

**EFFECTS OF RESERVOIR OPERATIONS AT
MINIMUM POOL AND REGULATED INFLOWS OF LOW
TEMPERATURE WATER ON RESIDENT FISHES
IN LOWER GRANITE RESERVOIR,
IDAHO-WASHINGTON**

Draft

by

**David H. Bennett
Thomas J. Dresser, Jr.
and
Melissa A. Madsen**

**Department of Fish and Wildlife
College of Forestry, Wildlife and Range Sciences
University of Idaho
Moscow, Idaho 83843**

March 1994

TABLE OF CONTENTS

	<u>Page</u>
List of Figures.....	ii
List of Tables.....	iv
ABSTRACT.....	v
Introduction.....	2
Objectives.....	4
Study Area.....	5
Methods.....	9
Results.....	13
Abundance of Larval Fishes.....	13
Larval Predator Abundance.....	20
Northern Squawfish.....	20
Smallmouth Bass.....	26
Year-Class Strength.....	26
Northern Squawfish.....	26
Smallmouth Bass.....	29
Growth of Smallmouth Bass.....	29
Total Length Attained in Fall.....	29
Back-Calculated Length at Age.....	34
Age, Environmental and Age*Environmental Effects.....	34
Discussion.....	36
MOP Operations and Abundance of Larval Fishes.....	36
Larval Predator Abundance.....	37
Northern Squawfish.....	37
Smallmouth Bass.....	38
Year-Class Strength.....	39
Northern Squawfish.....	39
Smallmouth Bass.....	40
Low Temperature Inflows and Growth of Smallmouth Bass.....	41
Body Length in Fall Samples.....	41
Age, Environmental and Age*Environmental Effects.....	44
Conclusions.....	45
References.....	47

LIST OF FIGURES

	<u>Page</u>
Figure 1. Map of sampling stations and locations in Lower Granite Reservoir.....	6
Figure 2. Water levels (ft above MSL) and temperatures (°C) in Lower Granite Reservoir from May through September, 1991.....	7
Figure 3. Water levels (ft above MSL) and temperatures (°C) in Lower Granite Reservoir from May through September 1992.....	8
Figure 4. Water levels (ft above MSL) and temperatures (°C) in Lower Granite Reservoir from May through September 1989.....	10
Figure 5. Water levels (ft above MSL) and temperatures (°C) in Lower Granite Reservoir from May through September 1990.....	11
Figure 6. Numbers of larval fishes sampled in Lower Granite Reservoir from 1989 through 1992.....	14
Figure 7. Comparison by stations and years of numbers of larval fishes sampled in Lower Granite Reservoir from 1989 through 1992...19	19
Figure 8. Numbers of larval fishes collected among stations by handbeam trawl and paired plankton nets in Lower Granite Reservoir from June through September, 1989.....	21
Figure 9. Numbers of larval fishes collected among stations by handbeam trawl and paired plankton nets in Lower Granite Reservoir from June through September, 1990.....	22
Figure 10. Numbers of larval fishes collected among stations by handbeam trawl and paired plankton nets in Lower Granite Reservoir from June through September, 1991.....	23
Figure 11. Numbers of larval fishes collected among stations by handbeam trawl and paired plankton nets in Lower Granite Reservoir from June through September, 1992.....	24
Figure 12. Comparisons by stations and years of larval northern squawfish sampled in Lower Granite Reservoir from 1989 through 1992.....	25
Figure 13. Comparisons by stations and years of larval smallmouth bass sampled in Lower Granite Reservoir from 1989 through 1992...27	27

- Figure 14. Graphical and statistical comparisons of the mean of ranks for age 0 northern squawfish abundance sampled by nighttime electrofishing in Lower Granite Reservoir during 1989-1993. The horizontal line under year-class indicates statistical nonsignificance ($P > 0.05$).....28
- Figure 15. Graphical and statistical comparisons of the mean of ranks for age 1+ northern squawfish abundance sampled by nighttime electrofishing in Lower Granite Reservoir during 1988-1992. Horizontal lines under year-class indicate statistical nonsignificance ($P > 0.05$).....30
- Figure 16. Graphical and statistical comparisons of the mean of ranks for age 0 smallmouth bass abundance sampled by beach seining in Lower Granite Reservoir during 1989-1993. Horizontal lines under year-class indicate statistical nonsignificance ($P > 0.05$)..31
- Figure 17. Graphical and statistical comparisons of the mean of ranks for age 1+ smallmouth bass abundance sampled by beach seining in Lower Granite Reservoir during 1988-1992. The horizontal line under year-class indicates statistical nonsignificance ($P > 0.05$).....32

LIST OF TABLES

	<u>Page</u>
Table 1. Numbers of larval fishes sampled by handbeam trawl and paired plankton nets during 1989 in Lower Granite Reservoir.....	15
Table 2. Number of larval fishes sampled by handbeam trawl and paired plankton nets during 1990 in Lower Granite Reservoir.....	16
Table 3. Number of larval fishes sampled by handbeam trawl and paired plankton nets during 1991 in Lower Granite Reservoir.....	17
Table 4. Number of larval fishes sampled by handbeam trawl and paired plankton nets during 1992 in Lower Granite Reservoir.....	18
Table 5. Mean, variance and coefficient of variation (CV) of total length of 1989 through 1993 year classes of smallmouth bass based on fall collections from Lower Granite Reservoir, Idaho-Washington. Like letters indicate no significant ($P>0.05$) differences in length.....	33
Table 6. Back-calculated length (mm) at age 1 from scale reading verified by examination of otoliths of smallmouth bass collected from Lower Granite Reservoir.....	35

ABSTRACT

Fluctuating water levels can adversely affect year-class strength of many fishes and conversely, stable water levels can enhance recruitment of some fishes. In 1991 and 1992, water levels were maintained at minimum operating pool (MOP - 733 ft) in Lower Granite Reservoir. We found that MOP contributed to exceptionally high larval fish abundance in 1991. Higher abundance was also found during 1992 although 2 weeks of water level fluctuations probably decreased larval abundance from 1991. Many larvae collected were northern squawfish *Ptychocheilus oregonensis* and smallmouth bass *Micropterus dolomieu* and numbers from these year classes also were highly abundant at ages 0+ and 1+. We believe that stronger than "average" year-classes of predators will develop under stable MOP conditions in Lower Granite Reservoir.

We found no unique effects to growth and survival of smallmouth bass of low temperatures in flows in Lower Granite Reservoir from upstream reservoir sources. Wide variation in growth of smallmouth bass was found and "environmental" effects significantly affected growth but not beyond the "normal" variation. Limited evidence suggested cool water inflows may be more deleterious to growth of older bass (4-6) but that was not the focus of our project.

INTRODUCTION

Widely fluctuating water levels in reservoirs are commonly associated with decreased recruitment of fishes whereas strong year-classes of many freshwater fishes have been associated with rising or high water levels during and after the spawning season (Ploskey 1986). Water levels also determine the quantity and quality of rearing habitat. Benson (1976), Nelson and Walburg (1977) and others reported increased year-class strength associated with increased water levels in Missouri River reservoirs. High spawning success does not ensure a strong year-class but may increase its probability of occurring.

During spring and summer 1991 and 1992, water management in Lower Granite Reservoir was modified. Water levels in Lower Granite Reservoir were stabilized and maintained at minimum operating pool (MOP). Maintaining operations at minimum water levels in the lower Snake River reservoirs could potentially enhance recruitment of fishes that require stable water levels for spawning and/or rearing in shallow water. For example, predator species such as northern squawfish *Ptychocheilus oregonensis* and smallmouth bass *Micropterus dolomieu* that rear in shallow water may have increased survival at MOP than under "normal" operating conditions when water levels can fluctuate about 5 ft (1.5 m) in the lower Snake River reservoirs. Stable water levels may increase spawning success and reduce stranding of larval and juvenile fishes and result in stronger year-classes.

The release of low temperature water in 1991 (Karr et al. 1992) and 1992 (Bennett et al. 1994a) as an experiment to assess whether the lower Snake River reservoirs could be cooled also could affect year-class strength, growth and survival of fishes in Lower Granite

Reservoir. Changing the temperature regimen in the Clearwater River because of operational needs at Dworshak National Fish Hatchery has shifted the fish community from a smallmouth bass fishery to a cold water trout fishery. Decreasing the number of thermal units in Lower Granite Reservoir could result in similar shifts in the fish community to fishes that favor lower temperatures. Decreasing water temperatures in the Columbia River resulted in nest abandonment and direct mortality to smallmouth bass embryos (Henderson and Foster 1957). Also, over-winter survival has been closely linked to body size in smallmouth bass (Oliver et al. 1979). Lower water temperatures result in slower growth rates and small body sizes entering the winter. Smaller fish may be more susceptible to higher predation rates that could also contribute to higher mortality and weaker year-classes; other potential indirect effects of reduced water temperatures. Other resident fishes in Lower Granite Reservoir could be impacted by changes in the thermal habitats, although much of the research on water levels and water temperatures has been conducted on smallmouth and largemouth *N. salmoides* bass.

The purpose of this study was to evaluate effects of maintaining a constant water level at MOP in Lower Granite Reservoir and assess effects of low temperature water inflows on resident fishes.

OBJECTIVES

1. To assess year-class strength of potential predator species from 1991 when water levels in Lower Granite Reservoir were maintained at minimum operating pool;
2. To quantify and compare abundance of larval fishes from 1991 and 1992 when minimum operating pool levels were maintained with abundance from previous years of greater water level fluctuations in Lower Granite Reservoir; and
3. To compare growth and survival of age 0 smallmouth bass in Lower Granite Reservoir as an indicator of possible deleterious effects from upstream cool water releases.

STUDY AREA

Sampling was conducted at several stations in Lower Granite Reservoir (Figure 1). Three stations were associated with disposal of dredged material at shallow (stations 1 and 2) and mid-depth (station 4) locations. Additional shallow water stations (reference stations 3, 5, 9, 10 and 11) were sampled. Specific locations of the sampling stations and a brief description follows:

<u>Station</u>	<u>Location</u>	<u>Type of Station</u>
1	RM 120	Shallow water disposal station; shoreline of the island created in 1989 from dredged material adjacent to the natural shoreline;
2	RM 120	Shallow water disposal station; off-shore, shoreline associated with the island;
3	RM 120	Shallow water reference station; shoreline adjacent to mid-depth disposal and island sites;
4	RM 120	Mid-depth disposal station that created the underwater bench (Bennett et al. 1988);
5	RM 127	Shallow water reference station (SR2S in Bennett and Shrier 1986; LG2S in Bennett et al. 1988);
9	RM 111	Shallow water reference station (LG1S in Bennett et al. 1988);
10	RM 110	Shallow water reference station on the south side of the reservoir (Bennett et al. 1990); and
11	RM 135.0	Shallow water reference station on the north side of the reservoir (LG5S in Bennett et al. 1988).

During June through mid-August 1991 and June through mid-September 1992, water levels were generally stabilized and maintained at MOP or between 733 and 734 ft (223 m) elevation in Lower Granite Reservoir (Figures 2 and 3). These levels were generally maintained during both years with < 1 ft (<0.3 m) fluctuation. Water levels in 1991 and 1992 were considerably more stable than those in the past that have

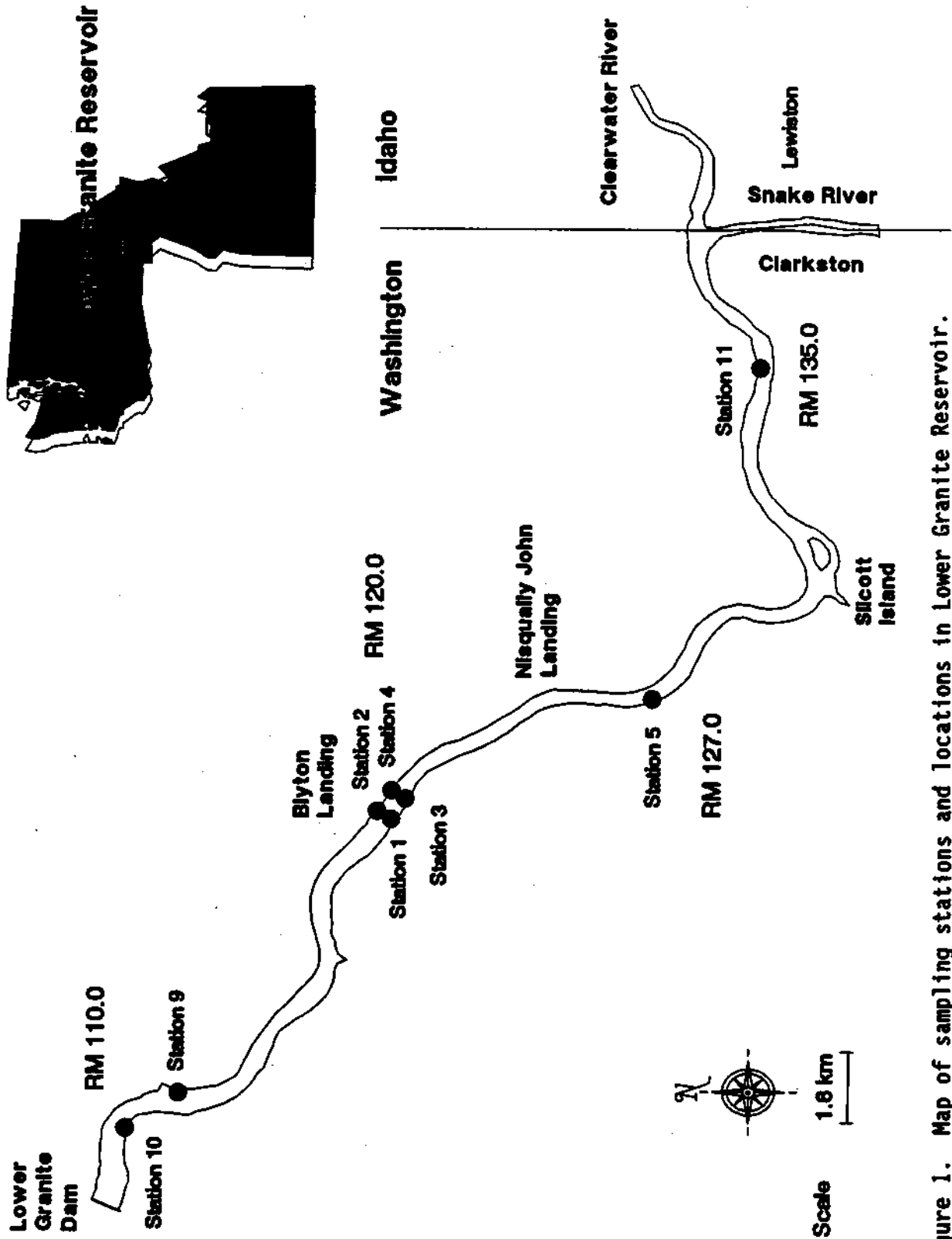


Figure 1. Map of sampling stations and locations in Lower Granite Reservoir.

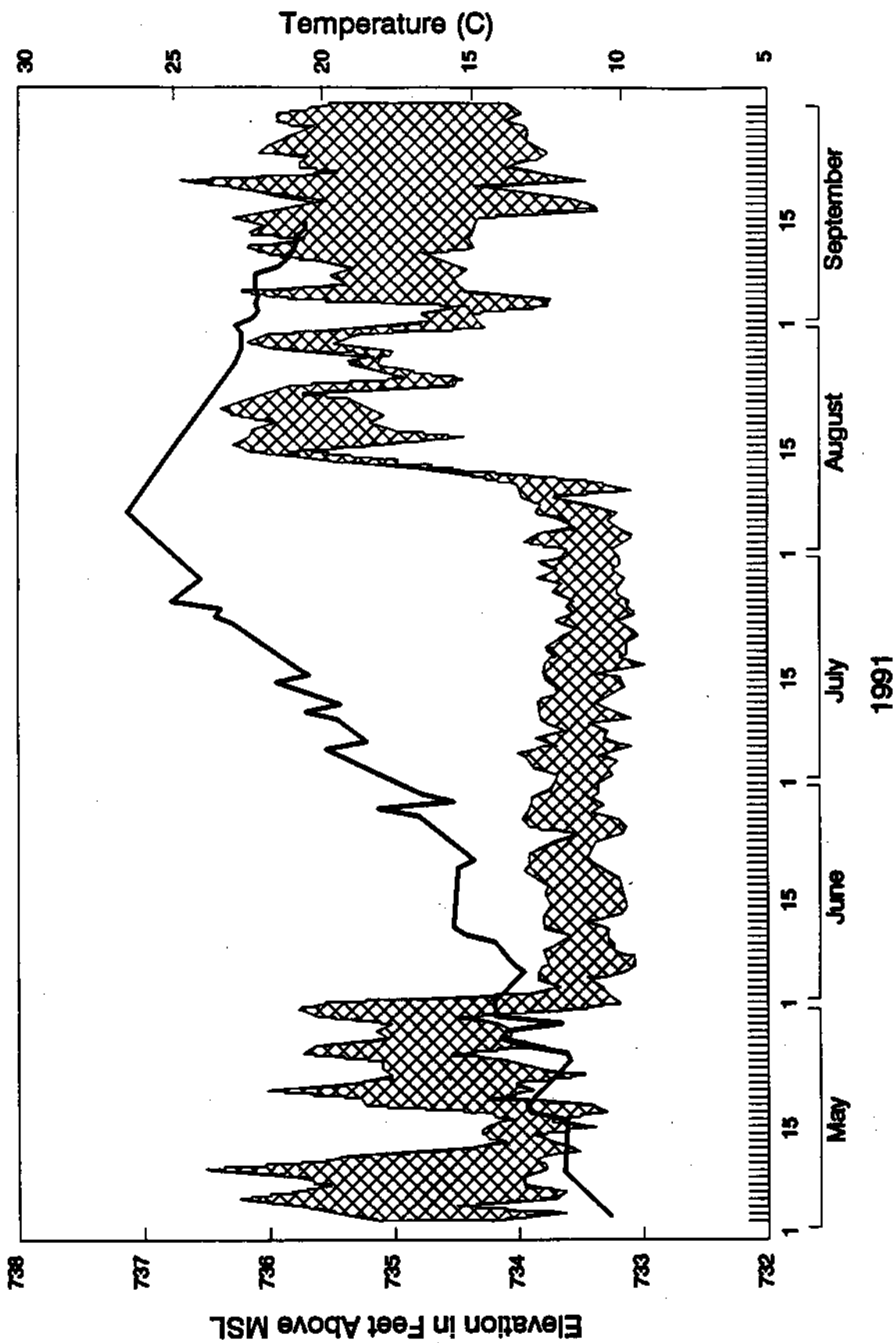


Figure 2. Water levels (ft above MSL) and temperatures ($^{\circ}\text{C}$) in Lower Granite Reservoir from May through September, 1991.

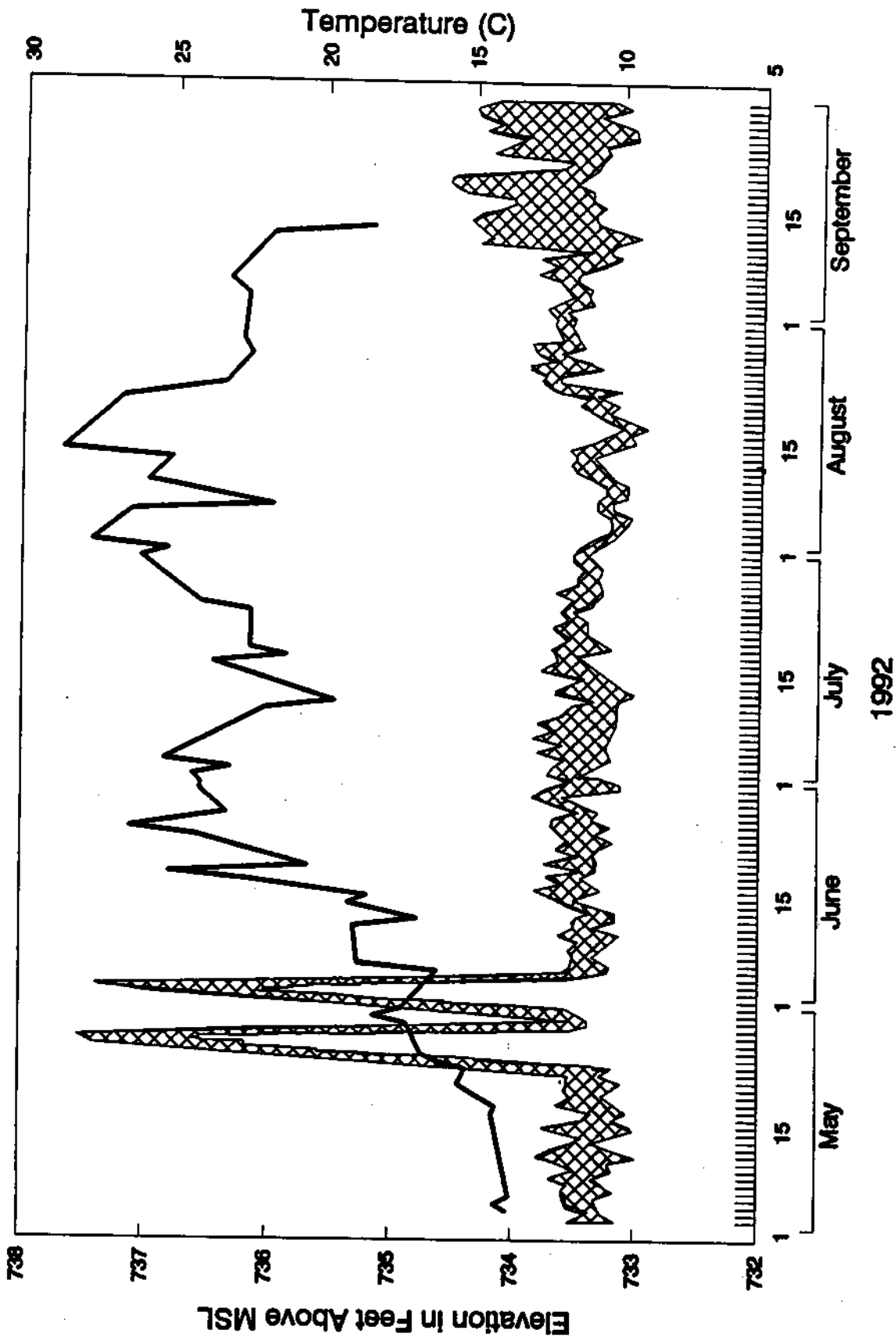


Figure 3. Water levels (ft above MSL) and temperatures (°C) in Lower Granite Reservoir from May through September 1992.

frequently fluctuated from 738 to 733 ft (225 to 223 m) elevation within a few days (Figures 4 and 5).

METHODS

Larval fish abundance was determined using 1/2 m (1.6 ft) paired plankton nets and a hand-drawn beam trawl (Bennett et al. 1991, 1993). We sampled generally at biweekly intervals from late May or June through August or mid-September from 1989 through 1992. Paired 1/2 m nets were towed at night approximately 1.6 m/s (5.1 ft/s) at the surface and 1 m (3.28 ft) in depth for 3 minutes at each depth. Three paired hauls were made at each station during each night of sampling. Samples from each net were preserved separately and provided six samples/sampling location/sampling date. During the daytime, the hand-drawn beam trawl (LaBolle et al. 1985) was pulled by two people along the shoreline over a standard distance of 15 m (49.2 ft). Three hauls were made along the shoreline in shallow (<1 m) and deeper (>1 m) water for a total of six hauls/station/sampling date. All samples were preserved in a 10% formalin solution for later enumeration.

During fall 1992 and 1993, we sampled by beach seining and nighttime electrofishing at selected shallow water habitats in Lower Granite Reservoir to assess year-class strength of predator fishes from both 1991 and 1992. Beach seining was conducted similarly to methods used in previous years to facilitate comparisons of results (Bennett and Shrier 1986; Bennett et al. 1988, 1990, 1991, 1993). We sampled twice monthly during September and October in the daytime using a 100 x 8 ft (30.5 x 2.4 m) seine constructed of 1/4 inch (0.64 cm) knotless nylon mesh with an 8 x 8 x 8 ft (25.4 m³) bag. A standard haul was made by

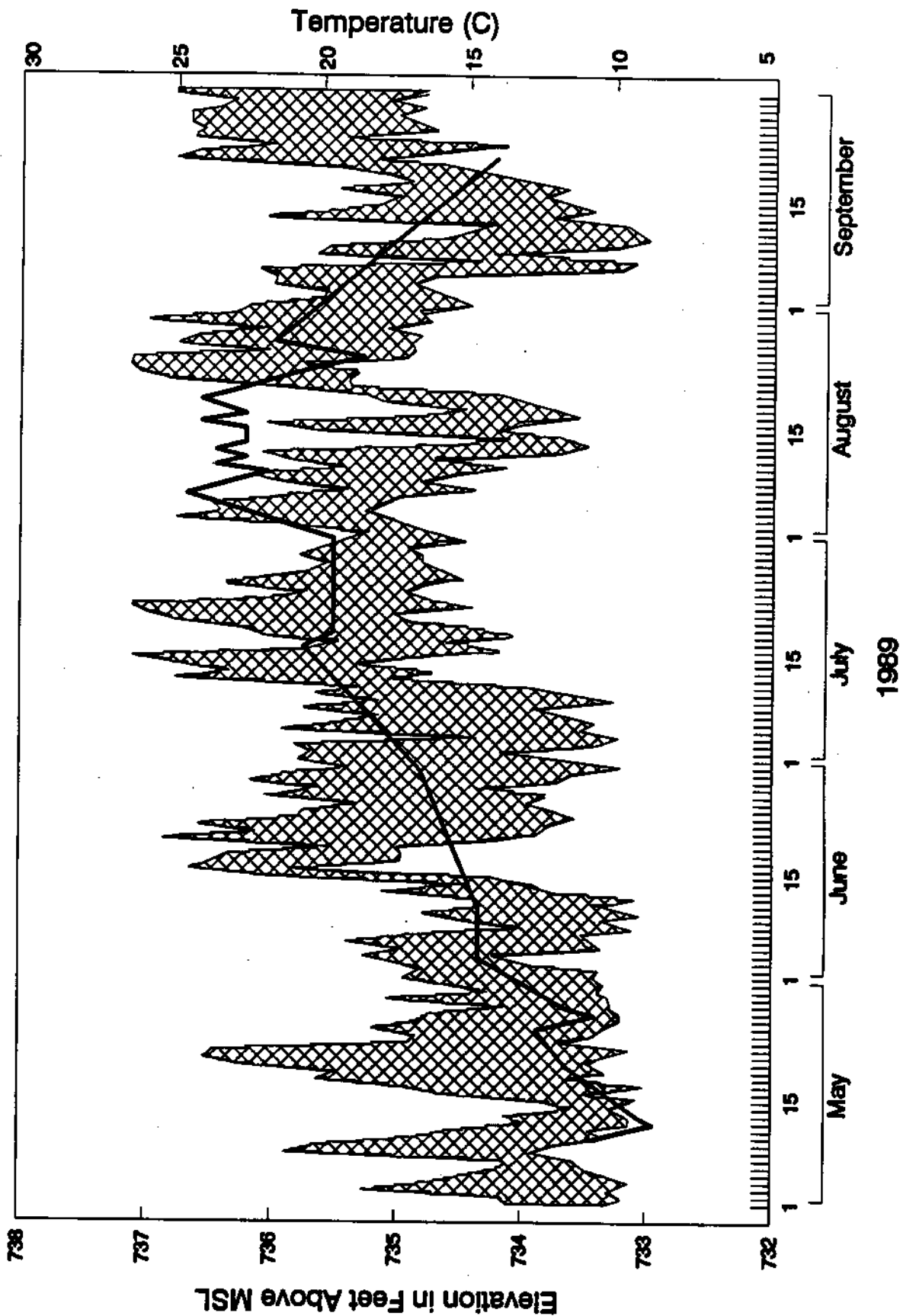


Figure 4. Water levels (ft above MSL) and temperatures ($^{\circ}$ C) in Lower Granite Reservoir from May through September 1989.

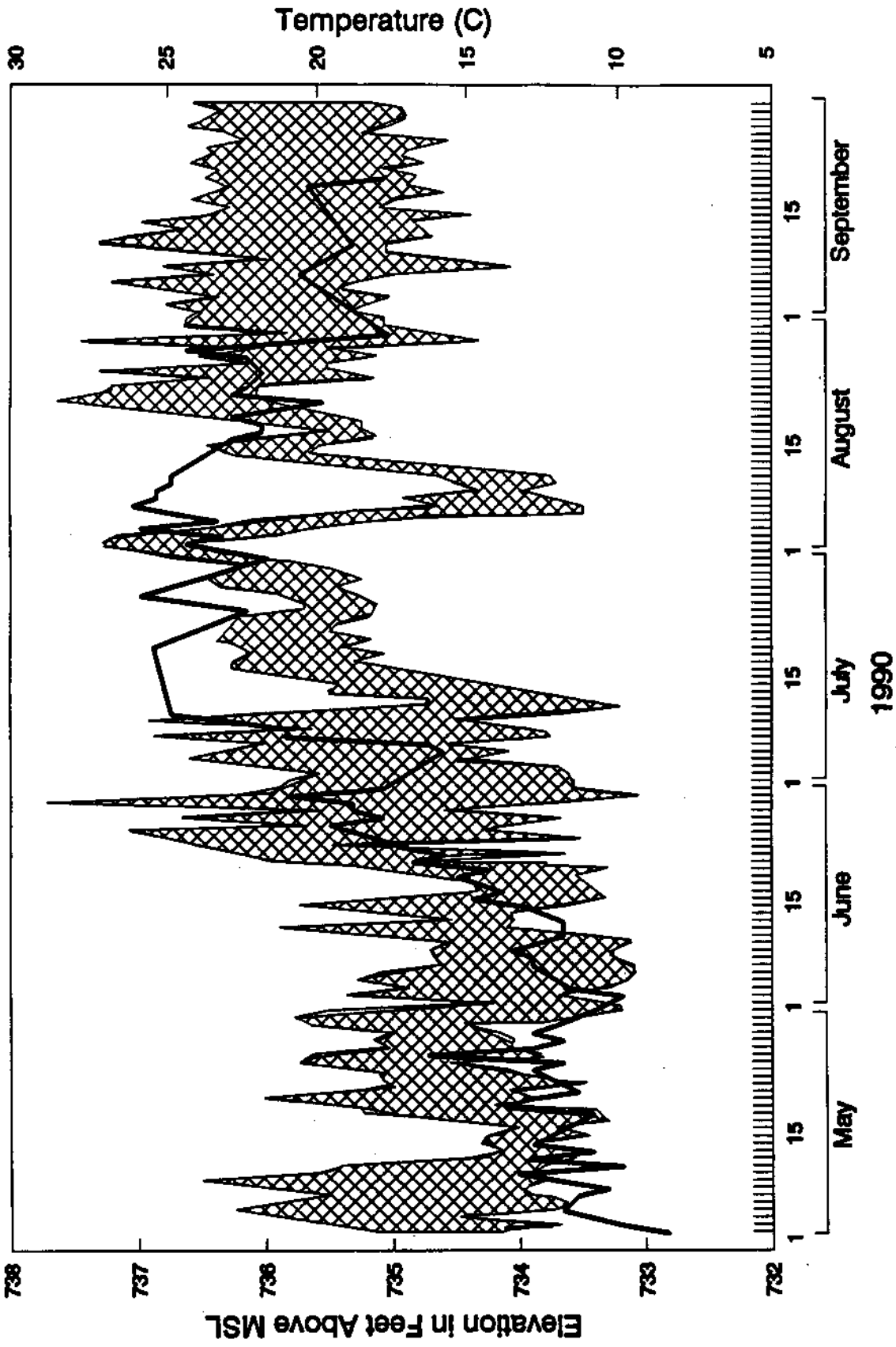


Figure 5. Water levels (ft above MSL) and temperatures (°C) in Lower Granite Reservoir from May through September 1990.

setting the seine parallel to the shoreline using 50 ft (15.2 m) extension ropes which sample approximately 0.08 acres (454 m²). Three hauls/station were made each time sampling was conducted. Standardized nighttime electrofishing was conducted by paralleling the shoreline as close as possible. Effort generally consisted of three periods of 5 minutes at each station. A constant output of 400 volts at 3-5 amps was found to adequately stun fish without causing mortality or visual evidence of injury.

Comparison of year-class strength among years was made by comparing catch/effort using analysis of variance ($P=0.10$). Because the assumptions of analysis of variance of normality and equal variances could not be satisfied ($P<0.01$), we transformed catches into ranks and used the rank values as observations in the analysis.

We sampled during spring and summer 1992 and collected scales and some otoliths from smallmouth bass to assess growth of bass in Lower Granite Reservoir. Scales were collected at the extension of the pectoral fin, below the lateral line and placed in labeled envelopes. Otoliths were collected from bass ranging from 70-140 mm to verify scale readings. Scales were cleaned in water in the laboratory and impressions made into acetate slides. Age and growth determinations were made by counting annuli and measuring the distance from the focus to annuli on a digitizer using the program, DISBCAL (Frie 1982). Mean length at age was calculated by DISBCAL using the Frazer-Lee method (Carlander 1982).

Comparison of annual growth was conducted by analysis of variance using a series of linear models developed by Weisberg and Frie (1987) to separate age, environmental and age*environmental effects using actual

scale measurements. An additive linear model: expected growth = age + environment + age*environment was fit to smallmouth bass scale increment data to determine if growth were affected by age, environmental, or an interaction of age and environmental effects. These models do not include an intercept, and the age variables are fit before environmental variables which are then adjusted for age effects, thereby enabling the separation of age and environmental effects (Weisberg and Frie 1987).

RESULTS

Abundance of Larval Fishes

Numbers of larval fishes sampled in Lower Granite Reservoir from 1989 through 1992 differed among years (Figure 6) and months (Tables 1-4). The highest abundance of larval fishes was collected during July 1991 (78%) followed by July 1992 (62.8%) and July 1990 (43.8%). The highest total number of larval fishes was collected in 1991 (24,417) when numbers were about eight times higher than in 1989 (2,945) and 1990 (2,079). Numbers collected in 1992 (8,688) were higher than those in 1989 and 1990, however they were about 30% of collections in 1991. Yearly differences in numbers of larvals collected were highly significant ($\chi^2=4310$; $P<0.0001$).

Numbers of larval fishes collected among sampling stations from 1989 through 1992 in Lower Granite Reservoir were not highly different among years except in 1991 (Figure 7). The difference among years occurred at station 11 where the majority of larval fishes was collected. Differences in larval fish numbers collected among years at station 11 were substantial (1,000-21,000), whereas comparisons among years at other stations were not highly different.

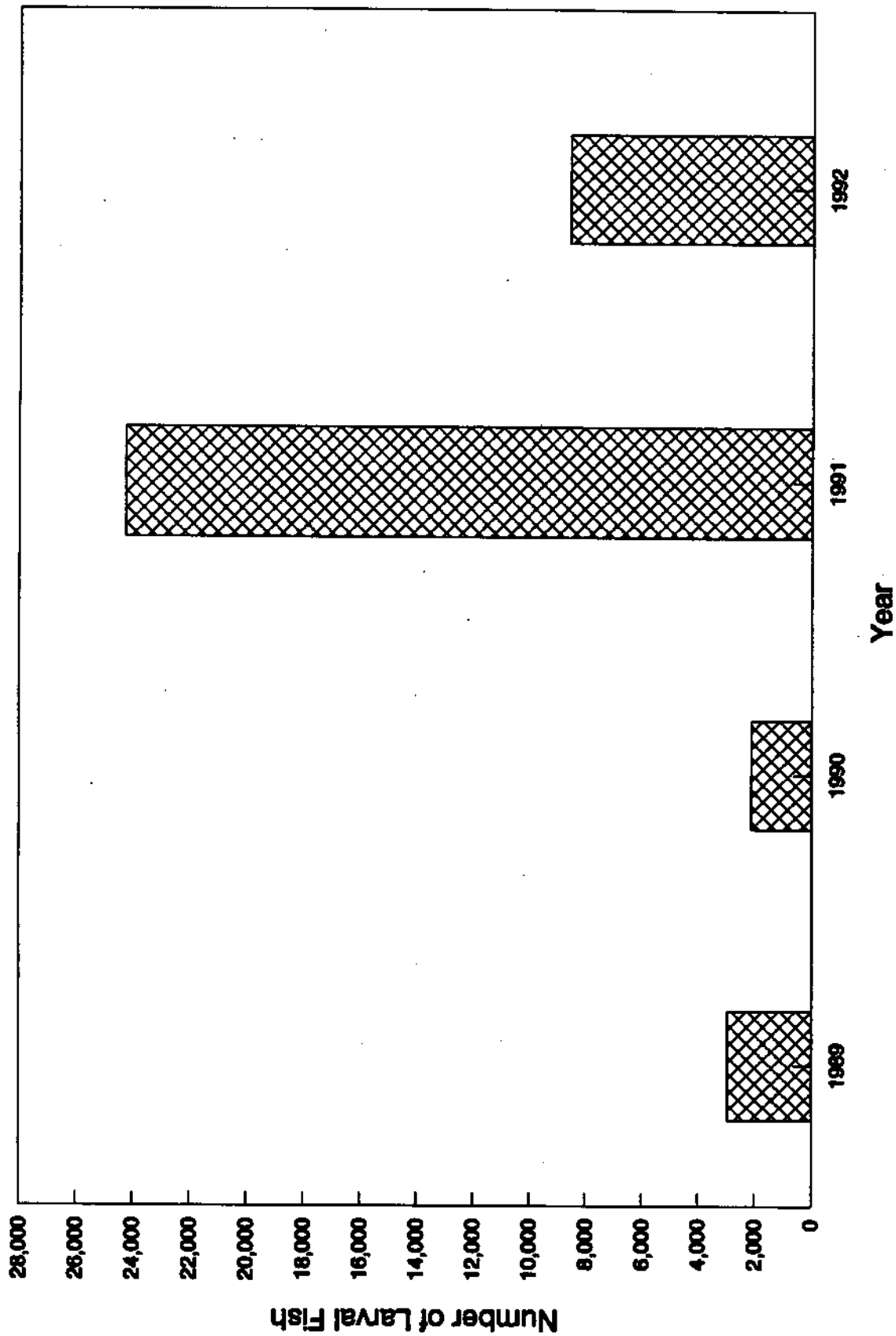


Figure 6. Numbers of larval fishes sampled in Lower Granite Reservoir from 1989 through 1992.

Table 1. Numbers of larval fishes sampled by handbeam trawl and paired plankton nets during 1989 in Lower Granite Reservoir.

Species	Month				Total	%
	June	July	August	Septemeber		
American shad		11			11	0.3
carp			1		1	0.03
northern squawfish		2	223		225	7.6
redside shiner	2	1			3	0.1
peamouth		278	11		289	9.8
Cyprinid spp.		189	35		224	7.6
Catostomid spp.	407	349	79		835	28.4
brown bullhead			8		8	0.3
Ictalurus spp.			1		1	0.03
pumpkinseed		3			3	0.1
Lepomis spp.		85	848	48	981	33.3
black crappie		103	4		107	3.6
white crappie		48	1	5	54	1.8
Pomoxis spp.		7	1		8	0.3
smallmouth bass		6	14		20	1.0
Micropterus spp.		173			173	5.9
Centrarchid spp.			2		2	0.1
Total	409	1,255	1,228	53	2,945	

Table 2. Number of larval fishes sampled by handbeam trawl and paired plankton nets during 1990 in Lower Granite Reservoir.

Species	Month				Total	%
	June	July	August	September		
American shad		1			1	0.04
chiselmouth		1			1	0.04
carp		11			11	0.5
northern squawfish		90	113	32	235	11.3
redside shiner		5		3	8	0.4
Cyprinid spp.	66	366	7	1	440	21.2
largescale sucker		2			2	0.1
bridgelip sucker		1			1	0.04
Catostomid spp.	88	275			363	17.5
brown bullhead			1		1	0.04
yellow bullhead		8			8	0.4
Ictalurus spp.				1	1	0.04
Lepomis spp.		110	608	212	930	44.7
black crappie		1	10	17	28	1.3
white crappie			2	1	3	0.1
Pomoxis spp.		27			27	1.3
smallmouth bass		11	3		14	1.0
Micropterus spp.		2	1	1	4	0.2
Centrarchid spp.	1				1	0.04
Total	155	911	745	268	2,079	

Table 3. Number of larval fishes sampled by handbeam trawl and paired plankton nets during 1991 in Lower Granite Reservoir.

Species	Month				Total	%
	June	July	August	September		
American shad		4	12		16	0.1
mountain whitefish	1				1	<0.01
chiselmouth		110	18		128	0.5
carp	1		55		56	0.2
peamouth	149	308	89		546	2.2
northern squawfish	202	3,351	2,963		6,516	26.7
redside shiner		10	3		13	0.1
Cyprinid spp.		1,124	37		1,161	4.8
largescale sucker			2		2	<0.01
Catostomid spp.	1,024	13,827	131		14,782	60.5
yellow bullhead			20		20	0.1
pumpkinseed		3			3	0.01
Lepomis spp.	2	280	324		586	2.4
white crappie		3			3	0.01
Pomoxis spp.		85	136		221	0.9
smallmouth bass		84	17		101	0.4
Centrarchid spp.		34	177		211	0.9
yellow perch		3	1		4	0.01
unknown spp.		42	5		47	0.2
Total	1,379	19,048	3,990	0	24,417	

Table 4. Number of larval fishes sampled by handbeam trawl and paired plankton nets during 1992 in Lower Granite Reservoir.

Species	Month				Total	%
	June	July	August	September		
American shad		13	2		15	0.2
chiselmouth		52			52	0.6
carp		2			2	0.02
peamouth	1	160			161	1.9
northern squawfish		1,242	6		1,248	14.4
redside shiner	1	12			13	0.1
Cyprinid spp.	81	1,903	5		1,989	22.9
largescale sucker		1			1	0.01
Catostomid spp.	38	22	4		64	0.7
channel catfish			1		1	0.01
pumpkinseed			1		1	0.01
bluegill		1	140		141	1.5
Lepomis spp.		27	277	282	586	6.7
black crappie		8	17		25	0.3
white crappie		196	15		211	2.4
Pomoxis spp.		11	375	24	410	4.7
smallmouth bass	356	138	4		498	5.7
Centrarchid spp.	172	1,659	1,271	141	3,243	37.3
yellow perch			17		17	0.2
Cottus spp.	1	1			2	0.02
unknown spp.	1	5	1	1	8	0.1
Total	651	5,453	2,136	448	8,688	

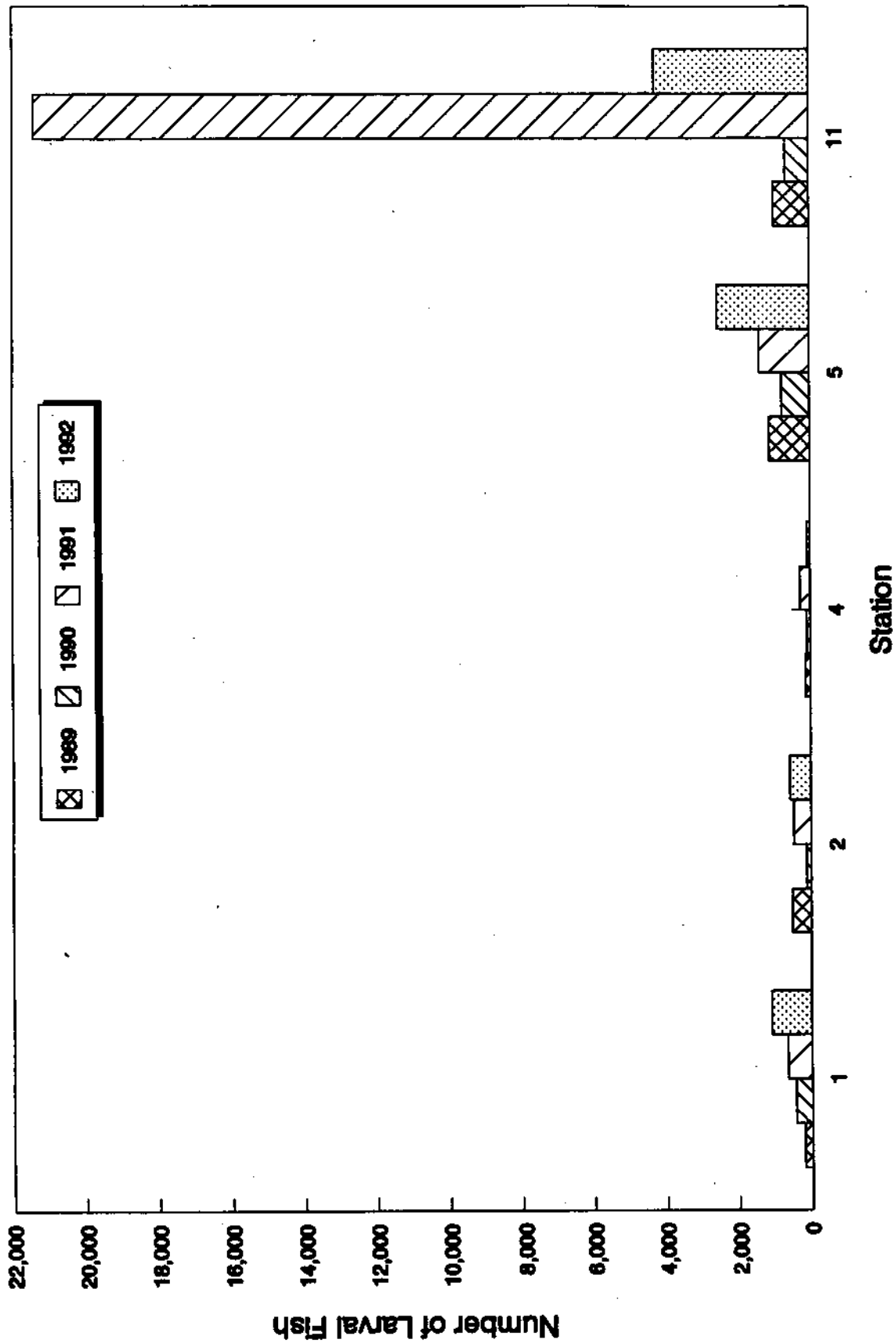


Figure 7. Comparison by stations and years of numbers of larval fishes sampled in Lower Granite Reservoir from 1989 through 1992.

Differences in the abundance of larval fishes collected among stations in Lower Granite Reservoir were large (Figures 8-11). During the period of sampling from 1989 to 1992, high numbers were collected at stations 11 and 5. Numbers collected at other stations in Lower Granite Reservoir were variable, although they followed a similar trend among years. During 1991 and 1992, the highest numbers of larval fishes were collected at station 11 (Figures 10-11), whereas in 1989 and 1990 the highest numbers were collected at station 5 (Figures 8-9).

Comparison of the abundance of larval fishes from shoreline versus pelagic waters indicate differences in abundance between habitat types among years (Figures 8-11). Approximately 90% of the larval fishes were collected adjacent to the shoreline by handbeam trawl during 1991 and 1992, whereas during 1989 and 1990 about 65-75% were collected there. The proportion of larval fishes collected at station 11 along the shoreline in 1990 was about 15%, whereas in 1991 and 1992 about 90% were collected there.

Larval Predator Abundance

Northern Squawfish

Numbers of larval northern squawfish collected at the sampling stations in Lower Granite Reservoir were generally low except during 1991 and 1992 (Figure 12). The number collected in 1991 was about 4-5 times higher than in 1992 and the number collected in 1992 was 4-5 times higher than 1989 and 1990.

The highest number of larval northern squawfish collected in Lower Granite Reservoir was at station 11 (Figure 12). Numbers of larval squawfish collected at all stations were similar between 1989 (n=225)

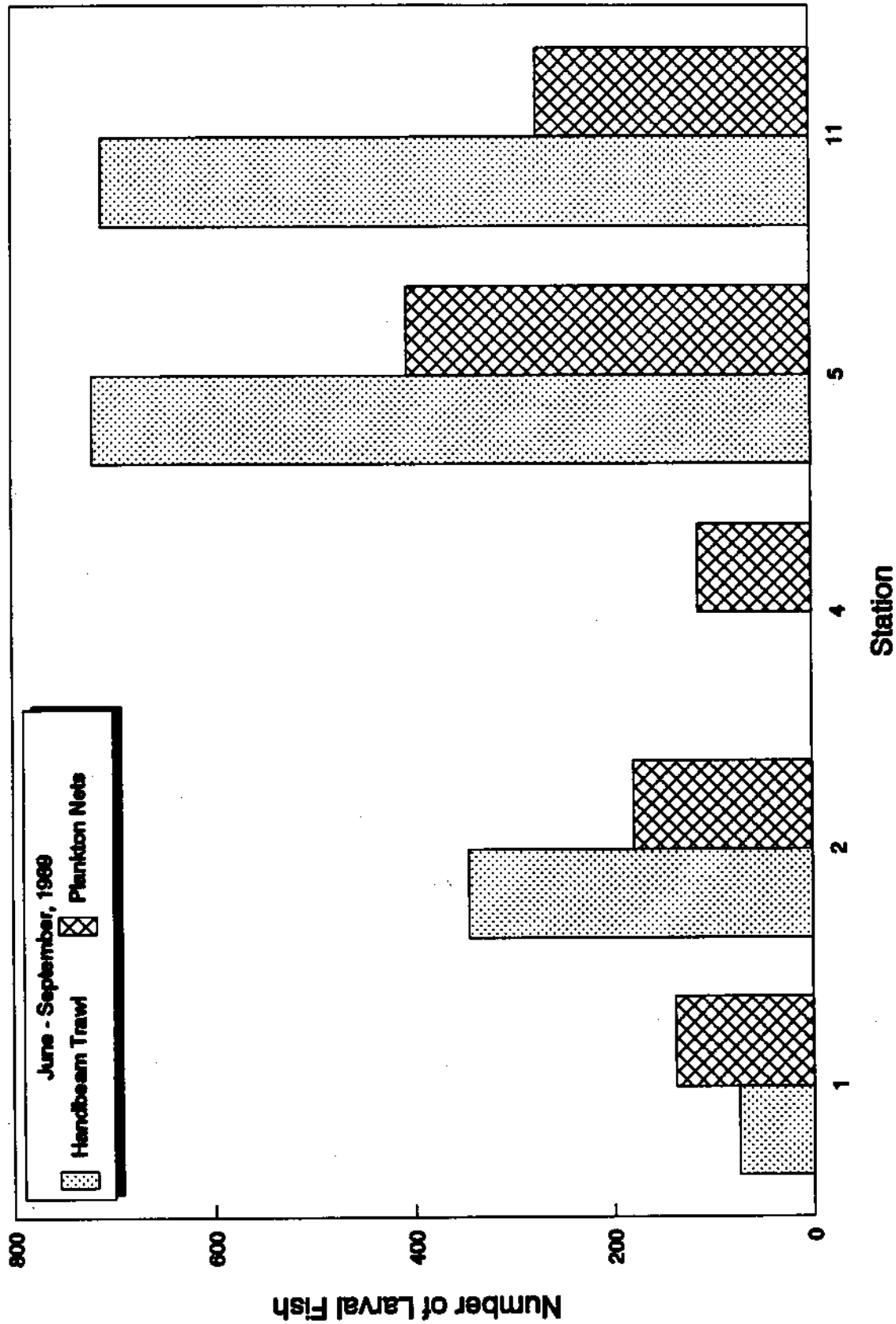


Figure 8. Numbers of larval fishes collected among stations by handbeam trawl and paired plankton nets in Lower Granite Reservoir from June through September, 1989.

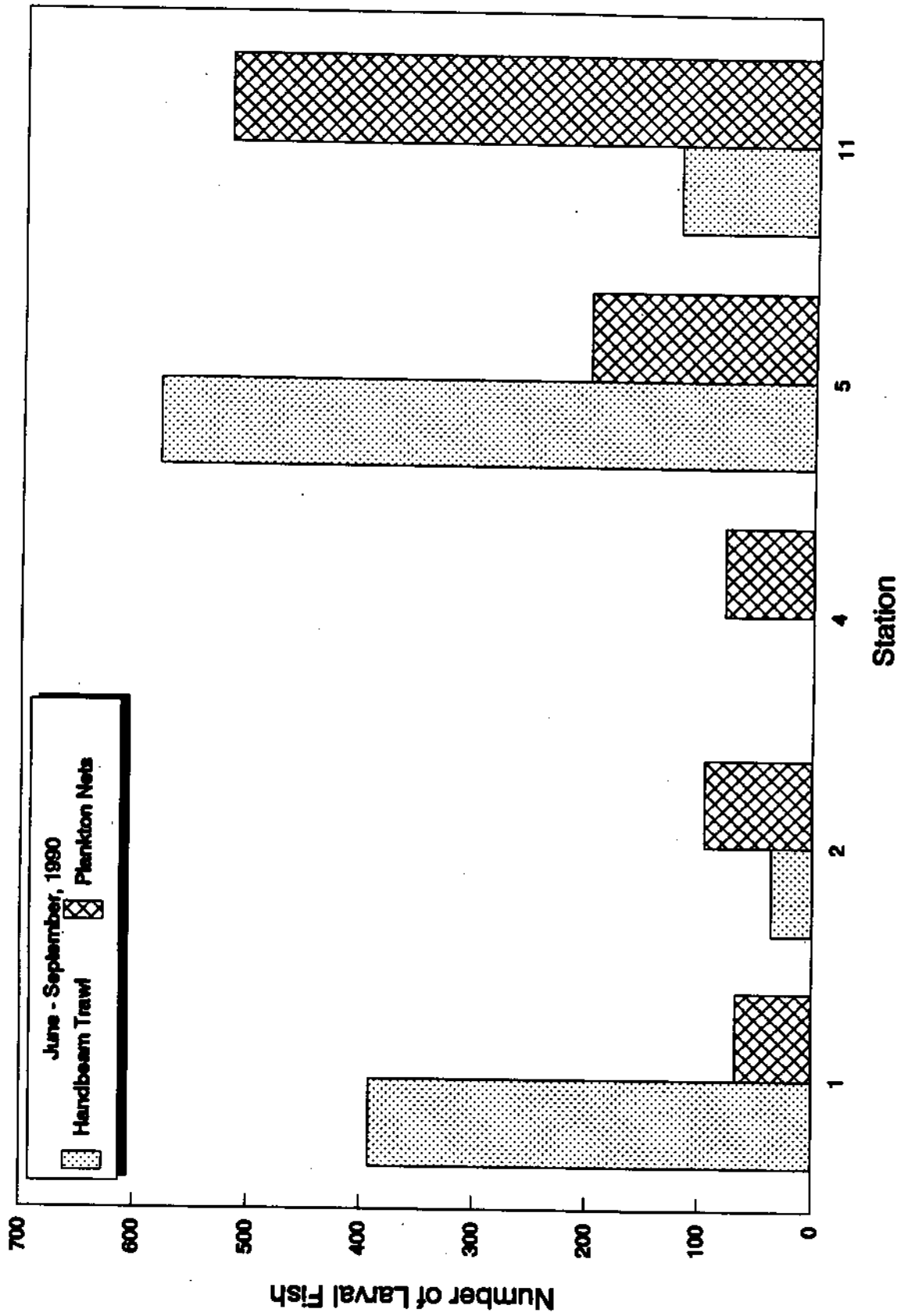


Figure 9. Numbers of larval fishes collected among stations by handbeam trawl and paired plankton nets in Lower Granite Reservoir from June through September, 1990.

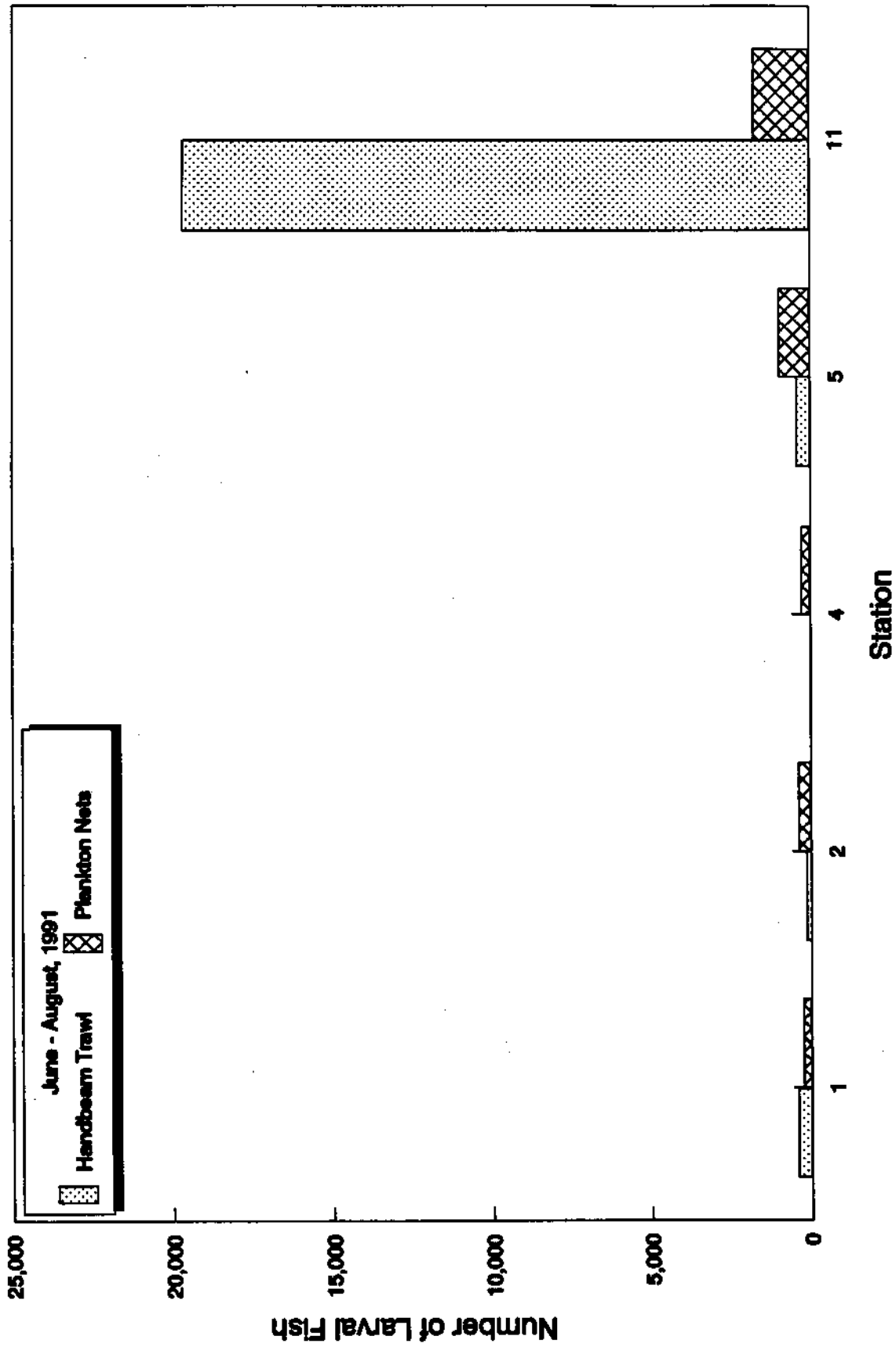


Figure 10. Numbers of larval fishes collected among stations by handbeam trawl and paired plankton nets in Lower Granite Reservoir from June through September, 1991.

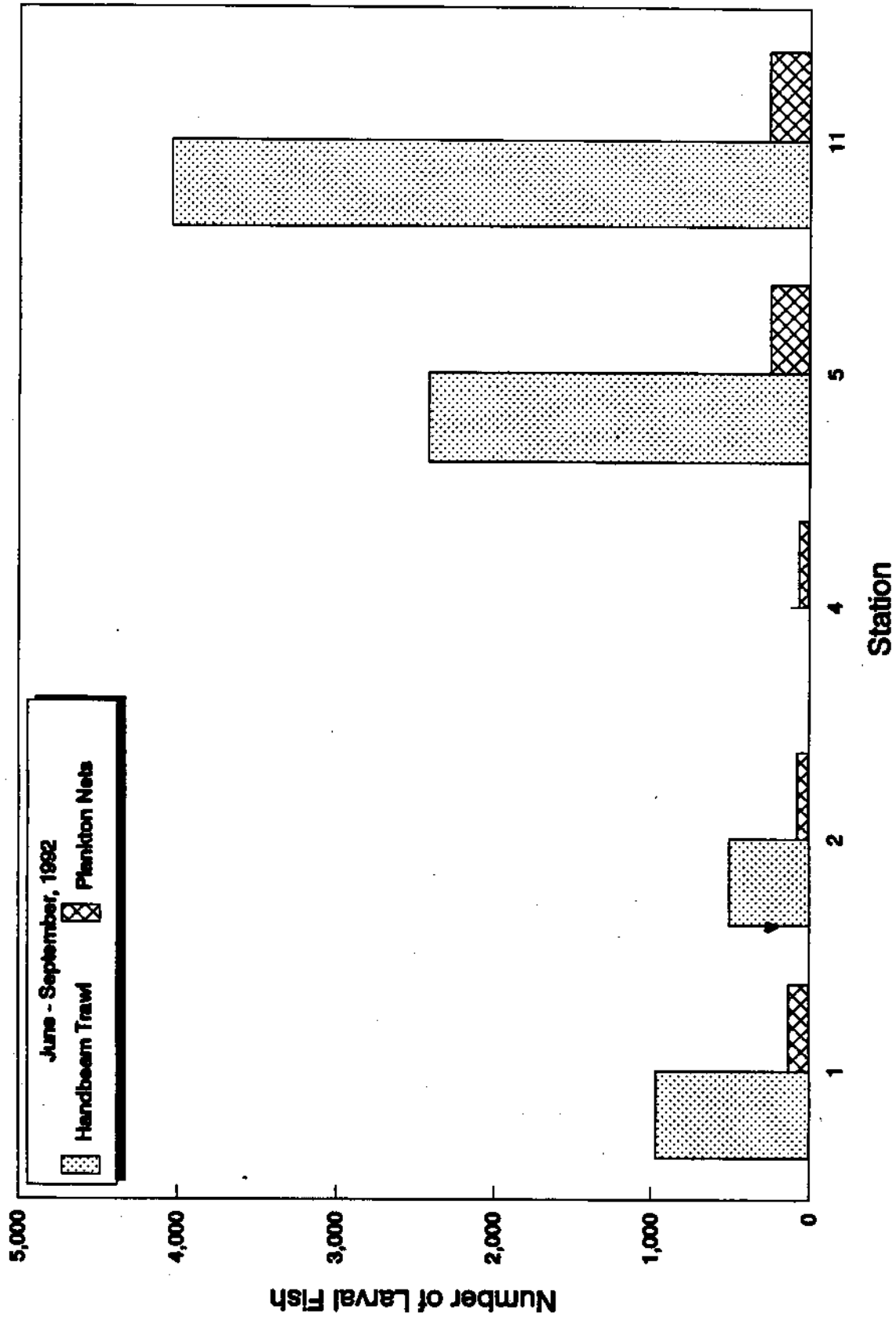


Figure 11. Numbers of larval fishes collected among stations by handbeam trawl and paired plankton nets in Lower Granite Reservoir from June through September, 1992.

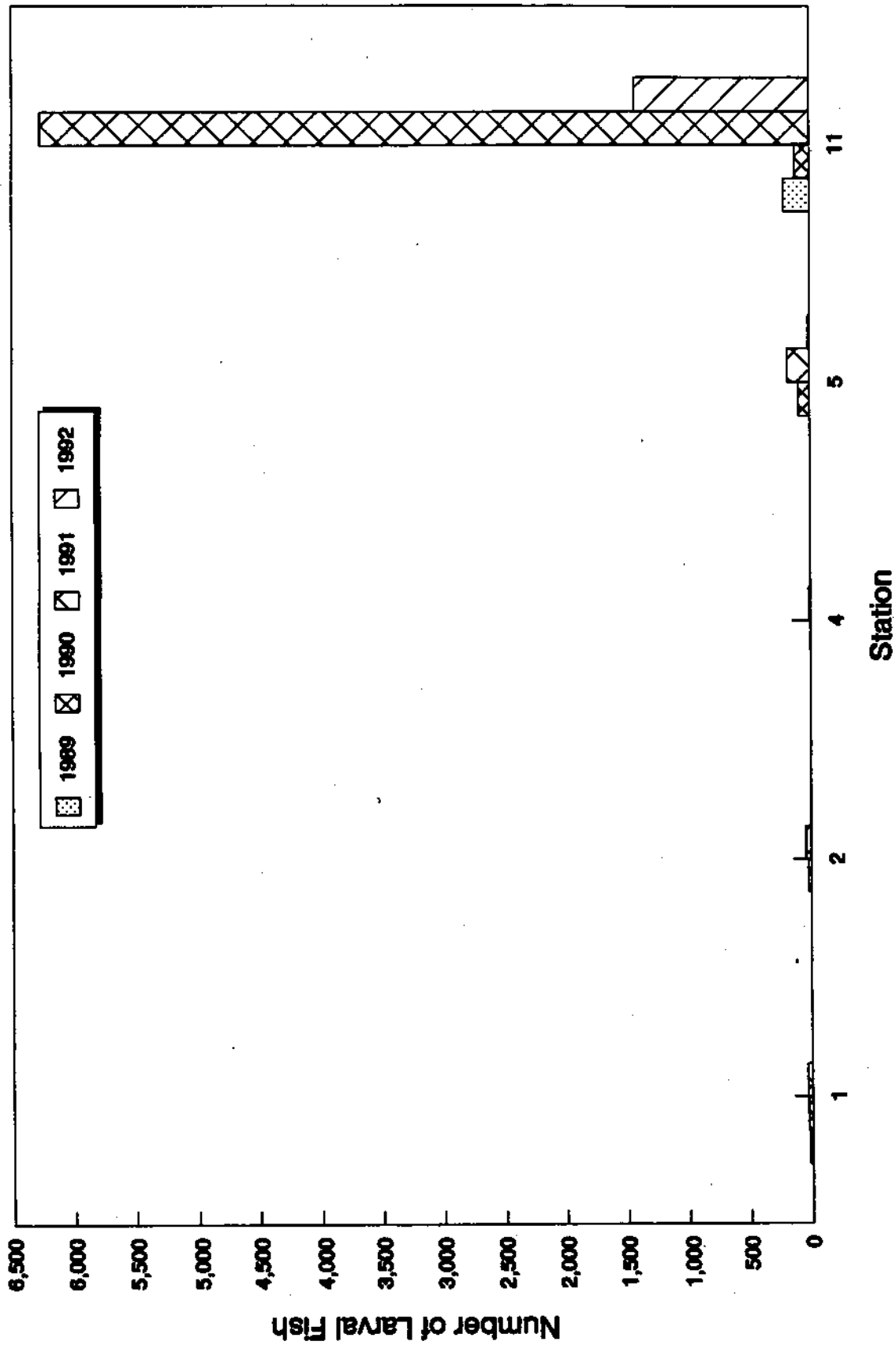


Figure 12. Comparisons by stations and years of larval northern squawfish sampled in Lower Granite Reservoir from 1989 through 1992.

and 1990 (n=235), although numbers in 1991 (n=6,516) and 1992 (n=1,248) were higher (Tables 1-4). The proportion of larval northern squawfish collected ranged from 7.6-11.3% in 1989 and 1990 to 26.7-14.4% in 1991 and 1992.

Smallmouth Bass

Numbers of larval smallmouth bass collected from 1989 to 1992 were variable among years and stations (Figure 13). The total number of smallmouth bass (n=4,981; Table 4) collected in 1992 was highest of all years and collections at stations 1 and 5 were highest (Figure 13). Abundance of larval smallmouth bass collected was high in 1989 at station 2 which may be related to spawning use of the newly constructed spawning habitat at Centennial Island (Bennett et al. 1993).

Numbers of larval smallmouth bass collected have been low among years compared to numbers of larval northern squawfish. The proportion of larval smallmouth bass collected remained about 1% from 1989 to 1991 and increased to about 6% in 1992 (Tables 1-4).

Year-Class Strength

Northern Squawfish

Numbers of larval northern squawfish collected by handbeam trawl and paired plankton nets appear to be an indicator of year-class strength. The highest number of larval northern squawfish was collected by larval fish sampling in 1991 (Table 3) followed by the highest number of age 0+ northern squawfish collected by electrofishing during fall 1991 (Figure 14). Catch/effort of age 0+ northern squawfish sampled during fall 1991 was significantly ($P < 0.05$) higher than those for years

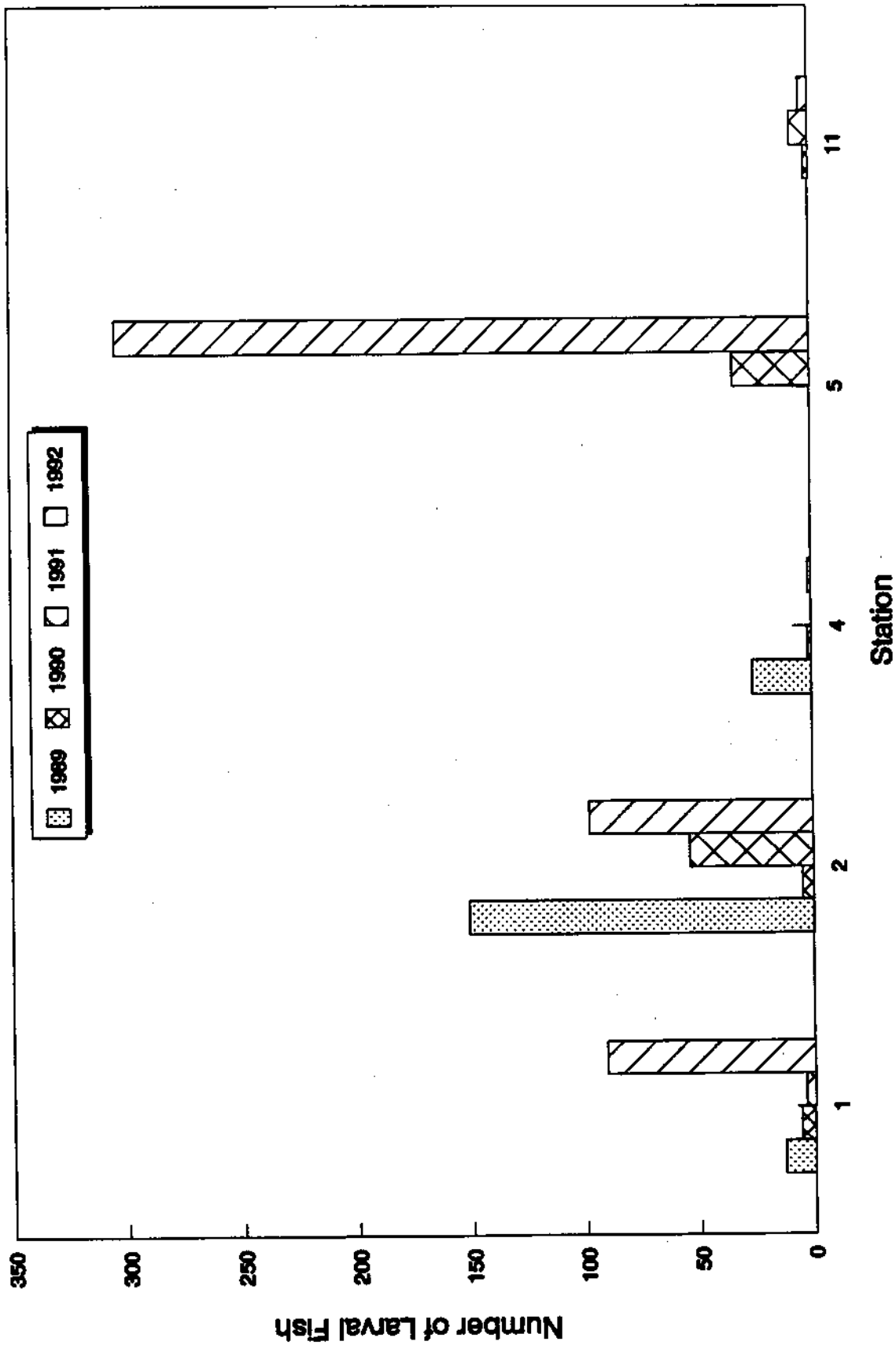


Figure 13. Comparisons by stations and years of larval smallmouth bass sampled in Lower Granite Reservoir from 1989 through 1992.

Mean of Ranks

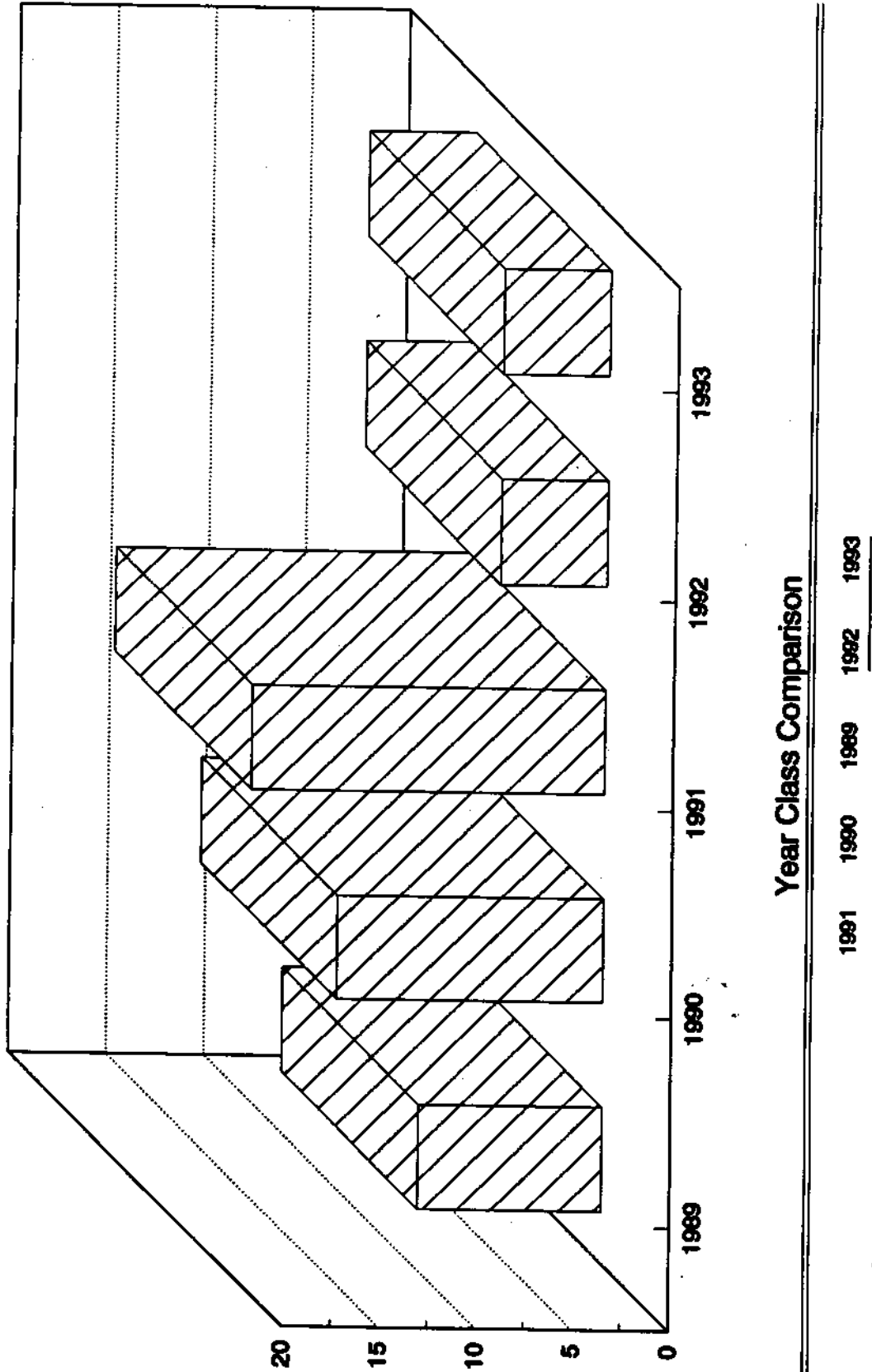


Figure 14. Graphical and statistical comparisons of the mean of ranks for age 0 northern squawfish abundance sampled by nighttime electrofishing in Lower Granite Reservoir during 1989-1993. The horizontal line under year-class indicates statistical nonsignificance ($P > 0.05$).

1989, 1990, 1992 and 1993. The catch/effort of age 1+ northern squawfish by electrofishing was highest for the 1988 year-class followed by the 1991 year-class (Figure 15). The catch/effort of age 1+ northern squawfish was not significantly ($P>0.05$) different between the 1988 and the 1991 year-classes, but catch/effort from 1988 was significantly ($P<0.05$) different from 1990, 1989 and 1992.

Smallmouth Bass

Catch/effort for age 0+ smallmouth bass indicate significantly ($P<0.05$) higher catch rates during fall 1992 and 1991 than other years (Figure 16). The lowest number of age 0+ smallmouth bass based on comparison of catch/effort was in 1993. The 1991 year-class for age 1+ smallmouth bass provided significantly ($P<0.05$) higher catch/effort than in all other years compared (Figure 17). The lowest catch/effort for age 1+ smallmouth bass occurred for the 1992 year-class.

Growth of Smallmouth Bass

Total Length Attained in Fall

Size of smallmouth bass entering their first winter was variable among 1989 through 1993 in Lower Granite Reservoir (Table 5). The largest size for age 0+ smallmouth bass entering the winter was in 1990 (78.3 mm) and the smallest (56.3 mm) was in 1989. Age 0+ smallmouth bass in the fall were significantly smaller ($P<0.05$) in 1989 than during the other 4 years examined. Size of age 0+ bass was similar between 1990 and 1992, and between 1991 and 1993, however total length was significantly different ($P<0.05$) from 1990 and 1992 compared with 1991 and 1993 (Table 5). During 1991 when upstream releases cooled

Mean of Ranks

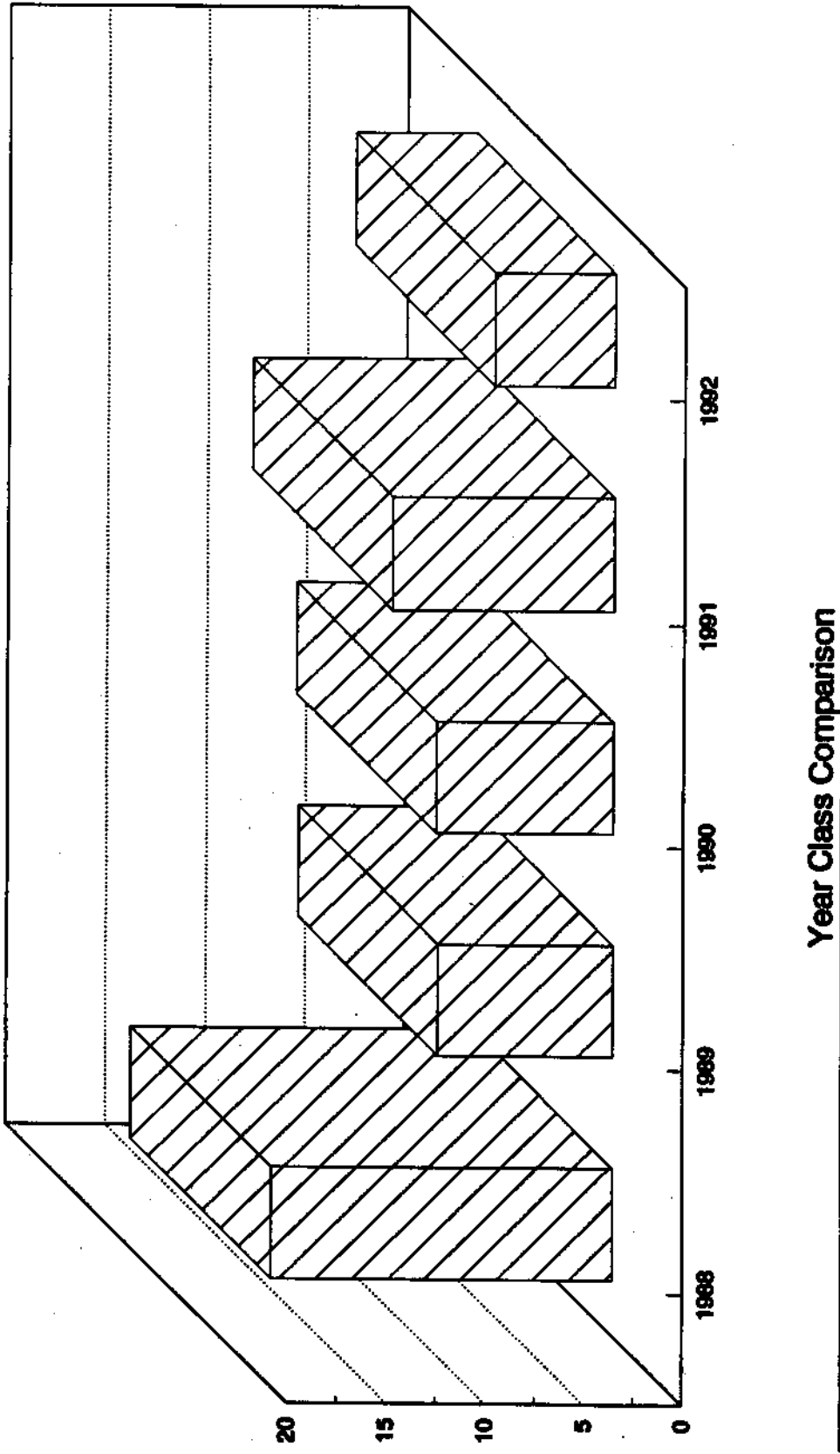
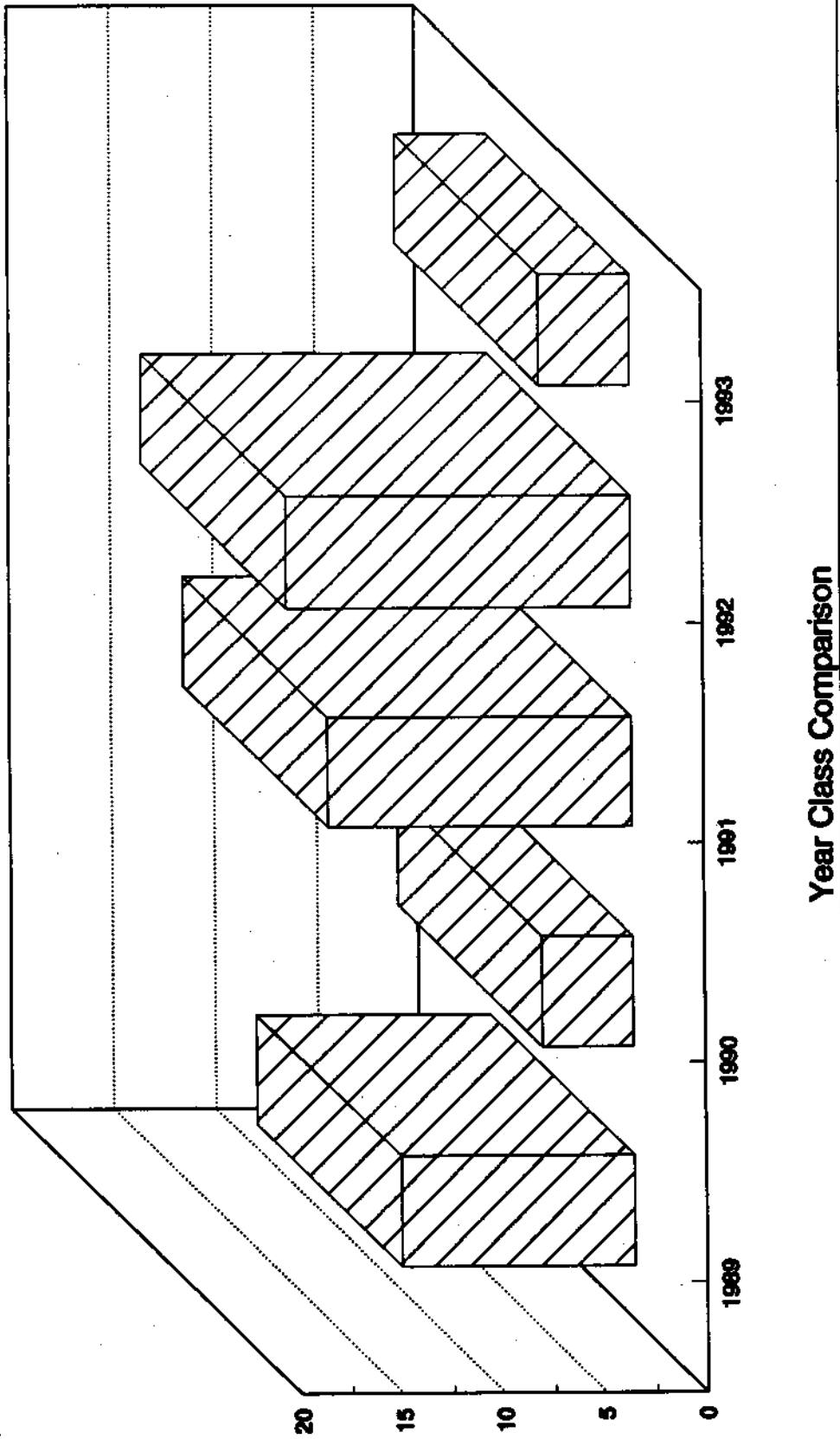


Figure 15. Graphical and statistical comparisons of the mean of ranks for age 1+ northern squawfish abundance sampled by nighttime electrofishing in Lower Granite Reservoir during 1988-1992. Horizontal lines under year-class indicate statistical nonsignificance ($P > 0.05$).

Mean of Ranks

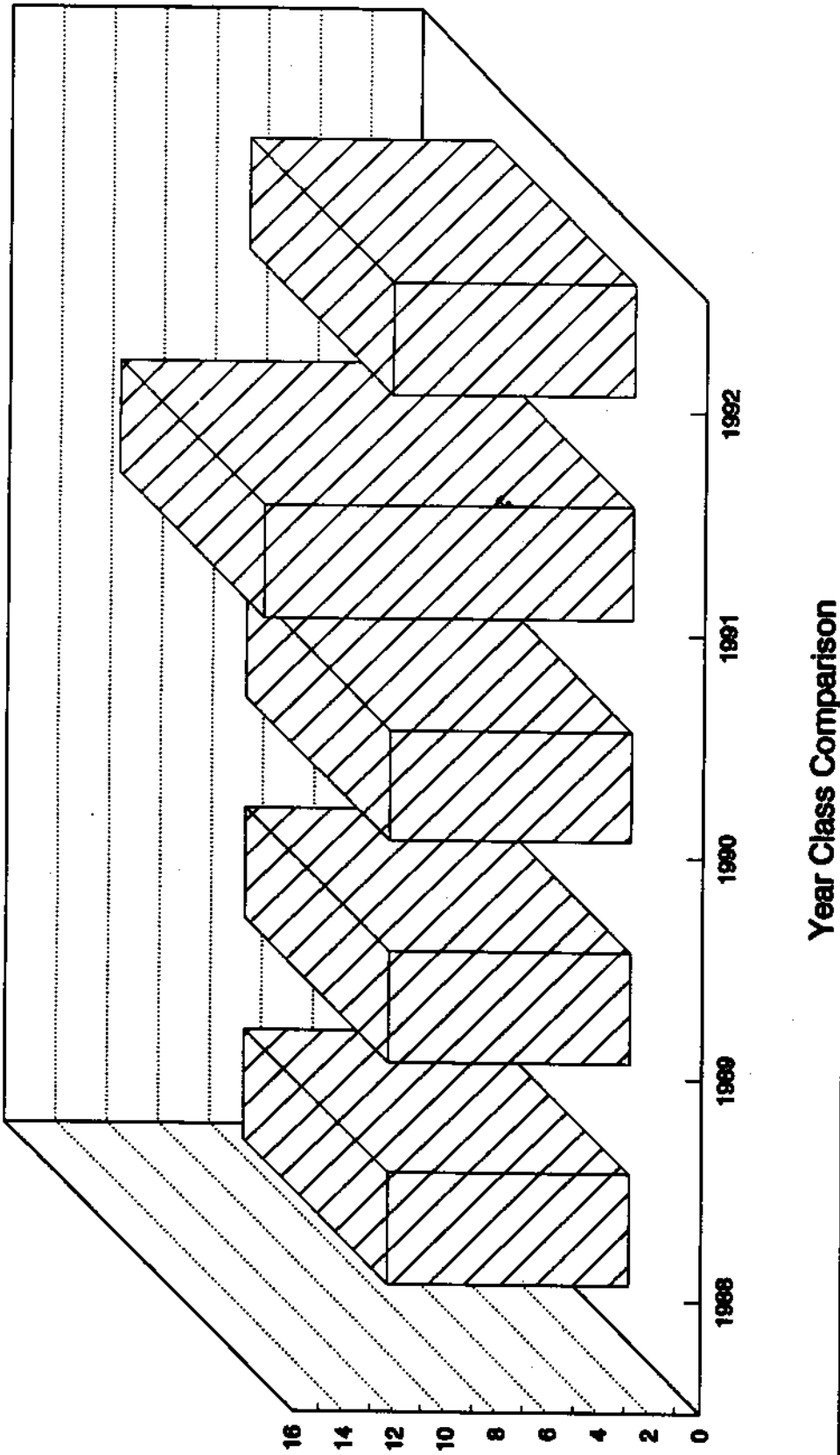


Year Class Comparison

1989 1990 1991 1992 1993

Figure 16. Graphical and statistical comparisons of the mean of ranks for age 0 smallmouth bass abundance sampled by beach seining in Lower Granite Reservoir during 1989-1993. Horizontal lines under year-class indicate statistical nonsignificance ($P > 0.05$).

Mean of Ranks



1988 1989 1990 1991 1992

Figure 17. Graphical and statistical comparisons of the mean of ranks for age 1+ smallmouth bass abundance sampled by beach seining in Lower Granite Reservoir during 1988-1992. The horizontal line under year-class indicates statistical nonsignificance ($P > 0.05$).

Table 5. Mean, variance and coefficient of variation (CV) of total length of 1989 through 1993 year classes of smallmouth bass based on fall collections from Lower Granite Reservoir, Idaho-Washington. Like letters indicate no significant ($P>0.05$) differences in length.

<u>Year</u>	<u>Mean</u>	<u>Variance</u>	<u>CV</u>	<u>N</u>
1989	56.3 ^c	106.1	137.3	238
1990	78.3 ^b	146.3	136.7	126
1991	66.9 ^a	186.2	166.8	322
1992	77.6 ^b	91.2	108.4	228
1993	64.1 ^a	822.9	358.3	21

Lower Granite Reservoir in August and September, age 0+ smallmouth bass attained similar mean size to those sampled in 1993, a naturally cooler summer. Variation in size of age 0+ smallmouth bass was highest in 1993 followed by 1991; variances were significantly ($P < 0.05$) larger for both 1991 and 1993 than other years.

Back-Calculated Length at Age

Back-calculated length at age indicates generally similar lengths at age 1 between year classes (Table 6). Maximum back-calculated lengths at age 1 among year-classes ranged from 70 to 82 mm for the years examined. Variation in first year growth can be about 12 mm (1/2 inch) based on the 4 years examined. Mean length of smallmouth bass collected from Lower Granite Reservoir in 1991 was more similar to the back-calculated lengths during 1988 and 1990.

Age, Environmental and Age*Environmental Effects

Analysis of variance indicated that smallmouth bass growth in Lower Granite Reservoir was affected by age ($P < 0.0005$) and environmental ($P < 0.0005$) effects and the interaction between age*environmental effects ($P < 0.005$). Analysis of variance also showed environmental effects on age 1 ($P < 0.001$) and age 4 ($P < 0.005$) smallmouth bass among cohorts were significant, however other age classes were not significant ($P > 0.05$). Age effects in a "fixed environment" were significant for age classes 1-4.

An evaluation of years 1990 and 1991, 2 years when age and growth data were obtained, indicated that in 1991 growth of smallmouth bass was poorer for ages 4-6 but not bass < age 4. Observed growth rates during

Table 6. Back calculated length (mm) at age 1 from scale reading verified by examination of otoliths of smallmouth bass collected from Lower Granite Reservoir.

<u>Year</u>	<u>Mean</u>	<u>Standard Error</u>	<u>N</u>
1987	82	2.75	8
1988	71	7.88	8
1989	78	0.94	127
1990	70	1.06	95
1991	67 ^a		238

^aBased on fall field sampling

the first 2 years of growth in 1991 were generally similar to those fit by the growth model.

DISCUSSION

MOP Operations and Abundance of Larval Fishes

To assess abundance of larval fishes in Lower Granite Reservoir, we used data from "pre-MOP" operations in 1989 and 1990 (Figures 2 and 3) as a "control" and made comparisons to data from 1991 and 1992, 2 years of MOP operations (Figures 4 and 5). Results indicated that larval fish abundance, and probably more importantly larval northern squawfish abundance, was substantially higher during the two summers of MOP operations.

Although MOP was maintained in 1992 through August, larval fish numbers were lower than those in 1991. Differences in pool levels between 1991 and 1992 were significant, however, in regards to their effects on larval fish abundance. During 1992, 2 weeks of widely fluctuating water levels occurred the end of May and early June (Figure 3) that may have been related to lower numbers of larval fishes than in 1991. Water temperatures reached 15°C (59°F) in the third week of May, 1992 about the time of wide water level fluctuations, whereas in 1991, that same temperature occurred in mid-June at a time when the water levels were stable. Our data show the effects of stable water levels at MOP on larval fish abundance in 1992 were probably confounded by temperature.

Timing of MOP operations and water temperatures seem to interact. Minimum operating pool conditions following 15°C appears related to higher larval fish abundance as occurred in 1991. Stable water levels

in mid-May, 1992 followed by 2 weeks of 4.5 ft (1.4 m) fluctuations resulted in intermediate numbers of larval fish. Although limited, the data do suggest that the typical operations of about 5 ft (1.5 m) fluctuations in Lower Granite Reservoir can adversely affect larval fish abundance and conversely, operations at MOP can create more favorable conditions for higher larval fish abundance.

Larval Predator Abundance

Concern over the potential for increased abundance of predators in Lower Granite Reservoir at MOP appears warranted based on 2 years, 1991 and 1992, of operations at MOP. Results from our 2 year study should be cautiously interpreted that reservoir operations at MOP in Lower Granite Reservoir will increase fish predator numbers. Two years of data at MOP only permitted limited comparisons to non-MOP operations, and the possible interactions with flows and temperatures are not clearly understood. However, our data show a relationship between higher larval fish numbers with more stable water levels and survival, and the resulting abundance of age 0+ and 1+ smallmouth bass and northern squawfish also were high from these years.

Northern Squawfish

Relative abundance of larval northern squawfish increased from 7.6-11.3% in 1989 and 1990 to 14.4-26.7% in 1991 and 1992 of all larval fishes collected. The highest abundance of larval northern squawfish was in 1991 when water levels were maintained +/-6 inches (± 15.2 cm) of MOP in Lower Granite Reservoir from early June through mid-August.

The mechanism how fluctuating water levels adversely affects larval fish abundance is not clear, especially in a species like northern squawfish. Spawning for northern squawfish probably occurs in the lotic waters of the Snake and Clearwater rivers when water temperatures reach 15°C, and larvae possibly migrate downstream. We hypothesize that most larval fish recruit to our station 11 site at Wilma, the first low gradient, sandy shoreline habitat downstream from these lotic waters. Under stable water levels at MOP, the probability that northern squawfish larvae would be washed upon the shoreline and desiccate is probably reduced, thus resulting in higher survival. Conversely, with wider water level fluctuations stranding may be prevalent. Our sampling data supports this hypothesis, as during years of MOP operations shoreline abundance of larval fishes based on handbeam trawl captures was higher than in open waters sampled by paired 1/2 m nets. At present, the life cycle of both smallmouth bass and northern squawfish is not clearly understood to refute or corroborate this hypothesis. The Wilma area in Lower Granite Reservoir is an important rearing habitat for larval fishes, including northern squawfish and also subyearling chinook salmon that are likely fall chinook (Bennett et al. 1985).

Smallmouth Bass

Examination of the 1991 water temperature increase in Lower Granite Reservoir suggests the wide fluctuations in water levels that occurred during late May may have adversely affected smallmouth bass spawning activities. Fluctuating water levels in Little Goose Reservoir were shown to adversely affect spawning success of smallmouth bass

(Bratovich 1985) and centrarchid fishes in other reservoirs (Bennett et al. 1985). Smallmouth bass, as with other centrarchid fishes, spawn in relatively shallow water; thus fluctuating water levels can desiccate incubating embryos and larvae in the spawning nest. Centrarchid fishes, such as smallmouth bass, pumpkinseed *Lepomis gibbosus* and crappie *Pomoxis* spp., spawn in Lower Granite Reservoir when water temperatures reach about 60°F (15.5°C; Cobble 1975). Centrarchid fishes were abundant in larval fish samples from Lower Granite Reservoir in 1989 (*Lepomis* spp.; Table 1), 1990 (*Lepomis* spp.; Table 2) and 1992 (Centrarchid spp.; Table 4) but were lower in 1991 (Table 3). The difference in abundance among years appears related to the timing of temperature increases and the existing water level fluctuations. In 1989, 1990, 1991 and 1992, a 60°F (15.5°C) water temperature occurred on June 1, 17, 11 and 19, respectively.

Year-Class Strength

Northern Squawfish

Year-class strength of northern squawfish seems to be linked to larval fish abundance. The highest number of larval northern squawfish were collected in 1991 followed by the highest number of age 0+ squawfish in the fall. These differences in catch/effort were significant. Also, abundance of age 1+ squawfish from the 1991 year-class was also significantly higher than in 1990, 1989 and 1992. Although limited in time, our data strongly suggests MOP can contribute to higher northern squawfish abundance and stronger year-classes, at least through age 1+.

Smallmouth Bass

Stable water levels during the spawning season of centrarchid fishes can enhance year-class strength because these species spawn in relatively shallow waters (Bennett et al. 1985). Fluctuations in water levels immediately prior to the time of spawning influence the depth of spawning; i.e. wider fluctuations immediately prior to spawning drives the fish to a deeper depth for spawning. During 1992, reduced fluctuations in Lower Granite Reservoir immediately prior to the onset of spawning may have "keyed" centrarchid fishes to a shallower depth of spawning which was then followed by 2 weeks of widely fluctuating water levels (Figure 3). Although the magnitude of water level fluctuations can be significant, Bennett et al. (1985) suggested that "regular" water level fluctuations of about 13 ft (4 m) immediately preceding the time of spawning cued centrarchid fishes to spawn deeper than the maximum depth of fluctuation.

Although the number of larval smallmouth bass collected in 1991 was low, numbers of age 0+ and 1+ bass collected in the first and second fall following spawning suggest a strong year-class originated. Smallmouth bass have not been commonly sampled in abundance in larval fish collections in Lower Granite (Bennett et al. 1990, 1991, 1993) or Little Goose reservoirs (Bennett et al. 1983) and larval abundance is probably not representative of actual abundance. Beach seine hauls/electrofishing collections during the fall probably provide a more definitive estimate of abundance. Catch/effort for age 0+ smallmouth bass were high in both 1991 and 1992 (Figure 16), although abundance of age 1+ bass from the 1992 year-class was low in the 1993 fall collections (Figure 17).

The unknown influence of the spring 1992 experimental drawdown confounds inferences to year-class strength based on catch/effort. Smallmouth bass from the 1991 year-class may have been entrained by the increased flows during the 1992 drawdown and therefore, affected the numbers that we sampled in the reservoir during fall 1992. Also, the number of potential spawning adults following the 1992 drawdown also may have decreased as a result of entrainment. Bennett and Hatch (1991) suggested that drawdowns in Long Lake, Spokane River, Washington, adversely affected the abundance of age 1 largemouth bass and may have been related to the unusually high estimate of natural mortality for adult bass.

Low Temperature Inflows and Growth of Smallmouth Bass

Body Length in Fall Samples

We used smallmouth bass as a target species to assess the influence of lower temperature inflows on growth and survival. Our 5 years of combined pre and post cool water release data suggest lower temperature inflows Lower Granite Reservoir probably have not deleteriously affected growth and survival of age 0 and age 1 smallmouth bass beyond that from "normal" conditions. The highest volume of cool water released as a test from Dworshak Reservoir to cool the lower Snake River reservoirs was in 1991 (Bennett et al. 1994a, 1994b, 1994c). Catch/effort data indicate that smallmouth bass were abundant in the fall and lengths of age 0+ bass were similar to that for years with "naturally" lower temperatures. If adverse effects from the release of low temperature water were being experienced by fishes in Lower Granite

Reservoir, the effects are more subtle than we have been able to detect in growth and survival of smallmouth bass.

Temperature not only affects the size of fish in the fall but also affects growth indirectly by affecting the timing of spawning. Smallmouth bass spawn with increasing photoperiod and water temperatures (Cobble 1975). Smallmouth bass initiate their spawning activities when temperatures warm to 15.5°C (60°F). In Lower Granite Reservoir, the time when temperatures reached 15.5°C (60°F) from 1989 to 1993 varied from May 19, 1992 to June 17, 1993. Smallmouth bass that are able to spawn earlier in the spring generally have larger juveniles in the fall. Back-calculated lengths of smallmouth bass were 78 mm in 1989 compared to an estimated average fall length of 64 mm. The quality of the growth season is also a factor. Water temperatures can directly affect growth of smallmouth bass by providing a low number of thermal units. Coble (1967) indicated that systems with < 1,000 thermal units per growing season generally do not provide adequate growth to maintain a good population. The thermal units in Lower Granite Reservoir ranged from about 1,014 in 1993 to 1,559 in 1992. The highest number of thermal units coincided with the second largest body size of smallmouth bass in the fall, whereas the lowest number of thermal units coincided with the second smallest body size (Table 5).

Size of fish is an important factor that affects survival. Predation is a function of size; smaller individuals are more susceptible to predation and more likely to die during overwintering. Size is a limiting factor for smallmouth bass populations in the northern part of their range. Oliver et al. (1979) showed that smallmouth bass < 50 mm in the fall generally do not survive the

winter, as smaller bass do not have sufficient energy reserves to last the winter. The stronger year-classes of smallmouth bass in Lower Granite Reservoir coincide with either earlier spawning or a high quality growing season. During 1989, some smaller smallmouth bass probably died as a result of their small body size. In the fall, mean length of age 0+ bass was 56 mm whereas the average back-calculated length at age 1 during that year was 78 mm. Age 0+ smallmouth bass collected in fall 1989 were the smallest of the 5 years examined (Table 5), although back-calculated lengths were the second largest (Table 6). We believe the smaller age 0+ bass died during that winter and only the larger bass survived. This hypothesis is supported by generally close agreement between the back-calculated lengths at age 1 and the average total lengths attained at the time of the fall sampling. The 1989 year-class of bass was generally stronger when assessed by the abundance of age 0+ than when age 1+ bass were sampled (Figures 16 and 17) which further supports this hypothesis.

Our data from the fall collections and from back-calculated lengths at age show high variability in lengths among years. The field collections indicate that 1989, 1991 and 1993 were years when the average length of bass in the fall was lower than either 1990 and 1992 (Table 5). Smallmouth bass were small in the fall collections of 1991, although similar in size to those collected at similar times in 1993. Age 0+ smallmouth bass collected in fall 1989 were the smallest of the 5 years examined (Table 5), although back-calculated lengths were the second largest (Table 6). Runoff was high in 1993 and water temperatures warmed slowly (Bennett et al. 1994b) which probably accounted for the small size in 1993. Regardless, we have not found any

evidence in the fall collections or back-calculated lengths that the lower temperatures in Lower Granite Reservoir in 1991 resulted in unusually smaller sized bass than would occur from annual variation in "natural" conditions.

Age, Environmental, and Age and Environmental Effects

Age and growth analysis indicate the Lower Granite Reservoir environment can affect growth of smallmouth bass. We used actual scale increments as the response variable in this analysis. This procedure was highly recommended by Weisberg (1986) and Weisberg and Frie (1987) over that of using back-calculated lengths. Scale growth of smallmouth bass in Lower Granite Reservoir showed year to year variability and a fair amount was attributed to age. Environmental effects contributed about equally to the variability. Age, environmental effects and the interaction of age*environment all were highly significant ($P < 0.01$). Growth during the first year was variable and the modeling showed environmental effects were significant. This suggests environmental conditions endured by age 1 smallmouth bass are variable among years. However, comparison of growth data indicate that the release of upstream waters to cool Lower Granite Reservoir in 1991 has not significantly affected growth of smallmouth bass ages 1-3 in the reservoir. In 1991, growth was significantly poorer for ages 4-6, but our emphasis was on growth and survival of younger fish and data collected on growth of older age classes is limited. As with the other analyses, we have to conclude that although the cool water inflows contributed to the high environmental variability in Lower Granite Reservoir, this variability seems to be similar to the "natural" variability.

CONCLUSIONS

1. Based on 4 years of larval fish data, operations of Lower Granite Reservoir at MOP can result in high abundance of larval fishes that can contribute to stronger year-classes of predators. Fluctuations in water levels during late May and early June, 1992 resulted in lower numbers of larval fishes than when levels were completely stabilized as in 1991 but higher than during years of "normal" water level fluctuations.

Therefore, stable water levels at MOP during the late spring season can result in abundant larval fishes.

2. A significant proportion of larval fishes sampled in Lower Granite Reservoir were larval cyprinid fishes and northern squawfish. Many of the larval cyprinid fishes could not be identified because of their small size and early development but were likely larval northern squawfish. Our larval fish and fall collections of age 0+ and 1+ northern squawfish suggest stronger year-classes resulted during 1991, a year of stable water levels at MOP. Therefore, if operations at MOP were maintained and management interests were to decrease northern squawfish numbers, we believe that 2 weeks of water level fluctuations when water temperatures are at about 15.5°C (60°F) may adversely affect year-class strength and may result in weaker year-classes of northern squawfish in Lower Granite Reservoir.

3. Inflows of cool water into Lower Granite Reservoir from upstream reservoir sources have not adversely affected survival and growth of ages 1-3 smallmouth bass and presumably other species. The decreased temperatures have contributed to a high environmental variability

component on smallmouth bass growth but not beyond that from "normal" year to year variation. Therefore, if management decisions were to release low temperature water to enhance conditions for anadromous salmonid fishes, these releases, if similar to those in 1991, should not adversely affect survival and growth of smallmouth bass and probably other resident fishes.

REFERENCES

- Bennett, D.H., P.M. Bratovich, W. Knox, D. Palmer, and H. Hansel. 1983. Status of the warmwater fishery and the potential of improving warmwater fish habitat in the lower Snake River reservoirs. Completion Report. US Army Corps of Engineers, Walla Walla, Washington.
- Bennett, D.H., O.E. Maughan, and D.B. Jester, Jr. 1985. Generalized model for predicting spawning success of fish in reservoirs with fluctuating water levels. North American Journal of Fisheries Management. 5(1): 12-20.
- Bennett, D.H., and F.C. Shrier. 1986. Effects of sediment dredging and in-water disposal on fishes in Lower Granite Reservoir, Washington. Completion Report. US Army Corps of Engineers, Walla Walla, Washington.
- Bennett, D.H., L.K. Dunsmoor, and J.A. Chandler. 1988. Fish and benthic community abundance at proposed in-water disposal sites, Lower Granite Reservoir. Completion Report. US Army Corps of Engineers, Walla Walla, Washington.
- Bennett, D.H., J.A. Chandler, and L.K. Dunsmoor. 1990. Lower Granite Reservoir in-water disposal test: Results of the fishery, benthic, and habitat monitoring program Year-1 (1988). Completion Report. US Army Corps of Engineers, Walla Walla, Washington.
- Bennett, D.H., J.A. Chandler, and G. Chandler. 1991. Lower Granite Reservoir in-water disposal test: Results of the fishery, benthic, and habitat monitoring program Year-2 (1989). Completion Report. US Army Corps of Engineers, Walla Walla, Washington.
- Bennett, D.H., and D.R. Hatch. 1991. Factors limiting the fish community with emphasis on largemouth bass in Long Lake, Spokane County, Washington. Completion Report to Washington Water Power Company (Project Number 4) Spokane, Washington.
- Bennett, D.H., T.J. Dresser, Jr., T.S. Curet, K. B. Leppla and M.A. Madsen. 1993. Lower Granite Reservoir in-water disposal test: Results of the fishery, benthic, and habitat monitoring program Year-2 (1990). Completion Report. US Army Corps of Engineers, Walla Walla, Washington.
- Bennett, D.H., M.H. Karr, and M.A. Madsen. 1994a. Thermal and velocity characteristics in the Lower Snake River reservoir, Washington, as a result of regulated upstream water releases. Completion Report. US Army Corps of Engineers, Walla Walla, Washington.

- Bennett, D.H., M.A. Madsen, and M.H. Karr. 1994b. Water velocity characteristics of the Clearwater River, Idaho and Lower Granite, Little Goose, Lower Monumental and Ice Harbor reservoirs, lower Snake River, Washington, during 1991-1992 with emphasis on upstream releases. Data Volume I. US Army Corps of Engineers, Walla Walla, Washington.
- Bennett, D.H., M.A. Madsen, and M.H. Karr. 1994c. Water velocity characteristics of the Clearwater River, Idaho and Lower Granite, Little Goose, Lower Monumental and Ice Harbor reservoirs, lower Snake River, Washington, during 1991-1993 with emphasis on upstream releases. Data Volume II. US Army Corps of Engineers, Walla Walla, Washington.
- Benson, N.G. 1976. Water management and fish production in Missouri River main stem reservoirs. Pages 141-147 *in* J.F. Osborn and C.H. Allman, editors. Instream Flow Needs, Volume II. American Fisheries Society, Bethesda, Maryland.
- Bratovich, P.M. 1985. Reproduction and early life histories of selected resident fishes in Lower Snake River reservoirs. Master's thesis. University of Idaho, Moscow.
- Carlander, K.D. 1982. Standard intercepts for calculating lengths from scale measurements from some centrarchid and percid fishes. Transactions of the American Fisheries Society 111:332-356.
- Coble, D.W. 1967. Relationship of temperature to total annual growth in adult smallmouth bass. Journal of the Fisheries Research Board of Canada 21(1):87-99.
- Coble, D.W. 1975. Smallmouth bass. Pages 21-33 *in* H. Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D.C.
- Frie, R.V. 1982. Measurement of fish scale and back-calculation of body lengths using a digitizing pad and microcomputer. Fisheries (Bethesda) 7(6):5-8.
- Henderson, C. and R.F. Foster. 1957. Studies of smallmouth black bass (*Micropterus dolomieu*) in the Columbia River near Richland, Washington. Transactions of the American Fisheries Society 86:112-127.
- Karr, M.H., B. Tanovan, R. Rudder, and D.H. Bennett. 1992. Interim report: Model studies and 1991 operations. Completion Report. US Army Corps of Engineers, North Pacific Division, Portland, Oregon.
- LaBolle, L. Jr., H.W. Li, and B.C. Mundy. 1985. Comparison of two samplers for quantitatively collecting larval fishes in upper littoral habitats. Journal of Fish Biology 26(2):139-146.

- Oliver, J.D., G.F. Holeton, and K.E. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. *Transactions of the American Fisheries Society* 108:130-136.
- Nelson, W.R., and C.H. Walburg. 1977. Population dynamics of yellow perch *Perca flavescens*, sauger *Stizostedion canadense*, and walleye *Stizostedion vitreum vitreum* in four main stem Missouri River reservoirs. *Journal of the Fisheries Research Board of Canada* 34: 1748-1763.
- Ploskey, G.R. 1986. Effects of water-level changes on reservoir ecosystems, with implications for fisheries management. Pages 86-93 in G.E. Hall and M.J. Van Den Avyle, editors. *Reservoir fisheries management-Strategies for the 80's*. American Fisheries Society, Bethesda, Maryland.
- Weisberg, S. 1986. A linear model approach to back-calculation of fish length. *Journal of the American Statistical Association*.
- Weisberg, S. and R.V. Frie. 1987. Linear models for the growth of fish. Pages 127-143 in R.C. Summerfelt and G.E. Hall, editors. *The age and growth of fish*. The Iowa State University Press, Ames.