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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF TABLES

ABSTRACT

The results of maximizing the lake rearing capacity for juvenile sockeye through stocking and later fertilization of Pass Lake, and stocking of Esther Passage Lake, demonstrated dramatic changes in previously predator-free zooplankton communities. These two oligotrophic lakes located on Esther Island in Prince William Sound have barriered outlets that prevent access to adult salmon. In 1988 and 1989 sockeye salmon fry were stocked at equivalent densities based on euphotic volume in both of these lakes, and in 1989 and 1990 Pass Lake was fertilized. In 1990, pre-smolts (fall fingerlings) were released in both lakes to compare overwinter survival, and in 1991 both lakes were left untreated. The introduction of sockeye fry in Pass Lake resulted in a major collapse of the zooplankton community after the first year of stocking. The zooplankton community (biomass and species composition) did not recover despite lake fertilization, a low density pre-smolt release, or leaving the lake untreated for one year. The zooplankton community of Esther Passage Lake was also affected by stocking of sockeye fry; however, this lake was somewhat more resilient, as after termination of stocking the zooplankton biomass approached near pre-stocking levels. Although after the termination of stocking Esther Passage Lake, the species composition remained restructured and zooplankton sizes were still depressed. The results of these whole-lake manipulations indicated that the degree to which juvenile sockeye restructure the zooplankton community appears to influence the ability of zooplankton to recover.

INTRODUCTION

In nursery lakes supporting sockeye salmon (*Oncorhynchus nerka*) fry, predation can dramatically influence the zooplankton community (Hrbacek et al. 1961; Brooks and Dodson 1965; Brocksen et al. 1970; Stenson 1972, 1976; Zaret 1980; Post and McQueen 1987; Kyle et al.1988). In turn, changes in the structure of the zooplankton community can subsequently lead to changes in lower trophic levels in the form of cascading events (e.g., Carpenter et al. 1985; Mazumder 1990). In addition, density-dependent responses in the form of reduced growth of sockeye salmon can result from intense competition for food (Johnson 1964, 1965; Brocksen et al. 1970; Hartman and Burger 1972; Goodlad et al. 1974; Kyle et al. 1988). Such top-down effects related to over-grazing the forage base can be reversible by lake enrichment (Hyatt and Stockner 1985; Koenings and Burkett 1987; Stockner 1987; Kyle et al. 1992). Since it has been assumed that zooplankton exponentially recuperate after a severe predation event (Welch and Noakes 1990), we conducted whole-lake experiments in two lakes to monitor the response of zooplankton to predation pressure, and assess the potential for reversal of top-down effects through nutrient enrichment and short-term natural recovery.

Previous investigations (Barto 1982, 1983) indicated that sockeye salmon fry could be introduced into barren Pass and Esther Passage lakes to take advantage of available natural forage. Sockeye salmon fry were planted in the spring of 1988 and 1989 at densities consistent with a modeled rearing capacity (Koenings and Burkett 1987), and sockeye pre-smolts were stocked at low levels in the fall of 1990 in both lakes. Pass Lake was treated with nutrient additions in 1989 and 1990 to monitor bottom-up responses, and in 1991 both lakes were left untreated.

METHODS AND MATERIALS

Study Site Description

Pass Lake (60° 55' N, 148° 3' W) and Esther Passage Lake (60° 52' N, 147° 56' W) are located on Esther Island in western Prince William Sound. These lakes are relatively small in surface area (0.49 and 0.19 km^2), with similar mean depths of 12-13 m (Figures 1 and 2). Both watersheds are located in steep valleys at elevations of 22-24 m, which contributes to relatively fast flushing rates of 0.37 y (Pass Lake) and 0.18 y (Esther Passage Lake). The outlet streams consist of large waterfalls which prevent the access to adult salmon. These lakes are nutrient limited (primarily nitrogen and phosphorus) with organically-stained (color > 15 pt) Esther Passage Lake having lower chlorophyll a values. Both lakes were dominated by *Cyclops* before treatment, followed by *Diaptomus* in Pass Lake and *Bosmina* in Esther Passage Lake.

Limnological Investigations

Studies initiated before treatment of Pass Lake were aimed at gathering baseline information regarding the physical, chemical, and biological characteristics during the summer growing season (May-October) of 1981-1982, and 1984-1986. Similarly, pre-treatment investigations at Esther Passage Lake were conducted during 1983, 1985, and 1986. Beginning with the initial year of treatment (1988), and continuing until a year after treatment (1991), identical monitoring of characteristics was conducted in both lakes to assess interlake and treatment response.

Limnological surveys were conducted at Pass and Esther Passage lakes at approximately one month intervals, or as weather permitted. One station located in the single basin of each lake was used for sampling (Figures 1 and 2). Measurements of temperature and dissolved oxygen were recorded at

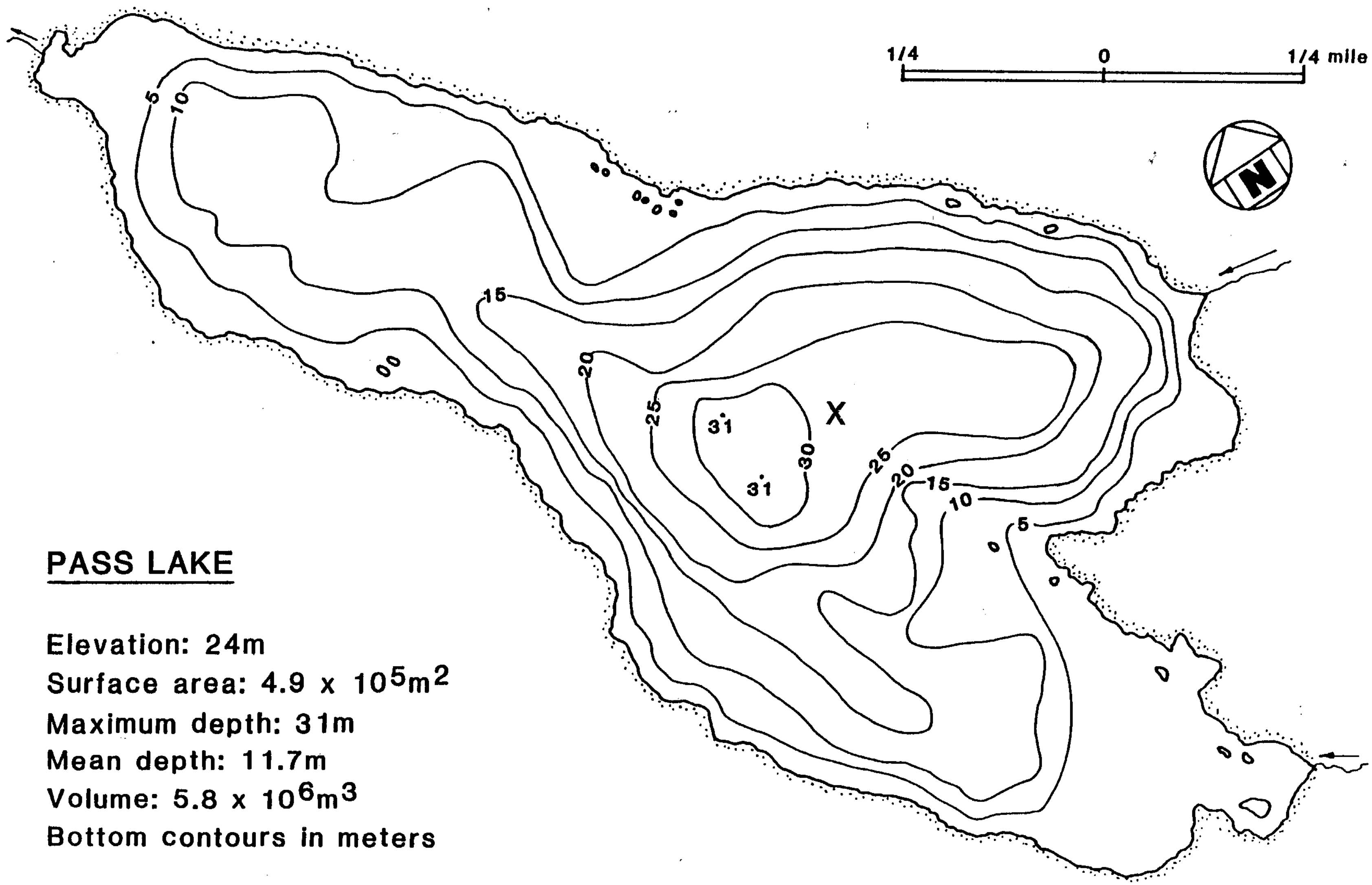

Figure 1. Morphometric map of Pass Lake showing location of the limnological station.

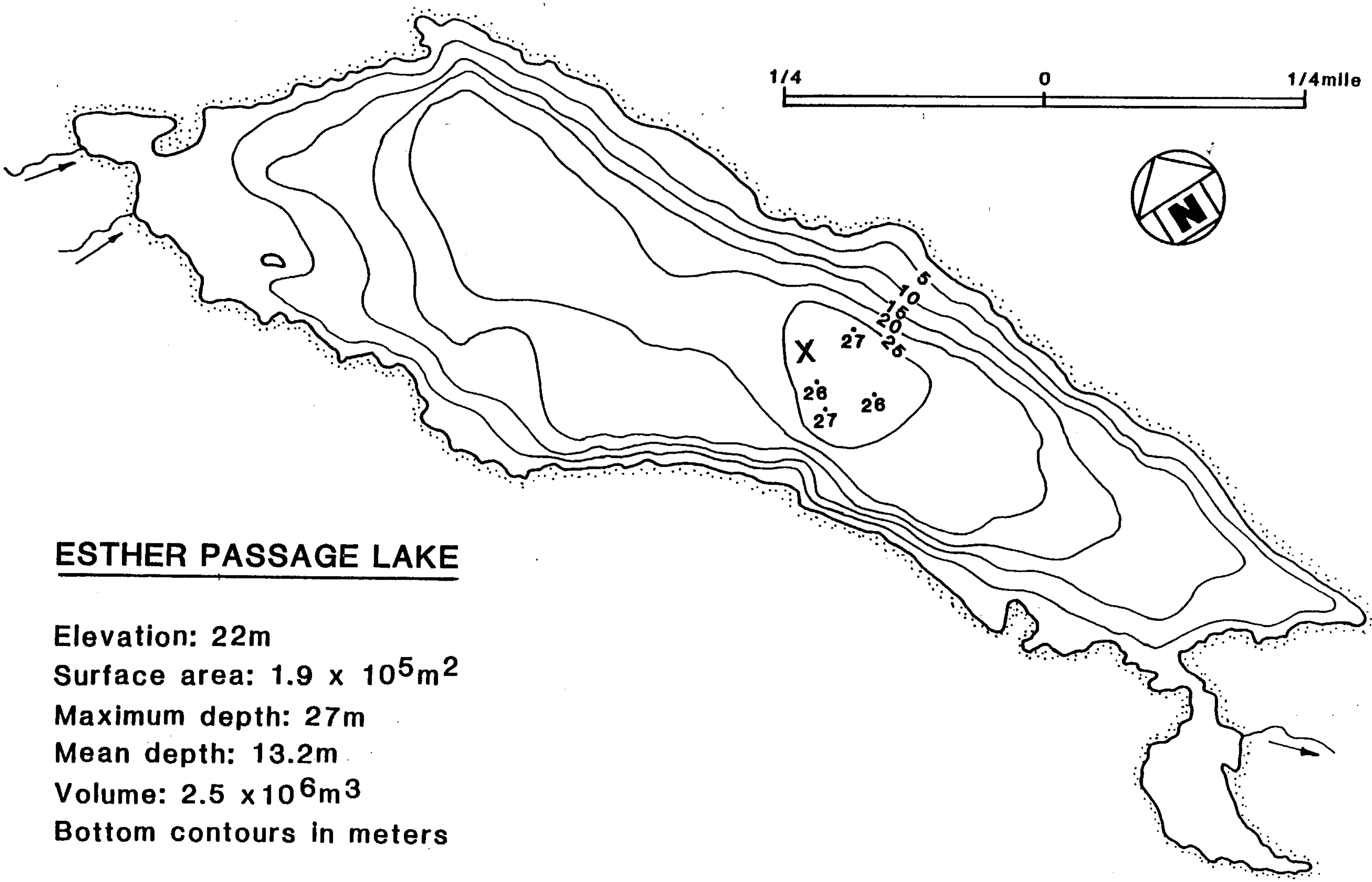

Figure 2. Morphometric map of Esther Passage Lake showing location of the limnological station.

1-m intervals throughout the water column. Water samples for nutrient analysis were taken with a Van Dorn sampler at 1 m and the mid-hypolimnion (75% of the lake depth). Euphotic zone depth (EZD), or the depth to which 1% of the photosynthetically available radiation (PAR) penetrates, was recorded at 0.5-m intervals from the surface to a depth equivalent to 1% of the subsurface light reading using a submarine photometer.

Total phosphorus was determined using molybdate-blue/ascorbic-acid method of Murphy and Riley (1962), as modified by Eisenreich et al. (1975). after persulfate digestion. Water samples (1-2 L) for chlorophyll a (chl a) analysis were filtered through 4.25-cm GF/F filters to which 1-2 mls of a saturated $MgCO_3$ solution were added just prior to the completion of filtration. The filters were then stored frozen in individual plexislides for later analysis. Chlorophyll a analysis followed the fluorometric procedure of Strickland and Parsons (1972). The low-strength acid addition recommended by Riemann (1978) was used to estimate phaeophytin.

Macrozooplankton were collected from duplicate, vertical hauls using a 0.2-m diameter, 153-μ mesh, conical plankton net. The net was pulled at a constant 1 m/s, and all organisms were preserved in a 10% neutralized formalin solution. Identification of *Daphnia* followed Brooks (1957), *Bosmina* after Pennak (1978), and the copepods after both Wilson (1959) and Yeatman (1959). Enumeration consisted of counting triplicate 1-ml subsamples taken with a Hansen-Stempel pipette in a 1-ml Sedgewick-Rafter cell. Zooplankton body sizes were obtained by measuring the length to the nearest 0.01 mm of at least 10 individuals along a transect in each 1-ml subsample (Koenings et al. 1987). Finally, zooplankton biomass was estimated from an empirical regression between zooplankton body-length and dry weight, and was weighted by organism density (Koenings et al. 1987).

Juvenile Sockeye Salmon Stocking

The number of sockeye fry released in Pass and Esther Passage lakes was based on the euphotic volume (EV) model (Koenings and Burkett 1987). The euphotic volume is the volume of water within a lake in which photosynthesis (the basis of the aquatic food chain leading to fish production) occurs. One million cubic meters of lake water within the euphotic zone represent one EV unit. This model predicts the production of 23,000 age-1 threshold-size smolts (~60 mm; 2.0-2.2 g) from a stocking of 110,000 fry per EV unit. Also, empirical data reported by Koenings and Burkett (1987) indicated that a stocking level of 54,000 juveniles per EV unit produced optimum size smolts relative to ocean. In this study we were interested in maximizing the rearing capacity to monitor the response in the zooplankton community; thus, both lakes were stocked at a density of ~110,000 spring fry/EV unit. Pass Lake has an average of 6 EV units (1981-1986) and Esther Passage Lake has an average of 1.4 EV units (1983-1986).

Juvenile sockeye salmon stocked into both lakes were incubated at Main Bay Hatchery located in western Prince William Sound. Stocking was initiated in the spring (late June) of 1988 with Esther Passage Lake receiving 153,000 fry and Pass Lake 594,000 fry. In the spring of 1989, Esther Passage Lake received 155,000 fry and Pass Lake was stocked with 603,000 fry. In late October of 1990, 125,000 pre-smolts (2 g fall fingerlings) were stocked in Esther Passage Lake and 100,000 were released in Pass Lake to compare overwintering survival (to the age-1 smolt stage). All stocking was accomplished with the use of aerated tanks mounted in a float plane. The juvenile fish were released upon landing, and transport mortality was negligible.

Smolt Enumeration and Sampling

Emigrating sockeye smolts were captured with a fyke net and temporarily retained in live boxes. The smolts were hand counted and released three times each day. Also, a daily subsample of 40 sockeye smolts was anesthetized in a solution of tricane methansulfate (MS-222), and measured for weight (nearest 0.1 g) and fork length (nearest millimeter). A scale smear was taken from each of the sampled smolts to determine age.

Nutrient Enrichment

Pass Lake received nitrogen and phosphorous additions by aerial application in 1989 and 1990 to ultimately stimulate secondary (zooplankton) production for rearing juvenile sockeye salmon during the summer period. The surface-specific and critical loading of phosphorus followed Vollenweider (1976), and the supplemental loading was based on 90% of the critical load of 10 µg/L minus the specific load (Kyle et al. 1992). In 1989, a total of 4.6 tons of 24-7-0 and 8 tons of 32-0-0 were applied during 11 June and 16 September. In 1990, a total of 4.8 tons of 20-5-0 was applied during 27 June and 25 August.

RESULTS

Primary Production Response to Nutrient Enrichment of Pass Lake

Following nutrient additions in 1989 and 1990, the phosphorus levels and consequently primary production (chl a) increased dramatically in Pass Lake. Specifically, total phosphorous levels (1 m) before treatment averaged 2.8 µg/L over the season, increased to 12.6 µg/L during nutrient enrichment, and returned to slightly above the pre-enrichment average to 3.5 µg/L a year after the cessation of nutrient additions (Figure 3A). Chlorophyll a (1 m) during pre-enrichment averaged 0.37 µg/L over the season, increased to 1.85 µg/L during

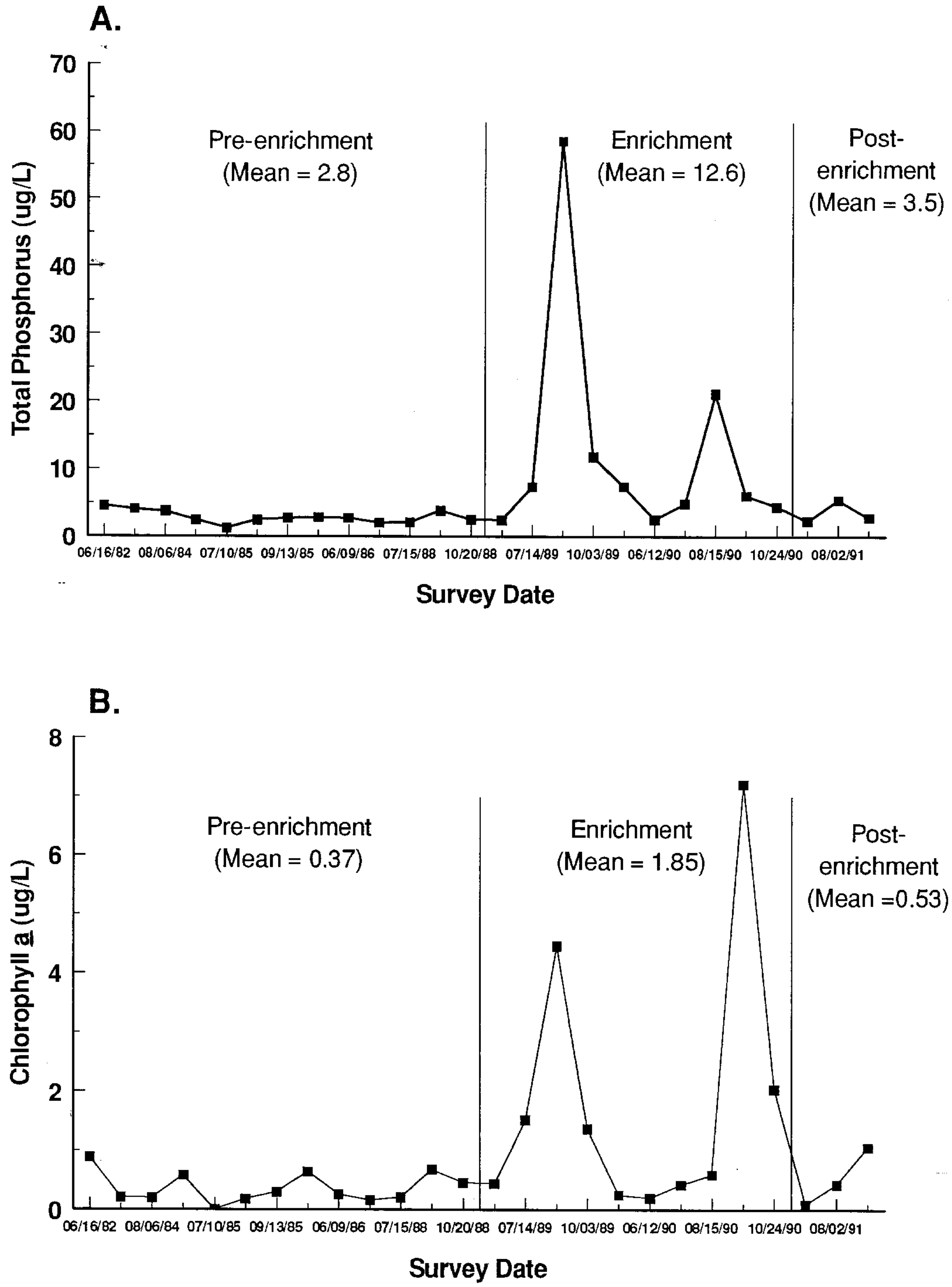

Figure 3. Total phosphorus (A) and chlorophyll a (B) before, during, and after nutrient enrichment of Pass Lake.

nutrient enrichment, and in 1991, the year after nutrient additions halted, the chl a level dropped to 0.53 μg/L (Figure 3B).

Zooplankton Community Response to Stocking, Nutrient Enrichment, and Decreased Planktivory in Pass Lake

For pre-stocking years (1981-1986), total macrozooplankton biomass (TMB) averaged 541 mg/m^2 (Figure 4A), and the zooplankton community was dominated by *Cyclops*, followed by *Diaptomus*, *Bosmina*, *Daphnia*, and *Holopedium* (Figure 4B). As a result of fry stocking (1988 and 1989), mean TMB decreased by 92% to 42 mg/m^2 (Figure 4A), and except for the dominance of *Cyclops*, the zooplankton community structure dramatically changed (Figure 4B). Specifically, during the first year of stocking, *Dipatomus* disappeared in June and by October both *Daphnia* and *Holopedium* were virtually eliminated. After the second year of stocking and the first year of fertilization, only the evasive *Cyclops* were present in sufficient numbers to be counted without concentrating the samples.

The seasonal biomass for *Diaptomus*, *Cyclops*, *Bosmina*, *Daphnia*, and *Holopedium* during pre-treatment averaged 126, 270, 87, 12, and 46 mg/m^2, respectively (Figure 4B). During the years when fry were stocked and the lake was fertilized, the seasonal mean biomass for these zooplankton taxa dropped dramatically to 0.04, 21, 9, 0.7, and 0.04 mg/m^2, respectively. In 1991, when the lake was left untreated, the mean biomass remained depressed for all taxa (0, 0.5, 3, 0.1, and 0 mg/m^2), and the TMB remained depleted at 4 mg/m^2 (Figure 4A), which represents an overall decline in macrozooplankton biomass of 94% since pre-treatment.

The seasonal mean lengths of zooplankton taxa decreased dramatically after stocking Pass Lake (Figure 5). The largest drop in body size (77%) was for *Diaptomus*, followed by *Holopedium*, *Daphnia*, *Bosmina*, and *Cyclops*. Of the

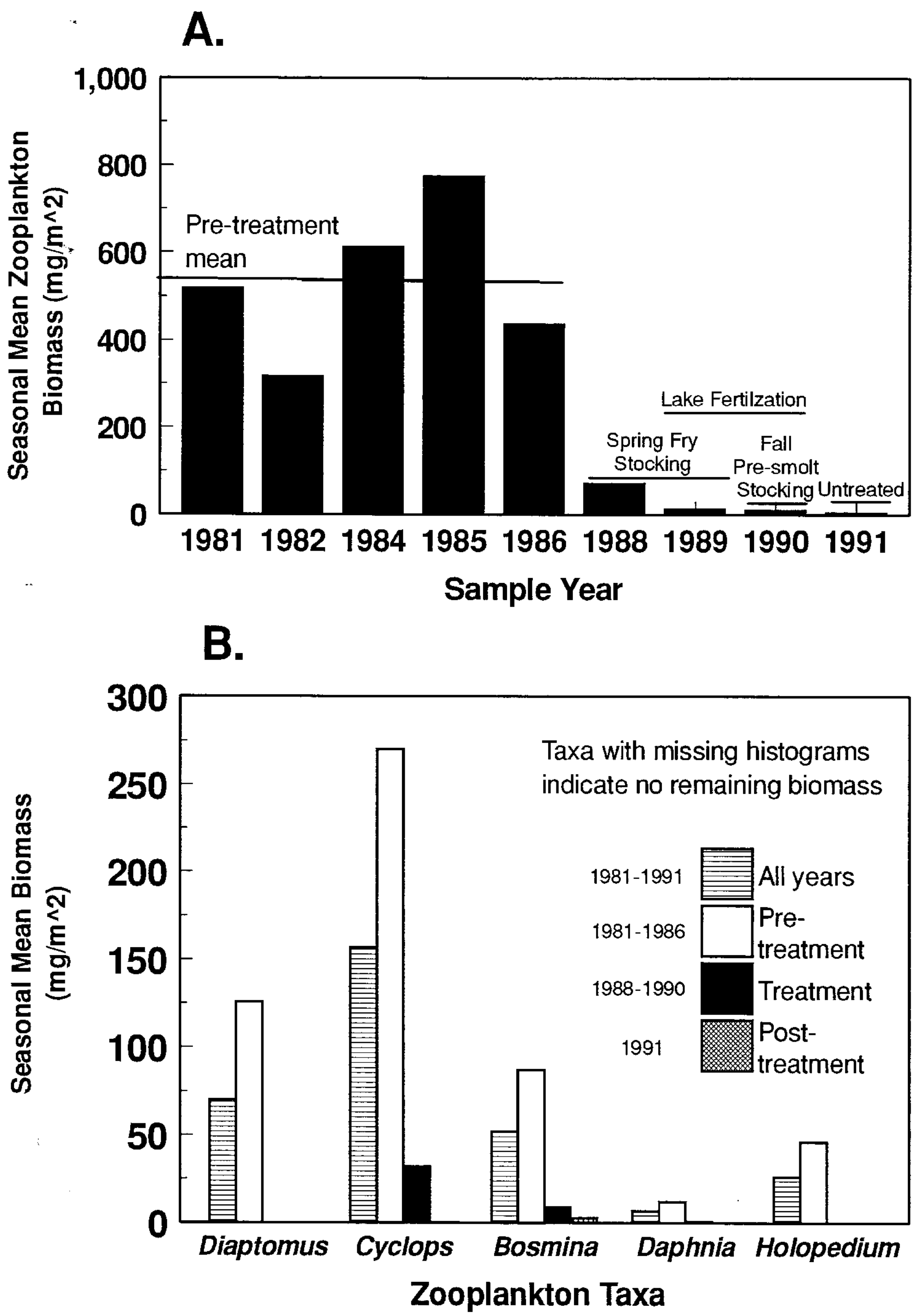

Figure 4. Mean zooplankton biomass before, during, and after treatment by year (A), and taxa (B) in Pass Lake.

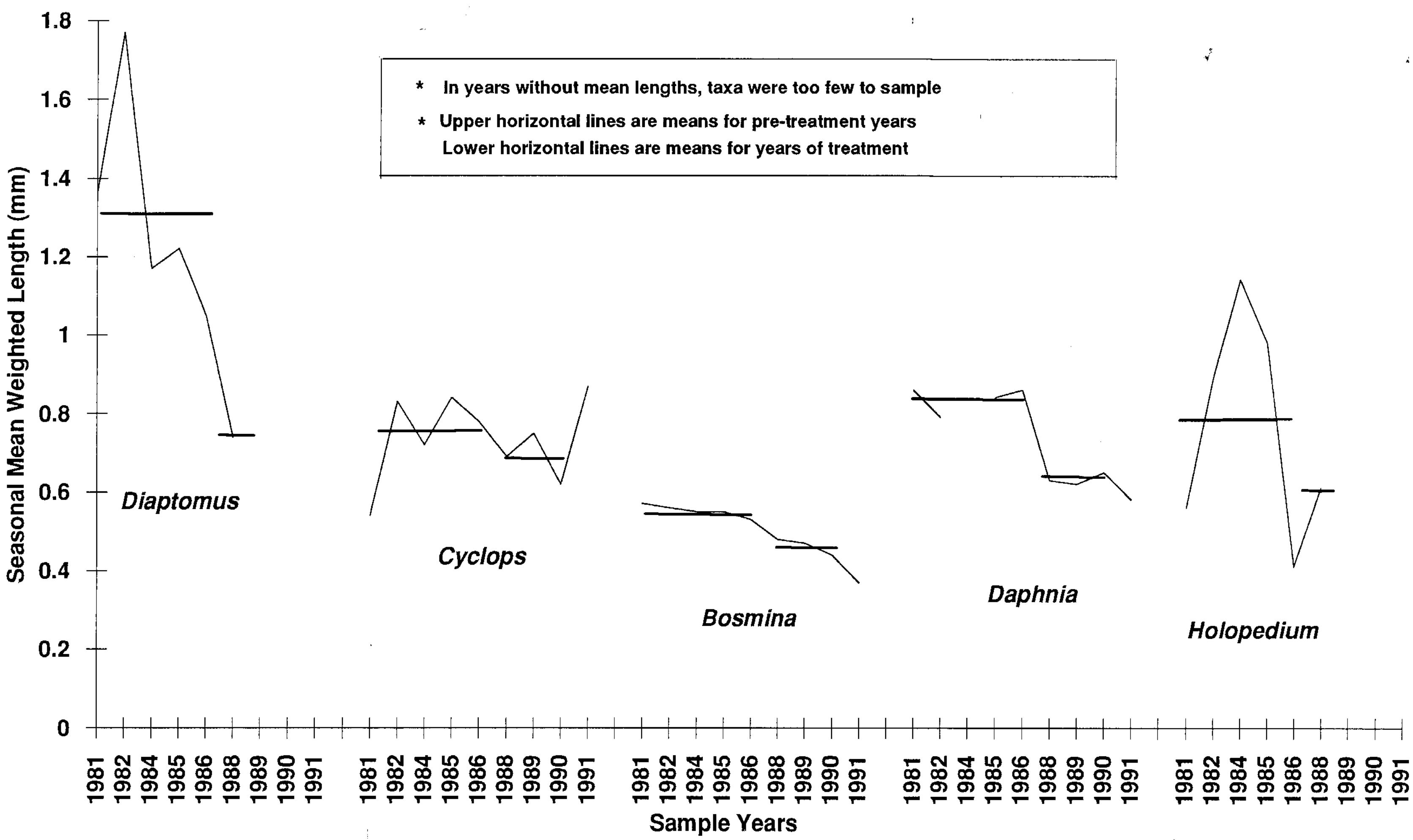

Figure 5. Seasonal mean weighted length of zooplankton taxa by year in Pass Lake.

taxa present in suitable numbers to measure in 1991 (the year the lake was left fallow), *Cyclops* increased in body size by 21% to 0.87 mm from 0.69 mm during treatment, while *Bosmina* and *Daphnia* continued to decline in body size.

Zooplankton Community Response to Stocking and Decreased Planktivory in Esther Passage Lake

Pre-stocking seasonal TMB in Esther Passage Lake ranged from 396 mg/m^2 in 1985 to 154 mg/m^2 in 1983, and averaged 241 mg/m^2 (Figure 6A). During stocking (1988-1990) TMB dropped by 58% to 101 mg/m^2. In 1991, when the lake was left fallow, TMB increased to 160 mg/m^2. Thus, after cessation of stocking the zooplankton biomass began to recover, with only 29% less biomass during the first year of no stocking than during pre-stocking.

Similar to Pass Lake, most of the zooplankton taxa decreased following the stocking of fry. The seasonal biomass for *Cyclops*, *Bosmina*, *Daphnia*, and *Holopedium* during pre-stocking averaged 126, 62, 14, and 40 mg/m^2, respectively (Figure 6B). The cladocerans (*Bosmina* and *Daphnia*) during the years of spring fry stocking (1988 and 1989) suffered a major decline in biomass (~ 45% each year). However, after 1989 (the last year of spring fry stocking) the cladoceran biomass exceeded pre-stocking levels; *Daphnia* increased by 43% and *Bosmina* increased by 85% compared to pre-stocking. The seasonal mean biomass of *Cyclops* dropped 86% after the spring fry stockings, but unlike the cladocerans, did not recover a year after the cessation of stocking (Figure 6B), probably due to their slower reproductive capacity.

The drop in body size (length) of zooplankton commensurate with spring fry stocking was much less pronounce than in Pass Lake. The seasonal mean lengths for *Cyclops*, *Bosmina*, *Daphnia*, and *Holopedium* in Esther Passage

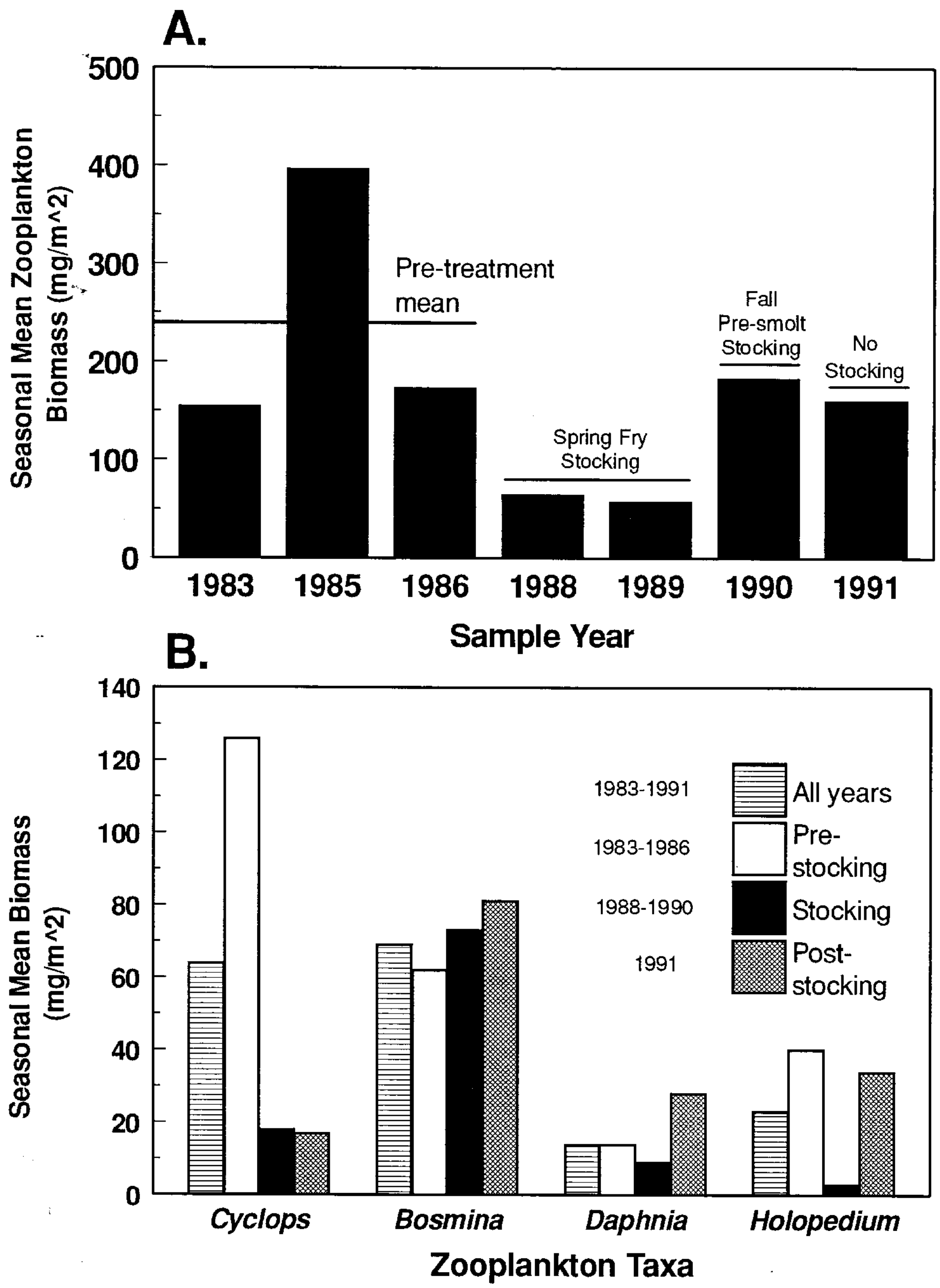

Figure 6. Mean zooplankton biomass before, during, and after treatment by year (A), and taxa (B) in Esther Passage Lake.

Lake were 0.73, 0.53, 0.80, and 0.72 mm, respectively (Figure 7). After stocking, *Bosmina* and *Daphnia* body sizes decreased 7.5% and 17% respectively; far less than that which occurred in Pass Lake (Figure 5).

<u>Smolt Production from Spring Fry and Fall Pre-Smolt Stocking in Pass and Esther Passage Lakes</u>

For Pass Lake, the EV model predicts an annual mean smolt production of 138,000 threshold sized age-1 smolts. Actual production in 1989 was 70,600 threshold-sized (2.3 g) age-1 smolts or about half the predicted number (Table 1). The survival to the smolt stage from the fry released in 1988 was 12%. Moreover, the EV model indicates a mean smolt biomass production of 304 kg; however, only 162 kg was actually produced. The age-1 smolts comprised 98% of the total, and only 1,696 age-2 smolts (3.5 g) were produced from the 1988 plant. For Esther Passage Lake, about 32,200 threshold-sized age-1 smolts were predicted to be produced by the model; however, in 1989 only 12,627 were produced, or 39% of the expected. The fry-to-smolt survival for the 1988 release was 8.5%. The age-1 smolts were larger (5.5 g) than those produced in Pass Lake, and expressed as biomass, the age-1 smolt production of 69 kg was very close to the 71 kg predicted from the EV model. In addition the age-1 smolts comprised 97% of the total smolt production from the 1988 fry plant.

In 1990, fewer and smaller age-1 smolts were produced from both lakes. From the stocking of 603,000 fry into Pass Lake in 1989, 19,686 age-1 smolts were produced that averaged 2.1 g (Table 1). This represented a biomass of 41 kg, or 13% of the expected. An almost equivalent number of age-2 smolts were produced (19,860) that averaged 5.8 g. The fry-to-smolt survival for the 1989 plant was 6.6% or a decrease of 80% compared to the 1988 plant. In Esther Passage Lake, a total of 14,735 age-1 smolts were produced with an average size of 4.9 g and a biomass of 72 kg. The number of age-1 smolts produced

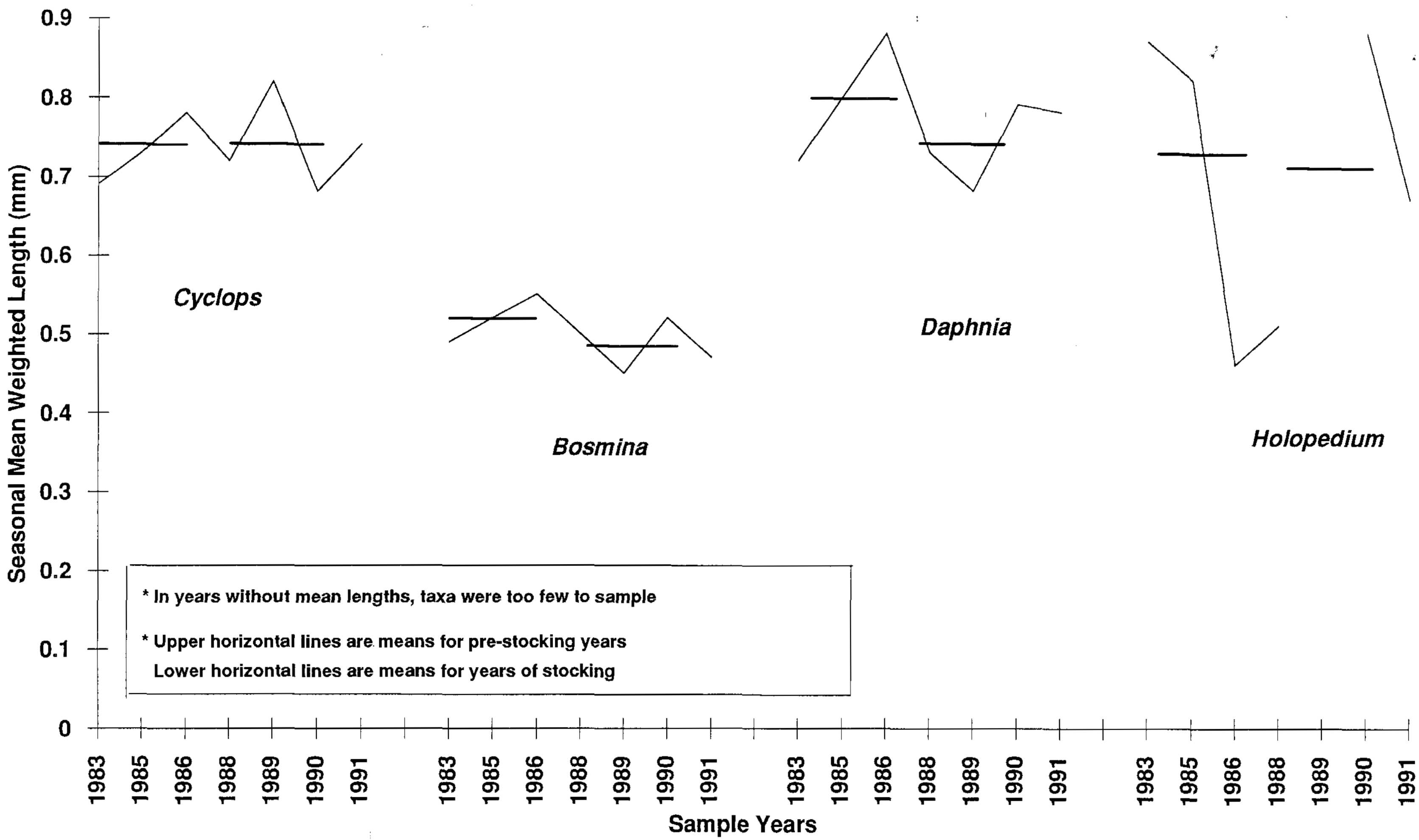

Figure 7. Seasonal mean weighted length of zooplankton taxa by year in Esther Passage Lake.

Table 1. Smolt production summary for spring fry and fall pre-smolt plants of sockeye salmon in Pass and Esther Passage lakes.

Year of plant	Number stocked	Number of age-1	Percent age-1	Age-1 weight (g)	Age-1 biomass (kg)	Number of age-2	Percent age-2	Age-2 weight (g)	Age -2 biomass (kg)	Number of age-3	Percent age-3	Age-3 weight (g)	Age-3 biomass (kg)	Fry-to-smolt survival (%)
PASS LAKE														
1988	594,000	70,600	98	2.3	162	1,696	2	3.5	6	0	0	----	----	12.0
1989	603,000	19,686	50	2.1	41	19,860	50	5.8	115	NA	NA	NA	NA	6.6
1990	100,000 (pre-smolt)	43,299	NA	2.1	91	NA	NA	NA	NA	NA	NA	NA	NA	43.3 \a
ESTHER PASSAGE LAKE														
1988	153,000	12,627	97	5.5	69	344	3	12.0	4	20	0.2	28.3	0.6	8.5
1989	155,000	14,735	97	4.9	72	420	3	16.8	7	NA	NA	NA	NA	9.8
1990	125,000 (pre-smolt)	15,886	NA	3.3	52	NA	NA	NA	NA	NA	NA	NA	NA	12.7 \a

\a Includes only age-1 smolts.

was about half of the expected, but the smolt biomass matched the predicted. Age-1 smolts comprised 97% of total smolt production from this plant, and the total fry-to-smolt survival was 9.8%.

Following the two years of spring fry plants, the lakes were stocked with pre-smolts in 1990 to compare overwinter survival (to the age-1 smolt stage) between the lakes and with the spring fry releases. Quite surprisingly, very different results were observed. In Pass Lake, 43,299 age-1 smolts were produced for a survival of 43.3% (Table 1), compared to 3.3% and 11.9% for the 1989 and 1988 spring fry releases, respectively. The 1991 age-1 smolts were similar in size to previous years despite being released at an average size of 2 g in the preceding fall. In Esther Passage Lake, a total of 15,886 age-1 smolts were produced, representing a survival of 12.7%, compared to 9.5% and 8.3% from the spring fry releases in 1989 and 1988, respectively. The 1991 age-1 smolts were smaller than in previous years, and were also released in the fall of 1990 at an average size of 2 g.

DISCUSSION

Biomass for all taxa of zooplankton in both Pass and Esther Passage lakes declined dramatically after the introduction of juvenile sockeye salmon in 1988 and 1989 (Figures 4 and 6). Some zooplankton such as *Diaptomus* and *Holopedium* in Pass Lake (Figure 8A) and *Holopedium* in Esther Pass Lake (Figure 9A) had declined or was beginning to before fry stocking, which suggests natural cyclic population fluctuations typical of unproductive, oligotrophic systems. After the second year of stocking (1989) in Pass Lake only *Cyclops* were present in large enough numbers to count without concentrating the zooplankton samples (Figure 8B). In 1990 (fall pre-smolt release) and 1991 (no treatment), *Bosmina* and *Daphnia* were detectable in Pass Lake, but still at very low levels. In Esther Passage Lake, after the first and second year of stocking (1988 and 1989), the biomass was lowered but

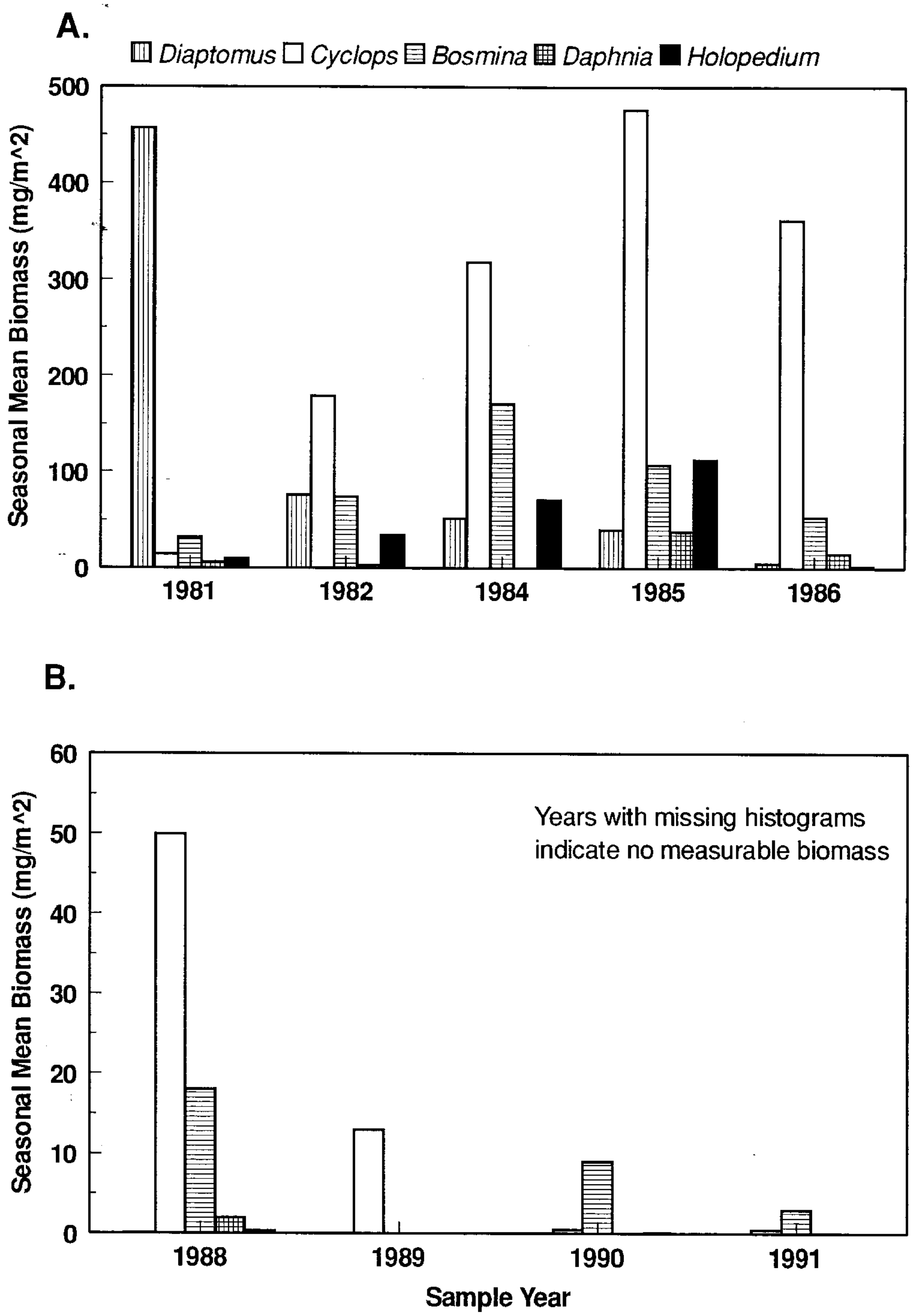

Figure 8. Zooplankton biomass by taxa and year before treatment (A), and (B) during treatment (1988-1990) and after treatment (1991) in Pass Lake.

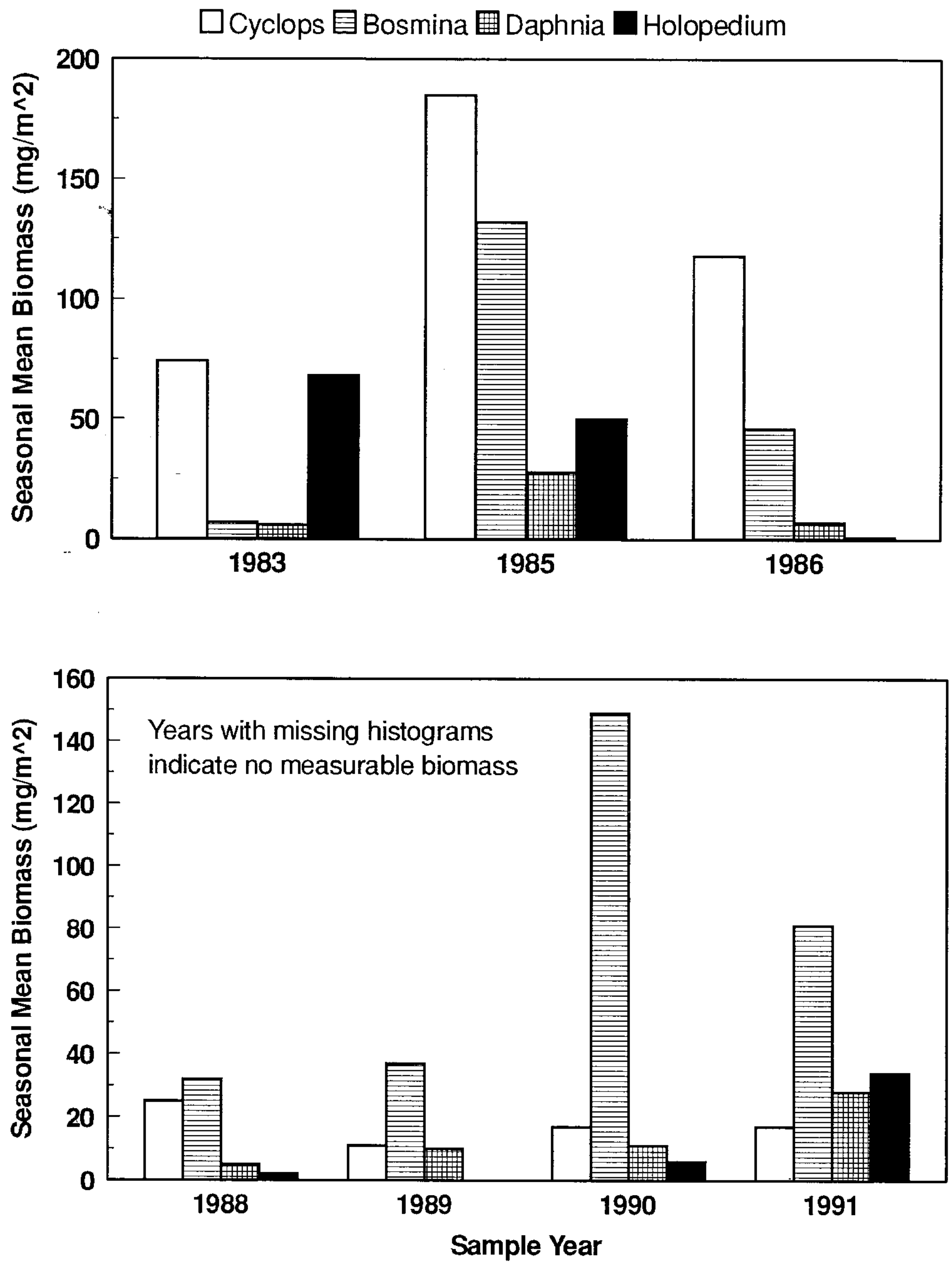

Figure 9. Zooplankton biomass by taxa and year before stocking (A), and (B) during stocking (1988-1990) and after stocking (1991) in Esther Passage Lake.

essentially the taxa composition remain intact (Figure 9B). Also, the zooplankton biomass and taxa composition in Esther Passage Lake improved in 1991, when the lake was not stocked (Figure 9B). Consequently, an accentuated effect of fry predation was observed in Pass Lake that appeared to cause a "population pit" where the zooplankton were cropped below a level such that short-term recovery was impossible.

Although predation effects were quite dramatic in Pass Lake, nutrient additions appeared to sustain *Bosmina* and *Daphnia* at numbers capable of surviving to reproduce. That is, in 1990, during the second year of nutrient treatment and when Pass Lake was not stocked with spring fry, the macrozooplankton remained depressed (Figure 8B); however, *Bosmina* dominated the zooplankton community (92% by biomass), and *Daphnia* and *Holopedium* reappeared. This is not an uncommon occurrence as enriched lake conditions are known to favor herbivorous zooplankton such as *Bosmina* and *Daphnia* (Brooks 1969; Allen 1976; Vanni 1986).

Moreover, Esther Passage and Pass lakes are oligotrophic, as chl a levels were at or below the threshold food concentration found by Lambert and Schober (1980) to be necessary for zooplankton (e.g., *Daphnia)* egg production. The added burden of a sudden and intense predation pressure by feeding juvenile sockeye, coupled with low food levels (primary productivity), causes the development of a predator-sensitive zooplankton community. Similar and other effects on zooplankton populations caused by predation are well documented (Brocksen et al. 1970; Hartman and Burgner 1972; Goodlad et al. 1974; Kyle et al. 1988; Reiman and Myers 1990; and others). In general, large bodied and\or easily captured forms such as *Diaptomus* or *Daphnia* are eliminated first and smaller bodied forms such as *Bosmina* become dominant. In Pass Lake, we found not only a reduction in large forms, but similar to that found by Gliwicz (1985), the near extinction of entire taxa within the first rearing season. Unlike Pass Lake, the zooplankton community found in

Esther Passage Lake, particularly the cladocerans (*Bosmina* and *Daphnia)* appeared capable of maintaining their populations. However, both of these zooplankters were subject to considerable predation pressure as evidenced by their reduced body sizes in 1988 and 1990 (Figure 7). Thus, the degree to which juvenile sockeye restructure the zooplankton community appears to influence the ability of zooplankton to recover.

The low productivity (oligotrophy) of these lakes, combined with the loss of nutrients from migrating smolts and the lack of nutrients from adult carcasses, short circuit the natural cycle of nutrient replenishment (Krokhin 1975). Thus, these lakes are driven to an even greater degree of oligotrophy and are hardly representative of nursery lakes having anadromous access. In addition, physical features common to both of these lakes that contribute to the accentuated lowering of zooplankton abundance are small surface area and relatively shallow depths. These conditions provide limited littoral and deep water refuge for zooplankton from juvenile sockeye, and consequently suffer increased probability of encountering a predator. Also, both lakes have relatively fast flushing rates (0.37 y for Pass Lake and 0.18 y for Esther Passage Lake), which during periods of high precipitation could flush zooplankton from the system (Brook and Woodward 1956).

Finally, smolt production, in particular smolt size, and survival from the fall fingerling releases in these two lakes were quite different. In Pass Lake, age-1 smolts were produced at a threshold size of about 2.2 g, whereas in Esther Passage Lake the age-1 smolts ranged from 3.3-5.5 g. The increased size of sockeye smolts in Esther Passage Lake is indicative of a better rearing environment. In both lakes, the spring fry-to-smolt survival was not substantially different and averaged less than 10% (Table 1). In contrast, the 2-g fall fingerlings released in both lakes survived to the age-1 smolt stage at a rate of almost four-times higher in Pass Lake than in Esther Passage Lake. This would be quite surprising if overwintering survival of fall fingerlings was strictly dependent upon the food base, especially given that the zooplankton community of Esther Passage Lake showed signs of recovery after the termination of spring fry stocking compared to Pass Lake. However, as the overwintering juvenile sockeye did not put on much growth in either lake, the resulting fall fingerling-to-smolt survivals are likely influenced by other factors.

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