ABUNDANCE, FOOD HABITS, AND SALMONID FISH CONSUMPTION OF SMALLMOUTH BASS AND DISTRIBUTION OF CRAYFISH IN LOWER GRANITE RESERVOIR, IDAHO-WASHINGTON

A Thesis
Presented in Partial Fulfillment of the Requirements for the
Degree of Master of Science
with a
Major in Fisheries Resources
in the
College of Graduate Studies
University of Idaho

by
Steven M. Anglea

June, 1997

Major Professor: David H. Bennett, Ph.D.

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ABSTRACT

I estimated absolute abundance of smallmouth bass *Micropterus dolomieu* and their consumption rate of juvenile salmonids in Lower Granite Reservoir, Idaho-Washington in 1994 and 1995. Crayfish are an important forage item for smallmouth bass and in Lower Granite Reservoir may alleviate predation on juvenile salmonids. I therefore collected baseline data on crayfish length composition and distribution throughout Lower Granite Reservoir.

From April-June 1994, 2,520 smallmouth bass ≥ 175 mm were tagged. I recaptured 9% of the tagged bass, and estimated the population size to be 20,911 smallmouth bass ≥ 175 mm. Pooled beach seine collections from 1988 to 1995 indicated an annual survival rate of 0.47 and instantaneous mortality rate of 0.75 for smallmouth bass 70 to 174 mm. The estimated survival rate, combined with the estimated abundance of smallmouth bass > 174 mm, indicated an abundance of approximately 44,490 smallmouth bass from 70 to 174 mm in Lower Granite Reservoir.

Approximately 1,001 (1994) and 3,036 (1995) smallmouth bass stomachs from four length groups (70-174 mm, 175-249 mm, 250-389 mm, and > 389 mm) were analyzed. Crayfish were the most important food item, based on percent weight, of smallmouth bass < 250 mm. Fish were the principal food item, followed by crayfish, of smallmouth bass > 249 mm. Peaks in consumption of salmonids coincided with peak passage of juvenile salmonids at Lower Granite Dam during 1994 and 1995, and were highest for smallmouth bass > 389 mm (8.939 mg salmonid/g predator/day). Consumption rates (smolts/bass/day) of out-migrating juvenile salmonids by smallmouth bass were similar to those previously reported for John Day Reservoir, Washington and Lower Granite Reservoir. In 1994, consumption rates of salmonids ranged from 0.00 to 0.38 smolts/bass/day, but were lower in 1995, ranging between

0.01 and 0.03 smolts/bass/day. In 1994 and 1995, approximately 20 million juvenile salmonids were released above Lower Granite Reservoir (Fish Passage Center, Portland, Oregon), suggesting predation may have been enhanced in 1994 as a result of lower flows, higher water temperature, and lower turbidity rather than changes in salmonid abundance. Approximately 82,476 and 64,020 juvenile salmonids were consumed by smallmouth bass in 1994 and 1995, respectively. The influence of predation, proportion of outmigrant population consumed by smallmouth bass, on subyearling chinook salmon *Oncorhynchus tshawytscha* was higher than on steelhead *O. mykiss* and yearling chinook salmon. Subyearling chinook salmon are smaller and fewer in number than steelhead and yearling chinook salmon, and rear in the reservoir for a prolonged period at a time when water temperatures are conducive to higher feeding activity of smallmouth bass.

Crayfish were captured using modified GEE brand minnow traps with 2, 3, or 4 cm entrance diameters. A total of 717 (1994) and 1,958 (1995) crayfish was captured. Mean carapace lengths of crayfish captured were significantly different ($P < 0.05$) among entrance diameters. In 1995, few crayfish were captured with carapace lengths between 28 and 32 cm, approximately age 3, suggesting the test drawdown of Lower Granite Reservoir that occurred in March 1992 may have significantly decreased survival of the 1992 cohort. The distribution of crayfish catch/effort among transects was not significantly different ($P > 0.05$) between years. Catch/effort of crayfish was highest at mid and upper reservoir transects in Lower Granite Reservoir. Catch/effort of crayfish may be higher at upstream reservoir locations as a result of more crevices and uneven substrate that provide refugia for non-burrowing crayfish.

ACKNOWLEDGMENTS

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I thank my parents for providing me with foundation and encouragement necessary to undertake and complete my Master's project. I would also like to thank Jim and Joan Bauer for their friendship and providing me with a personal look into farming in the Palouse and helping me to place smallmouth bass and crayfish into a broader perspective. I am forever indebted to my wife Karen, as the completion of this task would not have been possible without her love, continuous support, and numerous sacrifices.

TABLE OF CONTENTS

Page

Page

LIST OF FIGURES

LIST OF TABLES

APPENDIX TABLES

INTRODUCTION

Effects of over-harvest, increased hatchery releases, loss of spawning and rearing habitat, and mortality of adults and juveniles at hydropower dams have contributed to the decline of Pacific salmon *Oncorhynchus* spp. stocks within the Snake River system (Salo and Stober 1977; Raymond 1979). Rieman et al. (1991) stated that smolt losses as a result of predation in John Day Reservoir, Washington may be similar to mortality at dams and could represent the single most important source of smolt mortality during down-river migration.

The construction of reservoirs on the Columbia River has led to an increase in northern squawfish *Ptychocheilus oregonensis* abundance (Poe et al. 1991) and has also provided suitable habitat for introduced species (Bennett et al. 1991a) such as smallmouth bass *Micropterus dolomieu*. Northern squawfish has been recognized as a substantial natural predator of juvenile salmonids (Ricker 1941), but recently scientists have begun to evaluate the predatory influence of other resident fishes.

Curet (1993) was the first to evaluate smallmouth bass consumption of out-migrating juvenile salmonids in Lower Granite Reservoir, Idaho-Washington. Though his results were similar to those reported by Vigg et al. (1991) for John Day Reservoir, with mean daily consumption of subyearling chinook salmon by smallmouth bass < 390 mm ranging from 0.04-0.05 subyearling/smallmouth bass/day, Curet's (1993) study was conducted shortly after an experimental drawdown of Lower Granite Reservoir and the study area was restricted to the upper one third of the reservoir. Also, low flow and higher water temperatures in the 1992 out-migration period may have enhanced the predatory influence of smallmouth bass upon juvenile salmonids. Crayfish are an important dietary component of smallmouth bass

(Munther 1970; Curet 1993) in the Snake River, and may alleviate smallmouth bass predation on juvenile salmonids.

I evaluated the predatory influence of smallmouth bass on juvenile salmonids throughout the entire Lower Granite Reservoir during 2 years of lower (1994) and higher (1995) flows. My findings enable fishery managers to compare consumption rates of juvenile salmonids by smallmouth bass among reservoirs and reservoir conditions, and also evaluate the influence of reservoir management on crayfish populations.

OBJECTIVES

1). *Determine growth increments, absolute abundance, relative abundance, proportional stock density, population density, and standing crop of smallmouth bass in Lower Granite Reservoir;*

2). *Estimate consumption of juvenile salmonids (smolts/smallmouth bass/day and total loss) by smallmouth bass in Lower Granite Reservoir; and*

3). *Determine length composition and relative abundance of crayfish in Lower Granite Reservoir.*

STUDY AREA

Lower Granite Reservoir was formed in 1975 with the completion of the Lower Granite Lock and Dam project, and is the first impoundment encountered by juvenile salmonids migrating downstream through the Snake and Clearwater rivers. Lower Granite Dam provides electrical power generation, flood control, navigation, and recreation (Bennett et al. 1993). Lower Granite Reservoir has a total surface area of 3,602 ha, 16.6 m mean depth, and maximum depth of 42.1 m, and extends from Lower Granite Dam (Rkm 173.1) upstream beyond the confluence of the Snake and Clearwater rivers in Idaho (Rkm 224.6). My study area was approximately 53 km long, extending from Lower Granite Dam to the confluence of the Snake and Clearwater rivers (Rkm 224.6; Figure 1). I divided approximately 102 km of shoreline within Lower Granite Reservoir into 255 sampling sites (0.40 km) and three strata: stratum 1 (Rkm 211.3-224.6), stratum 2 (Rkm 193.5-211.3), and stratum 3 (Rkm 173.1-193.5; Figure 1). The habitat type present at each sampling site was recorded as either cliff, talus, cobble, sand, or rip-rap. The main channel substrate in the lower reservoir consists largely of silt, while the substrate in the upper reservoir is characterized by sand, large cobble, and boulders (Lepla 1994).

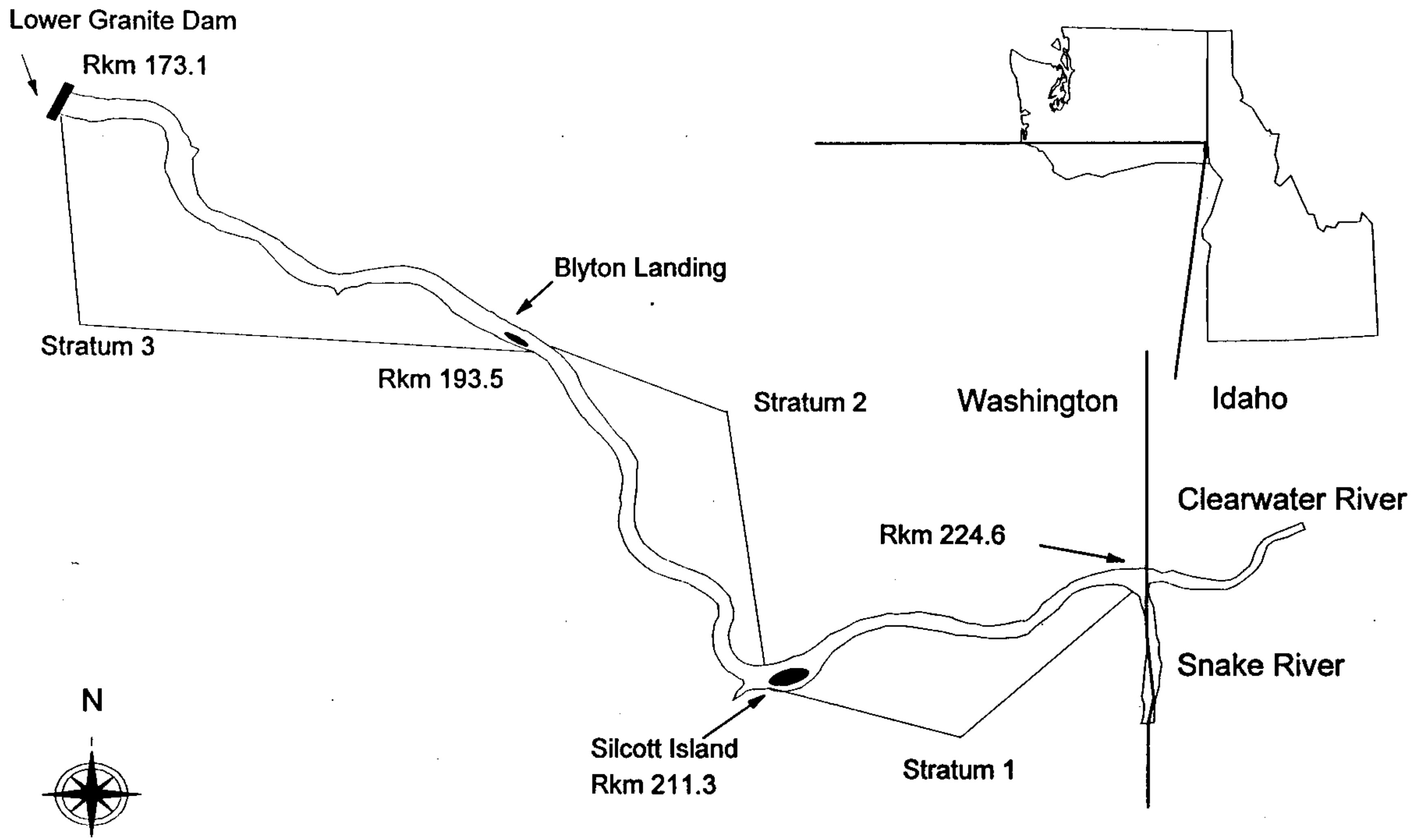

Figure 1. Location of strata in Lower Granite Reservoir, Idaho-Washington where smallmouth bass were sampled from April-November 1994-1995.

LOWER GRANITE RESERVOIR SMOLT OUT-MIGRATION

Stocks of juvenile anadromous salmonids that currently migrate through Lower Granite Reservoir are steelhead *Oncorhynchus mykiss*, yearling chinook salmon *O. tshawytscha*, and subyearling chinook salmon. Based on counts conducted at the Lower Granite Dam juvenile collection facility in 1995, steelhead and yearling chinook salmon passed through the reservoir fairly rapidly, with out-migration beginning in early April, peaking (numbers collected per day at Lower Granite Dam) in late April, and early May, and ending in June. Subyearling chinook salmon passage was relatively protracted, with initial passage in April and peak passage not occurring until late July and early August (Figure 2).

In 1995, approximately 5,900,000 steelhead, 3,700,000 yearling chinook salmon, and 31, 000 subyearling chinook salmon were collected at Lower Granite Dam. A total of 175 fall chinook salmon redds was counted in 1994, which should have produced approximately 210,000-525,000 subyearling chinook salmon entering the reservoir in 1995. Redds were observed in the Clearwater (122), Salmon (37), Grand Ronde (15), and Snake (1) rivers in 1994 (W. Connor, U.S. Fish and Wildlife Service, Ahsahka, Idaho, personal communication). Estimates of 30% (W. Connor, personal communication) and 75% (C. Eaton, University of Idaho, Moscow, personal communication) were used to determine the range of expected egg-to-fry survival. The lower estimate of 30% survival reflects the increase in mortality experienced by chinook salmon eggs as a result of prolonged exposure to incubation water temperatures < 4.5°C (Combs and Burrows 1957). Survival estimates of 90% and 95% were used for fry-to-smolt and smolt-to-reservoir life stages (W. Connor, personal communication).

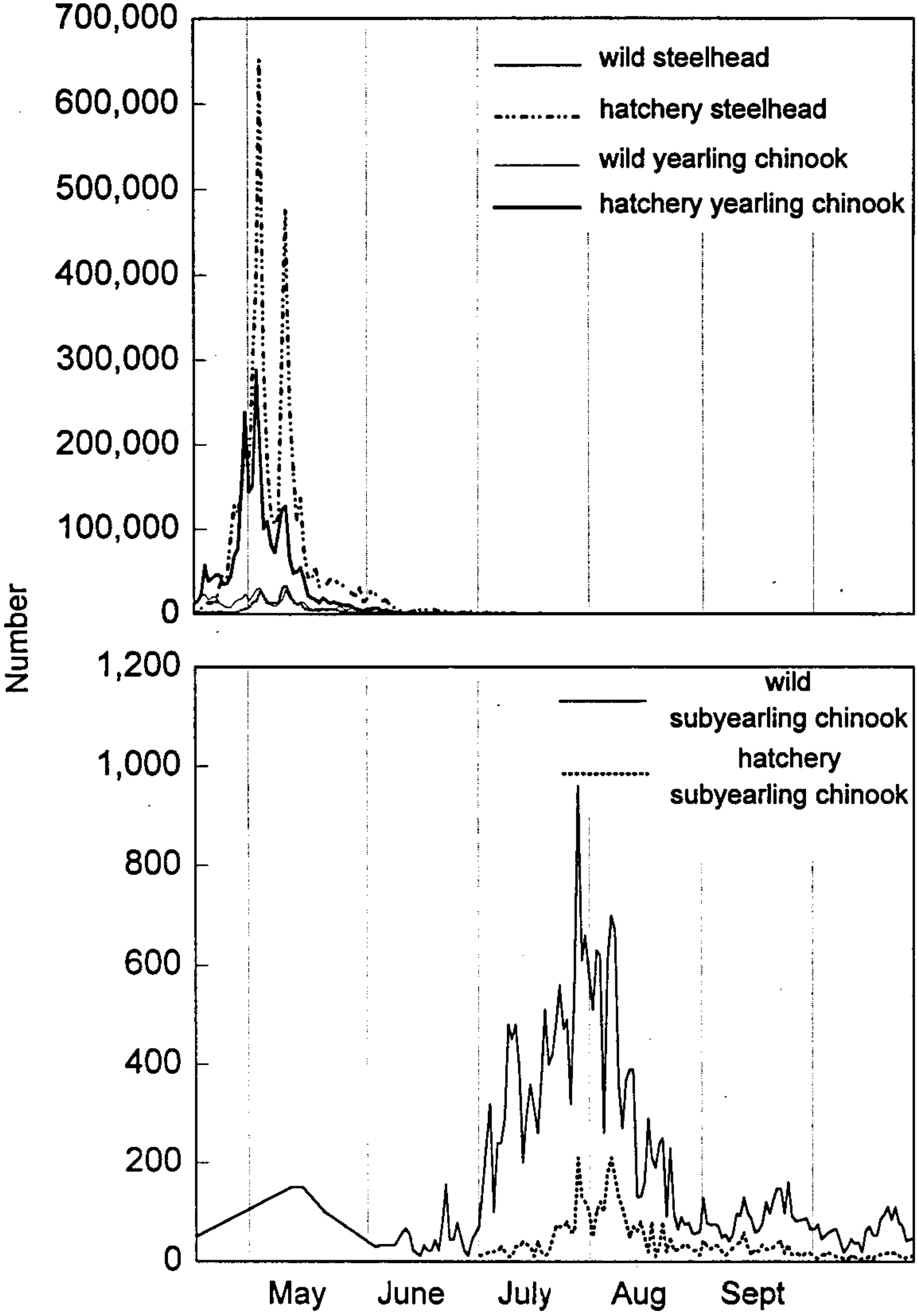

Figure 2. Timing and magnitude of salmonid out-migration through Lower Granite Reservoir, based on counts at Lower Granite Dam, 1995.

Objective 1. Determine growth increments, absolute abundance, relative abundance, proportional stock density, population density, and standing crop of smallmouth bass in Lower Granite Reservoir.

ABSTRACT

The absolute abundance of smallmouth bass in Lower Granite Reservoir was evaluated in 1994 and 1995 using a multiple-census mark-release and recapture study design. From April through June 1994, 2,520 smallmouth bass (> 174 mm) were tagged. I recaptured 9% of the tagged bass, providing an estimated absolute abundance of 20,911 smallmouth bass > 174 mm. Analysis of pooled beach seine collections from 1988 to 1995 in Lower Granite Reservoir indicated an annual survival rate of 0.47 and instantaneous mortality rate of 0.75 for smallmouth bass 70 to 174 mm. The survival rate, combined with the estimated abundance of smallmouth bass (> 174 mm), indicated an abundance of approximately 44,490 smallmouth bass from 70 to 174 mm in Lower Granite Reservoir. From the two abundance estimates, I determined that a population of approximately 65,400 smallmouth bass (> 69 mm) inhabits Lower Granite Reservoir: 44,490 from 70-174 mm, 17,565 from 175-249 mm, 3,137 from 250-389 mm, and 209 > 389 mm.

I calculated proportional stock densities of 8% (1994) and 5% (1995) for smallmouth bass in Lower Granite Reservoir. Smallmouth bass > 69 mm exhibited a density of 18.2 fish/ha and a standing crop of 1.02 kg/ha. The estimated density of smallmouth bass > 199 mm was 3.4 fish/ha and the standing crop was 0.75 kg/ha (1994) and 0.57 kg/ha (1995).

INTRODUCTION

The first introduction of smallmouth bass into the Snake River reportedly occurred between the late 1800's (Munther 1970) and the 1940's (Keating 1970). Populations of smallmouth bass in the Columbia River received little fishing pressure in the early 1900's, as abundant populations of trout, steelhead, and salmon were the principal fishes sought by fishermen (Henderson and Foster 1956). More recently, fishing pressure on regional bass populations has increased as coldwater fishing opportunities have declined (Rieman 1987). The construction of dams in the Snake River has transformed the riverine environment into a series of impoundments suitable for non-native fish (Bennett et al. 1991a) such as smallmouth bass. Smallmouth bass are found throughout lower and middle reaches of the Snake River and many of its major tributaries (Munther 1970). Temperature may be the most important environmental factor regulating abundance of northern populations of smallmouth bass (Clady 1975).

Impoundment of the lower Snake River appears to have affected annual growth increments of smallmouth bass. Keating (1970) reported a length at age 1 of 85 mm for smallmouth bass collected from the lower Snake River (the 77 km section from the Salmon River to the confluence of the Snake and Clearwater rivers) prior to impoundment; whereas, Bennett et al. (1983) reported a length of 71 mm for age 1 smallmouth bass collected in Little Goose Reservoir, Washington. Additionally, Keating (1970) reported annual growth increments of 35 to 15 mm for smallmouth bass ages 4 to 8 prior to impoundment, while Bennett et al. (1983) found annual growth increments of 54 to 27 mm for the same aged smallmouth bass from Little Goose Reservoir. Growth rates of smallmouth bass in the Snake River are substantially lower than those reported for John Day Reservoir (Bennett et al.

1991b) and also for populations within the native range of the species (Keating 1970). Bennett et al. (1983) reported annual growth increments ranging from 71 to 23 mm for smallmouth bass ages 1 to 10; whereas, Nigro et al. (1985a) reported annual growth increments ranging from 81 to 29 mm for John Day Reservoir. Carlander (1977) reported mean lengths for age 1 smallmouth bass ranging from 82 mm for populations in the northeastern U.S. to 107 mm for populations in the southeast. Cool water temperatures in the Snake River are probably the major environmental factor influencing growth increments, and may also influence abundance and cohort strength. Survival of age 0 fish is an important factor in determining recruitment and cohort strength in fish populations (Kramer and Smith 1960; Shuter et al. 1980; Coutant and DeAngelis 1983)

Shuter et al. (1985) reported that in years of poor growth, smallmouth bass < 60 mm rarely survive the winter. Similarly, Bowles (1985) noted a positive relationship between the length of largemouth bass *M. salmoides* at the end the first growing season and overwinter survival in northern Idaho. Populations of smallmouth bass in the Snake River are likely subject to high rates of overwinter mortality after the first growing season, and low year-class strength due to the short growing season and slow rate of growth (Bennett et al. 1983; Bennett and Dunsmoor 1986). Oliver et al. (1979) determined larger smallmouth bass (> 80 mm) survive their first winter better than smaller ones possibly due to greater energy reserves. Smallmouth bass that forage on fish or crayfish early in their first growing season may be larger and acquire greater energy reserves by the end of the growing season, compared to bass whose diet consists primarily of zooplankton and insects.

Smallmouth bass diet composition is influenced by the abundance and availability of prey (Coble 1975). In the lower Snake River, smallmouth bass diets are dominated by insects during spring, by fish and crayfish during summer, and by insects in the fall (Bennett et al. 1983). Smallmouth bass become torpid as water temperature decreases in the fall and rarely feed at temperatures < 10°C (Coble 1975).

Empirical determination of smallmouth bass abundance in the Columbia River Basin is limited to research conducted in John Day Reservoir. Beamesderfer and Rieman (1991) determined an average of 34,954 (1.8 fish/hectare) smallmouth bass ≥ 200 mm was present in John Day Reservoir in 1985 and 1986, compared to density estimates of midwestern smallmouth bass populations (16 to 164 fish/ha) reported by Carlander (1977). Proportional stock density estimates of smallmouth bass populations in the Columbia River Basin ranged from 45% for John Day Reservoir (Nigro et al. 1985a; Nigro et al. 1985b), to 38% for Ice Harbor Reservoir, Washington and 9% for Lower Granite Reservoir (Bennett, University of Idaho, unpublished data). Bennett et al. (unpublished data) calculated a mean smallmouth bass standing crop of 0.53 kg/ha for Little Goose Reservoir. Currently, estimates of standing crop are not available for other smallmouth bass populations in the Columbia River Basin.

As stocks of anadromous salmonids have declined, scientists have begun to evaluate more closely the influence of predation on out-migrating salmonids. Reservoir specific estimates of predator abundance and length composition are necessary to accurately describe this predator-prey relationship.

OBJECTIVE

1). *Determine growth increments, absolute abundance, relative abundance, proportional stock density, population density, and standing crop of smallmouth bass in Lower Granite Reservoir.*

METHODS

Smallmouth Bass Collection

Smallmouth bass were collected in each of the three strata to assess spatial differences in abundance. The number of sites sampled within each stratum and of each habitat type was determined using the proportional allocation formula (Scheaffer et al. 1990). Sampling sites were then randomly selected from a list of potential sites. In 1994, I sampled 50 sites on a monthly basis from April through June. In 1995, I sampled 60 sites in April and semimonthly from May through July.

Smallmouth bass were collected by electrofishing, beach seining, and angling. Nighttime electrofishing was conducted by boat, traveling parallel to the shoreline and operating with an electrical output of approximately 400 volts at 3-5 amps. I restricted beach seine hauls to sites consisting of talus, cobble, or sand habitats. One to three beach seine hauls were conducted at each sampling site using a 30.5 x 2.4 m beach seine with a 2.4 x 2.4 x 2.4 m bag constructed of 0.64 cm knotless nylon mesh. The beach seine was deployed parallel to and approximately 15 m from the shoreline and pulled toward shore to sample an area of approximately 454 m^2. Angling was conducted during April and May of 1994 at rocky outcroppings and underwater benches using a variety of natural and artificial baits. All captured smallmouth bass were measured to total length (mm), weighed (g), and released. From April through June 1994, I marked all captured smallmouth bass > 174 mm with individually numbered Floy anchor tags.

Age and Growth

I used scale analysis to determine annual growth increments of smallmouth bass collected during spring 1994. Scales were removed at the extension of the pectoral fin ventral to the lateral line. Impressions of each scale were made on acetate slides using 52°C heat and a 350 kg/cm^2 press. Scales were aged using a Vantage Com IV Microform 45X reader. Each scale was read two to three times before the position of the focus, annuli, and scale edge were marked on a piece of paper. I used a Houston Hipad tablet to digitize the scale readings. Back-calculated mean length-at-age was determined with DISBCAL (Frie 1982) using the Frazer Lee method (Carlander 1982):

$$Ln = a + \frac{Sn}{Sc}\left(Lc - a\right)$$

where: a = intercept value of best straight line relationship,

Sn = scale measurement to a given annulus, n,

Sc = scale measurement to edge,

Lc = length of fish at capture.

Absolute Abundance Estimation

I used a multiple-census mark-release and recapture study design (Schnabel 1938) to estimate the absolute abundance of smallmouth bass in Lower Granite Reservoir. I assumed that smallmouth bass in Lower Granite Reservoir represented a "closed" population, suggesting no births, deaths, or migrations occurred over the period of sampling (Garthwaite and Buckland 1990). Additional assumptions were that marked and unmarked smallmouth bass have equal mortality and capture rates, marked smallmouth bass were randomly distributed throughout the entire reservoir or sampling of marked smallmouth bass was random, marks were not lost, and all marked smallmouth bass recaptured were recognized and counted (Lagler 1956).

The Schnabel Estimator (Schnabel 1938) as modified from Overton (1965) was used to estimate absolute abundance of smallmouth bass in Lower Granite Reservoir:

$$\hat{N} = \frac{\sum (c_t m_t)}{((\sum r_t) + 1)}$$

where: c_t = total sample taken on day t,

m_t = number of marked fish in population at start of day t,

r_t = number of recaptures on day t.

I used a Poisson Distribution to calculate confidence intervals due to the low number of recaptures (5-10%) and normalized the variance estimation using the following equation (Ricker 1975):

$$r' = \sum r_t + 1.92 \pm 1.96\sqrt{\sum r_t + 1}\ .$$

To determine upper and lower bounds of the confidence interval for the absolute abundance estimate, r' was inserted into the following equation: $\hat{N} = \sum (c_t m_t)/r'$.

The population estimate was expanded to include smallmouth bass 70-174 mm (ages 1 to 3). Scale analysis of smallmouth bass collected during spring (April-June) 1994 was used to determine smallmouth bass length-at-age in Lower Granite Reservoir. Catch/effort of smallmouth bass ages 1 to 3 from beach seine collections conducted during spring 1988 through 1995 was used as an index of abundance. Assuming constant recruitment and survival, I estimated total annual survival ($\hat{S}$) of smallmouth bass ages 1, 2, and 3 using the Heincke Method (Seber 1982): $\hat{S} = (n - n_0)/n$. Total sample size is represented by n and the abundance of age 1 smallmouth bass in the sample by n_0. The instantaneous mortality rate ($\hat{Z}$) was then determined using: $\hat{Z} = -\ln(\hat{S})$. Variance of $\hat{S}$ was estimated using: $V[\hat{S}] = S(1-S)/n$ (Seber 1982). The abundance of smallmouth bass 70-174 was back-calculated from the estimated absolute abundance of smallmouth bass > 174 mm using the estimated survival rate.

Relative Abundance Estimation

Relative abundance based on catch/effort was used to determine if the abundance of smallmouth bass differed among strata. Catch/effort estimates from individual sites within a stratum were averaged to determine a mean catch/effort value for the entire stratum. Absolute abundance of smallmouth bass within each stratum was estimated to facilitate estimation of smolt losses due to smallmouth bass predation in Lower Granite Reservoir (Objective 2). Monthly stratum abundance of each length class was estimated using the equation:

$$\hat{N}_{ijk} = \hat{N}_{i\_} * \frac{A_j * CE_{ijk}}{\sum\left(A_j * CE_{ijk}\right)}$$

where: $\hat{N}_{i\_}$ = Schnabel abundance estimate * frequency of length class *i*,

A_j = percent reservoir area of stratum *j*,

CE_{ijk} = catch/effort of length class *i* in stratum *j* in month *k*.

Proportional Stock Density, Population Density, and Standing Crop

Electrofishing data collected from April through June 1994 and 1995 were used to estimate proportional stock density (PSD), population density (fish/ha), and standing crop (kg/ha) of smallmouth bass in Lower Granite Reservoir. I used stock and quality lengths of 180 and 280 mm, respectively to calculate the PSD (Anderson and Weithman 1978). I calculated population density and standing crop by estimating the absolute abundance and mean lengths of six length classes of smallmouth bass in Lower Granite Reservoir: 70-174 mm, 175-199 mm, 200-249 mm, 250-399 mm, 300-349 mm, and > 349 mm. The mean weight of each length class was determined by inserting the mean length of each length class into the following equation developed for smallmouth bass in Little Goose Reservoir by Bennett et al. (1983): $W = 1.64\text{x}10^{-5}*(L^{2.94})$, where W is weight (g) and L is total length (mm). I determined population density and standing crop for two length classes of smallmouth bass (> 69 mm and > 199 mm) by combining length class abundance and biomass estimates, and dividing by the surface area of Lower Granite Reservoir (3,602 ha). Confidence intervals (95%) for population density and standing crop estimates were constructed using upper and lower bounds of the absolute abundance estimate.

RESULTS

Age and Growth

I aged scales from 314 smallmouth bass to determine length-at-age and annual growth increments. Mean annual growth increments ranged from 81 to 26 mm for smallmouth bass ages 1 to 8 (Table 1). Annual growth increments decreased to 37 mm during the fourth year of growth and were < 35 mm for all successive age classes.

Absolute Abundance

A total of 2,396 smallmouth bass, ranging in length from 175 to 473 mm was marked with Floy anchor tags from 12 April to 30 June 1994. The recapture effort was conducted from 14 June through 30 June 1994 and consisted of sampling 148 randomly selected 0.40 km sites distributed throughout the reservoir. During the recovery effort, I collected 910

Table 1. Total length (mm) at age, annual growth increments, and number of smallmouth bass examined for age and growth from Lower Granite Reservoir during spring 1994.

	Age							
Variable	1	2	3	4	5	6	7	8
Length	81	145	202	246	289	324	350	383
Increment	81	64	52	37	34	30	31	26
n	314	313	233	141	56	19	8	6

smallmouth bass, 84 of which were tagged, yielding an overall tag recovery rate of approximately 9%. The modified Schnabel estimator yielded an absolute abundance estimate of 20,911 (17,092-26,197; 95% confidence intervals) smallmouth bass > 174 mm. Spring (April-June) electrofishing catches of smallmouth bass > 174 mm in 1994 and 1995 indicated > 80% of the smallmouth bass were between 175 and 249 mm, and < 1% were > 389 mm (Figure 3).

Pooled beach seine collections from 1988 to 1995 in Lower Granite Reservoir, indicated an annual survival rate of 0.47 (0.465-0.475; $Z = 0.76$) for smallmouth bass 70 to 174 mm. The estimated instantaneous mortality rate combined with the estimated absolute abundance of smallmouth bass > 174 mm indicates approximately 44,490 (43,931-44,969) smallmouth bass from 70 to 174 mm inhabit Lower Granite Reservoir. Combining the two abundance estimates yields a population abundance of approximately 65,400 (61,023-71,166) smallmouth bass > 69 mm in Lower Granite Reservoir: 44,490 from 70-174 mm, 17,565 from 175-249 mm, 3,137 from 250-389 mm, and 209 > 389 mm.

Relative Abundance

Electrofishing catch-per-unit-effort (catch/effort) increased for all length classes from April through July 1995 in all strata (Figure 4). Catch/effort of smallmouth bass 70-174 mm during June in stratum 1 (3.11 fish/min) was significantly higher ($P < 0.05$) than observed in stratum 2 (0.99 fish/min) and stratum 3 (0.71 fish/min). Catch/effort of smallmouth bass 70-174 mm was significantly different ($P < 0.05$) among strata in July, with stratum 1 having the highest catch/effort (2.83 fish/min) and stratum 3 the lowest (1.09 fish/min). Catch/effort of smallmouth bass 175-249 mm in April and July was significantly ($P < 0.05$) higher in stratum 3 (1.92 fish/min) than in stratum 1 (1.17 fish/min) and stratum 2 (1.09 fish/min). No

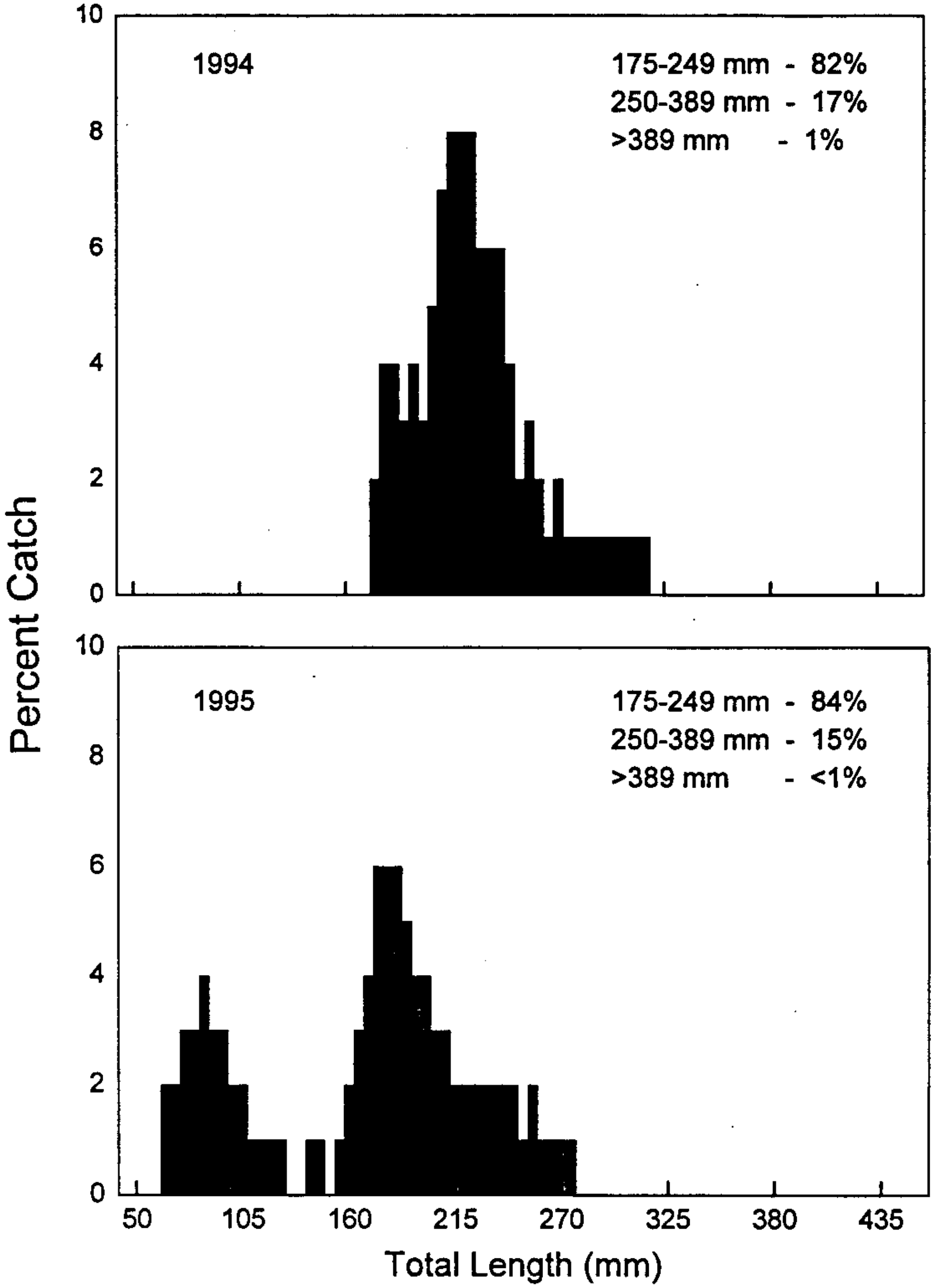

Figure 3. Length distribution of smallmouth bass sampled by electrofishing during spring 1994-1995, Lower Granite Reservoir. Smallmouth bass > 174 mm were collected in spring 1994.

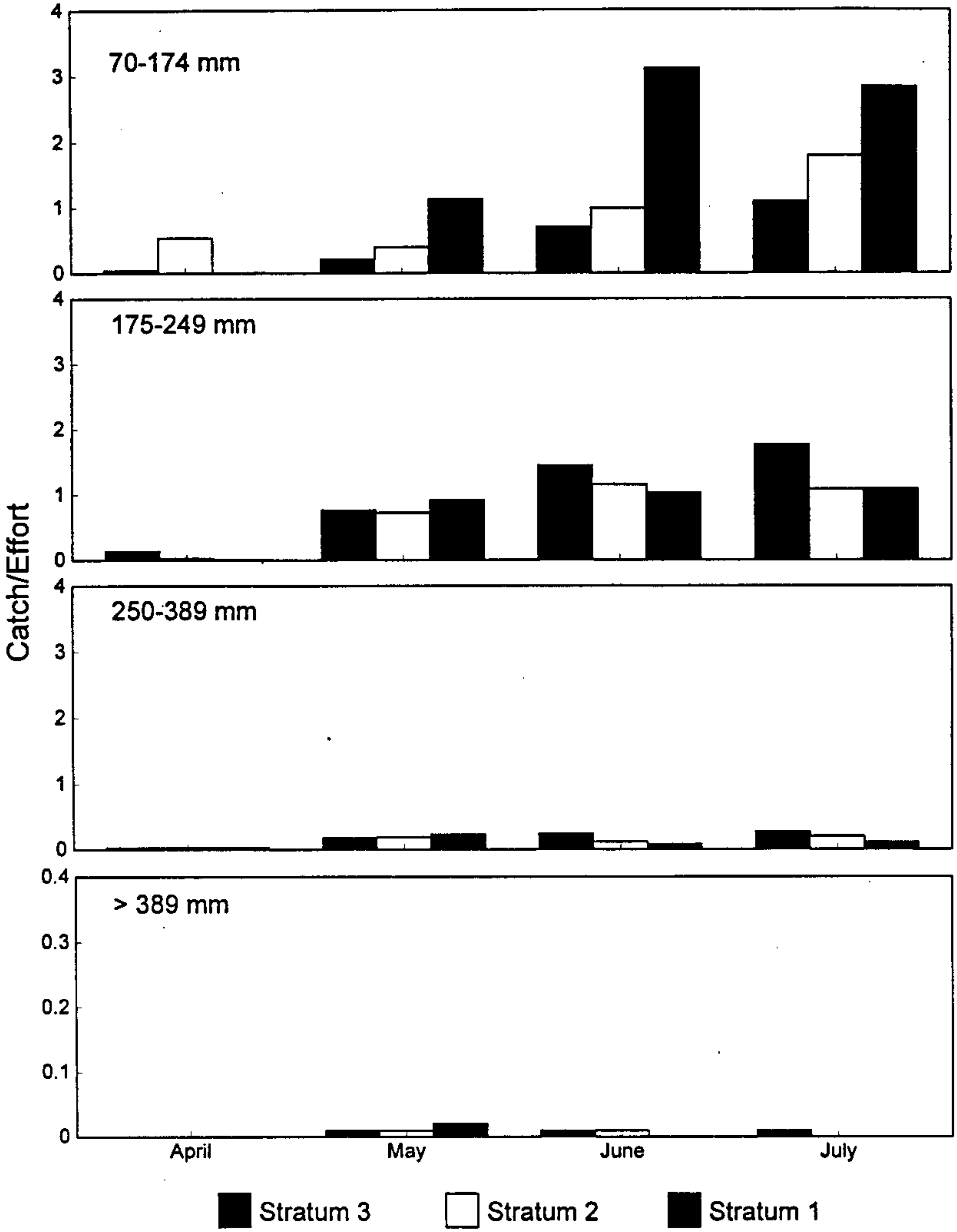

Figure 4. Catch/effort of smallmouth bass collected from April-July by electrofishing in Lower Granite Reservoir, 1995.

significant difference ($P > 0.05$) in catch/effort of 175-249 mm smallmouth bass was observed among strata during May or June. I found similar catch/effort ($P > 0.05$) of smallmouth bass 250-389 mm among strata during April, May, and June. In July, catch/effort of smallmouth bass 250-389 mm was significantly higher ($P < 0.05$) in stratum 3 (0.27 fish/min) than in stratum 1 (0.11 fish/min). No significant difference ($P > 0.05$) was observed in catch/effort of smallmouth bass > 389 mm among strata and months.

Proportional Stock Density, Population Density and Standing Crop

A PSD of 8% was calculated from 1994 spring electrofishing samples, whereas a PSD of 5% was found for smallmouth bass collected during spring 1995 in Lower Granite Reservoir. The estimated abundance of 65,400 smallmouth bass > 69 mm in Lower Granite Reservoir is equivalent to 18.2 fish/ha (16.9-19.8 fish/ha) and 3.4 fish/ha (2.8-4.3 fish/ha) for smallmouth bass > 199 mm. Estimated standing crop of smallmouth bass > 69 mm in 1995 was 1.02 kg/ha (0.88-1.21 kg/ha). Standing crop estimates of smallmouth bass > 199 mm in Lower Granite Reservoir were 0.75 kg/ha (0.62-0.95 kg/ha; 1994) and 0.57 kg/ha (0.46-0.71 kg/ha; 1995).

DISCUSSION

Age and Growth

The length at first annulus formation (81 mm) that I observed for smallmouth bass collected from Lower Granite Reservoir in 1994 is similar to the lower range of values reported for other populations of smallmouth bass in the Pacific Northwest (Table 2). My scale analysis results indicate that smallmouth bass ages 1 and 2 are between 70 and 174 mm, smallmouth bass ages 2 to 4 are between 175 and 249 mm, smallmouth bass ages 4 through 8

Table 2. Total lengths (mm) at age and annual growth increments from selected populations of smallmouth bass in the Pacific Northwest.

		Age												
Location	Measurement	1	2	3	4	5	6	7	8	9	10	11	12	13
Lower Granite Reservoir, ID-.WA	Length	81	145	202	246	289	324	350	383					
(1994)	Increment	81	64	52	37	34	30	31	26					
Little Goose Reservoir, WA	Length	71	132	190	244	298	336	363	390	411	434	454	478	497
(Bennett et al. 1983)	Increment	71	61	58	54	54	38	27	27	21	23	20	24	19
Upper Snake River, ID	Length	87	151	212	249	273	296	310	326					
(Keating 1970)	Increment	87	64	61	37	24	23	14	16					
Lower Snake River, ID	Length	85	145	205	240	267	291	309	324					
(Keating 1970)	Increment	85	60	60	35	27	24	18	15					
Lower John Day Reservoir, WA	Length	81	145	210	261	306	346	375	395	434	463			
(Nigro et al. 1985b)	Increment	81	64	65	51	45	40	29	20	39	29			
Upper John Day Reservoir, WA	Length	100	183	261	317	358	393	416	437	440	436	458	449	
(Nigro et al. 1985b)	Increment	100	83	78	56	41	35	23	21	3	NA	22	NA	
Lake Sammamish, WA	Length	101	185	260	314	357	383	414						
(Pflug and Pauley 1984)	Increment	101	84	75	54	43	26	31						

range from 250 to 389 mm, and smallmouth bass age 9 and older are > 389 mm. Annual growth increments and length-at-age are similar to those reported by Bennett et al. (1983) for smallmouth bass in Little Goose Reservoir. Annual growth increments of smallmouth bass collected in Lower Granite Reservoir during 1994 ranged from 81 to 26 mm and are representative of what Anderson and Weithman (1978) considered a small growth increment.

My determination of annual growth increments coupled with those of Keating (1970) provides a pre and post reservoir perspective of smallmouth bass growth in the lower Snake River. Annual growth increments were > 30 mm for smallmouth bass ages 5 through 7 collected during 1994, whereas Keating (1970) reported annual growth increments < 30 mm for ages 5 through 7. Annual degree days (> 10°C) differed little between the time of my sampling effort and that of Keating (1970). From 1987 through 1995, annual degree days in Lower Granite Reservoir ranged from 1,113 to 1,550 degree-days and averaged 1,318 degree-days. Keating (1970) reported mean degree days from 1960 through 1967 of 1,330 and 1,554 for lower and upper (the 68 km section from Johnson Bar within Hells Canyon to the Salmon River) regions of the Snake River, respectively, and related cool temperatures as a possible reason for slower growth among older ages of smallmouth bass.

I believe that differences in growth rates observed in my study and Keating's (1970) study, despite the similarity in degree days and thus growing period between the two studies, indicates a factor other than temperature may be regulating growth of larger smallmouth bass. Food supply was identified by Coble (1967) as being more important than water temperature in influencing growth of larger smallmouth bass. Crayfish were important prey items for smallmouth bass captured by Keating (1970), as well as for smallmouth bass I sampled in

Lower Granite Reservoir during 1994 and 1995 (Objective 2). The formation of Lower Granite Reservoir in 1975 may have provided abundant unexploited habitat for crayfish, potentially increasing their availability to larger smallmouth bass, and resulting in increased annual growth increments.

Annual growth increments of smallmouth bass collected in 1994 in Lower Granite Reservoir were considerably smaller than those noted for populations of smallmouth bass in the upper region of John Day Reservoir (Nigro et al. 1985b) and in Lake Sammamish, Washington (Pflug and Pauley 1984). Smallmouth bass in upper John Day Reservoir attained a total length of 100 mm by first annulus formation and smallmouth bass in Lake Sammamish were 101 mm at age 1, compared to 81 mm for smallmouth bass in Lower Granite Reservoir.

Abundance

I consider my population estimate to be precise and representative of the abundance of smallmouth bass in Lower Granite Reservoir. Confidence intervals for the absolute abundance estimate of smallmouth bass > 174 mm in Lower Granite Reservoir were relatively narrow (17,092-26,197) compared to those reported for smallmouth bass > 200 mm in John Day Reservoir (18,967-44,929; 29,019-46,899) by Beamesderfer and Rieman (1991). My research probably represents the best estimate of smallmouth bass abundance and density within the Columbia River Basin.

The validity of my smallmouth bass abundance estimate is based largely on the time and duration (April through June 1994) of the sampling effort. Overton (1965) suggests that the effect of changes in population abundance over time, can be reduced by limiting the duration of the sampling period. The 91 day period I used was short relative to the estimate made in John Day Reservoir (153 days; Beamesderfer and Rieman 1991). I conducted the mark-release and recapture effort during spring to more effectively sample smallmouth bass with shoreline oriented gear. Smallmouth bass redistribute in the spring, moving from deep to shallow water where they resume feeding activity (Coble 1975). Water temperatures ranged from 8 to 19°C during April through June in Lower Granite Reservoir and catch/effort of smallmouth bass is high during this period (Arthaud 1992). Catch/effort of smallmouth bass with electrofishing gear in the Red Cedar River, Wisconsin was highest in mid June when water temperature was 20°C (Paragamian and Coble 1975). Smallmouth bass forage and spawn within the shallow water habitats and then move into deeper water after spawning (Montgomery et al. 1980). Suitable water temperatures for spawning (13 to 21°C; Carlander 1977; 12 to 25°C; Graham and Orth 1986), typically occur from mid June to late July in Lower Granite Reservoir.

The difference in relative abundance of smallmouth bass 70-174 mm among strata is most likely related to the distribution of spawning habitat within the reservoir. Bennett et al. (1983) observed smallmouth bass nests exclusively on low gradient, gravel shorelines in Little Goose Reservoir. Suitable spawning habitat for smallmouth bass in Lower Granite Reservoir is located predominately in the upper region of the reservoir. I believe that the density of smallmouth bass nests in the upper region of the reservoir may be higher than in downstream locations, probably resulting in higher densities of juvenile smallmouth bass within this area. Dispersal of juvenile smallmouth bass from their natal areas may reduce strata differences in density of smallmouth bass > 174 mm.

Proportional Stock Density, Population Density and Standing Crop

My estimates of PSD for smallmouth bass in Lower Granite Reservoir for 1994 (8%) and 1995 (5%) are consistent with PSD estimated by Bennett et al. (9%; unpublished data) for Lower Granite Reservoir. Bennett et al. (unpublished data) estimated PSD's of 38%, 19%, 15%, and 9% for smallmouth bass within Ice Harbor, Lower Monumental, Little Goose, and Lower Granite reservoirs, respectively (Figure 5). Length frequency distributions of smallmouth bass collected during 1984 and 1985 in John Day Reservoir indicated a PSD of 45% (Nigro et al. 1985a; Nigro et al. 1985b). Proportional stock densities in Lower Granite Reservoir ranged from 5 to 16% during the last 8 years (Bennett et al. unpublished data), which confirms the observation by Bennett et al. (1991b) that northwestern reservoirs contained low numbers of quality-sized smallmouth bass. Low PSD values are indicative of a population consisting largely of small individuals and may result from slow growth rates or high mortality of quality-sized bass (Anderson and Weithman 1978). Anderson and Weithman (1978) noted that populations in which quality length was attained at age 5 or older may demonstrate low PSD values due to slow growth. My collections of smallmouth bass during 1994 indicate attainment of quality length at age 5. I determined the mean smallmouth bass harvest length to be 285 mm (n = 42) from voluntarily tag returns by Lower Granite Reservoir anglers in 1994 and 1995, suggesting larger smallmouth bass are being selectively removed from the population.

Densities of ten smallmouth bass populations reported by Carlander (1977) ranged from 16 to 164 fish/ha. Paragamian (1991) reported smallmouth bass densities that ranged from 2 to 911 fish/ha for 22 sites examined in Iowa, while Beamesderfer and Rieman (1991) reported a density of 1.8 fish/ha for smallmouth bass (>199 mm) in John Day Reservoir. My

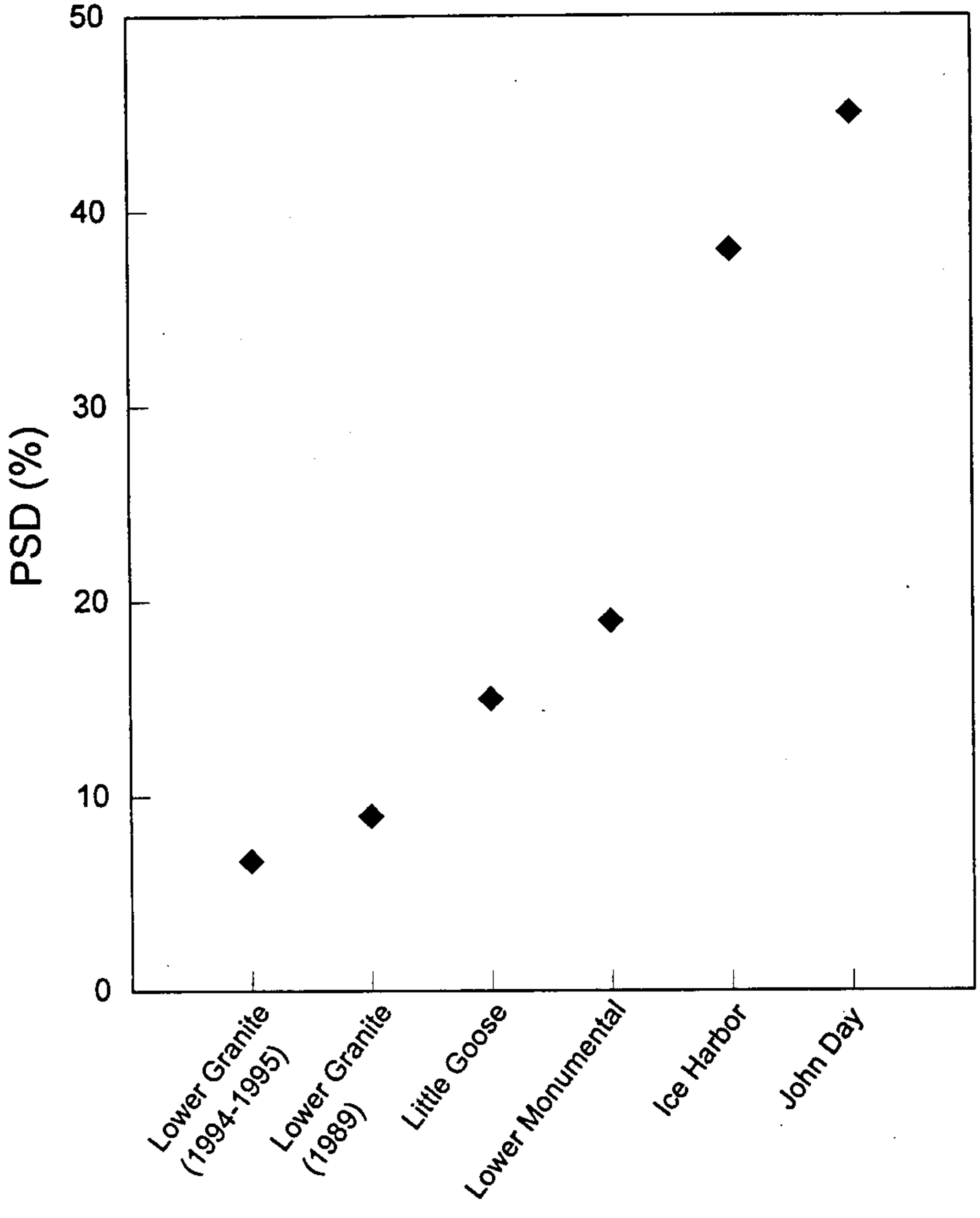

Figure 5. Proportional stock densities for smallmouth bass populations in lower Snake River reservoirs and John Day Reservoir, Columbia River.

data indicate that the density of smallmouth bass (> 199 mm; 3.4 fish/ha) in Lower Granite Reservoir is higher than that reported for John Day Reservoir and is consistent with the lower range of values reported in literature.

Estimated standing crops of smallmouth bass > 199 mm in Lower Granite Reservoir were 0.75 kg/ha (1994) and 0.57 kg/ha (1995), consistent with the estimate of Bennett et al. (1983) who reported a standing crop of 0.53 kg/ha for smallmouth bass > 200 mm in Little Goose Reservoir. The standing crop values I found are similar to the lower values noted for populations of smallmouth bass from other geographic areas (Schneider 1973; Fajen 1975; Funk 1975). Schneider (1973) observed a standing crop of 1.13 kg/ha for smallmouth bass in a Michigan lake and standing crops of smallmouth bass in a Missouri creek ranged from 4.4 to 15.5 kg/ha (Fajen 1975). Funk (1975) reported standing crops for populations of smallmouth bass in Oklahoma, Ohio, and Indiana ranging from 0.2 to 46.3 kg/ha. Fajen (1975) speculated that consistently low standing crops of smallmouth bass may be a function of high exploitation and low recruitment. My data show the standing crop of smallmouth bass in Lower Granite Reservoir is on the lower end of values reported in literature.

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Objective 2. Estimate consumption of juvenile salmonids (smolts/smallmouth bass/day and total loss) by smallmouth bass in Lower Granite Reservoir.

ABSTRACT

Diet composition and consumption rates of juvenile salmonids were determined for four length groups of smallmouth bass: 70-174 mm, 175-249 mm, 250-389 mm, and > 389 mm in Lower Granite Reservoir. A total of 1,001 (1994) and 3,036 (1985) smallmouth bass stomachs were analyzed. Crayfish were the most important food item, based on percent weight, of smallmouth bass < 250 mm. Fish were the principal food item, followed by crayfish, of smallmouth bass > 249 mm.

Peaks in mean daily ration (mg prey/g predator) of salmonids coincided with peak passage of juvenile salmonids at Lower Granite Dam in 1994 and 1995, and was highest for smallmouth bass > 389 mm (8.939 mg prey/g predator). Consumption rates (smolts/bass/day) of out-migrating juvenile salmonids by smallmouth bass were similar to those reported for John Day Reservoir and for Lower Granite Reservoir in earlier studies. In 1994, consumption rates of salmonids ranged from 0.00 to 0.38 smolts/bass/day, but were lower in 1995, ranging between 0.01 and 0.03 smolts/bass/day. In 1994 and 1995, approximately 20 million juvenile salmonids were released above Lower Granite Reservoir (Fish Passage Center, Portland, Oregon), suggesting predation may have been enhanced in 1994 as a result of lower flows, higher water temperature, and lower turbidity rather than changes in salmonid abundance.

Assuming a constant predator abundance, approximately 82,476 and 64,020 juvenile salmonids were consumed in Lower Granite Reservoir by smallmouth bass > 69 mm in 1994 and 1995, respectively. The influence of predation by smallmouth bass was highest on

subyearling chinook compared to steelhead and yearling chinook. Smallmouth bass consumed approximately 7% of the subyearling chinook salmon migrating through the reservoir and < 0.02% of the steelhead and yearling chinook salmon outmigrants. Subyearling chinook salmon are fewer in number, of smaller length, and rear in the reservoir for a prolonged period of time when water temperatures are conducive to higher feeding activity by smallmouth bass.

INTRODUCTION

Analyses of smallmouth bass dietary habits in the Snake River have focused primarily on describing seasonal changes in diet composition (Keating 1970; Bennett and Shrier 1986; Bennett and Dunsmoor 1986). However, recent interest in the predatory influence of resident fishes on out-migrating juvenile salmonids requires a more rigorous approach to dietary analysis. Vigg et al. (1991) described the consumption rates of juvenile salmonids by northern squawfish, walleye *Stizostedion vitreum*, channel catfish *Ictalurus punctatus*, and smallmouth bass in John Day Reservoir using methods detailed by Swenson and Smith (1973). The method detailed by Swenson and Smith (1973) accounts for differences among predators and environments to produce fine-scale feeding chronologies and consumption rates.

Smolt losses as a result of predation may be similar to mortality at dams and could represent the single most important source of mortality (Rieman et al. 1991). Juvenile salmonids pass through several reservoirs during their out-migration. Differences in reservoir environments, predator populations, and composition and abundance of outmigrants requires a reservoir-by-reservoir approach to describing the influence of predation on out-migrating juvenile salmonids.

Curet (1993) was the first to describe the predatory influence of smallmouth bass on juvenile salmonids in Lower Granite Reservoir. He determined that smallmouth bass consumed 0.04-0.05 smolts/smallmouth bass/day and approximately 31,512 subyearling chinook salmon in May 1992. A drawdown of Lower Granite and Little Goose reservoirs was conducted in March 1992 as a physical test on the dams and related structures, and may have influenced consumption rates by concentrating predators and prey, and also by reducing the abundance of benthic invertebrates in the reservoirs (Bennett et al. 1994). Crayfish are an important forage item of smallmouth bass in the Snake River (Bennett and Shrier 1986). Low flow and reduced turbidity following the drawdown may have also provided an environment conducive to higher feeding activity by smallmouth bass.

I evaluated the diet composition and consumption rates of juvenile salmonids and alternative prey fish of smallmouth bass throughout the entire reservoir from April through November in 1994 and 1995. Current estimates of consumption rates coupled with reservoir specific abundance estimates (Objective 1) will provide the best estimate of smolt losses due to predation by smallmouth bass in Lower Granite Reservoir.

OBJECTIVE

1). *Estimate consumption of juvenile salmonids (smolts/smallmouth bass/day and total loss) by smallmouth bass in Lower Granite Reservoir.*

METHODS

Smallmouth Bass Collection

Shoreline collections occurred in each of the three strata to evaluate possible spatial differences in the consumption rate of juvenile anadromous salmonids. Smallmouth bass were collected following procedures outlined in Objective 1. I used daytime and nighttime electrofishing and angling to collect smallmouth bass for dietary analyses.

Dietary Collection and Analyses

Stomach contents of smallmouth bass > 69 mm collected from April through November in 1994 and 1995, were analyzed to describe seasonal changes in diet and determine consumption rates of juvenile salmonids. Captured smallmouth bass were immediately placed in a live-well. Stomach contents were evacuated using a modified lavage technique (Seaburg 1957), flushed onto a mesh filter, and then transferred to a sample container where they were preserved in 10% formalin solution. Crayfish and fish prey items were removed from smallmouth bass stomachs with forceps when lavage was not successful. When possible, species of prey fish were identified immediately upon removal from the stomach. Total length and weight of each predator was recorded after removal of prey items.

Prey items removed from stomachs of smallmouth bass were identified to the lowest practical taxon. Number and digested weight of each prey item were recorded. When possible, parts of insects were combined with similar prey items and total number estimated. Partially digested, unidentifiable insects were weighed as a group. Digested weights were obtained by blotting prey items dry and weighing to the nearest mg.

Estimated live weights of prey fish were used in the analysis. Live weights of prey fish were estimated from fork length (FL-nearest mm) to weight (g) regression equations developed by Vigg et al. (1991). When prey fish were too digested to measure lengths, diagnostic bone lengths and nape to tail lengths were used to determine FL using regression equations developed by Hansel et al. (1988). Lengths of diagnostic bones were taken from cleithrum, opercle, dentary, and hypural bones found in stomach samples. Vertebrae shape was used to distinguish between salmonid and non-salmonid prey fish when preferred bony structures were absent.

Stock identification of salmonid prey fish (steelhead, yearling chinook salmon, and subyearling chinook salmon) was determined by comparing prey fish FL to stock specific length frequencies of smolts collected at Lower Granite Dam. Comparisons were restricted to length frequencies of smolts that passed through Lower Granite Dam within 7 days of the predator collection. Bennett et al. (1993) and Curet (1993) used the range of lengths of juvenile salmonids captured during routine sampling to identify unknown salmonids in stomach samples of northern squawfish and smallmouth bass in Lower Granite Reservoir.

Due to the possibility of length related differences in dietary composition and salmonid consumption, analyses were conducted using four length classes of smallmouth bass: 70-174 mm, 175-249 mm, 250-389 mm, and > 389 mm. Curet (1993) used three length classes of smallmouth bass (< 250 mm, 250-389 mm, and > 389 mm) to describe daily consumption of subyearling chinook salmon in Lower Granite Reservoir.

Seasonal changes in diets of smallmouth bass were determined using frequency of occurrence (FO) and percent weight (WT) of prey items. Prey items were consolidated into categories of salmonid, non-salmonid, unknown fish, crayfish, insects, and miscellaneous. Frequency of occurrence and WT values were determined for specific prey items and groups.

Prey items within each category were consolidated prior to calculating FO and WT since they are not additive (Dunsmoor 1990).

Consumption rates of juvenile salmonids by smallmouth bass were calculated for each length class of predator. Vigg et al. (1991) outlined the eight steps involved in estimating mean daily consumption and daily ration (Figure 6): (1) Stomach contents were first evaluated on a diel time period. Six, 4 hr time intervals were used to describe diel differences in consumption of juvenile salmonids in 1994 and 1995. (2) The original prey weight was back-calculated from regressions of weight versus body length and bone measurements determined by Hansel et al. (1988). (3) Percent digestion or mass evacuation by predator was calculated as the difference between the estimated original prey weight and sample (digested) weight. (4) Evacuation rates (digestion time in hours) of smallmouth bass were predicted from regression equations presented by Rogers and Burley (1991) and were a function of predator size (g), mass evacuated (g), and water temperature (°C). Duration of digestion (h) was determined by solving the following evacuation rate equation for smallmouth bass as presented by Vigg et al. (1991):

$$268.529(E+0.01)^{0.696}S^{-0.364}e^{-0.139T}P^{-0.175};$$

E represents prey mass evacuated (g), S is prey meal weight (g), T is temperature (°C), and P is predator weight (g). Prey meal weight (g) was calculated as described by Vigg et al. (1991) using the following equation:

$$S = O_i + O_j + D_k;$$

O_i is the original weight of the specified prey fish item, O_j is the original weight of other prey fish items in the sample that were within 10% of their original weight and 20% of the

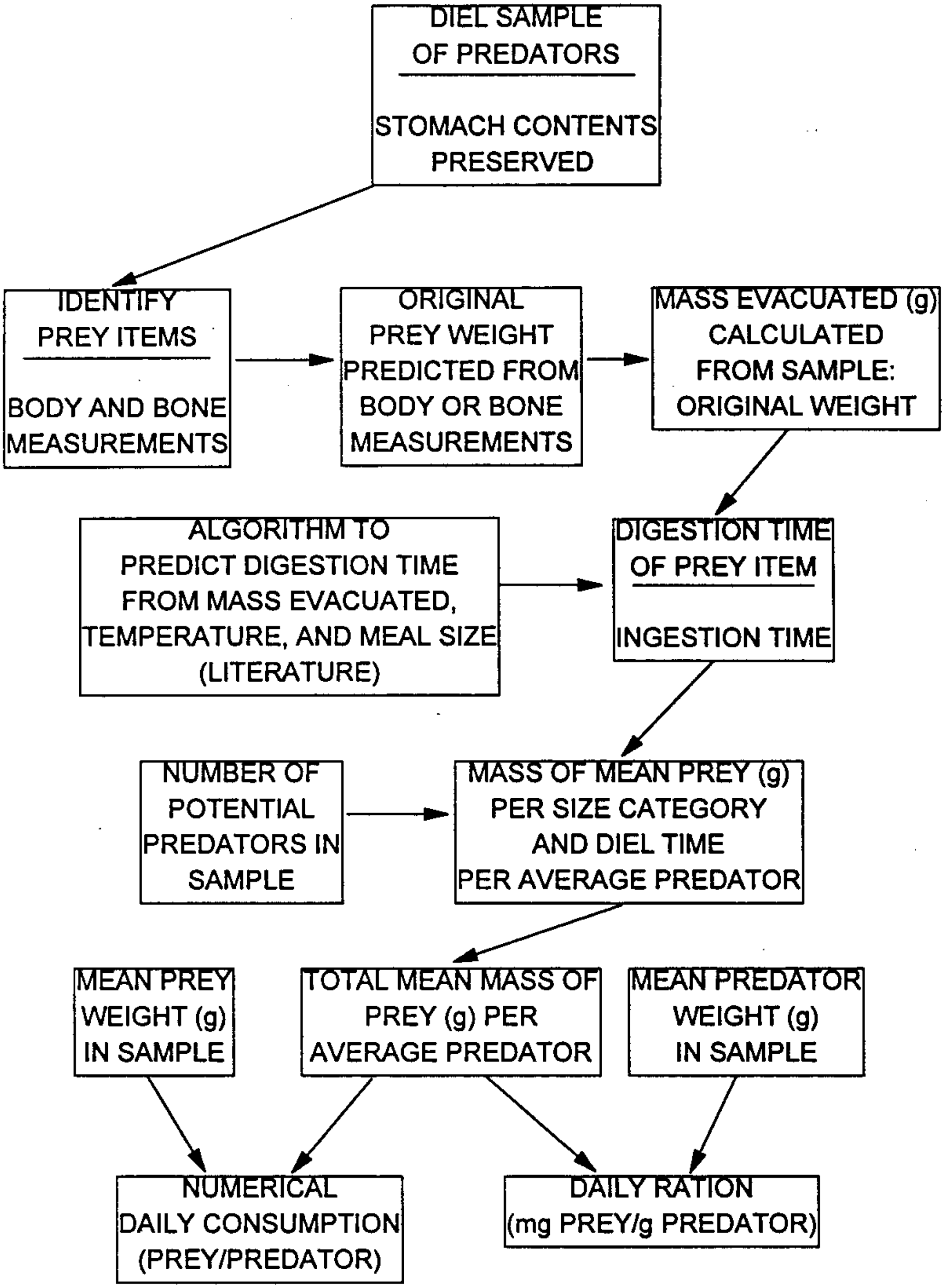

Figure 6. Flow diagram showing the processes involved in calculating consumption rates of juvenile salmonids by smallmouth bass (from Vigg et al. 1991).

percent digestion of the specified prey item, and D_k is the digested weight of all other food items in the sample. (5) Time of ingestion of each prey fish was derived from steps (3) and (4) by back-calculating from the time of predator collection and the degree of prey fish digestion. (6) The mass of prey consumed per diel time period per prey size category per day was calculated. (7) Data from step (6) was divided by the number of predators in the sample that could have ingested the selected prey fish type, of size *j* during time period *i,* to estimate average mass consumed per average predator. Mean daily consumption rates of juvenile salmonids were determined for each month, April through November, following procedures outlined in Vigg et al. (1991):

$$C = \sum_{i=1}^{t} \sum_{j=1}^{s} \frac{\sum_{k=1}^{p} W_{ij}}{F_{ij}};$$

C is the daily consumption (g) by an average predator, W_{ij} is the undigested weight of prey fish *k* of *p*, in a given 10 g size category *j* of *t* ($t = 11$) during a given diel time interval *i* of *s* ($s = 6$), and F_{ij} is the number of potential predators from the sample that could have contained prey fish of size *j* that were no more than 90% digested during period *i* (i.e. a smallmouth bass was considered a predator in all 4 hr time intervals from the time of capture back to when a prey item would have been detectable; Wahl and Nielsen 1985). (8) Daily ration (mg prey/g predator/day) and numerical consumption (prey/predator/day) are determined by dividing C, total mean mass of prey (g) per average predator per day, by mean predator and prey weights for the sample as follows:

Daily Ration (mg prey/g predator/day) = C * 1000 / Mean Predator Weight (g);

Numerical Consumption (prey/predator/day) = C / Mean Prey Weight (g).

Data from individual smallmouth bass stomachs, based on the selection criteria of predator length, prey type, reservoir location, and month were pooled to estimate mean daily ration and numerical consumption. Pooling of predator stomachs yields a single estimate of mean daily ration and numerical consumption, making direct calculation of confidence intervals difficult. Confidence intervals (95%) were therefore estimated using the bootstrap resampling method (Shao and Dongsheng 1995). The mean consumption rate estimated from the initial pooling of selected smallmouth bass stomachs was used as the point estimate for the 95% confidence interval. The resampling procedure randomly selected records from the entire smallmouth bass data set and selected those, with replacement, that met the specified selection criteria. Each iteration generated a new data set from the smallmouth bass records that met the specified selection criteria. The new data set contained a number of predator records equal to the number of records that met the specified selection criteria used to generate the point estimate. One-thousand iterations were performed, which resulted in a data set of 1,000 estimates of numerical consumption that were then used to generate standard error estimates for the initial point estimate.

Estimated Loss

Procedures presented by Rieman et al. (1991) were used to calculate total loss of juvenile salmonids to smallmouth bass predation:

$$L_{ij} = PS_iC_{ij}D_jG_{ij};$$

L_{ij} is the loss of salmonids to predator size group i during month j, P is the number of smallmouth bass > 69 mm, S_i is the proportion of each predator population within size group i, C_{ij} is consumption of predator size group i during month j, D_j is the number of days in month *j*, and G_{ij} is the proportion of juvenile salmonids in the diet of predator size group *i* during month *j*.

RESULTS

Diet Composition

A total of 1,207 and 3,059 smallmouth bass stomachs > 69 mm was sampled in 1994 and 1995, respectively. Approximately 80% of the samples were from bass ranging in length between 70 and 249 mm , whereas < 1% were from smallmouth bass > 389 mm (Figure 7).

Fish were the most abundant prey item, by weight, from April-June, whereas crustaceans and insects increased in abundance after June in both years (Figure 8). Salmonids accounted for 89% (1994) and 56% (1995) of the total diet weight during April-June (Figure 8).

In 1994 and 1995, distinct differences in the percent weight of salmonids, non-salmonids, crustaceans, and insects were found among length classes of smallmouth bass (Figure 9). As smallmouth bass length increased, fish increased in abundance while insects decreased. Crayfish composed 43.4% (1994) and 37.7% (1995) of the total diet weight of smallmouth bass 70-174 mm (Table 3). Salmonids were absent from stomach samples of smallmouth bass 70-174 mm in 1994 and contributed 0.28% of the total diet weight in 1995.

Crayfish were the most abundant food item by weight of smallmouth bass 175-249 mm in 1994 and 1995 (55.0% and 64.0% of total, respectively; Table 3). Finfish were second in abundance, constituting 28.7% (1994) and 26.3% (1995) of the total diet weight. Salmonid prey accounted for 5.5% and 3.5% of the total diet weight in 1994 and 1995, respectively.

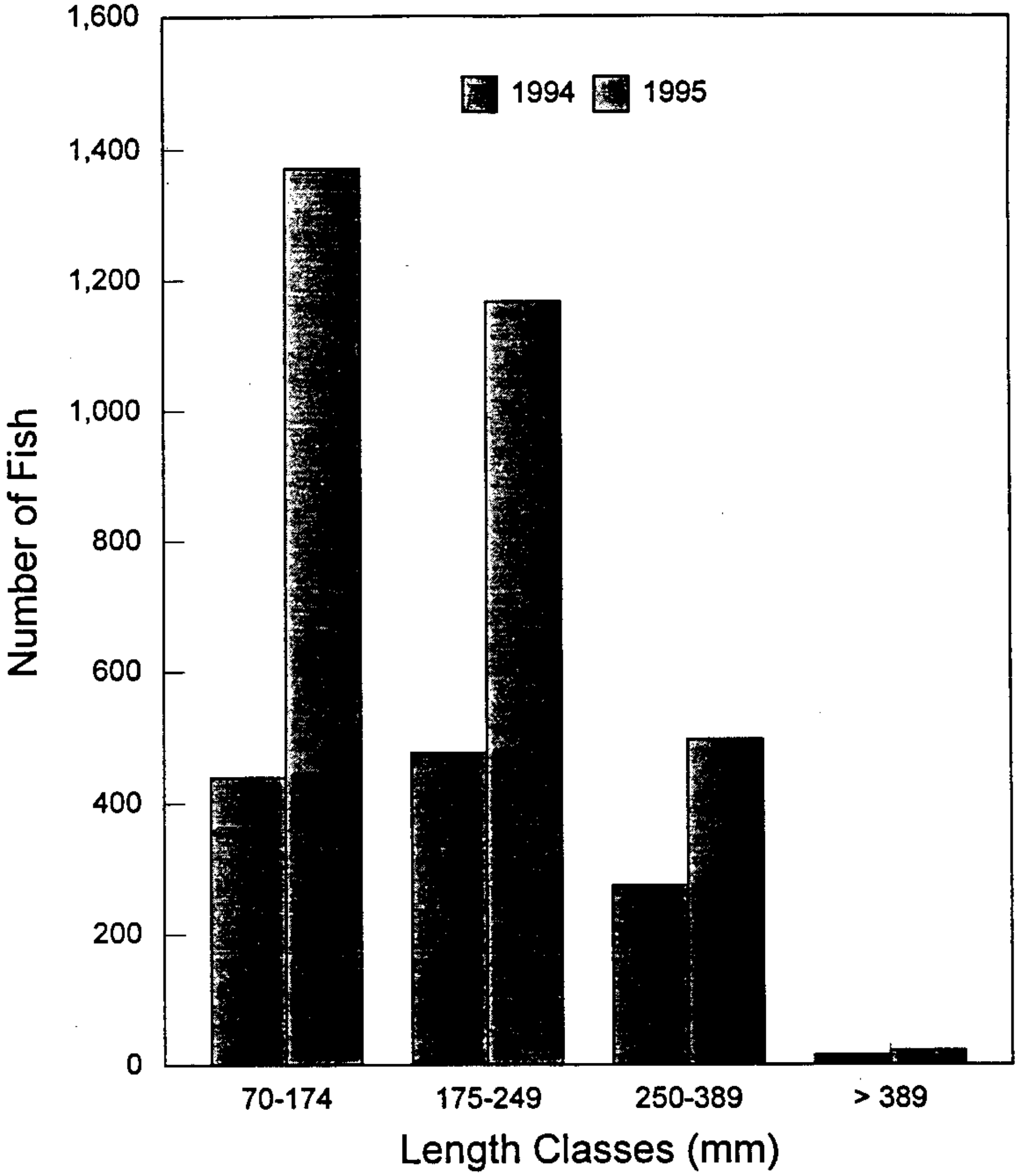

Figure 7. Length frequency of smallmouth bass sampled for dietary analyses in Lower Grantite Reservoir, 1994-1995.

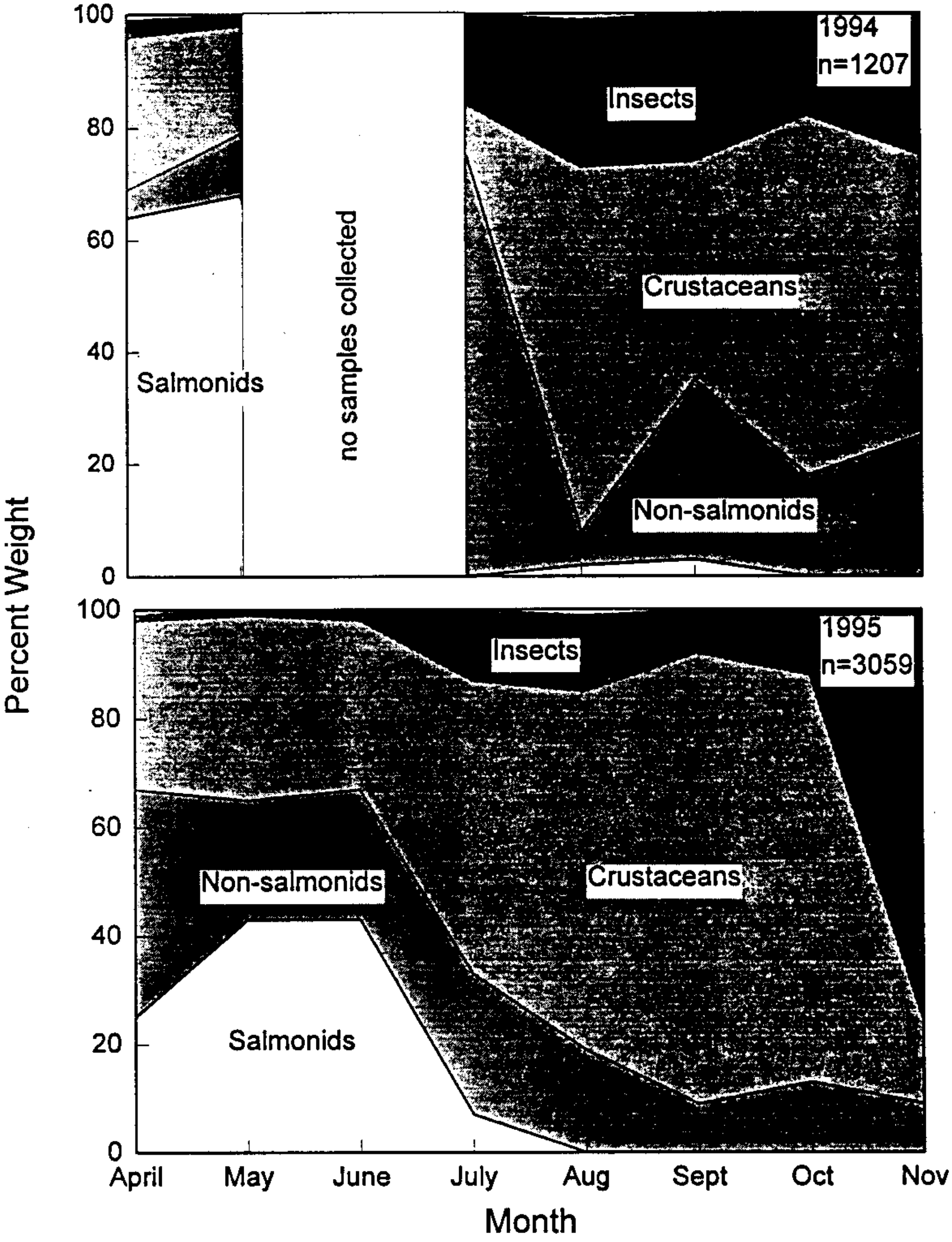

Figure 8. Monthly variation in diet composition, based on percent weight, of smallmouth bass diets in Lower Granite Reservoir, 1994-1995 (all lengths combined).

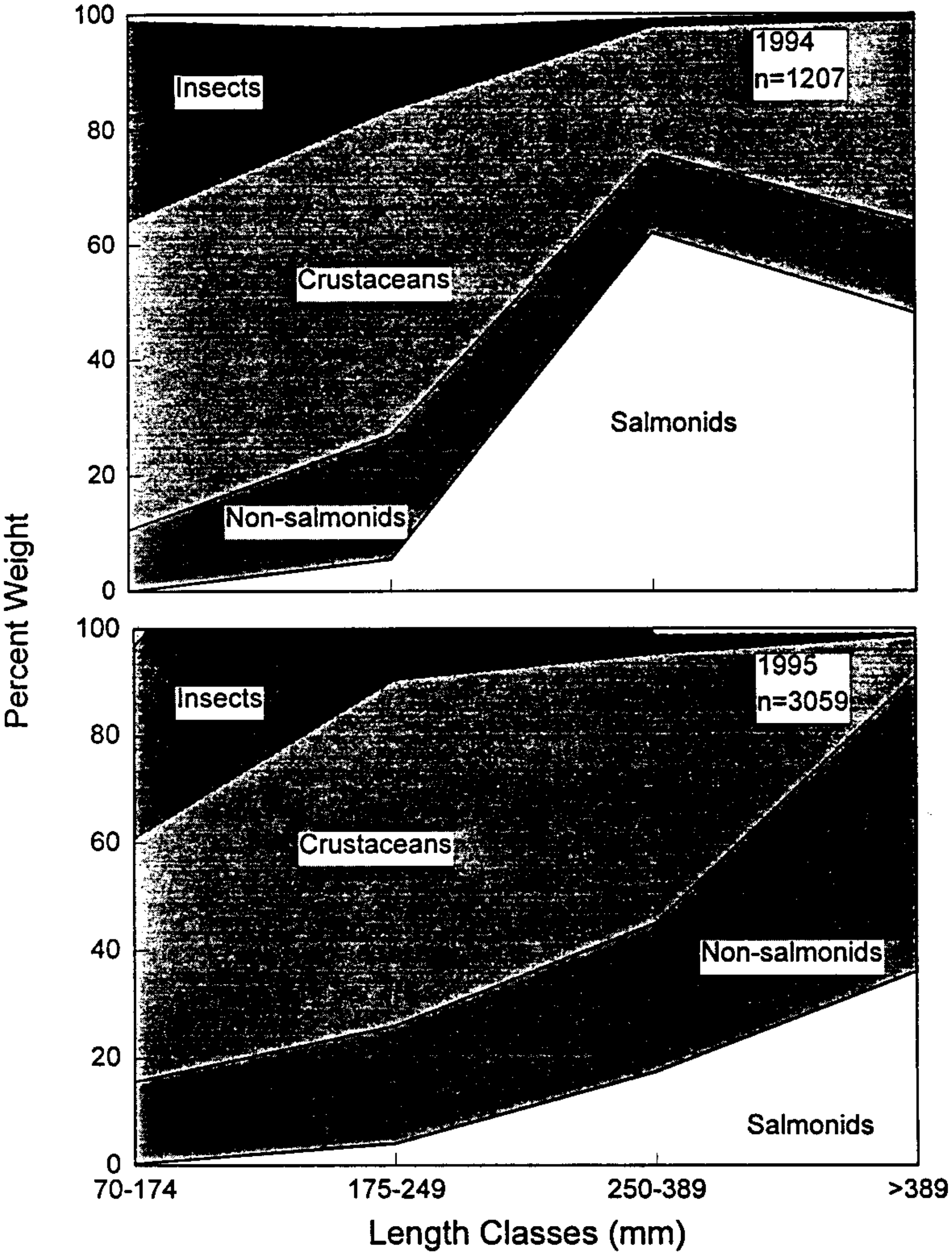

Figure 9. Variation in diet composition, based on percent weight, of four length classes of smallmouth bass in Lower Granite Reservoir, 1994-1995.

Table 3. Relative importance of prey items based on frequency of occurrence (FO) and percent weight (WT) for four length classes (mm) of smallmouth bass collected from Lower Granite Reservoir, 1994-1995.

1994	Length Class							
	70-174		175-249		250-389		> 389	
Prey Items	(FO)	(WT)	(FO)	(WT)	(FO)	(WT)	(FO)	(WT)
Osteichthyes	8.92	10.73	26.82	28.74	49.21	76.45	85.71	63.77
Unidentified fish	1.05	0.07	4.96	1.77	6.35	0.57	28.57	0.00
Chinook	0.00	0.00	3.79	3.45	11.64	46.60	14.29	47.99
Steelhead	0.00	0.00	0.00	0.00	2.65	13.92	0.00	0.00
Unidentified salmonids	0.00	0.00	1.46	2.00	3.17	1.54	0.00	0.00
Cyprinidae	2.10	2.64	4.66	2.33	4.76	3.37	0.00	0.00
Catostomidae	1.31	2.17	2.33	0.70	2.65	0.88	0.00	0.00
Centrarchidae	2.36	2.93	1.75	11.75	2.65	2.89	0.00	0.00
Cottidae	0.00	0.00	0.87	0.22	2.65	0.70	0.00	0.00
Ictaluridae	0.52	2.19	2.62	5.03	2.65	1.01	0.00	0.00
Percidae	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00
Larval fish	0.26	0.09	0.87	0.16	0.00	0.00	0.00	0.00
Unidentified non-salmonids	1.57	0.64	6.12	1.34	15.34	4.99	42.86	15.79
Crustacea	82.15	53.55	83.09	56.62	64.55	21.94	42.86	35.16
Cladocera	30.71	5.39	13.70	0.52	3.17	0.01	0.00	0.00
Copepoda	6.56	0.00	4.37	0.00	3.70	0.00	0.00	0.00
Amphipoda	56.17	4.06	48.10	1.05	30.69	0.07	28.57	0.16
Isopoda	2.62	0.16	1.46	0.01	0.53	0.00	0.00	0.00
Decapoda	31.50	43.93	53.64	55.04	46.03	21.86	42.86	34.99
Insecta	91.34	34.69	91.84	14.00	79.37	1.41	57.14	1.07
Unidentified	30.18	3.32	34.40	2.37	27.51	0.24	28.57	0.00
Diptera	85.56	25.86	86.01	7.46	71.96	0.92	57.14	1.02
Ephemeroptera	14.70	2.81	24.49	1.53	13.23	0.14	14.29	0.05
Hemiptera	3.94	0.04	2.33	0.11	0.53	0.00	0.00	0.00
Homoptera	1.84	0.03	1.17	0.00	0.00	0.00	0.00	0.00
Hymnoptera	6.56	1.01	7.29	0.92	3.17	0.09	0.00	0.00
Coleoptera	2.36	0.18	4.37	0.17	2.65	0.00	0.00	0.00
Trichoptera	14.17	1.44	14.58	0.50	4.23	0.01	0.00	0.00
Mollusca	0.26	0.01	0.29	0.00	0.00	0.00	0.00	0.00
Other Food	6.04	1.02	4.66	0.64	1.59	0.20	0.00	0.00

Table 3. continued.

1995	Length Class							
	70-174		175-249		250-389		> 389	
Prey Items	(FO)	(WT)	(FO)	(WT)	(FO)	(WT)	(FO)	(WT)
Osteichthyes	7.48	17.67	18.86	26.32	29.31	45.85	47.37	92.23
Unidentified fish	2.94	2.10	4.52	0.87	6.15	0.83	10.53	0.90
Chinook	0.27	0.27	1.28	3.45	2.36	7.42	0.00	0.00
Steelhead	0.00	0.00	0.00	0.00	0.71	8.20	21.05	35.42
Unidentified salmonids	0.09	0.01	0.10	0.02	0.95	1.78	5.26	0.58
Cyprinidae	0.62	5.39	2.06	4.48	1.89	3.97	5.26	3.23
Catostomidae	0.27	3.07	2.06	3.95	3.78	4.64	0.00	0.00
Centrarchidae	0.45	3.77	3.24	8.60	7.09	11.58	5.26	51.58
Cottidae	0.09	0.22	0.00	0.00	0.95	0.13	0.00	0.00
Ictaluridae	0.53	0.29	2.65	3.75	3.55	5.71	5.26	0.53
Percidae	0.27	1.69	1.47	0.60	2.36	1.32	0.00	0.00
Larval fish	1.96	0.87	2.85	0.19	2.13	0.02	0.00	0.00
Unidentified non-salmonids	0.53	0.00	1.38	0.42	2.13	0.24	0.00	0.00
Crustacea	74.62	45.32	76.82	64.44	65.72	50.27	47.37	7.36
Cladocera	20.93	1.73	6.58	0.01	1.42	0.00	0.00	0.00
Copepoda	8.46	0.00	6.97	0.00	7.57	0.00	21.05	0.00
Amphipoda	58.41	5.27	39.98	0.42	19.15	0.06	5.26	0.00
Isopoda	8.82	0.58	4.62	0.05	2.13	0.01	0.00	0.00
Decapoda	18.70	37.73	51.67	63.96	52.25	50.21	26.32	7.36
Insecta	77.92	35.97	73.77	8.77	67.38	3.59	47.37	0.41
Unidentified	20.57	7.54	18.17	1.81	9.69	0.51	10.53	0.12
Diptera	58.06	12.14	55.11	2.00	46.57	0.29	15.79	0.00
Ephemeroptera	34.37	12.24	34.18	4.06	32.15	2.44	31.58	0.29
Hemiptera	3.12	0.09	2.55	0.04	1.89	0.01	0.00	0.00
Homoptera	1.51	0.19	0.98	0.08	1.18	0.03	0.00	0.00
Hymnoptera	8.19	2.58	8.94	0.40	3.78	0.13	0.00	0.00
Coleoptera	3.21	0.21	3.34	0.12	1.89	0.09	0.00	0.00
Trichoptera	13.54	0.98	14.24	0.25	7.80	0.09	0.00	0.00
Mollusca	0.00	0.00	0.29	0.01	0.00	0.00	0.00	0.00
Other Food	4.10	1.04	4.32	0.45	3.55	0.28	0.00	0.00

Salmonids composed 62.1% of the total diet weight for smallmouth bass 250-389 mm in 1994, whereas in 1995, salmonids decreased in abundance accounting for 17.4% of the total diet weight. In 1995, finfish and crayfish were about equal in abundance accounting for 45.9% and 50.2% of the total diet weight, respectively (Table 3).

Fish were the dominant prey item of smallmouth bass > 389 mm in both years, accounting for 63.8% (1994) and 92.2% (1995) of the total diet weight (Table 3). Salmonids composed 75.3% and 39.3% of the total weight of fish in the diet during 1994 and 1995, respectively.

Daily Ration

Mean daily ration (mg prey/g predator) of smallmouth bass of all prey fishes was low during spring (April-June), increased through summer (July-September), and then decreased in fall (October-November) during both years (Figure 10). Mean daily ration of salmonids was 2.580 mg/g during spring 1994 and 1.725 mg/g during spring 1995. Mean daily salmonid ration in summer 1994 (6.190 mg/g) was substantially higher than that observed during summer 1995 (0.940 mg/g). Salmonids were absent from fall samples of smallmouth bass stomachs in 1994 and 1995.

No salmonids were identified in stomach samples of smallmouth bass 70-174 mm or > 389 mm in April 1995 (Figure 11). Mean daily salmonid ration was 0.232 mg/g for smallmouth bass 175-249 mm and 0.242 mg/g for smallmouth bass 250-389 mm during April 1995.

Salmonids were consumed by all length classes of smallmouth bass examined during May 1995 (Figure 11). Salmonid ration was lowest for smallmouth bass 70-174 mm (0.903

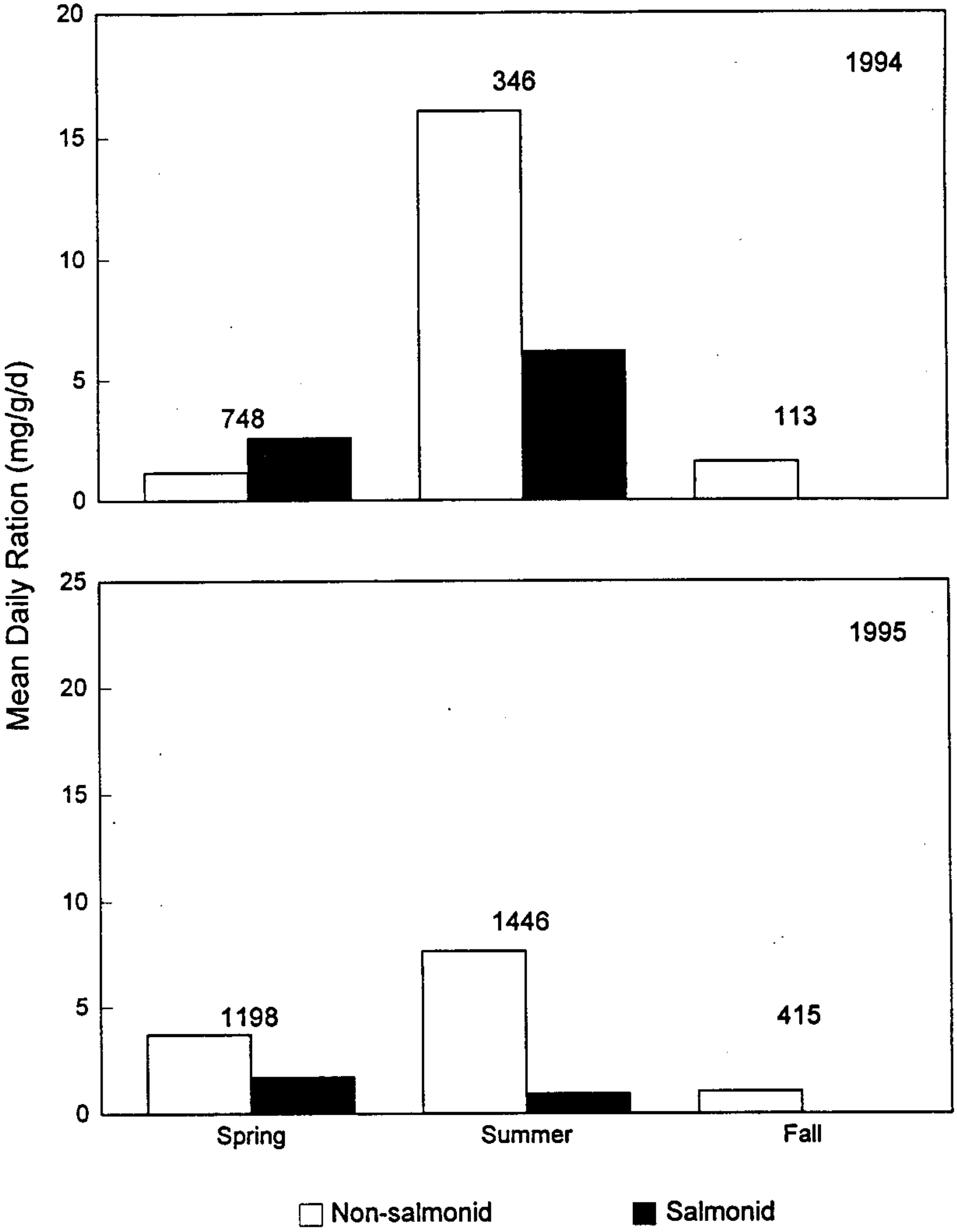

Figure 10. Mean daily ration of fishes consumed by smallmouth bass in spring (April-June), summer (July-September), and fall (October-November) in Lower Granite Reservoir, 1994-1995. Number above bar indicates sample size.

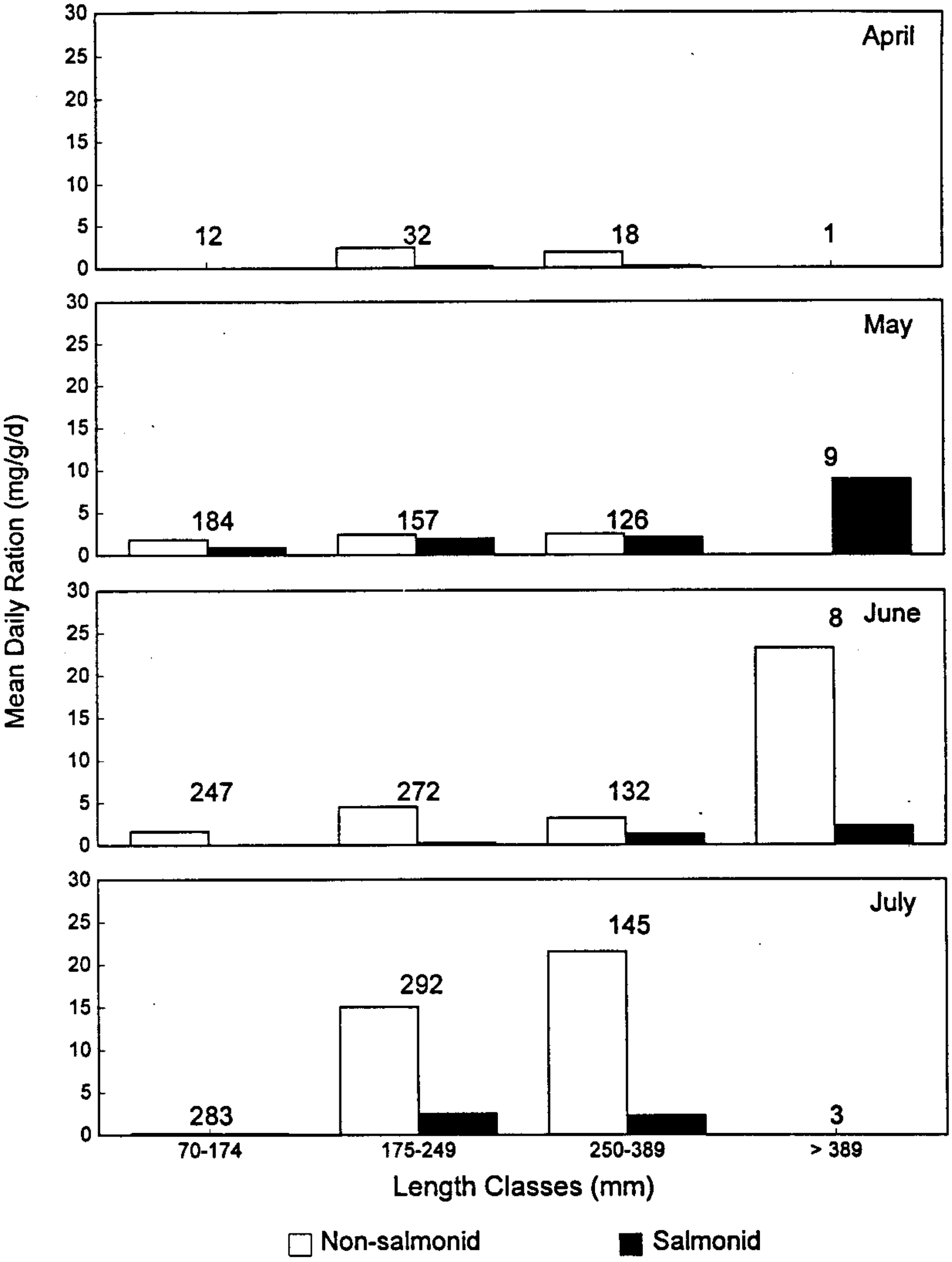

Figure 11. Mean daily ration of fishes consumed by four length classes of smallmouth bass in Lower Granite Reservoir, April-July 1995. Number above bar indicates sample size.

mg/g), similar between smallmouth bass 175-249 mm (1.917 mg/g) and 250-389 mm (2.066 mg/g), and highest for smallmouth bass > 389 mm (8.939 mg/g).

Mean daily ration of salmonids decreased for all length classes of smallmouth bass in June 1995 (Figure 11). Juvenile salmonids were not observed in stomachs of smallmouth bass 70-174 mm sampled in June. Mean daily salmonid ration of smallmouth bass 175-249 mm for June was 0.263 mg/g, and 1.288 mg/g for smallmouth bass 250-389 mm. Smallmouth bass > 389 mm exhibited the highest mean daily salmonid ration (2.243 mg/g) in June.

Mean daily salmonid ration for smallmouth bass 70-174 mm in July 1995 was 0.144 mg/g compared to 2.507 mg/g for smallmouth bass 175-249 mm, and 2.297 mg/g for smallmouth bass 250-389 mm (Figure 11). No salmonids were observed in stomach samples of smallmouth bass > 389 mm in July.

Numerical Consumption

Mean consumption of juvenile salmonids, as measured by prey-per-smallmouth bass > 69 mm-per-day (p/p/d), was low during April (0.054 p/p/d) and May (0.024 p/p/d), highest in August (0.375 p/p/d), and then decreased in September (0.162 p/p/d; Table 4) 1994. Consumption rate of non-salmonids by smallmouth bass > 69 mm was 0.015 p/p/d in May 1994, exceeded 0.300 p/p/d from July through October, and then decreased in November (0.036 p/p/d).

In 1995, mean daily consumption of salmonids by smallmouth bass > 69 mm was 0.014 p/p/d in April, increased to 0.018 p/p/d in May, decreased in June (0.007 p/p/d), and then increased again in July (0.013 p/p/d; Table 4). Consumption of non-salmonids by

Table 4. Mean daily consumption (prey/predator) of salmonids and non-salmonids for smallmouth bass in Lower Granite Reservoir, 1994-1995. Consumption statistics are: sample size (N), mean predator weight (W), mean consumption (n), and mean prey weight (w).

Year	Length Group (mm)	Prey Group	Consumption Statistic	Month							
				April	May	June	July	Aug	Sept	Oct	Nov
1994	> 69		N	40	708	NA	18	168	160	84	29
			W(g)	200	168	NA	136	88	74	101	62
		Salmonid	n	0.054	0.024	NA	0	0.375	0.162	0	0
			w(g)	12.6	17.4	NA	0	3.2	1.6	0	0
		Non-salmonid	n	0	0.015	NA	0.385	0.438	0.485	0.304	0.036
			w(g)	0	14.1	NA	0.2	5.0	1.9	1.9	1.4
	70-174		N	0	222	NA	1	83	81	33	20
			W(g)	0	41	NA	60	38	29	45	14
		Salmonid	n	0	0	NA	0	0	0	0	0
			w(g)	0	0	NA	0	0	0	0	0
		Non-salmonid	n	0	0.003	NA	0.000	1.427	0.514	0	0
			w(g)	0	1.3	NA	0.3	0.5	0.5	0	0
	175-249		N	24	249	NA	16	71	71	40	6
			W(g)	131	124	NA	125	120	109	101	99
		Salmonid	n	0.037	0.020	NA	0	0.000	1.862	0	0
			w(g)	0.1	8.2	NA	0	0.1	1.6	0	0
		Non-salmonid	n	0	0.024	NA	0.734	0.807	2.813	0.000	0.175
			w(g)	0	2.8	NA	0.1	10.5	3.4	2.1	1.4

Table 4. continued.

Year	Length Group (mm)	Prey Group	Consumption Statistic	Month							
				April	May	June	July	Aug	Sept	Oct	Nov
1994	250-389		N	16	222	NA	1	14	8	11	3
			W(g)	303	298	NA	401	225	226	265	306
		Salmonid	n	0.100	0.054	NA	0	0.000	0	0	0
			w(g)	16.7	21.0	NA	0	9.3	0	0	0
		Non-salmonid	n	0	0.029	NA	0	0.774	0	0.452	0
			w(g)	0	21.0	NA	0	0.6	0	1.8	0
	> 389		N	0	15	NA	0	0	0	0	0
			W(g)	0	831	NA	0	0	0	0	0
		Salmonid	n	0	0.043	NA	0	0	0	0	0
			w(g)	0	12.0	NA	0	0	0	0	0
		Non-salmonid	n	0	0	NA	0	0	0	0	0
			w(g)	0	0	NA	0	0	0	0	0

Table 4. continued

Year	Length Group (mm)	Prey Group	Consumption Statistic	Month							
				April	May	June	July	Aug	Sept	Oct	Nov
1995	> 69		N	63	476	659	723	377	346	280	135
			W(g)	165	142	118	104	70	78	61	24
		Salmonid	n	0.014	0.018	0.007	0.013	0	0	0	0
			w(g)	2.4	23.0	15.7	13.9	0	0	0	0
		Non-salmonid	n	0.051	0.054	0.054	0.082	0.064	0.013	0.011	0.002
			w(g)	5.8	5.3	12.6	12.3	10.0	13.3	5.6	0.9
	70-174		N	12	184	247	283	206	171	146	123
			W(g)	31	21	25	22	23	24	22	17
		Salmonid	n	0	0.005	0	0.005	0	0	0	0
			w(g)	0	4.1	0	0.6	0	0	0	0
		Non-salmonid	n	0	0.016	0.006	0.004	0.046	0	0.006	0.002
			w(g)	0	2.3	7.1	0.9	4.4	0	2.1	0.9
	175-249		N	32	157	272	292	141	147	118	9
			W(g)	112	110	108	107	109	106	91	82
		Salmonid	n	0.012	0.023	0.006	0.030	0	0	0	0
			w(g)	2.1	9.3	4.9	9.1	0	0	0	0
		Non-salmonid	n	0.040	0.062	0.058	0.145	0.117	0.018	0.017	0
			w(g)	6.7	4.3	8.4	11.1	10.0	4.7	7.8	0

Table 4. continued.

Year	Length Group (mm)	Prey Group	Consumption Statistic	Month							
				April	May	June	July	Aug	Sept	Oct	Nov
1995	250-389		N	18	126	132	145	30	27	16	3
			W(g)	289	291	255	244	215	217	185	149
		Salmonid	n	0.027	0.017	0.018	0.024	0	0	0	0
			w(g)	2.6	35.7	17.9	23.0	0	0	0	0
		Non-salmonid	n	0.108	0.104	0.050	0.381	0.138	0.171	0	0
			w(g)	5.0	6.8	16.2	13.8	24.7	17.6	0	0
	> 389		N	1	9	8	3	0	1	0	0
			W(g)	1242	1073	1056	741	0	1296	0	0
		Salmonid	n	0	0.248	0.064	0	0	0	0	0
			w(g)	0	38.7	37.1	0	0	0	0	0
		Non-salmonid	n	0	0	0.266	0	0	0	0	0
			w(g)	0	0	92.3	0	0	0	0	0

smallmouth bass > 69 mm ranged from 0.051 to 0.082 p/p/d from April through August 1995, and then decreased in September (0.013 p/p/d) and November (0.002 p/p/d).

Spatial Trends in Salmonid Consumption and Prey Weight

Consumption rates of juvenile salmonids by smallmouth bass > 69 mm were highly variable among strata from April through July 1995 (Table 5). Standard errors for consumption rate estimates were based on bootstrapping procedures using 1,000 iterations. Consumption of salmonids was observed exclusively in stratum 3 during April (0.024 p/p/d). In May, the mean daily consumption rate of salmonids was highest in stratum 3 (0.027 p/p/d) and lowest in stratum 1 (0.009 p/p/d). The mean daily consumption rate of salmonids was 0.013 p/p/d in stratum 3 during June. In July, mean daily consumption rate of salmonids was highest in stratum 1 (0.032 p/p/d) compared to stratum 2 (0.012 p/p/d) and stratum 3 (0.003 p/p/d). Consumption rates were generally lower within strata 1 and 2 in May and strata 2 and 3 in July. The mean weight (g) of salmonids consumed in stratum 3 during April 1995 was 2.4 g (Figure 12). During May, mean salmonid prey weights were 27.2 g in stratum 1, 15.7 g in stratum 2, and 26.8 g in stratum 3, compared to 15.7 g in stratum 3 in June. Mean salmonid prey weights varied among strata in July, with mean weights ranging from 9.7 g in stratum 1, to 3.5 g in stratum 2, and 51.0 g in stratum 3.

Size Selectivity

Smallmouth bass that consumed salmonids ranged between 85 and 474 mm and salmonids detected in smallmouth bass stomachs ranged from 21 to 293 mm (Figure 13). Approximately 32% of ingested salmonids were < 76 mm, 57% ranged from 76-150 mm, and 11% were > 150 mm. A positive linear relationship ($P < 0.05$; $r^2=0.34$) between smallmouth

Table 5. Mean daily consumption rate (prey/predator/day) and standard error (SE) of salmonids by smallmouth bass by strata and month in Lower Granite Reservoir, 1995.

	Consumption Rate					
	Stratum 1		Stratum 2		Stratum 3	
Month	Mean	SE	Mean	SE	Mean	SE
April	0.000	0.0000	0.000	0.0000	0.024	0.0005
May	0.009	0.0002	0.018	0.0003	0.027	0.0003
June	0.000	0.0000	0.000	0.0000	0.013	0.0001
July	0.032	0.0005	0.012	0.0003	0.003	0.0001

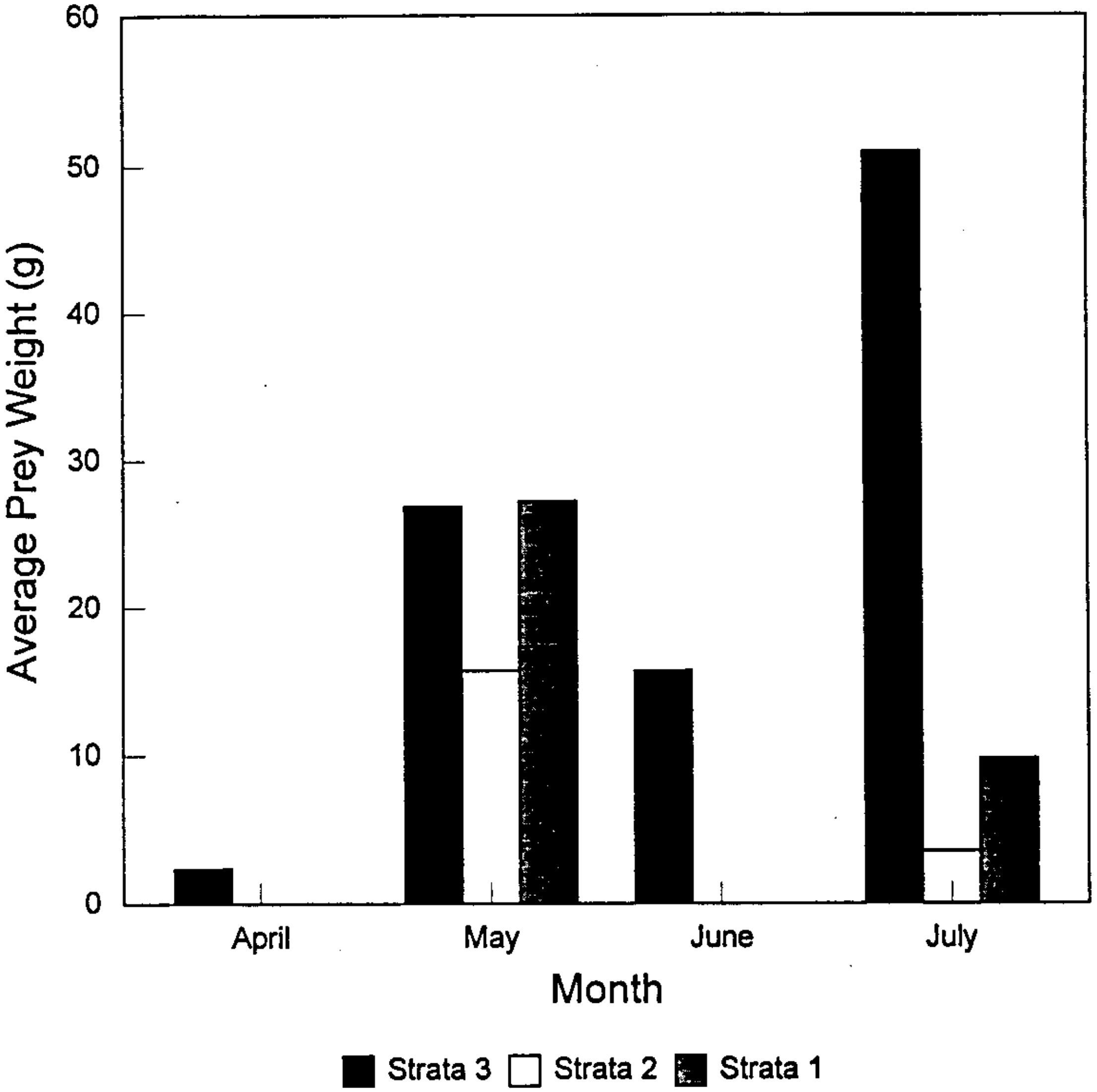

Figure 12. Average weight (g) of salmonids consumed by smallmouth bass (all lengths combined), by strata and month in Lower Granite Reservoir, 1995.

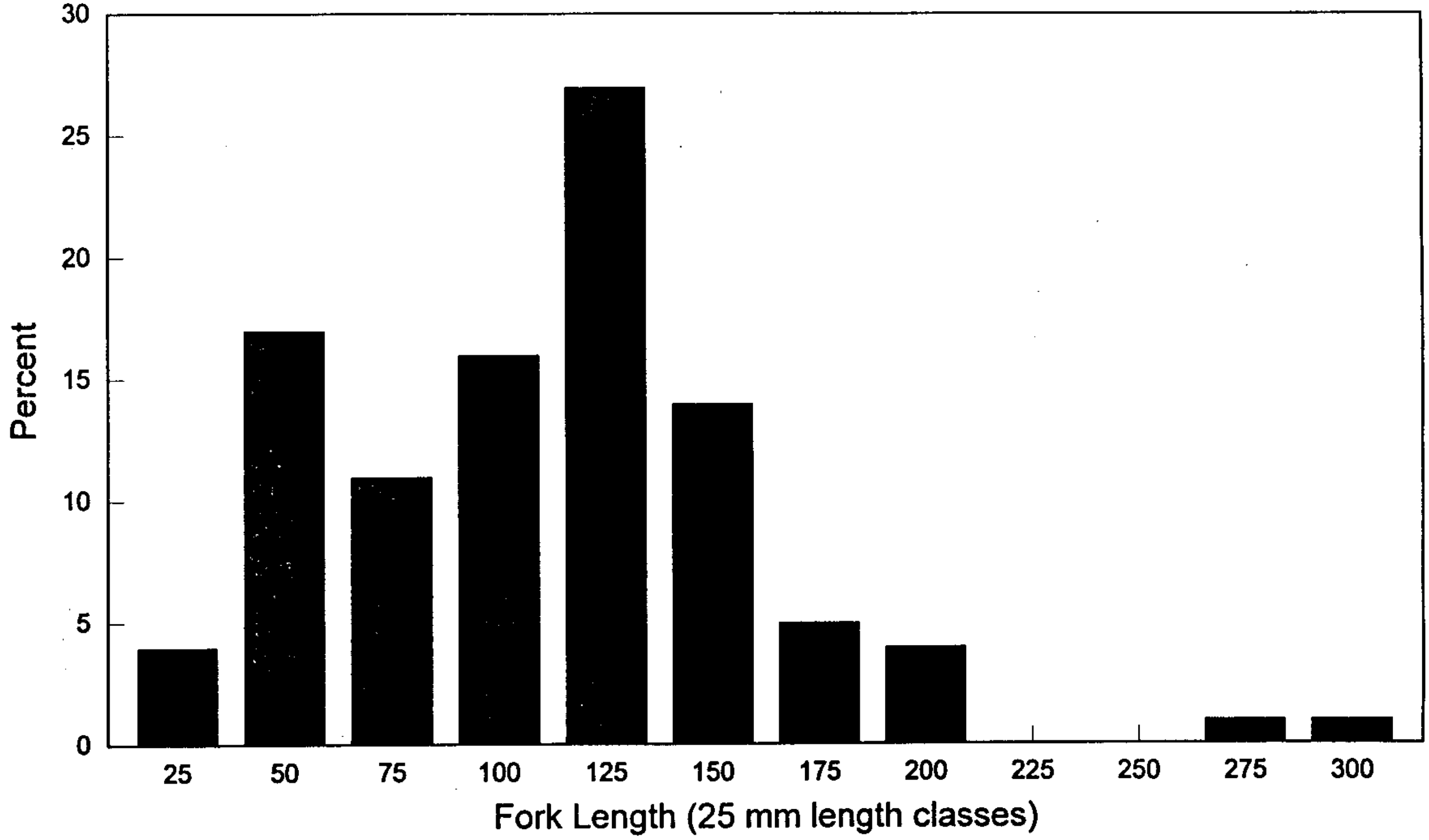

Figure 13. Length distribution of salmonids identified in smallmouth bass stomachs from Lower Granite Reservoir, 1994-1995.

bass and salmonid prey lengths was determined pooling data from 1994 and 1995 (Figure 14).

Fork lengths of ingested salmonids were similar to average daily fork lengths of juvenile chinook salmon collected at Lower Granite Dam during April and May 1994 (Figure 15). Lengths of ingested salmonids and lengths of subyearling chinook salmon collected at Lower Granite Dam were similar during April, May, and July 1995 (Figure 16).

Estimated Loss

In 1994, approximately 82,476 juvenile salmonids were consumed by smallmouth bass in Lower Granite Reservoir (Table 6) and approximately 64,020 juvenile salmonids were consumed in 1995 (Table 7). Juvenile chinook salmon composed 93% (1994) and 81% (1995) of all salmonids ingested (Tables 6 and 7).

Smolt losses in May 1994 accounted for 42% of the total annual loss due to smallmouth bass predation, and 62% of the loss occurred in stratum 1 (Table 6). In 1995, a substantial difference in estimated losses was found among strata. In April and May, losses occurred predominately in strata 2 and 3 (44% of total), whereas 40% of the total annual smolt losses occurred in strata 1 and 2 during July (Table 7).

Diel Consumption

Fish were consumed throughout the diel period by smallmouth bass 70-249 mm, with elevated rates of salmonid consumption occurring during early morning hours for smallmouth bass 175-249 mm (0000-0800 hrs; Figure 17). Diel consumption rates of salmonids were higher for smallmouth bass > 249 mm (Figure 18). Salmonid consumption was highest between 1600-2000 hrs for smallmouth bass 250-389 mm and between 0000-0400 for smallmouth bass > 389 mm.

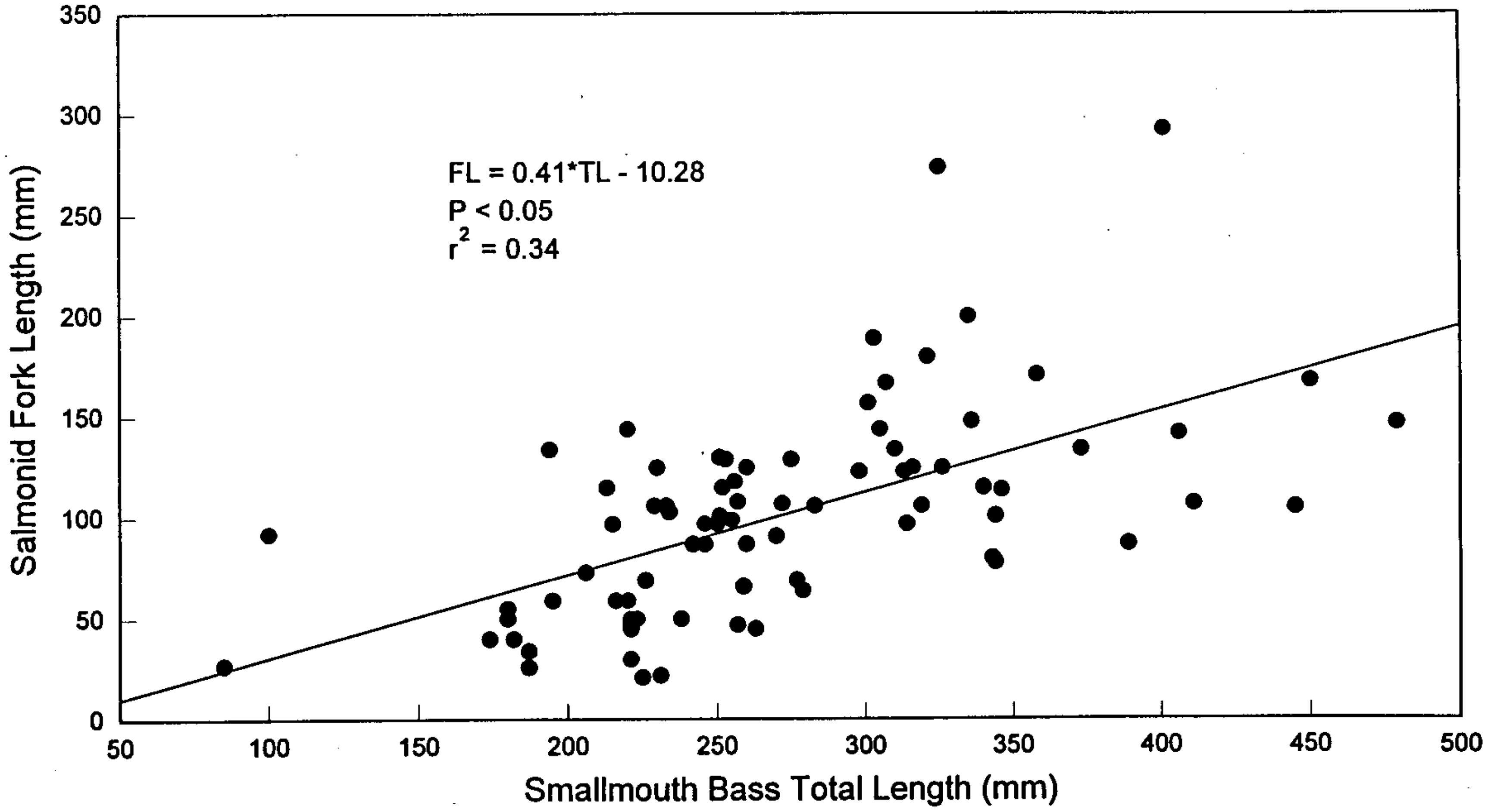

Figure 14. Relationship between smallmouth bass total length (TL) and fork length (FL) of ingested salmonids from Lower Granite Reservoir, 1994-1995.

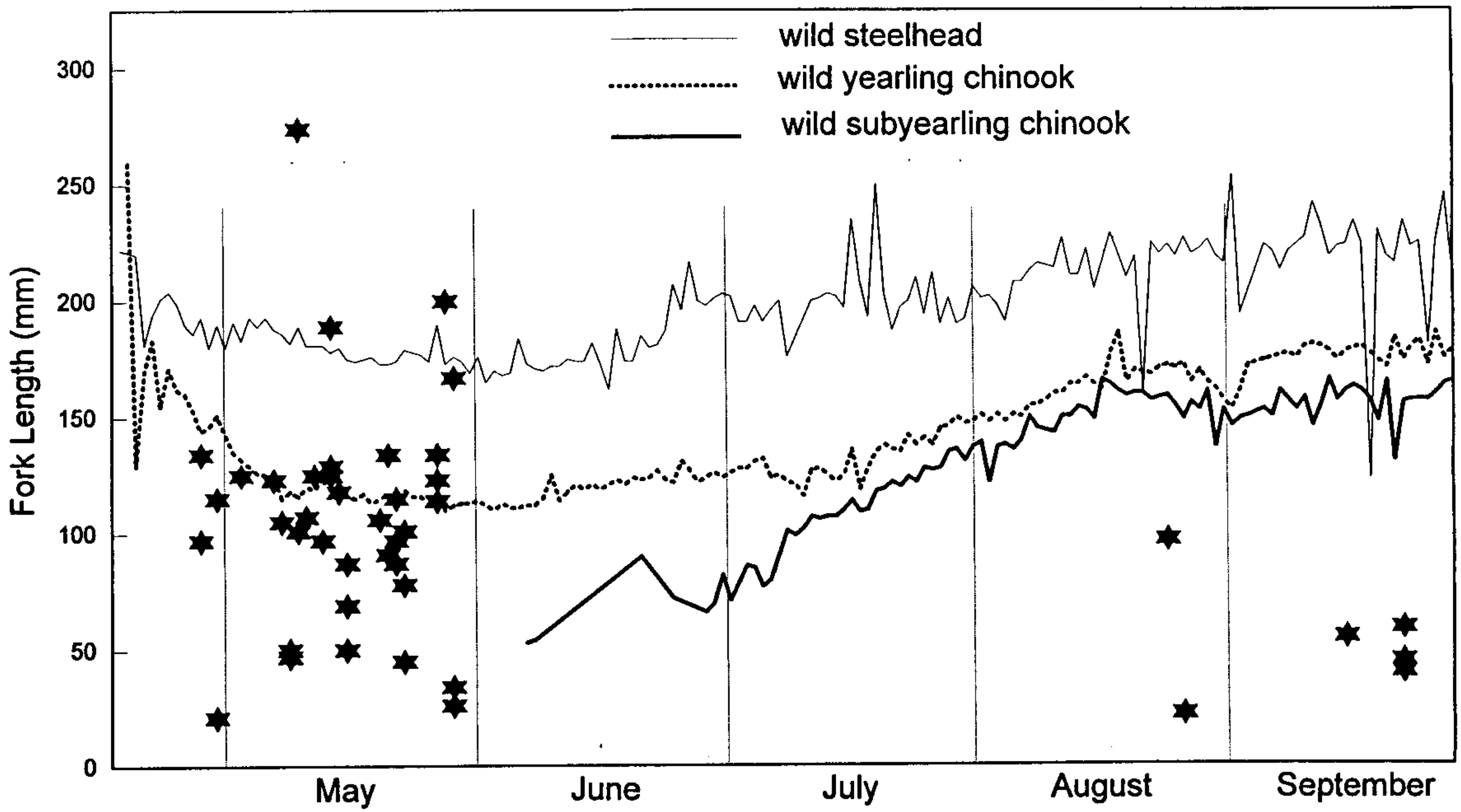

Figure 15. Salmonid prey fork length (stars) overlaid with average daily lengths (lines) of salmonids as determined by catches at the juvenile bypass facility, Lower Granite Dam, 1994. Average out-migrant lengths were estimated for dates when no passage occurred.

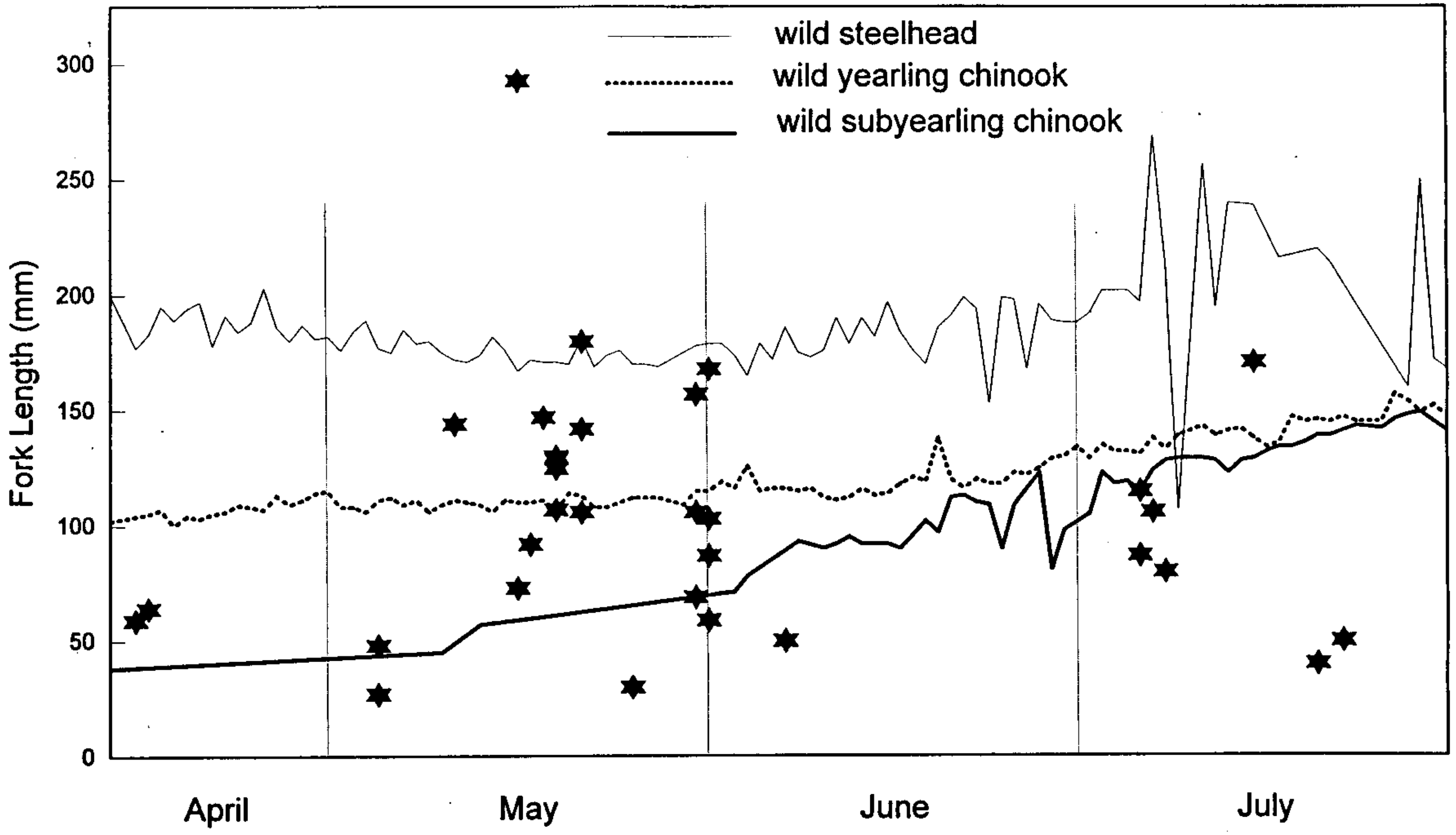

Figure 16. Salmonid prey fork length (stars) overlaid with average daily lengths (lines) of salmonids as determined by catches at the juvenile bypass facility, Lower Granite Dam, 1995. Average out-migrant lengths were estimated for dates when no passage occurred.

Table 6. Estimated loss of juvenile salmon and steelhead to predation by smallmouth bass in Lower Granite Reservoir from April-September 1994, by length class (mm), month, and strata.

				Month			
Strata	Length Class	April	May	June	July	Aug	Sept
1	70-174	0	0	NA	0	0	0
	175-249	21,276	21,515	NA	0	0	8,429
	250-389	0	0	NA	0	0	0
	> 389	0	0	NA	0	0	0
Monthly loss in Stratum 1		21,276	21,515	NA	0	0	8,429
Percent of Total		26	26	NA	0	0	10
2	70-174	0	0	NA	0	0	0
	175-249	0	7,059	NA	0	0	11,275
	250-389	2,640	1,399	NA	0	0	0
	> 389	0	0	NA	0	0	0
Monthly loss in Stratum 2		2,640	8,458	NA	0	0	11,275
Percent of Total		3	10	NA	0	0	14
3	70-174	0	0	NA	0	0	0
	175-249	0	1,968	NA	0	0	0
	250-389	4,197	2,574	NA	0	0	0
	> 389	0	144	NA	0	0	0
Monthly loss in Stratum 3		4,197	4,686	NA	0	0	0
Percent of Total		5	6	NA	0	0	0
Total Monthly loss		28,113	34,659	NA	0	0	19,704
Percent of Total		34	42	NA	0	0	24
							0
Loss of chinook		28,113	28,767	NA	0	0	19,704
Percent of Monthly Total		100	83	NA	0	0	100
Loss of steelhead		0	5,892	NA	0	0	0
Percent of Monthly Total		0	17	NA	0	0	0
Total chinook loss	76,584						
Percent of Total	93						
Total steelhead loss	5,892						
Percent of Total	7						
Total Loss	82,476						

Table 7. Estimated loss of juvenile salmon and steelhead to predation by smallmouth bass in Lower Granite Reservoir from April-July 1995, by length class (mm), month, and strata.

		Month			
Strata	Length Class	April	May	June	July
1	70-174	0	0	0	10,746
	175-249	0	4,883	0	7,704
	250-389	0	0	0	495
	> 389	0	355	0	0
Monthly loss in Stratum 1		0	5,238	0	18,945
Percent of Total		0	8	0	30
2	70-174	0	2,528	0	0
	175-249	0	7,024	0	5,397
	250-389	0	805	0	1,148
	> 389	0	513	0	0
Monthly loss in Stratum 2		0	10,670	0	6,545
Percent of Total		0	17	0	10
3	70-174	0	2,749	0	0
	175-249	7,421	3,568	2,258	0
	250-389	2,257	711	1,617	751
	> 389	0	848	242	0
Monthly loss in Stratum 3		9,678	7,876	4,117	751
Percent of Total		15	12	6	1
Total Monthly loss		9,678	23,984	4,117	26,241
Percent of Total		15	37	6	41
Loss of chinook		9,678	16,069	3,623	22,567
Percent of Monthly Total		100	67	88	86
Loss of steelhead		0	7,915	494	3,674
Percent of Monthly Total		0	33	12	14
Total chinook loss	51,937				
Percent of Total	81				
Total steelhead loss	12,083				
Percent of Total	19				
Total Loss	64,020				

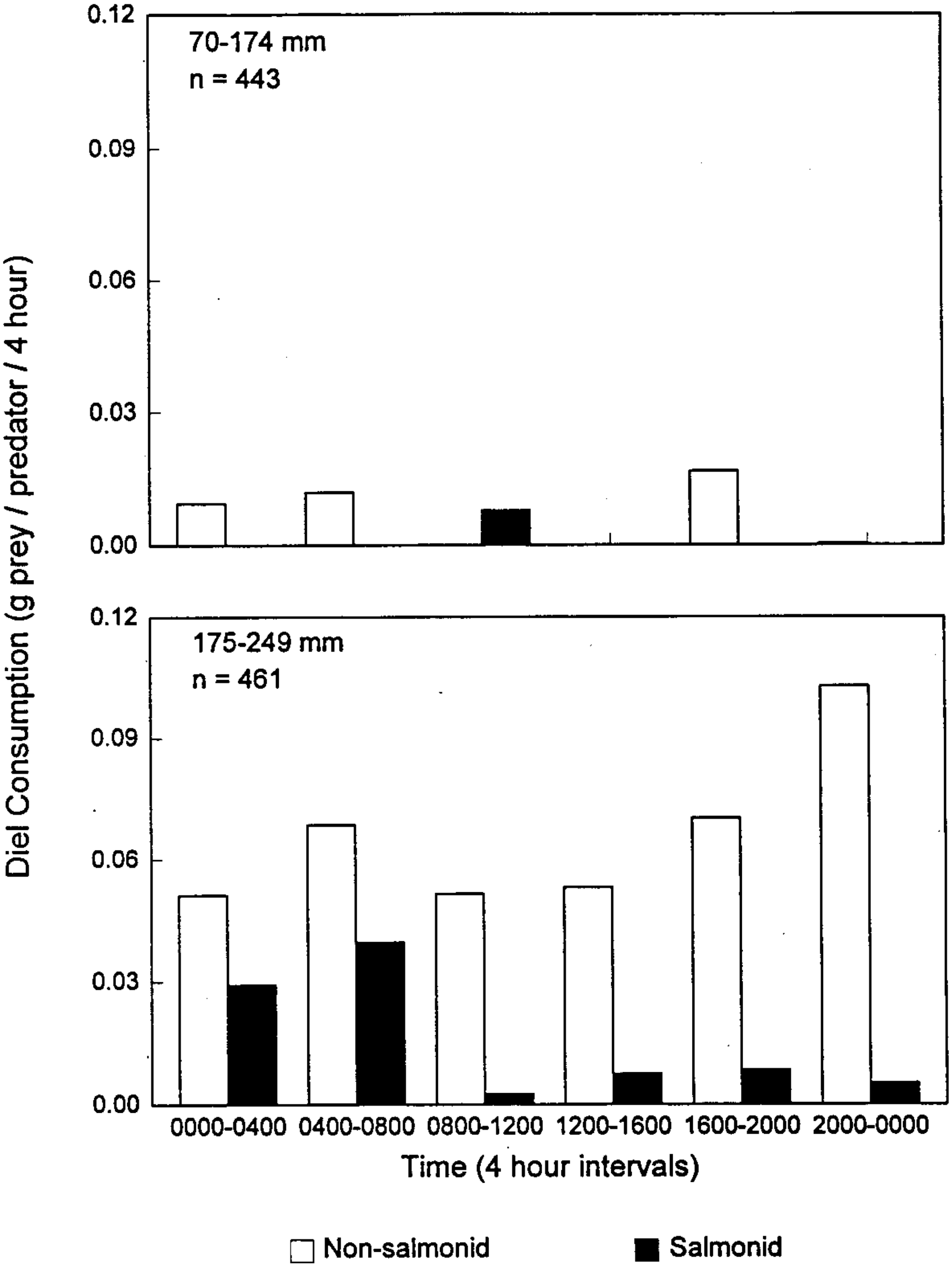

Figure 17. Diel consumption, in four hour intervals, of prey fishes for smallmouth bass 70-174 mm and 175-249 mm in Lower Granite Reservoir, April-June 1995.

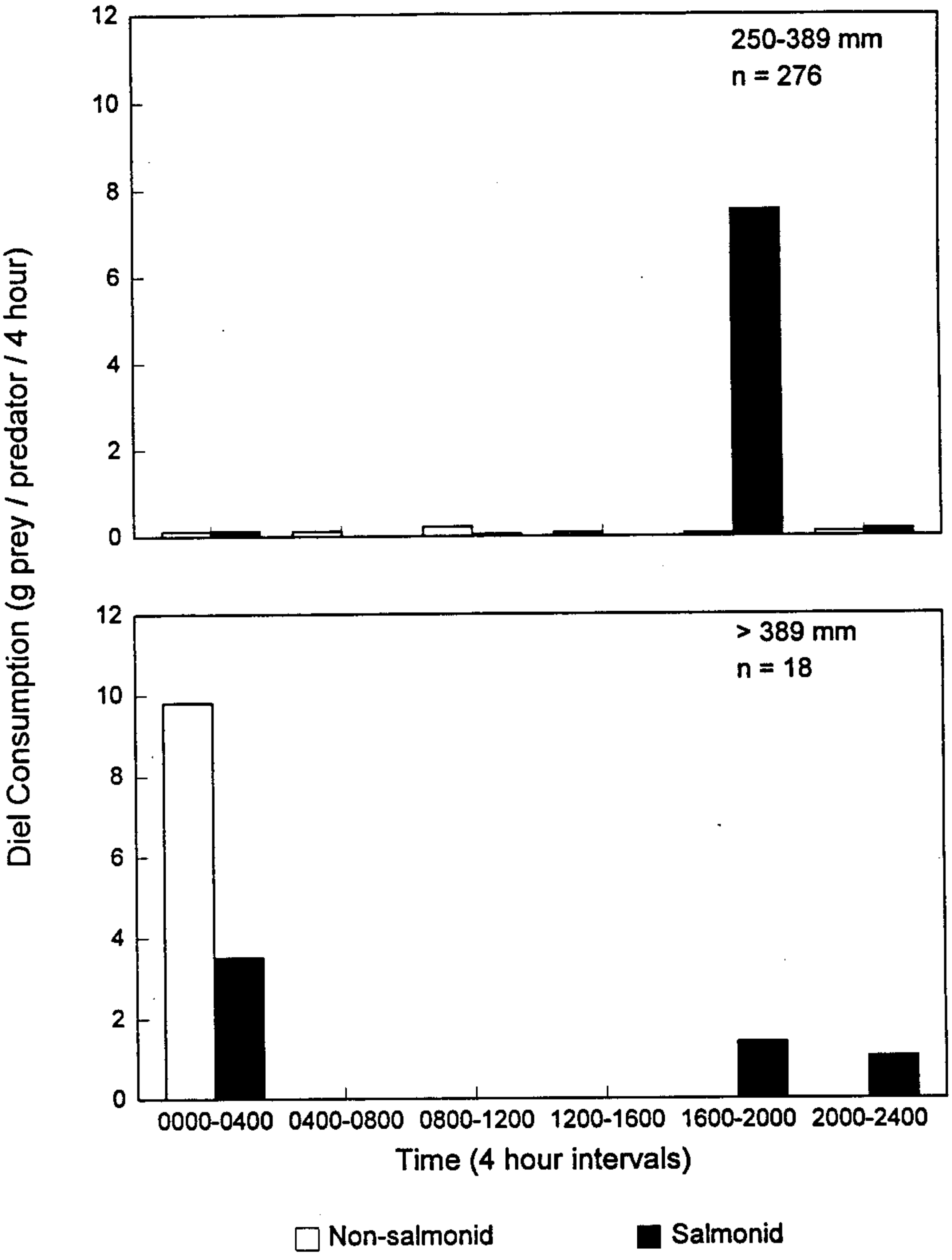

Figure 18. Diel consumption, in four hour intervals, of prey fishes for smallmouth bass 250-389 mm and > 389 mm in Lower Granite Reservoir, April-June 1995.

DISCUSSION

Diet Composition

Seasonal changes in diet composition observed in 1994 and 1995 demonstrated the opportunistic feeding behavior commonly reported for smallmouth bass (Keating 1970; Coble 1975; Pflug and Pauley 1984). Smallmouth bass fed heavily upon fish, from April through July in both years, and as passage rates of juvenile salmonids decreased at Lower Granite Dam (Figure 2), fed more heavily on crayfish and non-salmonids. Salmonids were absent from the stomachs of smallmouth bass sampled after July 1995. Stomach samples of adult smallmouth bass sampled in Lower Granite Reservoir by Bennett and Shrier (1986) contained about equal amounts (% wet weight) of salmonids (26.0%) and decapoda (22.8%) during spring, but the diet was dominated by decapoda (86.5%) during summer. An increase in the occurrence of salmonids in the diets of smallmouth bass coincided with the emigration of juvenile hatchery salmonids through Lake Sammamish, Washington (Pflug and Pauley 1984). Shively et al. (1996) documented the ability of northern squawfish in the Clearwater River, Idaho, to switch rapidly from a diet consisting mostly of crayfish (38% of diet weight) to one primarily of salmonids (86% of diet weight). The increase in salmonids in the diet was attributed to an increase in juvenile salmonid density resulting from hatchery releases upstream. Smallmouth bass in Lower Granite Reservoir demonstrated the same ability to respond to changes in prey abundance.

I found a major shift in the diet of smallmouth bass from insects to fish as predator length increased. Poe et al. (1991) reported the same trend for smallmouth bass in John Day Reservoir. Smallmouth bass shift from relatively small to larger prey items as they grow (Coble 1975; George and Hadley 1979). Dunsmoor et al. (1991) reported that zooplankton were the most abundant food item of smallmouth bass < 201 mm in Brownlee Reservoir, Idaho-Oregon, while smallmouth bass > 200 mm preyed chiefly on crayfish and fish. Fish (salmonids and non-salmonids) accounted for > 60% of the total diet weight of smallmouth bass > 249 mm in Lower Granite Reservoir in 1994 and 1995. Diets of smallmouth bass > 199 mm in John Day Reservoir averaged 82% fish (Vigg et al. 1991), and though predator lengths are not the same, clearly demonstrate the importance of fish in the diets of larger smallmouth bass. Percent weight of salmonids in smallmouth bass diets in 1994 increased from 0% for smallmouth bass 70-174 mm to 48% for smallmouth bass > 389 mm, similarly in 1995, salmonids accounted for 0.28% of the total diet weight of smallmouth bass 70-174 mm and 36% of the total diet weight of smallmouth bass > 389 mm.

Daily Ration

Smallmouth bass mean daily ration of all prey fishes increased steadily from April through August 1994, and April through July 1995. Increases in mean daily ration paralleled increases in reservoir water temperatures in 1994 and 1995 (Figure 19). Vigg et al. (1991) also observed an increase in daily fish ration of smallmouth bass in John Day Reservoir from April through August.

In Lower Granite Reservoir, peaks in daily ration of salmonids were observed during May and July 1995. These increases coincided with peak passage of juvenile salmonids at Lower Granite Dam. Daily counts of steelhead and yearling chinook salmon were highest in May, and subyearling chinook salmon passage was highest in July (Figure 2), suggesting a possible density dependent relationship between salmonid consumption by smallmouth bass and juvenile salmonid abundance. The relationship between daily ration and smolt passage observed for smallmouth bass in Lower Granite Reservoir was similar to that reported for

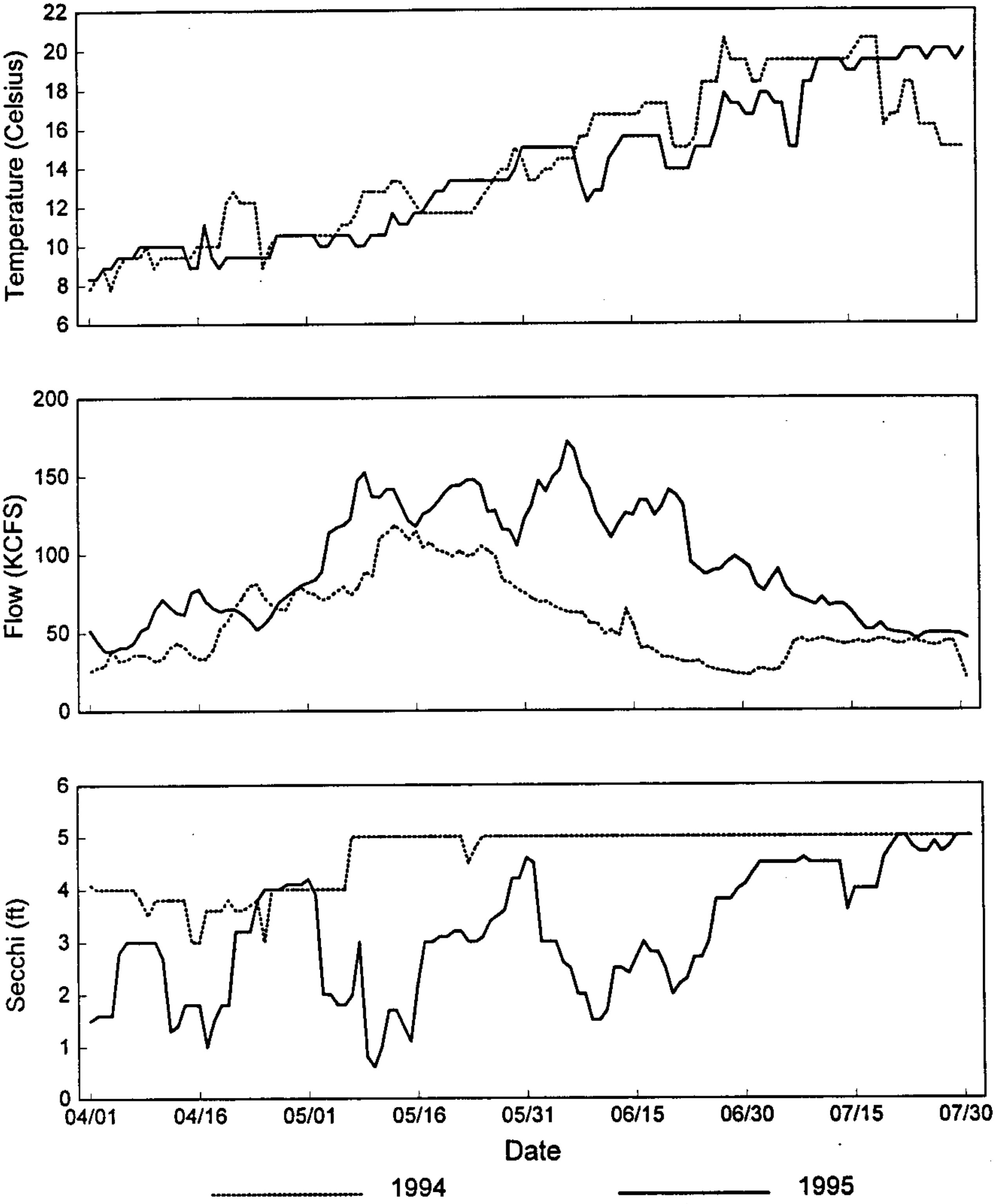

Figure 19. Average daily temperature, total daily outflow, and daily secchi disk measurements at Lower Granite Dam, from April-July 1994 and 1995.

northern squawfish by Petersen et al. (1990). They observed a density dependent relationship between the smolt consumption rate of northern squawfish and smolt density in the boat restricted zone of McNary Dam, Washington.

Daily fish ration of smallmouth bass in Lower Granite Reservoir increased with predator size in 1995. The highest daily ration of salmonids (8.94 mg/g) was observed for smallmouth bass > 389 mm. The highest daily ration of all prey fishes (25.46 mg/g), was slightly lower than that reported for 2,886 smallmouth bass sampled in John Day Reservoir (28.7 mg/g; Vigg et al. 1991). Mean daily ration was highest for smallmouth bass > 389 mm, which differs from the results of Vigg et al. (1991), who reported that fish ration was highest for smallmouth bass 200 mm (30.4 mg/g), and then decreased for larger smallmouth bass in John Day Reservoir.

Numerical Consumption

Vigg et al. (1991) noted that temperature may be the most influential factor regulating consumption rates of fishes. Consumption rates of smallmouth bass appeared to be linked to increasing water temperatures in 1994 and 1995, as they were relatively low during April and May and were highest from July through September. Optimal water temperature for smallmouth bass can range from 12 to 31°C depending on age and acclimation (Ferguson 1958; Barans and Tubb 1973). Water temperatures in both years were approximately 8°C at the beginning of April and reached a maximum of 23°C in August 1994 and 20°C in July 1995.

Higher water temperatures and lower flows and turbidity that occurred during spring 1994 compared to spring 1995 (Figure 19), may have enhanced predation by smallmouth bass. Consumption rates of salmonids in April and May 1994 were 0.054 and 0.024 prey/predator, whereas consumption rates were 0.014 and 0.018 prey/predator during April and May 1995. The increased turbidity in 1995 may have diminished the ability of smallmouth bass to locate and capture prey, as they are visually oriented predators (Carlander 1977) and are generally associated with areas of low turbidity (Todd and Rabeni 1989). My observations are similar to the findings of Bennett et al. (1993) who indicated high flows and resulting higher turbidity resulted in lower salmonid consumption by northern squawfish in Lower Granite Reservoir.

Salmonid Prey Weight

Salmonid prey weights fluctuated seasonally, with larger salmonids consumed in April and May, when steelhead and yearling chinook salmon abundance in the reservoir was highest, and smaller salmonids consumed in July, when subyearling chinook salmon rear and migrate through the reservoir (Figure 2). Salmonid prey weights were consistent between strata 1 (27.2 g) and 3 (26.8 g) in May, which may be indicative of steelhead and yearling chinook salmon actively migrating through the reservoir. The distribution of salmonid prey in July appeared to be clumped, with considerably smaller prey consumed in strata 1 (9.7 g) and 2 (3.5 g) compared to stratum 3 (51.0 g). The smaller prey sizes in strata 1 and 2 are probably representative of subyearling chinook salmon rearing in the upper portion of the reservoir. Bennett et al. (1993) collected subyearling chinook salmon almost exclusively over sand and sand/cobble substrate located in the upper portion of Lower Granite Reservoir. Curet (1993) reported that subyearling chinook salmon generally rear in the littoral areas of Lower Granite Reservoir until shoreline water temperatures exceed 18°C. The abundance and suitable forage size of subyearling chinook salmon within rearing areas may expose them to higher predation rates by smallmouth bass (Tabor et al. 1993). Comparison of subyearling chinook salmon habitat use and mean salmonid prey lengths and weights suggest that subyearling chinook salmon composed the majority of juvenile salmonids consumed during July 1995 in Lower Granite Reservoir.

Estimated Loss

Estimated losses of salmonids by smallmouth bass varied among months and strata. Highest losses coincided with peaks observed in steelhead, yearling chinook salmon, and subyearling chinook salmon passage at Lower Granite Dam during May and July. Predation by resident fishes in John Day Reservoir also coincided with peak abundance of juvenile salmonids (Rieman et al. 1991). Peaks in estimated losses may be a function smolt abundance, water temperature, and reproductive activity of smallmouth bass.

The onset of the smolt out-migration through Lower Granite Reservoir generally occurs in the beginning of April, and consists primarily of steelhead and yearling chinook salmon (Figure 2). Water temperatures in Lower Granite Reservoir in April are typically < 10°C, and feeding activity of smallmouth bass is minimal. Feeding activity increases as water temperatures near 15°C (Carlander 1977). Rising water temperatures also precipitate an increase in spawning activity by smallmouth bass. Suitable water temperatures for spawning (13 to 21°C; Carlander 1977; 12 to 25°C; Graham and Orth 1986), typically occur from mid June to late July in Lower Granite Reservoir. Feeding activity of male smallmouth and largemouth bass is depressed or absent during the spawning period (Carlander 1977; Adams et al. 1982) due to their nest guarding behavior and caring for newly hatched fry

(Heidinger 1976). Reduced feeding probably results in relatively low growth and energy storage of male centrarchids during spring (Adams et al. 1982). Daily ration of largemouth bass increased during late spring and summer following the nonfeeding reproductive period (Adams et al. 1982). Male smallmouth bass may also increase their feeding activity to replenish energy reserves, after the month or more reproductive period (Coble 1975; Carlander 1977). Bennett et al. (1983) observed active spawning nests of smallmouth bass from mid June to late July 1979 and 1980 in Little Goose Reservoir. In contrast to steelhead and yearling chinook salmon, subyearling chinook salmon are present in the reservoir when water temperatures are near annual maximums and spawning activity has subsided, potentially exposing them to increased predation.

The influence of smallmouth bass predation on subyearling chinook salmon in Lower Granite Reservoir may also be greater than that on any other stock as a result of their relatively low numbers, their smaller body size, and timing and duration of rearing in and migration through the reservoir. Subyearling chinook salmon are not fully smoltified as they begin their seaward journey and can rear from 22 to 112 days within a particular reservoir (Miller and Sims 1984; Bennett et al. 1993; Curet 1993). Poe et al. (1991) related the increase in smallmouth bass predation that occurred during August in John Day Reservoir to the overlapped distributions of smallmouth bass and subyearling chinook salmon within the littoral areas of the reservoir. Due to differences in the number of out-migrants among stocks, I believe that losses should be estimated for each stock of juvenile salmonid: steelhead, yearling chinook salmon, and subyearling chinook salmon.

The estimated loss of juvenile salmonids in Lower Granite Reservoir (82,476, 1994, 64,020, 1995) is substantially less than that attributed to smallmouth bass predation in John salmon by reducing shoreline water temperatures, thus resulting in increased encounters and higher predation by smallmouth bass.

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Objective 3. Determine length composition and relative abundance of crayfish in Lower Granite Reservoir.

ABSTRACT

Length frequency and relative abundance of crayfish *Pacifastacus leniusculus* in Lower Granite Reservoir were determined in 1994 and 1995. Crayfish were captured using modified GEE brand minnow traps with 2, 3, or 4 cm entrance diameters. A total of 717 (1994) and 1,958 (1995) crayfish was captured.

Carapace lengths of crayfish differed significantly ($P < 0.05$) among trap sizes in both years. In 1995, few crayfish were captured with carapace lengths between 28 and 32 cm, approximately age 3, suggesting the March 1992 test drawdown of Lower Granite Reservoir may have significantly decreased survival of the 1992 cohort. Carapace lengths of crayfish captured in shoreline and adjacent channel transects in 1995 were similar ($P > 0.05$).

The distribution of crayfish catch/effort among transects was not significantly different ($P > 0.05$) between years. Catch/effort was significantly different ($P < 0.05$) among transects within years and was higher at mid and upper reservoir transects in Lower Granite Reservoir, probably related to substrate differences. Main channel substrate in downstream areas consists largely of silt, while main channel substrate in the upper reservoir is characterized by sand, large cobble, and boulders. The higher frequency of crevices and uneven substrate at upstream locations provides refugia for non-burrowing crayfish potentially resulting in higher catch/effort of crayfish.

INTRODUCTION

Crayfish of the family Astacidae are common inhabitants of western lakes, streams, and reservoirs (Bouchard 1978; Hogger 1988). Bennett and Dunsmoor (1986) noted the presence of two species, *Pacifastacus leniusculus* and *P. gambeli* in the middle Snake River. The signal crayfish *P. leniusculus* "is aggressive, vagrant and grows and reproduces rapidly" (Lowery and Holdich 1988). Much of the information pertaining to crayfish habitat use and distribution in the Snake River has come about indirectly through studies of resident fishes such as smallmouth bass and white sturgeon *Acipenser transmontanus* (Munther 1970; Cochnauer 1983).

In the Snake River, abundance of smallmouth bass and white sturgeon may be a function of crayfish distribution (Munther 1970; Bennett et al. 1993). Higher densities of smallmouth bass and white sturgeon were observed over substrates consisting of gravel and boulders, substrate commonly inhabited by the non-burrowing crayfish *P. leniusculus* (Munther 1970; Hogger 1988).

Size distribution and density of crayfish may be a function of substrate quality (Abrahamsson and Goldman 1970; Shimizu and Goldman 1983). Areas of medium-sized rocks typically contain higher densities of medium-sized crayfish, compared to sandy bottom habitats which contain fewer, but larger crayfish (Hogger 1988). Higher densities of *P. leniusculus* were observed in areas of the Sacramento-San Joaquin delta protected by granite rip-rap compared to areas consisting primarily of mud-clay banks (Shimizu and Goldman 1983). Due to the non-burrowing nature of *P. leniusculus* (Hogger 1988), rocky substrate is utilized for cover (Abrahamsson and Goldman 1970). Relatively high fecundity (Lowery 1988) and reduced intraspecific competition may allow crayfish populations to recover quickly from massive die-offs. Crayfish are important elements within the food web of an ecosystem, functioning both as consumers and as forage for other organisms (Hogger 1988).

In Lower Granite Reservoir, crayfish are found in the diets of resident fishes such as smallmouth bass, white sturgeon, and northern squawfish (Bennett et al. 1983; Cochnauer 1983; Chandler 1993). Reduction in the abundance of crayfish as a forage item may lead to an increase in smolt predation as both smallmouth bass and northern squawfish consume juvenile salmonids (Poe et al. 1991).

OBJECTIVE

1). *Determine length composition and relative abundance of crayfish in Lower Granite Reservoir.*

METHODS

Crayfish Collection

Crayfish were sampled at 50 randomly selected transects in stratum 1, 40 in stratum 2, and 30 in stratum 3 from June through October 1994 (Figure 1). In June and July 1995, a total of 27 transects was sampled in stratum 1, 33 in stratum 2, and 15 in stratum 3.

Crayfish were collected in 1994 and 1995 using commercial GEE brand minnow traps with modified funnel entrances of 2, 3, or 4 cm. Each trap had two funnel entrances of equal diameter. In 1994, a total of five traplines, having equal numbers of traps with 2, 3, or 4 cm entrance diameters, randomly attached to traplines, was used to capture crayfish. Each trapline consisted of six traps individually attached at 3 m intervals. In 1995, six traplines with 15 traps at 3 m intervals were used to capture crayfish. Traplines were anchored on and deployed perpendicular to the shoreline with the first trap 3 to 5 m from shore. Traplines sampled shoreline transects in 1994 and shoreline and main channel transects in 1995. In 1995, a 45-90 m length of nylon rope separated pairs of traplines, allowing simultaneous sampling of shoreline and adjacent main channel transects. Maximum and minimum depths of each transect were determined with an Eagle Model Mach 1 depth recorder. Traps were baited with Pacific herring *Clupea pallasii* approximately 180 mm total length and fished for approximately 24-72 hrs in one location. Bait was maintained to ensure a consistent attraction mechanism existed among traps. Traplines were retrieved in the early morning to reduce crayfish escapement (Westman et al. 1978a), as crayfish feed principally at night and retreat to crevices and holes during daylight hours (Abrahamsson 1983; Collins et al. 1983).

Crayfish were removed from traps and placed in shallow basins containing water. Sex, carapace length (0.1 mm), and number of crayfish caught per entrance size were recorded in 1994 and 1995. Rostral length (0.1 mm) and crayfish weight (g) were also recorded in 1995. Length of carapace (rostral tip to posteriomedian edge of carapace) and rostral length (tip of rostrum to posteriomedian edge of orbit) were measured with vernier calipers. Crayfish were released at the capture site after being measured. Each trapline was retrieved, crayfish measurements recorded, and trapline re-set at a different sampling location before the next trapline was checked.

Crayfish Length, Sex Ratio, and Distribution Analyses

I conducted a two-way analysis of variance (ANOVA), using the STATISTICA (StatSoft 1997) analysis program, to test the null hypotheses that mean carapace length was similar among funnel opening sizes, between years, and was not influenced by a funnel opening size by year interaction. I tested the linear model: $CL_{ijk} = \mu + F_i + Y_j + FY_{ij} + \varepsilon_{ijk}$;

where CL_{ijk} represents the mean carapace length of crayfish captured in a trap with funnel opening size F_i in year Y_j and FY_{ij} represents the potential funnel opening size by year interaction, and ε_{ijk} the random error term. Statistically significant terms ($\alpha = 0.05$) were further evaluated using the Student-Newman-Keuls (SNK) multiple range test (Ott 1993) to identify pairwise differences. The general linear model procedure (GLM; SAS 1995) was used to determine if carapace lengths of crayfish captured in traps with similar funnel opening sizes differed between shoreline and channel locations. Statistical tests were conducted independently for each trap size using the model; $CL_{ij} = \mu + L_i + \varepsilon_{ij}$; where CL_{ij} represents the mean carapace length of crayfish captured in location L_j.

The Chi-square test of homogeneity (Ott 1993) was used to test for differences in sex ratios between summer (June-August) and fall (September-October) 1994 collections and between summer collections in 1994 and 1995.

Using a permutation test, I tested the null hypothesis that the distribution of catch/effort throughout the entire reservoir was similar between years. The permutation test does not require the data be normally distributed, only that the distributions from which the two samples were drawn from are the same (Good 1994). Additionally, a test using a linear model would require the test statistic be compared to a theoretical distribution, while the permutation test allows the researcher to identify the test statistic best suited for the problem at hand and generate a distribution of test statistic values using the collected data. A permutation distribution generated in GAUSS was compared to the test statistic D, to determine if the distribution of catch/effort among transects was similar between years. The number of crayfish-per-trap-per-night (catch/effort) at each transect was used as an expression of relative abundance. The test statistic, D = $\sum|R_{94i} - R_{95i}|$, is the sum of the absolute differences between ranks, R_{94i} is the rank of the catch/effort at transect i in 1994 and R_{95i} is the rank of the catch/effort at transect i in 1995. Values of D less than the expected value for a random distribution of ranks, indicate similar distributions of ranks between years and no year * transects interaction. A two-way GLM (SAS 1995) using weighted least squares due to nonconstant variance (Draper and Smith 1966), was used to test for differences in transformed catch/effort (ln(catch/effort + 1), to correct for nonnormality) among transects and between years (Ott 1993): $\ln(CE+1)_{ijk} = \mu + T_i + Y_j + \varepsilon_{ijk}$; where $\ln(CE+1)_{ijk}$ represents the transformed catch/effort of crayfish at transect T_i in year Y_j and random error term ε_{ijk}. Comparison of catch/effort among transects was conducted using the SNK multiple range test.

RESULTS

A total of 717 (1994) and 1,958 (1995) signal crayfish *P. leniusculus* was captured. Each trap entrance size was fished for 510 trap-nights in 1994, and in 1995 total trap-nights were similar: 2 cm (878), 3 cm (815), and 4 cm (883). In 1995, mean depths of shoreline transects were 9.0, 8.5, and 8.0 m while mean depths of channel locations were 17.1, 22.0, and 23.2 m in strata 1, 2, and 3, respectively.

Crayfish Length Distribution

Mean carapace lengths of crayfish collected in shoreline transects were significantly different ($P < 0.05$) among trap sizes for both years (Figure 20). Mean carapace lengths of crayfish captured in 2 and 3 cm traps were similar ($P > 0.05$) between years, while mean

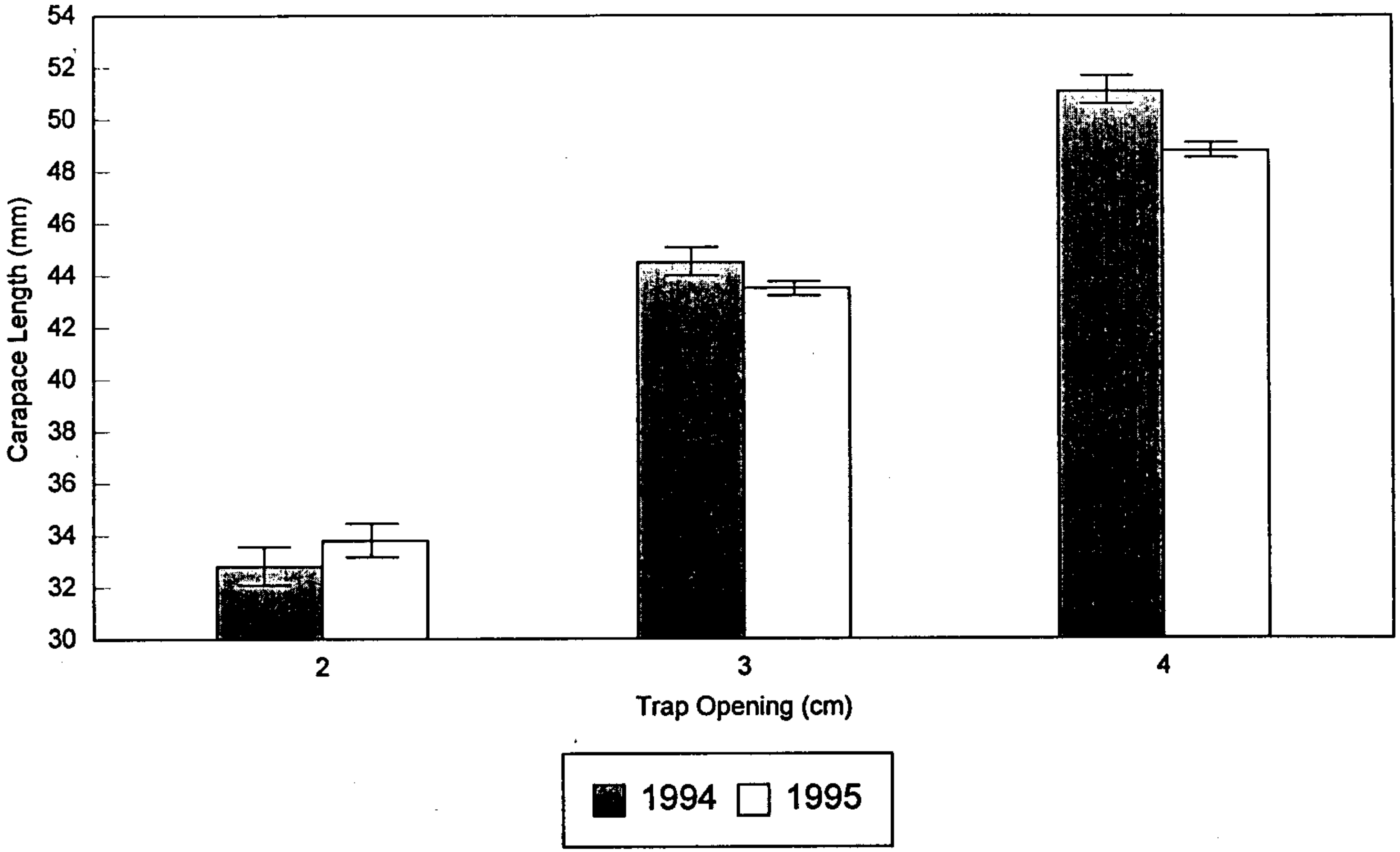

Figure 20. Mean carapace length ± 2*standard error (2SE) of crayfish captured by three trap openings in Lower Granite Reservoir, 1994-1995. Bar represents mean carapace length and tick marks represent upper and lower values of 2SE.

lengths of crayfish captured in traps with 4 cm openings were significantly ($P < 0.05$) larger in 1994. The two-way ANOVA indicated some degree of interaction between funnel opening size and year ($P < 0.05$). The range of crayfish carapace lengths was similar between years (Figure 21). In 1995, small crayfish (< 40 mm carapace length) constituted a majority (78%) of crayfish captured in traps with 2 cm openings, compared to traps with 4 cm openings (10%; Figure 22). However, more crayfish < 40 mm carapace length were collected in traps with 4 cm openings ($n = 121$) compared to traps with 2 cm openings ($n = 72$; Figure 22).

In 1995, mean carapace lengths of crayfish captured in traps with 2 cm funnel entrances were similar ($P > 0.05$) among shoreline (33.9 mm) and channel transects (33.7 mm; Figure 23). Mean carapace lengths of crayfish captured in traps with 3 cm openings were significantly ($P < 0.05$) larger in shoreline (43.9 mm) versus channel transects (42.8 mm; Figure 23). Traps with 4 cm funnel entrances captured significantly larger crayfish in shoreline (49.3 mm) versus channel transects (48.1 mm; Figure 23).

A significant positive relationship was found between carapace length and crayfish weight ($P < 0.05$; $r^2 = 0.84$; Figure 24). Rostral length was linearly related to carapace length ($P < 0.05$; $r^2 = 0.65$; Figure 24) for crayfish captured.

Sex Ratio

Sex ratios of crayfish captured varied between summer (June-August) and fall (September-October) trapping periods. In 1994, female-to-male sex ratios were similar ($P > 0.05$) between summer and fall collections in 2 cm traps (Figure 25), but were significantly different ($P < 0.05$) for crayfish captured in 3 cm and 4 cm traps. Female-to-male sex ratios in 1995 summer collections were: 57:43, 63:37, and 66:34 for 2, 3, and 4 cm traps,

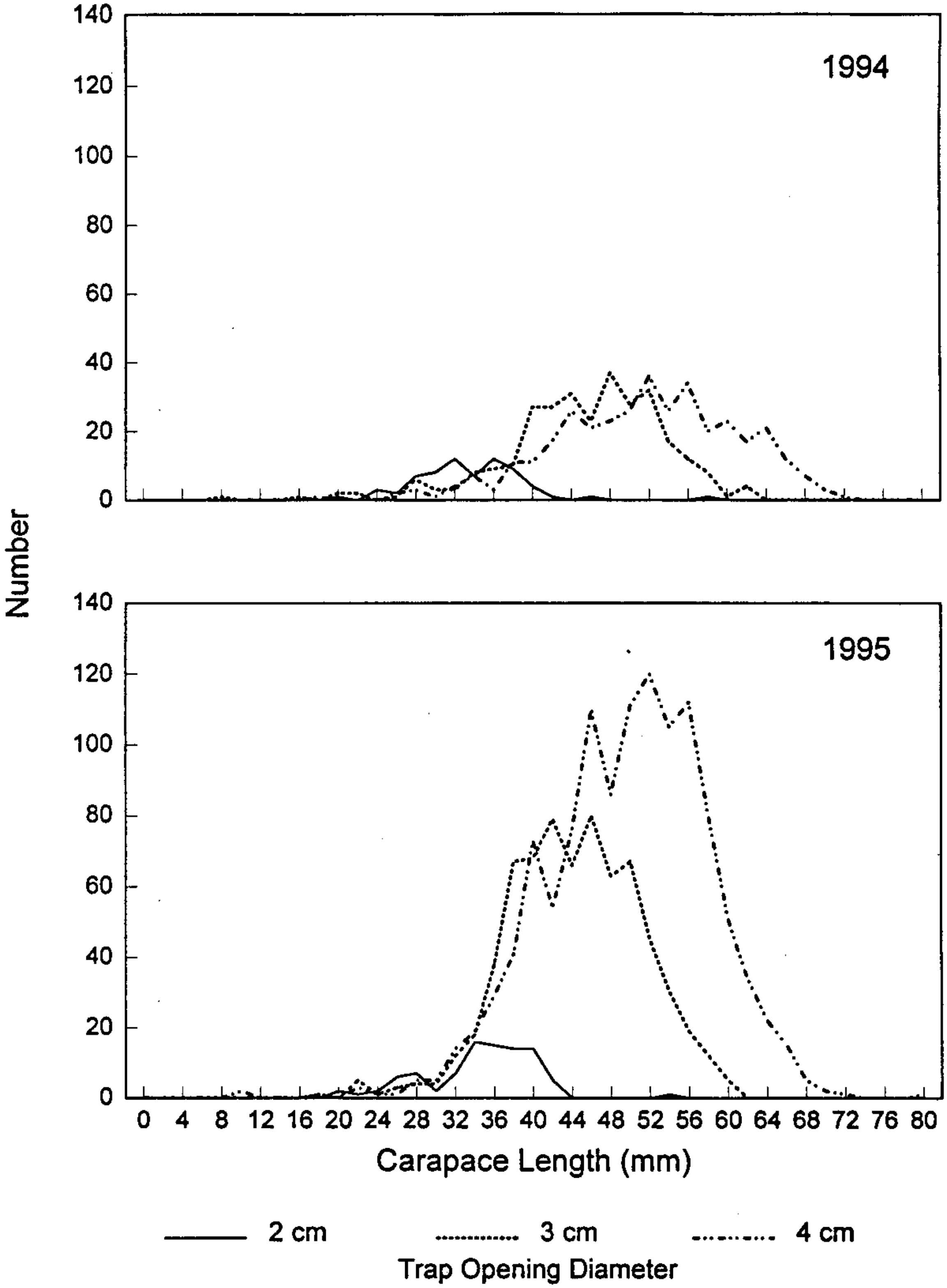

Figure 21. Carapace lengths of crayfish captured by three trap openings in Lower Granite Reservoir, 1994-1995.

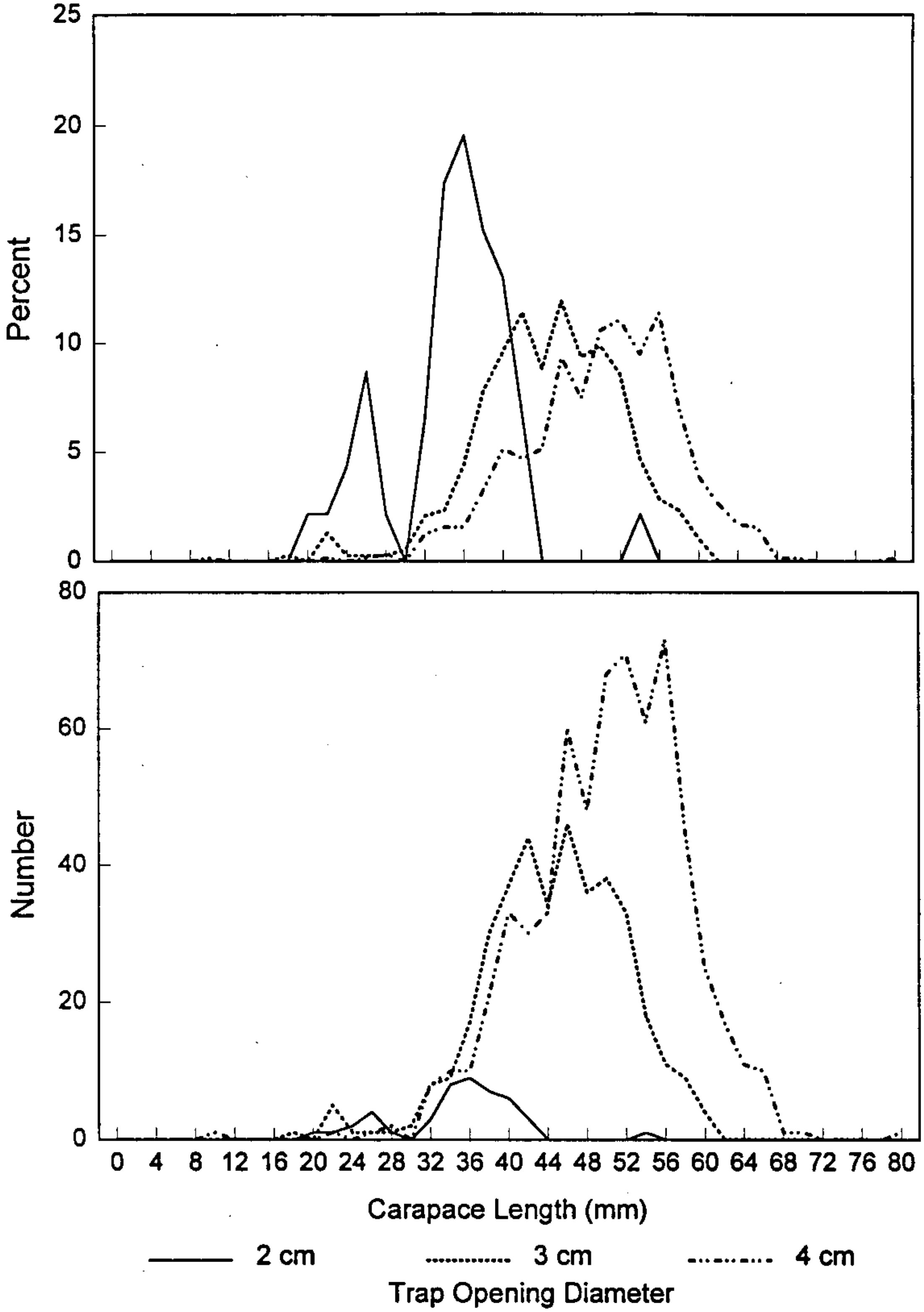

Figure 22. Distributions of carapace lengths, by trap opening diameter, based on percent and number of individuals per 2 mm size classes for crayfish captured in Lower Granite Reservoir, 1995.

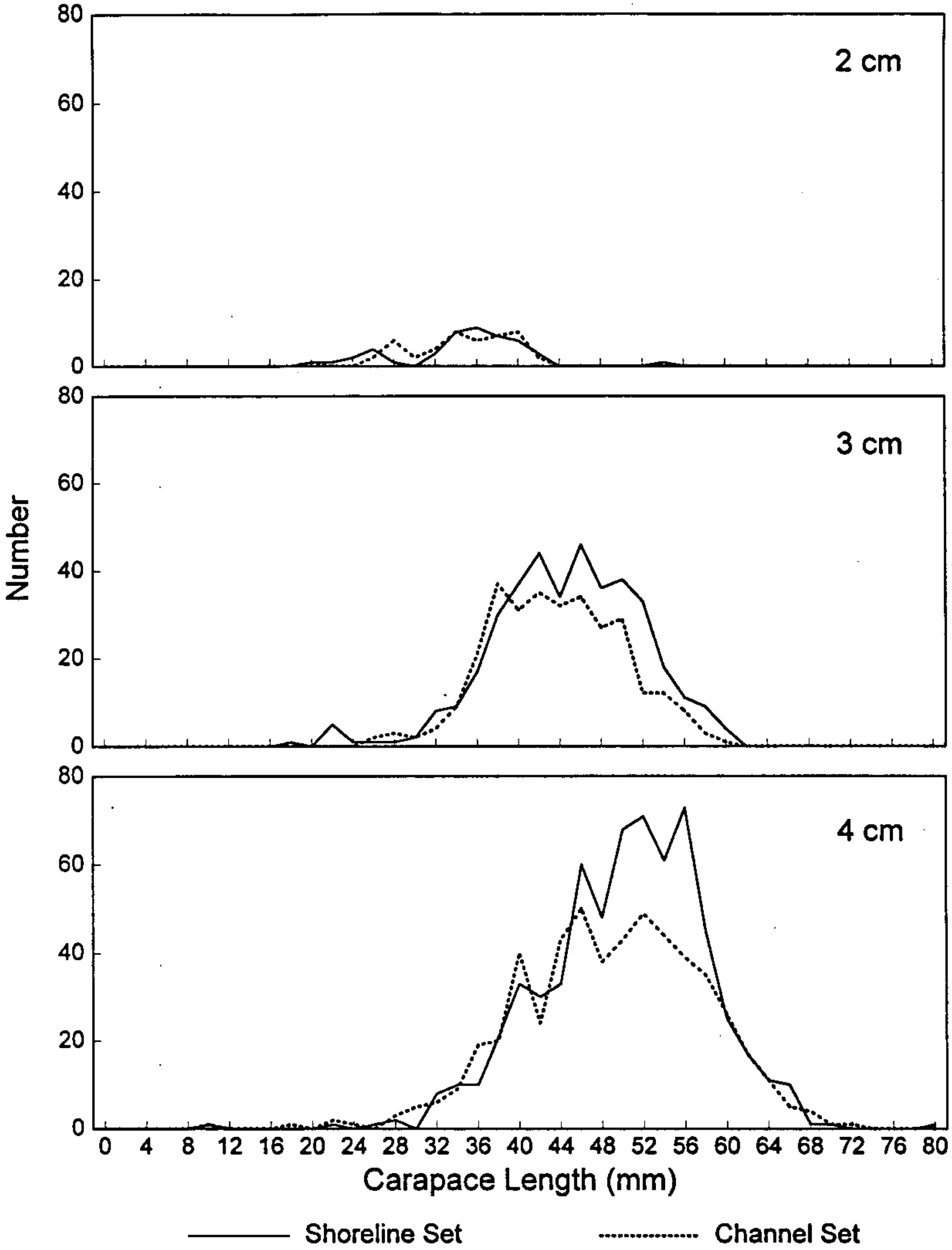

Figure 23. Carapace length-frequency distributions by funnel opening size of crayfish captured shoreline and channel locations Lower Granite Reservoir, 1995.

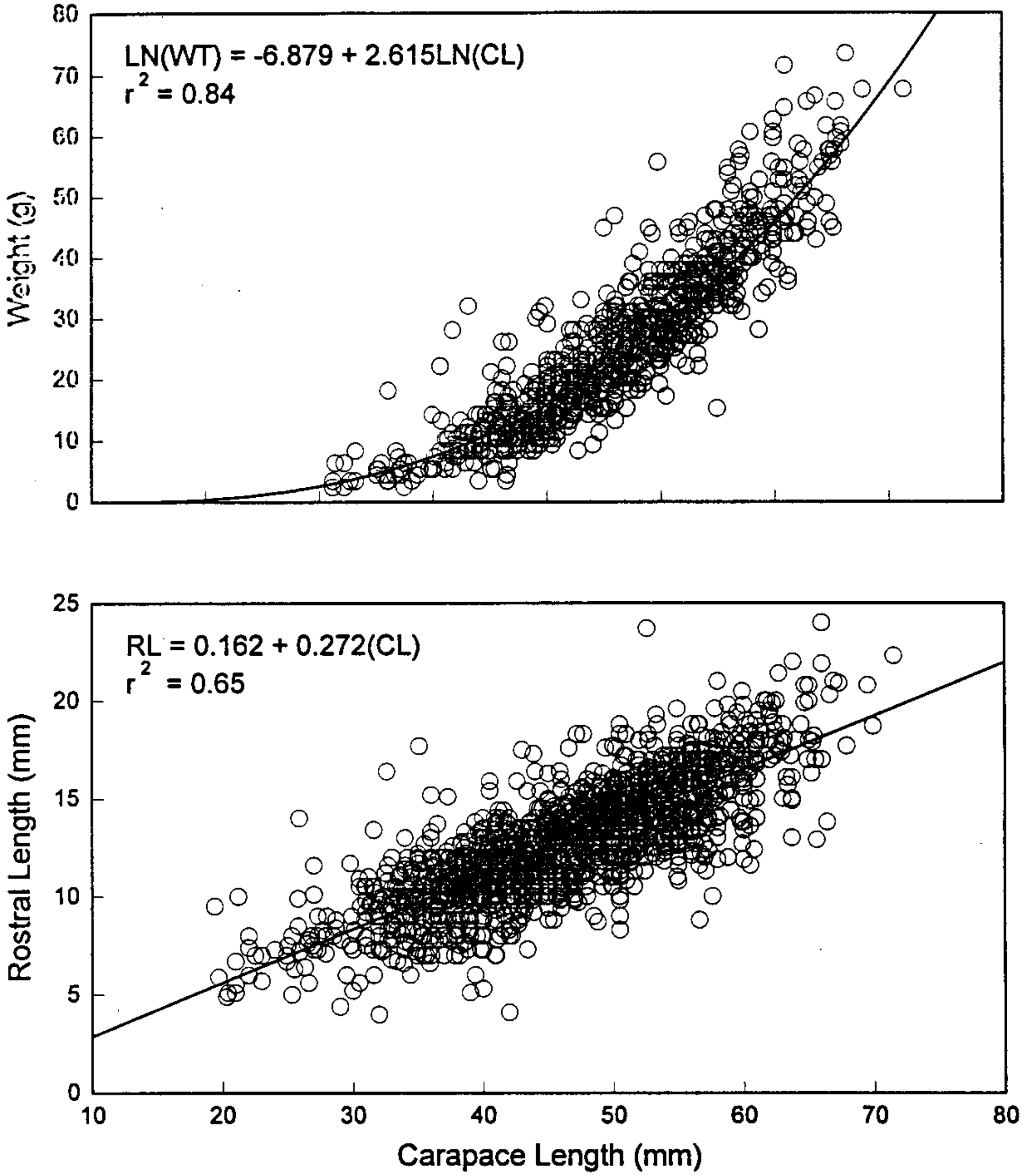

Figure 24. Relationship between carapace length (CL) and weight (WT), and carapace and rostral length (RL) for crayfish collected from Lower Granite Reservoir in 1995.

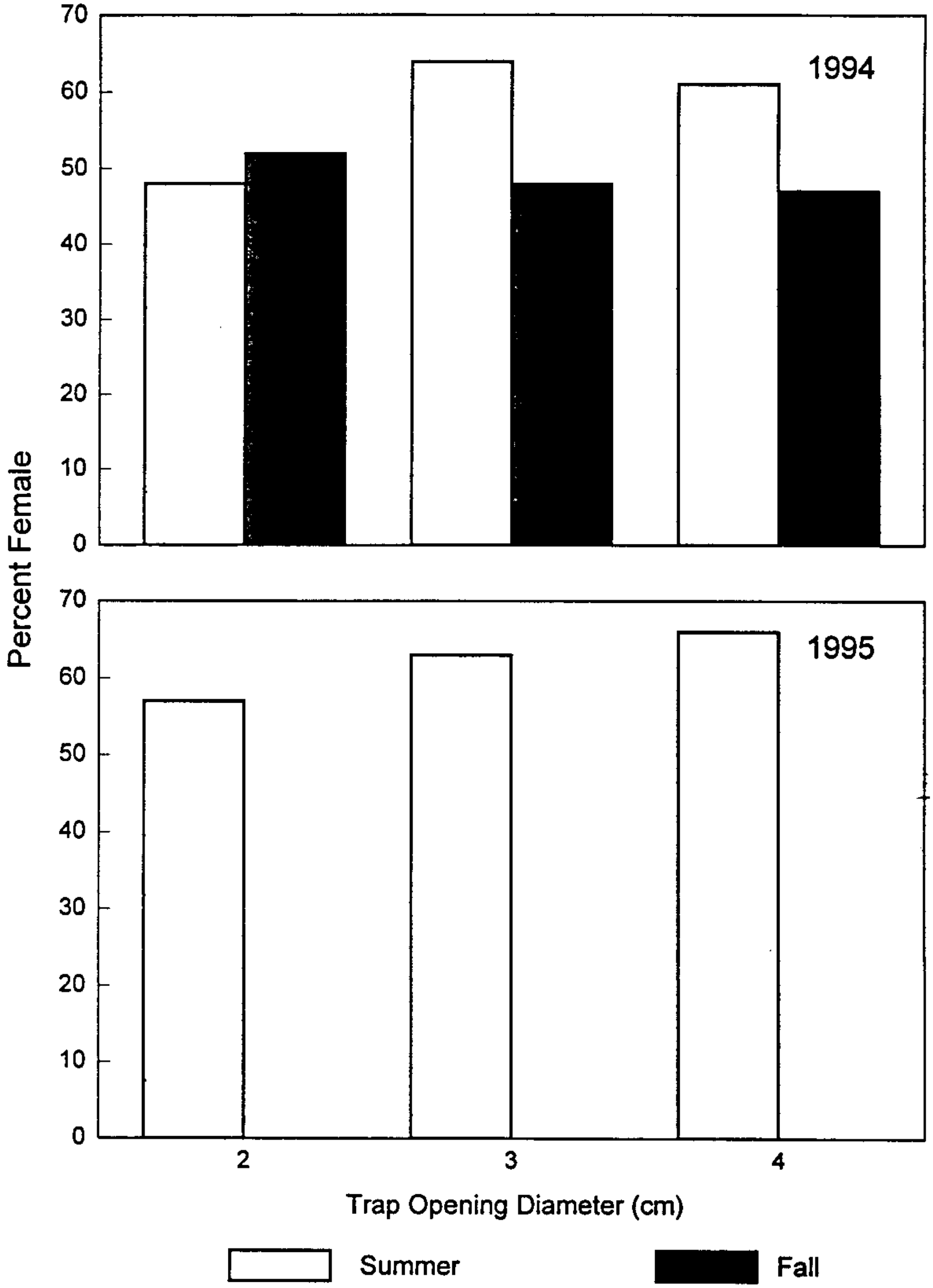

Figure 25. Percent female crayfish captured by three trap openings in Lower Granite Reservoir, 1994-1995.

respectively (Figure 25); no sampling was conducted in the fall. No significant difference ($P > 0.05$) in sex ratios was detected between 1994 and 1995 summer collections.

Crayfish Distribution

Based on the permutation test, the distribution of catch/effort throughout the reservoir was similar ($P > 0.05$; Figure 26) between years. The GLM indicated a significant difference ($P < 0.05$) in transformed catch/effort among transects. The SNK multiple range test identified significant differences ($P < 0.05$) in catch/effort among transects within the same stratum, which precluded pooling catch/effort values to test for stratum differences. Grouping generated by the procedure indicated catch/effort was generally higher in mid and upper portions of the reservoir (Figure 26). Catch/effort was similar ($P > 0.05$) between shoreline and channel transects in 1995 (Figure 27).

DISCUSSION

Crayfish Length Distribution

My results agree with those of Stuecheli (1991) who found that the size composition of crayfish caught in traps is related to funnel entrance diameter. Collections were dominated by the largest individuals capable of entering a trap. Large crayfish may be more successful at defending a prey item (Stein 1976) and preventing subdominant crayfish from entering a baited trap. Stuecheli (1991) also reported that crayfish > 40 mm were unable to enter traps with 2 cm openings and crayfish > 50 mm were unable to enter traps with 3 cm openings. However, I observed carapace lengths up to 58 mm in 2 cm traps and 62 mm in 3 cm traps. Differences in upper limits may be related to morphological differences between species of crayfish studied, as Stuecheli (1991) collected virile crayfish *Oronectes virilis* and I collected

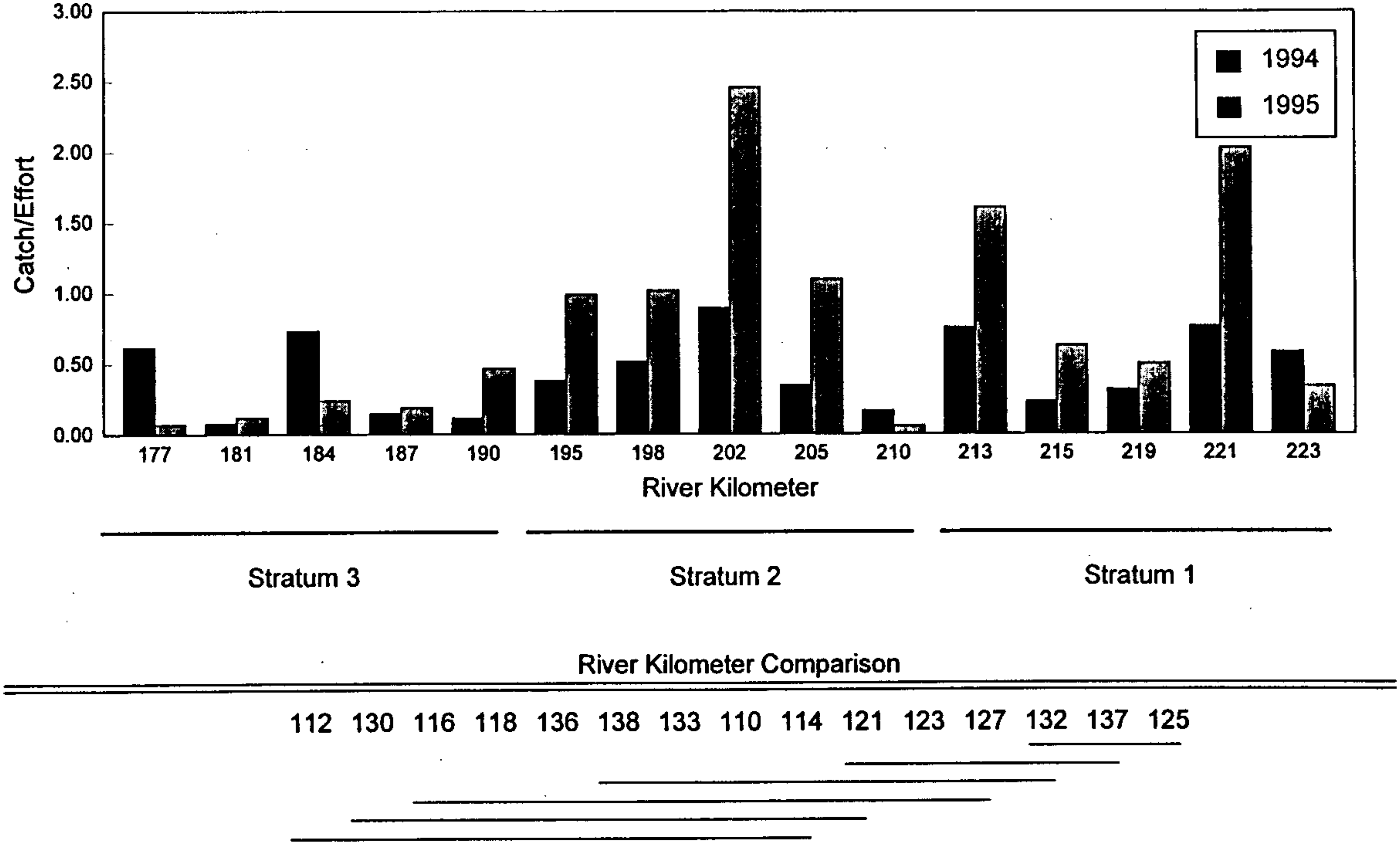

Figure 26. Catch/effort and river kilometer comparisons of crayfish collected in Lower Granite Reservoir, 1994-1995. Horizontal lines below river kilometers indicate statistical nonsignificance ($P > 0.05$).

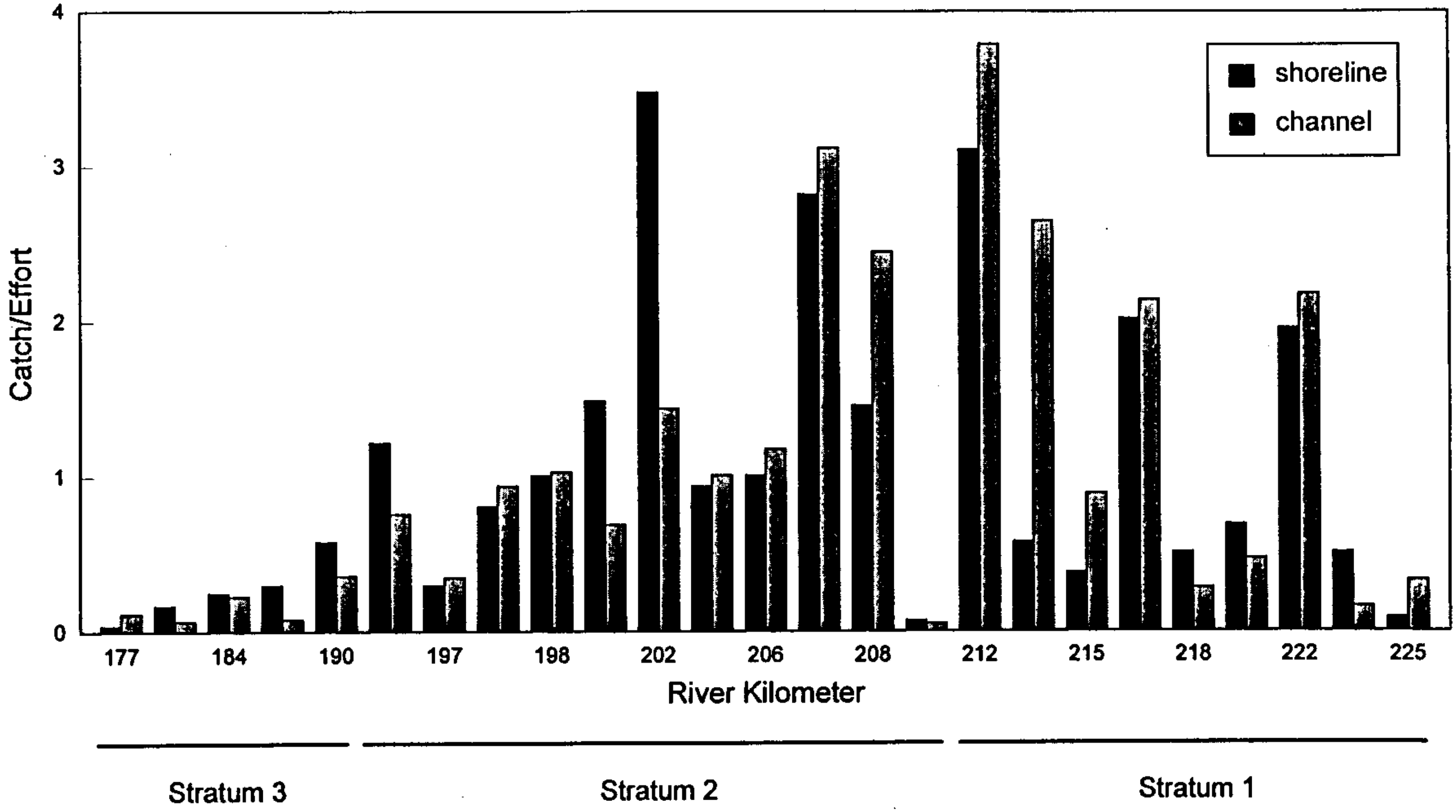

Figure 27. Catch/effort of crayfish collected at shoreline and channel transects in Lower Granite Reservoir, 1995.

signal crayfish *P. leniusculus*. The carapace diameter of *O. virilis* may be greater than that of *P. leniusculus* for a given carapace length. The size composition of crayfish collected using baited traps may also be directly or indirectly influenced by predators (Mather and Stein 1993).

Predators may influence crayfish study results directly through consumption or indirectly through behavior modification. Small crayfish are most vulnerable to consumption by fish (Rabeni 1992; Mather and Stein 1993). Mather and Stein (1993) and Collins et al. (1983) found reduced locomotory activity of small crayfish in the presence of predatory fish. In lakes with high predator (smallmouth bass, largemouth bass, and rock bass *Ambloplites rupestris*) and crayfish densities, samples using baited GEE brand minnow traps with 5 cm trap entrances resulted in low catches of crayfish; catches were higher in lakes with similar crayfish densities , but with lower predator densities (Collins et al. 1983). Density of smallmouth bass in Lower Granite Reservoir is relatively low (3.4 fish/ha; Objective 1), and therefore may not dramatically influence trapping results. The size composition of crayfish samples may be influenced by intra and interspecific interaction, as well as trap design.

Funnel entrance size may physically prevent relatively large crayfish from entering a trap. Stuecheli (1991) suggested using a variety of trap opening sizes, to sample a broader segment of the population. I believe if he presented carapace length-frequency distributions in terms of numbers captured per trap size rather than percent, the disparity in effectiveness among trap sizes would have been reduced (Figure 28). Based on percentages of size classes trapped, 2 cm traps are most effective at capturing small individuals, 3 cm traps intermediate sizes, and 4 cm traps large crayfish. Conclusions based on numbers of individuals trapped

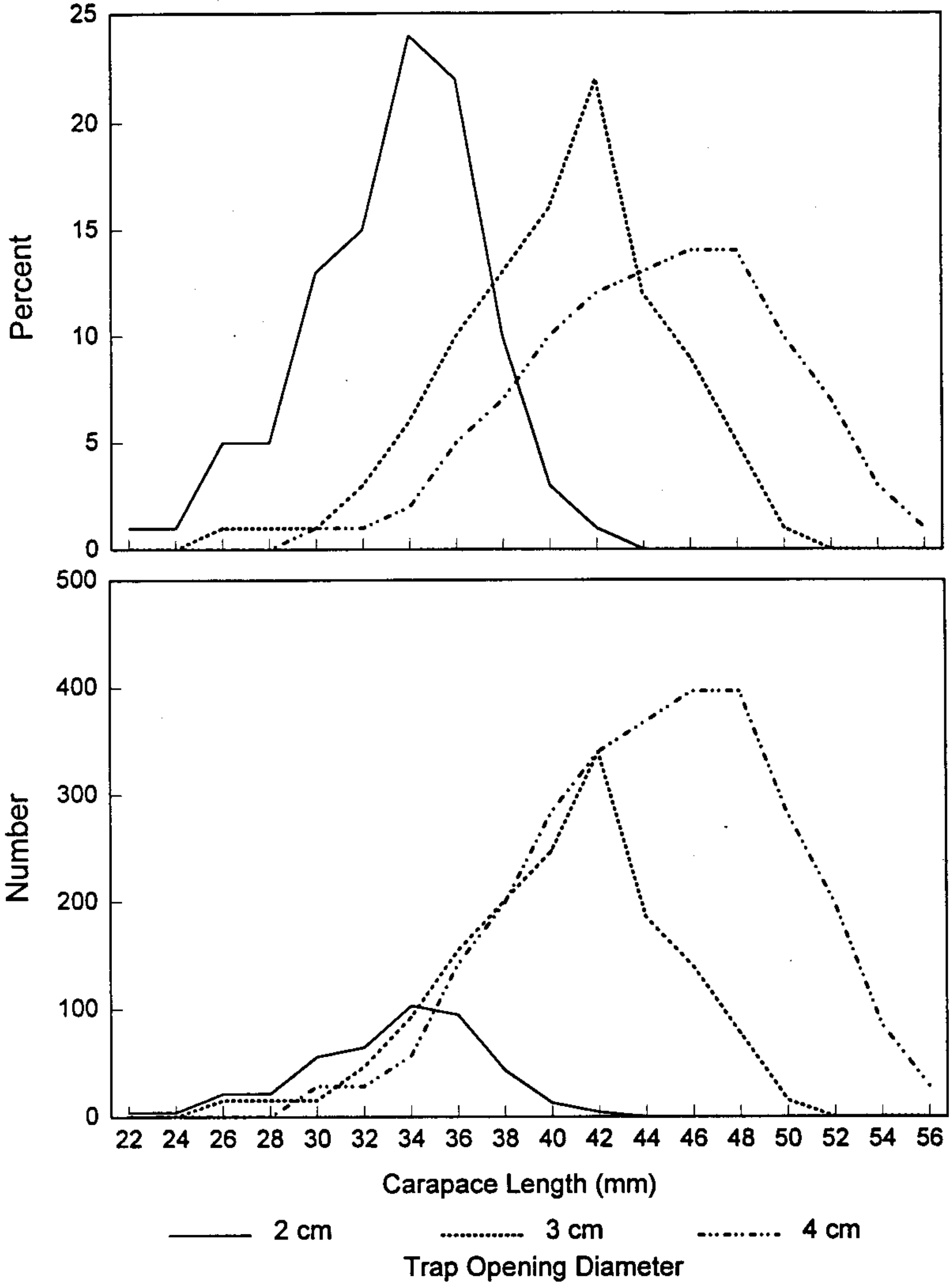

Figure 28. Length frequency-distributions of virile crayfish based on percentage and number of crayfish captured by three funnel openings. (Adapted from Stuecheli 1991)

suggest small differences in trappability of smaller crayfish (< 34 mm carapace length) among funnel entrance diameters (Figures 22 and 28).

Length-frequency and growth data suggest that the test drawdown of Lower Granite Reservoir, conducted during March 1992, may have resulted in a partial collapse of the 1992 cohort. In 1995, few crayfish with carapace lengths from 28 to 32 cm were captured (Figures 21 and 22). Signal crayfish of this size may be 3 to 4 years of age. Lowery (1988) identified seven populations of *P. leniusculus* whose carapace length at age 3 ranged from 28 to 62 cm, the smallest of which was reported for Lake Tahoe, California-Nevada. Annual water temperatures in Lower Granite Reservoir (4 to 23°C) are similar to those reported for Lake Tahoe (5 to 20°C), indicating length-at-age of crayfish within the two populations may be similar. Shimizu and Goldman (1983) and Lowery (1988) identified water temperature as the single most influential environmental variable affecting crayfish growth. Collections of the 1992 cohort in 1994 were likely too few to yield the resolution required to identify age classes in the lower end of the length-frequency distribution. Juveniles generally hatch (release from females) between late March and April (Shimizu and Goldman 1983). Mortality of juveniles during the drawdown may have resulted from juveniles being dislodged from the host female, desiccation, or through entrainment into downstream reservoirs. Artificial reduction of crayfish abundance may have reduced intraspecific competition for food and space. Reduced competition and relatively high fecundity (Lowery 1988) of surviving crayfish may have resulted in rapid recolonization of previously dewatered reservoir habitat following the drawdown.

I believe the statistically significant interaction between funnel opening size and year is an artifact of my large sample size and not biologically significant. Had the differences in means been more substantial (5-10 mm), I would not have proceeded with the pairwise comparisons of mean carapace length and funnel opening size. Differences in carapace lengths of crayfish sampled in shoreline and adjacent channel transects were statistically significant for traps with 3 or 4 cm openings, but may not have been biologically significant, and may be related to large sample sizes (385:302, 3 cm trap opening; 642:657, 4 cm trap opening; shoreline:channel respectively). Crayfish collected from shoreline transects in Lower Granite Reservoir were 1.1 (3 cm trap opening) and 1.2 mm (4 cm trap opening) longer than crayfish collected in adjacent channel transects. Abrahamsson and Goldman (1970) noted a substantial difference (5-10 mm) between body lengths of crayfish captured in shallow (0-40 m) and deep (40-200 m) water in Lake Tahoe. Shimizu and Goldman (1983) reported that crayfish tagged on one side of a river channel were often captured on the opposite side, a distance of approximately 110 m, and related this movement to random dispersal. The distance between shoreline and adjacent channel transects in Lower Granite Reservoir ranged from 45 to 90 m. Short distances between transects and overlapping depths of shoreline (1-60 m) and main channel (8-110 m) transects in Lower Granite Reservoir probably permitted mixing of individuals, resulting in similar size compositions. Future studies of crayfish trappability may benefit from determining *a priori* differences in mean carapace lengths that would be considered biologically significant.

Sex Ratio

Mating activity of *P. leniusculus* generally begins in mid to late October (Abrahamsson 1983; Shimizu and Goldman 1983) and may influence the sex and length composition of crayfish trapped. Chelipeds of males become larger in the mating period, allowing them to interact more successfully with larger, more fecund females (Stein 1976). The percentage of males trapped increased from summer to fall indicating that males may be more effective at preventing subdominant crayfish from entering traps in the fall. During non-mating periods, chelipeds of males become smaller (Stein 1976), potentially reducing their ability to defend a prey item. Westman et al. (1978b) reported that large male crayfish push aggressively into baited traps to feed, resulting in their over-representation in catches. The behavioral characteristic of berried females may also result in a predominance of males. Females stop eating, reduce or eliminate locomotory activity, and remain in seclusion until juveniles hatch (Taylor 1983).

Sampling technique may also influence the observed sex ratios of crayfish populations. Collections of crayfish using SCUBA reveal near even female-to-male ratios (Abrahamsson and Goldman 1970; Somers and Stechey 1986). Westman et al. (1978b) determined that electro fishing provided a representative sample of the sex and length structure of crayfish populations. Trapping studies generally show a predominance of males in the population (Somers and Stechey 1986; France et al. 1991; Stuecheli 1991). My results agree with those of Abrahamsson (1983), who noted a predominance of females in mid July collections of *P. leniusculus* in Lake Tahoe.

Crayfish Distribution

Catch/effort of crayfish in Lower Granite Reservoir was higher in mid and upper reservoir locations, similar to the distribution observed by Bennett et al. (1993). Klosterman and Goldman (1983) suggested that *P. leniusculus* distribution is nonrandom and may be related to substrate quality. Abrahamsson and Goldman (1970) observed higher densities and production of *P. leniusculus* in areas of Lake Tahoe that were dominated by rocky substrate. Substrate at upstream main channel locations in Lower Granite Reservoir is characterized by sand, large cobble, and boulders, while main channel substrate in lower regions of the reservoir consists largely of silt (Lepla 1994). Difference in substrate quality between upstream and downstream reservoir areas may account for the difference in crayfish relative abundance. Alternatively, Collins et al. (1983) cautioned that variable predator density among sampling locations may influence indices of crayfish density. Predator density throughout Lower Granite Reservoir probably had little influence on indices of crayfish density, as catch/effort of smallmouth bass was similar among strata in June 1995 and slightly higher in stratum 3 in July 1995 (Objective 1). Factors such as substrate quality, water velocity, wave action, depth, food availability, and predator density may influence crayfish density (Flint and Goldman 1975; Klosterman and Goldman 1983; Collins et al. 1983). Simultaneous measurements of several factors may be required to characterize the regulating mechanism of crayfish density.

Similarity in catch/effort between shoreline and adjacent channel transects in 1995 may be more evidence that crayfish migrate between the two areas. Crayfish in the American River, California were captured in traps on the opposite side of the river 12 days after release (Abrahamsson 1983). Crossing the river channel, which is approximately 20 m at its maximum depth, required that crayfish travel about 700 m (Abrahamsson 1983). This ability to move substantial distances may have enhanced dispersal of crayfish following the 1992 drawdown. Emigration followed by recolonization is often the response of stream inhabitants to drought (Larimore et al. 1959). Crayfish in Lower Granite Reservoir may not have been able to respond quickly enough to the decreasing pool elevation and emigrate to deeper water. Densities of desiccated crayfish were high throughout most of the exposed shorelines (Bennett, unpublished data). The shoreline and main channel regions of the upper reservoir were most dramatically affected by the test drawdown. Density of crayfish within main channel regions of Lower Granite Reservoir that were not dewatered during the drawdown may have reached carrying capacity, resulting in greater contact, more frequent behavioral interaction (Lowery 1988), and the migration of crayfish into unexploited shoreline areas after water levels were raised to pre-drawdown levels. Reduced density of large adults within the shoreline area would reduce the amount of adult cannibalism on juveniles (Taylor 1983). Taylor (1983) also observed large populations of juveniles and small adults available for recolonization following a drought in a Georgia stream. The ability of crayfish in Lower Granite Reservoir to recover from a cohort collapse may help reduce the amount of predation on juvenile anadromous salmonids migrating through the reservoir by providing an alternate prey for resident predatory fishes.

Crayfish are valuable to aquatic ecosystems for the role they play in controlling productivity and also as an alternative food source for fish (Abrahamsson and Goldman 1970; Bouchard 1978; Rabeni 1992). Hogger (1988) reported that crayfish can comprise 30% of the biomass in stream ecosystems. Flint and Goldman (1975) identified *P. leniusculus* as an important source of ammonia in Lake Tahoe and suggested the crayfish population influences the entire benthic community through its nutrient recycling. Nutrient cycling by crayfish may indirectly enhance benthic forage abundance (Lowery 1988) and ultimately food for juvenile anadromous salmonids. Additionally, following the test drawdown of Lower Granite Reservoir in 1992, smallmouth bass consumption rates of subyearling chinook in the upper reservoir ranged from 0.04-0.05 subyearling chinook/smallmouth bass/day (Curet 1993), compared to 0.009-0.032 smolts/smallmouth bass/day in 1995 (Objective 2). The higher consumption rates following the drawdown may be related to reduced abundance of crayfish in the upper reservoir, or low flow and resulting benefits to fish predators (Objective 2).

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Appendix Table 1. Estimated mean catch per unit effort (C/E) and sample variance (Var) for smallmouth bass by length class (mm), month, and location in Lower Granite Reservoir, 1995. Effort was minutes of electrofishing current-on time.

Strata	Month	Number	Length Class (mm)							
			70-174		175-249		250-389		> 389	
		of samples	C/E	Var	C/E	Var	C/E	Var	C/E	Var
1	April	16	0.01	0.002	0.01	0.002	0.03	0.006	0.00	0.000
	May	34	1.13	1.232	0.92	0.864	0.23	0.080	0.02	0.003
	June	31	3.11	8.313	1.03	0.622	0.08	0.011	0.00	0.001
	July	31	2.83	7.049	1.10	1.177	0.11	0.012	0.00	0.000
2	April	45	0.54	0.540	0.03	0.004	0.03	0.007	0.00	0.001
	May	61	0.40	0.453	0.73	0.360	0.19	0.030	0.01	0.001
	June	40	0.99	1.029	1.16	0.478	0.12	0.026	0.01	0.001
	July	48	1.79	1.634	1.09	0.726	0.20	0.038	0.00	0.000
3	April	24	0.05	0.007	0.14	0.069	0.03	0.002	0.00	0.000
	May	52	0.22	0.060	0.77	0.496	0.18	0.052	0.01	0.001
	June	58	0.71	0.709	1.45	2.809	0.24	0.339	0.01	0.001
	July	48	1.09	0.870	1.77	1.922	0.27	0.132	0.01	0.001

Appendix Table 2. Estimated abundance of smallmouth bass by length class (mm), strata, and month in Lower Granite Reservoir, 1995.

		Length Class (mm)				
Strata	Month	70-174	175-249	250-389	> 389	TOTAL
1	April	608	763	867	0	2238
	May	25230	5286	938	72	31526
	June	25096	3779	419	35	29329
	July	18341	3687	444	0	22472
	August	18341	3687	444	0	22472
	September	18341	3687	444	0	22472
2	April	39982	2335	1167	209	43693
	May	11992	5665	1069	58	18784
	June	10776	5777	839	95	17487
	July	15593	4932	1089	0	21614
	August	15593	4932	1089	0	21614
	September	15593	4932	1089	0	21614
3	April	3899	14467	1103	0	19469
	May	7268	6615	1130	79	15092
	June	8618	8008	1878	79	18583
	July	10555	8946	1604	209	21314
	August	10555	8946	1604	209	21314
	September	10555	8946	1604	209	21314