised this estimate to approximately 1.4 million when spatial patterns of predation were accounted for. Ward et al. (1995) found that high levels of predation occur throughout the lower Columbia and Snake rivers, and are greater in some areas than in John Day Reservoir.

The management of northern squawfish is one of many recent efforts to increase survival of juvenile salmonids in the Columbia and Snake rivers. Rieman and Beamesderfer (1990) predicted that exploiting northern squawfish > 275 mm fork length at a sustained annual rate of 10-20% would result in a 50% annual decrease in salmonid losses to predation. The success of test fisheries by the Northern Squawfish Management Program (NSMP) in 1990 led to full-scale implementation of two major removal fisheries in 1991. The "sport-reward" fishery pays public anglers US$3 to $5 (depending on their total catch for the season) for each northern squawfish turned in to agency-operated check stations. A "dam-angling" fishery employs fisheries agency personnel to angle for northern squawfish directly from dams, or from boats operated in close proximity to the dams. In addition, a gillnet fishery has been in operation since 1994 to remove northern squawfish near hatchery release points, dams, tributary mouths, and other areas where high levels of predation may occur (Collis et al. 1995). Other fisheries were employed for various amounts of time but discontinued because of their failure to capture large numbers of northern squawfish or because of unacceptably high catch rates of other species (Beamesderfer et al. 1996).

Northern squawfish become significant predators of juvenile salmonids at approximately 250 mm fork length (Vigg et al. 1991). In addition, fish of this size are approximately 11 inches in total length (Carlander 1969), a convenient measurement for public anglers participating in the sport-reward fishery. Therefore, northern squawfish ≥ 250 mm fork length are targeted by all fisheries.

Numerous confounding factors limit our ability to measure the success of the NSMP in terms of increased numbers of juvenile salmonids reaching the estuary or increased numbers of adult salmonid returns. Beamesderfer et al. (1996) proposed that evaluations of the NSMP be based on indirect measures, such as mark-recapture estimates of exploitation. In this paper we use indirect measures to evaluate the performance of the three major northern squawfish fisheries, and estimate the degree to which potential predation on juvenile salmonids has been reduced by the NSMP over the first six years of operation. To evaluate the fisheries, we (1) determined annual and total northern squawfish harvest, harvest effort, and catch per unit of harvest effort (CPUE) for each fishery, (2) used mark-recapture data to compare the exploitation of northern squawfish among years, fisheries, and areas, and (3) compared size of northern squawfish harvested by each fishery. We used this information to develop a simple model to estimate predation on juvenile salmonids by northern squawfish relative to predation that would occur without implementation of the NSMP.

METHODS

Fishery Evaluation

The sport-reward fishery was first implemented in John Day Reservoir (Figure 1) in 1990 to gauge the level of public participation in the program. From 1991-96, the fishery was conducted from May to mid-September on the Columbia River from the mouth to the boat-restricted zone (BRZ) below Priest Rapids Dam, and on the Snake River from the mouth to the BRZ below Hell's Canyon Dam. After one year (1990) of experimental fishing was conducted at Bonneville, The Dalles, John Day, McNary, and Ice Harbor dams, dam-angling was implemented annually (May-September) at each of the eight dams of the lower Columbia and Snake rivers. Dam-angling was conducted primarily in tailrace (the section of river directly downstream from a dam) BRZs. From 1994-96, the gillnet fishery was implemented from April or May through June throughout the lower Columbia and Snake rivers. We monitored these fisheries from 1990-96 to determine annual and total harvest of northern squawfish, harvest effort, and CPUE.

We used mark-recapture data to evaluate exploitation of northern squawfish in each fishery from 1992-96. We used electrofishing boats and gillnets to collect and mark northern squawfish from April through June of each year. Fish were marked with serially- numbered spaghetti tags and given a year-specific secondary mark consisting of a pelvic or caudal fin clip. We randomly allocated sampling effort in all river kilometers (RKm) of the Columbia River from RKm 71 to RKm 639, and in the Snake River from the mouth to RKm 248 (Figure 1). We generally sampled from 1800 hours to 0100 hours, near shorelines or structure, and in water less than 6 m deep. Sampling was discontinued in Ice Harbor Reservoir after 1992, as we were unable to capture a sufficient number of northern squawfish to estimate exploitation.

We based our calculation of exploitation rates for 1992-96 on the number of tagged northern squawfish recovered by each fishery. Fisheries started each year before our

Figure 1. Lower Columbia and Snake rivers, with dashed lines representing upstream boundaries of northern squawfish management fisheries from 1990-96. Dams (with corresponding reservoirs) within the area are labeled.

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tagging was complete; therefore, we calculated weekly estimates of exploitation by dividing the number of tagged northern squawfish recovered by the number of tagged fish at large and summed these estimates to yield overall estimates of exploitation. We adjusted exploitation estimates for tag loss (4.2%), determined from the recovery of secondary-marked fish with no tag. Because of uncertainties regarding tag loss over a period of two or more years, we used only northern squawfish tagged and recaptured within a given year to determine exploitation. We calculated annual exploitation estimates for each fishery and area (reservoir or free-flowing reach downstream from Bonneville Dam) when possible, as well as "systemwide" estimates for all fisheries and areas combined. Only northern squawfish recaptured in the same area in which they were tagged were included in estimates of exploitation.

In 1992, sampling downstream from Bonneville Dam was conducted as in other years. However, due to time constraints, we sampled only the forebay (the section of river immediately upstream from a dam), tailrace, and a randomly selected portion of the mid-reservoir area of each impoundment above Bonneville Dam, increasing the potential for bias in our estimates of exploitation. We therefore used two methods to estimate exploitation for 1992: (1) we assumed full mixing of tagged and untagged fish and random allocation of fishing effort throughout each reservoir, and (2) we assumed no mixing of fish outside the areas they were tagged, with fishery effort restricted to areas in which fish were tagged. We determined exploitation estimates for method 1 as described previously, giving a maximum estimate. For method 2, we adjusted the number of tagged northern squawfish in mid-reservoir areas by dividing the number of fish actually tagged by the proportion of mid-reservoir area sampled. We used the adjusted number of tags and calculated exploitation as in method 1, giving a minimum estimate. We used the mean of estimates (1) and (2) as the overall exploitation estimate.

We calculated 95% confidence intervals for the number of tagged fish recovered each week. We determined confidence bounds for variables distributed in a Poisson distribution from Ricker (1975) for weeks when tagging and fishing occurred simultaneously. After tagging was complete, we estimated bounds by using the formula

$$m \pm 1.96 \sqrt{m/n}, \text{ if } mn > 30$$

where

m = the mean number of tagged fish recovered per week, and
n = the number of sampling periods (weeks) remaining (Elliott 1977).

We summed estimates for each week to give overall confidence limits. Because we calculated two exploitation estimates for 1992, we used the high confidence bound from estimate (1) and the low confidence bound from estimate (2) as overall confidence limits.

We were unable to calculate exploitation rates in 1991 using mark-and-recapture data because no northern squawfish were tagged. To estimate exploitation rates for 1991, we divided the fisheries' total catch in each reservoir or area by a population estimate of northern squawfish for that area. Population estimates were derived using abundance indices for northern squawfish from Ward et al. (1995) and the relationship between abundance indices and population estimates from Zimmerman and Ward (1997). Because the area downstream from Bonneville Dam, The Dalles Reservoir, and McNary Reservoir were not sampled in 1991, we used abundance indices from 1990 (The Dalles and McNary reservoirs) and 1992 (downstream from Bonneville Dam) to estimate population sizes.

Because the goal of the NSMP is to harvest fish ≥ 250 mm, we further analyzed the relative efficiency of each fishery by comparing the mean size of northern squawfish harvested. We used data from subsamples of fish collected from the fisheries to compare length-frequency distributions and calculate mean fork lengths for each fishery and year. To determine the degree of association between exploitation and fork length for each fishery, we calculated catch rates of tagged fish by 50-mm length groups, and used linear regression to describe the relationships between exploitation and fork length. We again used only fish recaptured in a given year in the analysis to reduce biases associated with tag loss among multiple years.

Reduction in Predation

We developed a simple model to estimate predation on juvenile salmonids by northern squawfish relative to predation that would occur without implementation of the NSMP. The model was designed to estimate the effects of the NSMP if all other factors (river and ocean conditions, numbers of juvenile salmonids migrating, turbine mortality, etc.) were held constant. The model also assumed no compensation (increased growth, fecundity, consumption, etc.) by remaining northern squawfish and other predators in response to sustained removals of northern squawfish.

Model inputs included (1) an "average" population structure (age distribution, length at age, and natural mortality) for northern squawfish prior to implementation of the NSMP, (2) "average" rates of consumption of juvenile salmonids by northern squawfish, (3) age distribution adjusted by observed exploitation and natural mortality, and (4) an index of age-specific relative predation on juvenile salmonids by northern squawfish. Few juvenile salmonids are consumed by northern squawfish less than 250-mm fork length (Vigg et al. 1991), which are about 5 years old (Parker et al. 1995). We therefore only evaluated predation by northern squawfish ≥ age 5. Model output was relative predation for each year expressed as the percent of the loss prior to implementation of the NSMP. Calculations were made for each reservoir and the Columbia River downstream from Bonneville Dam, with results summed to yield a systemwide estimate for the model output.

Uncertainty inherent in some inputs to the model generated a range of potential predation indices. Calculation of 95% confidence limits for exploitation provided three inputs for age-specific exploitation estimates. We also used three formulas to describe the relationship between northern squawfish length and consumption of juvenile salmonids. We summarized model uncertainty by reporting the median and the range (minimum and maximum) for the nine potential loss indices.

Population Structure

We used length distributions for northern squawfish collected prior to implementation of the NSMP (Ward et al. 1995) for each reservoir. We pooled length-at-age data from 1990-96 (Knutsen and Ward 1997) to estimate the age distribution of fish in each 25-mm length interval, and to estimate mean length at each age. Because growth, annual mortality, and maximum age differ between female and male northern squawfish (Parker et al. 1995), we summarized data for each sex separately.

Because different sizes of northern squawfish are differentially vulnerable to capture (Beamesderfer and Rieman 1988), we divided the unadjusted proportion of fish at each age by an index of vulnerability for the mean length at that age (Knutsen and Ward 1997). We then pooled the adjusted data for females and males to estimate an average age composition prior to implementation of the NSMP. We used linear regression on a catch curve constructed from adjusted age frequencies (Ricker 1975) to estimate annual natural mortality rate and mean index of recruitment to age 5. The mean abundance index for each age was then calculated as

$$A_h = A_5 \bullet (1-M)^{h-5} \qquad (1)$$

where

   A_h = mean abundance index for age h,
   A_5 = mean abundance index (mean recruitment) for age 5, and
   M = annual natural mortality rate.

Consumption

An index of consumption of juvenile salmonids by northern squawfish was estimated by examining digestive tracts of northern squawfish collected by electrofishing (Ward et al. 1995). A consumption index (CI) was calculated for spring and summer separately as

$$CI = 0.0209 \bullet T^{1.60} \bullet MW^{0.27} \bullet (S \bullet GW^{-0.61}) \qquad (2)$$

where

   T = water temperature (^{o}C),
  MW = mean weight (g) of northern squawfish in sample,
   S = mean number of salmonids per northern squawfish in sample, and
  GW = mean total gut weight (g) of northern squawfish in sample.
We collected consumption information from 1990-96 (Zimmerman 1997), to compute mean spring and summer consumption indices. Consumption indices were converted to consumption rates (C; juvenile salmonids per northern squawfish per day) by the formula from Zimmerman and Ward (1997):

$$C = -0.077 + 0.618(CI) \qquad (3).$$

Size of northern squawfish used in estimates of consumption is important because consumption rates increase with northern squawfish length (Vigg et al. 1991). Consumption rates were therefore adjusted to reflect differences in mean size of northern squawfish in samples. The three formulas used to estimate the potential relationship between relative consumption rate (RC) and fork length (L) of northern squawfish were:

$$RC = -0.858 + 0.003703(L) \qquad (4)$$
$$RC = 1.631 \times 10^{-8} (L^{2.986}) \qquad (5)$$
$$RC = 1.58 \times 10^{-15} (L^{6.02}) \qquad (6)$$

We used 50-mm length groups, and pooled 1993-96 consumption data from all reservoirs and both seasons to develop Equation (4). Equation (5) assumed a direct relationship between consumption rate and weight of northern squawfish (Tabor et al. 1993), then utilized the standard weight equation for northern squawfish (Parker et al. 1995) to estimate the relationship between consumption and length. Equation (6) was used by Rieman and Beamesderfer (1990) to estimate relative salmonid consumption by northern squawfish of different sizes.

After the mean age and fork length of northern squawfish used in developing a consumption index was determined, a consumption rate for each age was calculated as

$$CR_h = C \bullet (RC_h/RC_m) \tag{7}$$

where

Cr_h = consumption rate for age h fish,
C = consumption rate for fish in sample from Equation (3),
Rc_h = relative consumption rate for age h fish from Equations 4-6, and
Rc_m = relative consumption rate for mean age fish in sample from Equations 4-6.

Exploitation

Length-specific exploitation rates and length-at-age information were used to estimate age-specific exploitation rates. The preliminary exploitation rate was computed as

$$PE_{h,f} = E_f \bullet F_f \tag{8}$$

where

$Pe_{h,f}$ = preliminary exploitation estimate for age h fish in fishery f,
E_f = overall exploitation estimate for fishery f, and
F_f = relationship between fork length and exploitation rate for fishery f.

Although Equation (8) addresses the relationship between exploitation and northern squawfish size, the sum of the age-specific exploitation estimates may not equal the overall exploitation rate. Age-specific exploitation rates were therefore corrected as

$$E_{h,f} = PE_{h,f} \bullet (E_f / \sum_h Pe_{h,f}) \tag{9}$$

where

$E_{h,f}$ = exploitation estimate for age h fish in fishery f.

Total exploitation rate for each age was calculated as the sum of the fishery-specific exploitation estimates, with a maximum exploitation of 1.0 for each age.

Relative Predation

Northern squawfish age structure after implementation of the NSMP was adjusted by exploitation and natural mortality:

$$A_{h,j} = A_{h-1,j-1} \bullet (1 - E_{h-1,j-1}) \bullet (1 - M) \tag{10}$$

where

$A_{h,j}$ = abundance index of age h fish in year j,
$A_{h-1,j-1}$ = abundance index of age h-1 fish in year j-1, and
$E_{h-1,j-1}$ = exploitation rate on age h-1 fish in year j-1.

This assumes that natural mortality occurs after fishing ends and that forces of natural mortality remain constant (Ricker 1975). The recruitment of fish to age 5 remains constant at the average level.

Seasonal predation by each age of northern squawfish is calculated and summed to yield annual predation by age:

$$P_{h,j} = \sum_m (A_{h,j} \bullet CR_h \bullet D_m) \tag{11}$$

where

$P_{h,j}$ = predation index to age h northern squawfish in year j, and
D_m = number of days in season m.

Predation indices are summed for all reservoirs then expressed as a percentage of the predation index for the "average" northern squawfish population prior to implementation of the NSMP.

RESULTS

Fishery Evaluation

During the period of full implementation of the NSMP (1991-96 for the sport-reward and dam-angling fisheries; 1994-96 for the gillnet fishery), the three major fisheries removed approximately 1.1 million northern squawfish ≥ 250 mm from the lower Columbia and Snake rivers (Table 1). The sport-reward fishery accounted for 86.5% of the harvest, the dam-angling fishery contributed 11.2%, and the gillnet fishery 2.3%. Harvest effort for the sport-reward fishery averaged 55,354 angler days per season, and catch per angler-day increased every year from 1992-96. Dam-angling effort (angler-hours) decreased markedly from 1991-96; catch per angler-hour ranged from 0.7 in 1995 to 2.1 in 1991. Effort (net-hours) in the gillnet fishery increased during each year of operation, while catch per net-hour decreased.

Mean systemwide exploitation (all fisheries combined) of northern squawfish ≥ 250 mm from 1991-96 was 12.0% and ranged from 8.1% in 1993 to 15.5% in 1995 (Figure 2). Systemwide exploitation was > 10% all years except 1993 (Figure 3). Total exploitation was usually highest in The Dalles, McNary, and Lower Granite reservoirs, and downstream from Bonneville Dam. The contribution of dam-angling to total exploitation varied among years, but declined considerably from 1991-96. From 1994-96, the gillnet fishery made an important contribution to exploitation in Bonneville Reservoir.

Sample sizes were sufficient (mn>30) to calculate 95% confidence intervals of exploitation estimates for all fisheries combined downstream from Bonneville Dam, in Bonneville Reservoir, and systemwide (Figure 2). Values of mn<30 resulted in unrealistically large confidence intervals; we do not report confidence bounds for areas with small sample sizes. Confidence bounds for estimates of exploitation averaged 69% of the point estimate for the low confidence bound (range 32%-90%) and 155% of the point estimate for the high confidence bound (range 118%-245%).

Mean fork length of northern squawfish harvested by all three fisheries and all years (1990-96) combined was 366 mm (Figure 4); all fisheries harvested a high proportion of northern squawfish ≥ 250 mm. Mean fork length of northern squawfish was highest for the gillnet fishery and lowest for the sport-reward fishery. The dam-angling fishery harvested a slightly higher proportion of northern squawfish ≥ 250 mm (99.5%) than the gillnet (98.7%) or sport-reward (96.1%) fisheries.

Table 1. Catch, effort, and catch per unit effort (CPUE) for northern squawfish $\geq$ 250 mm fork length harvested in the lower Columbia and Snake rivers by management fisheries from 1990-96. Units of effort are angler-days (sport reward), angler-hours (dam angling) and net-hours (gillnet).

	Sport Reward			Dam Angling			Gillnet		
Year	Catch	Effort	CPUE	Catch	Effort	CPUE	Catch	Effort	CPUE
1990	4,681	2,376[a]	2.0	11,001	6,374[b]	1.7	--	--	--
1991	153,508	67,384	2.3	39,196	19,298	2.0	--	--	--
1992	186,095	88,494	2.1	27,442	16,759	1.7	--	--	--
1993	104,536	34,879	3.0	17,105	9,718	1.8	--	--	--
1994	129,384	40,783	3.2	15,938	10,002	1.6	9,018	1,442	6.3
1995	199,788	62,725	3.2	5,397	7,289	0.7	9,484	2,431	3.9
1996	157,230	35,485	4.4	5,381	3,666	1.5	6,167	2,878	2.1
Total	935,222	332,126	2.8	121,460	73,106	1.7	24,669	6,751	3.7

[a] John Day Reservoir only.
[b] Bonneville, The Dalles, John Day, McNary, and Ice Harbor dams only.

Relationships between relative exploitation rate and fork length varied among fisheries; however, exploitation generally increased with increasing fork length (Figure 5). This was especially true for the dam-angling and sport-reward fisheries, although the rate of increase for the sport-reward fishery declined somewhat as fork length increased. For the site-specific gillnet fishery, exploitation rose sharply but then peaked and declined for fork lengths greater than 450-500 mm.

Reduction in Predation

Potential predation on juvenile salmonids by northern squawfish has decreased to approximately 45% to 75% of pre-NSMP levels, with a median estimate of 62% (Figure 6). Relative benefits of a given exploitation decreased over time as the number of large northern squawfish was reduced. Therefore, continued exploitation at mean 1991-96 levels will not result in further reductions in potential predation. Exploitation in recent years (1994-1996) has been higher than the 1991-96 mean; therefore, further reductions in potential predation will be realized if exploitation is maintained at mean 1994-96 levels.

Contribution by various age-classes to overall predation by the unexploited population depended on the relationship between consumption rate and fork length (Figure 7). With exploitation, predation declined in older fish, and the relative prey consumption by age shifted toward younger fish. Predation was negligible by fish older than age 13.
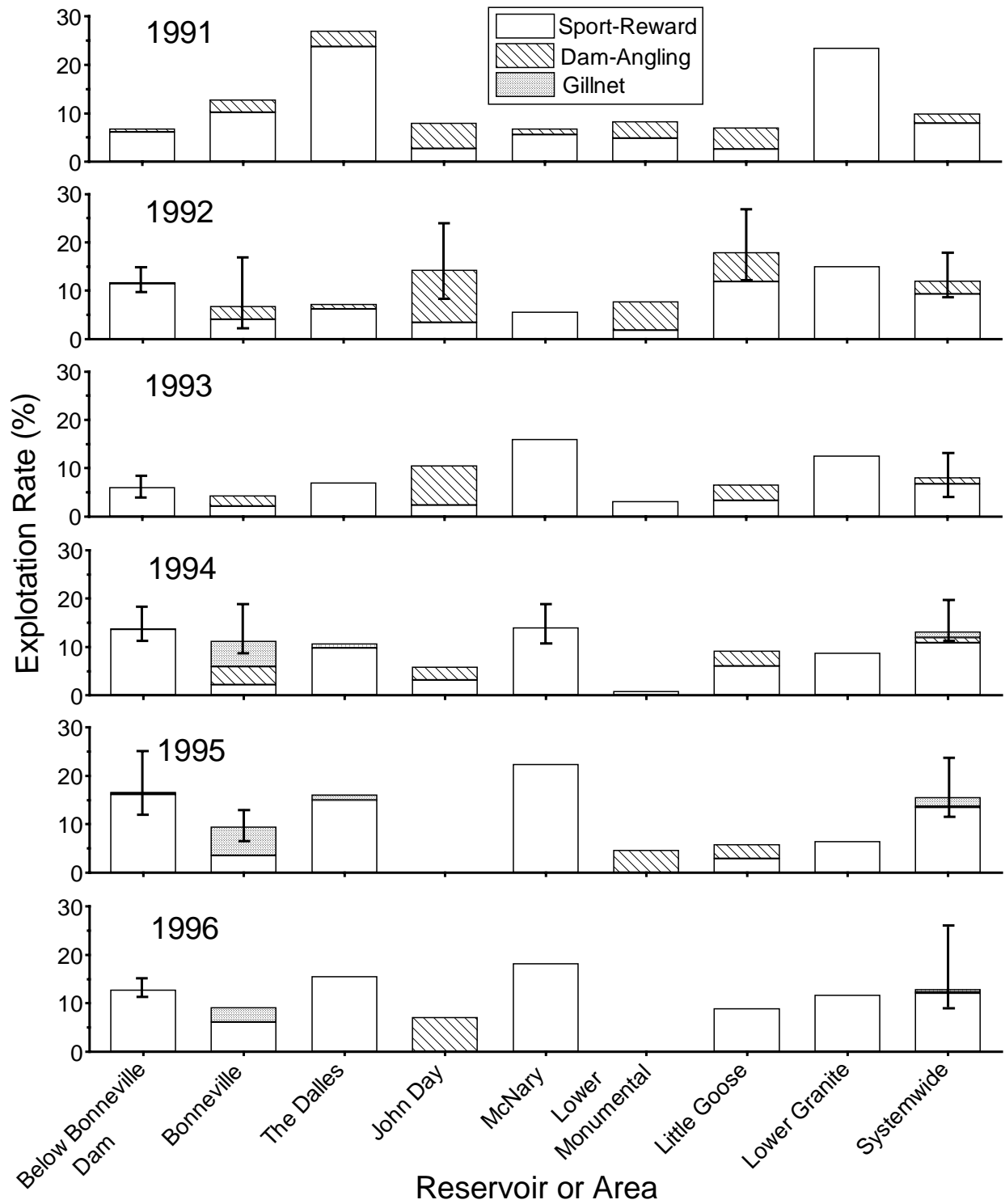
Figure 2. Annual exploitation of northern squawfish ≥ 250 mm fork length by fishery and area, 1991-1996. Confidence intervals for all fisheries combined (95%; vertical bars) are included where a sufficient number of tagged northern squawfish were recaptured to estimate upper and lower bounds.
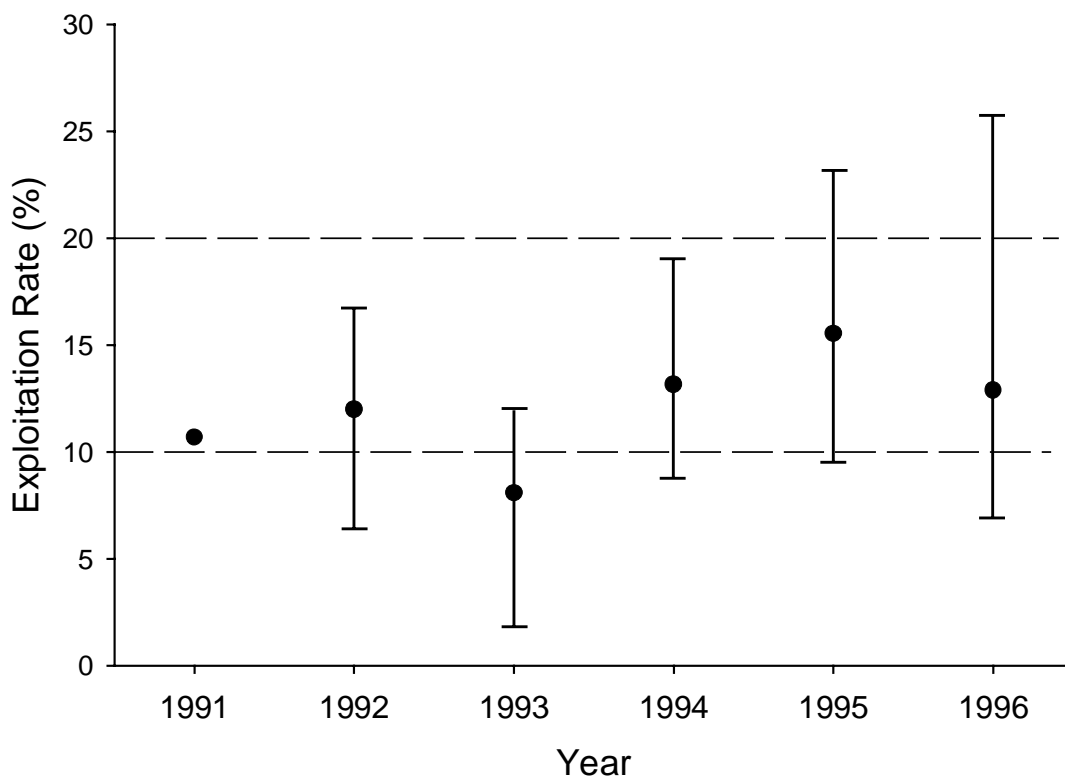
Figure 3. Systemwide exploitation rate of northern squawfish ≥ 250 mm fork length from 1991-96 relative to target exploitation rate (dashed lines; Rieman and Beamesderfer 1990). Vertical bars represent 95% confidence intervals and are included for years in which exploitation was determined using mark-and-recapture data.

DISCUSSION

Management fisheries in the Columbia and Snake rivers are highly effective at removing large northern squawfish. The sport-reward fishery is most effective in terms of total northern squawfish harvested, due primarily to the large amount of effort afforded by the involvement of public anglers. Although harvest effort varies annually (likely due to weather and river conditions), sport-reward CPUE has increased as veteran anglers become more efficient at catching northern squawfish and new anglers are recruited to the fishery.
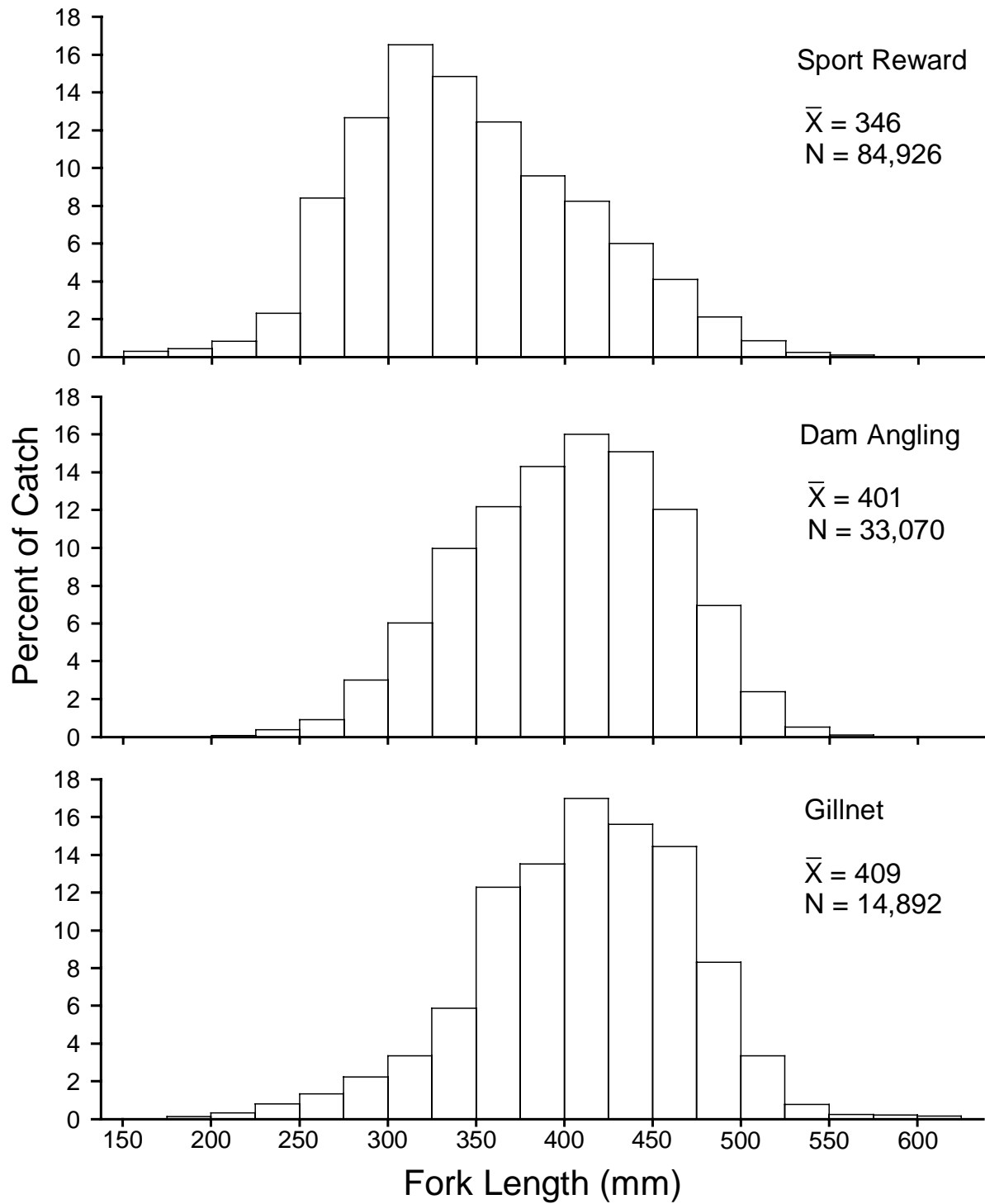
Figure 4. Length-frequencies and mean fork lengths of northern squawfish from subsamples of fish harvested in the lower Columbia and Snake rivers by the sport-reward (1990-1996), dam-angling (1990-1996), and gillnet (1994-1996) fisheries..

Sport Reward

$Y = -10.66 + 1.988 \times \mathrm{Log}_e(X)$

$r^2 = 0.98$

Dam Angling

$Y = -1.993 + 0.0085(X)$

$r^2 = 0.97$

Gillnet

$Y = 1.837e^{\frac{-(478.4-X)^2}{8316.4}}$

$r^2 = 0.92$

Proportion of Overall Fishery-Specific Exploitation
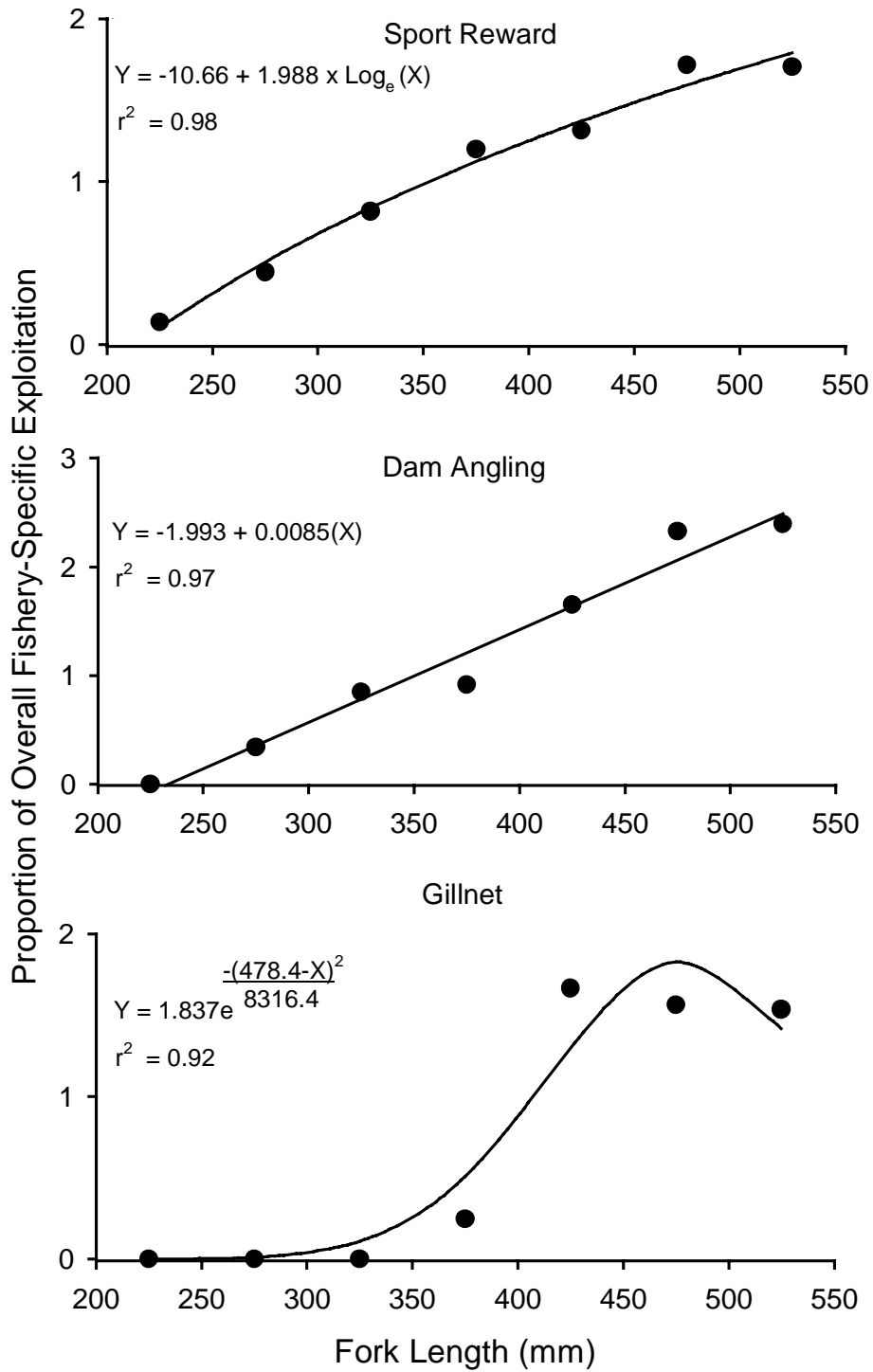
Fork Length (mm)

Figure 5. Relative exploitation of northern squawfish by fork length for sport-reward (1992-1996), dam-angling (1992-1996), and gillnet (1994-1996) fisheries.

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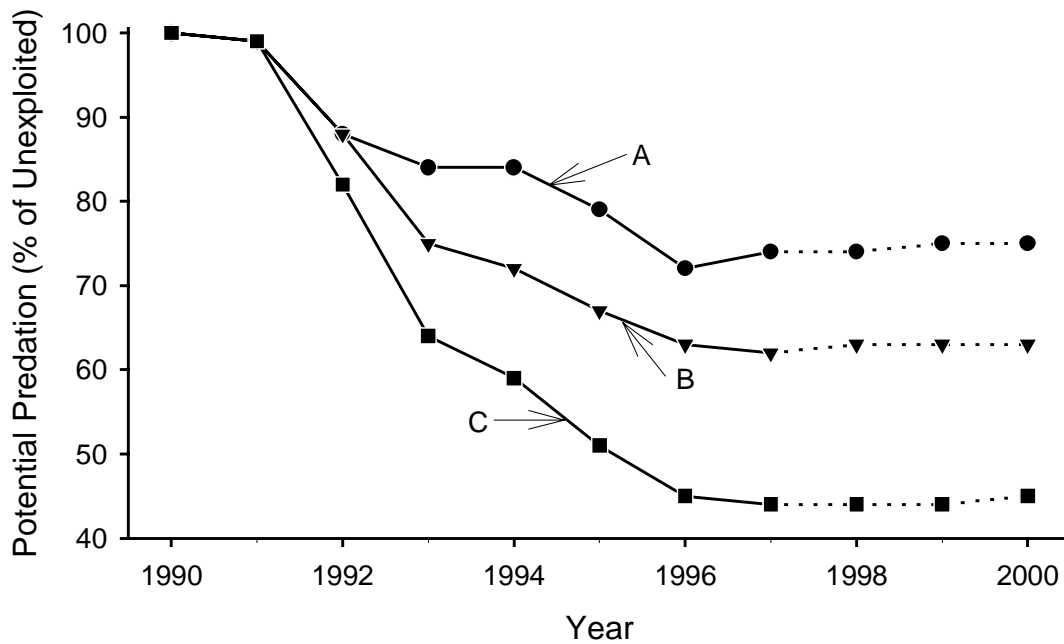
Figure 6. Range of estimates of potential predation on juvenile salmonids by northern squawfish relative to predation by the unexploited population. Limited management of northern squawfish began in 1990; full implementation of management began in 1991. Scenarios represent (A) length-predation relationship and exploitation estimates resulting in minimum estimate of eventual reduction in potential predation, (B) median estimate of potential predation, and (C) maximum estimate of eventual reduction in potential predation.

Though the dam-angling fishery contributes far less to the total catch of northern squawfish, the fish harvested are larger, and therefore more piscivorous (Vigg et al. 1991), than those captured in the sport-reward fishery. In addition, this fishery targets northern squawfish primarily in tailrace BRZs, where high levels of predation occur (Ward et al. 1995). These areas are also inaccessible to members of the public participating in the sport-reward fishery. Low catch rates in the dam-angling fishery have resulted in a
decrease in harvest effort and harvest of northern squawfish in recent years, which may be partially attributed to declining abundance of large northern squawfish throughout the Columbia and Snake rivers (Knutsen and Ward 1997). Very high river flows in 1995 and 1996 (Fish Passage Center, unpublished data) also undoubtedly affected this fishery. Faler et al. (1988) found that northern squawfish avoid areas of high flow associated with spillgate operation in the tailrace of McNary Dam on the Columbia River.
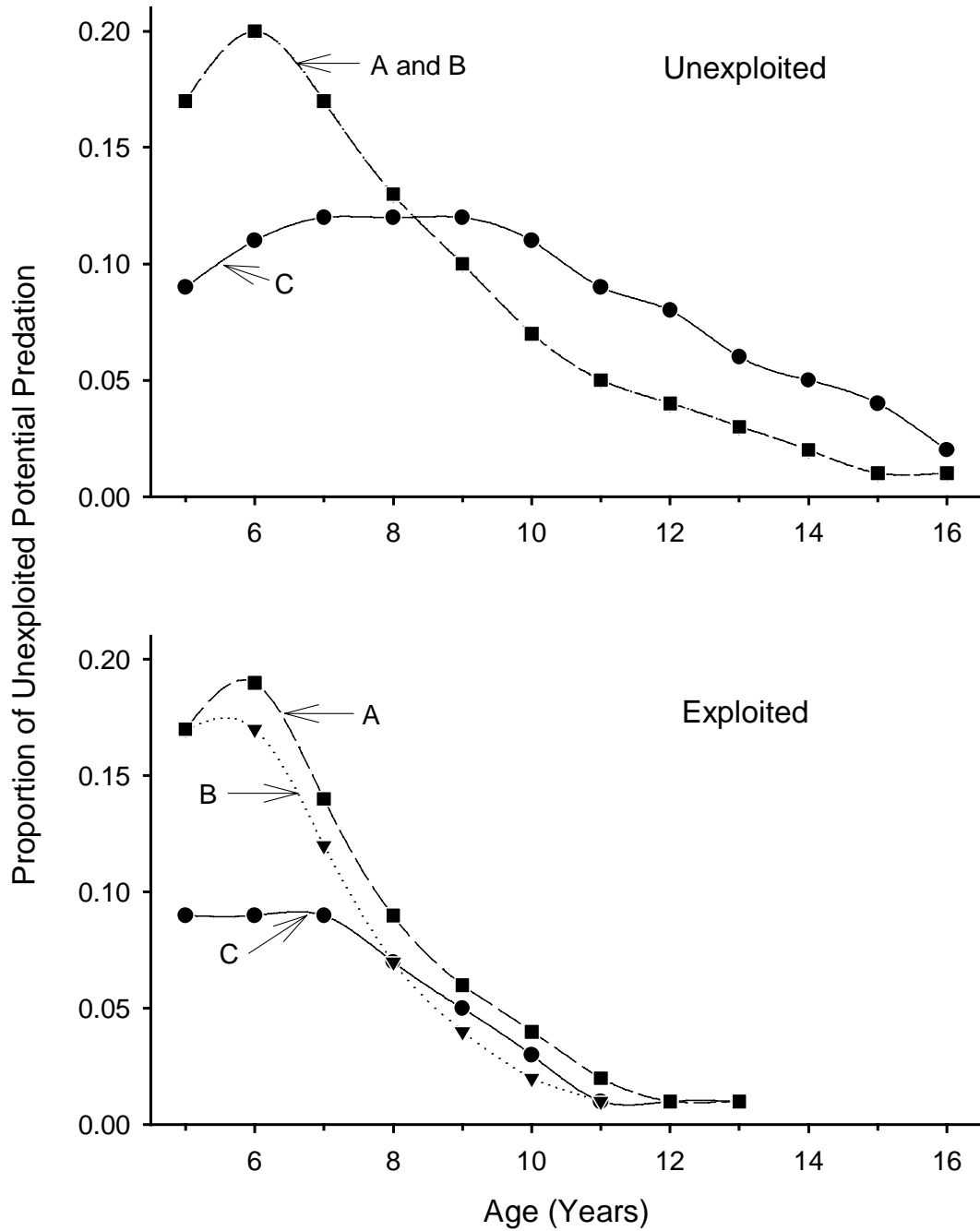
Figure 7. Potential predation by age-classes of northern squawfish in the lower Columbia River basin with no exploitation and with observed exploitation. Scenarios represent (A) length-predation relationship and exploitation estimates resulting in minimum estimate of eventual reduction in potential predation, (B) median estimate of potential predation, and (C) maximum estimate of eventual reduction in potential predation.

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Like the dam-angling fishery, the gillnet fishery captures northern squawfish considerably larger than those harvested by the sport-reward fishery, and harvest effort is concentrated in areas with potentially high predation. Collis et al. (1995) documented increased catches of northern squawfish in gillnets following juvenile salmonid releases, and suggested that northern squawfish may aggregate to feed on salmonids during peak release times. For this reason, the contribution of the gillnet fishery to northern squawfish exploitation is important, despite a relatively low number of fish harvested.

If exploitation is not sustained, northern squawfish populations may recover within a few years (Rieman and Beamesderfer 1990); therefore, fisheries exploiting northern squawfish at a low level must be sustainable. Our systemwide exploitation estimates for 1991-92 and 1994-96 consistently exceeded 10%, despite variations in harvest effort and CPUE. Lower rates of exploitation (as in 1993) will also have significant effects on predation. For example, Beamesderfer et al. (1996) predicted a 15-30% reduction in predation if exploitation is sustained at a rate of only 5%.

Our estimates of reductions in potential predation by northern squawfish are within the range predicted by Rieman and Beamesderfer (1990), and summarized by Beamesderfer et al. (1996). Based on information from John Day Reservoir, Rieman and Beamesderfer (1990) estimated that if northern squawfish recruitment was constant, sustained exploitation of 12% would reduce potential predation to about 55% of the unexploited level, compared to our median estimate of about 62%. The estimates differ in part because population dynamics of northern squawfish vary among areas of the Columbia River basin (Parker et al. 1995). Northern squawfish downstream from Bonneville Dam comprise 35% to 50% of the population in the lower Columbia River basin (Ward et al. 1995; Zimmerman and Ward 1997), so our results are highly dependent on reductions in predation by these fish. Natural mortality is higher, and proportional stock density is generally lower downstream from Bonneville Dam than in Columbia River reservoirs (Parker et al. 1995; Knutsen and Ward 1997); therefore, the unexploited population contained a smaller proportion of old, highly piscivorous individuals. Consequently, exploitation downstream from Bonneville Dam had a proportionately smaller effect on predation than exploitation in reservoirs.

Although our model to estimate reductions in predation is similar to the model developed by Rieman and Beamesderfer (1990), important differences add significance to the similarity in results. We were able to use information on northern squawfish abundance, diet, and population dynamics from throughout the lower Columbia River basin (Parker et al. 1995; Knutsen and Ward 1997; Zimmerman 1997), but the only data available to Rieman and Beamesderfer (1990) was from John Day Reservoir. Biological characteristics of northern squawfish vary considerably throughout the Columbia River basin (Parker et al. 1995; Knutsen and Ward 1997). Because exploitation of northern squawfish was virtually non-existent prior to implementation of the NSMP, Rieman and Beamesderfer (1990) could not predict the relationships between northern squawfish size and exploitation rates, or how exploitation would differ among areas.

The assumption of constant recruitment by northern squawfish seems suitable for our analyses. Parker et al. (1995) found no correlation between northern squawfish density and other population characteristics. Extensive information on year-class strength of northern squawfish in the Columbia River (Rieman and Beamesderfer 1990), including information gathered since implementation of the NSMP (Knutsen and Ward 1997), indicates that recruitment is not related to density. Year-class strengths fluctuate randomly, or in some unknown response to environmental conditions, and average out over a period of years. An assumption of constant recruitment should be relatively accurate if extended over that period of years.

Other assumptions inherent in our method to estimate reductions in potential predation have been verified by recent findings. Knutsen and Ward (1997) found that relative abundance of large, highly piscivorous northern squawfish has declined, and that growth and reproduction of surviving northern squawfish have not increased. Zimmerman (1997) found no evidence of increased predation by surviving northern squawfish. Ward and Zimmerman (1997) found no evidence of response by smallmouth bass *Micropterus dolomieu* to sustained removals of northern squawfish, and Friesen and Ward (1997) found no evidence of response by walleye *Stizostedion vitreum*.

Our modeling results can be used to estimate increases in the number of surviving juvenile salmonids that may result from sustained exploitation of northern squawfish. Mean annual losses of juvenile salmonids to northern squawfish predation in the Columbia River from the mouth to the Priest Rapids Dam tailrace, and in the Snake river from the mouth to the Hells Canyon Dam tailrace were estimated at 15.2 million individuals (Beamesderfer et al. 1996). Our estimate of percent reduction in potential predation indicates that annual losses may be reduced to 9.4 (range 6.8-11.4) million, a net gain of 5.8 (range 3.8-8.4) million juvenile salmonids.

The relative success of the NSMP can also be measured in comparisons to other fish control programs. Brown and Moyle (1981) observed that past projects targeting northern squawfish were often based on anecdotal evidence or inconclusive studies. Meronek et al. (1996) judged 250 fish control programs on the basis of benefits to fisheries, and found 29% to be unsuccessful and 28% to have insufficient data to determine success. They concluded that all fish control programs should include (1) critical evaluation of assumptions and of suspected causes of problems, (2) explicit rationale and objectives, and (3) pre-treatment and long-term post-treatment study. A review of northern squawfish studies in the Columbia River basin during the past 15 years suggests that these criteria have been met by the NSMP. Evaluation of assumptions and problems was addressed by Petersen (1994), Ward and Zimmerman (1997), Knutsen and Ward (1997), and Friesen and Ward (1997). Program rationale and objectives were established primarily by Rieman and Beamesderfer (1990); pre-program biology, population dynamics, and predation potential of northern squawfish were investigated by Rieman et al. (1991), Vigg et al. (1991), Poe et al. (1991), Ward et al. (1995), and Parker et al. (1995). Recent work constitutes steps towards post-treatment evaluation. Zimmerman (1997) compared diet and piscivory in predatory fish species during implementation of the NSMP; Zimmerman and Ward (1997) described predation on juvenile salmonids by northern squawfish from 1994-96. Studies of biological responses of resident piscivores to sustained exploitation of northern squawfish (Knutsen and Ward 1997; Ward and Zimmerman 1997; Friesen and Ward 1997) are also important post-treatment evaluations.

Based on our use of indirect methods to evaluate the NSMP, we conclude that management fisheries are successful at removing large numbers of northern squawfish ≥ 250 mm, exploitation rates of 10-15% are sustainable, and this exploitation translates to a considerable reduction in predation on juvenile salmonids. The NSMP is an effective management tool for improving salmonid survival in the Columbia and Snake rivers.

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Index of Predation on Juvenile Salmonids by Northern Squawfish
in the Lower Columbia River Basin from 1994-96

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October 1997

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INTRODUCTION

The first critical assessment of the magnitude of juvenile salmonid predation by resident fishes in the Columbia River was conducted in John Day Reservoir from 1983-86. Rieman et al. (1991) used rigorous estimates of predator population sizes (Beamesderfer and Rieman 1991) and individual consumption rates (Vigg et al. 1991) to demonstrate that (1) mean annual loss of juvenile salmonids to predators was equivalent to mortality associated with dam passage, and (2) northern squawfish *Ptychocheilus oregonensis* accounted for 78% of estimated loss of juvenile salmonids. These findings led to the question of whether mean losses in John Day Reservoir were representative of losses throughout the lower Columbia Basin.

The data requirements of estimating northern squawfish abundance and consumption in a river reach over 1,000 km in length required a different approach. Ward et al. (1995) developed surrogate indices of northern squawfish abundance and consumption that were linearly related to population estimates and absolute consumption rates. The indices were used to evaluate juvenile salmonid predation by unexploited northern squawfish throughout the lower and mid-Columbia Basin from 1990-93. The study provided a snapshot of spatial variation in predation relative to John Day Reservoir.

These studies added greatly to our knowledge of salmonid predation by unexploited populations of northern squawfish in the Columbia Basin. They also provided a sound biological basis for the implementation of a regulated predator control program in 1990 (Beamesderfer et al. 1996). Approximately 1.1 million northern squawfish have been harvested from the lower Columbia and Snake rivers from 1990-96 (Friesen and Ward 1997). Program benefits would be less than expected if surviving northern squawfish consumed juvenile salmonids at higher rates.

Consumption by an individual predator is regulated by many factors, including temperature, body size, metabolic rate, evacuation rate, physiological state, presence of conspecifics or predators, and prey density (Wootton 1991). Estimates of absolute consumption by northern squawfish have been related to temperature (Vigg and Burley 1991), body size (Vigg et al. 1991), and density of juvenile salmonid prey (Petersen and DeAngelis 1992). The index of juvenile salmonid consumption by northern squawfish is a function of water temperature, predator size, weight of food in the gut, and number of juvenile salmonids in the gut (Ward et al. 1995).

Relations between salmonid prey density and consumption by northern squawfish may also be related to levels of flow and spill near dams. Northern squawfish avoid areas where water velocities exceed 100 cm/s (Faler et al. 1988). Velocities are generally highest in tailraces, particularly during periods of spill. Migration rates of juvenile salmonids increase with flow (Sims and Ossiander 1981; Berggren and Filardo 1993). Spatial and temporal variation in consumption might therefore reflect variation in project flow or spill because faster migration rates may decrease encounter times between predator and prey. Alternatively, the efficiency with which juvenile salmonids are collected for transport from dams to down-river sites is

reduced during high flow periods, leaving greater numbers of juvenile salmonids susceptible to in-river sources of mortality including predation.

Beamesderfer et al. (1996) argued that direct measurement of the benefits of northern squawfish removals is not feasible, and program evaluation must rely on a long time series of indirect measures to separate confounding environmental effects from biological responses to removals. Repeated sampling in selected reservoirs and reaches would lend greater confidence in spatial variation in predation, reveal temporal trends, and facilitate analysis of sources of variability associated with estimates of consumption and predation.

The primary objective of this study was to estimate predation by northern squawfish on juvenile salmonids at fixed sites sampled annually from 1994-96, and compare estimates with relative abundance and consumption of northern squawfish in 1990-93. Relationships were examined between abundance indices and population estimates, and between consumption indices and consumption rates. Associations between consumption indices and temperature, flow, spill, and juvenile salmonid passage indices from 1990-96 were analyzed to interpret annual variability in predation.

METHODS

Field Sampling

Northern squawfish were sampled from 1994-96 at fixed sites throughout the lower Columbia and Snake rivers (Figure 1; Table 1). Sites in the unimpounded Columbia River included Bonneville Dam tailrace (the 6-km reach immediately downstream from Bonneville Dam), and river kilometer (RKm) 117-121, RKm 172-178, and RKm 190-197. For subsequent data analyses, the three reaches downstream from the tailrace were assumed to be representative of RKm 71-121, RKm 122-177, and RKm 178-224, respectively. Sites in lower Columbia River reservoirs included the 6-km reaches in the forebay and tailrace zones within Bonneville, The Dalles, and John Day reservoirs. Mid-reservoir sites within Bonneville (RKm 275-281) and John Day (RKm 390-396) reservoirs were also sampled, and assumed to be representative of the entire mid-reservoir area between forebay and tailrace zones. Sites in the lower Snake River included the 6-km reaches in Little Goose and Lower Granite Dam tailraces, 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.

Each sampling site was subdivided into 24 fixed, near-shore transects approximately 500 m in length. Northern squawfish were captured by electrofishing a minimum of six randomly selected transects per day within each site. Standardized effort in each transect was 15 minutes of continuous output at 4-5 A. A total effort of 8 boat-days was allocated annually in each site, with effort equally divided between spring (April-June) and summer (July-September). Exceptions to seasonal stratification are noted in Table 1. Sampling was scheduled to coincide with dates of historic peak passage of juvenile salmonids. Sampling
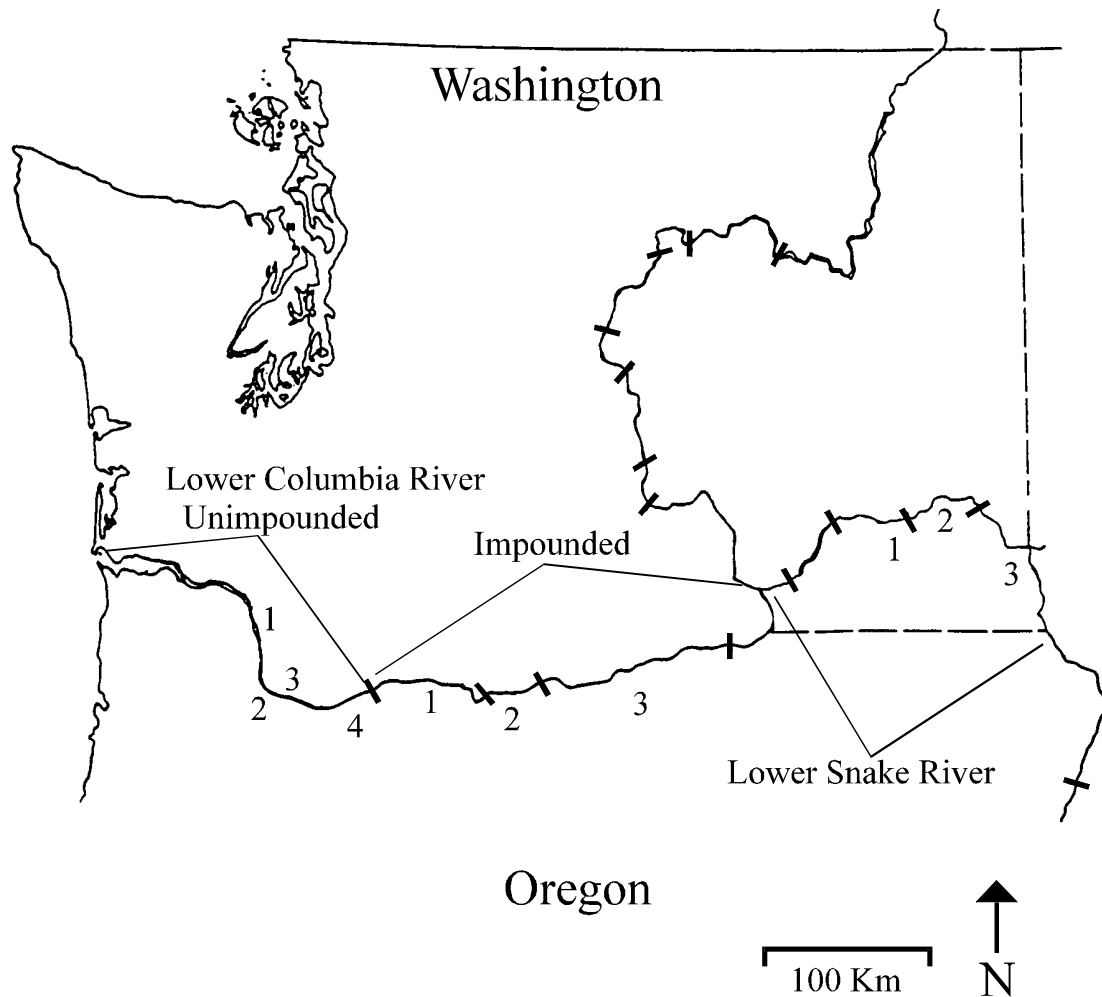
Figure 1. Sampling sites in the lower Columbia River basin in 1994-96. Sites in the unimpounded lower Columbia River are (1) river kilometer (RKm) 115-121, (2) RKm 172-178, (3) RKm 190-197, and (4) the 6-km tailrace reach immediately downstream Bonneville Dam. Sites in the impounded lower Columbia River are (1) Bonneville Reservoir forebay, mid-reservoir, and tailrace, (2) The Dalles Reservoir forebay and tailrace, and (3) John Day Reservoir forebay, mid-reservoir, and tailrace. Sites in the lower Snake River are (1) Little Goose Dam tailrace, (2) Lower Granite Dam tailrace, and (3) RKm 222-228.

Table 1. Areas sampled for northern squawfish abundance and consumption in the lower Columbia River basin from 1990-93 (Ward et al. 1995) and 1994-96 (this study). All sites were sampled during both spring (April-June) and summer (July-September) except where indicated.

Sampling site	1990	1991	1992	1993	1994-96
Unimpounded Lower Columbia River					
RKm 115-121	--	--	X	--	X
RKm 172-178	--	--	X	--	X
RKm 190-197	--	--	X	--	X
Bonneville Dam Tailrace	X	--	X	X	X
Lower Columbia River Reservoirs					
Bonneville					
Forebay	X	--	--	X	X
Mid-reservoir	X	--	--	X	X
Tailrace	X	--	--	X	X
The Dalles					
Forebay	X	--	--	X	X
Tailrace	X	--	--	X	X[a]
John Day					
Forebay	X	X	X	X	X
Mid-reservoir	X	X	X	X	X
Tailrace	X	X	X	X	X
Lower Snake River[b]					
Little Goose Dam Tailrace	--	X	--	--	X
Lower Granite Dam Tailrace	--	X	--	--	X
RKm 222-228	--	X	--	--	X

[a] Sampled during summer only.
[b] Sampled during spring only.

was conducted between 0300 and 1200 hours, which encompassed peaks in diel consumption rates of northern squawfish (Vigg et al. 1991). Northern squawfish ≥250 mm fork length were measured, weighed, sacrificed, and dissected to remove the entire digestive tract.

Laboratory Analysis

Digestive tracts were placed in sample bags on ice and later frozen until subsequent laboratory analysis. Gut contents were thawed in the laboratory, blotted dry, and weighed to the nearest 0.01g . To speed processing of samples, gut contents were digested in a solution of lukewarm tapwater, 2% (wet weight) pancreatin (8x porcine digestive enzyme), and 1% (wet

weight) sodium sulfide (Ward et al. 1995). Samples were placed in a 40°C desiccating oven for approximately 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). In 1995 and 1996, intact diagnostic bones of prey fishes were measured to the nearest 0.05 mm with hand calipers.

Abundance Index

The density of northern squawfish ≥250 mm fork length in each area was estimated by mean catch per 15-min electrofishing run (CPUE). An index of northern squawfish abundance (AI) was calculated using the equation

$$AI_i = D_i \bullet S_i \tag{1}$$

where

Ai_i = abundance index in area I,
D_i = density in area i, and
S_i = surface area (hectares) in area i (Ward et al. 1995).

The relationship between AI and mark-recapture estimates of population size was examined by linear regression. Northern squawfish were marked throughout the study area each year from 1992-96 (Friesen and Ward 1997), and angler returns of marked fish were used to estimate abundance. Adjusted Petersen estimates (Ricker 1975) were calculated for areas and years in which at least 10 marked fish were recaptured.

Consumption Index

An index of juvenile salmonid consumption (CI) by northern squawfish was calculated using the equation of Ward et al. (1995):

$$CI = 0.0209 \bullet T^{1.60} \bullet W^{0.27}(S \bullet GW^{-0.61}) \tag{2}$$

where

T = mean water temperature ($^{\circ}$C),
W = mean predator weight (g),
S = mean number of salmonids per northern squawfish, and
GW = mean total gut weight (g).

Consumption indices were calculated separately for spring and summer periods.
The relationship between area-specific consumption indices and average daily consumption rates from 1995 and 1996 was examined by linear regression. The approach of Tabor et al. (1993) was used to estimate average daily consumption rates of northern squawfish

on juvenile salmonids. Original fork lengths of consumed fishes were estimated from diagnostic bone measurements (Hansel et al. 1988). Original meal weight was estimated from length-weight regressions of common forage fishes (Vigg et al. 1991). The frequency of occurrence of food among northern squawfish, the proportion of juvenile salmonids among consumed prey fishes, and weights of non-fish prey items were obtained from Zimmerman (1997).

Correlation analyses were used to examine relationships between consumption indices and variables that may have contributed to annual variation in consumption, such as mean predator weight and various measures of dam operations, water temperature, and passage indices for juvenile chinook salmon *Oncorhynchus tshawytscha* (Table 2). Seven-day and 30-day means for variables in Table 2 were selected to represent average conditions prior to and including the day of sampling. Seven-day mean indices of chinook salmon passage were expressed as a proportion of maximum passage each year, which measured the timing of predator sampling relative to peak passage periods. Other species of juvenile salmonids were not included in the analysis because of the predominance of chinook salmon in the diets of northern squawfish (Zimmerman 1997). Flow, spill, temperature, and juvenile chinook salmon passage data were obtained from the Fish Passage Center, Portland, Oregon. Consumption indices from 1990-93 were obtained from Ward et al. (1995).

Correlation analyses were restricted to (1) data obtained from areas adjacent to dams (forebays and tailraces), (2) data series of five or more years, except in the Snake River where data from Little Goose and Lower Granite Dam tailraces (each sampled for four years) were combined, and (3) data series for which the index of consumption equaled zero in no more than one year. Consumption indices were related to each variable in Table 2 using the nonparametric Spearman's rank correlation procedure (Zar 1974). Decisions on statistical significance for individual correlations were avoided because the analysis was exploratory and many correlations were examined. Correlation coefficients $> |0.60|$ were considered to provide evidence for a relationship between consumption indices and a particular variable.

Predation Index

The predation index (PI), a product of the northern squawfish abundance and consumption indices (Ward et al. 1995), was calculated as

$$PI_{ij} = Ai_i \bullet CI_{ij} \tag{3}$$

where

   Pi_{ij} = predation index in area i in season j,
   Ai_i = abundance index in area i (both seasons pooled), and
   Ci_{ij} = consumption index in area i in season j.

RESULTS

Abundance Index

Relative abundance of northern squawfish ≥250 mm fork length in 1994-96 was highest downstream from Bonneville Dam (Figure 2). Since 1994, relative abundance in impoundments was highest in Bonneville Reservoir and lowest in Snake River areas. Mean abundance in areas sampled at least five years (Bonneville Dam tailrace, Bonneville Reservoir, The Dalles Reservoir forebay and tailrace, and John Day Reservoir) was 48-60% lower in 1994-96 than 1990-93.

Petersen abundance estimates for northern squawfish were linearly related to abundance indices (Figure 3). Areas and years represented by the relationship include the Columbia River downstream from Bonneville Dam (1992, 1994-96), Bonneville Reservoir (1993-94), The Dalles Reservoir (1993), and John Day Reservoir (1994).

Consumption Index

Consumption in spring was lower in 1994-96 than the pre-1994 period in Columbia River reservoirs and downstream from Bonneville Dam, and similar between periods in Bonneville Dam tailrace and the Snake River (Figure 4). In summer, consumption in 1994-96 was similar or less than 1990-93 in all locations except RKm 115-121 and The Dalles Reservoir forebay and tailrace (Figure 5). Among areas sampled at least five years, mean consumption in 1994-96 was 21-41% lower in spring and 13-64% lower in summer than 1990-93. Indices of juvenile salmonid consumption were linearly related to mean daily consumption rates from 1995-96 (Figure 6).

Correlation analyses provided evidence for relationships between consumption indices and flow, spill, temperature, and relative passage indices for chinook salmon at particular dams and seasons, although no single variable was consistently related to consumption at all sampling areas. In spring, consumption of juvenile salmonids was negatively correlated with mean outflow at Bonneville Dam tailrace, John Day Dam forebay, and Little Goose and Lower Granite Dam tailraces (Table 3). Spring consumption was inversely related to either seven or 30-day mean spill at all dams, and inversely related to spill as a proportion of total outflow in Bonneville Dam tailrace, John Day Dam forebay, and combined Snake River dam tailraces. Consumption increased with 30-day mean water temperature at Bonneville Dam tailrace and McNary Dam tailrace. Consumption in McNary Dam tailrace was positively correlated with relative passage indices for age-1 chinook salmon.

Table 2. Variables used in correlations with consumption indices of northern squawfish.

Variable	Period[a]
Mean predator weight in sample (g)	--
Mean daily outflow (m^3/s $\times$ 1,000)	7 d
	30 d
Mean daily spill (m^3/s $\times$ 1,000)	7 d
	30 d
Mean spill as a proportion of total project outflow	7 d
	30 d
Mean daily water temperature ($^\circ$C)	7 d
	30 d
Mean juvenile chinook salmon passage index (proportion of maximum daily index each year)[b]	7 d

[a] Calculated for days prior to and including the date of sampling.
[b] Passage indices for age-1 chinook salmon were used in correlations with consumption indices in spring, and passage indices for age-0 chinook salmon were used in correlations with consumption indices in summer.

In summer, juvenile salmonid consumption by northern squawfish increased with mean weight of predators in samples collected at Bonneville Dam forebay, The Dalles Dam tailrace, and McNary Dam tailrace (Table 4). Consumption in The Dalles Dam tailrace was negatively correlated with project outflow at The Dalles Dam, whereas consumption in John Day Dam tailrace increased with mean flow at John Day Dam. Consumption was negatively correlated with seven-day mean spill in Bonneville Dam tailrace and seven and 30-day mean spill at The Dalles Dam tailrace. Conversely, consumption in John Day Dam tailrace increased with 30-day mean spill at John Day Dam. Juvenile salmonid consumption in Bonneville Dam tailrace and forebay, and The Dalles Dam tailrace was negatively related to the relative volume of water spilled at Bonneville Dam and The Dalles Dam, respectively. In John Day Dam tailrace, consumption increased with the proportion of project outflow spilled at John Day Dam. Summer consumption was positively correlated with mean temperature in The Dalles and McNary Dam tailraces, but decreased with summer temperatures in John Day Dam forebay and tailrace. Consumption in John Day and McNary Dam tailrace increased with passage of age-0 chinook salmon at John Day and McNary Dam, respectively.
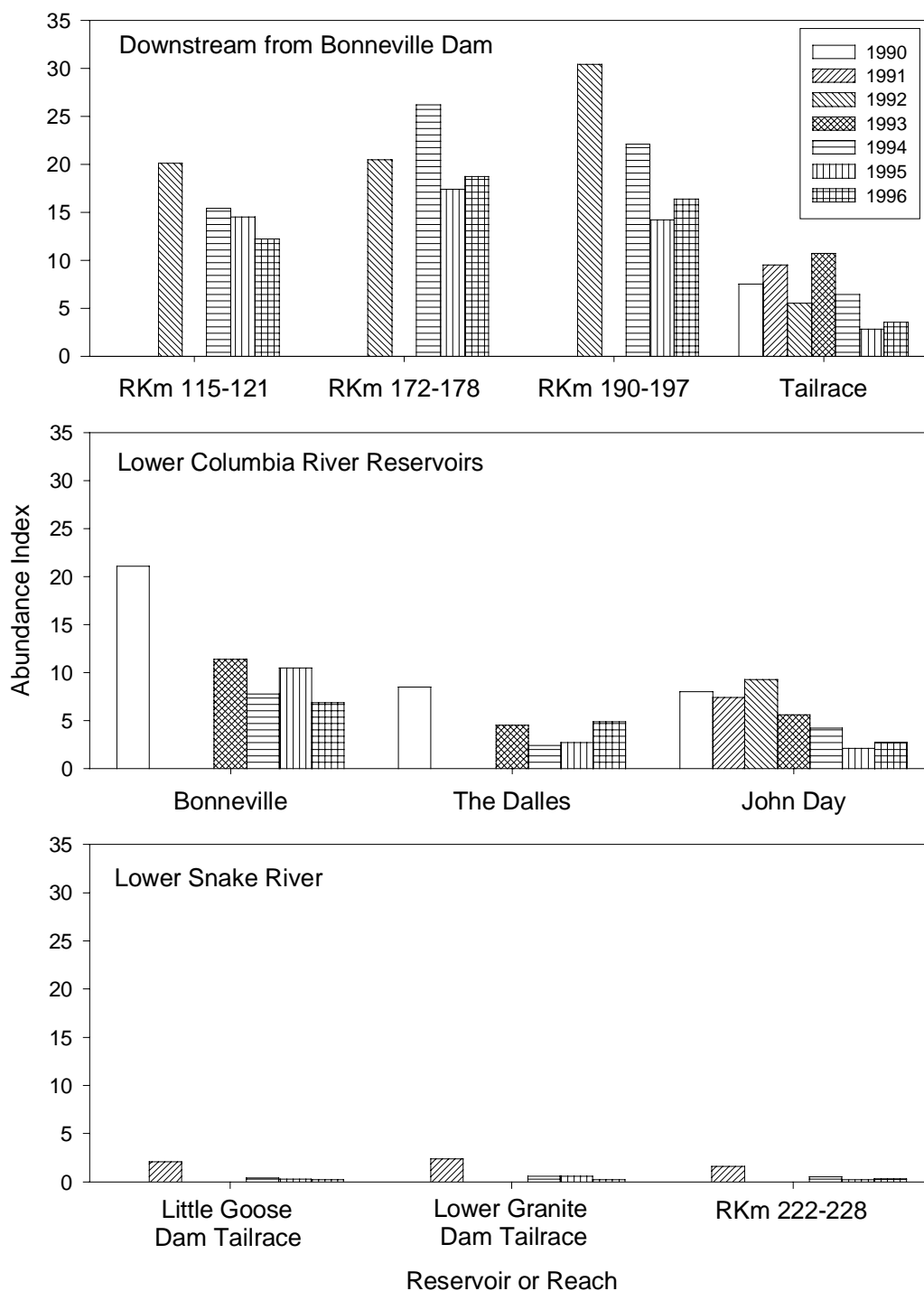
Figure 2. Relative abundance of northern squawfish ≥250 mm fork length in the Columbia River downstream from Bonneville Dam, lower Columbia River reservoirs, and the lower Snake River, 1990-96. 1990-93 abundance indices from Ward et al. (1995).
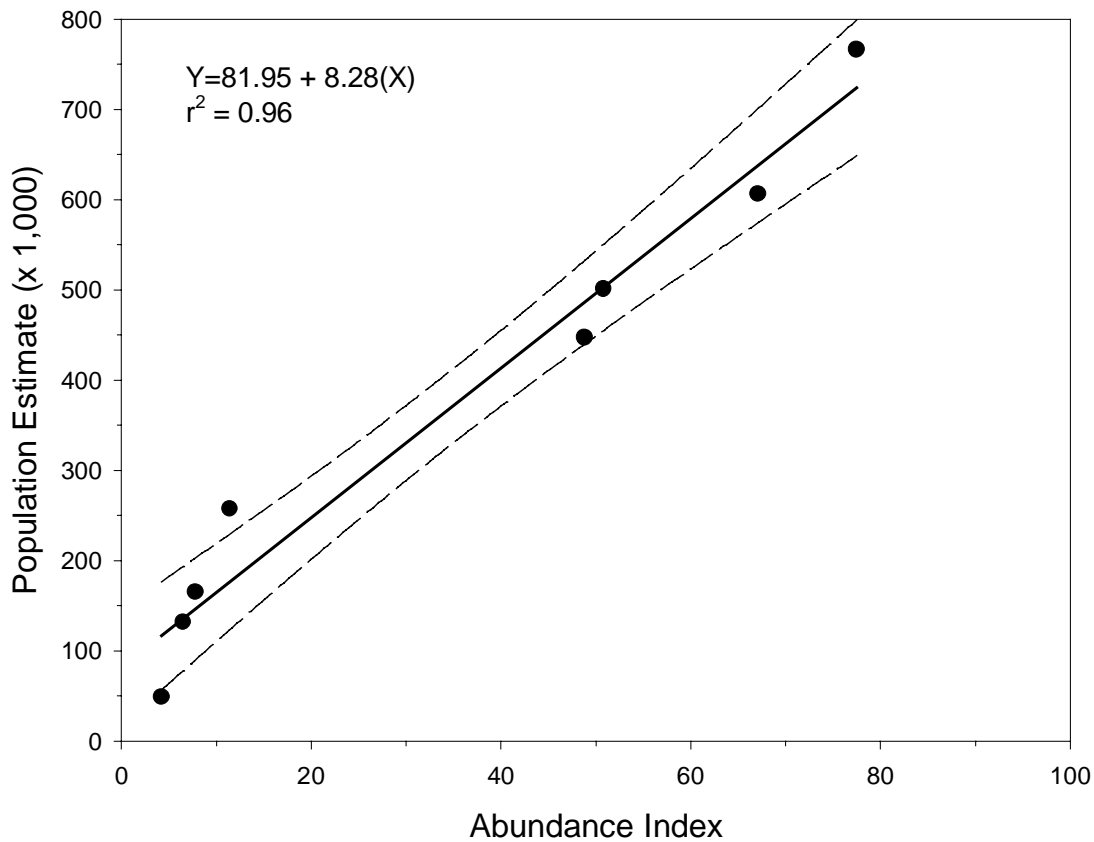
Figure 3. Relationship between northern squawfish abundance indices (X) and Petersen population estimates of northern squawfish (Y) in the lower Columbia River.

Predation Index

Spring predation indices in 1995 and 1996 were similar or less than previous years in all locations (Figure 7). Summer predation indices in RKm 71-121 and RKm 122-177 increased from 1992 to 1994, and then declined to zero in 1996 (Figure 8). Predation indices in Bonneville Dam tailrace were lower in 1994-96 than previous years. Summer predation in Bonneville and John Day reservoirs declined from a maximum in 1991 to a minimum in 1996. Predation in The Dalles reservoir increased from 1993 to 1996, but predation in those years was far less than in 1991.

The mean decline in spring predation indices from 1990-93 to 1994-96 ranged from 47% in Bonneville Dam tailrace to 95% in the forebay of The Dalles Reservoir (Table 5). The mean decline in summer predation indices from 1990-93 to 1994-96 ranged from 59%
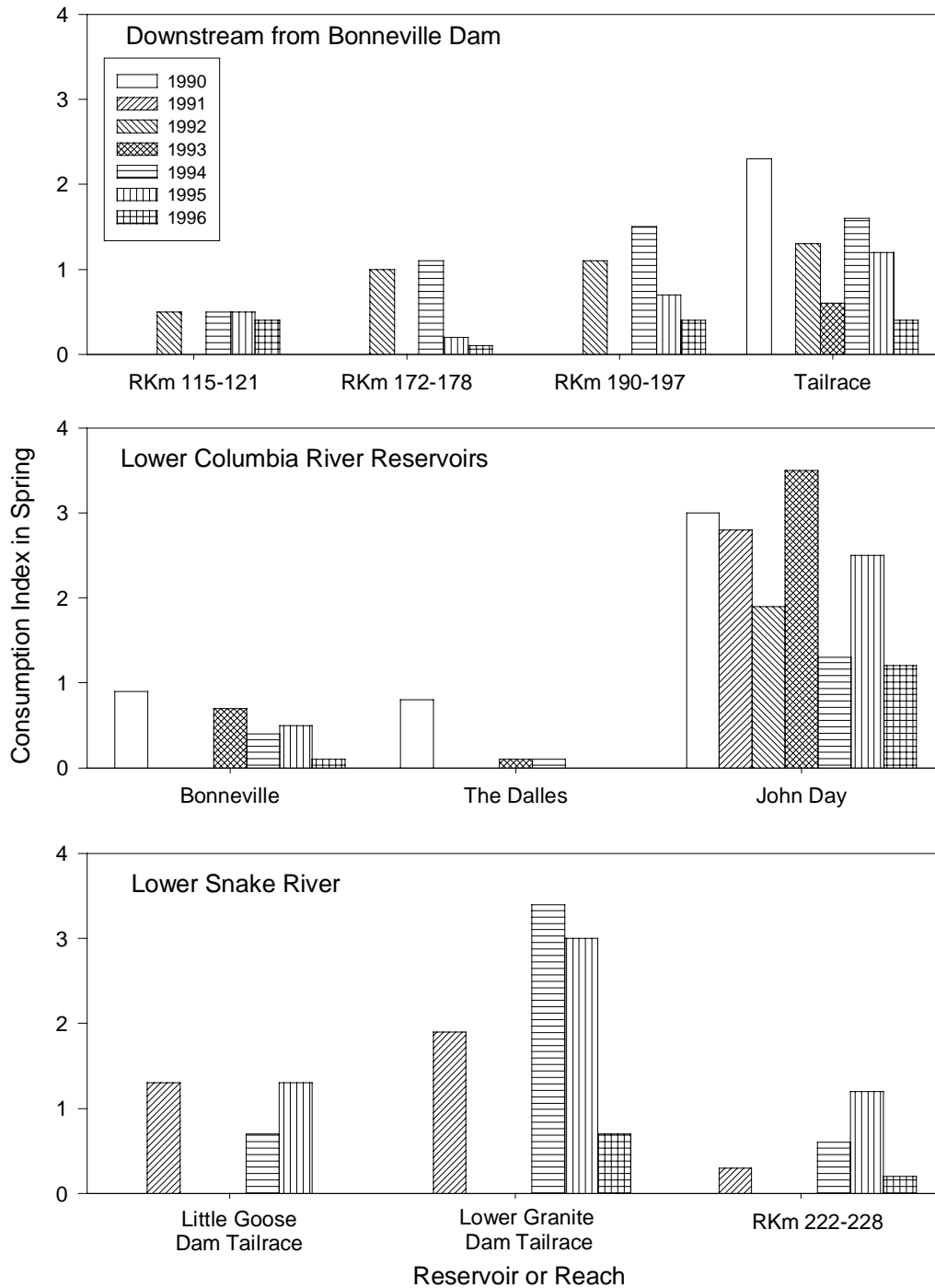
Figure 4. Consumption index values for northern squawfish in the Columbia River downstream from Bonneville Dam, lower Columbia River reservoirs, and the lower Snake River, spring (April-June) 1990-96. 1990-93 consumption indices from Ward et al. (1995).
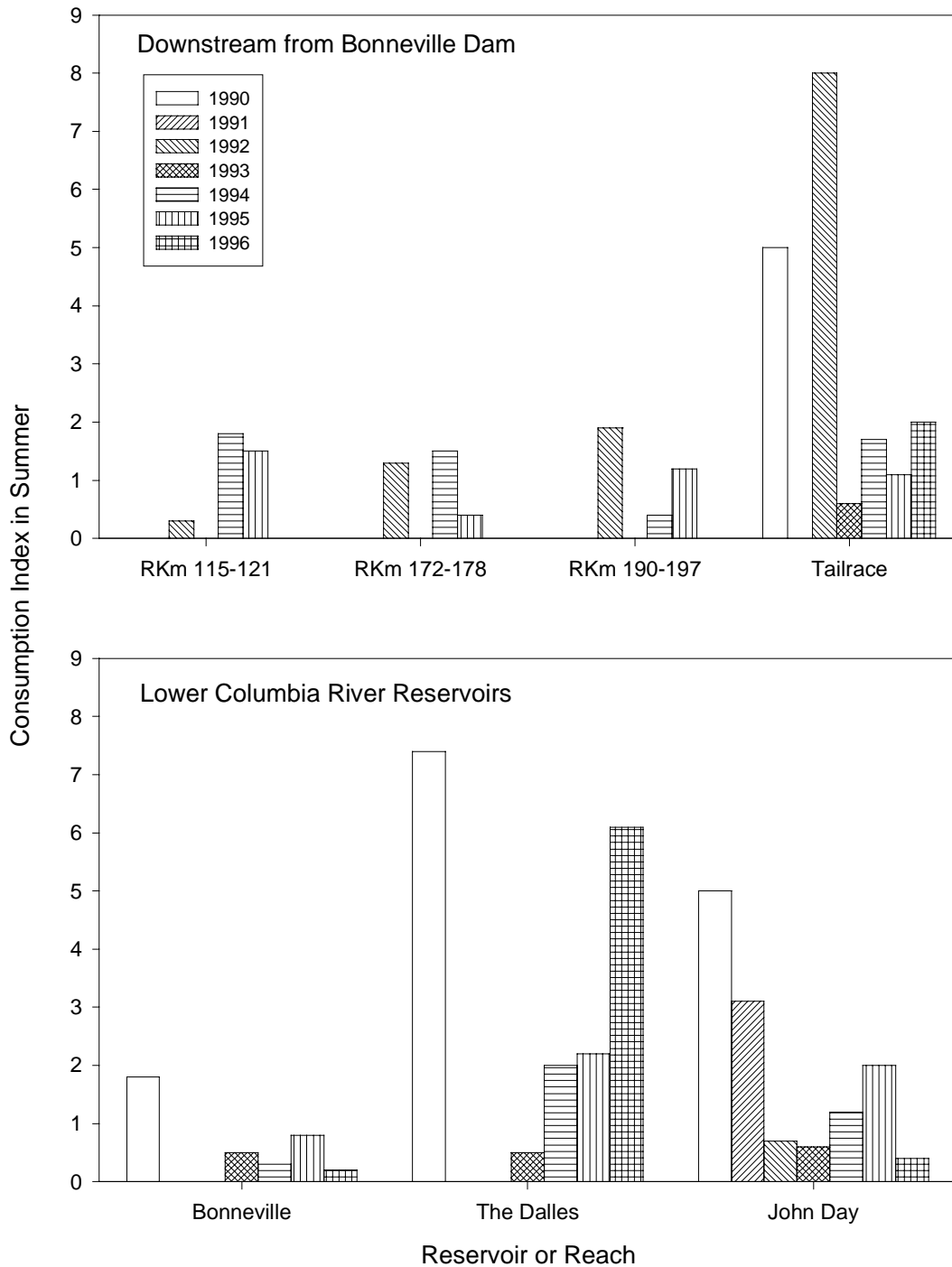
Figure 5. Consumption index values for northern squawfish in the Columbia River downstream from Bonneville Dam and lower Columbia River reservoirs, summer (July-September) 1990-96. 1990-93 consumption indices from Ward et al. (1995).
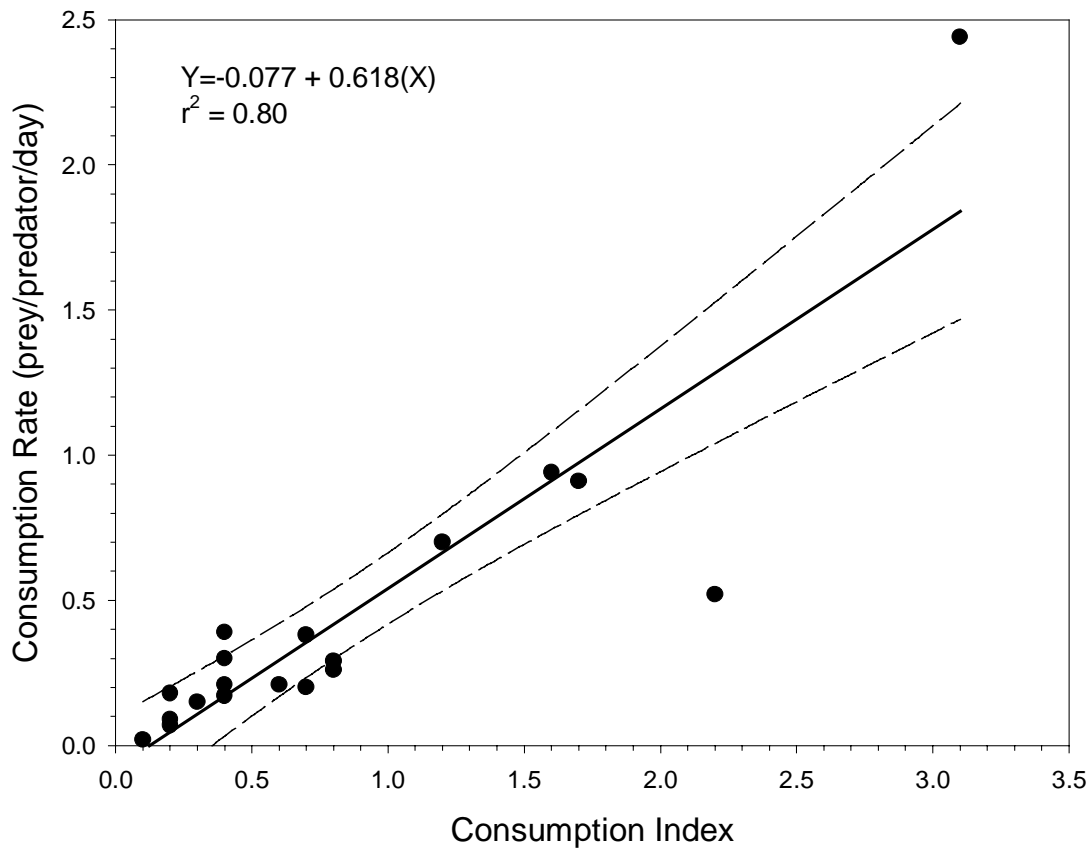
Figure 6. Relationship between northern squawfish consumption indices (X) and daily consumption rates of northern squawfish on juvenile salmonids (Y) in the lower Columbia River basin.

downstream from Bonneville Dam tailrace to 91% in Bonneville Reservoir (Table 5). The mean decline in all areas combined was 69% in spring and 76% in summer.

DISCUSSION

Spatial variation in northern squawfish abundance and predation from 1994-96 was consistent with variation from 1990-93 summarized by Ward et al. (1995). Northern squawfish abundance was greatest in the Columbia River downstream from Bonneville Dam, and declined in an upstream direction to the Snake River. Predation downstream from Bonneville Dam was an order of magnitude higher than Columbia River reservoirs and two orders of magnitude higher than Snake River reservoirs. In this study, the same

Table 3. Spearman's rank coefficients and associated probabilities between juvenile salmonid consumption indices by northern squawfish and mean weight of northern squawfish, seven and 30-day mean outflow, seven and 30-day mean spill, seven and 30-day mean spill as a proportion of project outflow (spill/flow), seven and 30-day mean temperature, and relative passage of age-1 chinook salmon (CHN-1) at Bonneville Dam tailrace and forebay, John Day Dam forebay, McNary Dam tailrace, and Little Goose and Lower Granite Dam tailraces combined in spring (April-June), 1990-96. Sample size is the number of year and location-specific consumption index values used in each correlation.

Correlation Coefficient (Probability)

Variable	Bonneville Tailrace	Forebay	John Day Forebay	McNary Tailrace	Little Goose and Lower Granite Tailraces
Sample size	6	5	7	7	8
Mean Weight	0.46	0.35	-0.23	0.54	0.37
	(0.36)	(0.56)	(0.62)	(0.21)	(0.36)
$Outflow_7$	-0.88	-0.43	-0.19	-0.10	-0.72
	(0.02)	(0.47)	(0.68)	(0.84)	(0.04)
$Outflow_{30}$	-0.27	-0.53	-0.70	-0.34	-0.72
	(0.60)	(0.36)	(0.08)	(0.46)	(0.04)
$Spill_7$	-0.90	-0.20	-0.56	-0.21	-0.82
	(0.01)	(0.74)	(0.19)	(0.66)	(0.01)
$Spill_{30}$	-0.75	-0.82	-0.71	-0.63	-0.84
	(0.09)	(0.09)	(0.08)	(0.13)	(0.01)
$Spill/flow_7$	-0.64	-0.05	-0.60	-0.26	-0.74
	(0.17)	(0.93)	(0.15)	(0.57)	(0.04)
$Spill/flow_{30}$	-0.79	-0.12	-0.71	-0.52	-0.79
	(0.06)	(0.84)	(0.08)	(0.23)	(0.02)
$Temp._7$	0.27	-0.24	0.03	0.50	-0.08
	(0.60)	(0.70)	(0.95)	(0.26)	(0.86)
$Temp._{30}$	0.85	-0.27	0.19	0.60	0.24
	(0.03)	(0.66)	(0.68)	(0.15)	(0.56)
CHN-1	0.14	0.10	-0.25	0.81	0.27
	(0.02)	(0.87)	(0.58)	(0.03)	(0.53)

Table 4. Spearman's rank coefficients and associated probabilities between juvenile salmonid consumption indices by northern squawfish and mean weight of northern squawfish, seven and 30-day mean outflow, seven and 30-day mean spill, seven and 30-day mean spill as a proportion of project outflow (spill/flow), seven and 30-day mean temperature, and relative passage of age-0 chinook salmon (CHN-0) at Bonneville Dam tailrace and forebay, The Dalles Dam tailrace, John Day Dam tailrace and forebay, and McNary Dam tailrace in summer (July-September), 1990-96. Sample size is the number of year and location-specific consumption index values used in each correlation.

Correlation Coefficient (Probability)

| | Bonneville | | | John Day | | |
| | | | The Dalles | | | McNary |
Variable	Tailrace	Forebay	Tailrace	Tailrace	Forebay	Tailrace
Sample size	6	5	5	5	7	7
Mean Weight	0.09	0.79	0.86	-0.03	0.40	0.69
	(0.87)	(0.12)	(0.06)	(0.96)	(0.37)	(0.09)
$Outflow_7$	-0.34	-0.33	-0.98	0.84	0.25	-0.23
	(0.51)	(0.59)	(<0.01)	(0.07)	(0.59)	(0.63)
$Outflow_{30}$	-0.44	-0.14	-0.92	0.91	0.44	-0.37
	(0.38)	(0.82)	(0.02)	(0.03)	(0.33)	(0.42)
$Spill_7$	-0.71	-0.47	-0.76	0.56	-0.07	-0.31
	(0.11)	(0.42)	(0.13)	(0.32)	(0.88)	(0.50)
$Spill_{30}$	-0.57	-0.45	-0.82	0.78	-0.04	-0.42
	(0.24)	(0.45)	(0.09)	(0.12)	(0.93)	(0.35)
$Spill/flow_7$	-0.72	-0.76	-0.46	0.56	-0.04	-0.34
	(0.10)	(0.14)	(0.44)	(0.32)	(0.93)	(0.45)
$Spill/flow_{30}$	-0.38	-0.60	-0.60	0.66	-0.20	-0.50
	(0.46)	(0.28)	(0.28)	(0.22)	(0.67)	(0.26)
$Temp._7$	0.05	-0.52	0.85	-0.69	-0.18	0.61
	(0.93)	(0.37)	(0.07)	(0.20)	(0.70)	(0.15)
$Temp._{30}$	0.24	-0.17	0.74	-0.95	-0.66	0.25
	(0.65)	(0.79)	(0.16)	(0.01)	(0.12)	(0.59)
CHN-0	0.14	0.46	0.05	0.87	0	0.81
	(0.79)	(0.43)	(0.93)	(0.05)	(1.00)	(0.03)

Figure 7. Relative predation on juvenile salmonids by northern squawfish in the Columbia River downstream from Bonneville Dam, lower Columbia River reservoirs, and the lower Snake River in spring (April-June), 1990-96. 1990-93 predation indices from Ward et al. (1995).
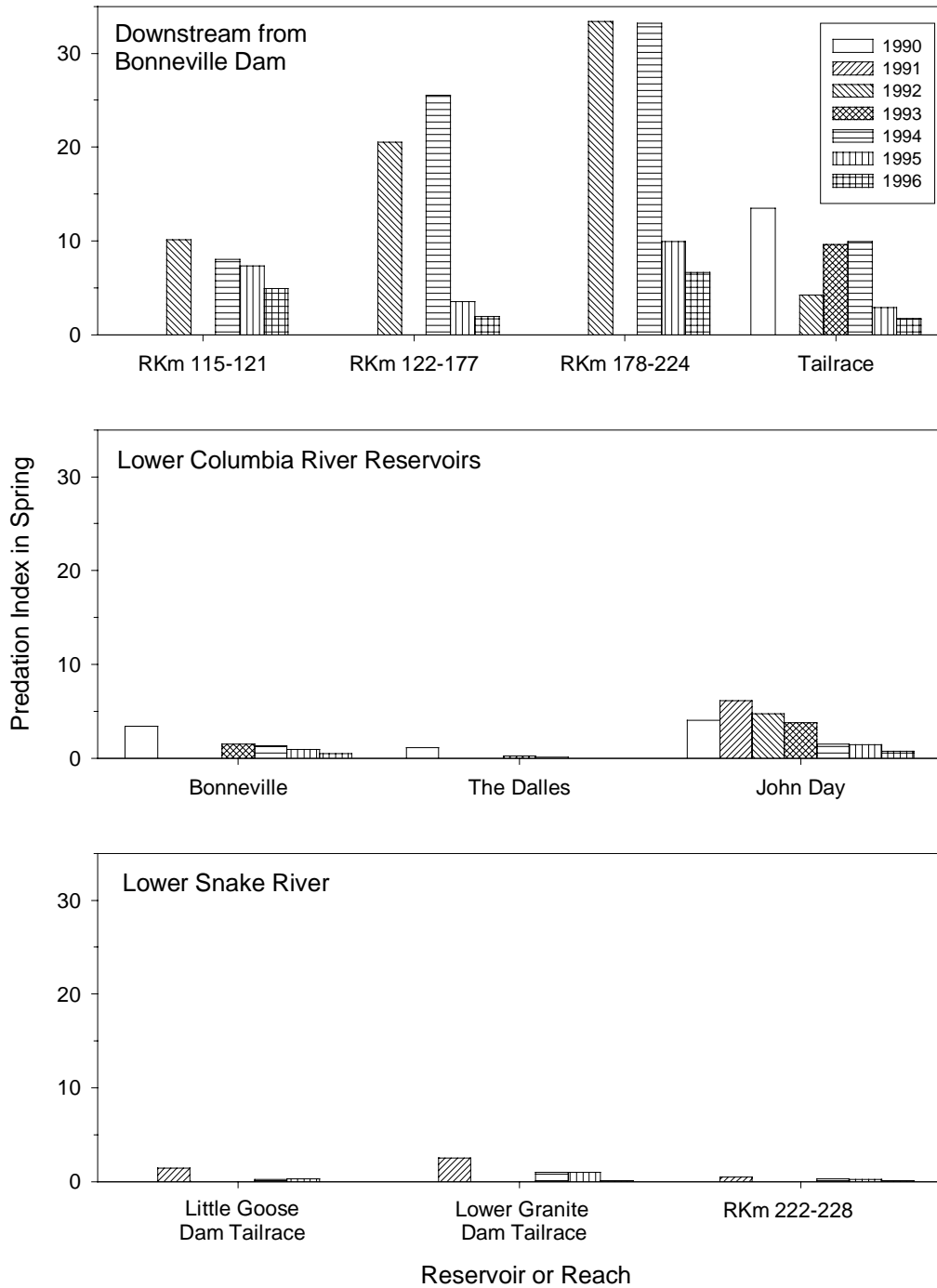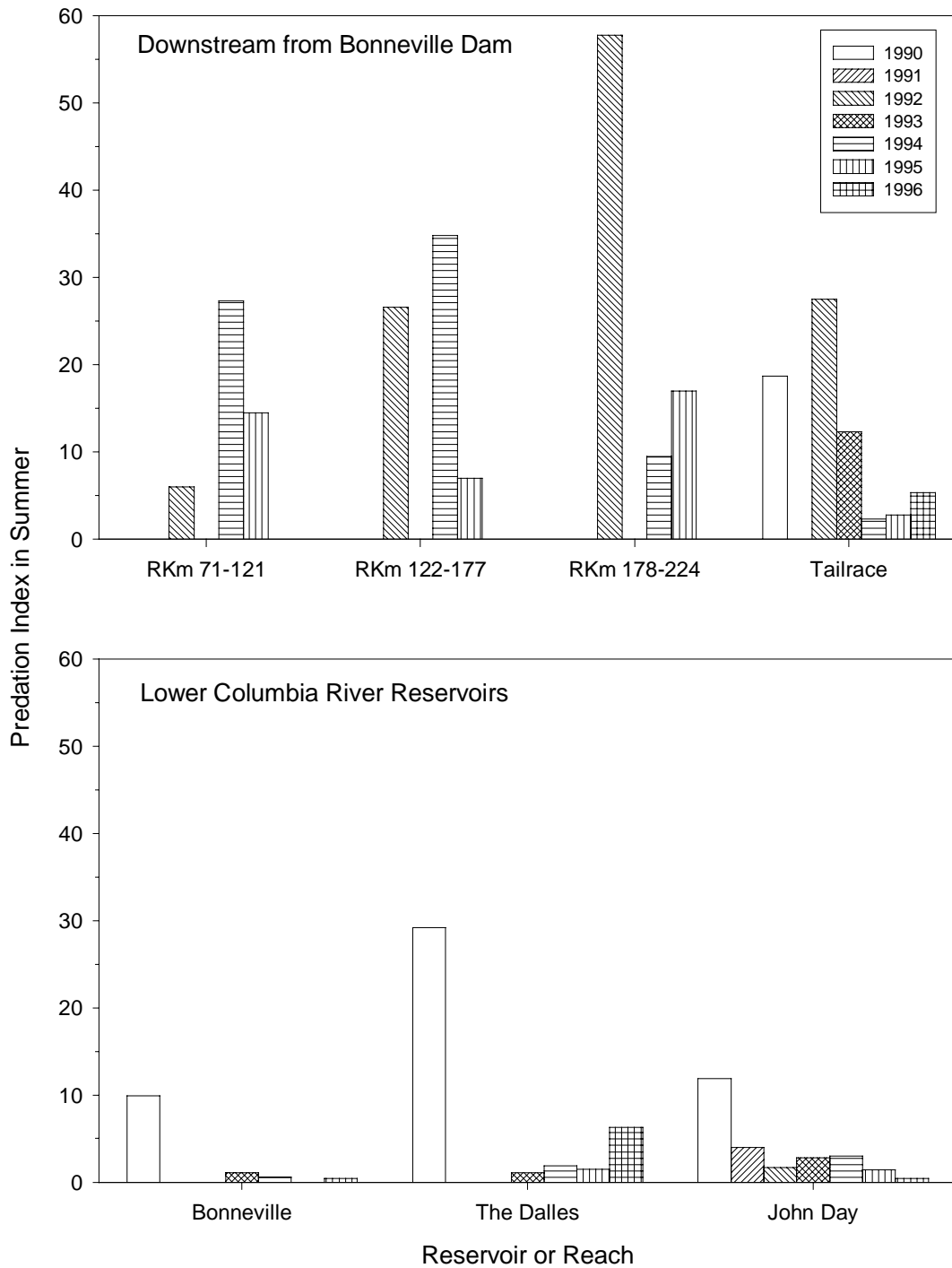
Figure 8. Relative predation on juvenile salmonids by northern squawfish in the Columbia River downstream from Bonneville Dam and lower Columbia River reservoirs in summer (July-September), 1990-96. 1990-93 predation indices from Ward et al. (1995).

Table 5. Mean decline (%) in northern squawfish predation indices from 1990-93 to 1994-96 in spring (April-June) and summer (July-September). N = number of years sampled.

Season, area	Mean Predation Index (N)		Mean Decline
	1990-93[a]	1994-96	
Spring			
Unimpounded Lower Columbia River			
RKm 71-224	64.0 (1)	33.6 (3)	48%
Bonneville Dam tailrace	9.1 (3)	4.8 (3)	47%
Lower Columbia River Reservoirs			
Bonneville	2.4 (2)	0.9 (3)	62%
The Dalles[b]	0.6 (2)	<0.1 (3)	95%
John Day	4.6 (4)	1.2 (3)	74%
Lower Snake River			
Little Goose Dam tailrace	1.4 (1)	0.2 (3)	86%
Lower Granite Dam tailrace	2.5 (1)	0.4 (3)	84%
RKm 222-228	0.5 (1)	0.2 (3)	60%
Summer			
Unimpounded Lower Columbia River			
RKm 71-224	90.4 (1)	36.7 (3)	59%
Bonneville Dam tailrace	19.5 (3)	3.5 (3)	82%
Lower Columbia River Reservoirs			
Bonneville	5.5 (2)	0.5 (3)	91%
The Dalles[c]	15.1 (2)	3.2 (3)	79%
John Day	5.1 (4)	1.6 (3)	69%

[a] Ward et al. (1995).
[b] Forebay only.
[c] Forebay and tailrace only.

areas were sampled annually from 1994-96 and our results reinforced those of Ward et al. (1995), which were obtained from areas sampled in different years.

Significant linear regressions between mark-recapture population estimates and an abundance index based on catch per unit of effort, and between area-specific estimates of daily ration and a consumption index based on easily measured variables, demonstrated the reliability of surrogate measures of relative abundance and consumption. The results increase confidence

in spatial differences in predation reported by Ward et al. (1995) and temporal trends in predation from 1990-96.

Declines in relative abundance of northern squawfish, relative consumption rates on juvenile salmonids, or both abundance and consumption from 1990-96 have led to declines in northern squawfish indices of predation on juvenile salmonids in nearly all areas sampled. Several factors probably contributed to temporal differences in relative predation from 1990-96, including changes in population characteristics of northern squawfish associated with exploitation, and annual variation in river flow, dam operations, and densities of juvenile salmonids.

Exploitation of northern squawfish was minimal prior to the implementation of predator control efforts in 1990. Approximately 1.1 million northern squawfish ≥250 mm fork length have been harvested from the lower Columbia and Snake rivers from 1990 to 1996, with annual harvest rates averaging 12% (Friesen and Ward 1997). Knutsen and Ward (1997) found that populations of northern squawfish populations have shifted toward smaller, younger individuals since 1990. Because fisheries are selective for large northern squawfish (Friesen and Ward 1997) and consumption rates on juvenile salmonids increase with northern squawfish size (Vigg et al. 1991), predation on juvenile salmonids would be reduced in the absence of other factors. Positive correlations between consumption indices and mean weight of northern squawfish in samples collected during summer in Bonneville Dam forebay, The Dalles Dam tailrace, and McNary Dam tailrace were consistent with the changes observed in proportional stock density of northern squawfish populations from 1990-96 (Friesen and Ward 1997).

Juvenile salmonid consumption in spring and summer at many projects was negatively related to project outflow and spill variables. High water velocities reduce the feeding efficiency of northern squawfish and exclude northern squawfish from areas within tailraces where salmonids are most vulnerable to predation (Faler et al. 1988; Mesa and Olson 1993). High velocities also reduce the travel times of juvenile salmonids (Berggren and Filardo 1993), which may reduce encounters between predator and prey. Total spill and the proportion of total discharge spilled at most projects were greater in 1995-96 than previous years, and may have contributed to declines in consumption indices of northern squawfish from 1990-96. Our results provide evidence that river conditions which enhance juvenile salmonid passage also reduce the losses of juvenile salmonids to northern squawfish.

Positive correlations between consumption indices and relative passage indices for chinook salmon at McNary Dam tailrace (spring and summer) and John Day Dam tailrace (summer) were consistent with the functional response relationship described by Petersen and DeAngelis (1992). Variation in consumption indices associated with passage indices should reflect the degree to which our sampling efforts coincided with peak periods of juvenile salmonid passage. However, passage indices are not necessarily an accurate estimate of juvenile salmonid densities, and a complex relationship exists between total discharge, spill, and the numbers of juvenile salmonids counted at dams.

Friesen and Ward (1997) estimated that harvests of northern squawfish since 1990 have reduced predation on juvenile salmonids by 38% relative to predation prior to the implementation of the Northern Squawfish Management Program. Annual variation in flow and spill from 1990-96 may have contributed to further reductions in juvenile salmonid predation by northern squawfish.

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Biological Characteristics of Northern Squawfish in the Lower Columbia and Snake Rivers
Before and After Sustained Exploitation

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INTRODUCTION

The northern squawfish *Ptychocheilus oregonensis* is a native cyprinid that is widely distributed throughout the Columbia and Snake river systems. Intensive predation by northern squawfish on juvenile Pacific salmon *Oncorhynchus* spp. has been well documented throughout the lower Columbia River basin (Vigg et al. 1991; Rieman et al. 1991; Ward et al. 1995), where extensive hydropower development has greatly increased the vulnerability of migrating juvenile salmonids to predation (Raymond 1979; Rieman et al. 1991). Concern about this predation led to the development of a large-scale management program for northern squawfish (Beamesderfer et al. 1996; Friesen and Ward 1997). The Northern Squawfish Management Program (NSMP) consists of both public and agency-operated fisheries, with the goal of sustaining annual exploitation at 10-20% of northern squawfish exceeding 250 mm fork length. Over 1.1 million northern squawfish were removed by this program from 1990 through 1996, and relative densities appear to have declined in many areas (Zimmerman and Ward 1997).

Although annual exploitation from 1991 through 1996 averaged approximately 12% (Friesen and Ward 1997), success of the NSMP relies in part on the response of northern squawfish populations to sustained exploitation. Because vulnerability of northern squawfish to fisheries generally increases with size (Friesen and Ward 1997), sustained exploitation decreases the relative abundance of large fish. This will lead to a decrease in predation because consumption of juvenile salmonids increases with size of northern squawfish (Vigg et al. 1991). Compensation by northern squawfish in the form of enhanced reproduction and growth would limit the benefits of removals. Rieman and Beamesderfer (1990) concluded that life history characteristics of northern squawfish suggest a species with a limited capacity for compensation, and Parker et al. (1995) found no correlations between biological characteristics and density of northern squawfish. However, uncertainty still exists regarding resiliency of northern squawfish to changes in their density, particularly because biological compensation has been documented for other species after intensive removals. Johnson (1977) demonstrated increased growth in immature white suckers *Catostomus commersoni* following an 85% reduction in the adult standing crop. Healy (1978) showed that fecundity of exploited populations of lake whitefish *Coregonus clupeaformis* and lake trout *Salvelinus namaycush* increased following intensive removals.

Parker et al. (1995) collected baseline biological data on pre-exploitation populations of northern squawfish in lower Columbia and Snake River reservoirs from 1990 through 1992. The purpose of this paper is to compare northern squawfish biological characteristics within reservoirs and areas of the lower Columbia and Snake rivers before and after sustained exploitation. We focus our analyses on testing the hypothesis that sustained removals have not resulted in a density-dependent response of northern squawfish population structure, mortality, growth, and fecundity. In this report we (1) compare northern squawfish size structure among years and contrast observed results with those that would be expected without implementation of the NSMP, (2) examine annual mortality rates to detect increases attributable to removal fisheries and identify decreases that may offset benefits of sustained removals, (3) compare

growth and relative weight among years to identify increases in growth rate or condition that could result in increased predation rates among younger-aged fish, and (4) compare changes in individual northern squawfish fecundity among years to determine if reproductive potential has been enhanced as a result of removals.

METHODS

Data Collection and Laboratory Analysis

We used boat electrofishing from 1990 through 1996 to collect northern squawfish in four areas in the lower Columbia and Snake rivers: (1) the unimpounded Columbia River downstream from Bonneville Dam, (2) Bonneville Reservoir, (3) John Day Reservoir, and (4) Lower Granite Reservoir (Figure 1). Because the large size of each area precluded sampling the entire reach, we partitioned each area into sampling zones. The area downstream from Bonneville Dam was subdivided into three sampling zones: river kilometer (RKm) 115-121, RKm 172-178, and RKm 190-197. We sampled in three 6-km-long reaches in Bonneville and John Day reservoirs corresponding to forebay (immediately upstream from the dam), mid-reservoir, and tailrace (immediately downstream from the next dam). In Lower Granite Reservoir, we sampled the transition zone (RKm 222-228) between the uppermost portion of the reservoir and the free-flowing reach of the Snake River downstream from Hell's Canyon Dam. Details of sampling methods and gear specifications are given in Zimmerman and Ward (1997).

We measured fork length (mm) and weight (g), collected scale samples, and when possible, determined the sex of northern squawfish collected by electrofishing. Wherever samples sizes from electrofishing were insufficient, we used subsamples collected from fish harvested in NSMP fisheries. We used standard methods to determine ages of northern squawfish from scales (Jearld 1983). Ovaries were excised from ripe northern squawfish and preserved following methods described by Bagenal and Braum (1978). In the laboratory, fecundity was estimated following procedures described in Parker et al. (1995). Ovaries were not collected in 1990.

Data Analysis

Year-class Strength

We used the method of El-Zarka (1959) to index relative year-class strengths of northern squawfish cohorts (1985-92) in the area downstream from Bonneville Dam, and in Bonneville and John Day reservoirs. The El-Zarka (1959) procedure compared the relative abundance of each year class in catches from standardized sampling over a number of years. Because the relative abundance of year classes in our standardized electrofishing were biased by exploitation rates that varied among years (Friesen and Ward 1997), we limited our comparisons to the relative abundance of northern squawfish large enough to be effectively sampled (ages 3 and older), but small enough to be excluded from the NSMP (ages 5 and younger).
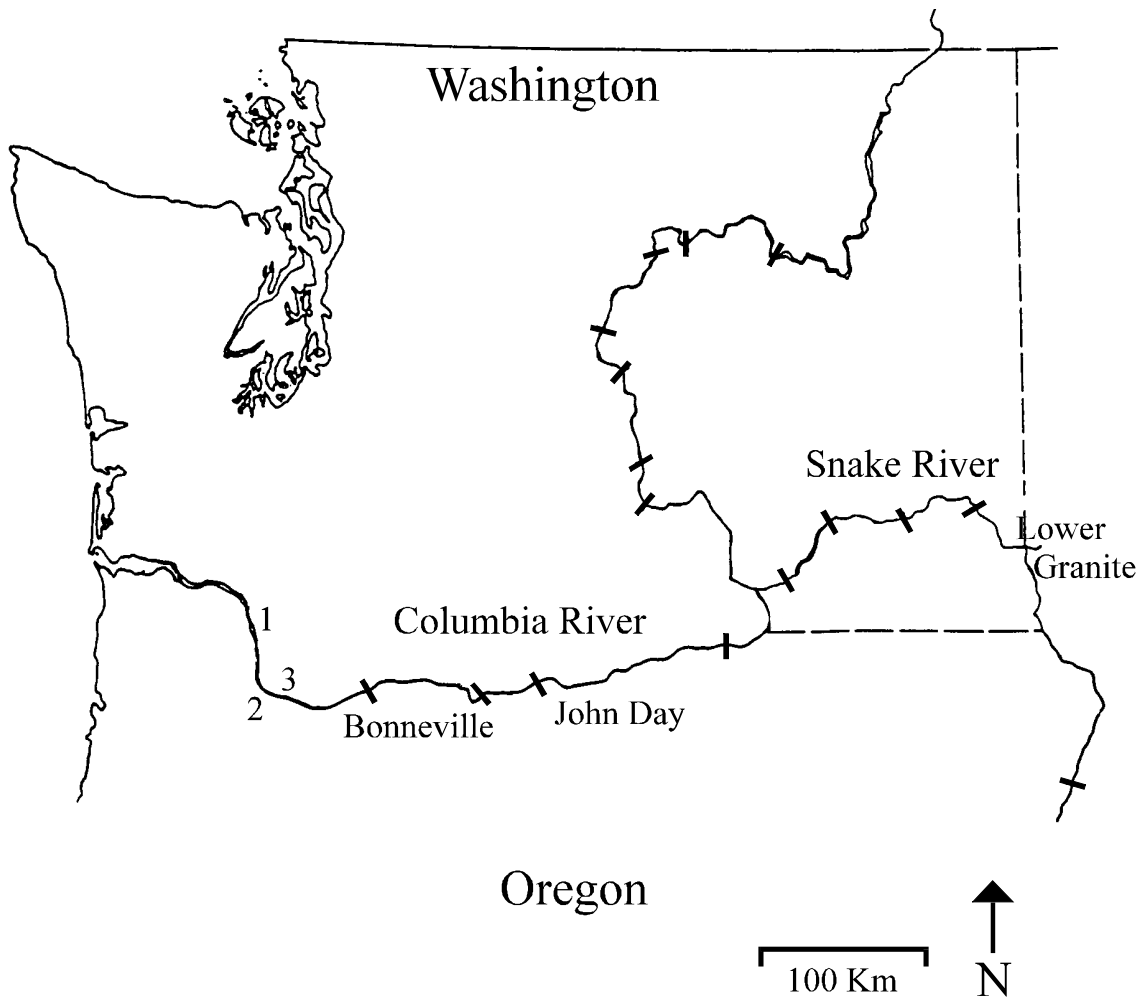
Figure 1. The Columbia and Snake rivers in Oregon and Washington. Reservoirs sampled (and associated dams) are labeled. Reaches sampled downstream from Bonneville Dam tailrace were (1) river kilometer (RKm) 115-121, (2) RKm 172-178, and (3) RKm 190-197.

Population Size Structure

We used proportional stock density (PSD = 100[number of fish at least quality length]/[number of fish at least stock length]) to compare size structure of northern squawfish populations among years from 1990-96 (Anderson 1980). Stock and quality sizes for northern squawfish have been defined as 250 and 380 mm fork length (Beamesderfer and Rieman 1988; Parker et al. 1995). We compared observed PSDs to estimates of PSDs that would be expected with and without implementation of the NSMP in the area downstream from Bonneville Dam, and in Bonneville and John Day reservoirs. Insufficient data were available to calculate PSD in Lower Granite Reservoir.

To facilitate comparison of observed and expected PSDs, we used age composition of our catches rather than size composition to estimate PSD. We used pooled 1990-96 age-at-length data to (1) back-calculate age-specific lengths for female and male northern squawfish, (2) estimate sex-specific age composition within 25-mm length intervals, and (3) estimate for each sex the proportion of each age (≥ 5 years) that were at least stock and quality size. We summarized sex-specific catch data into 25-mm length intervals, and calculated observed PSDs by summing the number of stock and quality size fish each year. We then computed 95% confidence intervals (Fleiss 1981) for these observed PSDs.

To estimate expected PSDs, we (1) calculated age distributions for the first year sampled as previously explained, (2) estimated recruitment to age 5 in subsequent years as a linear function of relative year-class strengths, and (3) estimated relative abundance of other ages as a function of natural mortality rates (Parker et al. 1995) and exploitation rates (Friesen and Ward 1997). The expected number of stock and quality size fish for each sex was estimated from the expected age distributions, and PSDs were estimated by summing the total number of expected stock and quality size fish each year. We then used a Tukey-type nonparametric multiple comparison procedure (Zar 1984) to test for significant differences between observed and expected PSDs.

Relative Weight

We used mean relative weight (W_r) to compare condition of northern squawfish among years (Anderson and Gutreuter 1983). We used the standard weight (W_s) equation for northern squawfish developed by Parker et al. (1995), $\log_{10}(W_s) = -4.886 + 2.986[\log_{10}(\text{fork length})$, in calculations ($W_r = 100[\text{weight}]/W_s$). We calculated W_r separately for females and males.

Annual Mortality

We used age-specific catch of male and female northern squawfish from 1990-1996 (corrected for differences in sampling effort among years) to produce year-class-specific catch curves. We then estimated total annual mortality over ages 8 through 11 by calculating a separate regression for each year-class (Rieman and Beamesderfer 1990). A lack of time series data for the area downstream from Bonneville Dam limited our analysis to the 1985-86 cohorts.

Growth

We used scales collected from female northern squawfish and calculated annual growth increments from 1989 to 1995. We then used analysis of variance (ANOVA; SAS Institute, Inc. 1990) to compare growth increments of like-aged female northern squawfish among years. We limited our analysis to ages 6 through 10 because these were the ages in which sample sizes were most complete. When the F-value in the ANOVA indicated significant differences ($P<0.05$) in growth among years, we used Tukey's multiple comparison test to determine in which years growth differed.

Fecundity

      To identify changes in fecundity from 1991 through 1996 we calculated mean relative fecundity (number of developed eggs per gram of body weight) for the area downstream from Bonneville Dam, and Bonneville, John Day and Lower Granite reservoirs. Because fecundity data did not meet assumptions of parametric analyses, we used Kruskal-Wallis (KW) analysis of variance by ranks to identify differences in relative fecundity among years. When differences were significant ($P < 0.05$), we used a nonparametric Tukey-type multiple comparison procedure described by Zar (1984) to make pairwise comparisons among years. Relative fecundity quantiles were then plotted for each area.

RESULTS

Year-class Strength

      Year-class strengths of northern squawfish varied considerably in all areas (Figure 2). Relatively strong year-class strengths in 1985 were followed by relatively weak 1987-88 year-classes in the area downstream from Bonneville Dam and John Day Reservoir. Year-class strengths in Bonneville Reservoir were highest in 1987 and 1991, and lowest in 1988. Relative year-class strengths generally increased in most areas between 1988 and 1991.

Population Size Structure

      Proportional stock density of northern squawfish has decreased in most areas since implementation of the NSMP (Figure 3). Observed PSDs initially remained stable or increased, as the relatively strong 1985 year class (Figure 2) was recruited from stock to quality size. Observed PSDs then generally decreased as harvest was sustained over a number of years, and as relatively strong 1989-91 year classes were recruited to stock size. In Bonneville and John Day reservoirs, observed PSDs were lower than estimates of PSDs expected without implementation of the NSMP. Differences were not always significant ($P<0.05$) however, in part because small sample sizes resulted in large confidence intervals for observed PSDs. From 1993-96, observed PSDs were very similar to estimates of PSDs expected with the NSMP. Observed and expected PSDs were similar downstream from Bonneville Dam until 1995, when PSD increased when it was expected to decrease. Although observed PSD decreased from 1995 to 1996, it was still higher than expected.

Relative Weight

      Relative weight varied among years and areas, but we found no evidence of an increase or decrease in W_r with time for any area (Figure 4). Relative weight was generally lower downstream from Bonneville Dam than in the reservoirs. Relative weight of males
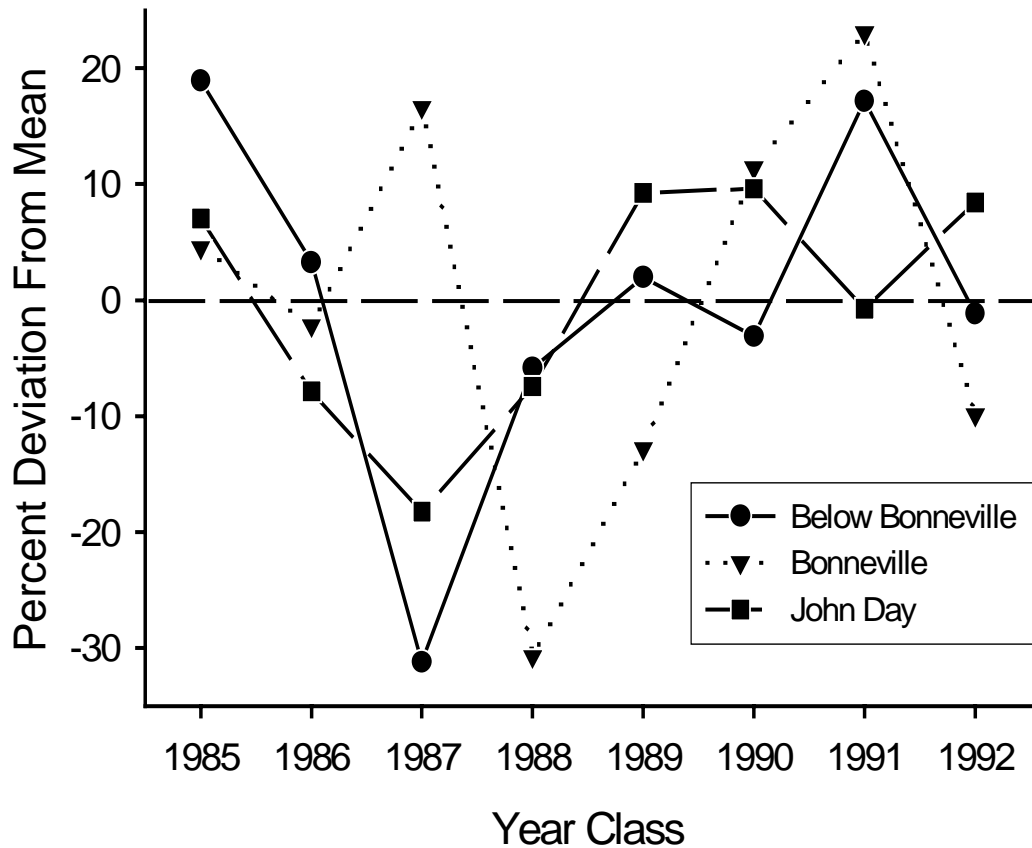
Figure 2. Index of relative year-class strength of northern squawfish in the Columbia River downstream from Bonneville Dam, in Bonneville Reservoir, and in John Day Reservoir.

was always lower than W_r of females. Female W_r was usually greater than 100, whereas W_r of males exceeded 100 only once.

Annual Mortality

Estimates of total annual mortality were generally high but varied among areas (range 18% - 72%; Table 1). Mortality estimates were typically highest in John Day Reservoir and lowest in Bonneville Reservoir. In John Day Reservoir, annual mortality of
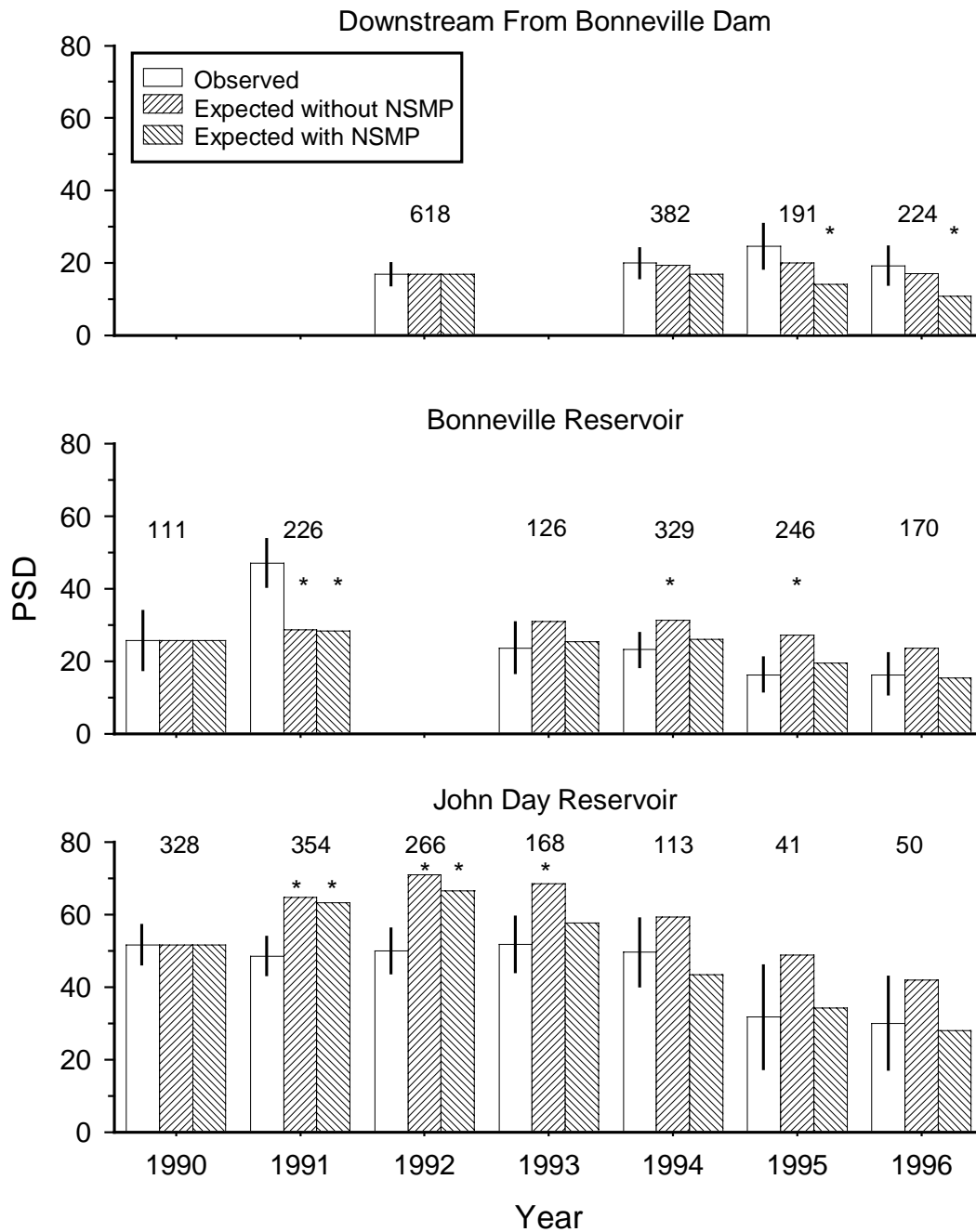
Figure 3. Observed and expected proportional stock density (PSD) with and without implementation of the Northern Squawfish Management Program from 1990-1996 in the Columbia River downstream from Bonneville Dam, in Bonneville Reservoir, and in John Day Reservoir. Vertical bars represent 95% confidence intervals for observed PSDs. Asterisks indicate where expected PSD differed (*P*<0.05) from observed PSD. Number of stock-length fish is given above each group.
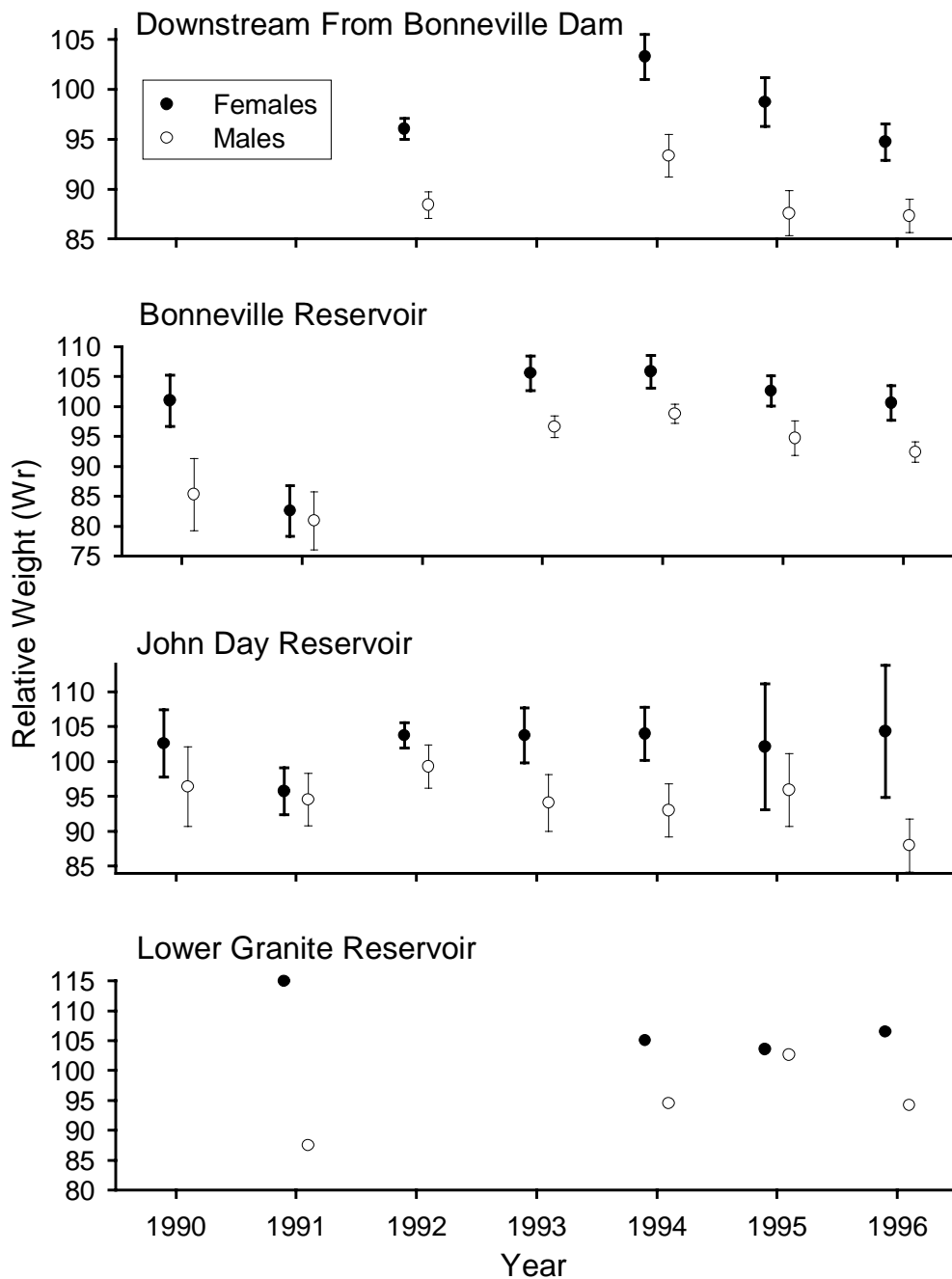
Figure 4. Mean relative weight (W_r) of female and male northern squawfish in the Columbia River downstream from Bonneville Dam, and in Bonneville, John Day, and Lower Granite reservoirs, 1990-1996. 95% confidence intervals are indicated by vertical bars. Insufficient data were available to generate confidence intervals for Lower Granite Reservoir.

Table 1. Age-specific catch (number of fish, corrected for effort) and estimates of annual mortality (A) for year-classes of northern squawfish in the area downstream from Bonneville Dam, Bonneville Reservoir, and John Day Reservoir.

| Area, year-class	Catch at Age				A	r^2
	8	9	10	11		
Downstream from Bonneville Dam						
1985	--	119	62	50	0.35	0.92
1986	130	64	58	--	0.33	0.83
Bonneville Reservoir						
1982	40	33	--	13	0.32	0.97
1983	73	--	32	30	0.27	0.93
1984	--	34	31	23	0.18	0.91
1985	36	31	23	14	0.27	0.94
1986	34	19	14	--	0.36	0.97
John Day Reservoir						
1982	79	72	36	27	0.32	0.92
1983	141	83	90	10	0.54	0.74
1984	111	145	24	3	0.72	0.84
1985	155	24	5	5	0.69	0.88
1986	21	5	6	--	0.47	0.65

successive year classes initially increased, but has decreased somewhat in recent years. Mortality initially decreased in Bonneville Reservoir, but has since increased so that mortality of recent year classes was higher than that of early year classes.

Growth

Analysis of female northern squawfish growth increments indicated considerable variation in growth among years; however, no trends of increasing or decreasing growth were evident for any area (Figure 5). Growth increments were generally smallest in 1992, and highest in 1993 and 1994. Despite these differences, growth in 1994 and 1995 was never significantly ($P <0.05$) greater than growth in any previous year.
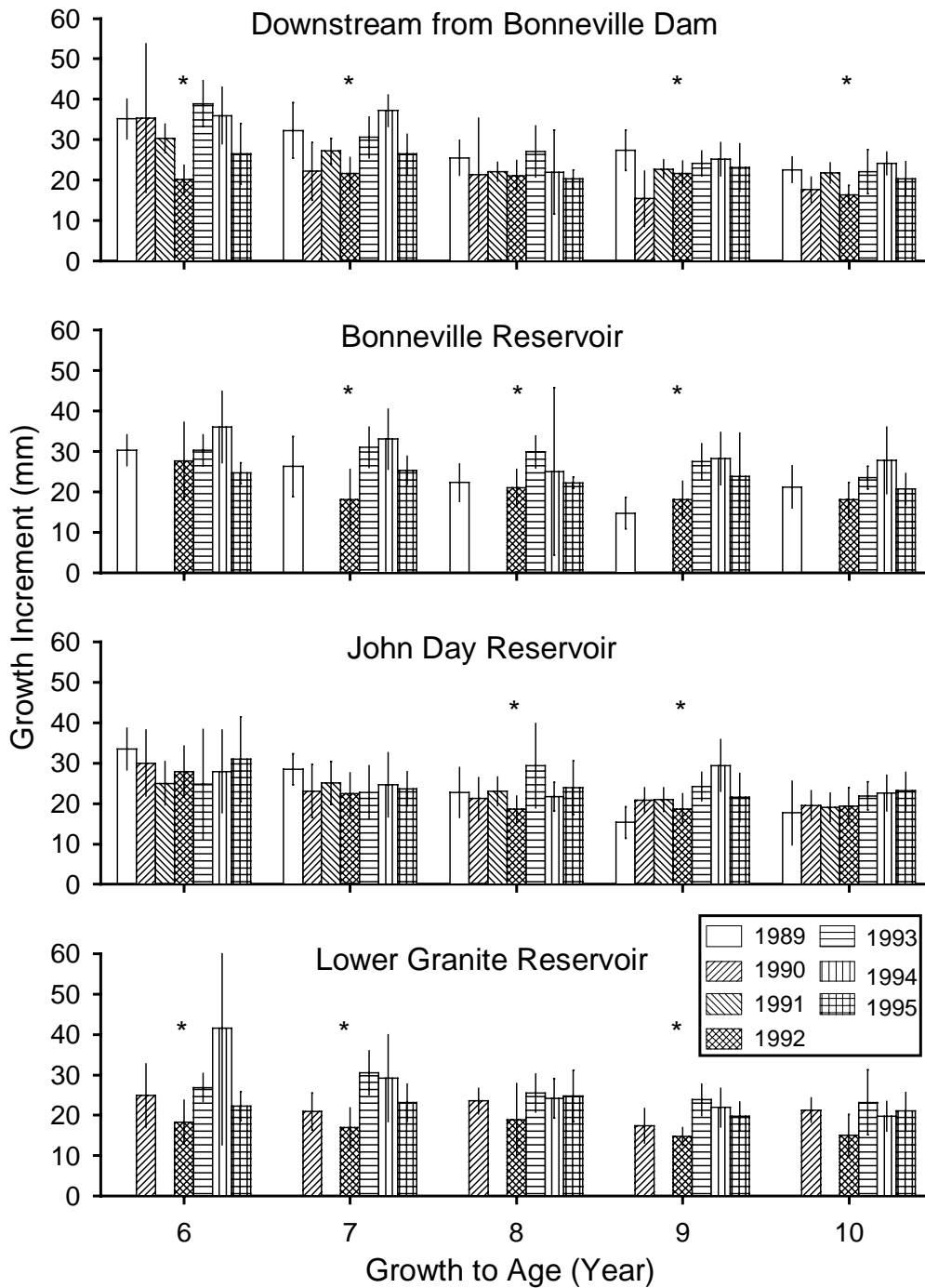
Figure 5. Mean annual growth increments for age 6 through 10 female northern squawfish in the Columbia River downstream from Bonneville Dam, and in Bonneville, John Day, and Lower Granite reservoirs. Asterisks indicate significant differences ($P<0.05$) in growth among years.

Fecundity

Relative fecundity varied significantly ($P < 0.05$) among years in all areas except Lower Granite Reservoir (KW = 7.4, df = 5, P = 0.19; Figure 6); however, we detected no consistent increases or decreases in relative fecundity over time. Relative fecundities in 1996 were not significantly different from those observed in 1991 in the area downstream from Bonneville Dam (KW = 38.3, df = 5, $P < 0.05$), Bonneville Reservoir (KW = 17.3, df = 5, $P < 0.05$), or John Day Reservoir (KW = 55.0, df = 5, $P < 0.05$). Relative fecundity in 1995 was significantly lower than all other years downstream from Bonneville Dam, and lower than the two preceding years in Bonneville and John Day reservoirs.

DISCUSSION

Decreases in PSD in John Day and Bonneville Reservoirs were greater than could be explained by fluctuations in year-class strength, and indicate that sustained removals may be altering the size structure of predator-sized northern squawfish. Our method for estimating expected PSD appeared to be reasonably accurate as observed and expected PSDs differed significantly less than 36% of the time. Observed and expected PSDs often differed in early years of the NSMP, in part because estimates of expected PSD incorporate estimates of natural mortality and growth. Annual variations in mortality and growth are unpredictable; we therefore used estimates of natural mortality developed prior to sustained removals (Parker et al. 1995), and pooled 1990-96 growth data to estimate age-specific lengths. These data are representative of long-term averages, but do not reflect annual variation around those averages. Differences between observed and expected PSDs have become smaller over a period of years, as annual variations in mortality and growth "average out".

Differences between observed and expected PSDs downstream from Bonneville Dam should also become smaller over time. Because we did not collect data for PSD estimates until 1992, annual variations in mortality and growth have had less time to "average out". Information from 1996 suggests that differences in observed and expected PSDs are becoming smaller.

We found no evidence that condition of surviving northern squawfish has improved concurrent with sustained removals. Although variable, W_r has not increased in any area. Differences in W_r among areas have also remained similar. Our finding that W_r is generally lowest downstream from Bonneville Dam is similar to findings prior to sustained removals (Parker et al. 1995). Consistent differences in W_r between sexes indicate that it may be appropriate to develop separate standard weight equations for female and male northern squawfish. Furthermore, separate standard weight equations for pre- and post-spawn female northern squawfish may also be needed. Although Parker et al. (1995) developed a single equation, they found that differences in weight-length relationships between sexes within an area were as great as differences among areas for each sex.
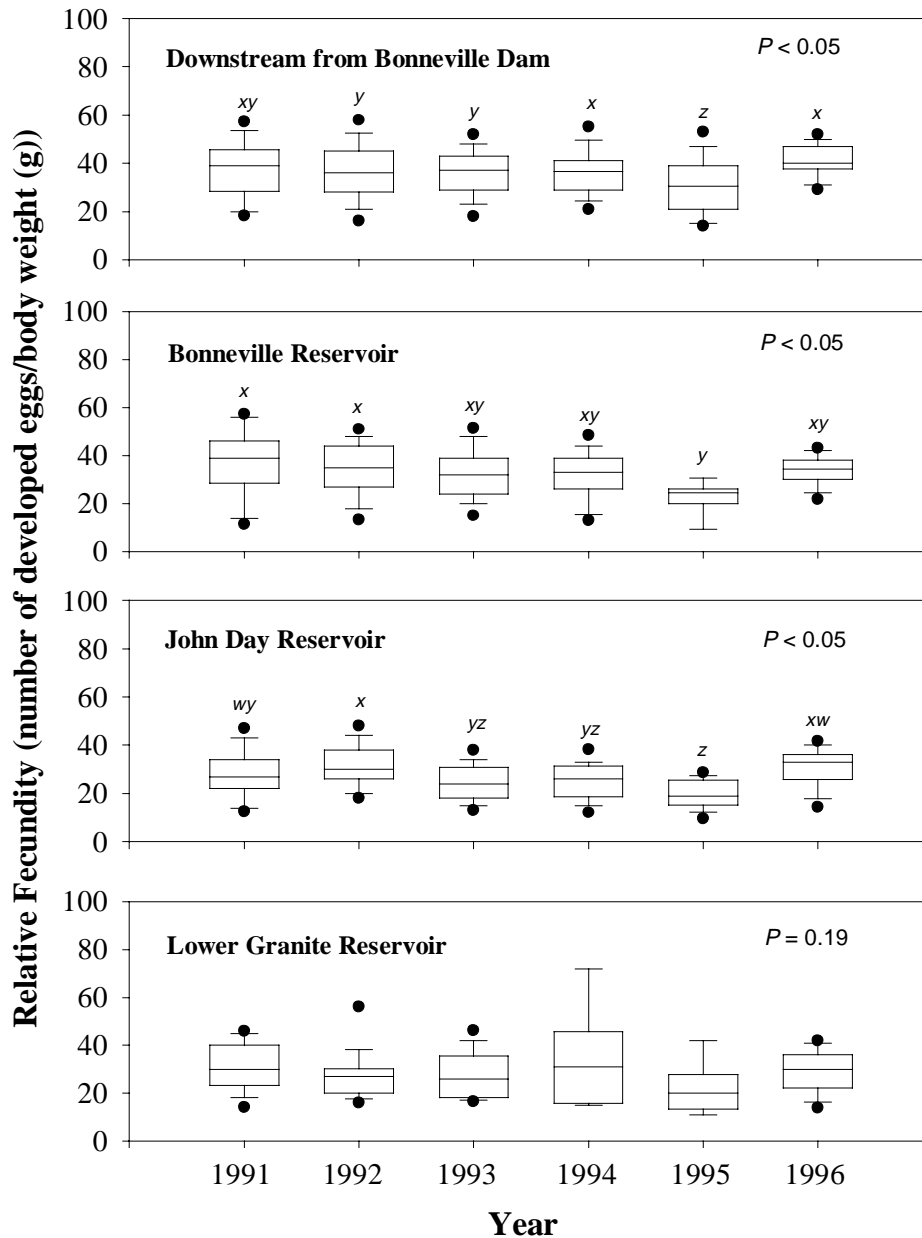
Figure 6. Relative fecundity (number of developed eggs per gram of body weight) for northern squawfish in the Columbia River downstream from Bonneville Dam, and in Bonneville, John Day, and Lower Granite reservoirs, 1990-1996. Samples sizes and percentiles for each year within a reservoir are indicated. Lines represent percentiles of 10, 25, 50, 75, and 90 (the box encompasses the 25th through 75th percentiles). The 5th and 95th percentiles are indicated below and above the 10th and 90th percentile caps. For each area, relative fecundities followed by the same letter are not significantly different (Kruskal-Wallis analysis of variance by ranks, $P \geq 0.05$).

Estimates of annual mortality were higher than pre-exploitation levels previously reported for the Columbia River. Our estimates probably best represent annual mortality rates of female northern squawfish as the majority of 8 to 11 year-olds in the lower Columbia River are females (Oregon Department of Fish and Wildlife, unpublished data). In the area downstream from Bonneville Dam, our estimates were higher than those reported by Parker et al. (1995) for female northern squawfish. Similar mortality estimates among the 1985-86 cohorts probably reflects consistency in harvest rates occurring downstream from Bonneville Dam between 1994 and 1996 (Friesen and Ward 1997).

In Bonneville Reservoir, estimates of annual mortality were higher than those previously reported by Parker et al. (1995); however, estimates were variable and somewhat cyclic. High harvest rates in 1991 and 1994-96 (Friesen and Ward 1997) probably contributed to variations in mortality estimates among the 1982-86 cohorts.

Annual mortality estimates for northern squawfish in John Day Reservoir were considerably higher than those previously reported by Parker et al. (1995) who estimated annual mortality as 18% for females and 46% for males. Our estimates ranged from 32% to 72% for both sexes combined. High harvest rates from 1991 to 1993 followed by a 60% decrease in 1994-96 harvest rates (Friesen and Ward 1997) may explain the observed decrease in annual mortality estimates among more recent cohorts.

We observed no trends in growth of northern squawfish that indicate a density-dependent response to sustained removals. Although density-dependent variation in growth is common in many fish populations (Goodyear 1980), our findings are consistent with Rieman and Beamesderfer (1990) who found no correlation between growth and year-class size of northern squawfish in John Day Reservoir in the 1980's. Because growth rates of fishes are often the most dynamic among biological characteristics (Spangler et al. 1977), their utility in drawing comparisons over such a short period may be limited.

Although our estimates of relative fecundity varied, there was no evidence to suggest that individual northern squawfish reproductive potential has increased in any area. Although compensation in reproduction may be more important to production in exploited populations than compensation in growth and mortality (Cushing and Harris 1973; Gulland 1978), reproductive response of northern squawfish to sustained removals is probably unlikely given their relatively low fecundity compared to known resilient fish populations (Cushing 1971).

We believe that changes in northern squawfish population structure resulting from 5-7 years of sustained exploitation have not resulted in measurable differences in their biological characteristics. Compensatory predation by northern squawfish and other predators in response to northern squawfish removals are other factors that could limit anticipated benefits of the NSMP. However, Zimmerman and Ward (1997) found no evidence of increased consumption of juvenile salmonids by northern squawfish or smallmouth bass *Micropterus dolomieui* concurrent with the implementation of the NSMP. Similarly, Ward and Zimmerman (1997) indicated that

densities of smallmouth bass have also not increased. Continued sustained exploitation of northern squawfish at 1990-1996 levels will probably not result in biological compensation. However, because of uncertainties associated with effects of long-term removal programs on northern squawfish populations, monitoring of population level characteristics should continue as a parallel component of the NSMP.

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

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October 1997

INTRODUCTION

A large-scale management program for northern squawfish *Ptychocheilus oregonensis* was begun in 1990 to increase survival of juvenile salmonids in the Columbia River basin (Parker et al. 1995; Beamesderfer et al. 1996). The program consists of both public and agency-operated fisheries that target northern squawfish ≥250 mm in fork length, approximately the size at which northern squawfish become important predators on juvenile salmonids (Poe et al. 1991). The goal of the program is to sustain annual exploitation of "predator-size" northern squawfish at 10-20%, which may reduce losses of juvenile salmonids by as much as 50% (Rieman and Beamesderfer 1990). Over 1.1 million northern squawfish were removed by this program from 1990-96, with estimates of annual exploitation in the lower Columbia and Snake rivers from 1991-96 averaging 12.1%, and ranging from 8.1% to 15.5% (Friesen and Ward 1997).

Although predation by native northern squawfish has been well documented throughout the lower Columbia River basin (Rieman et al. 1991; Ward et al. 1995), other predators such as introduced smallmouth bass *Micropterus dolomieu* are also present. Smallmouth bass are distributed throughout the lower Columbia and Snake rivers, with densities highest in Snake River reservoirs (Zimmerman and Parker 1995). Estimates of smallmouth bass abundance ranged from under 40% of northern squawfish abundance in John Day Reservoir (Beamesderfer and Rieman 1991) to more than 100% of northern squawfish abundance in Lower Granite Reservoir (Curet 1993). Smallmouth bass were responsible for only 7% of the total predation on juvenile salmonids in John Day Reservoir
(Rieman et al. 1991); however, in some areas and times of year, smallmouth bass may be more important predators than northern squawfish (Tabor et al. 1993).

The effects of large-scale removals of northern squawfish on smallmouth bass are unknown and difficult to predict. If mortality of juvenile salmonids is significantly reduced by sustained removals of northern squawfish, predation by smallmouth bass may be enhanced due to increased availability of juvenile salmonid prey. A change in growth rate might accompany dietary shifts, altering size distributions and abundance. Johnson (1977) and Hayes et al. (1992) found that populations of yellow perch *Perca flavescens* were enhanced by intensive removals of white sucker *Catostomus commersoni*; however, removals were far more intensive (80-85% of adult white suckers), and competition between yellow perch and white sucker was strongly indicated. Although diets of smallmouth bass and northern squawfish overlap (Poe et al 1991; Zimmerman 1997), differences in distribution between the two species may limit competition. Densities of smallmouth bass are generally highest in forebays immediately upstream from dams and in mid-reservoir areas (Zimmerman and Parker 1995), whereas northern squawfish densities are generally highest in tailraces immediately downstream from dams, and lowest in mid-reservoir areas (Ward et al. 1995).

Our objective was to describe the response of smallmouth bass to sustained removals of northern squawfish. We examined smallmouth bass year-class strength, density, consumption of juvenile salmonids, population structure, growth, and mortality over a period of years coinciding with the Northern Squawfish Management Program. Information comparing smallmouth bass

populations before and after sustained removals of northern squawfish will help assess the effectiveness of the removal program in reducing predation on juvenile salmonids.

METHODS

Data Collection and Summary

We sampled from 1990-96 to collect information on smallmouth bass in the lower Columbia and Snake rivers (Figure 1). We sampled each year in the tailrace immediately downstream from Bonneville Dam, and in the forebay (immediately upstream from the dam), mid-reservoir, and tailrace (immediately downstream from the next dam) of Bonneville and John Day reservoirs, except that we did not sample Bonneville Reservoir in 1992. We sampled three reaches of the Columbia River downstream from Bonneville Dam tailrace in 1992, and 1994-96. We sampled the upper reach of Lower Granite Reservoir (there is no dam immediately upstream) in 1991, and 1994-96. Each sampling reach was approximately 6-km long, and was subdivided into 24 near-shore sampling sites of approximately 500 m.

We used boat electrofishing, and sampled 4-8 boat-days in each reach between early April and mid-September to collect smallmouth bass. Sampling was stratified so that efforts in spring (April-June) and summer (July-September) were approximately equal to accommodate differences in water temperature and in species of juvenile salmonids present (Ward et al. 1995). Sampling was scheduled to coincide with dates of peak passage of juvenile salmonids. We sampled at least six randomly selected sites each boat-day between 0300 and 1200 hours. Effort at each site consisted of a 15-min electrofishing run with continuous output of approximately 4 A.

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

In the laboratory, stomach contents were thawed, and weighed to the nearest 0.01 g. To speed processing of samples, we first digested them with a solution of lukewarm tapwater, 2% (wet weight) pancreatin (8x porcine digestive enzyme), and 1% (wet weight) sodium sulfide. The solution was poured into sample bags until contents were submersed, and the bags were sealed and contents mixed to ensure all food was in contact with the solution. Samples were placed in a desiccating oven at 40°C for 24 h. Digested samples were poured through a 425-μm sieve and rinsed with tap water. Diagnostic bones of prey fish were examined under a dissecting microscope and identified to the lowest possible
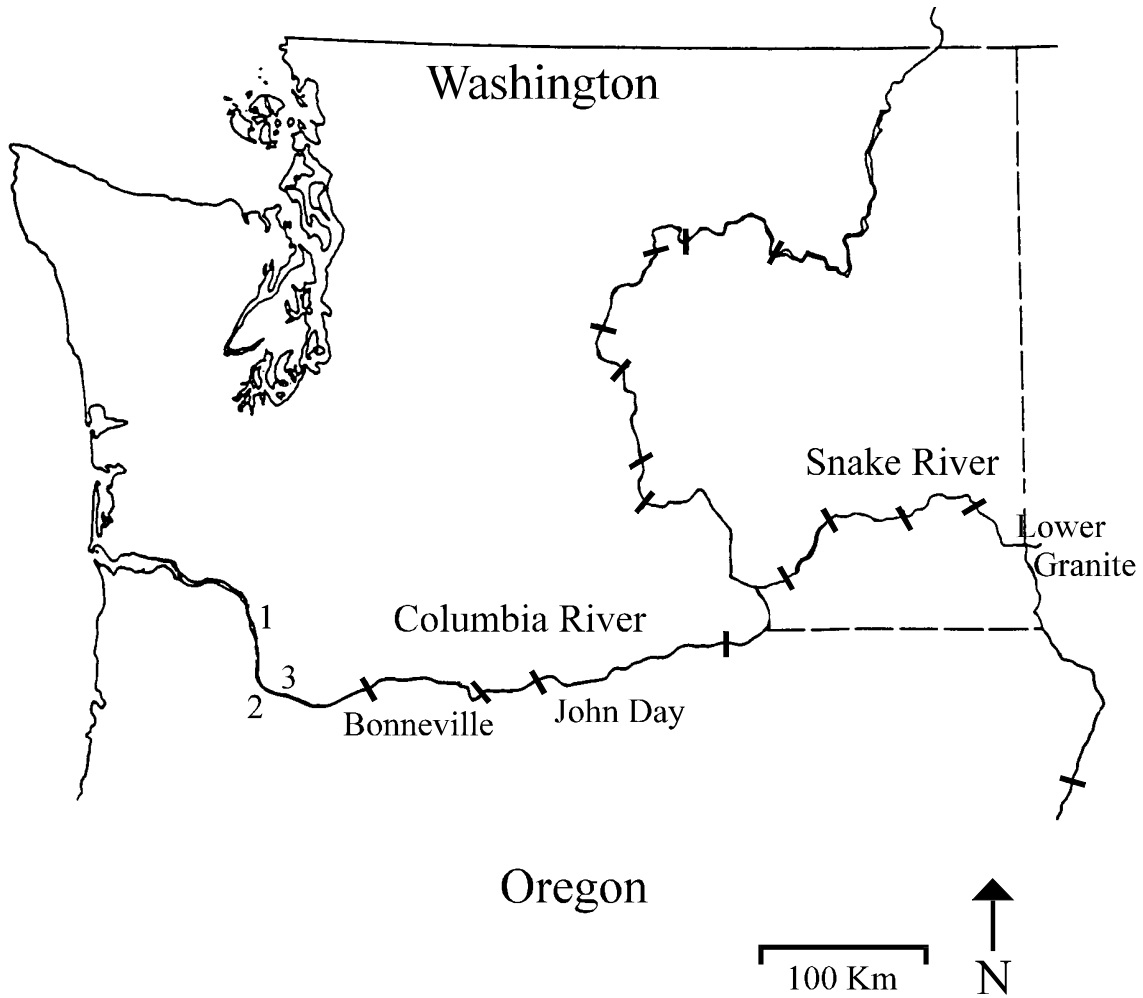
Figure 1. The Columbia and Snake rivers in Oregon and Washington. Reservoirs sampled (and associated dams) are labeled. Reaches sampled downstream from Bonneville Dam tailrace were (1) river kilometer (RKm) 115-121, (2) RKm 172-178, and (3) RKm 190-197.

taxon (Hansel et al. 1988). We enumerated prey fish consumed by adding the number of paired diagnostic bones to remaining unpaired bones.

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

Data Analysis

Although we sampled all reaches in both spring and summer, data were often pooled to achieve adequate sample sizes or to simplify data analyses. We pooled catch and effort data to produce yearly estimates of density for each reach; however, differences in water temperatures between seasons precluded pooling of consumption data. Year-class strength, population structure, growth, and mortality data were pooled to produce yearly estimates for each reservoir and for the Columbia River downstream from Bonneville Dam.

Year-Class Strength

We used the method of El-Zarka (1959) to index relative year-class strength for cohorts of smallmouth bass. The index was developed by comparing the relative abundance of each year class in catches from standardized sampling over a number of years. We used linear regression to determine if changes in the index were correlated with time for each reservoir and downstream from Bonneville Dam.

Density

We used catch per 15-minute electrofishing run (CPUE) as an index of smallmouth bass density for each reach. Beamesderfer and Rieman (1988) found that electrofishing captured the widest size range of smallmouth bass, and Zimmerman and Parker (1995) concluded that electrofishing CPUE was a good indicator of smallmouth bass density. We calculated mean CPUE and 95% confidence intervals for each reach each year, and used analysis of variance (ANOVA; SAS Institute, Inc. 1990) to compare mean catch among years for each reach. Catch was transformed to $\log_{10}(\text{catch} + 1)$ before analysis. We then used the Tukey multiple comparison procedure to determine where differences existed.

Consumption of Juvenile Salmonids

We developed an index to compare consumption of juvenile salmonids by smallmouth bass among years. Our consumption index was analogous to the consumption index for northern squawfish developed by Ward et al. (1995), which was highly correlated with direct estimates of consumption, and was easily obtained so that laboratory effort was minimized.

Rogers and Burley (1990) determined the days to 90% digestion (T90$_i$) for smallmouth bass as

$$T90_i = 24.542 \bullet M_i^{0.29} \bullet e^{-0.15T} \bullet W^{-0.23}.$$

where

M_i = meal size (g) at time of ingestion of salmonid prey item i,
T = water temperature ($^{\circ}$C), and
W = predator weight (g).

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

$$C = 0.0407 \bullet e^{0.15T} \bullet W^{0.23} \bullet \sum_{i=1}^{n} M_i^{-0.29}$$

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

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

We tested how well differences in consumption indices related to differences in direct estimates of consumption rate. Consumption indices and consumption rates were both computed for reaches sampled in 1995 and 1996, and the correlation between the index and the direct estimate was examined.

We used the simple meal turnover-time method of Tabor et al. (1993) to estimate smallmouth bass consumption rate of juvenile salmonids in 1995 and 1996:

$$C = (R \bullet P \bullet W) / SW$$

where

R = daily ration (% body weight/day) ,
P = proportion of diet (by weight) that is salmonid prey, and
SW = mean salmonid prey weight (g) before digestion.

Daily ration (R) was estimated as

$$R = (M \bullet n) / (T90_i \bullet N)$$

where

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

An estimate of original meal weight of fishes was based on lengths of prey fishes. Identity and original fork lengths of prey fishes were determined from diagnostic bones (Hansel et al. 1988), then original weights were estimated from length-weight regressions (Vigg et al. 1991). Original weights of other prey items were estimated by adjusting the observed non-fish weight with the same ratio used for fish weight (Tabor et al. 1993).

We adjusted estimates of consumption rate for diel feeding periodicity. Vigg et al. (1991) found that smallmouth bass consumed 32% of their daily ration during the hours we sampled.

Population Structure

We used proportional stock density (PSD) to compare size structure of smallmouth bass populations among years (PSD= 100 • number of fish of at least quality length/number of fish of at least stock length; Anderson 1980). Stock and quality sizes were defined as 180 mm and 280 mm total length, respectively (Anderson and Gutreuter 1983), where total length = 1.04 • fork length (Carlander 1977). We computed 95% confidence intervals for each PSD estimate (Gustafson 1988), and used a proportion comparison procedure analogous to a chi-square test (Zar 1984) to compare differences among PSDs. We then used a multiple comparisons procedure for proportions analogous to the Tukey test to determine where differences existed.

We used mean relative weight (W_r) to compare fish condition among years (W_r= 100 • weight/W_s; W_s is the length-specific standard weight of smallmouth bass). The standard weight equation defined by Kolander et al. (1993) for smallmouth bass at least 150 mm total length is

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

We computed 95% confidence intervals for each estimate of mean W_r, and used a Kruskal-Wallis test (SAS Institute, Inc. 1990) to compare differences in W_r among years for each reach.

Growth and Mortality

To identify trends in growth, we compared annual growth increments (mm) among years for smallmouth bass aged 2-5. We used scale measurements to estimate total growth during the year preceding capture. Because we collected scales from 1990-96, we were able to estimate growth from 1989-95. We used ANOVA to compare growth among years for each age, and used the Tukey test to determine where differences existed.

To evaluate total instantaneous mortality and annual mortality rates, we used relative catch (corrected for sampling effort) of individual year classes over a number of years to produce year-class-specific catch curves (Ricker 1975). We tested the descending limb of the catch curves (estimates of total instantaneous mortality) for homogeneity of slopes to determine if mortality differed among years.

RESULTS

Year-Class Strength

Year-class strengths of smallmouth bass were highly variable (Figure 2). Variations with year were generally similar among reservoirs; therefore, the pattern of variation did not appear to be strictly random. Generally strong year classes from 1990-92 were followed by a relatively weak year class in 1993. We found little correlation between year-class strength and time for the Columbia River downstream from Bonneville Dam ($r^2 = 0.25$), Bonneville Reservoir ($r^2 = 0.21$), John Day Reservoir ($r^2 = 0.19$), or Lower Granite Reservoir ($r^2 = 0.12$).

Density

Catch rate of smallmouth bass varied considerably among reaches and years (Figure 3), with catch generally highest in John Day and Lower Granite reservoirs. Although CPUE differed among years for a majority of reaches, we found no evidence of an increase in CPUE over time at any of the reaches sampled. Catch rate decreased from 1995 to 1996 in most reaches. Catch rate consistently decreased in Lower Granite Reservoir.

Consumption of Juvenile Salmonids

Our proposed consumption index for smallmouth bass,

$$CI = 0.0407 \bullet e^{0.15T} \bullet W^{0.23} \bullet (S \bullet GW^{-0.29}),$$

was linearly related to, and highly correlated with direct estimates of consumption rate (Figure 4). When the largest CI was excluded from the data, the correlation remained very high. We therefore used this index to evaluate consumption of juvenile salmonids by smallmouth bass.

Consumption of juvenile salmonids was highly variable among reaches and seasons, but was generally low (Figures 5 and 6), even though sampling was scheduled to coincide with peak abundance of juvenile salmonids. The CI was zero for 74 of 104 estimates, including 22 of 39 with relatively large sample sizes (at least 30 smallmouth bass
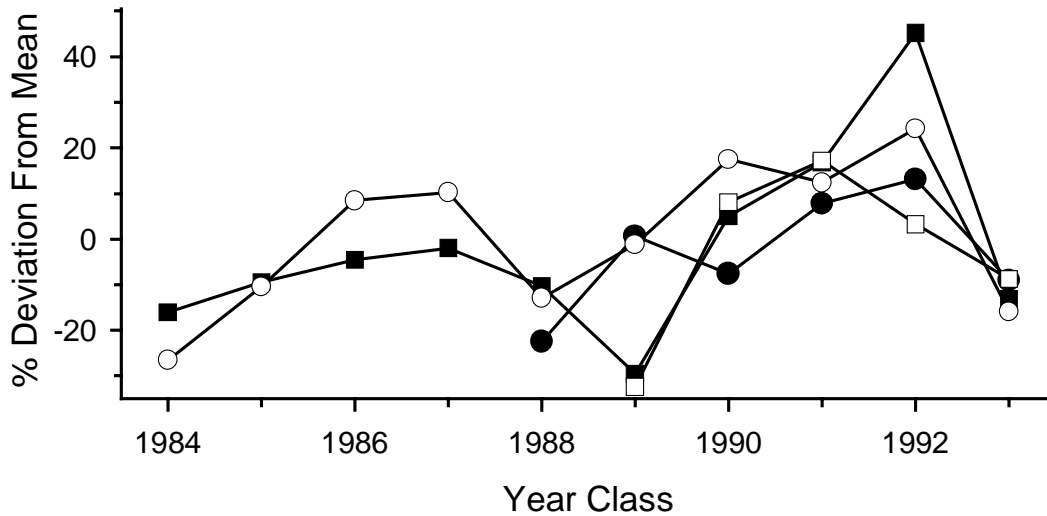
Figure 2. Indexes of relative year-class strength for smallmouth bass downstream from Bonneville Dam (●) and in Bonneville (■), John Day (○), and Lower Granite (□) reservoirs.

examined). Although consumption indices for spring were especially low, we found consistent evidence of predation on juvenile salmonids in Lower Granite Reservoir, and to a lesser extent in the forebay of John Day Reservoir. In summer, consumption was usually highest in the forebay of John Day Reservoir, and was also evident in the reach from RKm 190-197, downstream from Bonneville Dam. Most juvenile salmonids had migrated from Lower Granite Reservoir prior to our summer sampling. We found no trend of increasing consumption by smallmouth bass over time.

Population Structure

Proportional stock density of smallmouth bass varied among reservoirs (Figure 7), but was generally higher in the Columbia River than in the Snake River. Proportional stock density also varied among years for each reservoir and the Columbia River downstream from Bonneville Dam. Although PSD was relatively high in Bonneville and John Day reservoirs in 1996, we found no trend of increasing PSD's over time in either reservoir. Smallmouth bass PSD did appear to increase over time in Lower Granite Reservoir.

Mean W_r of smallmouth bass also varied among years, (Figure 7), but was usually highest in Bonneville Reservoir or in the Columbia River downstream from Bonneville
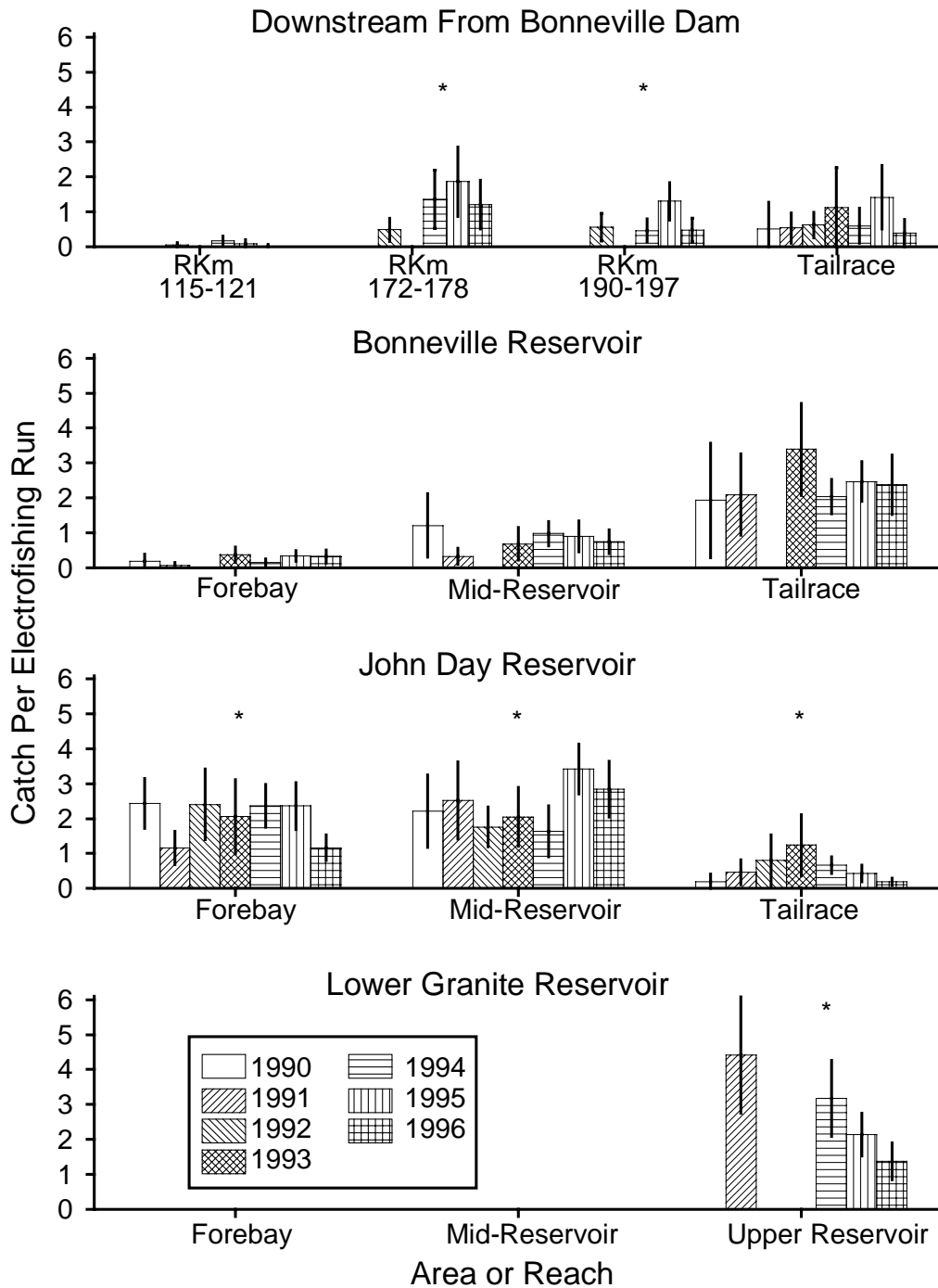
Figure 3. Relative density of smallmouth bass 200 mm fork length and larger in the lower Columbia and Snake rivers, 1990-96, as determined by catch per 15-minute electrofishing run. Vertical bars represent 95% confidence intervals. Asterisks indicate significant differences ($P<0.05$) among years. RKm = river kilometer.
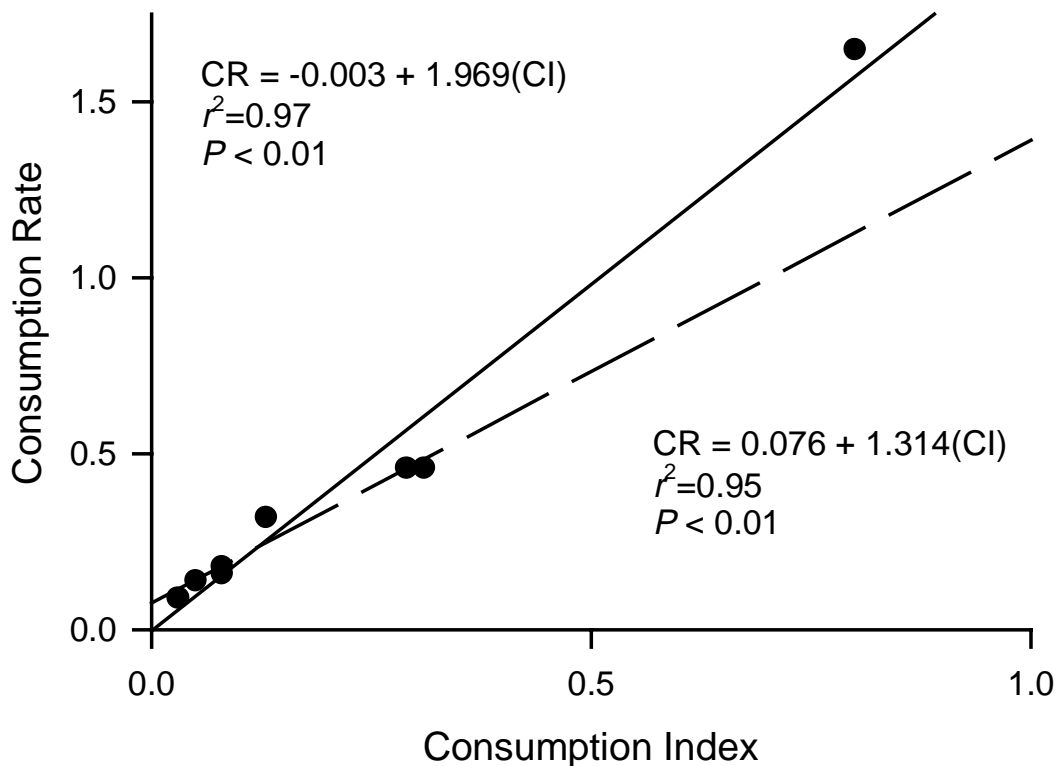
Figure 4. Relationship between proposed consumption index for smallmouth bass (CI) and direct estimate of consumption rate (CR); CR = number of juvenile salmonids per smallmouth bass per day. Dashed line indicates relationship when highest CI is excluded.

Dam. Relative weight remained relatively stable from 1990-93, but decreased from 1994 to 1996 in all areas.

Growth and Mortality

Annual growth of smallmouth bass varied among years for all ages in most areas (Figure 8); however, no temporal trends were evident. Growth in 1995 was similar to or less than growth in preceding years. Growth was generally greater in 1990, 1992, and 1994 than in other years.

Estimates of annual mortality of smallmouth bass varied among reservoirs, but consistently exceeded 50% (Table 1). Mortality did not decrease concurrent with removals of northern squawfish. We found no significant differences in slopes of the descending
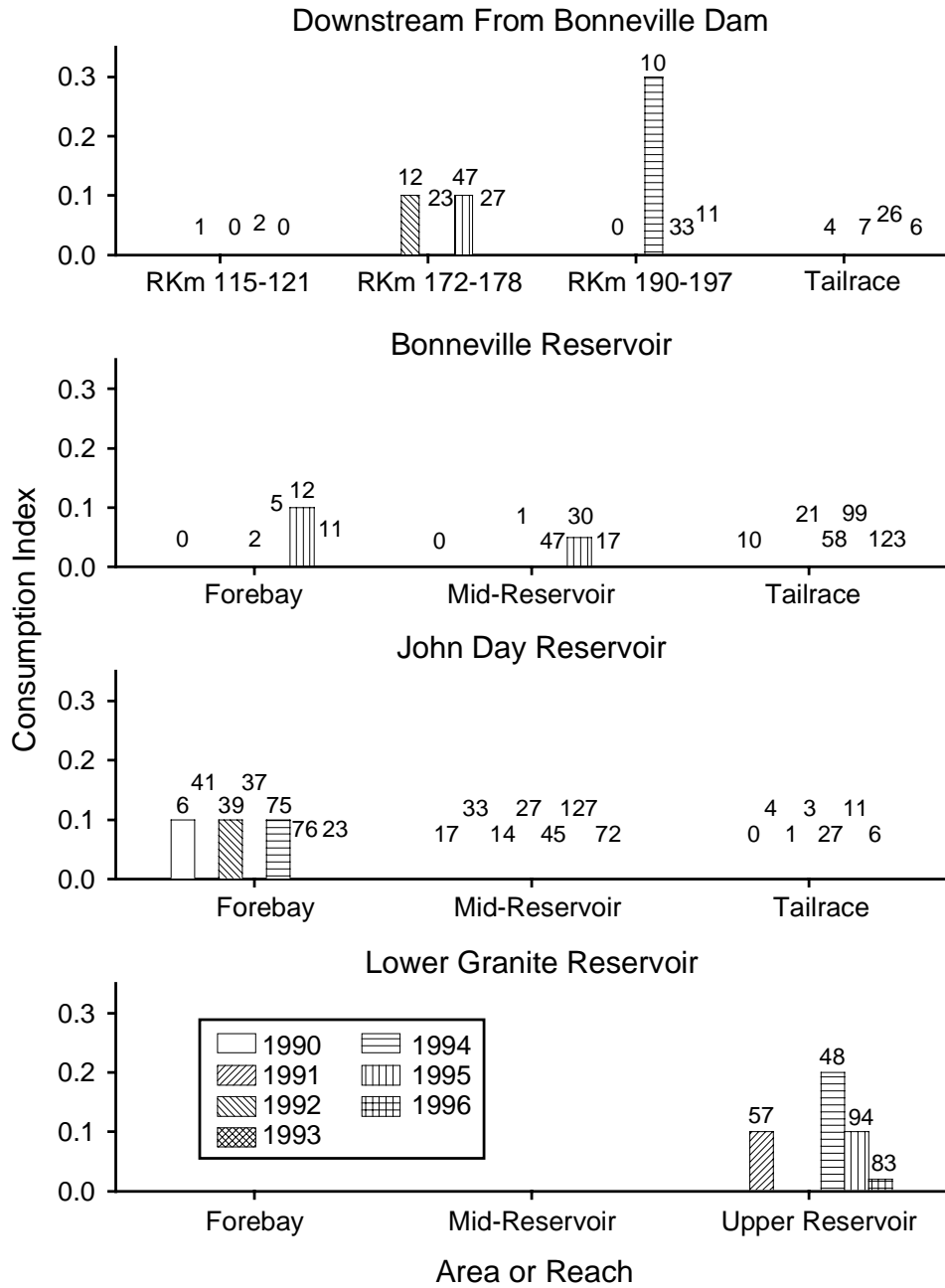
Figure 5. Consumption index values for smallmouth bass in the lower Columbia and Snake rivers, spring 1990-96. Number of fish examined is shown above each bar. Data were collected downstream from Bonneville Dam in 1992 and 1994-96, in Bonneville Reservoir in 1990 and 1993-96, in John Day Reservoir from 1990-96, and in Lower Granite Reservoir in 1991 and 1994-96. RKm = river kilometer.

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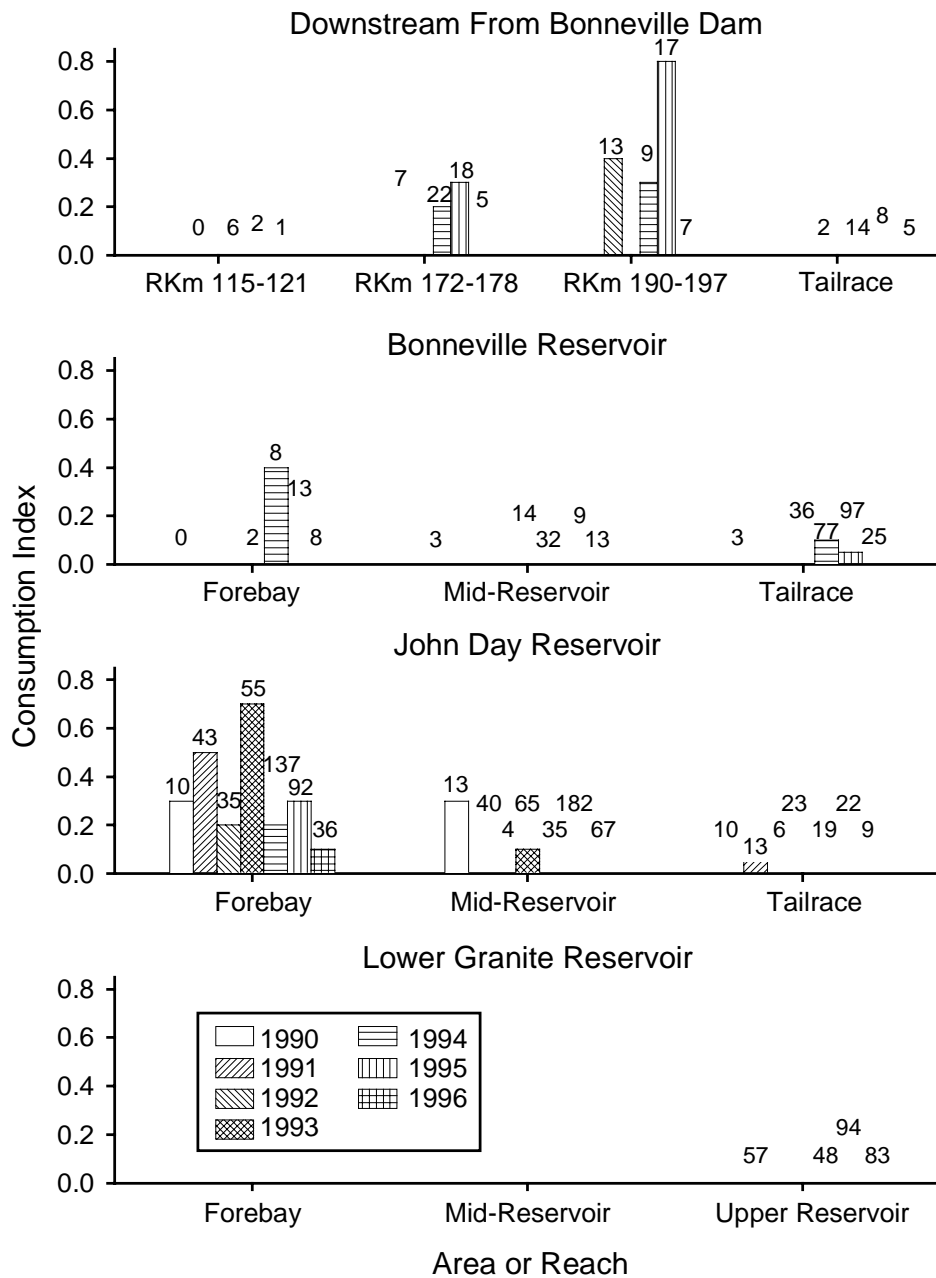
Figure 6. Consumption index values for smallmouth bass in the lower Columbia and Snake rivers, summer 1990-96. Number of fish examined is shown above each bar. Data were collected downstream from Bonneville Dam in 1992 and 1994-96, in Bonneville Reservoir in 1990 and 1993-96, in John Day Reservoir from 1990-96, and in Lower Granite Reservoir in 1991 and 1994-96. RKm = river kilometer.
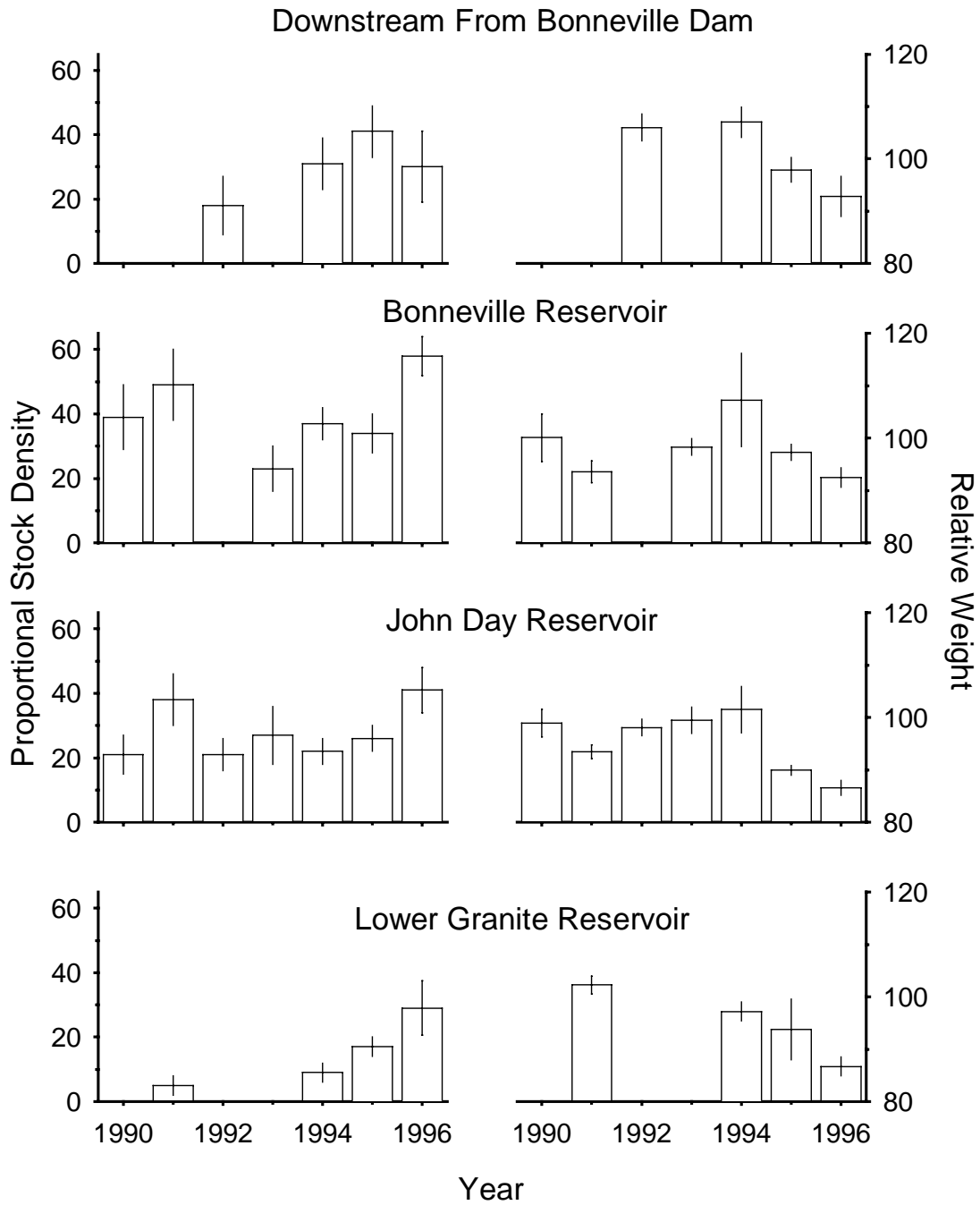
Figure 7. Proportional stock density (PSD) and mean relative weight (W_r) of smallmouth bass in the lower Columbia and Snake rivers 1990-96. Vertical bars represent 95% confidence intervals. Differences among years were significant ($P<0.05$) for both PSD and W_r for all reservoirs.
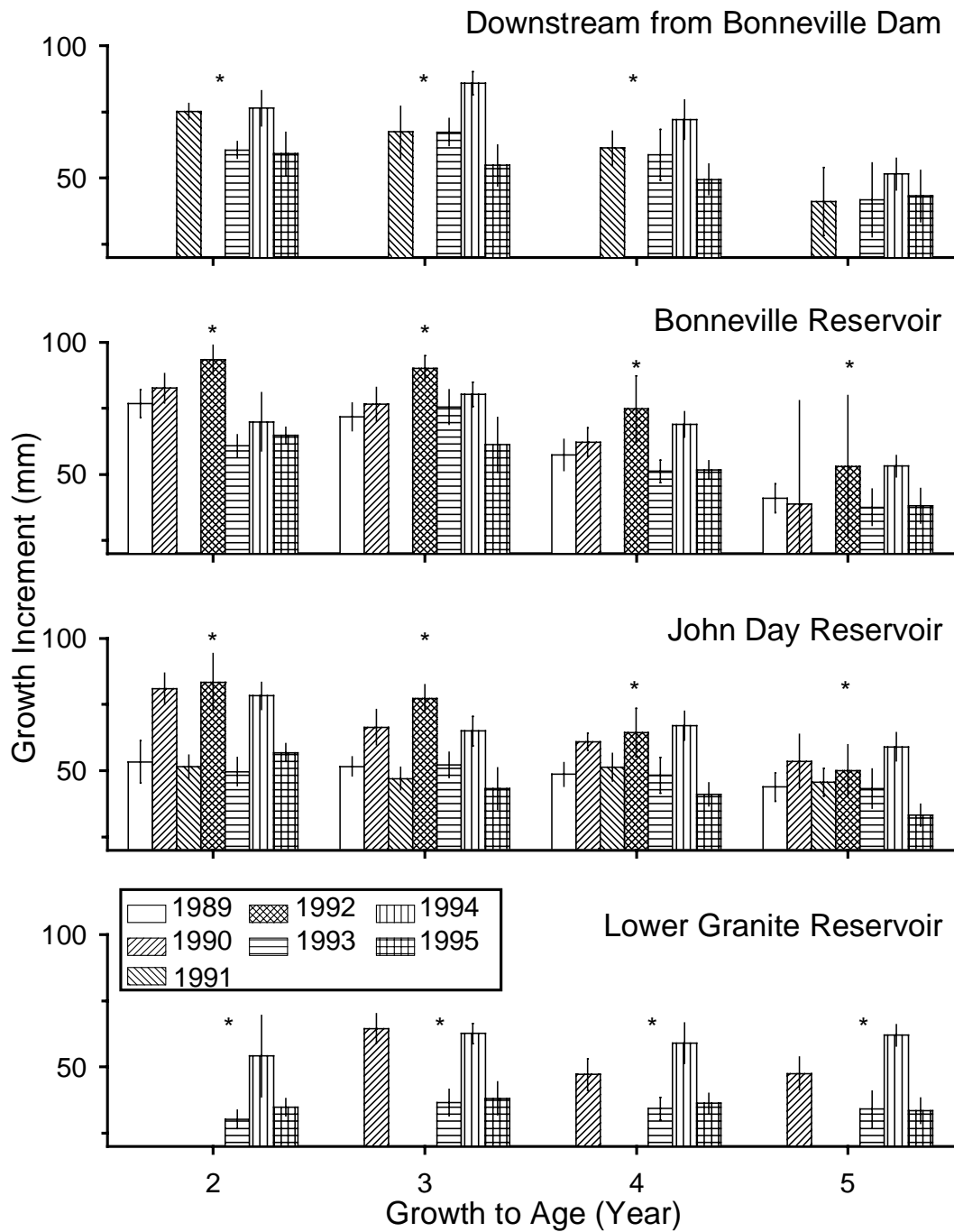
Figure 8. Annual growth increments (and 95% confidence intervals) for smallmouth bass aged 2-5 in the lower Columbia and Snake rivers, 1989-95. Vertical bars represent 95% confidence intervals. Asterisks indicate significant differences ($P<0.05$) among years.

Table 1. Age-specific catch and estimates of total instantaneous mortality (Z) and annual mortality rate (A) for individual year classes of smallmouth bass in the lower Columbia and Snake rivers. Catches at age for each year-class are corrected for differences in effort among years.

| Area, year(s) sampled	Year class	Catch at age				Mortality	
		3	4	5	6	Z	A
Downstream from Bonneville Dam							
1992, 1994-95	1989	61		10	7	0.75	0.53
1994-96	1990		26	15	1	1.63	0.80
1994-96	1991	52	43	5		1.17	0.69
Bonneville Reservoir							
1990-91, 1993	1987	60	26		5	0.83	0.56
1991, 1993-94	1988	83		25	9	0.72	0.51
1993-95	1989		87	23	10	1.08	0.66
1993-96	1990	208	74	25	10	1.02	0.64
1994-96	1991	118	88	35		0.61	0.46
John Day Reservoir							
1990-92	1986		63	31	9	0.97	0.62
1990-93	1987	136	67	26	13	0.80	0.55
1991-94	1988	144	138	49	13	0.82	0.56
1992-95	1989	333	155	51	22	0.93	0.60
1993-96	1990	225	160	69	19	0.83	0.56
1994-96	1991	280	188	56		0.80	0.55
Lower Granite Reservoir							
1994-96	1990		153	36	10	1.36	0.74
1994-96	1991	272	91	23		1.24	0.71

limbs of catch curves (estimates of total instantaneous mortality) for the Columbia River downstream from Bonneville Dam ($P = 0.35$), Bonneville Reservoir ($P = 0.07$), John Day Reservoir ($P = 0.96$), or Lower Granite Reservoir ($P = 0.91$).

DISCUSSION

We found no evidence of smallmouth bass response to sustained removals of northern squawfish. No trends in smallmouth bass year-class strength, density, consumption of juvenile salmonids, population structure (except PSD in Lower Granite Reservoir), growth, or mortality have been realized concurrent with sustained removals of northern squawfish. An ideal study would have included comparisons to an area not subject to removals of northern squawfish; however, northern squawfish management included the entire lower Columbia and Snake rivers (Friesen and Ward 1997), precluding the possibility of an appropriate control area. Confidence in our results is enhanced by the long time series of data available for most areas, and by comparing our results to those from previous studies in the lower Columbia River basin.

The first evidence of any response by smallmouth bass would likely be changes in diet, which could then lead to changes in growth (Johnson 1977; Hayes et al. 1992). Although the exploitation rate of northern squawfish in John Day Reservoir averaged about 12% annually from 1990-93 (Friesen and Ward 1997), Zimmerman (1997) found that the diet of smallmouth bass remained similar to that prior to northern squawfish removals (Poe et al. 1991). Sculpins *Cottus* spp. remained the most common fish in the diet, and crustaceans (primarily crayfish *Pasifisticus* spp.) remained the most common non-fish prey item. Consumption of juvenile salmonids has remained low, as originally reported by Vigg et al. (1991). Because our sampling was timed to coincide with peak abundance of juvenile salmonids, overall consumption of juvenile salmonids by smallmouth bass is probably even lower than our results indicate.

Of the population characteristics we examined, size structure may be the most likely to exhibit measurable change within the period studied. Small changes in growth, survival, and recruitment may all contribute to, and therefore be more apparent as changes in size structure. After a single-year removal of 80% of a white sucker population, Hayes et al. (1992) reported small changes in size structure of yellow perch for three years, and a much larger change in the fourth year. Although annual exploitation rates of northern squawfish were much lower, removals have been sustained for six years in most areas (seven years in John Day Reservoir), with little evidence of changing size structure of smallmouth bass. However, of the areas we sampled, exploitation of northern squawfish has been highest in Lower Granite Reservoir (Friesen and Ward 1997), where smallmouth bass PSD has consistently increased.

Analyses of PSD are complicated by variations in year-class strength because the presence or absence of strong year classes influences the number of stock-length fish over time. In Bonneville, John Day, and Lower Granite reservoirs, fish from relatively strong year classes from 1990-92 grew to stock length from 1993-95, which resulted in relatively low PSDs. The increase in PSDs seen in 1996 probably resulted from growth of these fish to quality size, combined with a relatively weak 1993 year class. Proportional stock density changed little from

1994-96 downstream from Bonneville Dam, where differences in year-class strengths from 1990-93 were small compared to other areas.

Mortality estimates from standard catch curves are also subject to uncertainty because of variations in year-class strengths. Reliability of our mortality estimates is enhanced, however, by our use of catch curves constructed from the relative catch of individual year classes over a number of years. Our estimates of total annual mortality for John Day Reservoir were similar to estimates made prior to removals of northern squawfish (Connolly and Rieman 1988; Beamesderfer and Ward 1994).

Although we found no evidence of changes in the annual mortality rate of smallmouth bass, we did not calculate separate estimates for fishing mortality and natural mortality. Decreases in natural mortality, a potential response to removals of northern squawfish, may be masked by increases in fishing mortality. Sizable increases in fishing mortality from 1993-95 were unlikely, however, because changes in annual effort by smallmouth bass anglers in Columbia River reservoirs were minimal (Washington Department of Fish and Wildlife, unpublished data). Beamesderfer and Ward (1994) found that 72-96% of the total annual mortality of smallmouth bass in John Day Reservoir was attributable to fishing, leaving little chance for large changes in natural mortality in response to removals of northern squawfish.

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

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Biological Characteristics of Walleye in Relation to Sustained Removals of Northern Squawfish
in the Columbia River

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INTRODUCTION

Though the method of their establishment is not entirely clear, walleye *Stizostedion vitreum* were introduced into the Columbia River in the mid-1900s (Brege 1981; Maule and Horton 1984). Regardless of origin, walleye now occur throughout the lower Columbia River basin and support a major sport fishery (Tinus and Beamesderfer 1994). Information concerning the biology of walleye in the Columbia River is limited, despite their importance as a game fish.

Much of the existing information on Columbia River walleye addresses their role as predators. Rieman et al. (1991) estimated that walleye accounted for 13% (351,000) of the annual loss of juvenile salmonids to predation in John Day Reservoir, Columbia River. During emigration periods of juvenile salmonids in John Day Reservoir, approximately 14% of the diet of walleye consists of juvenile salmon *Oncorhynchus* spp. and steelhead *O. mykiss* (Poe et al. 1991). However, walleye are far less abundant in the Columbia River than other major predators of juvenile salmonids, including northern squawfish *Ptychocheilus oregonensis*, smallmouth bass *Micropterus dolomieu*, and channel catfish *Ictalurus punctatus* (Beamesderfer and Rieman 1991; Zimmerman and Parker 1995).

The introduction, reduction or elimination of competing species may alter walleye populations significantly. Johnson (1977) reported an increase in the number of walleye when 85% of the standing stock of white sucker *Catostomus commersoni* were removed from a Minnesota lake. Johnson and Hale (1977) noted a significant decrease in walleye numbers when smallmouth bass were introduced to several lakes with established walleye populations. In the Columbia River, a large-scale program has been implemented to reduce predation on juvenile salmonids by removing large northern squawfish. From 1990 through 1996, approximately 1.1 million northern squawfish ≥ 250 mm were removed by the Northern Squawfish Management Program (NSMP), at an annual exploitation rate ranging from 8-16% (Friesen and Ward 1997). How the implementation of this program affects walleye populations is unknown. If walleye respond biologically to sustained exploitation of northern squawfish, benefits of the NSMP to juvenile salmonids may be reduced (Beamesderfer et al. 1996).

Our objective is to describe trends in year-class strength, abundance, population structure, growth, and mortality of walleye in the lower Columbia River from 1992-96, the period of full implementation of northern squawfish fisheries. We explore whether observed changes in walleye populations can be attributed to the sustained removal of large northern squawfish, and address the implications of these changes to the NSMP.

METHODS

Data Collection and Summary

We sampled from 1992-96 to collect information on walleye in the lower Columbia River (Figure 1). We sampled each year in Bonneville, The Dalles, and John Day reservoirs, and in the tailrace downstream from Bonneville Dam. In Bonneville and John Day reservoirs, sampling was equally distributed among forebay (immediately upstream from the dam), mid-reservoir, and tailrace (immediately downstream from the dam) areas. Sampling in The Dalles Reservoir was limited to the forebay. Sampling dates varied among years, but generally occurred between March 1 and August 31.

We used boat electrofishing to collect walleye. Effort consisted of 15-minute nearshore electrofishing runs with a continuous output of 3-5 A. Sampling was generally conducted from 1800 hours to 0100 hours (March-April) or 0200 hours to 1100 hours (May-August). We recorded fork length (mm) and obtained scale samples from all walleye collected. We also weighed (g) a subsample of walleye collected.

Because sample sizes from individual reservoirs and areas within reservoirs (forebay, mid-reservoir, tailrace) were generally small, we pooled data to provide information for the lower Columbia River. Supplemental catch data for 1992 and 1993 was provided by the U. S. Geological Service, Biological Resources Division (USGS), and additional scale samples were provided by Oregon Department of Fish and Wildlife (ODFW) sport fishery sampling.

We used standard methods (Jearld 1983) to determine ages of walleye from scales. We grouped scale samples by 20 mm size classes and aged a maximum of ten randomly selected scales per size class.

Data Analysis

Year-Class Strength

We used the method of El-Zarka (1959) to index relative year-class strength for cohorts of walleye. The index was developed by comparing the relative abundance of each year class in catches from standardized sampling over a number of years. We then evaluated the correlation between year-class strength and river flow, water temperature, length at age 1, and year-class strength from one year previous, all of which may be important influences on walleye year-class strength in the Columbia River (Connolly and Rieman 1988).

Density

Catch per unit of effort (CPUE) was found to be a reliable index of density for other large piscivores in the Columbia River basin, including northern squawfish (Ward et al.
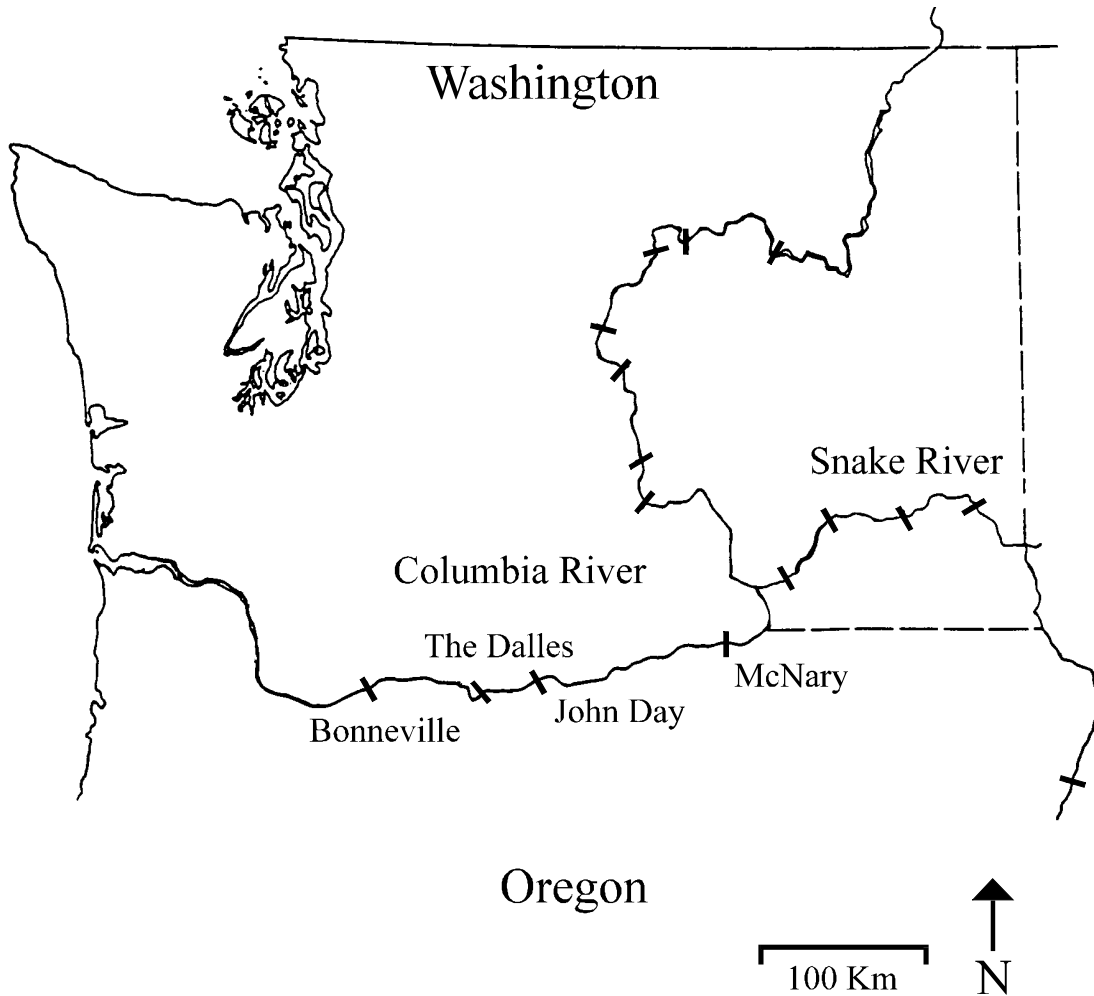
Figure 1. Lower Columbia River basin, with dams (and corresponding reservoirs) of the lower Columbia River labeled. Electrofishing was conducted throughout Bonneville and John Day reservoirs, in the forebay of The Dalles Reservoir, and in the tailrace downstream from Bonneville Dam.

1995), smallmouth bass, and channel catfish (Zimmerman and Parker 1995). We therefore used catch per 15-minute electrofishing run as an indicator of annual walleye density in the lower Columbia River. We calculated mean CPUE and 95% confidence intervals (Zar 1984) for each year, and used analysis of variance (ANOVA; SAS Institute, Inc. 1990) to compare differences in mean CPUE among years. We then used the Tukey multiple comparison test to determine where differences existed.

Population Structure

As size may be an important indicator of other changes within a population, we compared length frequencies for walleye collected from 1992-96. We calculated mean annual fork length and visually identified trends in length frequencies among years. We also used proportional

stock density (PSD; Anderson 1980) to compare size structure of walleye populations among years, where PSD = 100•(number of fish at least quality length / number of fish at least stock length). Stock and quality sizes were defined as 250 mm and 380 mm total length, respectively (Anderson and Gutreuter 1983), where total length (TL) = 0.236 + 1.060•fork length (Murphy et al. 1990). We calculated 95% confidence intervals for annual estimates of PSD (Fleiss 1981; Gustafson 1988), and used a proportion comparison procedure analogous to a chi-square test (Zar 1984) to compare differences among PSDs. We then used a multiple comparisons procedure for proportions analogous to the Tukey test to determine where differences existed.

We calculated relative weight (W_r) to provide an index of condition for walleye in the Columbia River. Relative weight is $W_r = 100 \bullet W/W_s$, where W is the weight of an individual fish and W_s is a length-specific standard-weight value for the species (Wege and Anderson 1978). We used the standard-weight equation for walleye developed by Murphy et al. (1990):
$$\log_{10}W_s(g) = -5.453 + 3.180 \log_{10}TL \text{ (mm)}.$$

We determined mean W_r and 95% confidence intervals for each year from 1992-96, and used a Kruskal-Wallis test (SAS Institute, Inc. 1990) to compare differences in W_r among years.

Growth and Mortality

To identify trends in growth, we compared annual growth increments (mm) among years for walleye aged 2-7. For each age, we used scale measurements to estimate total growth during the preceding year. Because we collected walleye scales from 1992-96, we were able to estimate growth for 1991-95. We used ANOVA to compare growth among years separately for each age, and used the Tukey test to determine where differences existed.

We used catch curves (Ricker 1975) to evaluate trends in mortality for Columbia River walleye. We tested the descending limb of the catch curves (estimates of total instantaneous mortality) for homogeneity of slopes.

RESULTS

Year-Class Strength

Year-class strengths of walleye were highly variable (Table 1). Relatively strong year classes in 1986 and 1987 were followed by relatively weak year classes from 1988 through 1990. Year-class strength rebounded in 1991 and 1992, but was again relatively weak in 1993. We found no indication that year-class strength was increasing with time.

Table 1. Indexes of relative year-class strength for walleye in the lower Columbia River, and corresponding values for environmental and population variables. Year-class strengths were standardized to a mean of 0.0. r = Pearson correlation coefficient for year-class strength and the applicable environmental or population variable.

Year Class	Relative year-class strength	Mean river flow (kcfs; January-December)	Mean water temperature ($^{\circ}$C; June-August)	Fork length (mm) at age 1	Strength of previous year class
1986	52.8	186.5	19.7	242	--
1987	24.0	144.4	19.3	230	52.8
1988	-16.9	140.0	19.2	243	24.0
1989	-41.1	157.1	19.3	221	-16.9
1990	-43.0	182.4	19.3	226	-41.1
1991	3.9	192.4	18.9	218	-43.0
1992	41.7	138.5	20.6	221	3.9
1993	-21.4	152.8	18.7	220	41.7
r	--	-0.02	0.62	0.29	0.35

We found little correlation between year-class strength and environmental or population variables (Table 1). The strongest correlation was with water temperature during the summer months. Mean daily river flow had little effect on year-class strength. Relative year-class strength was also not strongly correlated with the strength of the previous year class.

Density

Catch and effort varied widely among years. Catch ranged from 45 walleye in 1992 to 146 walleye in 1996; effort ranged from 515 electrofishing runs in 1993 to 884 electrofishing runs in 1994. Catch per electrofishing run decreased from 1992 to 1993, then increased every year through 1996 (Figure 2). Although CPUE increased each year after 1993, mean CPUE was not significantly higher in 1994 and 1995 than in 1992. CPUE also did not differ significantly from 1994-96.

Population Structure

Mean fork length of walleye captured by electrofishing varied considerably among years, ranging from 335 mm in 1993 to 540 mm in 1992 (Figure 3). Mean fork length followed the same trend as CPUE, increasing every year from 1993 to 1996. The greatest proportion of the catch was comprised of 200-249 mm individuals in 1993 and increasingly larger individuals in 1994 (350-374 mm) and 1995 (450-474 mm).
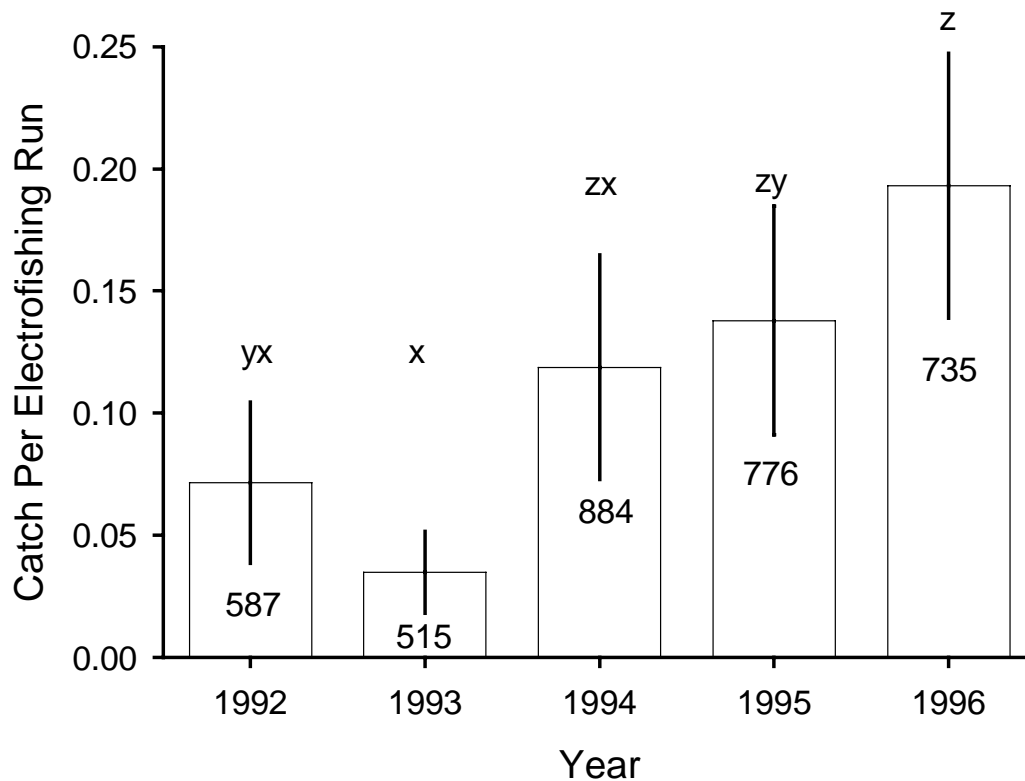
Figure 2. Walleye catch per electrofishing run (CPUE) and 95% confidence intervals for the lower Columbia River, 1992-96. Number of electrofishing runs shown within each bar. CPUE was not significantly different for years with the same letter.

Proportional stock density ranged from 45% in 1993 to 98% in 1992 (Figure 4), and increased considerably from 1993-96. We found no difference between estimates for 1992 and 1996, or for 1994 and 1995. Differences among other years were significant ($P<0.05$).

Mean W_r of walleye in the Columbia River from 1992-96 was 90% and ranged from 86% in 1992 and 1993 to 95% in 1994 (Figure 4). Relative weight differed significantly among years ($P<0.01$) ; however, we found no trend of increased W_r with time.

Growth and Mortality

Annual growth of walleye varied among years for most ages (Figure 5); however, no temporal trends were evident. Growth in 1995 was similar to or less than growth in
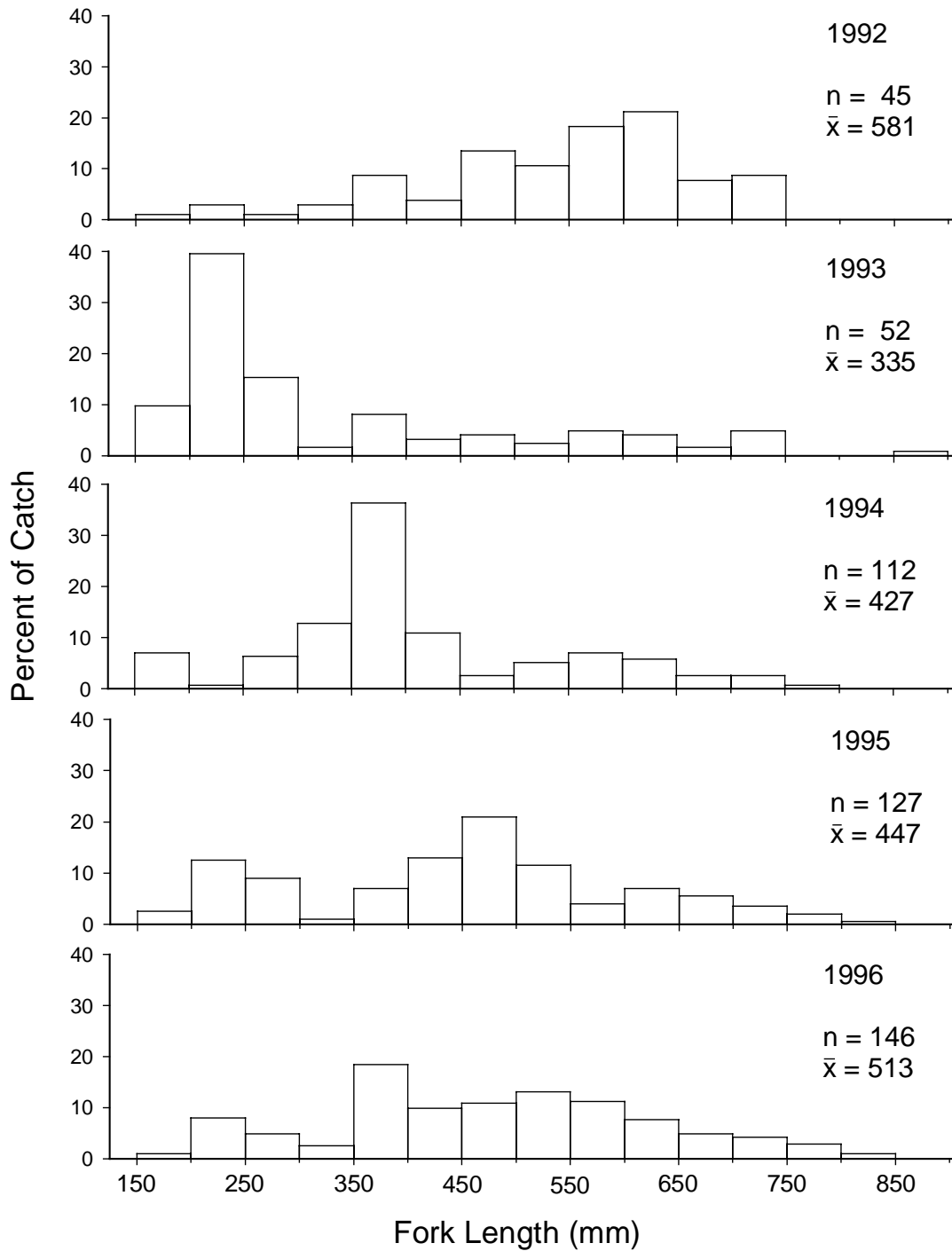
Figure 3. Length frequencies, sample size, and mean fork length of walleye collected from the lower Columbia River, 1992-96.
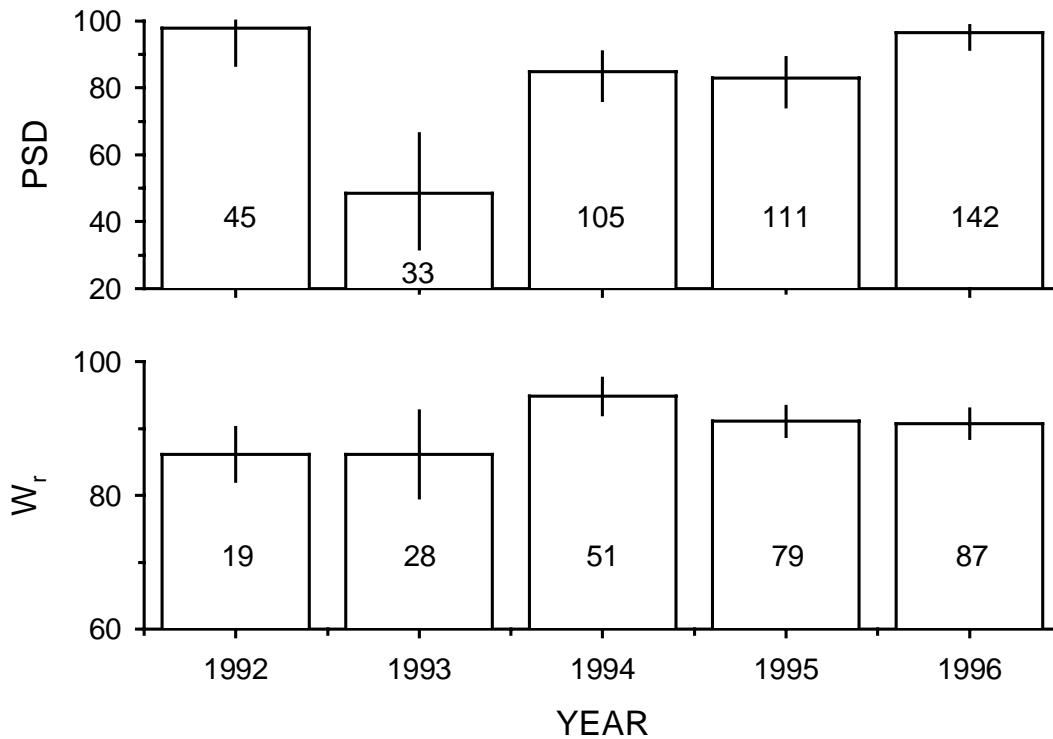
Figure 4. Proportional stock density (PSD) and mean relative weight (W_r) of walleye collected from the lower Columbia River, 1992-96, with 95% confidence intervals. Sample size shown within each bar.

preceding years for fish aged 2-5. Growth of older fish appeared to increase in 1995; however, differences among years were generally not significant.

Walleye appeared to be fully recruited at age 4; we therefore based estimates of mortality on regression parameters for age 4 to age 8 fish (Figure 6). Total annual mortality averaged 38%, with little variation apparent among years (range 32-42%) We found no differences among years in estimates of total instantaneous mortality (slopes of catch curves; *P*=0.44).

Figure 5. Annual growth increments (and 95% confidence intervals) for walleye aged 2-7 years in the lower Columbia river, 1991-95. For each age, years with the same letter are not significantly different (P > 0.05).

DISCUSSION

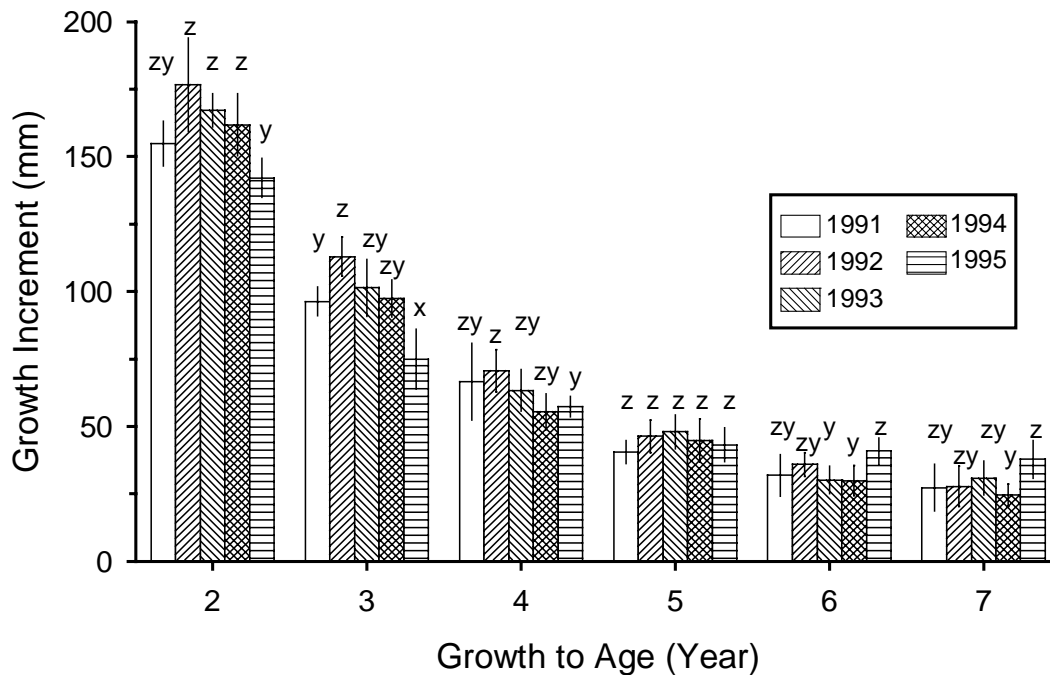Although we found an apparent trend of increased density of walleye in the lower Columbia River, it is unlikely that this trend is in response to sustained removals of northern squawfish. The observed increase in CPUE from 1993-96 appears to be driven by variations in year-class strength. Catch of walleye was low in 1992 as year-class strengths from 1988 to 1991 were relatively weak; this is evident by the large mean fork length of walleye collected in 1992. Though some fish from the strong 1992 year class were captured in 1993 (driving mean fork length down), catch remained low because these fish were not fully recruited to the sampling gear. In 1994 and 1995, CPUE increased as walleye from 1992 became more fully recruited to the gear; this is also evident in the observed increase in mean fork length. By 1996, walleye from the 1992 year class were fully recruited to the sampling gear and subsequent year classes were becoming vulnerable, resulting in high catch rates.
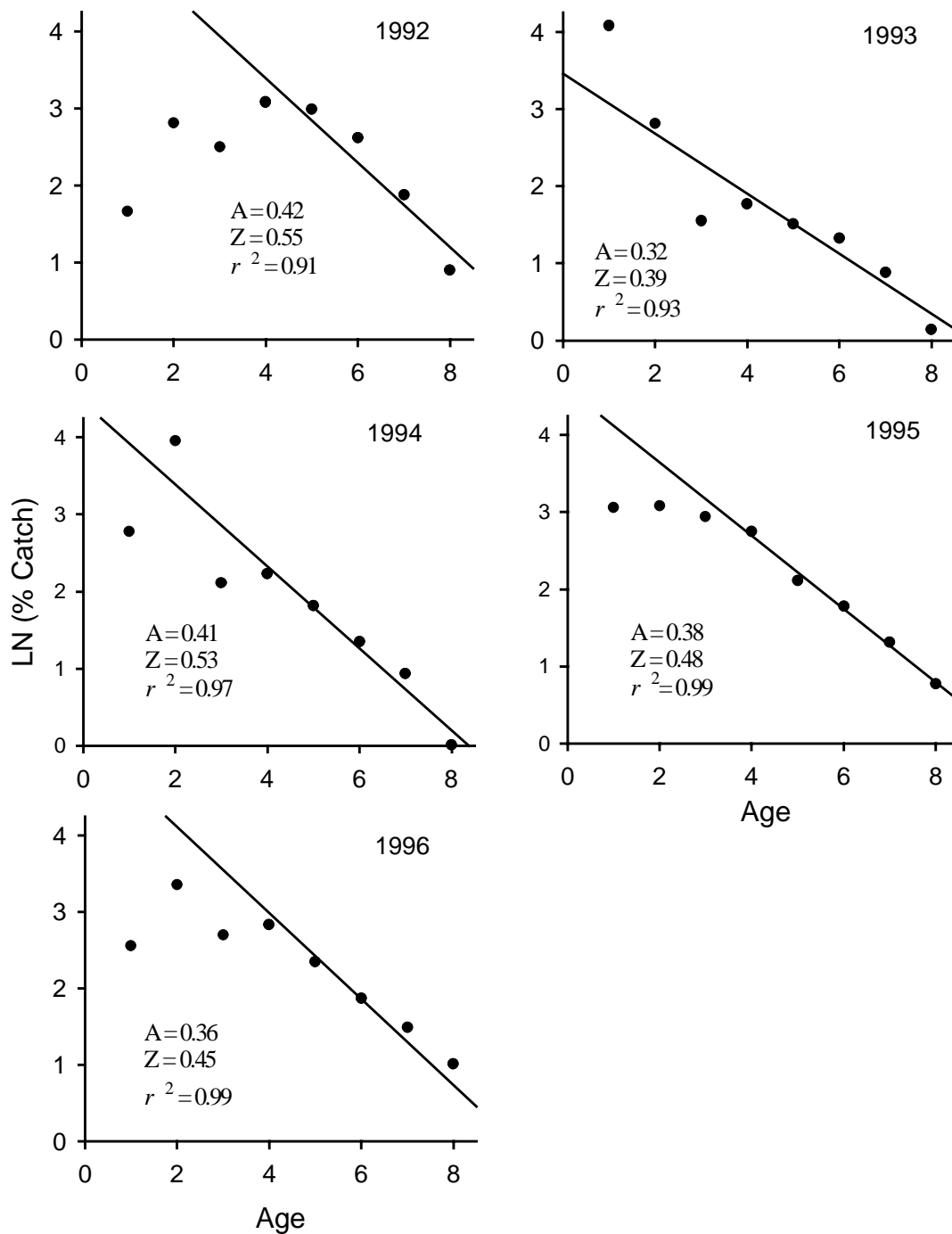
Figure 6. Catch curves for Columbia River walleye, 1992-96. Total instantaneous mortality (Z), and annual mortality rate (A) were calculated for ages 4 through 8.

Large fluctuations in walleye abundance such as these are not unprecedented in the Columbia River. Beamesderfer and Rieman (1991) found that the abundance of walleye ≥ 250 mm fork length increased 41% over one-year in John Day Reservoir. Tinus and Beamesderfer (1994) suggested that the population of walleye longer than 250 mm fork length in John Day Reservoir had doubled between 1986 and 1989.

Although we were unable to discern any mechanisms driving year-class strength of walleye, our estimates of relative year-class strengths are supported by independent data. Increased CPUE by sport anglers in John Day Reservoir from 1986 to 1989 (Tinus and Beamesderfer 1994) supports our finding of strong 1986 and 1987 year classes. Tinus and Beamesderfer (1994) also found that the majority of walleye sampled from sport and set-net fisheries in Bonneville and The Dalles reservoirs in 1990 and 1991 were from the 1986 and 1987 year classes. Low catch rates of walleye by sport anglers in 1992 and 1993, followed by higher catch rates in 1994 and 1995 (Washington Department of Fish and Wildlife, unpublished data), supports our finding that the 1989 and 1990 year classes were weak relative to the 1991 and 1992 year classes.

The influence of the 1992 year class is also evident in length frequencies, with dominant peaks occurring at 350-399 mm in 1994 and 450-499 mm in 1995. The strength of the 1992 year class was likely a major factor in the observed increase in mean fork length from 1993-96, though the influence of year classes beyond 1993 and other variables remains uncertain.

We found no evidence that these fluctuations in year-class strengths were related to removals of northern squawfish. Year-class strength was stronger in 1991 and 1992 than from 1988-90, but was relatively weak again in 1993. Year-class strength was highest in 1986, prior to implementation of the NSMP. Rieman and Beamesderfer (1990) also found that walleye year-class strengths in the Columbia River were highly variable, with occasional dominant years. Ward and Zimmerman (1997) found no relationship between year-class strengths of smallmouth bass in the lower Columbia and Snake rivers and removals of northern squawfish.

Analyses of PSD are also complicated by variations in year-class strength because the presence or absence of strong year-classes influences the number of stock-length fish over time. Walleye from the relatively strong 1992 year class grew to stock length during 1993, which resulted in a decrease in PSD from 1992. Increases in PSD from 1994 to 1996 probably resulted from growth of these fish to quality size, combined with a relatively weak 1993 year class.

Relative weight of walleye may have decreased since implementation of the NSMP. Our mean W_r for walleye collected from 1992-96 (90; n=264) is considerably lower than that of Murphy et al. (1990), who reported a mean W_r of 109 for 2,053 walleye collected from John Day Reservoir prior to 1990. Additional data collected by Tinus and Beamesderfer (1994) yielded a mean W_r of 99 for John Day, The Dalles, and Bonneville reservoirs from 1990-91 (n=233). Though walleye from our samples do not approach the ideal W_r of 100, this is not necessarily an indication of poor condition; only 21 of 114 North American walleye populations examined by Murphy et al. (1990) had relative weights ≥ 100.

Like other biological characteristics we examined, growth of walleye from 1992-96 shows variation among years, but no distinct trend over time, indicating a lack of response to sustained northern squawfish removals. Because growth and diet are closely linked, our results are supported by Zimmerman (1997) who found that walleye diet during 1990-93 and 1996 was similar to that prior to sustained northern squawfish exploitation (Poe et al. 1991).

Sustained removals of northern squawfish have not resulted in changes in walleye mortality during 1992-96. Slight variations in total instantaneous mortality and annual mortality rate among years appear to be random and are likely related to differences in year-class strength, fishing mortality, and environmental conditions.

Small sample size limited some of our analyses. Our sample sizes for PSD and W_r in 1992 and 1993 were smaller than recommended by Miranda (1993) for analyzing differences between proportions. These small sample sizes may have contributed to our finding of significant differences among PSDs even when confidence limits overlapped. Though the number of walleye collected in this study was relatively small, the large amount of standardized sampling we performed over the course of five years increases our confidence in the results.

We find no evidence of changes in walleye year-class strength, abundance, size, PSD, growth, or mortality in response to sustained exploitation of northern squawfish. While mean fork length, abundance, and PSD show increases since implementation of the NSMP, these trends appear to be driven by a relatively strong 1992 year class. Decreases in W_r suggest that walleye have not increased their consumption of juvenile salmonids in response to northern squawfish removals.   The lack of response by walleye supports the hypothesis that juvenile salmonid survival is enhanced by the exploitation of northern squawfish. Because the NSMP has been in place for a relatively short period of time, populations of salmonid predators should continue to be monitored for possible responses.

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Comparative Food Habits and Piscivory of Smallmouth Bass, Walleyes, and Northern Squawfish
in the Lower Columbia River Basin

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INTRODUCTION

Fish communities and trophic dynamics in the Columbia River basin have been shaped by numerous introductions of exotic species and severe habitat changes associated with extensive hydropower development. Basic research on food web structure and function is lacking, due in part to logistical constraints associated with sampling large rivers (Campbell 1979). Regional research and management is primarily directed toward understanding and ameliorating the effects of impoundments and flow management on anadromous salmonids (Bentley and Raymond 1976; Ebel and Raymond 1976; Raymond 1979; Zaugg et al. 1985; Berggren and Filardo 1993). Little is known of the effects of Columbia River basin impoundments on endemic nonsalmonids, invertebrates, and nutrient dynamics.

The fish community in the lower Columbia River basin is a diverse mix of endemic and introduced predator and forage fishes that include warm, cool, and cold water species (Table 1). Although this trophic classification based on piscivory by adult fish is highly simplified, it illustrates the potential complexity of food web interactions in the lower Columbia and Snake rivers, and suggests that predation on endemic prey species has increased since the introduction of smallmouth bass *Micropterus dolomieu*, walleyes *Stizostedion vitreum*, and channel catfish *Ictalurus punctatus*. Poe et al. (1994) hypothesized that exotic predators have affected prey population dynamics as well as the diets of endemic predators, particularly northern squawfish *Ptychocheilus oregonensis*.

Rigorous studies of predator food habits in the lower Columbia River basin have been limited in geographic scope to a single reservoir (Poe et al. 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 demonstrated the significance of juvenile salmonid predation by resident fishes, and provided a sound biological basis for a region-wide predator control program targeting northern squawfish (Rieman and Beamesderfer 1990; Beamesderfer et al. 1996).

The Northern Squawfish Management Program was implemented in 1990 to enhance survival of outmigrating juvenile salmonids through managed harvest of northern squawfish in the lower Columbia River basin. Approximately 1.1 million northern squawfish have been harvested since 1990 (Friesen and Ward 1997a), adding yet another potential influence on resident fish communities. The anticipated benefits of the program would be lessened by compensatory predation by other predators in response to northern squawfish removals (Beamesderfer et al. 1996).

General food habits and piscivory of smallmouth bass, walleyes, and northern squawfish were compared from 1990-96 among three 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. This study addresses (1) spatial variation in predators diets among the three reaches, (2) annual variation in piscivory within each reach, (3)

Table 1. Resident piscivores (based on adult diets) and potential prey species of the mainstem lower Columbia River basin. Asterisks denote introduced species.

Trophic classification,
     Common name   Scientific name

Piscivore
     Northern squawfish   Ptychocheilus oregonensis
     Channel catfish[*]   Ictalurus punctatus
     Smallmouth bass[*]   Micropterus dolomieu
     Walleye[*]   Stizostedion vitreum

Potential prey
     Pacific lamprey   Lampetra tridentata
     American shad[*]   Alosa sapidissima
     Chinook salmon   Oncorhynchus tschawytscha
     Steelhead   O. mykiss
     Mountain whitefish   Prosopium williamsoni
     Bullhead[*]   Amerius spp.
     Peamouth   Mylocheilus caurinus
     Chiselmouth   Acrocheilus alutaceus
     Common carp[*]   Cyprinus carpio
     Redside shiner   Richardsonius balteatus
     Longnose dace   Rhinichthys cataractae
     Largescale sucker   Catostomus macrocheilus
     Bridgelip sucker   Catostomus columbianus
     Threespine stickleback   Gasterosteus aculeatus
     Sand roller   Percopsis transmontana
     Bluegill[*]   Lepomis macrochirus
     Pumpkinseed[*]   L. gibbosus
     Crappie[*]   Pomoxis spp.
     Yellow perch[*]   Perca flavescens
     Prickly sculpin   Cottus asper

relationships between predator size and prey size for salmonid and nonsalmonid prey fishes, and (4) daily consumption rates on indigenous nonsalmonid forage fishes.

METHODS

Field Sampling

Predators were sampled at fixed sites established throughout three reaches of the lower Columbia River basin from 1990-96 (Figure 1). Sites in the unimpounded lower Columbia River were river kilometer (RKm) 115-121, 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 mid-reservoir areas away from dams (RKm 275-281 in Bonneville Reservoir and RKm 390-396 in John Day Reservoir). Snake River sampling sites included the tailrace 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 for seven consecutive years, whereas sampling years differed among sites in other reservoirs and reaches (Table 2). All sites were sampled annually from 1994-96.

Each sampling site was subdivided into 24 near-shore transects approximately 500 m in length. Predators were captured by electrofishing a minimum of 6 randomly selected transects per day within each site. Standardized effort in each transect was 15 minutes of continuous output at 4-5 A. A minimum of 8 boat-days of effort was allocated annually in each site, with effort 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 squawfish were collected every year from 1990-96, whereas walleye were collected from 1990-93 and in 1996.

Smallmouth bass, walleye, and northern squawfish were measured (fork length in mm) and weighed (g). Stomachs of smallmouth bass and walleye ≥200 mm were pumped with a modified Seaburg sampler (Seaburg 1957). Northern squawfish ≥250 mm were sacrificed and the entire digestive tracts removed. Samples were frozen until subsequent laboratory analysis.

Laboratory Analysis

Gut contents were thawed in the laboratory, blotted dry, and sorted into four prey categories: fish, crayfish, other invertebrates (molluscs, insects), and "miscellaneous" (all other prey items such as amphibians, aquatic plants, wheat). Prey types were weighed to the nearest 0.01 g and returned to the original sample bags. A solution of lukewarm tapwater, 2% (wet weight) pancreatin (8x porcine digestive enzyme), and 1% (wet weight) sodium sulfide was poured into each bag and mixed with the gut contents to speed sample
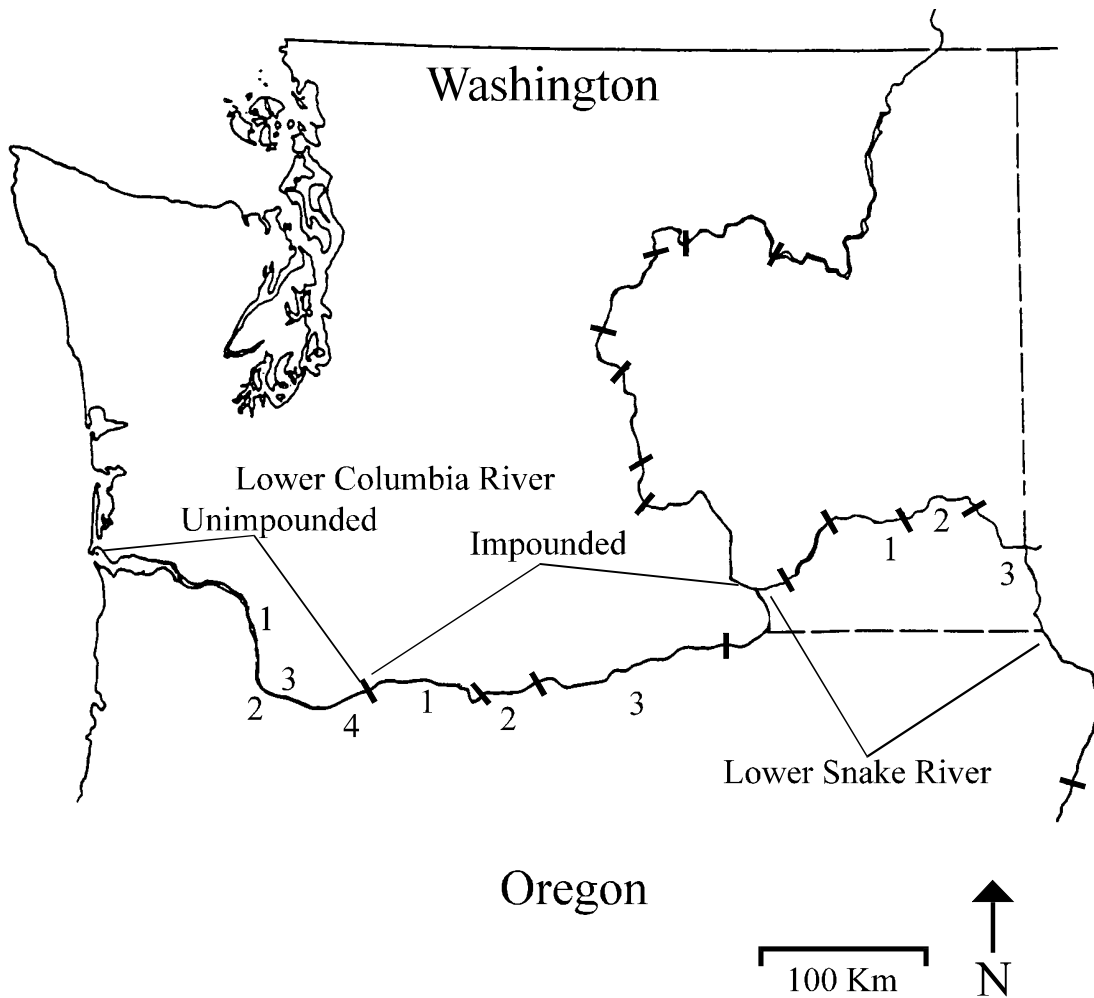
Figure 1. Sampling sites in the lower Columbia River basin, 1990-96. Sites in the unimpounded lower Columbia River are (1) river kilometer (RKm) 115-121, (2) RKm 172-178, (3) RKm 190-197, and (4) Bonneville Dam tailrace. Sites in the impounded lower Columbia River are (1) Bonneville Reservoir forebay, mid-reservoir, and tailrace, (2) The Dalles Reservoir forebay and tailrace, and (3) John Day Reservoir forebay, mid-reservoir, and tailrace. Sites in the lower Snake River are (1) Little Goose Dam tailrace, (2) Lower Granite Dam tailrace, and (3) RKm 222-228.

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 (X). All sites were sampled during spring (April-June) and summer (July-September) except where indicated.

Sampling site	1990	1991	1992	1993	1994-1996
Unimpounded Columbia River					
RKm 115-121	--	--	X	--	X
RKm 172-178	--	--	X	--	X
RKm 190-197	--	--	X	--	X
Bonneville Dam tailrace	X	--	X	X	X
Columbia River Reservoirs					
Bonneville					
Forebay	X	--	--	X	X
Mid-reservoir	X	--	--	X	X
Tailrace	X	--	--	X	X
The Dalles					
Forebay	X	--	--	X	X
Tailrace	X	--	--	X	X[a]
John Day					
Forebay	X	X	X	X	X
Mid-reservoir	X	X	X	X	X
Tailrace	X	X	X	X	X
Snake River Reservoirs[b]					
Lower Monumental					
Tailrace	--	X	--	--	X
Little Goose					
Tailrace	--	X	--	--	X
Lower Granite					
RKm 222-228	--	X	--	--	X

[a] Sampled in summer only.
[b] Sampled in spring only in 1991 and 1994.

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 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.

Data Analysis

Spatial Variation in Diets

Diet data was pooled across sites and years within each large sampling reach. Analyses of variance were used to compare predator weights and weights of stomach or gut contents and weights of each prey type among reaches. Chi-square analyses were used to compare the frequency of occurrence (FO) of food in samples. McCabe et al. (1993) used an Index of Feeding (IF) as another measure of feeding intensity. The IF is the relative weight of stomach or gut contents:

$$IF = (W_s/W_f) \times 100\%$$

where

W_s = weight (g) of gut or stomach contents, and
W_f = weight (g) of predator.

Analyses of variance were used to compare arcsine-transformed IF values. The Least Square Means procedure (SAS Institute, Inc. 1990) was used to analyze differences among areas. The FO's of each prey type (fish, crayfish, other invertebrates, and miscellaneous prey) and prey fish taxa (salmonids, cottids, and other prey fishes) were analyzed by chi-square tests. Probabilities less than 0.05 were considered indicative of a significant effect in all analyses.

Annual Variation in Piscivory

Chi-square analyses were used to compare FO of food and fish prey among years within each reach. Analyses of variance were used to test for differences in total weights of fish in stomach or gut contents among years, and differences in proportions (arcsine-transformed) of consumed prey fishes that were salmonids among years.

Predator and Prey Size Relationships

Linear regression equations of Hansel et al. (1988) were used to estimate original fork lengths from measurements of diagnostic bones of prey fishes consumed in 1995-96. Kolmogorov-Smirnov Two-Sample Tests (Sokal and Rohlf 1981) were used to compare

frequency distributions (10-mm fork length intervals) of juvenile salmonid prey between predator species, and between consumed salmonids and salmonids collected in juvenile bypass systems of dams beginning seven days prior to each sampling date. Salmonid length data were supplied by the National Marine Fisheries Service (Bonneville and John Day dams), Washington Department of Fish and Wildlife (McNary and Lower Granite dams), and Oregon Department of Fish and Wildlife (Little Goose Dam). For nonsalmonid prey taxa with a sample size of 10 or more individuals, frequency distributions (10-mm fork length intervals) of consumed prey were compared among predator species with the Kolmogorov-Smirnov Two Sample Test (Sokal and Rohlf 1981). Relationships between predator length (25-mm fork length intervals) and the maximum size of prey fish consumed were analyzed by linear regression.

Consumption Rates

The method of Diana (1979) was used to estimate average daily consumption rates of cyprinids, suckers, sand rollers, and sculpins by smallmouth bass and northern squawfish (sample sizes of walleye were insufficient to include in the analysis) in 1995-96. The method is based on meal turnover-time using the equation

$$R = (M \bullet n)/(ET90 \bullet n)$$

where

    R   = daily ration (% body weight/d),
    M = average size of ingested meal (% body weight) of those fish that contained food,
     n = number of fish that contained food,
ET90 = 90% emptying time (d) of digestive tract contents, and
    N = total number of fish.

Original meal weight of prey fishes was estimated from length-weight regressions of common forage fishes (Vigg et al. 1991). Since all prey fishes could not be identified to species, I assumed that all unidentified salmonids were chinook salmon, and all catostomids were largescale suckers. Original fork lengths and weights of redside shiners were approximated using regression equations for peamouth because regression equations were not available for redside shiners. 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 using digestion rate equations for smallmouth bass (Rogers and Burley 1991),

$$ET90 = 24.542 \; S^{0.29} \; e^{-0.15T} \; W^{-0.23}$$

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

$$ET90 = 47.792 \; S^{0.61} \; T^{-1.60} \; W^{-0.27}$$

where

    S   = meal weight (g),
    T   = temperature (°C), and
    W = predator weight (g).

Average daily consumption rates of cyprinids, catostomids, sand rollers, and cottids by smallmouth bass and northern squawfish during spring and summer were calculated as

$$C = \frac{R \bullet P \bullet \text{mean predator weight (g)}}{\text{mean original prey weight (g)}}$$

where

    C = prey/predator/d,
    R = daily ration (% body weight/d), and
    P = proportion (by weight) of cyprinids, catostomids, sand rollers, or cottids in diet.

Consumption rates were adjusted for diel feeding periodicity assuming that smallmouth bass consumed 32% and northern squawfish consumed 40.5% of their daily ration between 0400 and 1100 hours (Vigg et al. 1991).

Consumption rate estimates were calculated from a sample of predators, and therefore do not have an observed variance. To express some measure of the precision associated with each estimate, I calculated a low and high estimate using plus and minus two standard deviations of mean meal size (M), 90% emptying time (ET90), and predator weight.

RESULTS

Spatial Variation in Diets

Predator sample sizes totaled 3,827 smallmouth bass, 171 walleyes, and 5,386 northern squawfish from 1990-96 (Table 3). The FO of food in samples ranged from 68-74% for smallmouth bass, 45-47% for walleyes, and 55-68% for northern squawfish. Weights of smallmouth bass were greatest downstream from Bonneville Dam, and IF's were significantly greater in Snake River impoundments than both Columbia River areas. Walleyes weighed significantly more downstream from Bonneville Dam than in Columbia River reservoirs; however, there was no difference in stomach content weight and IF between areas. Weights of northern squawfish were largest in Columbia River reservoirs,

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Table 3. Number of gut samples examined (N), number of samples that contained food (N_{food}), mean predator weight, mean weight of gut contents, and mean Index of Feeding (IF) of smallmouth bass, walleyes, and northern squawfish from the lower Columbia River basin, 1990-96. Means are expressed as mean $\pm$ 2 SE.

Reach, parameter	Smallmouth bass		Walleye		Northern squawfish	
Downstream from Bonneville Dam						
N	355		38		1,697	
N_{food} (%)	262	(73.8)	17	(44.7)	931	(54.9)
Mean predator weight (g)	407	$\pm$ 33	1,886	$\pm$ 344	676	$\pm$ 21
Mean gut weight (g)[a]	4.0	$\pm$ 1.0	11.1	$\pm$ 12.5	13.4	$\pm$ 1.1
Mean IF[a]	1.0	$\pm$ 0.2	1.1	$\pm$ 1.2	1.8	$\pm$ 0.1
Columbia River reservoirs						
N	2,668		133		2,865	
N_{food} (%)	1,922	(72.0)	63	(47.4)	1,662	(58.0)
Mean predator weight (g)	346	$\pm$ 10	1,524	$\pm$ 165	715	$\pm$ 16
Mean gut weight (g)[a]	3.6	$\pm$ 0.3	13.6	$\pm$ 6.3	10.8	$\pm$ 0.7
Mean IF[a]	1.1	$\pm$ 0.1	0.8	$\pm$ 0.3	1.4	$\pm$ 0.1
Snake River reservoirs						
N	804		0		824	
N_{food} (%)	546	(67.9)	--		564	(68.4)
Mean predator weight (g)	300	$\pm$ 17	--		699	$\pm$ 30
Mean gut weight (g)[a]	4.1	$\pm$ 0.6	--		18.6	$\pm$ 1.9
Mean IF[a]	1.4	$\pm$ 0.2	--		2.3	$\pm$ 0.2

[a] Only samples that contained food.

and weights of northern squawfish gut contents and IF's were greatest in Snake River reservoirs.

Smallmouth bass in the Columbia River downstream from Bonneville Dam preyed upon fish to a greater extent and crayfish to a lesser extent than in other areas (Figure 2). The frequency of occurrence of fish among walleyes was higher in Columbia River reservoirs than the unimpounded lower Columbia River; however statistical power was too low (<0.80) to test the difference between reaches. Few walleyes utilized prey other than
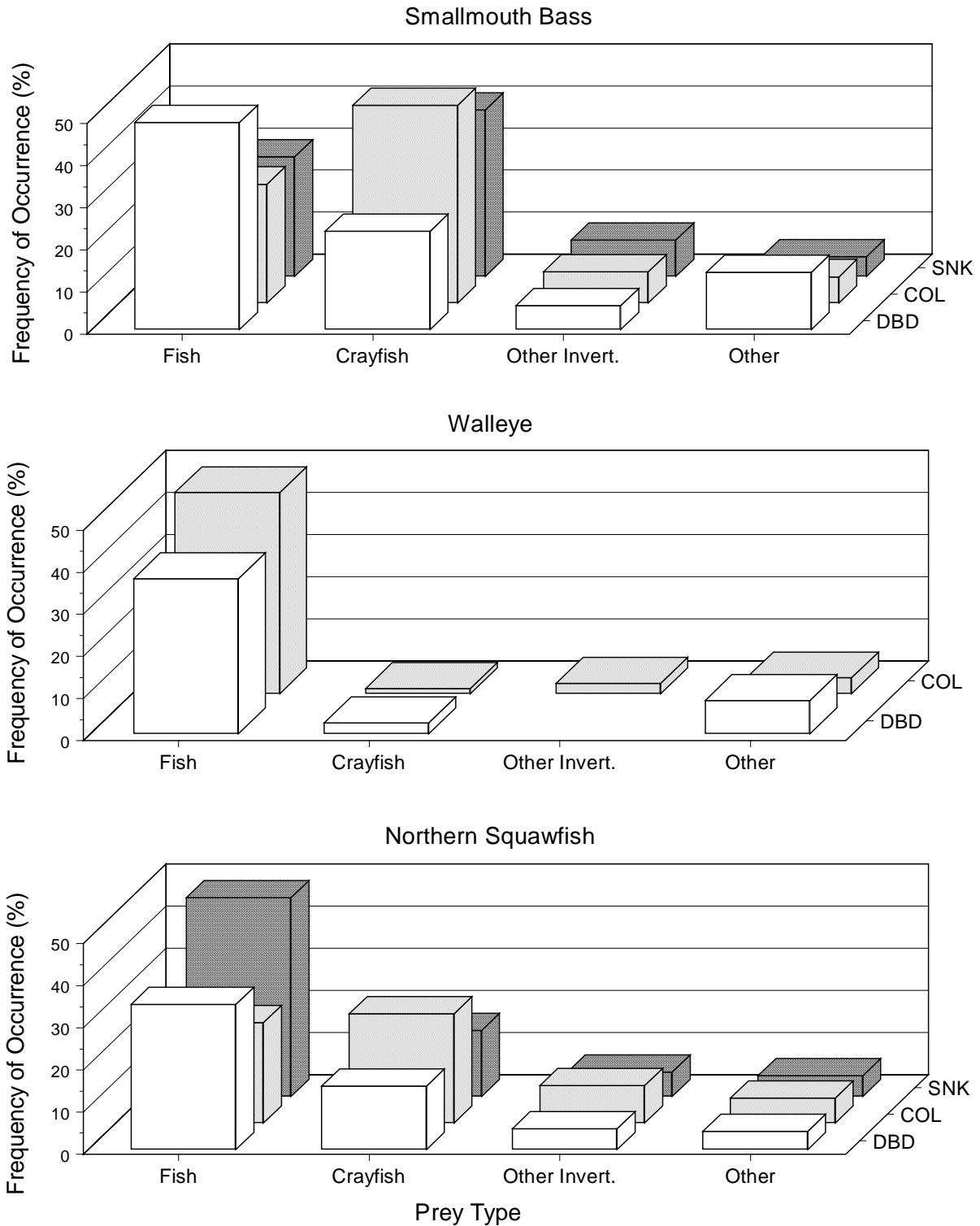
Figure 2. The frequency of occurrence (%) of fish, crayfish, other invertebrates, and other prey among gut samples of smallmouth bass, walleyes, and northern squawfish in the Columbia River downstream from Bonneville Dam (DBD), lower Columbia River reservoirs (COL), and lower Snake River reservoirs (SNK) from 1990-96. fish. Frequency of occurrence of fish prey among

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northern squawfish was greatest in Snake River reservoirs, whereas utilization of crayfish and other invertebrates (amphipods, mussels, and aquatic and terrestrial insects) was greatest in Columbia River reservoirs.

Weight of fish prey in smallmouth bass stomachs was greatest downstream from Bonneville Dam, and weight of crayfish was greatest in Columbia River reservoirs (Figure 3-A). Weights of all prey types in walleye stomachs were similar between the impounded and unimpounded lower Columbia River. Weight of fish prey in northern squawfish digestive tracts was greatest in Snake River reservoirs, whereas weights of all other prey types were greatest in Columbia River reservoirs.

The proportion of salmonids among prey fishes consumed by smallmouth bass and northern squawfish were greatest in the Snake River, whereas the proportions of cottids were greatest in Columbia River reservoirs (Figure 3-B). Cottids and other nonsalmonid prey were far more prevalent in smallmouth bass and walleye diets than northern squawfish diets.

Chinook salmon were consumed to a far greater extent than steelhead by smallmouth bass and northern squawfish, except in the Snake River where steelhead comprised 40% of identified salmonids ingested by northern squawfish (Table 4). Smallmouth bass and walleye consumed more native cyprinids, catostomids, sand rollers, and cottids than did northern squawfish. Smallmouth bass consumed threespine stickleback, ictalurids, and centrarchids to a greater extent than either walleye or northern squawfish. The proportional frequency of ictalurids and centrarchids in the diets of both smallmouth bass and northern squawfish was greatest in the Snake River.

Annual Variation in Piscivory

The frequency of occurrence of food and fish prey among smallmouth bass did not increase over time (Figure 4). Total weight of fish prey and proportion of salmonids among prey fishes consumed by smallmouth bass were similar among years downstream from Bonneville Dam, but differed among years in Columbia and Snake River reservoirs. Mean weight of fish prey and proportion of salmonids consumed in Columbia River reservoirs was lowest from 1994-96. Small sample sizes of walleye contributed to considerable annual variation in all diet variables (Figure 5); however, piscivory and salmonid predation did not increase over time. The proportion of northern squawfish that consumed food and fish prey declined over time in the Columbia River, but not in the Snake River (Figure 6). Weight of fish prey in northern squawfish gut contents declined over time in Columbia River reservoirs, and northern squawfish consumed fewer salmonids relative to other prey fishes downstream from Bonneville Reservoir from 1990-96.
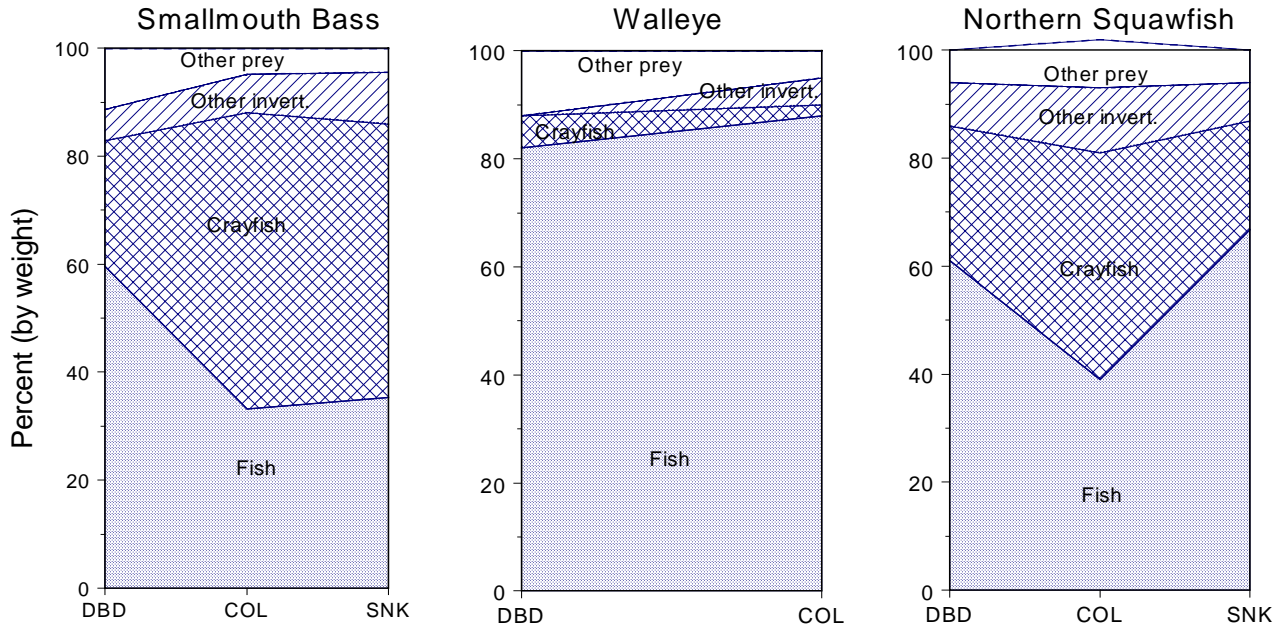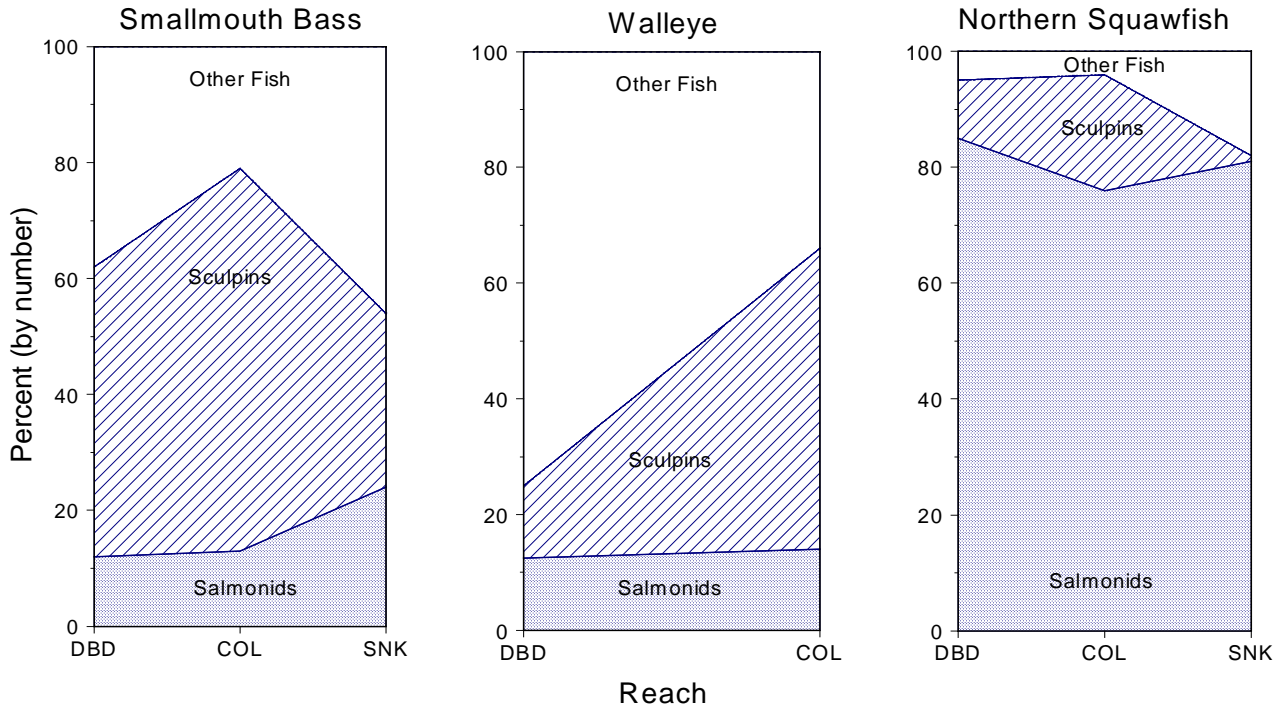
Figure 3. Composition (percent weight) of all prey (A) and composition (percent number) of fish prey (B) consumed by smallmouth bass, walleyes, and northern squawfish in the Columbia River downstream from Bonneville Dam (DBD), lower Columbia River reservoirs (COL), and lower Snake River reservoirs (SNK) from 1990-96.

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Table 4. Total number of fish (N_{total}), number of identifiable fish ($N_{identified}$), and species composition (%) of identified fish consumed by smallmouth bass, walleyes, and northern squawfish in the Columbia River downstream from Bonneville Dam (DBD), lower Columbia River reservoirs (COL), and lower Snake River reservoirs (SNK), 1990-96.

| Sample size and prey category	Smallmouth bass			Walleye		Northern squawfish		
	DBD	COL	SNK	DBD	COL	DBD	COL	SNK
N_{total}	221	983	299	14	117	1,619	1,393	380
$N_{identified}$	171	703	218	8	86	1,555	1,282	355
%Petromyzonidae	0	0.30	0	0	0.3		0.8	9.3
%Salmonidae	12.9	14.6	23.4	12.5	13.9	92.4	81.4	84.8
Chinook Salmon	8.8	8.0	11.5	0	5.8	64.2	28.8	49.0
Steelhead	0	0	2.3	0	0	2.3	2.7	21.1
Unidentified spp.	4.1	6.7	9.6	12.5	8.1	25.8	50.0	14.7
%Cyprinidae	17.0	11.8	12.8	50.0	13.9	0.8	0.9	0.3
Carp	0.6	0	0	0	0	0.1	0	0
Chiselmouth	1.2	0.3	3.2	0	0	0	0	0.3
Peamouth	6.4	5.6	2.7	0	7.0	0.4	0.6	0
Northern squawfish	5.9	4.3	3.2	12.5	4.6	0.2	0	0
Redside shiner	2.3	0.4	0	12.5	2.3	0.1	0.1	0
Unidentified spp.	0.6	1.3	3.7	25.0	0	0	0.2	0
%Catostomidae	14.6	3.3	7.8	0	5.8	0.1	0.2	0.3
%Ictaluridae	0	1.6	13.8	0	0	0	0	1.4
%Percopsidae	2.9	1.4	0	25.0	14.1	0.3	0.1	0
%Gasterosteidae	3.5	0.4	0	0	0	0.7	0.2	0
%Cottidae	47.9	64.0	33.5	12.5	51.8	5.3	16.1	0.9
%Centrarchidae	0.6	2.1	8.7	0	1.2	0.1	0.2	3.1
Smallmouth bass	0.6	1.7	2.7	--	0	0.1	0.2	0.9
Crappie spp.	0	0.1	3.7	--	1.2	0	0	1.7
Sunfish spp.	0	0.1	1.4	--	0	0	0.1	0
Unidentified spp.	0	0.1	0.9	--	0	0	0	0.6
%Percidae	0.6	0.3	0	0	0	0	0	0
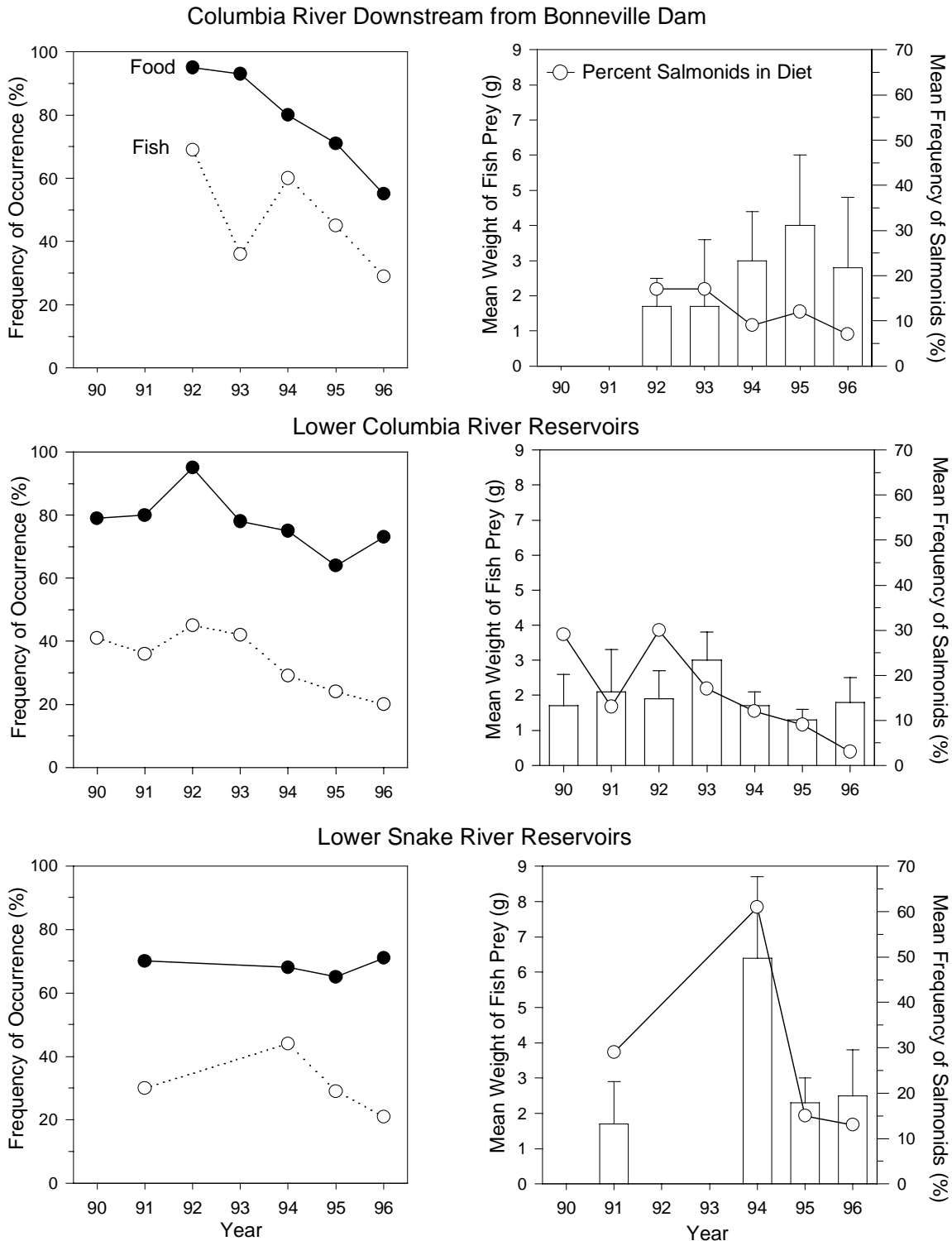
Figure 4. Temporal variation in the frequency of occurrence (%) of food and fish prey, mean wet weight of fish prey (bars + 2 SE), and the frequency (%) of juvenile salmonids among all identified prey fishes consumed by smallmouth bass.

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Columbia River Downstream from Bonneville Dam
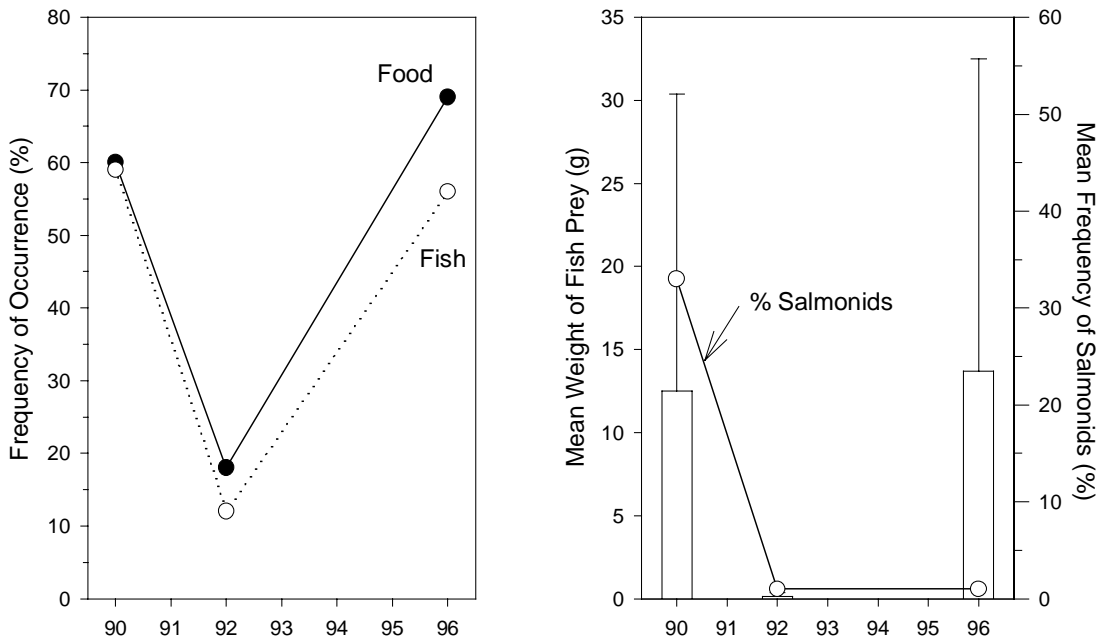
Lower Columbia River Reservoirs
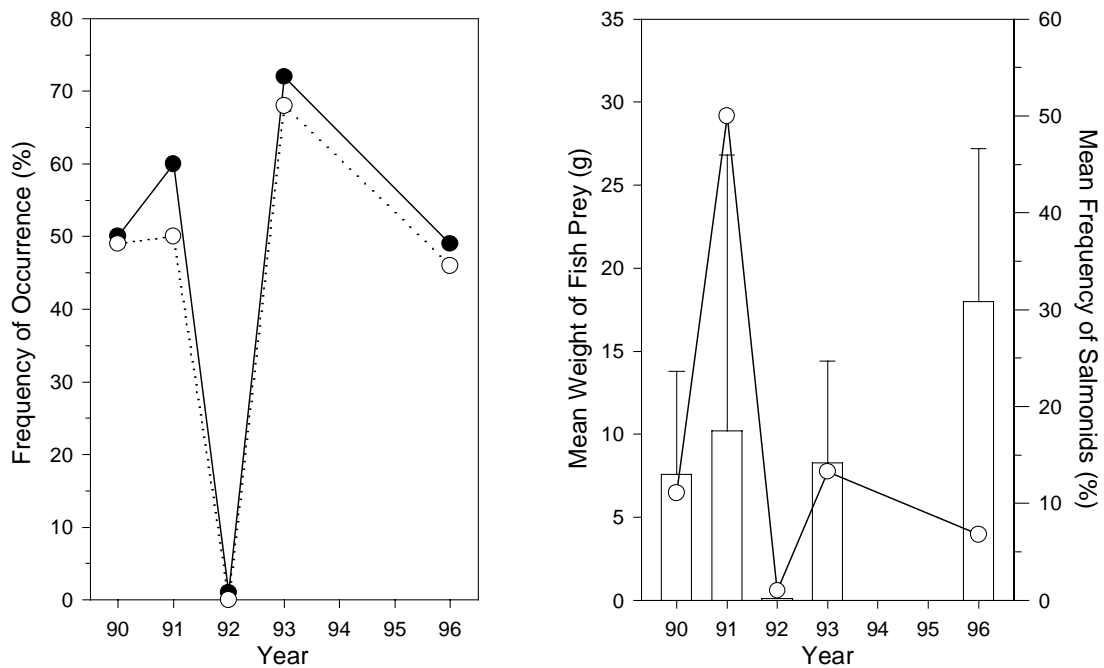
Figure 5. Temporal variation in the frequency of occurrence (%) of food and fish prey, mean wet weight of fish prey (bars + 2 SE), and the frequency (%) of juvenile salmonids among all identified prey fishes consumed by walleyes.

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Columbia River Downstream from Bonneville Dam

Lower Columbia River Reservoirs
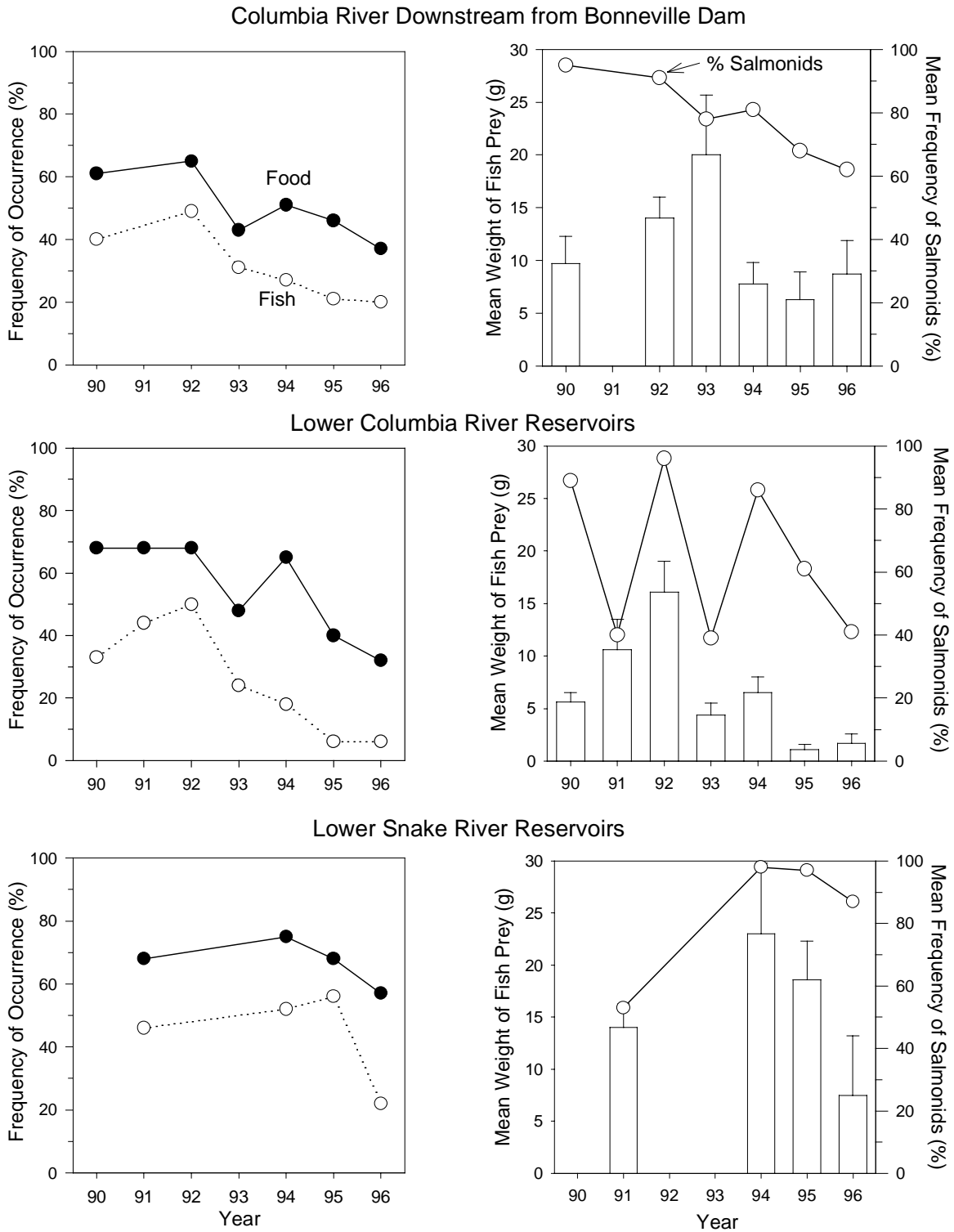

Lower Snake River Reservoirs

Figure 6. Temporal variation in the frequency of occurrence (%) of food and fish prey, mean wet weight of fish prey (bars + 2 SE), and the percent of juvenile salmonids among all prey fishes consumed by northern squawfish.

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Predator and Prey Size Relationships

In spring, smallmouth bass consumed chinook salmon only in the Snake River, where lengths of consumed chinook salmon were similar to those passing Little Goose and Lower Granite dams (Figure 7). In summer, chinook salmon consumed by smallmouth bass in Columbia River reaches were smaller than chinook salmon passing Bonneville, John Day, and McNary dams. Lengths of chinook salmon consumed by northern squawfish in Columbia River reservoirs were similar to lengths of chinook salmon passing John Day and McNary dams in spring and summer; however, chinook salmon consumed downstream from Bonneville Dam and in the Snake River differed in size from chinook salmon passing Bonneville and Lower Granite dams. Lengths of steelhead consumed by northern squawfish downstream from Bonneville Dam and in the Snake River combined were different from lengths of steelhead at Bonneville and Lower Granite dams. We found diagnostic bones of only five salmonids consumed by walleye, one in spring and four in summer.

Cottid prey ranged from 10-205 mm fork length, and smallmouth bass consumed smaller cottids than walleye and northern squawfish (Figure 8). Mean size of cyprinid prey was smaller for smallmouth bass than walleye, although the maximum size of cyprinid consumed was similar (241 and 252 mm) between species. We identified only four cyprinids in northern squawfish guts (range = 87-199 mm). Catostomids consumed by smallmouth bass ranged from 46-185 mm fork length. We identified only three catostomids in walleye samples (range = 58-284 mm), and two in northern squawfish samples (101 and 340 mm).

The maximum size of juvenile salmonid prey increased with predator length for northern squawfish and smallmouth bass, and maximum salmonid size consumed by northern squawfish was larger than smallmouth bass (Figure 9). Size of cottid prey increased with length of smallmouth bass and northern squawfish, but not walleye. Maximum size of cyprinid prey consumed by smallmouth bass and walleye increased with predator length.

Consumption Rates

Daily consumption rates of indigenous prey fishes by smallmouth bass generally exceeded consumption by northern squawfish, and consumption rates were generally higher in summer than spring (Figure 10). Consumption rate of cottids by smallmouth bass was highest in Columbia River reservoirs in summer (2.9 prey/predator/day), whereas consumption of cyprinid prey was highest in the unimpounded lower Columbia River in summer (1.9 prey/predator/day). Consumption of cottids by northern squawfish was highest in the unimpounded Columbia River in summer (0.8 prey/predator/day), and consumption of cyprinids was highest in Columbia River reservoirs in summer (0.2 prey/predator/day). Both predator species' consumption rates on catostomids and sand
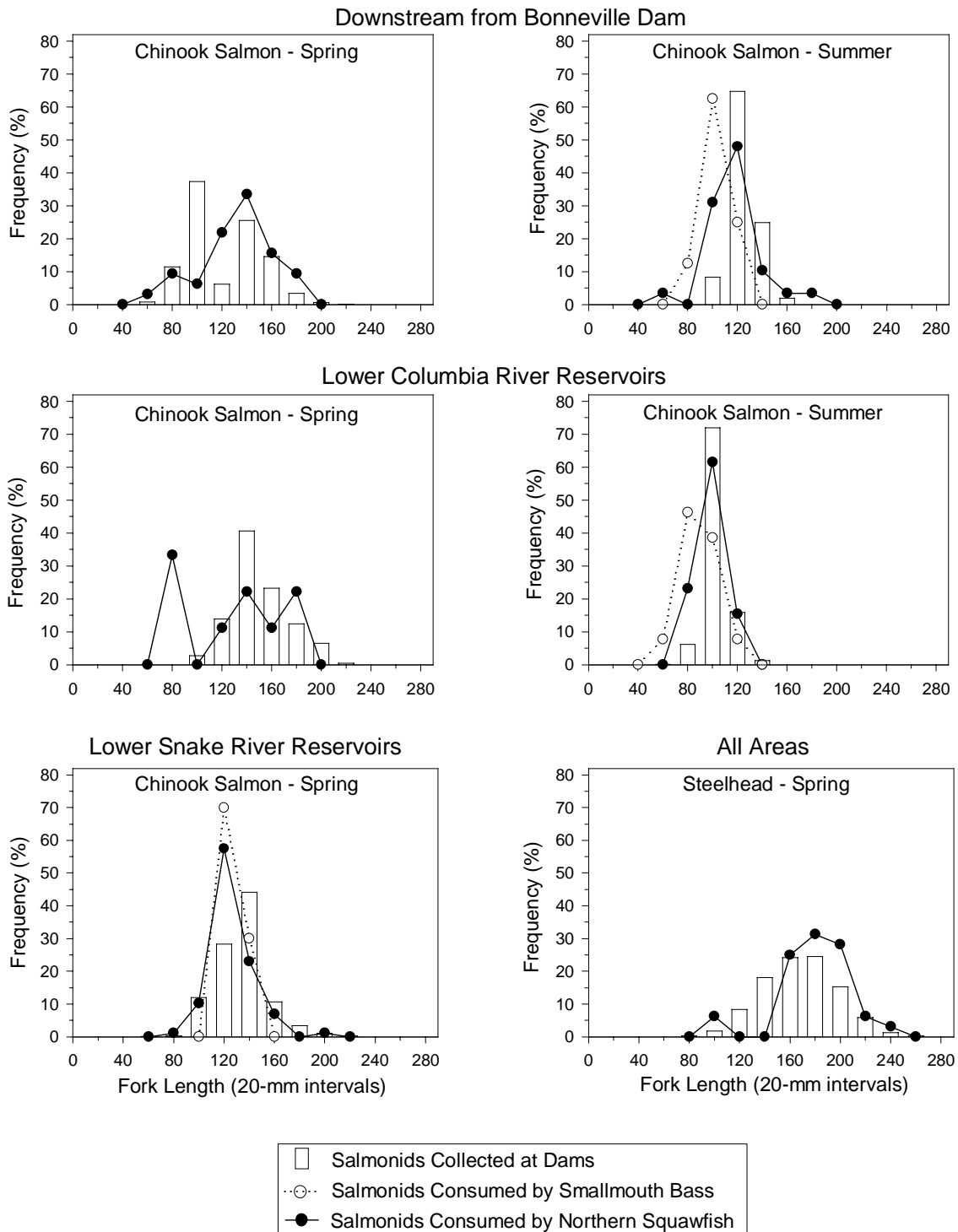
Figure 7. Fork lengths (20-mm intervals) of juvenile salmonids collected at dams in 1995-96 (bars), and fork lengths (20-mm intervals) of juvenile salmonids consumed by smallmouth bass (open circles) and northern squawfish (filled circles) in 1995-96.
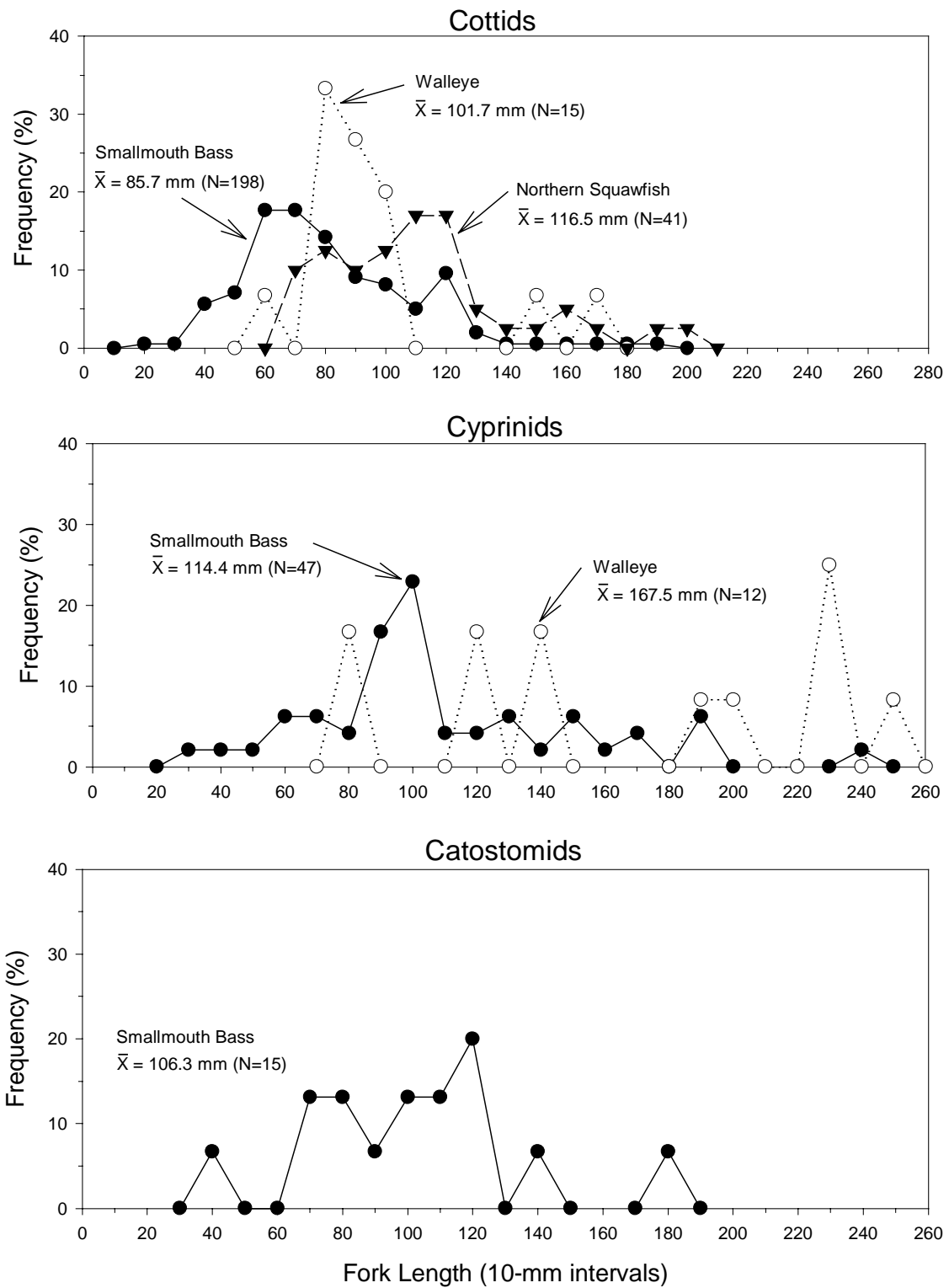
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Figure 8. Fork lengths (10-mm intervals) of cottids, cyprinids, and catostomids consumed by smallmouth bass, walleyes, and northern squawfish in 1995-96, all reaches combined.
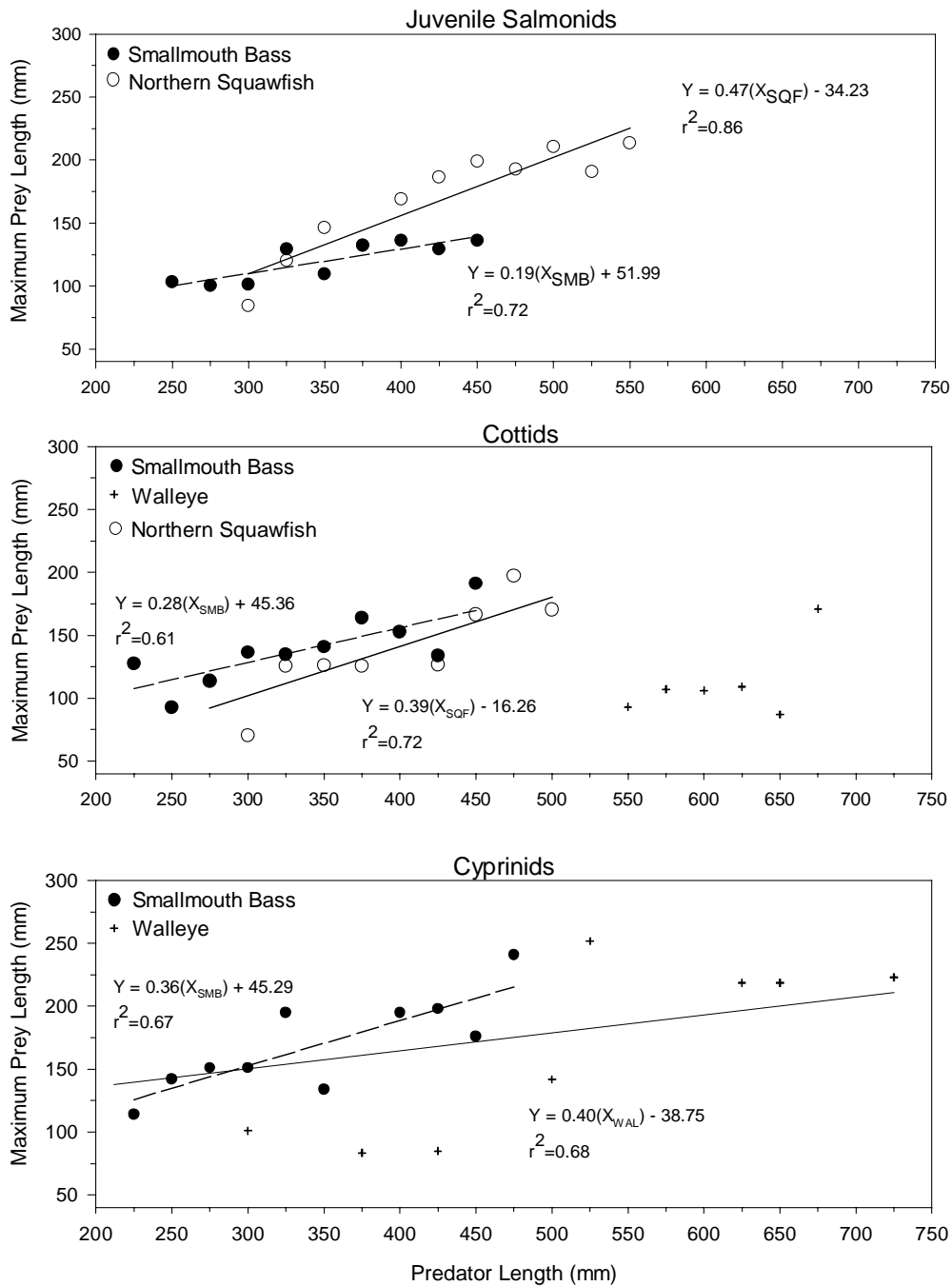
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Figure 9. Linear regressions of maximum size of prey consumed (Y) on predator fork length (X) for juvenile salmonids consumed by smallmouth bass (SMB) and northern squawfish (SQF), cottids consumed by smallmouth bass, walleyes (WAL) and northern squawfish, and cyprinids consumed by smallmouth bass and walleye. Data from 1995-96, all reaches combined.
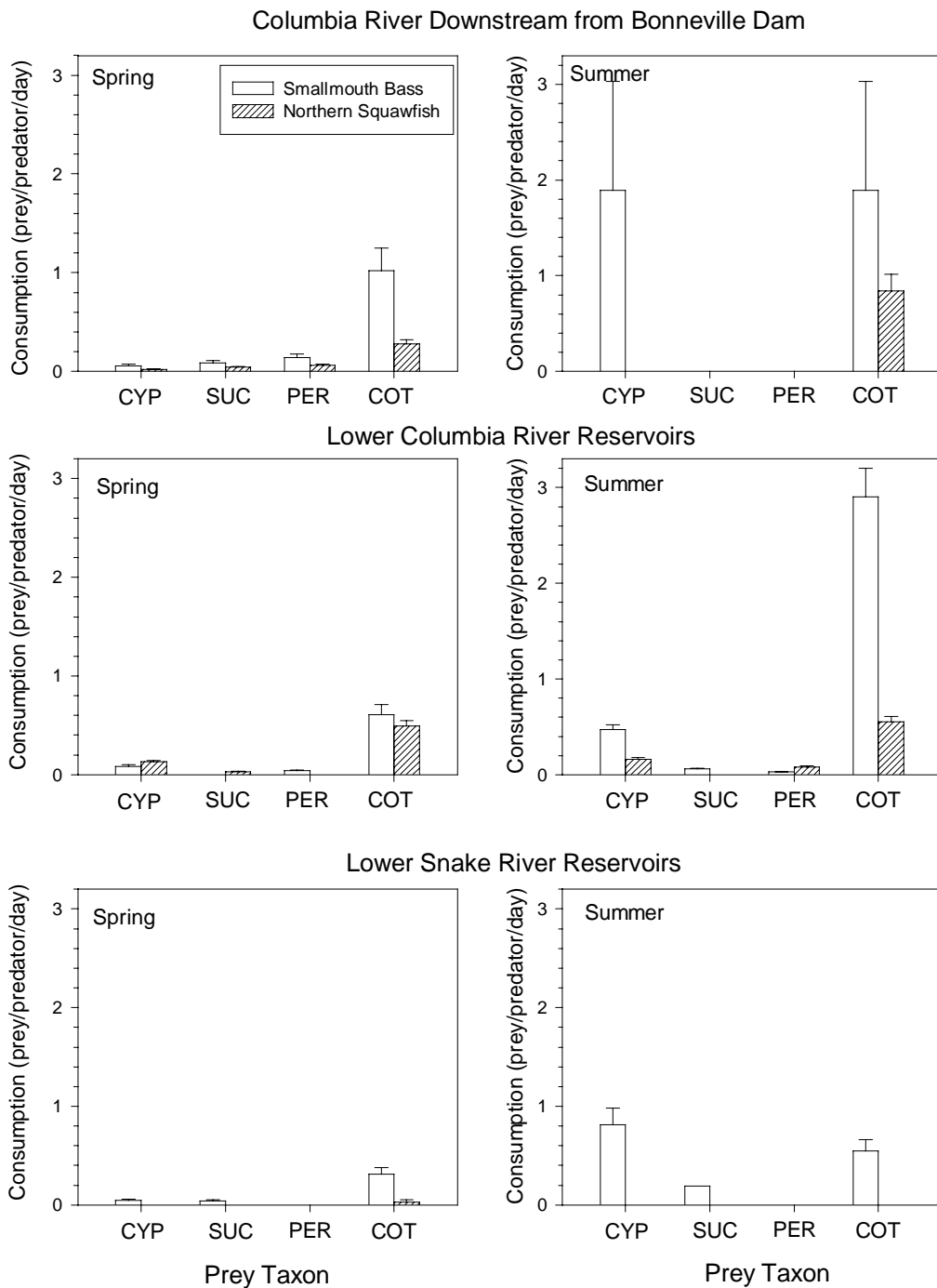
Figure 10. Consumption (prey/predator/day) of cyprinids (CYP), catostomids (SUC), sand rollers (PER), and cottids (COT) by smallmouth bass and northern squawfish in spring (April-June) and summer (July-September), 1995-96. Error bars represent consumption rates calculated from two standard errors of mean meal size, 90% emptying time, and predator weight. rollers were low (≤0.2 prey/predator/day) relative to consumption rates on cyprinids and cottids.

DISCUSSION

The food habits of smallmouth bass, walleyes, and northern squawfish throughout the lower Columbia basin were generally consistent with those reported in other studies. The primary prey of adult smallmouth bass throughout their range are crayfish and fish (Scott and Crossman 1973, Carlander 1977, Edwards et al. 1983, Austen and Orth 1985, Roell and Orth 1993). Smallmouth bass preyed on sculpins, suckers, cyprinids, sand rollers, and crayfish to a greater extent (by weight and %FO) than did northern squawfish in John Day Reservoir (Poe et al. 1991). Walleye diets throughout the lower Columbia River were dominated (by weight and %FO) by fish prey, particularly nonsalmonids. Cyprinids, catostomids, sand rollers, and cottids comprised 84% (by weight) of the total diet of walleyes in John Day Reservoir (Poe et al. 1991).

Smallmouth bass and walleyes consumed far fewer juvenile salmonids than did northern squawfish throughout the study area, consistent with their diets and consumption rates on salmonid and nonsalmonid prey in John Day Reservoir (Poe et al. 1991; Vigg et al. 1991). Estimated daily consumption rates of smallmouth bass on cottids and cyprinids generally exceeded consumption rates on salmonids (Ward and Zimmerman 1997). Nevertheless, smallmouth bass consumption rates exceeded one juvenile salmonid/predator/day in specific areas in summer (Tabor et al. 1993; Ward and Zimmerman 1997), when subyearling chinook salmon are the only available salmonid prey.

Poe et al. (1991) found that food habits of each predator species differed between near-dam and mid-reservoir areas within John Day Reservoir. Relative abundance of walleyes and northern squawfish is greatest in dam tailraces (Friesen and Ward 1997b; Zimmerman and Ward 1997), whereas smallmouth bass are generally more abundant in dam forebays. Although prey types utilized by walleyes and northern squawfish in areas away from dams were underrepresented, the impact of predation on those prey types would be relatively low because of low predator abundance. Differences in habitats occupied by each predator species would reduce the probability of competitive interactions within individual reservoirs.

Vigg et al. (1991) reported that nonsalmonid consumption rates by walleye were similar to smallmouth bass and greater than northern squawfish in John Day Reservoir. Potential impacts of walleye predation may be high, but are dependent upon temporal variability in abundance to a greater extent than other predator species. Walleye abundance in John Day Reservoir from 1983-86 was approximately 30% of smallmouth bass abundance; however, walleye abundance fluctuates widely with year-class strength (Beamesderfer and Rieman 1991; Friesen and Ward 1997b).

Spatial variation in prey fish composition often reflected differences in species composition of fish communities within the lower Columbia Basin. Trends in differential predation on resident fishes were most evident for smallmouth bass because they consumed nonsalmonids to a much greater extent than did northern squawfish. Both predator species consumed more exotic prey fishes such as ictalurids and centrarchids in the Snake River.

Ictalurids and centrarchids are more abundant in the Snake River than the lower Columbia River (Zimmerman and Parker 1995). Predation on sand rollers and threespine stickleback was restricted to the lower Columbia River. Non-targeted species were recorded while electrofishing for predators, and catch rates of sand rollers and threespine stickleback were greatest downstream from Bonneville Dam.

Beamesderfer et al. (1996) argued that dietary changes among other predator species following removal of northern squawfish are possible given enough time, but unlikely due to relatively low (<20%) exploitation rates on northern squawfish. Changes in food habits have been documented following removal of another species (Johnson 1977; Hayes et al. 1992). General feeding, piscivory, and juvenile salmonid consumption by smallmouth bass and walleyes exhibited annual variation; however, the pattern of variation appeared random and there was no evidence for a compensatory response by smallmouth bass or walleyes since 1990. Declining abundance of northern squawfish and salmonid predation by northern squawfish was attributed to predator removals (Friesen and Ward 1997a) and environmental variation from 1990-96 (Zimmerman and Ward 1997). Variation in flow, temperature, and dam operations probably contributed to annual variation in piscivory by smallmouth bass and walleyes.

Smallmouth bass consumed smaller chinook salmon in spring than did northern squawfish, 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 frequency of occurrence of food among smallmouth bass. Consequently, predator-prey size relationships may reflect the degree and timing of habitat overlap as suggested by Tabor et al. (1993), who attributed high levels of smallmouth bass predation on subyearling chinook to overlap of rearing habitat of subyearling chinook salmon with the preferred habitats of smallmouth bass in summer.

Skewed length distributions of juvenile salmonid prey might also result from size-related vulnerability of prey, for example associated with swimming speed (Poe et al. 1991). Alternatively, size distributions of salmonids collected in juvenile bypass systems may not have been representative of sizes of salmonids available to resident predators. Regardless of the mechanism, an important consequence of size-selective predation would be increased vulnerability of wild juvenile salmonids, which are smaller than chinook salmon and steelhead reared in hatcheries.

Predation by introduced piscivores was underestimated to an unknown extent for several reasons. Poe et al. (1991) found that fish were important prey for smallmouth bass and walleyes <200 mm in John Day Reservoir, whereas fish comprised a relatively small portion of the diets of northern squawfish <250 mm. Smallmouth bass and walleye less than 200 mm were excluded from this study. Only the direct effects of piscivory by adult predators were addressed, and other important levels of piscivory were ignored, such as predation by smaller individuals on fish eggs and early life stages. Additionally, fish can affect community structure and function through indirect mechanisms that can 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 squawfish for crayfish, sculpins and other nonsalmonid prey, and juvenile salmonid predation by northern squawfish has increased since the introduction of exotic predators. Results of this study yielded some indirect evidence for competition among predator species, particularly between smallmouth bass and northern squawfish. There was substantial dietary overlap between smallmouth bass and northern squawfish for some prey types, particularly crayfish and sculpins, and to a lesser extent, subyearling chinook salmon in summer. Northern squawfish consumed fewer cyprinids, catostomids, and cottids in the Snake River, where smallmouth bass greatly outnumber northern squawfish and utilized nonsalmonid prey extensively. Conversely, northern squawfish consumption rates on juvenile salmonids were high in the unimpounded lower Columbia River (Ward et al. 1995; Zimmerman et al. 1997), where smallmouth are least abundant (Zimmerman and Parker 1995).

Results of this study must be viewed in light of the sampling scheme. Sampling days were selected to coincide with peak migration periods of yearling chinook salmon and steelhead in spring, and subyearling chinook salmon in summer, except in the lower Snake River (see below). Consequently, juvenile salmonids were over-represented in the diets of each predator species, while other seasonally available prey were under-represented to an unknown extent. Logistical constraints required that summer sampling at lower Snake River sites occurred in August and September, after most subyearling chinook salmon had outmigrated.

There is little doubt that the aquatic ecosystem in the lower Columbia River basin has undergone profound biotic and abiotic change since the late 1800's. Changes in fish community structure (species composition) and function (piscivory) have become clearer by comparing predators' food habits throughout the lower Columbia and Snake rivers. Beamesderfer et al. (1996) pointed out that at least 15 years of research will be required to effectively evaluate biological responses to the recently implemented predator removal program. This study has established a reference point from which to evaluate long-term community-level changes in response to northern squawfish removals.

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