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Biological Characteristics of Northern Pikeminnow in the Lower Columbia and Snake Rivers before and after Sustained Exploitation

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Abstract.—We describe the response of northern pikeminnow *Ptychocheilus oregonensis* to a sustained removal program in the lower Columbia and Snake rivers. We compared catch rates of fish 250 mm fork length and larger before and after implementation of removals and examined relationships between catch rates and year-class strength. We also describe the response of mortality rates, relative weight, growth, and fecundity to sustained removals. Although annual exploitation of northern pikeminnow at least 250 mm long averaged 12.1% from 1991 to 1996, we found no evidence that surviving northern pikeminnow compensated for removals. In some areas, catch rates decreased in response to removals; however, we found no trend of increased relative weight, growth, or fecundity. Estimates of mortality were higher than those reported prior to removals, and variations in mortality generally corresponded to variations in annual exploitation rates. Our estimates of relative weight, growth, and fecundity were similar to estimates made prior to northern pikeminnow removals. Continued sustained exploitation of northern pikeminnow at 1991–1996 levels will probably not result in biological compensation, which increases confidence in the hypothesis that sustained removals increase survival of juvenile salmonids *Oncorhynchus* spp. Monitoring of population-level characteristics should continue as a parallel component of the removal program.

The northern pikeminnow *Ptychocheilus oregonensis* is a native cyprinid that is widely distributed throughout the Columbia and Snake river systems. Intensive predation by northern pikeminnow on juvenile Pacific salmon *Oncorhynchus* spp. has been well documented throughout the lower Columbia River basin (Rieman et al. 1991; Vigg 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 predation led to the development of a large-scale management program for northern pikeminnow (Beamesderfer et al. 1996; Friesen and Ward 1999). The management program consists of both sport and agency-operated fisheries; its goal is to sustain annual exploitation at 10–20% of northern pikeminnow exceeding 250 mm fork length. Over 1.1 million northern pikeminnow were removed by this program from 1990 through 1996, and densities appear to have declined in many areas (Zimmerman and Ward 1999, this issue).

Although annual exploitation from 1991 through 1996 averaged 12.1% (range, 8.1–15.5%; Friesen and Ward 1999), success of the management program relies in part on the response of northern pikeminnow populations to sustained exploitation. Because vulnerability of northern pikeminnow to capture generally increases with fish size (Friesen and Ward 1999), sustained exploitation should decrease the proportion of large fish in the remaining population. Presumably, this will lead to a decrease in predation because consumption of juvenile salmonids increases with size of northern pikeminnow (Vigg et al. 1991).

Compensation by northern pikeminnow in the form of enhanced reproduction and growth would limit the benefits of removals. Rieman and Beamesderfer (1990) concluded that compensation by northern pikeminnow was unlikely because the species' fecundity is much lower than fecundity of species considered resilient (Cushing 1971), its growth is slow and mortality low compared with other species, and it has not demonstrated obvious density-dependent growth. In addition, Parker et al. (1995) found that density of northern pikeminnow was not correlated with relative weight, von Bertalanffy growth parameters, annual mortality, slope of the weight–length equation, or fecundity. However, uncertainty still exists over the response of northern pikeminnow to changes in their density, particularly because biological compensation has been documented for other species

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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 preexploitation populations of northern pikeminnow in the lower Columbia and Snake rivers from 1990 through 1992. Although the management program began in 1990, no northern pikeminnow were removed from Columbia or Snake River reservoirs prior to initial sampling. Although approximately 65,000 northern pikeminnow were removed from the Columbia River downstream from Bonneville Dam prior to initial sampling in 1992, removals were small relative to abundance (<1% of fish ≥ 250 mm in 1991, and approximately 8% in 1992; Ward et al. 1995). The purpose of our study was to compare northern pikeminnow 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 pikeminnow population structure, mortality, growth, or fecundity. To this effect we (1) compare catch rates of northern pikeminnow among years and determine if differences in catch rates merely reflect differences in year-class strengths, (2) examine mortality rates to detect increases attributable to removal fisheries, (3) compare relative weight and growth among years to determine if compensation has occurred, and (4) compare changes in individual northern pikeminnow 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 pikeminnow 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 (for a map and description of the study area see Zimmerman and Ward 1999, this issue). Because the large size of each area precluded complete sampling, we partitioned each area into sampling 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), midreservoir, and tailrace (immediately downstream from the The Dalles Dam [Bonneville Reservoir] or McNary Dam [John Day Reservoir]). In Lower Granite Reservoir, we sampled the transition zone (Rkm 222–228) between the uppermost portion of the reservoir and the free-flowing reach of the Snake River downstream from Hell's Canyon Dam. Details of electrofishing methods and gear specifications are given in Zimmerman and Ward (1999).

We measured fork length (mm) and weight (g), collected scale samples, and when possible, determined the sex of northern pikeminnow collected by electrofishing. We used standard methods to determine ages of northern pikeminnow from scales (Jearld 1983). Ovaries were excised from ripe females and preserved by methods described by Bagenal and Braum (1978). In the laboratory, each sample was washed, drained through a sieve, and rinsed to remove any remaining preservative and separate clumped eggs. The total ovary was weighed to the nearest 0.001 g and thoroughly mixed. Three subsamples of eggs were removed and weighed, and the number of eggs was counted. We estimated fecundity as the product of the mean number of eggs per gram of subsample and the total ovarian weight (Parker et al. 1995). Ovaries were not collected in 1990.

Catch rates.—We used catch of northern pikeminnow 250 mm fork length and larger per 15-min electrofishing run to index the density of large fish. Because analysis of variance (ANOVA; $\alpha = 0.05$) on data transformed to $\log_{10}(\text{catch} + 1)$ indicated that catch rates differed between spring and summer for many reaches (Table 1), we calculated mean catch rates and 95% confidence intervals separately for each season, then used ANOVA to compare mean transformed catch rates among years. We used least-squares means analyses to determine where differences existed, with $\alpha = 0.01$ to control possible increases in type I error associated with multiple testing (Neter et al. 1990).

Year-class strength.—Differences in catch rates among years may reflect differences in relative strengths of year-classes collected, rather than differences due to removals. We therefore used the method of El-Zarka (1959) to index relative year-class strengths of northern pikeminnow cohorts

TABLE 1.—Mean catches of northern pikeminnow 250 mm fork length and larger during 15-m electrofishing runs in the Columbia and Snake rivers, transformed by $\log_{10}$(catch + 1). Values of $P \leq 0.05$ indicate significant differences between spring and summer catch rates, all years combined; RKm is river kilometer.

Area, reach	Years sampled	Mean catch (SD)		P
		Spring	Summer	
Downstream from Bonneville Dam				
Rkm 115–121	1992, 1994–1996	0.25 (0.26)	0.18 (0.23)	0.05
Rkm 172–178	1992, 1994–1996	0.42 (0.31)	0.20 (0.27)	<0.01
Rkm 190–197	1992, 1994–1996	0.38 (0.31)	0.23 (0.27)	<0.01
Bonneville Dam tailrace	1992, 1994–1996	0.63 (0.43)	0.40 (0.39)	<0.01
Bonneville Reservoir				
Forebay	1990–1992, 1994–1996	0.37 (0.35)	0.37 (0.38)	0.95
Midreservoir	1990–1992, 1994–1996	0.26 (0.29)	0.17 (0.24)	<0.01
The Dalles Dam tailrace	1990–1992, 1994–1996	0.19 (0.26)	0.20 (0.32)	0.87
John Day Reservoir				
Forebay	1990–1996	0.08 (0.17)	0.13 (0.25)	0.04
Midreservoir	1990–1996	0.03 (0.11)	0.05 (0.12)	0.22
McNary Dam tailrace	1990–1996	0.13 (0.27)	0.17 (0.34)	0.28
Lower Granite Reservoir				
Rkm 222–228	1991, 1994–1996	0.18 (0.21)	0.03 (0.09)	<0.01

(1985–1992) downstream from Bonneville Dam and in Bonneville and John Day reservoirs. For each year sampled we used results from scale analyses to determine which year-classes were collected and the percentage of the catch each year-class represented. To obtain the relative strengths of year-classes we (1) summed the catch percentages for each year-class, (2) calculated the percent change in sums between successive year-classes, (3) assigned the earliest year-class observed an arbitrary value of zero and succeeding year-classes values based on the percent change in sums, and (4) adjusted the scores to a mean of zero to give the final ranking. Because the relative abundance of year-classes in our standardized electrofishing samples might be affected by exploitation rates that varied among years (Friesen and Ward 1999), we limited our analyses to ages large enough to be effectively sampled (3 and older), but small enough to be excluded from the removal program (5 and younger). Most year-classes appeared in the catch at all three ages.

We used regression analysis to determine if catch rates of northern pikeminnow 250 mm fork length and larger were correlated with strengths of year-classes 5 and 6 years prior to sampling. We used these two ages because mean fork length of northern pikeminnow generally reaches 250 mm at age 5, virtually all northern pikeminnow exceed 250 mm by age 6 (Parker et al. 1995), and the majority of northern pikeminnow age 5 or older are ages 5 and 6 (natural mortality rates in areas we sampled are 13–29% for females and 34–46% for males, males comprising 49–62% of fish smaller than 380 mm; Parker et al. 1995). For the regressions we used the mean of year-class strengths 5 and 6 years prior to sampling, weighted to reflect natural mortality from age 5 to age 6 (38% downstream from Bonneville Dam, 23% in Bonneville Reservoir, and 35% in John Day Reservoir; Parker et al. 1995).

Mortality.—To estimate mortality rates, we used age-specific catch of northern pikeminnow from 1990 to 1996 to produce year-class-specific catch curves. However, age-specific catches for each year-class were biased by differences in sampling effort among years. To correct for these differences, we (1) determined sampling effort (number of electrofishing runs) during each year that fish from a given year-class were collected, (2) left the age-specific catch for the year with the highest effort unchanged, (3) determined the relative differences in effort between each of the other years and the year with the highest effort, and (4) increased age-specific catches by the same relative differences (Rieman and Beamesderfer 1990). We used analysis of covariance (ANCOVA; $\alpha = 0.05$) with year-class as the covariate to compare total instantaneous mortality over ages 8 through 11, and we used least-squares means analyses to test for differences among individual year-classes ($\alpha = 0.01$) downstream from Bonneville Dam, and in Bonneville and John Day reservoirs.

Relative weight.—We used the standard weight (W_s) equation for northern pikeminnow developed by Parker et al. (1995)—$\log_{10}(W_s) = -4.886 + 2.986[\log_{10}(\text{fork length})]$, to calculate relative weight (W_r; Anderson and Gutreuter 1983) of northern pikeminnow as 100(observed weight)/W_s. We then used ANOVA (α = 0.05) to compare differences in mean W_r between sexes and among years for each area or reservoir. If W_r differed between sexes, we tested for differences among years separately for each sex. We used least-squares means analyses to test for differences among individual years (α = 0.01).

Growth.—We used scales collected from 1990 to 1996 to calculate annual growth increments of female northern pikeminnow from 1989 to 1995. We then used ANOVA (α = 0.05) to compare growth increments of like-aged fish among years, and we used least-squares means analyses to test for differences among individual years (α = 0.01). We also used ANOVA to determine if trends in growth increments for each age varied among areas. We limited our analysis to ages 6–10 because these were the ages for which sample sizes were most complete. We limited our analysis to females because few males live to age 10, and males and females exhibit different growth patterns after about age 5 (Parker et al. 1995).

Fecundity.—We used ANCOVA (α = 0.05) with fish weight as a covariate to compare fecundity of northern pikeminnow among years for each area, and we used least-squares means analyses to compare differences (α = 0.01) among individual years from 1991 through 1996. We also calculated mean relative fecundity (number of developed eggs per gram of body weight).

Results

Catch Rates

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

Catch rates varied among years for 4 of 11 reaches in spring (Figure 1) and for 5 of 11 reaches in summer (Figure 2). In spring, catch rate decreased over time in the tailrace downstream from Bonneville Dam. Catch rate also decreased after initial sampling in Bonneville forebay and mid-reservoir, and in Lower Granite Reservoir. In summer, catch rates decreased over time in Bonneville forebay, John Day midreservoir, and Lower Granite Reservoir. Differences among years in the tailraces of Bonneville and John Day reservoirs were the result of high catches in a single year.

Catch rate differed among years for both spring and summer in only 2 of 11 reaches. Catches generally decreased over time for both seasons in Bonneville forebay and in Lower Granite Reservoir.

Year-Class Strength

Year-class strengths of northern pikeminnow varied considerably in all areas (Figure 3). Relatively strong year-class strengths in 1985 were followed by relatively weak 1987–1988 year-classes downstream from Bonneville Dam and in 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. We found no positive correlation between catch rate of northern pikeminnow 250 mm fork length and longer and year-class strength 5 and 6 years prior to sampling downstream from Bonneville Dam ($r = -0.09$, $P = 0.91$), in Bonneville Reservoir ($r = -0.12$, $P = 0.84$), or in John Day Reservoir ($r = -0.76$, $P = 0.08$).

Mortality

Estimates of total instantaneous mortality were generally high but varied among areas (range, 0.20–1.27; Table 2). Mortality estimates were typically highest in John Day Reservoir and lowest in Bonneville Reservoir. Although highly variable in John Day Reservoir, mortality differed significantly among year-classes only in Bonneville Reservoir.

Relative Weight

Mean W_r of female northern pikeminnow was greater than that of males ($P < 0.01$) in all areas (Figure 4). Female W_r was usually greater than 100 (except downstream from Bonneville Dam), whereas male W_r exceeded 100 only once. Although mean W_r differed among years for both sexes except in Lower Granite Reservoir, we found no evidence of an increase or decrease in W_r with time for any area. Mean W_r of males appeared to increase in Bonneville Reservoir; however, mean W_r in 1996 did not differ from that in 1990. Relative weight was generally lower downstream from Bonneville Dam than in the reservoirs.

Growth

Analysis of female northern pikeminnow growth increments indicated considerable variation in growth among years, especially downstream from Bonneville Dam (Figure 5); however, we found no evidence to indicate that growth has increased concurrent with removals. Other than growth to age

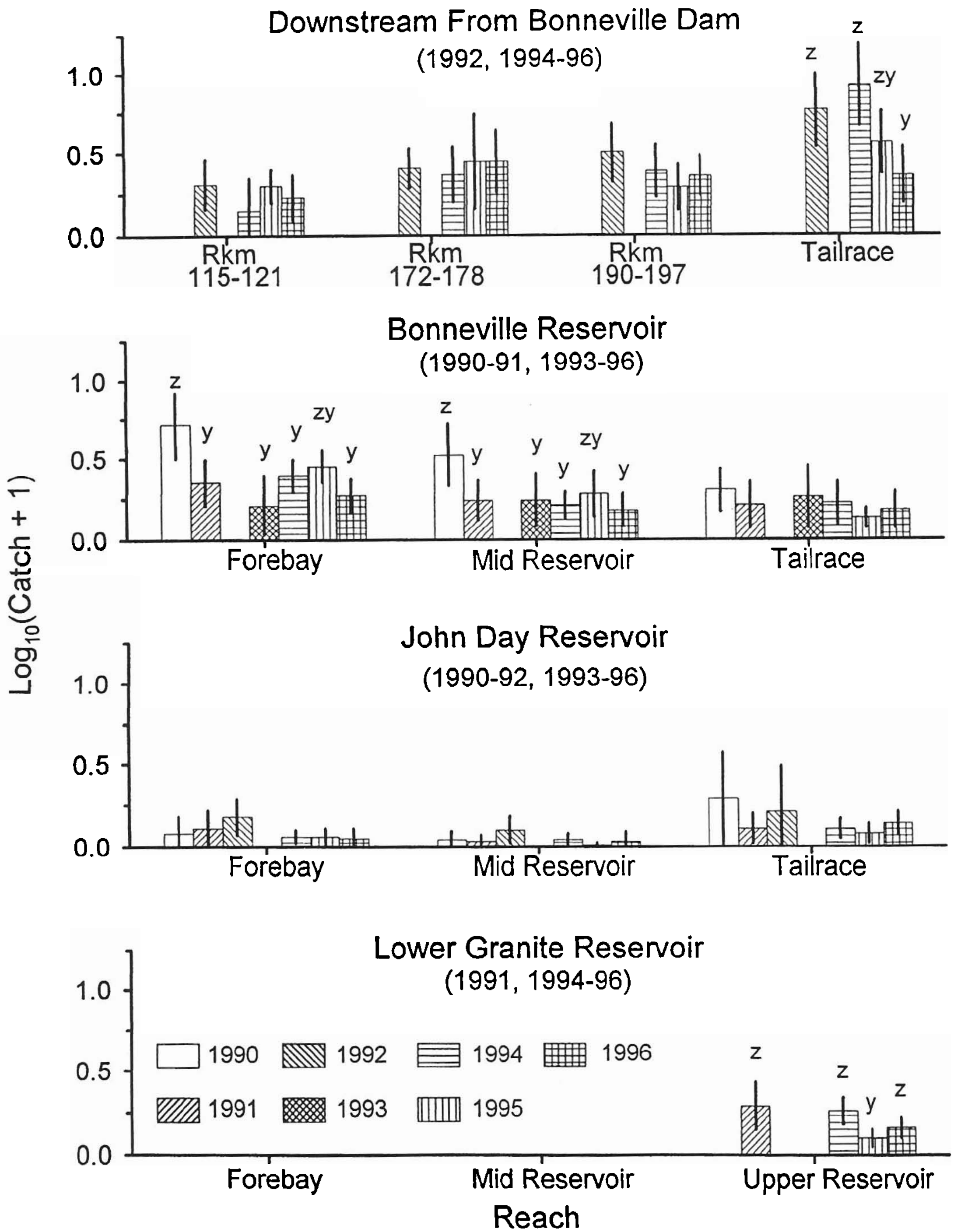

FIGURE 1.—Mean spring catches of northern pikeminnow 250 mm fork length and larger in the lower Columbia and Snake rivers during 15-min electrofishing runs, transformed to $\log_{10}$(catch + 1). Data sets with letters contain significant differences in catch among years (ANOVA; $P < 0.05$); catches in years without a letter in common differ ($P < 0.01$). Years sampled are indicated in parentheses. Vertical bars represent 95% confidence intervals; Rkm = river kilometer.

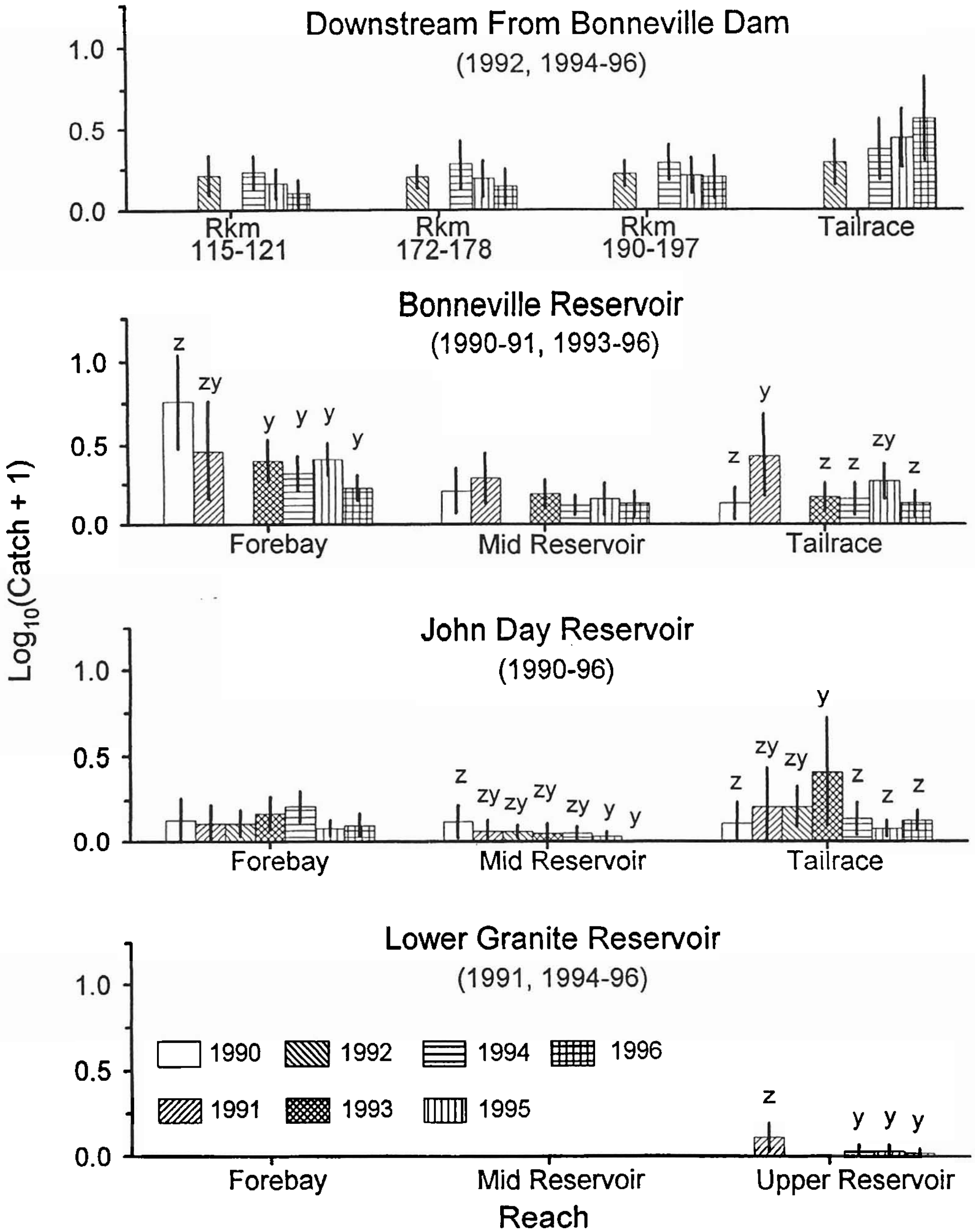

FIGURE 2.—Mean summer electrofishing catches of northern pikeminnow in the lower Columbia and Snake rivers. Conventions are those of Figure 1.

7 in 1994, growth downstream from Bonneville Dam was never significantly ($P < 0.01$) greater than in 1989 or 1990. In Bonneville Reservoir, only growth to age 8 in 1993 and to age 9 in 1993 and 1994 increased from growth in previous years. In John Day Reservoir, only growth to age 9 in 1994 was significantly greater than growth in previous years. In Lower Granite Reservoir, only growth to age 7 in 1993 was significantly greater than growth in previous years. In each of these cases, growth in subsequent years decreased, and no longer differed from growth in previous years.

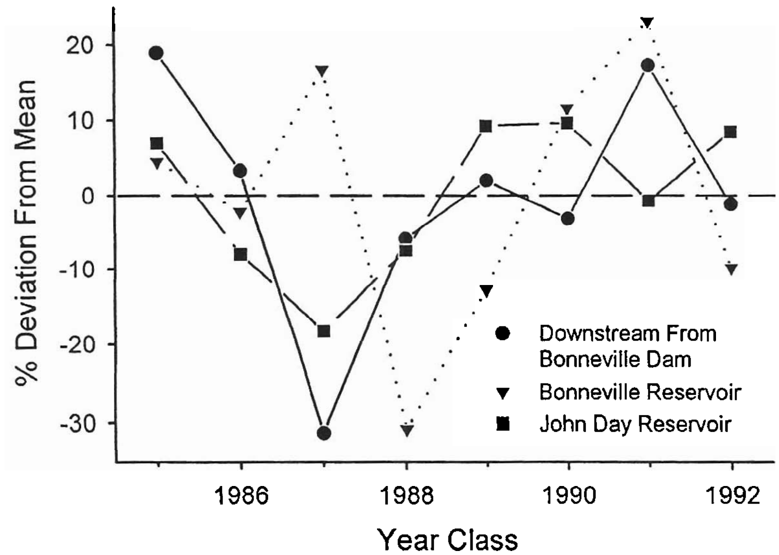

FIGURE 3.—Indexes of relative year-class strength for northern pikeminnow in the lower Columbia River.

Annual variations in growth increments were similar among areas ($P > 0.05$) except for age 6 ($P < 0.01$).

Fecundity

Fecundity (with weight as a covariate) varied significantly ($P < 0.05$) among years in all areas except Lower Granite Reservoir ($P = 0.31$; Table 3); however, we detected no increases in fecundity over time. Relative fecundities also varied among years but no trends were evident.

Discussion

Rieman and Beamesderfer (1990) suggested that sustained removals of northern pikeminnow would result in reduced predation on juvenile salmonids, primarily by reducing the relative abundance of large, piscivorous individuals. We found that catch rates of large northern pikeminnow have decreased in some areas concurrent with removals, indicating that sustained removals may indeed be altering the size structure of northern pikeminnow populations. The significant decrease in catch rates in

TABLE 2.—Age-specific catches (numbers of fish, corrected for effort) and estimates of total instantaneous mortality (Z) for year-classes of northern pikeminnow in the lower Columbia River. Mortality rates for each area without a letter in common are significantly different ($P < 0.01$).

Area, year-class	Catch at age				Z
	8	9	10	11	
Downstream from Bonneville Dam					
1985		119	62	50	0.43 z
1986	130	64	58		0.40 z
Bonneville Reservoir					
1982	40	33		13	0.39 zy
1983	73		32	30	0.32 zx
1984		34	31	23	0.20 z
1985	36	31	23	14	0.32 y
1986	34	19	14		0.45 yx
John Day Reservoir					
1982	79	72	36	27	0.39 z
1983	141	83	90	10	0.78 z
1984	111	145	24	3	1.27 z
1985	155	24	5	5	1.17 z
1986	21	5	6		0.64 z

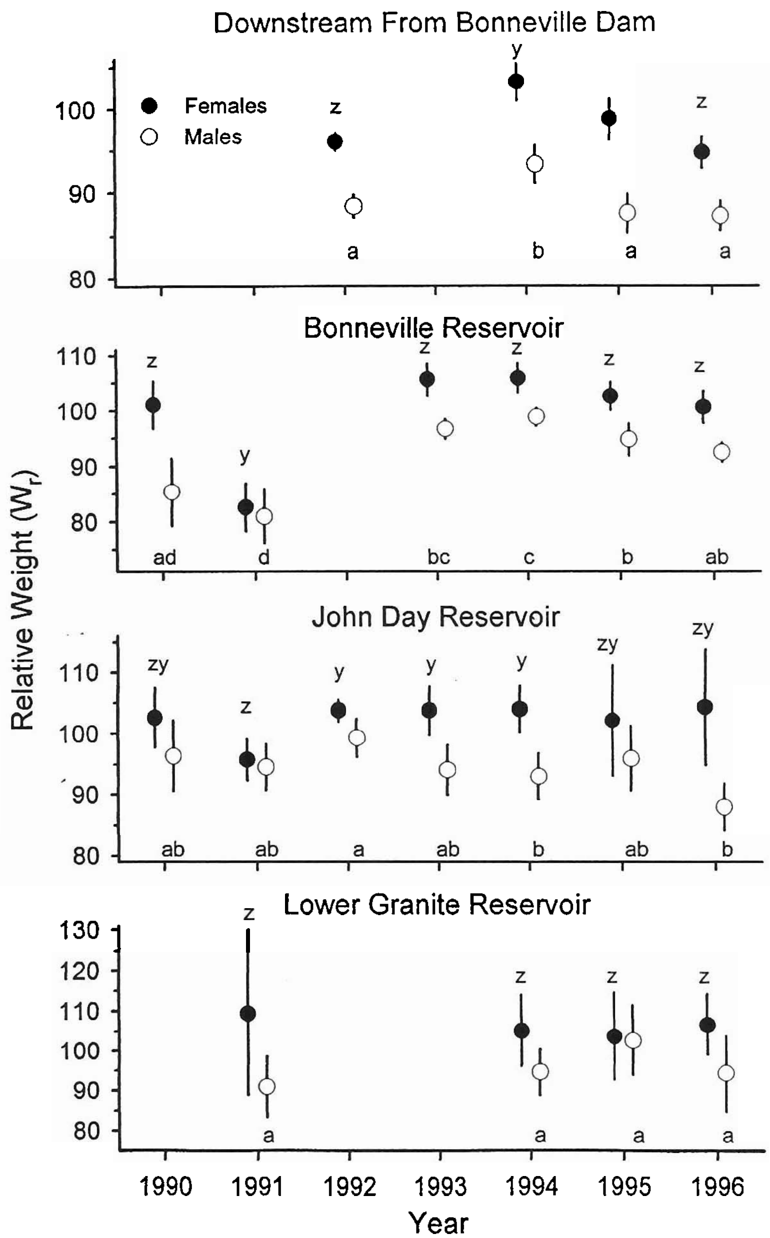

FIGURE 4.—Mean relative weight (W_r) of female and male northern pikeminnow in the lower Columbia and Snake rivers. Vertical bars represent 95% confidence intervals. Mean relative weights for each area and sex without a letter in common are significantly different ($P < 0.01$).

Bonneville Reservoir, particularly in the forebay, was greater than could be explained by fluctuations in year-class strength. Decreased catch rates in the midreach of John Day Reservoir also were not explained by variations in year-class strength. Although we do not have information on year-class strength in Lower Granite Reservoir, the significant decrease in catch rates there was proportionately similar to the decrease in Bonneville Reservoir, and far greater than any fluctuation in year-class strength observed.

Removals will have little benefit if numerically diminished northern pikeminnow populations exhibit increased growth or fecundity, or if exploi-

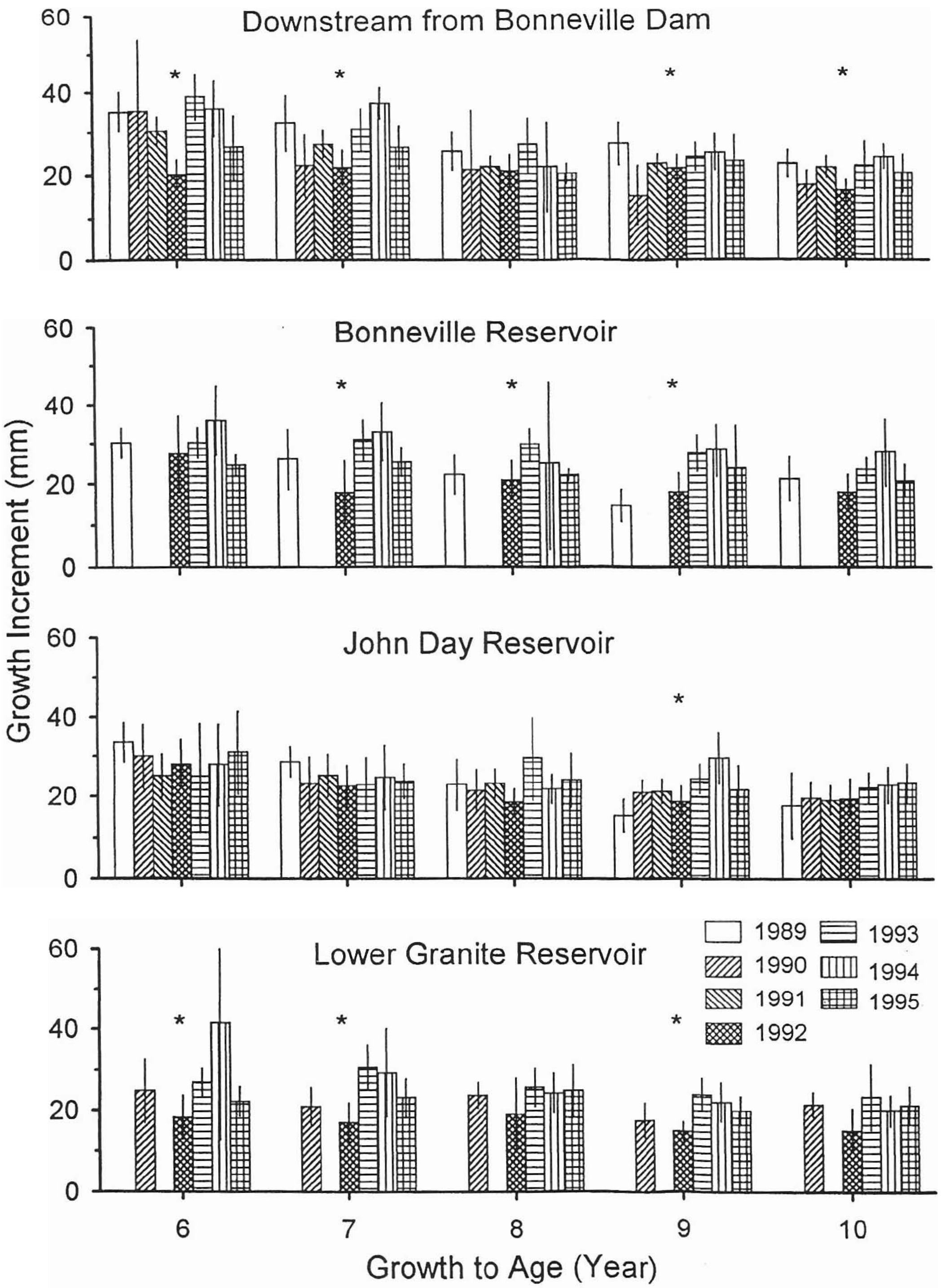

FIGURE 5.—Mean annual growth increments for female northern pikeminnow aged 6–10 in the lower Columbia and Snake rivers. Vertical bars represent 95% confidence intervals. Asterisks indicate significant differences ($P <$ 0.05) among years.

TABLE 3.—Mean fecundity and relative fecundity (number of eggs per gram body weight) of female northern pikeminnow in the lower Columbia basin. Fecundities (with weight as covariate) for each area without a letter in common are significantly different ($P < 0.01$). Analyses were limited to areas and years with $N \geq 10$ females.

Area, year	*N*	Fecundity, mean	Relative fecundity, mean (SD)
Downstream from Bonneville Dam			
1991	74	36,359 z	38.5 (15.9)
1992	294	25,036 zy	37.1 (15.0)
1993	295	22,465 y	36.2 (27.0)
1994	93	26,616 zy	35.8 (10.8)
1995	151	18,497 x	28.9 (12.1)
1996	50	24,567 zy	39.3 (8.6)
Bonneville Reservoir			
1991	46	35,820 z	43.5 (47.1)
1992	113	33,429 z	34.6 (11.4)
1993	106	29,846 zx	31.2 (11.4)
1994	116	28,347 yx	31.1 (12.2)
1995	6	18,550 –	22.3 (8.0)
1996	57	25,550 zy	31.6 (8.2)
John Day Reservoir			
1991	82	30,422 zy	28.1 (10.0)
1992	119	31,504 z	31.6 (8.8)
1993	108	25,340 x	23.7 (8.3)
1994	64	27,321 yx	24.5 (8.2)
1995	16	16,357 w	18.3 (6.7)
1996	66	35,044 z	29.7 (8.3)
Lower Granite Reservoir			
1991	51	26,594 z	31.6 (11.5)
1992	35	25,393 z	26.6 (11.0)
1993	20	30,422 z	26.1 (10.2)
1994	5	21,926 –	34.3 (22.9)
1995	8	24,053 –	20.1 (10.0)
1996	81	26,816 z	28.4 (9.1)

tation does not result in increased mortality. Significant increases in growth may allow individuals to reach predator size at a younger age than previously required and therefore be subject to fewer years of prepredation annual mortality. Increases in fecundity may offset the effect of removals on spawner abundance. Decreases in natural mortality may limit the benefit of increased mortality due to exploitation.

We found no evidence that surviving northern pikeminnow have responded to sustained removals. Mortality has increased since implementation of the removal program. Conversely, no increases in relative weight, growth, or fecundity have been realized concurrent with removals. An ideal study would have included comparisons with an area not subject to removals of northern pikeminnow; however, northern pikeminnow management has included the entire lower Columbia and Snake rivers (Friesen and Ward 1999), precluding the possibility of an appropriate control area. Confidence in our results is enhanced by the several years of data available for most areas and by comparisons of our results with those from previous studies in the lower Columbia River basin.

Our estimates of total instantaneous mortality were higher than preexploitation levels previously reported for northern pikeminnow in the Columbia and Snake rivers. Our estimates probably best represent annual mortality rates of female northern pikeminnow, because the majority of 8–11-year-olds in the lower Columbia River are females. Parker et al. (1995) found instantaneous mortality of females to be 0.34 downstream from Bonneville Dam, compared to our estimates of 0.40–0.43. Similar mortality estimates for the 1985 and 1986 cohorts probably reflects consistency in harvest rates occurring downstream from Bonneville Dam between 1994 and 1996 (13–17%; Friesen and Ward 1999).

In Bonneville Reservoir, our estimates of mortality were variable (0.20–0.45) and somewhat cyclic, but they were consistently higher than previously reported (0.14; Parker et al. 1995). Higher harvest rates occurred in 1991 and 1994–1996 (9–14%; Friesen and Ward 1999) than in 1992–1993

(4–7%), which probably contributed to variations in mortality estimates among the 1982–1986 cohorts.

Our mortality estimates for northern pikeminnow in John Day Reservoir (0.39–1.27) were considerably higher than those previously reported for females (0.20; Parker et al. 1995). Relatively high harvest rates in 1991–1993 (8–14%) followed by sharp decreases in 1994–1996 (0–7%; Friesen and Ward 1999) may explain the observed decrease in annual mortality estimates among more recent cohorts.

We found no evidence that condition of surviving northern pikeminnow has improved concurrently with sustained removals. This is consistent with Parker et al. (1995), who found no correlation between W_r and density of northern pikeminnow. Although variable, mean W_r of females has not increased in any area. Mean W_r of males appears to have increased in Bonneville Reservoir; however, decreases after 1994 resulted in the mean 1996 W_r being similar to that in 1990. 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 pikeminnow. 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.

We observed no trends in growth of northern pikeminnow that indicate a density-dependent response to sustained removals. Trends in growth were similar among areas (except for age 6) with different exploitation levels (Friesen and Ward 1999), suggesting that growth is a result of environmental or habitat conditions rather than exploitation. 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 pikeminnow in John Day Reservoir in the 1980s, and with Parker et al. (1995), who found no correlation between growth parameters and density of northern pikeminnow in the lower Columbia and Snake rivers. 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 fecundity varied, we found no evidence to suggest that individual northern pikeminnow 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 pikeminnow to sustained removals probably is unlikely, given their relatively low fecundity among known resilient fish species (Cushing 1971). We found fecundity (both pre- and postexploitation) to be within the range previously reported (Olney 1975; Parker et al. 1995).

Friesen and Ward (1999) estimated that potential predation by northern pikeminnow may have been reduced by 25% (range, 14–38%) since implementation of the management program if no compensation by surviving northern pikeminnow were occurring. Our findings indicate that changes in northern pikeminnow population structure resulting from 5–7 years of sustained exploitation have not resulted in measurable differences in their biological characteristics. Compensatory predation by northern pikeminnow and other predators in response to northern pikeminnow removals are other factors that could limit anticipated benefits of the management program. However, Zimmerman and Ward (1999) found no evidence of increased consumption of juvenile salmonids by northern pikeminnow or smallmouth bass *Micropterus dolomieu* concurrently with the implementation of the management program. Similarly, Ward and Zimmerman (1999, this issue) indicate that densities of smallmouth bass also have not increased. Continued sustained exploitation of northern pikeminnow at 1991–1996 levels probably will not result in biological compensation, which increases confidence in the hypothesis that sustained removals increase survival of juvenile salmonids. However, because of uncertainties associated with effects of long-term removal programs on northern pikeminnow populations, monitoring of population-level characteristics should continue as a parallel component of the management program.

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