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Reprinted from the
Alaska Fishery Research Bulletin
Vol. 4 No. 2, Winter 1997

Alaska Fishery Research Bulletin 4(2):120–135. 1997.

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ABSTRACT: Stocking of juvenile sockeye salmon *Oncorhynchus nerka* into nonanadromous lakes at levels comparable with juvenile densities in anadromous lakes supporting natural sockeye salmon populations effected up to a 90% reduction in zooplankton biomass. The zooplankton communities subsequently became resistant to predation as the vulnerable *Daphnia, Diaptomus*, and ovigerous *Cyclops* were virtually eliminated and the more agile (nonovigerous) *Cyclops* and smaller *Bosmina* persevered and became predominant. Relying on a standing crop of zooplankton that was severely depressed by intense grazing the previous season, juvenile sockeye salmon experienced at least a 3-fold reduction in numbers and biomass between fry and smolt stages from the previous year. Our experimental results confirmed our empirical findings that, in rearing-limited lakes, smolt biomass production becomes a function of zooplankton biomass. Once restructured by excessive predation, some zooplankton communities were unresponsive or slow to respond to either reduced grazing pressure and/or to subsequent nutrient treatment. This delayed recovery of overgrazed zooplankton populations reduced growth and survival (rearing efficiency) for ensuing cohorts. In response, Frazer Lake sockeye salmon populations fell far below replacement, the dominant-year run segment collapsed, and the amplitude of high versus low return per spawner ratios increased. In contrast, less damaged zooplankter populations responded to nutrient treatments, leading to a 3-fold increase in fry-to-smolt survival and a 6- to 20-fold increase in smolt biomass. The degree to which juvenile sockeye salmon foraging decreases biomass levels and changes the species composition of the zooplankton community ultimately determines the duration of zooplankton recovery and lowered sockeye salmon production.

INTRODUCTION

Spawner-recruit relationships (Ricker 1954) and cyclical dominance (Welch and Noakes 1990) affect cohort abundance of sockeye salmon *Oncorhynchus nerka*, but both processes assume zooplankton populations recover immediately from predation and for the most part are density-independent. Unfortunately, a vast majority of curves fit to spawner-recruit data are not statistically significant (Dahlberg 1973; Geiger and Koenings 1991). One reason for this might be that escapement/cohort effects on subsequent zooplankton populations are not independent but may carryover to subsequent years. These effects are included in some simulation models that use brood year interactions to forecast cyclic changes in sockeye salmon run strength in Alaska (Eggers and Rogers 1987) and Canada (Walters and Staley 1987), but for the most part, these effects have not been considered. Even though freshwater density-dependent effects have been clearly demonstrated in Alaskan (Koenings and Burkett 1987b; Kyle et al. 1988), Russian (Bugaev 1989), and Canadian (McDonald et al. 1987) sockeye salmon populations, biological mechanisms responsible for the negative interaction between cohorts are not well defined.

Koenings and Burkett (1987b) proposed that a lake's sockeye salmon rearing capacity is the fry density that produces smolts of minimal or threshold size (about 60 mm or 2 g). Loading densities above this capacity are excessive (Geiger and Koenings 1991) and may invoke changes (e.g., overgrazing) in rearing capacities for subsequent brood years. In fact, successive escapements 2–3 times above the rearing capacity in Frazer Lake (Kyle et al. 1988) caused the collapse of a dominant-year run, and subsequent brood year return per spawner ratios fell below replacement levels. Such top-down effects, if related to overgrazing

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Acknowledgments: Many fishery technicians and biologists — conducted field activities and collected data. The Limnology Laboratory in Soldotna — analyzed water and zooplankton samples.
Sponsorship: These lake investigations were funded by the Kodiak and Cook Inlet Aquaculture Associations, Lower Cook Inlet Seiners Association, and State of Alaska.

Table 1. Morphological characteristics and limnological characteristics of the 4 study lakes.

Lake	Lake type	Elevation (m)	Surface area (km^2)	Flushing rate (yr)	EZD[a] (m)	EV units[b]	TP[c] ($\mu g \cdot L^{-1}$)	TN[d] ($\mu g \cdot L^{-1}$)	Chl-*a*[e] ($\mu g \cdot L^{-1}$)
Leisure	clear	46	1.1	0.90	17.5	19.3	5.4	470	0.56
Pass	clear	24	0.5	0.37	12.7	6.4	2.6	67	0.35
Esther Pass	stain	22	0.2	0.18	6.1	1.2	3.2	77	0.35
Frazer	clear	108	16.6	2.10	16.9	280.5	5.8	138	0.86

[a] EZD = euphotic zone depth

[b] An EV unit = $10^6 m^3$

[c] TP = total phosphorus

[d] TN = total nitrogen

[e] Chl-*a* = chlorophyll-*a*

the forage base, are reversible by nutrient treatment (Hyatt and Stockner 1985; Koenings and Burkett 1987b; Kyle 1994; Kyle et al. 1997). Top-down control by rearing sockeye salmon reduces the size of prey items, lowers zooplankton fecundity and density, displaces vulnerable prey species, and thereby restructures the zooplankton into a predator-resistant community (Koenings and Burkett 1987b; Kyle et al. 1988). Once established, such an assemblage may resist immediate reversal to bottom-up (producer) control, either through decreased predation or increased primary production.

Based on observations from whole-lake manipulation experiments (lake stocking and nutrient treatment) on 4 lakes, we examine whether intense predation by high sockeye fry densities are independent and reversible. This information is useful to identify bottlenecks for enhancement (Koenings and Burkett 1987b) and has significant implications to management (Koenings and Burkett 1987a; Geiger and Koenings 1991).

METHODS

Study Lakes and Manipulations

Leisure Lake (59°35'N, 151°19'W) is located within Kachemak Bay State Park 16 km east of Homer, Alaska. This coastal clearwater lake (outlet flows 2 km to salt water) lies at an elevation of 46 m and has a surface area of 1.1 km^2 (Table 1). Juvenile sockeye salmon have been planted annually into this lake since 1980, and the lake has been treated with nutrient additions since 1985 (Kyle 1994). The outlet stream has a barrier that prohibits salmon access.

Pass Lake (60°55'N, 148°3'W) and Esther Pass Lake (60°52'N, 147°56'W) are located on Esther Island in western Prince William Sound, Alaska. These lakes are also coastal lakes, Esther Pass Lake being slightly smaller and more stained compared to Pass Lake (Table 1). Both lakes have outlet barriers that prevent salmon access, and both outlet streams flow <2 km to salt water. Sockeye salmon fry were planted into both lakes in 1988 and 1989. Pass Lake was treated with nutrients in 1989 and 1990; Esther Pass Lake was left untreated.

Frazer Lake (57°5'N, 154°10'W) is the second largest lake on Kodiak Island, Alaska, with a surface area of about 17 km^2 and an outlet stream that flows 14 km to salt water. This lake has a barrier falls that until 1962 precluded salmon access. In 1962 a single steeppass fishway was installed and another was added in 1979. The fishways enabled a major run of sockeye salmon to become established along with other salmon species (Blackett 1987). This lake has not been stocked in recent years, but nutrient treatment was conducted from 1988 to 1992 (Kyle 1994).

All 4 lakes are oligotrophic, seasonal mean concentrations of total phosphorus ranging from 2.6 to 5.8 $\mu g \cdot L^{-1}$, and chlorophyll-*a* concentrations of 0.35 to 0.86 $\mu g \cdot L^{-1}$ (Table 1). The macrozooplankton community in the lakes consists primarily of 2 cladocerans, *Bosmina longirostris* and *Daphnia longiremis*, and 2 copepods, *Diaptomus pribilofensis* and *Cyclops columbianus*. All 5 species of Pacific salmon are found in the Frazer Lake system; however, sockeye salmon are predominant in the limnetic rearing area. Other fish

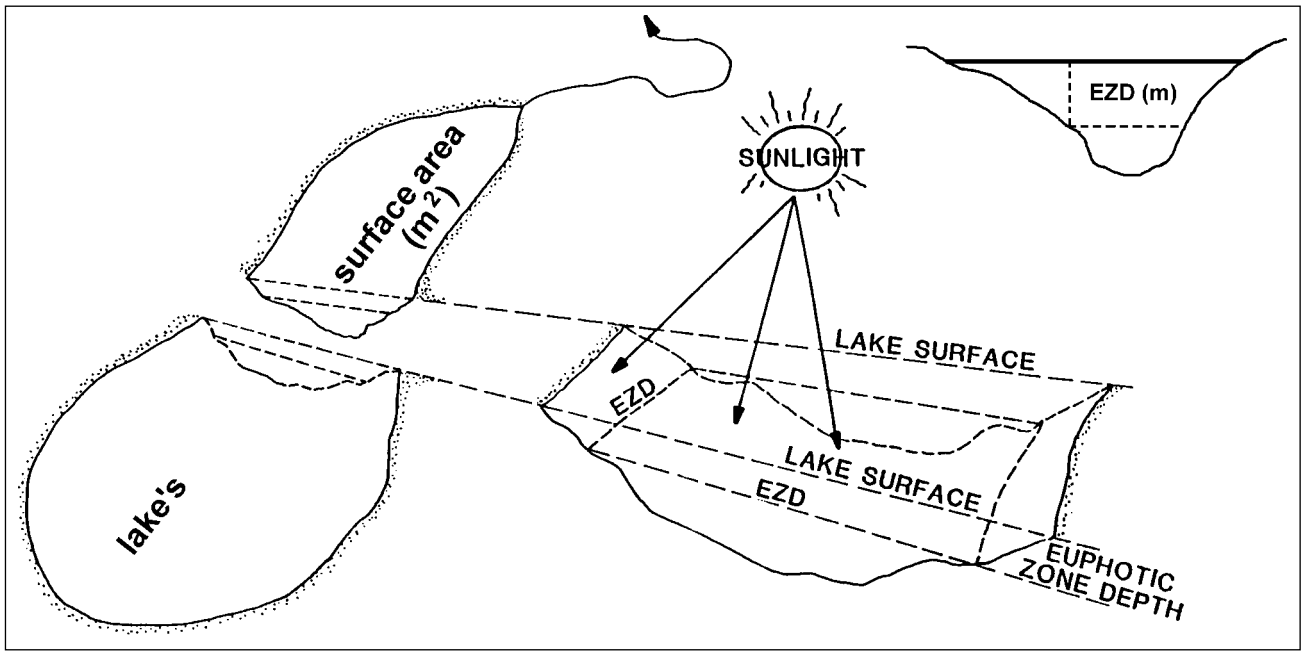

Figure 1. Schematic of a generalized lake showing the calculation of euphotic volume (EV) as the product of lake surface area (m^2) and euphotic zone depth (EZD; depth at which <1% of subsurface photosynthetically active radiation penetrates) in meters.

populations in the lakes include rainbow trout *O. mykiss*, Dolly Varden *Salvelinus malma*, three-spine stickleback *Gasterosteus aculeatus*, and coastrange sculpin *Cottus aleuticus*.

Juvenile sockeye salmon were planted at densities consistent with the maximum rearing capacity (Koenings and Burkett 1987b). Changes in the zooplankton community of Leisure, Pass, and Esther Pass Lakes were assessed before, during, and after stocking and compared to juvenile sockeye salmon survival and smolt biomass. Fry sizes and the zooplankton community in Frazer Lake were assessed in the fall and related to escapement fluctuations below and above the goal. The potential reversal of top-down effects was tested by nutrient treatment in 3 lakes (Esther Pass Lake was not treated) aimed at establishing bottom-up control. Finally, recovery of the zooplankton population after cessation of stocking was evaluated.

Euphotic Zone Depth

The algal light compensation point or euphotic zone depth (EZD) — i.e., the depth to which 1% of the subsurface photosynthetically active radiation penetrates (Schindler 1971) — was determined using a Protomatic[1] submersible photometer to measure light every 0.5 m to a depth of 5 m and thereafter at 1-m increments to the EZD. The EZD in meters times the lake surface area in square meters represented the lake's euphotic volume (EV), measured in EV units of 10^{+6} m^3 per unit (Figure 1).

Zooplankton Assessment

Zooplankters were collected at 2 stations on Leisure and Frazer Lakes, and at 1 station for Pass and Esther Pass Lakes. Vertical tows were replicated once every 3–4 weeks during May through October using a 0.2-m-diameter, 153-μm-mesh conical net at depths ranging from 15 to 55 m. The net was pulled at a speed of 0.5 $m \cdot s^{-1}$, and all zooplankton were preserved in a buffered 10% formalin solution (Haney and Hall 1973). Zooplankton from each tow were identified and enumerated by placing a 1.0-mL subsample, taken with a Hansen-Stemple pipette, onto a 1-mL Sedgewick-Rafter cell; all organisms within 5 of the inscribed 0.01-cm^2 grids were counted. Three 1-mL subsamples from each tow were processed in this manner. Macrozooplankton (copepods and cladocerans) were identified to species and expressed as number per square meter (cubic meter for Frazer Lake, for consistency

[1] Mention of a trade name is included for scientific completeness and does not imply endorsement.

with historical data). Body lengths of at least 10 zooplankters, selected from a transect in each of the three 1-mL subsamples, were measured to the nearest 0.01 mm. Zooplankton biomass was estimated from an empirical regression between zooplankton body length and dry weight (Koenings et al. 1987).

Fish Assessment

In Leisure, Pass, and Esther Pass Lakes total smolt counts were conducted by fencing off the entire outlet with mesh panels that led to either a fyke net or collection box (Bechtol and Dudiak 1988; Edmundson et al. 1993). In most years emigrating smolts were individually counted except when passage rates were too high; at these times the smolt biomass was estimated using a technique described by Bechtol and Dudiak (1988). Each day throughout the emigration, smolts were subsampled for age, length, and weight. Sampled smolts were anesthetized in a tricaine methanesulfonate (MS-222) solution, measured to the nearest millimeter (snout to fork of tail), and weighed to the nearest 0.1 g. In addition, a scale smear was taken from each measured fish, and from the glass slide containing the scales, ages were read using a Microfiche reader.

September townet surveys were conducted to estimate the size of juvenile sockeye salmon rearing in Frazer Lake. The net had a mouth opening of 2 x 2 m and was pulled by a boat as described by Gjernes (1979). Three 20-min tows were conducted along the axis of the lake. Species composition and abundance were recorded for each tow, and samples were preserved for 6 weeks in a buffered 10% formalin solution to allow stabilization. All captured sockeye juveniles were sampled for age, length, and weight.

Fry Stocking and Nutrient Treatment

Sockeye salmon fry (0.2–0.3 g) were planted in Leisure Lake during mid June by aerial dropping from a fixed-wing aircraft. The same size fry were stocked in Pass and Esther Pass Lakes; however, the fry were transported by an amphibious aircraft and released in these lakes after landing. Stocking of fry in Pass and Esther Pass Lakes occurred in early July.

A liquid white phosphorus and nitrogen fertilizer (27-7-0 or 20-5-0) was sprayed from a fixed-wing aircraft at Frazer and Pass lakes, and from a boat at Leisure Lake. However, in the third year (1987) at Leisure Lake, fertilizer was applied using a fixed-wing aircraft, but it was not an effective method because the lake was too small and too much of the fertilizer fell on the surrounding terrain. The fertilizer was composed of inorganic phosphate and nitrogen as a mixture of ammonium, nitrate, and urea. The fertilizer had an N-to-P ratio (by atoms) of 20:1, which is considered optimal for nonblue-green algal production (Rhee 1978; Schindler 1978; Smith 1982, 1983). Addition of supplemental phosphorus in the lakes was based on the annual surface-specific loading and 90% critical loading as defined by Vollenweider (1976). The fertilizer was added weekly from late May through August and was distributed in the upper area of each lake to minimize rapid flushing of nutrients.

Additional Lakes

Smolt/parr biomass and plankton biomass were also collected from 12 other Alaskan lakes (McDonald, Crescent, Tustumena, Packers, Hugh Smith, Tokun, Larson, Eshamy, Karluk, Chilkoot, Upper Russian, and Afognak Lakes) at similar times and using methods similar to those described above for the study lakes. Smolt and late-fall parr biomass estimates for sockeye salmon stocks in the 12 lakes were taken from Koenings and Burkett (1987a, 1987b). Biomass estimates of zooplankton and juvenile sockeye salmon biomass from Cultus, Black, and Great Central Lakes were obtained from Foerster (1944), Narver (1966), and LeBrasseur et al. (1978), respectively, and similar data for kokanee in Pend Oreille Lake were obtained from Reiman and Bowler (1980).

RESULTS AND DISCUSSION

Euphotic Volume and Sockeye Life-Stage Survivals

Koenings and Burkett (1987b) pioneered the use of EV (an index for primary production) as a normalizing function that converted absolute numbers of rearing sockeye salmon to numbers per EV unit, thereby enabling between-lake comparisons of sockeye salmon production potential, especially lakes impacted by organic stain and turbidity (Figure 1). Light penetration, reduced by stain and turbidity, lowers areal primary production (Koenings and Edmundson 1991), which ripples up the food chain to alter sockeye salmon production. Rearing capacity is reached when nursery lakes produce threshold-sized smolts (about 60 mm or 2 g) in one growing season (Geiger and Koenings 1991). At rearing capacity, sockeye salmon production at various life stages from Alaskan and Canadian lakes can be empirically related to freshwater areal production indexed by EV (Figure 2).

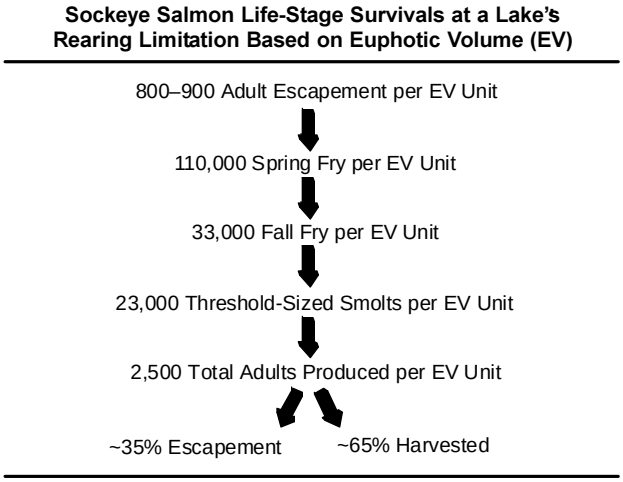

Figure 2. Sockeye salmon life-stage survivals in a typical Alaskan nursery lake at rearing limitation expressed on a euphotic-volume basis.

Based on experimental stocking in nonanadromous lake systems, the average number of sockeye salmon fry necessary to reach rearing capacity was estimated to be 110,000 fry per EV unit (Koenings and Burkett 1987b). The actual rearing capacity varies and depends on food web processes, plankton and fish community structure, and environmental factors. Survival rates and densities were determined from multiyear measurements at over a dozen nursery lakes: spring fry-to-smolt survival averaged 21%, mean smolt-to-adult survival was 12%, and harvest rates were around 65% for escapements of about 900 adults per EV unit. Many nursery lakes managed by the Alaska Department of Fish and Game have escapement goals ranging from 800 to 1,000 fish per EV unit. Assuming 50% of the spawners are female with an average fecundity of 3,000 eggs, an escapement of 900 fish per EV unit would equate to about 135,000 spring fry per EV unit at a maximum egg-to-fry survival of 10%. Thus, the experimental value of about 110,000 fry per EV unit seemed to be a reasonable estimate for fry production.

Recently, the Alaskan sockeye salmon production model (EV model), modified by using the photosynthetic rate, has been successfully used to estimate the juvenile sockeye salmon rearing capacity of 3 lakes in Canada's Fraser River system (Hume et al. 1996).

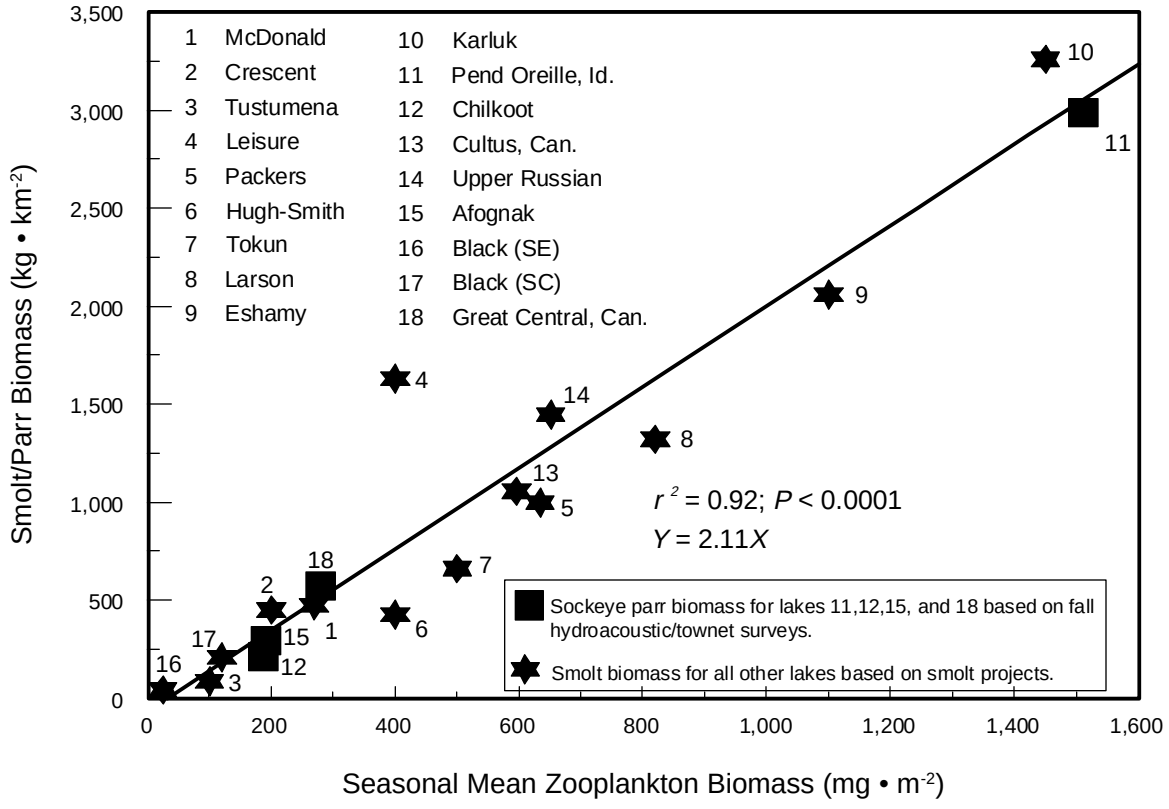

Figure 3. Relationship between seasonal mean macrozooplankton biomass and annual sockeye salmon smolt (or presmolt) biomass production for 18 nursery lakes.

Table 2. Comparison of zooplankton biomass, smolt production, and fry survival during stocking with and without nutrient treatment in Leisure Lake, 1983–1988.

Treatment	Number stocked (millions)	Smolt year	Zooplankton biomass ($mg \cdot m^{-2}$)[a]	Number of smolts and mean weight (g)	Total smolt biomass (kg)	Fry-to-age-1 smolt survival (%)	Total fry-to-smolt survival (%)
Stocking	1.5	1983	88	326,540 2.2	718	21	24
	2.1	1984	34	177,680 1.1	195	8	15
	2.1	1985	54	46,510 1.7	77	2	9
Mean			59		330	10	16
Stocking and Nutrient Treatment	2.0	1986	414	223,700 4.9	1,096	11	14
	2.4	1987	570	861,000 2.7	2,324	37	37[b]
	2.1	1988	167	650,000 3.4	2,210	31	31[c]
Mean			384		1,877	26	27

[a] Measured in the year preceding the smolt year.

[b] No age-2 smolts were produced.

[c] No age-2 smolt data available; includes only age-1 smolt survival.

Smolt Biomass as a Function of Zooplankton Biomass

The best evidence of intraspecific competition for food by sockeye salmon is the production of threshold-sized smolts after one rearing season (e.g., Ricker 1937). Under such conditions, the zooplankton community becomes predator-resistant, the standing crop biomass becomes fairly stable, and smolt production reflects the annual zooplankton turnover or production. Thus, when competition for food is severe enough to limit juvenile growth, smolt biomass production becomes a function of zooplankton biomass.

We examined this relationship for 18 lakes from Cook Inlet, Alaska, in the north, through British Columbia, Canada, to Pend Oreille, Idaho, in the south. For these lakes we found that average smolt biomass (in kilograms per square kilometer) at rearing limitation was approximately 2 times the seasonal (i.e., ice-free period from about May to October) mean dry weight (in milligrams per square meter) of the macrozooplankton community (Figure 3). However, caution should be used when applying the model to ensure the zooplankton community is fully available to rearing juvenile sockeye salmon. For example, in L-shaped Eshamy Lake, Alaska, spawner and hydroacoustic surveys indicated that spawners and rearing fry occupy only one arm of the lake, so smolt production based on the whole lake was 40% too low (authors' unpublished data). Similarly, in Great Central Lake (Canada), rearing sockeye salmon are excluded from the warmer surface stratum, and thus 50% of the macrozooplankton are unavailable to the rearing fry (LeBrasseur et al. 1978). After correcting for zooplankton biomass actually available to rearing fry in these 2 lakes, the magnitude of smolt biomass production was consistent with the model.

This model (Figure 3) estimates sockeye smolt biomass expected from a measured standing crop of zooplankton when the rearing area is used to capacity. By applying appropriate freshwater survival values (Figure 2), a cap can be set on the number of rearing juveniles delivered either by natural spawning or by hatchery stocking. Exceeding the cap and establishing top-down control of the zooplankton by rearing sockeye salmon may lead to indirect brood interactions

caused by intraspecific competition when ensuing broods forage on a depressed forage base.

Leisure Lake

Survival and Smolt Biomass: Food Deficient

As part of an experimental lake manipulation program, Leisure Lake was annually stocked with 1.5–2.1 million sockeye salmon fry in June during 1982–1984 (Table 2), which was equivalent to 76,000–106,000 fry per EV unit. The resultant age-1 smolt weights ranged from means of 1.1 to 2.2 g (mean = 1.7 g), a threshold size indicating that intraspecific competition for forage was limiting growth. In addition, these resultant age-1 smolts decreased in number from 326,540 to 46,510 (3-year mean of 184,000), in smolt biomass from 718 to 77 kg (3-year mean = 330 kg), and in fry-to-age-1 smolt survival from 21 to 2% (3-year mean = 10%). In addition, the smolt age structure shifted to a lower percentage of age-1 fish. Thus, smolt numbers, biomass, age structures, and fry-to-smolt survivals progressively degenerated over the 3 years of stocking, even though the numbers stocked each year were similar. This suggests that when limited by food, cohorts interact by reducing the growth and survival of subsequent cohorts through carryover effects on the forage base.

Survival and Smolt Biomass: Food Sufficient

From 1986 to 1988, when the lake was treated with nutrients to increase forage production, stocking levels were similar to the previous 3 years, ranging from 2.0 to 2.4 million fry or 101,000 to 121,000 fry per EV unit (Table 2). However, during this period the mean weight of age-1 smolts more than doubled, the average number of smolts tripled, and the smolt biomass increased nearly 6 fold compared to the previous 3 years preceding nutrient treatment. In addition, the fry-to-age-1 smolt survival averaged 26% (compared to 10% for the previous 3 years), and age-1 fish composed a higher percentage of the total. Thus, these results suggest that when food supply is not limiting to juvenile growth and survival, broods do not affect subsequent broods by diminishing the forage base.

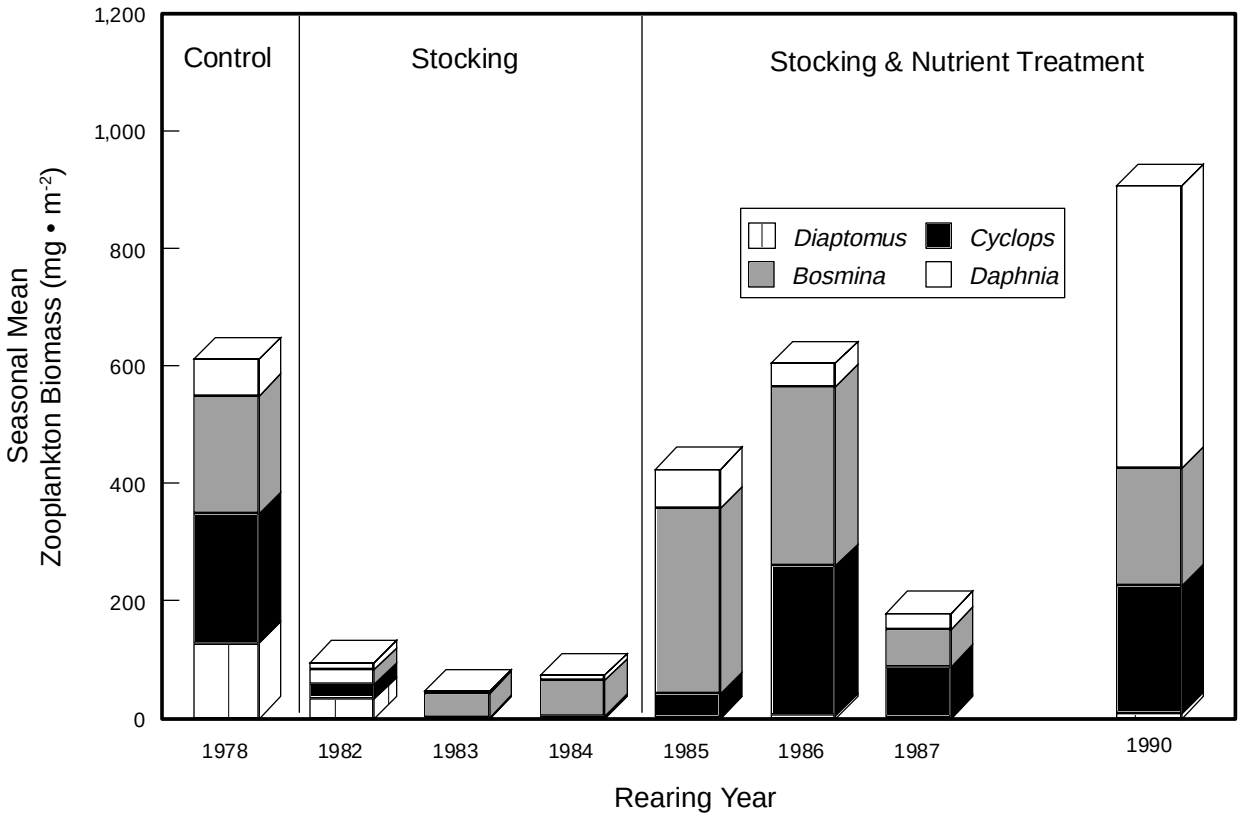

Figure 4. Seasonal mean macrozooplankton biomass, by taxa, in Leisure Lake before stocking of sockeye salmon fry (control), during stocking, and during both stocking and nutrient treatment.

Zooplankton Dynamics

In 1978, before the introduction of sockeye salmon fry, zooplankton biomass in Leisure Lake averaged 612 $mg \cdot m^{-2}$ (Figure 4). In contrast, during the 3 years preceding nutrient treatment (1982–1984), when the lake was stocked, zooplankton biomass was only 34 to 88 $mg \cdot m^{-2}$ and averaged 59 $mg \cdot m^{-2}$ (Table 2), or about 10% of the 1978 biomass.

Following the 1982 stocking, zooplankton biomass and density decreased by 85%, but the species composition remained similar to the 1978 season, so all species were consumed in similar proportions. However, in subsequent years the species composition dramatically changed. For example, *Cyclops* and *Diaptomus* combined made up 57% (348 $mg \cdot m^{-2}$) of the zooplankton biomass in 1978 and 65% (57 $mg \cdot m^{-2}$) in 1982. However, after the second year of stocking (1983), both *Diaptomus* and *Cyclops* were virtually eliminated (<1 $mg \cdot m^{-2}$ each), and small *Bosmina* (mean body size = 0.36 mm) composed 86% of the zooplankton biomass. Small *Bosmina* continued to predominate (78%) the depressed zooplankton biomass during the third year (1984) of stocking.

Juvenile sockeye salmon not only restructured the zooplankton community, nearly excluded some species, and reduced the overall biomass, but also reduced the mean zooplankton body size through size-selective predation. For example, during 1978 to 1984 the mean length of *Diaptomus* decreased from 1.24 to 0.56 mm. In addition to the decrease in length during the initial 3 stocking years, ovigerous copepods were observed in only 17% of the samples. Thus, during the 3 stocking years the zooplankton biomass was quite depressed, which changed the rearing conditions for subsequent juveniles (Figure 4). Serial changes in rearing conditions were reflected in successively lower fry-to-smolt survivals and smolt biomass of ensuing cohorts (Table 2).

During the 3 years of nutrient treatment and continued similar stocking practices, zooplankton biomass averaged 384 $mg \cdot m^{-2}$, which represented a 6-fold increase compared to the previous 3 years (Figure 4). *Bosmina* represented 74% of the biomass in the initial year of treatment (1985) and increased in biomass from 43 $mg \cdot m^{-2}$ in 1984 to 307 $mg \cdot m^{-2}$ in 1985, which exceeded the 201 $mg \cdot m^{-2}$ observed before stocking (1978). In contrast, the biomass of both *Cyclops* and *Diaptomus* remained depressed in 1985 at 40 and 1 $mg \cdot m^{-2}$, compared to 221 and 127 $mg \cdot m^{-2}$ prior to stocking. In 1986 *Cyclops* biomass did increase to 255 $mg \cdot m^{-2}$, but *Diaptomus* biomass remained depressed at 5 $mg \cdot m^{-2}$. During the third year (1987) of treatment, the zooplankton biomass dropped to 167 $mg \cdot m^{-2}$ in response to the ineffective aircraft application of the fertilizer. However, by 1990 the total zooplankton biomass was over 900 $mg \cdot m^{-2}$, primarily due to increases in *Daphnia*. Thus, the primary population response to the increase in primary productivity came first from *Bosmina* and then a year later from *Cyclops*, and by the second year of treatment the community had returned to prestocking (1978) biomass levels (Figure 4). However, *Diaptomus* never returned to 1978 levels of abundance, even after 6 years of nutrient treatment.

After nutrient treatment zooplankton body sizes increased; the mean length of *Cyclops* increased from 0.63 mm in 1984 to 0.89 mm in 1985 and to 0.90 mm in 1986. Similarly, *Bosmina* sizes increased from 0.35 mm in 1984 to 0.41 mm in 1985 and to 0.38 mm in 1986. In addition, *Diaptomus* averaged 0.56 mm in 1978, 1.01 mm in 1985, and 1.35 mm in 1986. In 1987, however, when nutrient additions were ineffectively applied, the mean lengths of *Diaptomus* (0.88 mm), *Cyclops* (0.73 mm), and *Bosmina* (0.37 mm) decreased, suggesting an immediate reversal from bottom-up to top-down control. The number of samples containing ovigerous copepods increased from 17% (1982–1984) to 83% (1985–1987). There was no station effect on the presence of ovigerous copepods (ANOVA two-way; $P = 0.80$), but there was an effect related to increased zooplankton density during treatment ($P < 0.05$). It was quite evident that nutrient treatment enabled zooplankton biomass, species composition, and body sizes to gradually rebound from 3 previous years of top-down control by sockeye salmon fry.

Pass and Esther Pass Lakes

Survival and Smolt Biomass at Rearing Capacity

In the spring of 1988, both Pass and Esther Pass Lakes were stocked with sockeye salmon fry at about 110,000 fry per EV unit (Table 3). At Pass Lake, the fry-to-age-1 smolt survival for the 1988 release was about 12%, and a total of 70,602 age-1 smolts with a biomass of 158 kg were produced. The small size of smolts (2.2 g) indicated the rearing limits were approached. At Esther Pass Lake, the fry-to-age-1 smolt survival for the 1988 release was 8%, and a total of 12,600 age-1 smolts having a biomass of 69 kg were produced. These smolts averaged 5.4 g, which was greater than threshold size and indicated that fry densities were not sufficient to limit rearing.

In 1989 both lakes were stocked again at densities of about 110,000 fry per EV unit. This release resulted

Table 3. Summary of zooplankton biomass, smolt production, and fry survival from stocking Pass and Esther Pass Lakes.

Lake	Number stocked	Smolt year	Zooplankton biomass ($mg \cdot m^{-2}$)[a]	Number of smolts and mean weight (g)	Total smolt biomass (kg)	Fry-to-age-1 smolt survival (%)
Pass	594,000	1989	73	70,602 2.2	158	12
	603,000	1990	13	21,200 2.1	45	4
Esther Pass	153,000	1989	65	12,600 5.4	68	8
	155,000	1990	57	15,100 4.8	72	10

[a] Measured in the year preceding the smolt year.

in a decrease in fry-to-age-1 smolt survival to 4% at Pass Lake, and only 21,200 age-1 smolts with a biomass of only 45 kg were produced. These age-1 smolts averaged 2.1 g, which again indicated the rearing limits were approached. The number of age-2 smolts in 1990 was 1,696 or about 2% of the brood year production. Thus, effects of interbrood competition during 1989 were minimal. At Esther Pass Lake, the 1989 fry release caused a slight increase from 8% to 10% in fry-to-age-1 smolt survival, and 15,100 age-1 smolts with a biomass of 72 kg were produced. These smolts averaged 4.8 g, which for the second year was above threshold size for smolts. The number of age-2 smolts in 1990 was 344 or <3% of the brood year production; thus, effects of interbrood competition during 1989 in this lake were also minimal.

The Pass Lake results indicate that when rearing sockeye densities approach the rearing limits (e.g., Pass Lake), the rearing efficiency (juvenile growth and survival) for ensuing cohorts can be reduced, and an indirect density-dependent response can result. In contrast, results from Esther Pass Lake show that when rearing sockeye salmon densities are not sufficient to limit rearing (e.g., Esther Pass Lake), the rearing efficiency for ensuing cohorts will generally remain unaltered.

Zooplankton Dynamics

In 1985, prior to the stocking of sockeye salmon fry, the seasonal mean macrozooplankton biomass in Pass Lake was 783 $mg \cdot m^{-2}$. The community was predominantly *Cyclops* (62% of biomass), followed by both *Holopedium* and *Bosmina* (each 14%) and then *Diaptomus* and *Daphnia* (each 5%; Figure 5A). In the absence of predation pressure by sockeye salmon fry, *Diaptomus* averaged 1.22 mm, followed in size by *Holopedium* (0.98 mm), *Daphnia* and *Cyclops* (0.84 mm), and *Bosmina* (0.55 mm; Figure 6A). After the first year of stocking (1988), zooplankton biomass decreased by 93% to 73 $mg \cdot m^{-2}$, and the community structure shifted to predominance by evasive, nonovigerous *Cyclops* (73%) and small-sized *Bosmina* (25%). *Diaptomus* disappeared soon after the June stocking, and by October both *Daphnia* and *Holopedium* were also eliminated. Under intense predation pressure, the body size of zooplankton decreased (Figure 6A). In 1989, after the second year of stocking, zooplankton biomass decreased by 98% to 13 $mg \cdot m^{-2}$ compared to 1985. Only *Cyclops* survived in sufficient densities to be counted, although both *Bosmina* and *Daphnia* were observed in concentrated samples. In addition to being the second year of stocking, 1989 was the first year the lake underwent nutrient treatment. Top-down effects still controlled zooplankton production, but it appears that nutrient treatment allowed *Bosmina* and especially *Daphnia* to survive.

Prior to stocking Esther Pass Lake in 1985, the seasonal macrozooplankton biomass averaged 402 $mg \cdot m^{-2}$. The community was composed of *Cyclops* at 48% of the biomass, followed by *Bosmina* at 33%, *Holopedium* at 13%, and *Daphnia* at 6% (Figure 5B). The body size of zooplankters was similar to those in Pass Lake, except *Holopedium* was slightly smaller (Figure 6B). In 1988, after the first year of stocking, zooplankton biomass decreased by 84% to 65 $mg \cdot m^{-2}$. The zooplankton community composition (Figure 5B)

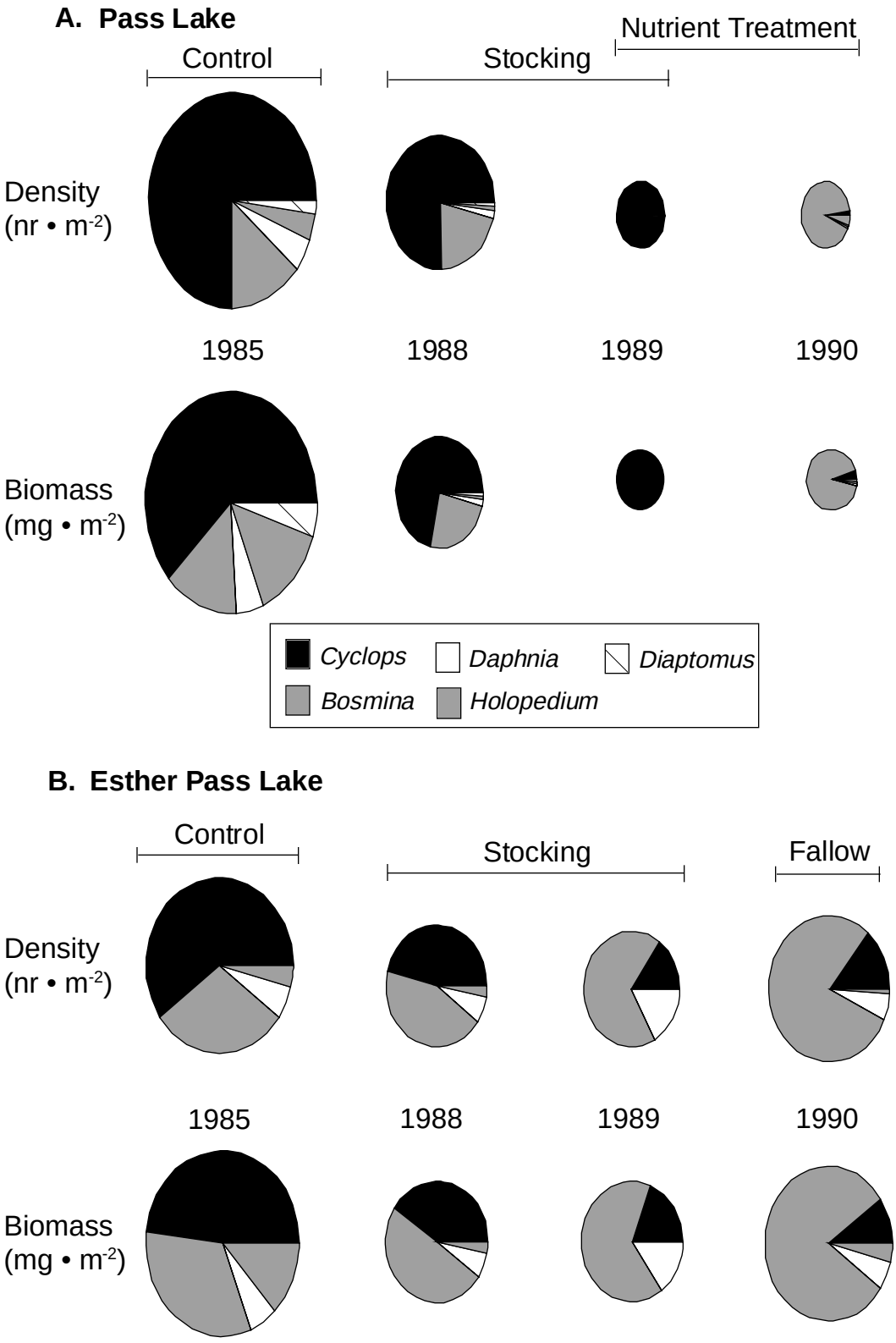

Figure 5. Seasonal mean macrozooplankton biomass and density by taxa in Pass Lake (A) and Esther Pass Lake (B) before stocking of sockeye salmon fry (control), during stocking, and during either nutrient treatment or no stocking.

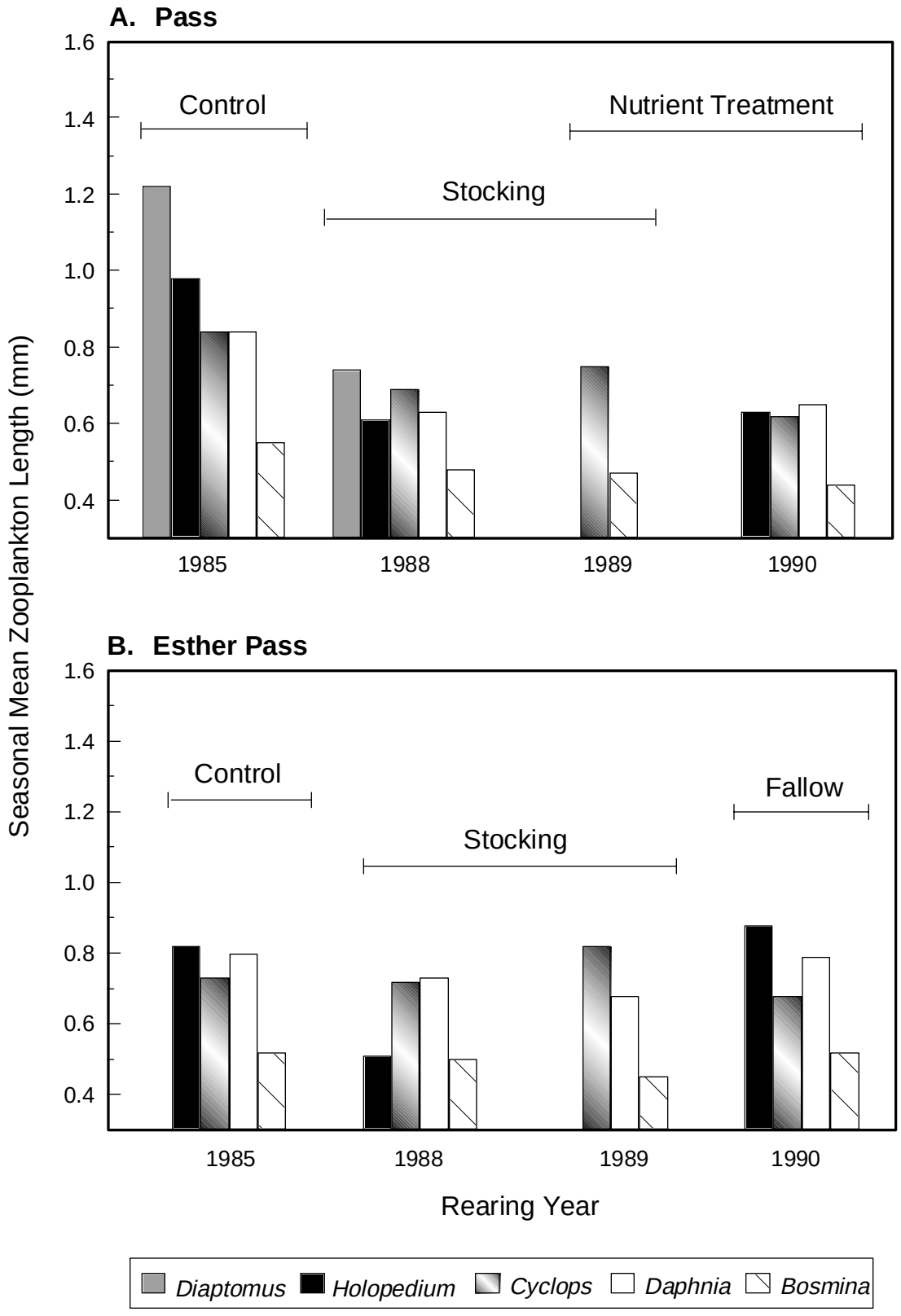

Figure 6. Seasonal mean macrozooplankton body sizes, by taxa, in Pass Lake (A) and Esther Pass Lake (B) before stocking of sockeye salmon fry (control), during stocking, and during either nutrient treatment or no stocking.

Table 4. Changes in zooplankton density and taxa and age-1 smolt size during periods of increasing sockeye salmon escapements at Frazer Lake (Kyle et al. 1988).

Historical period	Mean sockeye escapement	Macrozooplankton density ($mg \cdot m^{-3}$)	Cladoceran-to-copepod ratio	Smolt size (g)	Smolt size (mm)
Early (1964–1969)	14,684	10,620	0.06	29.5	148
Middle (1970–1976)	66,887	3,590	0.17	18.8	127
Late (1977–1986)	257,727	1,450	8.86	5.9	89

and zooplankton body sizes (Figure 6B) remained remarkably similar to those of 1985. *Cyclops* represented 41% of the biomass, *Bosmina* represented 50%, and *Daphnia* and *Holopedium* made up the remaining 9%. In 1989, the second year of stocking, the zooplankton biomass remained stable at 57 $mg \cdot m^{-2}$. Although *Holopedium* was absent, the remaining community was intact: *Bosmina* represented 65% of the biomass, followed by *Cyclops* at 19% and *Daphnia* at 15%.

Zooplankton Response to Reduced Predation

In 1990 Pass Lake was treated with nutrients a second year and was nearly devoid of rearing sockeye salmon (no stocking and few holdovers); the zooplankton biomass, however, remained depressed at 10 $mg \cdot m^{-2}$ (Figure 5A). The body sizes of zooplankton remained depressed as well (Figure 6A), but the zooplankton community composition responded to the combined treatments. *Bosmina* again became the predominant taxa (92% of biomass), followed by *Cyclops* (5%) and the return of *Daphnia* and *Holopedium*. The limnetic area was also invaded for the first time by the littoral-dwelling *Chydorid* and *Polyphemus.*

In 1990 rearing sockeye salmon were also absent from Esther Pass Lake because the lake was not stocked. The 1990 zooplankton biomass tripled 1989 levels to reach 184 $mg \cdot m^{-2}$, but the community structure (Figure 5B) and zooplankton body sizes (Figure 6B) remained similar to those found in previous years. *Bosmina* predominated (81% of the biomass), followed by *Cyclops* (10%) and *Daphnia* (6%). Also, in 1990 *Holopedium* reappeared (4% of biomass), and the limnetic area was invaded by the littoral-dwelling *Chydorid* and *Polyphemus*.

These results show the degree to which rearing sockeye salmon reduce and restructure the zooplankton community determines the time required for recovery. Intense predation pressure in Pass Lake caused an accentuated population decline that apparently crossed a reproductive threshold below which the zooplankton could not readily or promptly recover, even with the concomitant benefits of nutrient treatment and the absence of rearing sockeye salmon. In contrast, the lower pressure exerted on the forage base in Esther Pass Lake enabled zooplankton to at least partially recover in the absence of rearing sockeye salmon.

Frazer Lake

Stock Responses to Increased Escapements

Over a span of 22 years (1964–1986), sockeye escapements in Frazer Lake have increased from an average of about 15,000 adults in the first 6 years to 67,000 in the early 1970s to over 250,000 from 1977 through 1986 (Table 4). During this time macrozooplankton densities decreased by 84%, from 10,620 to 1,450 $\cdot m^{-3}$, and age-1 smolt sizes decreased from 148 to 89 mm, indicating the system was approaching its rearing limit. In addition, as the system's productivity changed, the stock acquired a dominant/subdominant run cycle, even though fishing pressure was quite limited during the run building period (Kyle et al. 1988).

The upper limit to the biological escapement goal for sockeye salmon in Frazer Lake is 200,000 adults or 800 adults per EV unit. An escapement that large produces about 120,000 fry per EV unit (Figure 2). The 1980–1982 sockeye salmon escapements averaged approximately 400,000 spawners. The return per

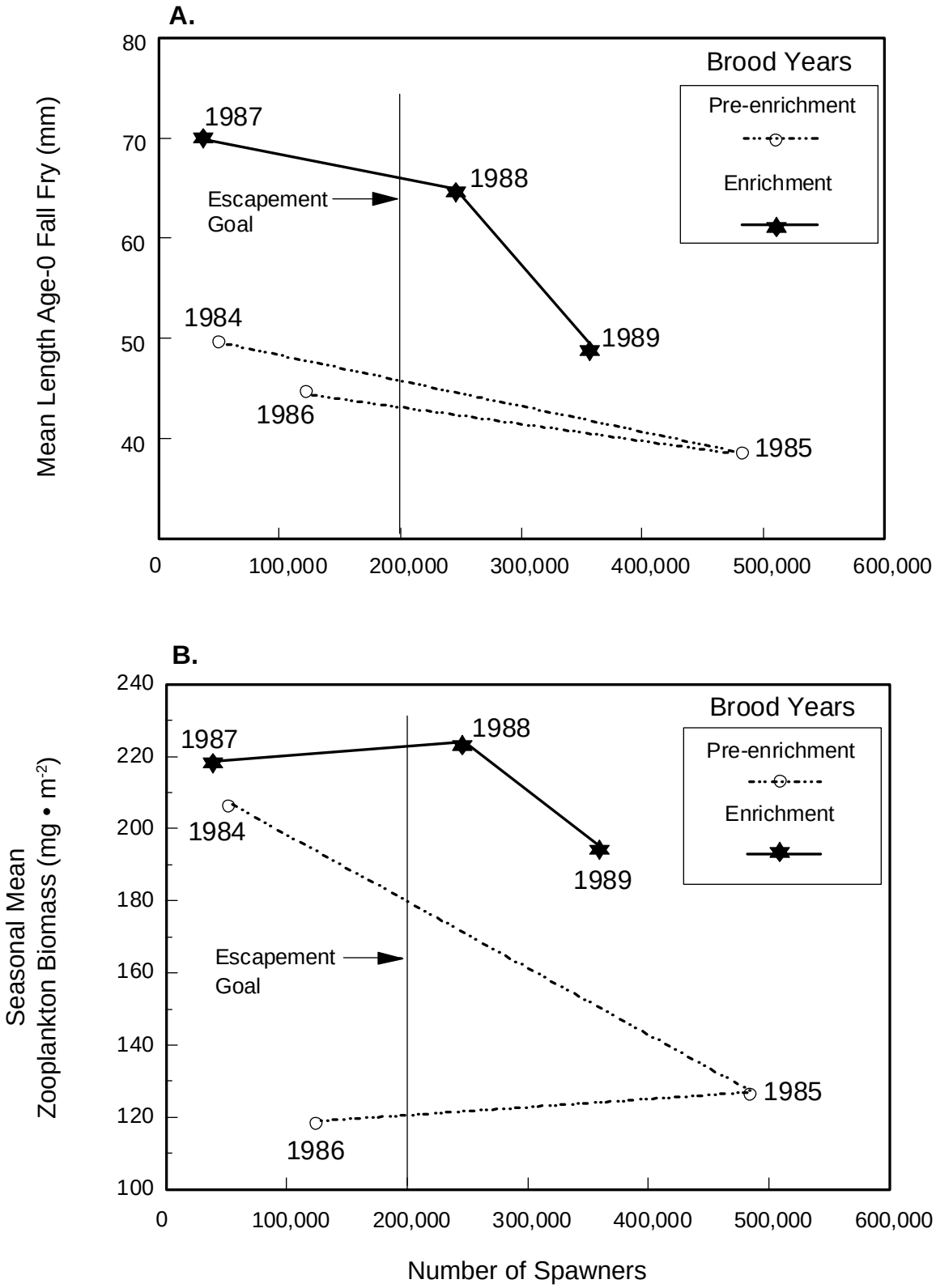

Figure 7. Changes in the length of age-0 sockeye salmon in the fall (A) and seasonal mean macrozooplankton biomass (B) corresponding to the rearing period for the various brood years for Frazer Lake.

spawner (R/S) ratio for the 1980 escapement was 1.9, presumably indicating that spawning and rearing capacity was not limiting production; however, R/S ratios for the 1981 and 1982 brood years decreased to 0.1 and 0.2, which indicated a delayed effect of the high 1980 escapement.

Fry and Zooplankton Interactions

Following the high 1980–1982 escapements, detailed in-lake data were collected to assess lake productivity and possible mechanisms responsible for the low R/S ratios. For 1984–1986, escapements were 53,500, 485,800, and 126,500 spawners, and during the next 3 years (1987–1989), escapements were 40,500, 246,700, and 360,400 (Figure 7). Sockeye salmon cohorts from the 1984–1986 escapements reared under natural conditions, whereas the 1987–1989 cohorts reared while the lake was treated with nutrients to increase the forage base.

During the 3 years before nutrient treatment, the mean length of age-0 cohorts in the fall (September) was 50 mm (1.5 g) in 1985, 37.4 mm (0.3 g) in 1986, and 46 mm (1.0 g) in 1987 (Figure 7A). The high escapement in 1985 produced minimal inseason fry growth, and even though the 1996 escapement was below the escapement goal, growth of those cohorts still lagged behind former years.

Reduced growth in the 1985 cohort noted in the fall of 1996 compared to 1984 cohort growth resulted from intense predation by rearing sockeye salmon, which lowered 1986 zooplankton biomass by 61% (Figure 7B). The 1986 escapement was only 60% of the goal, but the 1987 zooplankton standing crop not only remained depressed, but declined further. Thus, the zooplankton response to the high 1985 escapement was delayed to the next 2 years.

The 1987 escapement was comparable to 1984's, and both were below the goal; however, both the 1988 and 1989 escapements exceeded the goal (Figure 7A). The 1987 cohorts grew to a length of 70 mm (3.8 g) by fall of 1988, compared to 65 mm (3.3 g) and 50 mm (1.5 g) for the 1988 and 1989 cohorts (Figure 7A). This decrease in fry size also appeared to correspond to an increase in escapements. In 2 out of the 3 nutrient-treatment years (1987–1989), escapements exceeded the 200,000 goal, but the mean zooplankton biomass was 40% higher compared to the previous 3 years (Figure 7B). Although progeny from the large 1989 escapement reduced zooplankton biomass, even during nutrient treatment, the decrease was moderate compared to the decrease effected by the 1984–1986 cohorts. Such top-down effects are density-dependent, and from the above results, appear to be reversible and moderated through nutrient treatment.

Finally, when earlier (1980–1983) runs at Frazer Lake exceeded 375,000 spawners, zooplankton densities were comparable to those associated with the 1985 and 1986 cohorts (Kyle et al. 1988). High numbers of spawners in 1985 and 1989 reduced the rearing capacity for sockeye juveniles by depressing the forage base (Figure 7B).

CONCLUSIONS

1. Results of experimental studies at Leisure, Pass, and Esther Pass Lakes, and empirical findings at Frazer Lake, demonstrate that, although rearing sockeye salmon may prefer specific zooplankters and feed on larger individuals first, all macrozooplankters are consumed when predation pressure is intense. These results also support the use of total zooplankton biomass to predict sockeye biomass when rearing becomes limited.

2. Top-down control of zooplankton by intense predation of rearing sockeye salmon is easily established. The reversal of top-down control or the reestablishment of bottom-up control and the concomitant recovery of the zooplankton community is significantly more difficult to accomplish. Once the zooplankton community is restructured to become predator-resistant, the new community can be very resilient and resistant to change. That is, a temporal structure can be imposed that has stability, even when subsequent levels of predation are reduced. A massive effort to re-establish bottom-up control by nutrient treatment can be effective; however, recovery can be delayed by a year or more.

3. Brood year interactions have successfully modeled cyclic changes in sockeye abundance (e.g., Eggers and Rogers 1987); however, our findings did not fully support the assumption that a lake's zooplankton community exponentially recuperates after perturbation (Welch and Noakes 1990). We found that after a particularly severe or prolonged perturbation of the zooplankton community, zooplankton do not always recuperate promptly and growth and survival of ensuing young sockeye salmon is dramatically reduced. For example, high escapements at Frazer Lake lowered R/S ratios far below replacement levels, caused the collapse of a dominant-year run segment, and increased the

amplitude of high versus low R/S ratios (i.e., cyclic dominance).

4. The most basic assumption of the stock-recruitment analysis is that productivity of a system does not fundamentally change; i.e., stock parameters are fixed, and all instability is expressed only through a random variable assumed to have no temporal structure. However, our results refute the assumed independence of large escapements because predator-resistant zooplankton populations, formed after heavy predation by rearing sockeye salmon, became stable and demonstrated a delayed recovery.

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