Nutrient Treatment of 3 Coastal Alaskan Lakes: Trophic Level Responses and Sockeye Salmon Production Trends

Gary B. Kyle

Reprinted from the
Alaska Fishery Research Bulletin
Vol. 1 No. 2, Winter 1994

Alaska Fishery Research Bulletin 1(2):153–167. 1994.

Nutrient Treatment of 3 Coastal Alaskan Lakes: Trophic Level Responses and Sockeye Salmon Production Trends

Gary B. Kyle

ABSTRACT: Three coastal oligotrophic lakes with variable interannual production of sockeye salmon *Oncorhynchus nerka* were treated with additions of fertilizer to increase zooplankton biomass for the purpose of producing more numerous and larger smolts. Nutrient additions increased primary production (chlorophyll-*a*) by as much as 500% and resulted in a sustained higher level of zooplankton biomass than before treatment. Zooplankton biomass increased from 40% to 700% after nutrient treatment in the 3 lakes. For the 2 lakes in which data were available, sockeye smolt biomass increased from 50% to 250%, and in the third lake the mean weight of age-1 smolts increased by 35%. For all 3 lakes subsequent adult sockeye production increased. The phosphorus loading rates for these lakes exceeded that of treated coastal lakes in Canada by 2–5 times; however, the oligotrophic status of these lakes was not altered. The sustained high production of zooplankton and the consistent production of larger or more abundant smolts indicated that the higher phosphorus loading rates for these Alaskan lakes were advantageous to rearing sockeye salmon fry.

INTRODUCTION

Addition of nutrients to oligotrophic lakes in Canada stimulated productivity of lower trophic levels, which in turn, improved the growth and survival of juvenile sockeye salmon *Oncorhynchus nerka* and produced larger adult returns (LeBrasseur et al. 1978; Hyatt and Stockner 1985; Stockner and Shortreed 1985). The treated Pacific-coast lakes of Canada experienced smaller increases in zooplankton biomass than Canada's interior lakes and lower-than-expected production of adult sockeye salmon (Stockner 1987). The Canadian lakes were fertilized at phosphorus (P) loading rates of 3–5 mg $P \cdot m^{-2} \cdot week^{-1}$ for 18–20 weeks (Stockner 1987).

The Alaska Department of Fish and Game has investigated trophic responses to nutrient additions, salmon fry stocking, adult salmon escapements, and environmental factors in a variety of lakes in Alaska (Koenings and Burkett 1987; Kyle et al. 1988; Koenings et al. 1990; Koenings and Kyle *in press*; Koenings and Edmundson 1991; Edmundson et al. 1993; Kyle et al. *in press*; Kyle 1994). These investigations revealed a basic tenet of rearing efficiency of sockeye salmon in nursery lakes: that juvenile sockeye production is not an exclusive function of spawner density, and that a high-quality rearing environment improves juvenile sockeye growth and survival. The goal of Alaska's lake enrichment program is to increase zooplankton biomass without negatively altering the zooplankton species composition or changing the lake's oligotrophic state (Kyle et al. *in press*). This goal is based on the assumption that lake fertilization will lead to a higher-quality rearing environment for planktivorous juvenile sockeye salmon, and ultimately increase smolt production.

In this paper I present the results from 3 coastal Alaskan lakes treated with nutrient additions and examine whether (1) nutrient treatment simultaneously increased zooplankton biomass and sockeye smolt production (size/number), and (2) adding nutrients at phosphorus loading rates 2–5 times greater than those used in Canadian coastal lakes increased sockeye smolt production without adversely altering the lake's trophic state. Of the 10 lakes fertilized in southcentral Alaska (Kyle et al. *in press*), Frazer, Leisure, and Packers Lakes were selected for this paper because they were the only lakes that provided concurrent data for all trophic levels, as needed to examine the above-stated objectives. These 3 lakes also experienced interannual

Author: GARY B. KYLE is a regional limnologist with the Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, 34828 Kalifornsky Beach Road, Suite B, Soldotna, Alaska 99669.
Acknowledgments: Many fishery technicians and biologists — assisted with nutrient application and data collection. The Limnology Laboratory in Soldotna — analysis of water and zooplankton samples. Jeffery Koenings — reviewed an earlier version of this manuscript.
Project Sponsorship: This investigation was partially funded by the Kodiak and Cook Inlet Regional Aquaculture Associations and the Lower Cook Inlet Seiners Association.

variation in sockeye production prior to nutrient treatment, and their morphometry and degree of oligotrophy were similar to the treated Canadian lakes.

METHODS

This study focuses on the years before fertilization and between initiation of lake fertilization (mid to late 1980s) through 1992 (note: Frazer Lake fertilization ended in 1992, but fertilization of Leisure and Packers Lakes continued beyond 1992).

Nutrient Treatment

The 3 coastal Alaskan lakes treated with nutrients are located in southcentral Alaska (Figure 1). Frazer Lake (57°15'N, 154°10'W), on Kodiak Island, was first seeded with sockeye salmon eggs in 1951 and, with the installation of fishways, has developed into a major run (Blackett 1987). However, as the escapements increased, there was a concomitant decrease in macrozooplankton densities, which eventually caused a major collapse in adult sockeye production (Kyle et al. 1988). Consequently, in 1988 the escapement goal was reduced by 50% and nutrients were added annually to increase zooplankton biomass.

Leisure Lake (59°35'N, 151°19'W) is located on the east side of Kachemak Bay across from Homer, Alaska. This lake had no population of sockeye salmon due to an impassable falls. It was stocked with sockeye salmon fry (about 2 million per year) beginning in 1980 to enhance commercial and sport fisheries. A fertilization project was initiated in 1985 to bolster fry growth and survival.

Packers Lake (60°28'N, 151°55'W), located on Kalgin Island in Cook Inlet, has a natural run of sockeye salmon, but in the early 1980s the run decreased to a very low level. Nutrient additions in Packers Lake began in 1984, and beginning in 1988 lake stocking with sockeye salmon fry was initiated to enhance the adult return.

All 3 lakes are oligotrophic, as characterized by low phosphorus and nitrogen concentrations and low chlorophyll-*a* levels (Table 1). These lakes range in mean depth from 12 to 33 m, in surface area from 1 to 17 km^2, and in water resident time from 0.6 to 2.8 years. Frazer and Leisure Lakes are characterized as clear-water lakes (color range 5–10 Pt units), whereas Packers Lake is dystrophic (color range 20–35 Pt units), which reduces light penetration and the depth of the euphotic zone (Koenings and Edmundson 1991).

An aqueous nitrogen (N) fertilizer (32-0-0) and/or blended nitrogen and white phosphorus fertilizers (27-7-0; 20-5-0) were sprayed from a fixed-wing aircraft at Frazer Lake. Fertilizer was applied by boat at Packers and Leisure Lakes, although aircraft spraying was used at Packers Lake in 1983 (Table 2). The lakes received different types of fertilizer, depending on the ambient levels of both phosphorus and nitrogen. Phosphorus was added in the form of inorganic phosphate, whereas nitrogen was applied in a mixture of ammonium, nitrate, and urea. The blended fertilizer N-to-P ratio (by atoms) approximated 20:1, which is considered optimal for non-blue green algal production (Schindler 1978; Rhee 1978; Smith 1982, 1983). The annual mean loading of supplemental phosphorus in the 3 lakes ranged from 90 to 273 $mg \cdot m^{-2} \cdot year^{-1}$ based on the annual surface-specific and critical loading as defined by Vollenweider (1976). The attendant percentage increase in phosphorus from fertilizer ranged from 33% to 67%. Application of nitrogen fertilizer was based on pretreatment concentrations and any observed summer depletions.

Nutrient applications occurred from once per day to once per week. Applications were begun each year in late May to mid June and were usually terminated by the end of August (Table 2). The fertilizer was distributed over 33–60% of the total lake's surface area in areas selected to minimize rapid flushing of nutrients from the lake. The phosphorus loading rate from fertilizer averaged 10, 24, and 14 $mg \cdot P \cdot m^{-2} \cdot week^{-1}$ in Frazer, Leisure, and Packers Lakes. The number of weeks that each lake received phosphorus fertilizer varied from 10 to 11 weeks for Frazer Lake, 10 to 16 weeks for Leisure Lake, and 3 to 14 weeks for Packers Lake.

Nutrients

Water samples for nutrient analysis were collected from the 3 lakes at least once per month between May and September. However, to reduce the effects of climatic inconsistencies in May and September, I used nutrient data for only the June–August samples. In each of the lakes, nutrient (and zooplankton) samples were taken in each of the 3 years before treatment began and in each year during treatment. Two permanent sampling stations were established to characterize changes in lake productivity. At each station, water was collected from the epilimnion at 1 m with a Van Dorn sample bottle, stored in a 10-L translucent carboy, and preprocessed (i.e., filtered and frozen or cooled) for each appropriate test before shipment to the Limnology Laboratory in Soldotna, Alaska, for

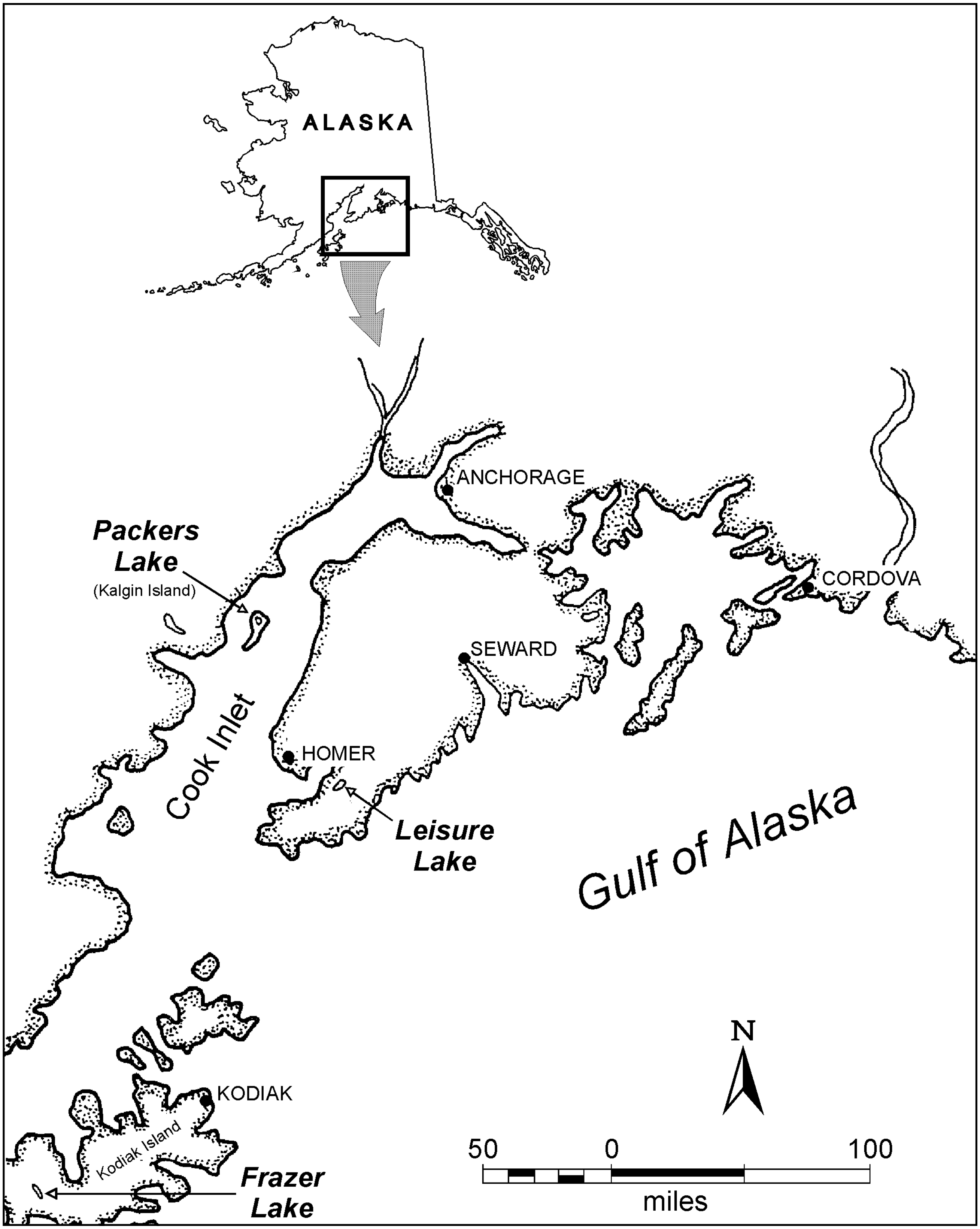

Figure 1. Geographical location of Frazer, Leisure, and Packers Lakes within southcentral Alaska.

Table 1. Morphometric information and epilimnetic means of pre-enrichment nutrient and algal concentrations (May–September) for 3 years and 2 sample stations in Frazer, Leisure, and Packers Lakes.

Lake	Lake type	Elevation (m)	Surface area (km^2)	Mean depth (m)	Water residence time (yr)	Euphotic zone depth (m)	Total phosphorus ($\mu g \cdot L^{-1}$)	Filterable reactive phosphorus ($\mu g \cdot L^{-1}$)	Total Kjeldahl nitrogen ($\mu g \cdot L^{-1}$)	Nitrate ($\mu g \cdot L^{-1}$)	Chlorophyll-*a* ($\mu g \cdot L^{-1}$)
Frazer	clear	108	16.60	33.2	2.10	16.7	5.8	2.3	91	60	0.95
Leisure	clear	46	1.05	16.4	0.57	14.7	4.8	2.0	83	379	0.56
Packers	stain	16	2.10	13.3	2.84	3.9	7.6	6.0	218	70	1.46

analysis. Nitrogen and phosphorus analyses followed procedures described by Koenings et al. (1987). Total phosphorus concentrations in Packers Lake were corrected for organic stain as described by Koenings et al. (1987).

Phytoplankton

Algal biomass from epilimnetic water samples taken at 1 m from June through August was estimated by chlorophyll-*a* analysis using the fluorometric

Table 2. Type, amount, and application rate of fertilizer added to Frazer, Leisure, and Packers Lakes.

Lake	Application area (km^2)	Application year	Fertilizer type	Amount (tons)	Application period, rate, and method	Phosphorus loading rate from fertilizer ($mg \cdot m^{-2} \cdot week^{-1}$)
Frazer	10	1988	27-7-0	60	Mid Jun – mid Aug; 7.5 tons/week: aerial[a]	12.5
		1989	20-5-0	65	Mid Jun – mid Aug; 8.1 tons/week: aerial	9.6
		1990	20-5-0	75	Mid Jun – Aug; 7.5 tons/week: aerial	8.9
		1991	20-5-0	75	Mid Jun – Aug; 7.5 tons/week: aerial	8.9
		1992	20-5-0	75	Mid Jun – Aug; 7.5 tons/week: aerial	8.9
Leisure	0.4	1985	27-7-0	14	Early Jun – early Oct; 0.12 ton/d: boat	22
		1986	27-7-0	14	Late May – late Aug; 0.27 ton every other d: boat	30
		1987	27-7-0	15	Early Jun – late Aug; 0.34 ton every other d: boat	33
		1988	27-7-0	14	Early Jun – late Aug; 1.17 ton once/week: boat	30
		1989	20-5-0	15	Early Jun – late Aug; 1.25 ton once/week: boat	24
		1990	20-5-0	15	Early Jun – late Aug; 1.25 ton once/week: boat	24
		1991	20-5-0	15	Early Jun – late Aug; 1.25 ton once/week: boat	24
		1992	20-5-0	15	Early Jun – late Aug; 1.25 ton once/week: boat	24
Packers	0.7	1983	32-0-0	14	Aug – mid Sep; 2 tons/week: aerial[b]	
		1984	27-7-0	13	Jun – mid Aug; 0.16 ton/d: boat	17
		1985	27-7-0	13	Jun – mid Aug; 0.16 ton/d: boat	17
		1986	32-0-0	4	Jun; 0.16 ton/d: boat	
			27-7-0	10	Jul – Aug; 0.16 ton/d: boat	17
		1987	27-7-0	15	Jun – mid Sep; 0.16 ton/d: boat	17
		1988	32-0-0	14	Jun – Aug; 0.16 ton/d: boat	
		1989	32-0-0	8	Late Jun – mid Aug; 0.16 ton/d: boat	
			20-5-0	6	Late Jun & late Aug; 0.16 ton/d: boat	20
		1990	32-0-0	13	Mid Jun – Aug; 0.17 ton/d: boat	
			20-5-0	2	End May – early Jun; 0.16 ton/d: boat	9.5
		1991	32-0-0	13	End May – early Aug; 0.17 ton/d: boat	
			20-5-0	2	End May – early Jun; 0.16 ton/d: boat	9.5
		1992	32-0-0	10	End May – early Aug; 0.17 ton/d: boat	
			20-5-0	2	End May – early Jun; 0.16 ton/d: boat	9.5

[a] Due to poor flying conditions, the application schedule was adjusted each year. The application rate represents the average during each year. Weekly applications required 3 d.
[b] Weekly applications required 2 d.

procedure of Strickland and Parsons (1972). The low-strength acid addition method recommended by Reimann (1978) was used to estimate phaeophytin. One or two liters of sampled water were filtered through 4.25-cm GF/F filters, to which 2 mL of a saturated $MgCO_3$ solution were added just before completion of filtration. Phytoplankton samples for estimates of cell density and taxa, collected primarily during the fertilized years, were analyzed by Eco-Logic, Ltd., of British Columbia, Canada. These samples were collected sporadically from June through August from the epilimnion of each lake at 1 m.

Zooplankton

Macrozooplankton (excluding nauplii and rotifers) were sampled monthly during May–September in each lake for 3 years before and during each year of nutrient treatment. Zooplankton were collected using a 0.2-m diameter, 153-µm mesh, cylinder-cone net. Duplicate vertical hauls from 1 m above the bottom to the surface of the lake were taken from the same 2 stations used to collect water for nutrient analysis. The net was pulled at a speed of 0.5 $m \cdot sec^{-1}$, and all contents were washed into a 250-mL polyethylene bottle containing a 10% neutralized sugar-formalin solution suggested by Haney and Hall (1973). Cladocerans were identified to lower taxa using the taxonomic keys by Brooks (1957) and by Pennak (1978); copepods were identified using the keys of Wilson (1959) and Yeatman (1959). Enumeration consisted of counting triplicate samples taken with a 1-mL Hansen-Stemple pipet on a 1-mL Sedgewick-Rafter counting chamber. In addition to enumeration and identification, zooplankton were individually measured to the nearest 0.01 mm and converted to biomass as described in Koenings et al. (1987).

Smolt Sampling

Sockeye salmon smolts were enumerated and subsampled for size and age at a complete barrier trap at Leisure and Packers Lakes (Bechtol and Dudiak 1988; Marcusen 1988). The traps diverted all migrating smolts into a live box for counting and sampling. During each day of the migration approximately 20–40 smolts were measured for fork length to the nearest millimeter and weighed to the nearest 0.1 g; their age was determined by placing several scales per fish on a glass slide and then reading the scales with a microfiche reader. At Frazer Lake, only smolt size and age data were collected through the use of a fyke net or inclined-plane trap.

Adult Sampling

Because a barrier falls prevents sockeye salmon from entering Leisure Lake, adult return information consisted of the number of sockeye salmon harvested in the sport and commercial fisheries. The number of Leisure Lake sockeye salmon commercially harvested was estimated based on geographic segregation, stock identification (i.e., adult size), and average run size before initiation of enhancement (L. Hammerstrom, Alaska Department of Fish and Game, Homer, personal communication). At Packers Lake, only escapement data (weir counts) were available. Effort targeting Packers Lake sockeye salmon in the commercial fishery was not increased after treatment, and the increase in escapements therefore provided an index that reflected the change in run size. For Frazer Lake, both escapement (weir count) and harvest data were available. However, all age classes from brood years that reared in the lake when it was treated with nutrients had not yet returned when this paper was prepared.

RESULTS

Nutrients

The mean epilimnetic total phosphorus (TP) concentrations before treatment were less than those following treatments in all 3 lakes (Figure 2). The largest increase in mean TP during treatment was observed in Leisure Lake (a 70% increase from 5.3 to 9.0 $\mu g \cdot L^{-1}$). Both Frazer and Packers Lakes increased 1.3 $\mu g \cdot L^{-1}$ (about 20%) in mean TP during treatment. In all 3 lakes the seasonal mean TP concentrations did not exceed 10 $\mu g \cdot L^{-1}$, which is the upper concentration normally used to categorize oligotrophic lakes (Carlson 1977; Woods 1986). Mean total Kjeldahl nitrogen (TN) concentrations were also higher during the treated years, and as with TP, the largest increase was in Leisure Lake. Mean nitrate concentrations were not different in Frazer and Leisure Lakes after treatment but increased 3 fold in Packers Lake. The atomic ratio of TN to TP for Frazer Lake changed very little during treatment, averaging 53:1 before treatment and 47:1 after treatment. Before treatment in Leisure Lake the TN:TP ratio was quite high at 200:1, indicating that phosphorus was severely limiting phytoplankton growth. During treatment the TN:TP ratio ranged from 92:1 to 181:1 and averaged 132:1. In Packers Lake the mean TN:TP ratio before treatment was 44:1 and during treatment through 1989 increased to 53:1;

however, from 1990 through 1992 the TN:TP ratio increased dramatically to an average of 120:1.

Algal Composition and Biomass

Algal composition and the density (number·m^{-3}) of phytoplankton taxa from samples collected during June–August were highly variable in the 3 lakes. In Frazer Lake the algal composition was predominated by diatoms, of which the inedible genera (inedible by zooplankton), most notably *Asterionella* and *Melosira*, were more abundant (Figure 3A). Although there is a broad category of environmental variables that affect algal assemblage (Reynolds 1984), the low density of edible phytoplankton is consistent with a high degree of grazing by zooplankton (Schindler 1992). In Leisure Lake the algal composition consisted of a mixture of taxa, including some temporary blooms of cyanophytes (Figure 3B). Unlike Frazer Lake, there was more edible phytoplankton (e.g., *Chromulina* and *Ankistrodesmus*) in samples collected from Leisure Lake during June–August, but for all the years and months sampled, inedible forms were slightly more prevalent than edible forms.

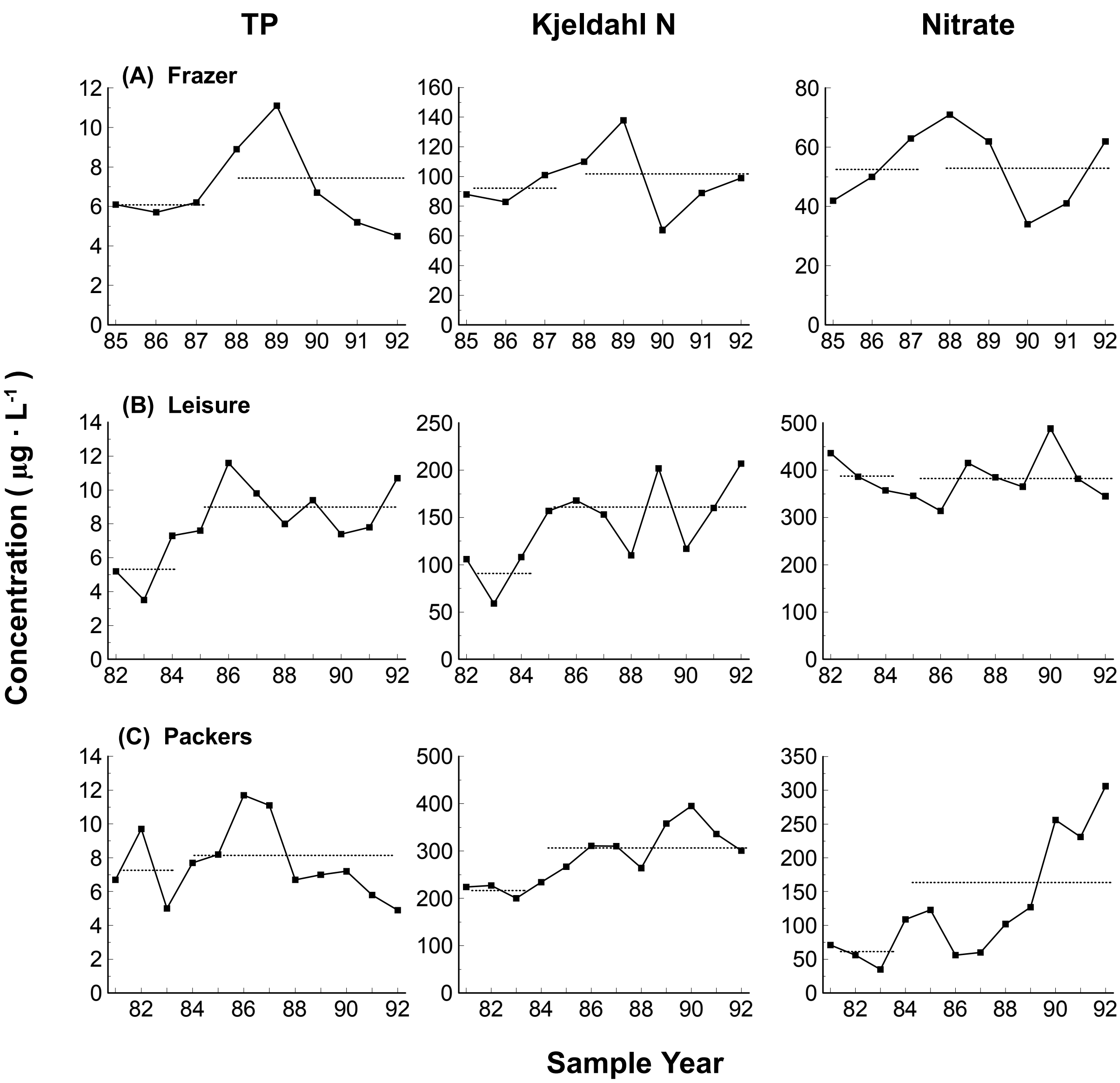

Figure 2. Mean concentrations of total phosphorus, Kjeldahl nitrogen, and nitrate for 2 epilimnetic (1 m) stations sampled during June–August in Frazer Lake (A), Leisure Lake (B), and Packers Lake (C). The first 3 years of each lake were untreated, and the remaining years were treated with nutrients.

Packers Lake had the highest density of phytoplankton, which was mainly composed of diatoms and crypto-chrysophytes (Figure 3C). The majority of phytoplankton sampled during June–August in Packers Lake were the edible variety (e.g., *Cyclotella*, *Chromulina*, and *Ankistrodesmus*), which is consistent with a low degree of grazing by zooplankton (Schindler 1992).

The mean chlorophyll-*a* concentration (June–August) in all 3 lakes was higher during years of nutrient treatment (Figure 4). Leisure Lake experienced the largest increase in algal biomass: chlorophyll-*a* averaged 0.65 $\mu g \cdot L^{-1}$ before treatment and 3.95 $\mu g \cdot L^{-1}$ during treatment (a 500% increase). In Frazer Lake, the mean chlorophyll-*a* concentration increased 37% during treatment and 63% in Packers Lake. Seasonal mean chlorophyll-*a* concentrations did not exceed values considered typical for oligotrophic lakes (Lambou et al. 1982).

Zooplankton Composition and Biomass

During the first 2 years of nutrient treatment (1988 and 1989) in Frazer Lake, the composition of zooplankton taxa was similar to those found before treatment (Figure 5A). However, beginning in 1990 and continuing through 1992, the composition of *Daphnia* was lower and *Cyclops* was higher. In Leisure Lake the pretreatment zooplankton community was predominated by *Bosmina*, except in 1982 when a slightly larger composition of *Diaptomus* was found (Figure 5B). During the first year of treatment, the zooplankton composition was similar; however, an increase in *Cyclops* and a concurrent decrease in *Bosmina* followed. The zooplankton community was predominated by *Bosmina* in 1989, by *Cyclops* (95%) in 1991, and became split between *Cyclops* and *Bosmina* in 1992. In Packers Lake the zooplankton composition remained essentially the

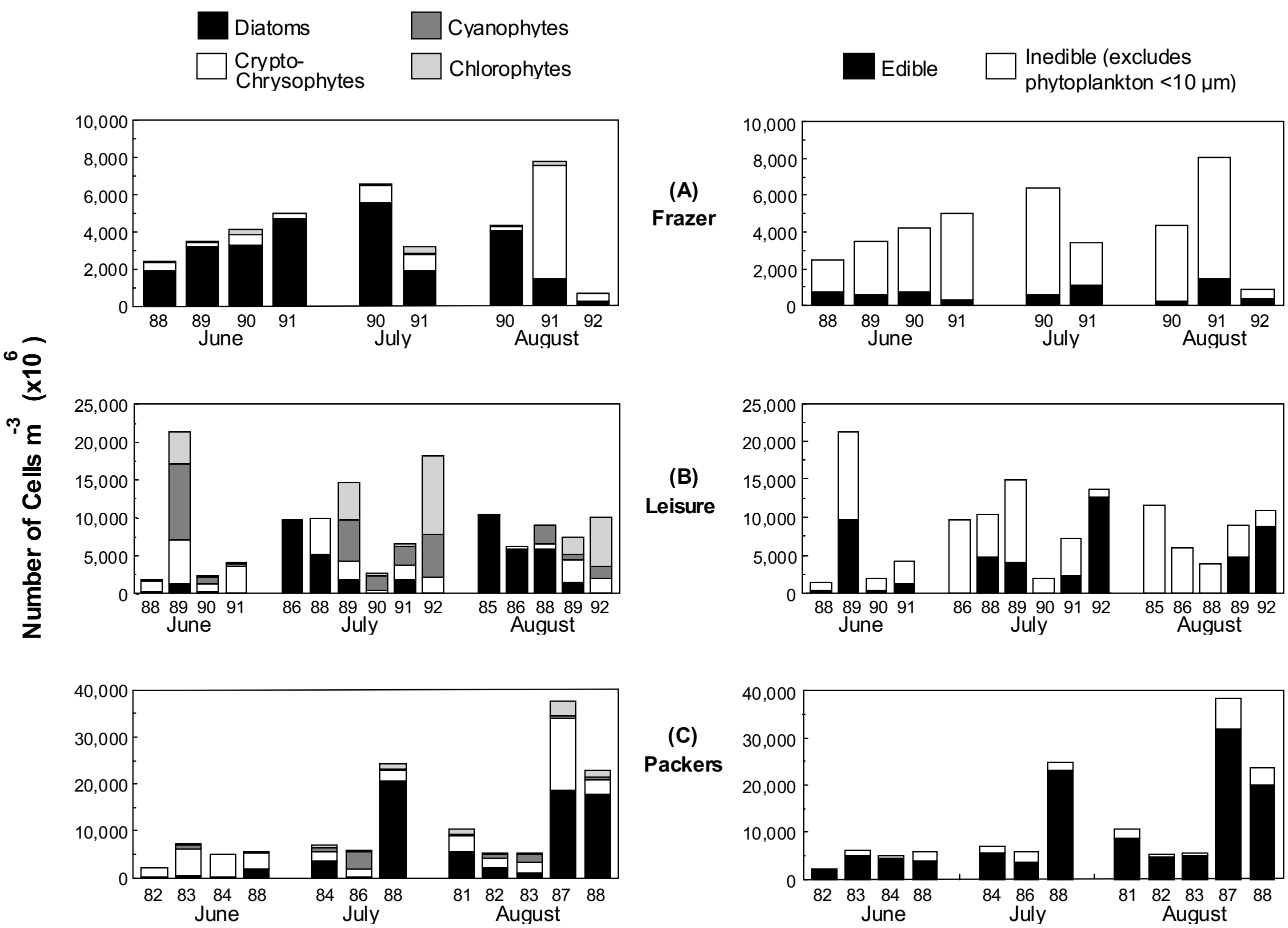

Figure 3. Mean phytoplankton density for 2 epilimnetic (1 m) sample stations by taxa and edible versus inedible forms and by month (June, July, and August) for Frazer Lake (A), Leisure Lake (B), and Packers Lake (C).

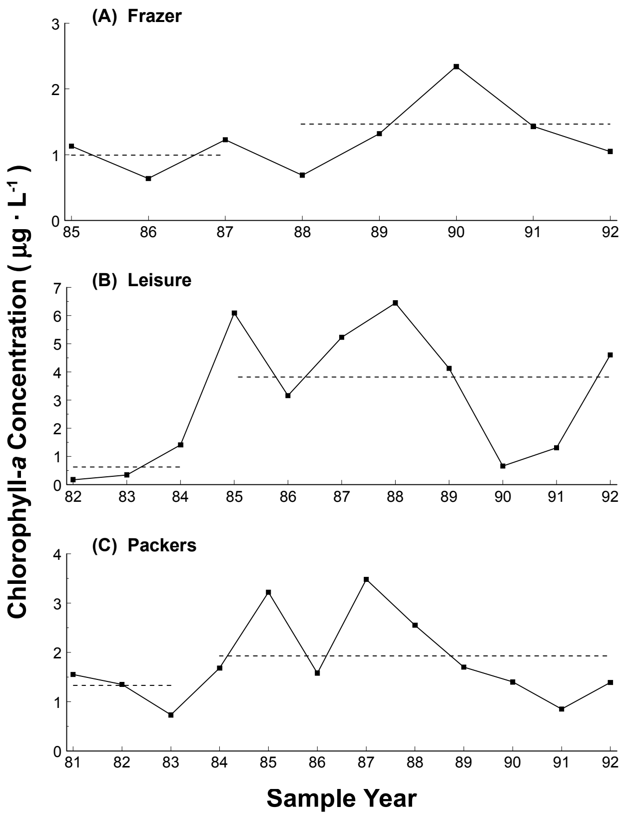

Figure 4. Mean concentrations of chlorophyll-*a* for 2 epilimnetic (1 m) stations sampled during June–August in Frazer Lake (A), Leisure Lake (B), and Packers Lake (C). The left-hand broken, horizontal line is the mean for 3 years preceding nutrient treatment and the right is for the treated years.

same after nutrient treatment began in 1984 (Figure 5C); the only exception was the virtual absence of *Cyclops* in 1992.

Comparison of zooplankton biomass before and during nutrient treatment indicates that there was a significant increase ($p < 0.05$; *t*-test) in the May–September mean for all 3 lakes (Figure 6). In Frazer Lake the mean zooplankton biomass increased from 150 $mg \cdot m^{-2}$ for 3 years (1985–1987) before treatment (average 1984–1986 escapement = 222,000) to just under 300 $mg \cdot m^{-2}$ for the 5 years (1988–1992) of treatment (average 1987–1991 escapement = 216,000; Figure 6A). (Note: Escapements were lagged by 1 year because the resulting effects of their progeny on zooplankton did not begin until the following year.)

In Leisure Lake the zooplankton biomass for the 3 years preceding treatment averaged 70 $mg \cdot m^{-2}$ and during treatment increased nearly 9 times to average just over 600 $mg \cdot m^{-2}$ (Figure 6B). This increase occurred despite a mean of 10% more fry stocked in the lake during the treated years. In Packers Lake the zooplankton biomass averaged about 500 $mg \cdot m^{-2}$ during the 3 years before treatment and reached an average of 700 $mg \cdot m^{-2}$ during the 9 years of treatment (Figure 6C). This 40% increase in mean zooplankton biomass occurred despite the initiation of lake stocking in 1988, which added about 2.5–3.3 million sockeye salmon fry per year (Figure 6C) plus additional fry from an average of 10,000 more natural spawners per year.

Smolt Production

Smolt abundance for Frazer Lake was not determined. However, an increase in escapements decreased the standing stock of zooplankton and smolt size due to increasing grazing pressure in this lake (Kyle et al. 1988). Therefore, an increase in smolt size after nutrient treatment, when the average escapement was nearly identical to the 3 years before treatment, would indicate a direct benefit from the treatment project. Age-1 smolts for the 5 years before nutrient treatment averaged 77.8 mm (range of 70–84 mm) and 3.6 g (range of 2.5–5.0 g; Figure 7A). After treatment age-1 smolts averaged 85.7 mm (range of 80–90 mm) and 5.1 g (range of 4.0–5.5 g), which represents a 10% increase in length and a 35% increase in weight compared to pretreatment size.

Smolt abundance (ages 1 and 2) in Leisure Lake during nutrient treatment increased 2.4 fold, whereas smolt biomass increased 3.5 fold compared to pretreatment levels (Figure 7B). During treatment an average of 10% more fry were stocked. However, the 3.5-fold increase in mean smolt biomass primarily resulted from the improved rearing conditions: specifically, a 9-fold increase in mean zooplankton biomass. The mean age-1 smolt composition increased by 38% (from 61% to 84%) during nutrient treatment of this lake. In addition, the average age-1 smolt size increased from 61 mm and 1.7 g during pretreatment to 78 mm and 3.6 g during treatment.

An extraordinarily high number of smolts in 1982 caused the mean pretreatment (1982–1984) smolt population in Packers Lake to be slightly higher than the mean smolt population during the years of nutrient treatment without fry stocking (1985–1988; Figure 7C). However, the mean smolt biomass during treatment without fry stocking increased 63% compared to the mean before treatment. After fry were stocked in Packers Lake, the mean smolt population increased about 3 fold compared to pretreatment and treatment without stocking. During treatment with

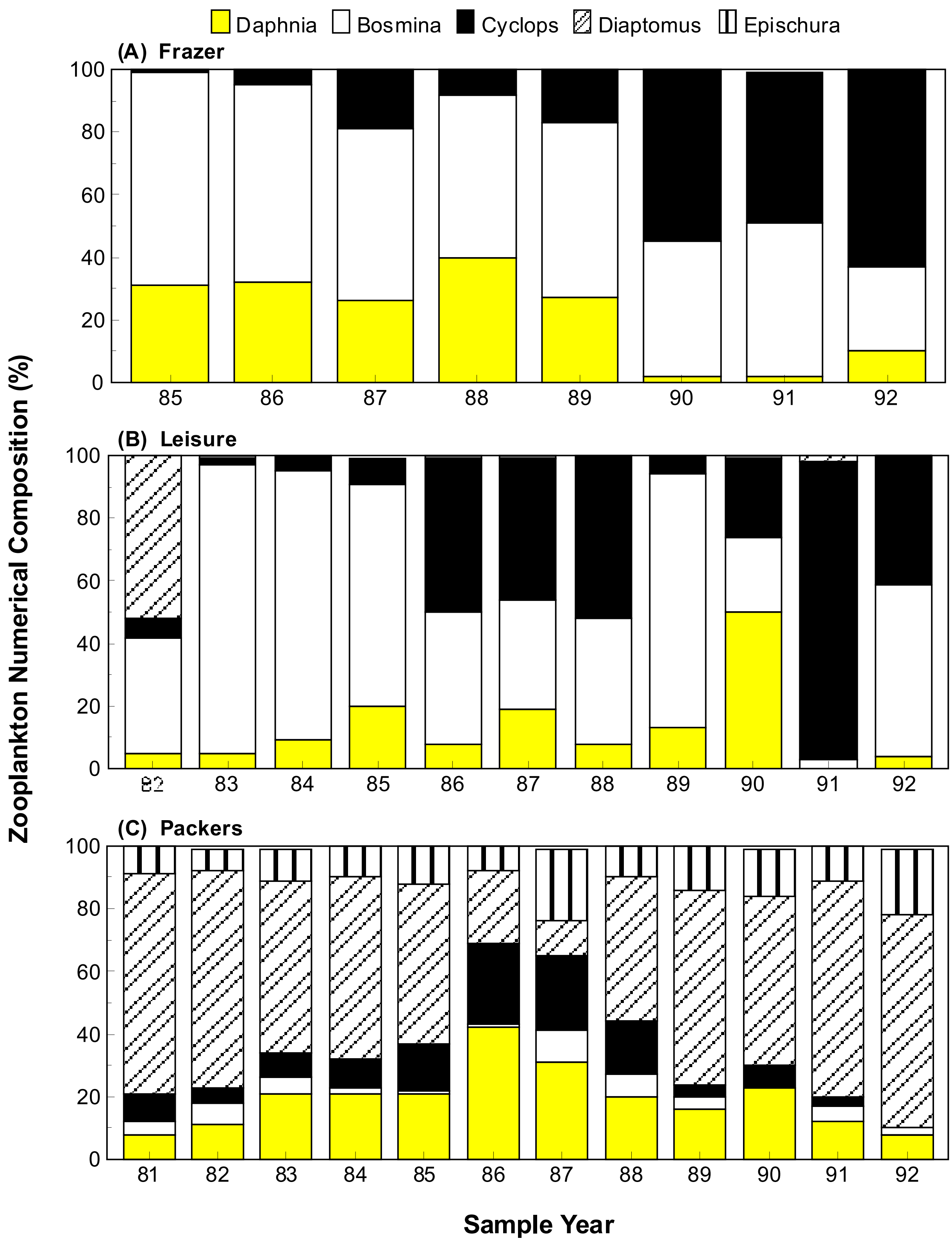

Figure 5. Mean zooplankton taxa composition for 2 stations sampled during May–September in Frazer Lake (A), Leisure Lake (B), and Packers Lake (C). The first 3 years of each lake were untreated and the remaining years were treated with nutrients.

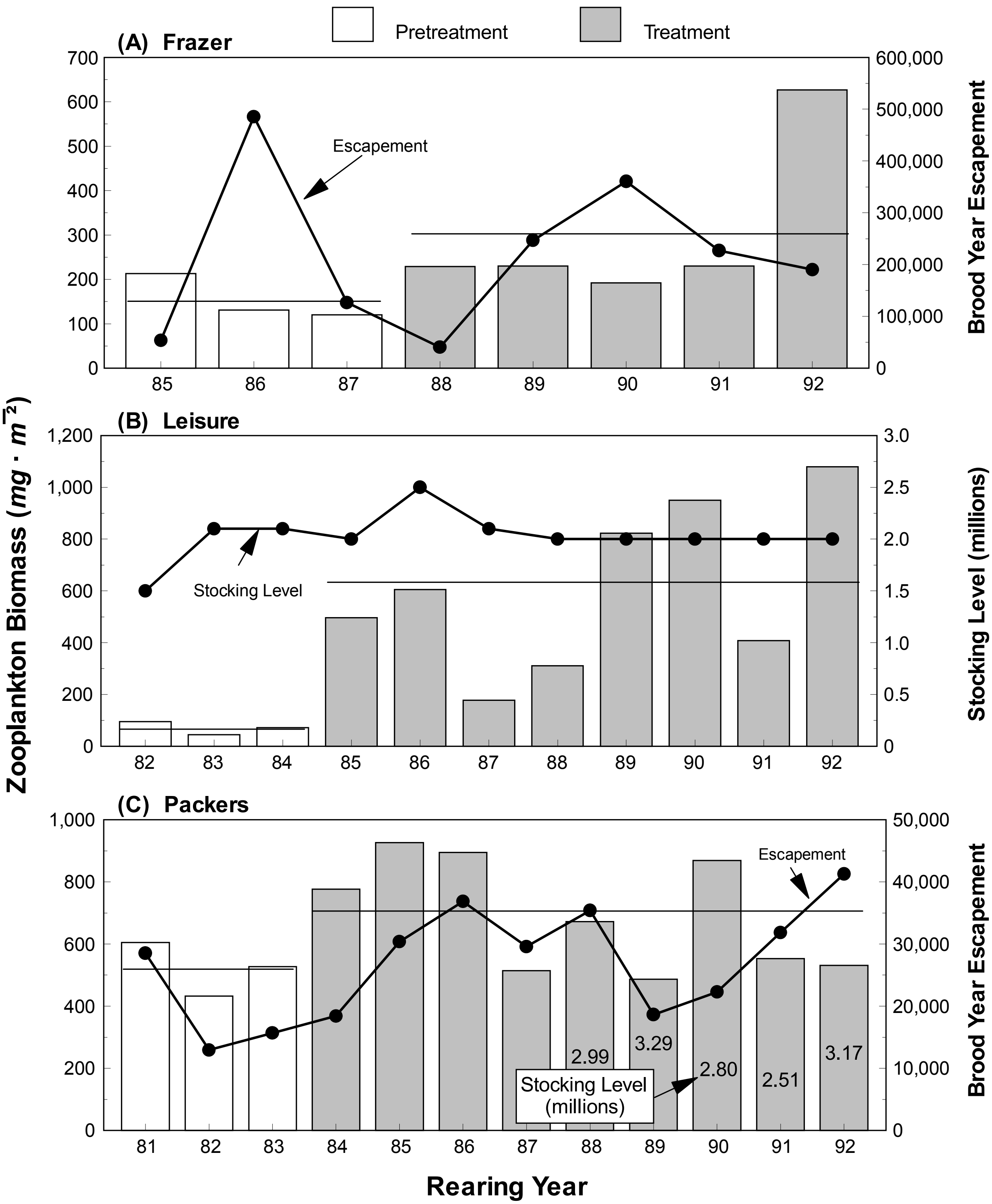

Figure 6. Mean zooplankton biomass for 2 stations sampled during May–September, associated escapements from the preceding year, and fry stocking levels in Frazer Lake (A), Leisure Lake (B), and Packers Lake (C). The horizontal lines indicate mean zooplankton biomass during the 3 years preceding nutrient treatment and during nutrient treatment (the remaining years).

stocking the mean smolt biomass decreased about 20% compared to treatment without stocking but was 35% higher than during pretreatment. The age-1 smolt composition averaged 8% during pretreatment, 42% during treatment without stocking, and 51% during treatment with stocking. The average age-1 smolt size increased from 83 mm and 5.2 g during pretreatment to 101 mm and 10.4 g during treatment without stocking; it decreased to 75 mm and 3.4 g during treatment with stocking.

Adult Production

Adult return data for juveniles that reared in Frazer Lake when nutrient treatment was conducted are still incomplete. However, for brood year (BY) 1986, in which the age-2 smolts reared under 1 year of nutrient treatment, the age-2.2 returns set a single age class record high of 972,000 (Table 3). Although the 1986 BY return was extraordinarily high for all age classes, nutrient treatment may have contributed to the record return of age-2.2 fish. For BY 1987, the return of age-1.2 and age-1.3 fish was dramatically lower than the average in recent years but unusually high relative to the low parent-year escapement of 40,500 fish. The high return of these latter age classes may also be related to the nutrient treatment project. For BY 1988, fish that spent 1 year in fresh water (ages 1.2 and 1.3) and reared in the lake during treatment were similar in abundance to returns before pretreatment.

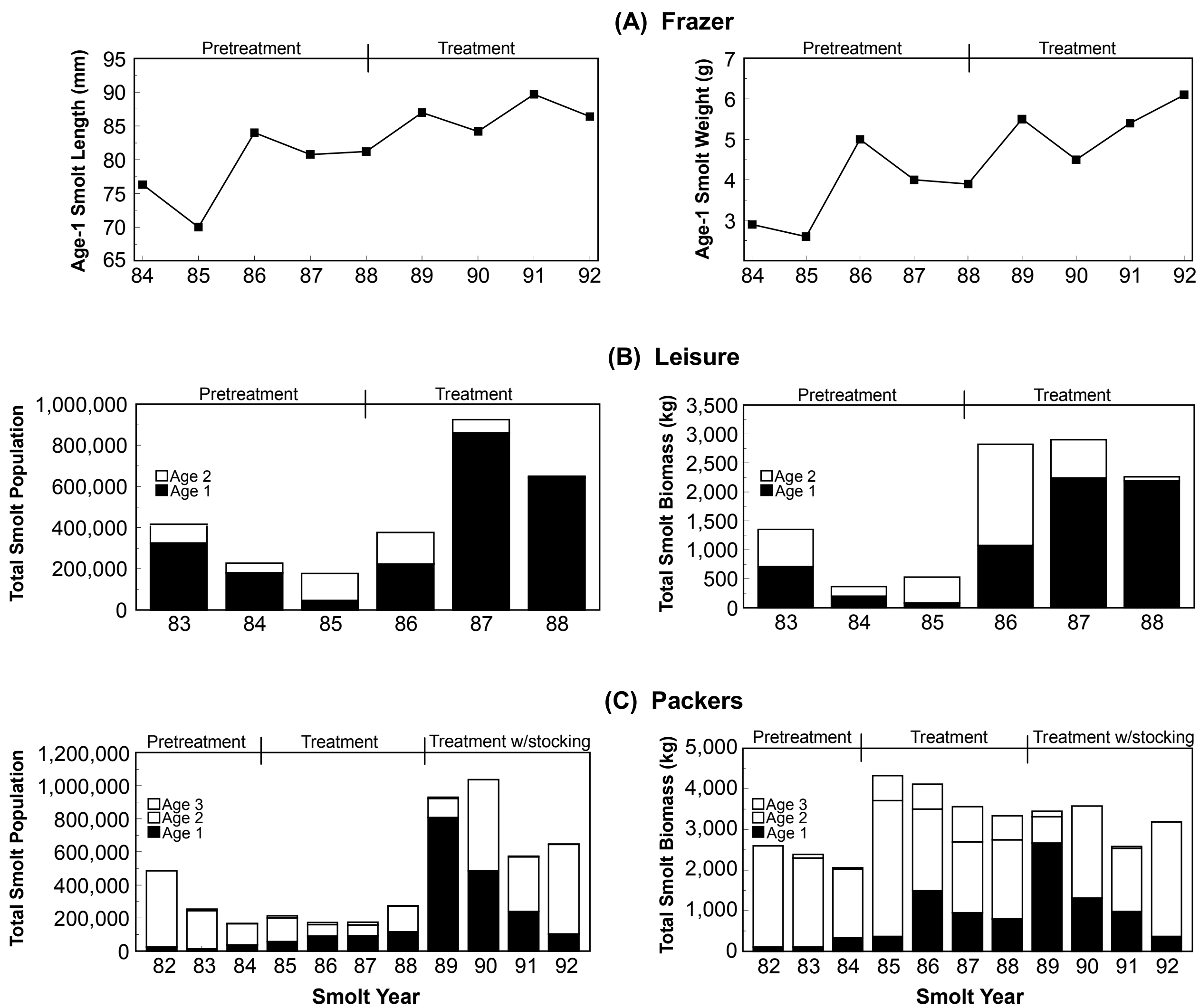

Figure 7. Comparison of smolt production during the 3 years preceding treatment and during treatment of Frazer Lake (A), Leisure Lake (B), and Packers Lake (C).

Table 3. Brood year production of adult sockeye salmon returning to Frazer Lake by major age classes. The outlined numbers indicate adults that reared in the lake as fry when it was treated with nutrients.

Brood year		Escapement	Return (no. by age) Age 1.2	Age 1.3	Age 2.2	Age 2.3
1962		3,090				
1963		11,857				4,009
1964		9,966		0	16,173	279
1965		9,074	0	475	12,518	2,571
1966		16,456	11,820	7,580	16,149	2,629
1967		21,834	38,626	38,395	11,553	5,114
1968		16,738	15,565	15,228	14,998	10,757
1969		14,041	14,654	9,306	30,137	6,007
1970		24,039	17,672	1,687	51,299	9,351
1971		55,366	1,417	769	92,226	20,151
1972		66,419	10,888	8,032	91,876	71,167
1973		56,255	2,677	4,825	31,706	15,969
1974		82,609	53,591	28,713	75,084	30,407
1975		64,199	22,571	20,732	173,687	72,701
1976		119,321	223,444	73,677	257,625	143,383
1977		139,548	73,189	92,211	107,917	146,064
1978		141,981	162,130	24,148	22,970	16,844
1979		126,742	1,374	2,965	24,323	26,791
1980		405,535	6,064	7,654	589,393	141,065
1981		377,716	12,120	2,455	7,748	5,239
1982		430,423	23,647	28,624	3,735	10,870
1983		158,340	8,935	13,438	380,531	586,833
1984		53,524	5,771	7,437	386,832	67,142
1985		485,835	16,502	49,290	53,978	22,578
	Mean	**136,476**	**34,412**	**20,840**	**116,014**	**67,316**
1986		126,529	727,658	230,893	972,290	168,815
1987		40,544	3,019	3,902	187,581	159,822
1988		246,704	21,073	30,096	210,586	
1989		360,373	327,929			
1990		226,707				
1991		190,358				
1992		185,825				
1993		198,412				

However, the age-2.2 return was much higher for BY 1988 (210,600) than it was before treatment (mean = 116,000). In contrast, the 328,000 age-1.2 fish produced from BY 1989 when the lake was treated represented the second highest number of age-1.2 fish since the early 1960s, when monitoring began.

The total number of sockeye salmon returning to Leisure Lake increased almost 2.5 times after the lake was treated with nutrients (Table 4). During pretreatment the run averaged 32,400 sockeye salmon compared to 79,100 during treatment. In addition, the smolt-to-adult survival increased by 25% (from 11.4% to 14.2%).

For Packers Lake the number of adults (based on escapements) increased modestly from 29,600 during pretreatment to 31,400 during treatment without stocking to 49,500 during treatment with fry stocking (for the 2 years with complete age class returns). However, because of the high production of smolts in 1982, the average number of smolts produced during nutrient treatment without stocking was about 40% less compared to pretreatment, but the smolt-to-adult return rate to the lake increased by more than half (from 9.5% to 15.1%; Table 4).

DISCUSSION

Whether nutrient treatment can simultaneously maintain higher levels of zooplankton and juvenile sockeye salmon can be examined by considering the individual results for each lake. In Frazer Lake,

Table 4. Number and survival rate of adult sockeye salmon returning to Leisure and Packers Lakes before and during nutrient treatment.

Lake	Smolt year	Number of smolts	Number of adults[a]	Survival or return rate[a] (%)
Leisure		Pretreatment		
	1983	416,900	57,500	13.8
	1984	227,000	15,400	6.8
	1985	178,100	24,400	13.7
	Mean	**274,000**	**32,400**	**11.4**
		Treatment		
	1986	375,900	91,900	24.4
	1987	925,000	91,800	9.9
	1988	657,100	53,600	8.2
	Mean	**652,700**	**79,100**	**14.2**
Packers		Pretreatment		
	1981	267,900	22,000	8.2
	1982	486,400	31,900	6.6
	1983	254,450	35,000	13.8
	Mean	**336,250**	**29,600**	**9.5**
		Treatment Without Stocking		
	1984	168,050	27,200	16.2
	1985	215,600	23,600	10.9
	1986	173,900	20,400	11.7
	1987	178,600	27,800	15.6
	1988	275,500	58,200	21.1
	Mean	**202,300**	**31,400**	**15.1**

[a] Includes total return (sport and commercial catches) for Leisure Lake. For Packers Lake, only escapement data are available (*see* Methods); thus, adult numbers and return rate represent only fish that returned to the lake.

escapements (1984–1986) before treatment averaged about 222,000 and ranged from about 25% to almost 250% of the escapement goal of 200,000. During the pretreatment period, zooplankton biomass was 205 mg·m^{-2} in 1985 when fry were produced from a relatively low 1984 escapement, decreased to 130 mg·m^{-2} in 1986 when fry were produced from a record high 1985 escapement, and remained depressed at 120 mg·m^{-2} in 1987 when fry were produced from the smaller 1986 escapement (Figure 6A). During the 5 treatment years (1988–1992) escapements (1987–1991) averaged 216,000 and ranged from 20% to 180% of the escapement goal. However, unlike the period before nutrient treatment, zooplankton biomass remained quite stable and nearly tripled during the last year of treatment (1992). In addition to the dramatic difference in zooplankton biomass between the 2 periods, the record 1985 escapement (well above the escapement goal) and attendant 1986 rearing had a carry-over effect that reduced zooplankton biomass in 1987 (pretreatment). In contrast, during the treated years, the large number of rearing fry in 1990 from the large 1989 escapement produced the lowest zooplankton biomass, reflecting the density-dependent rearing dynamics of Frazer Lake (Kyle et al. 1988). However, the decline compared to other treated years was relatively insignificant. Thus, in Frazer Lake, top-down or density-dependent effects appear to be reversible by bottom-up control of trophic dynamics through nutrient treatment.

Before treatment, Leisure Lake was annually stocked with an average of 1.9 million sockeye salmon fry from 1982 through 1984; from 1985 through 1992, when the lake was treated with nutrients to increase zooplankton production, an average of 2.1 million fry were stocked. After the first year of nutrient treatment (1985), zooplankton biomass increased by nearly 700% to 414 mg·m^{-2}, and in 1992 exceeded 1,000 mg·m^{-2} (Figure 6B). Thus, it is apparent that nutrient treatment provided conditions that allowed the zooplankton community to thrive at a higher level, despite a slightly higher (10%) average stocking level. During treatment the total smolt biomass (ages 1 and 2) from 1986 through 1988 increased 3.5 times compared to 1983–1985 pretreatment levels (Figure 7B). In contrast to the density-dependent responses in Frazer Lake, it is evident from the results of adding nutrients to Leisure Lake that when the forage-to-fry ratio is high, there is little carry-over effect on the zooplankton community that negatively affects growth and survival for subsequent rearing fry.

The effect of nutrient treatment in Packers Lake (without fry stocking) was similar to Frazer and Leisure Lakes in that smolt size increased, but unlike Leisure Lake smolt numbers did not (Figure 7C). Larger smolts are consistent with increased lake productivity. In Packers Lake a 63% increase in smolt biomass followed nutrient treatment without fry stocking, and the larger smolts apparently had a positive effect on survival, which increased from 9.5% to 15.1% in rate of return (based on escapements; Table 4).

During subsequent nutrient treatment with fry stocking, a 20% reduction in smolt biomass affirmed a density-dependent response. However, during all treated years, both with and without stocking, the 40% average increase in zooplankton biomass and 50% average increase in smolt biomass compared to pretreatment demonstrates that nutrient treatment can sustain a more robust rearing environment and produce a greater biomass of smolts.

Nutrient additions increased nutrient concentrations in all of the lakes and resulted in higher algal biomass (Figure 4). Although changes in nutrient supply often bring predictable changes to a lake's phytoplankton community, numerous other variables, such as solar radiance and penetration, temperature, zooplankton species composition and size structure, and changes in juvenile sockeye density, make it difficult to correlate phytoplankton changes on the basis of nutrients alone. These factors should be considered when interpreting results of phytoplankton sampling in the 3 lakes.

For example, in Frazer Lake there was a predominance of inedible phytoplankton that could be due to overgrazing by zooplankton. However, grazing by zooplankton, which is affected by planktivore density, seldom controls phytoplankton independently because, under equilibrium conditions, the size of the predator population is a function of prey biomass (Reynolds 1984). Likewise, the sporadic presence of inedible cyanophytes in Leisure Lake could have occurred because of unusually warm weather and a lack of vertical mixing rather than because of improper nutrient ratios. In Packers Lake, the relatively high density of phytoplankton and the preponderance of edible forms suggest low zooplankton grazing. Yet, zooplankton biomass in this lake increased by 40% during the treated years, and the N-to-P ratio increased beyond the optimal ratio for algal growth in recent years. Thus, to elucidate the pathways and efficiency of energy transfer among nutrients, phytoplankton, and macrozooplankton, further investigation is required.

Stockner (1987) found that at low phosphorus loading rates of 3–5 $mg{\cdot}m^{-2}{\cdot}week^{-1}$ for 18–20 weeks in Canada's Pacific-coast lakes, zooplankton biomass did not approach levels found in untreated interior Canadian lakes. He attributed this difference to the extreme oligotrophic nature of coastal lakes. For example, he found that in 15 fertilized coastal lakes, zooplankton biomass averaged 27 $mg{\cdot}m^{-3}$ in the northern lakes and 10 $mg{\cdot}m^{-3}$ in the southern lakes, compared to an average of 61 $mg{\cdot}m^{-3}$ in interior Babine Lake.

The higher fertilization rate (phosphorus loading rates 2–5 times greater) of the 3 Alaskan coastal lakes did not appear to result in an overwhelmingly higher zooplankton biomass compared to the coastal Canadian lakes; i.e., zooplankton biomass averaged 10 $mg{\cdot}m^{-3}$ in Frazer Lake, 12 $mg{\cdot}m^{-3}$ in Leisure Lake, and 46 $mg{\cdot}m^{-3}$ in Packers Lake during the treated years. Thus, if the higher rate of phosphorus additions in Alaska allowed a greater algal biomass for zooplankton, the standing stock of zooplankton (biomass) was a poor indicator of the benefit from a higher phosphorus loading rate, probably because of the confounding effect of variations in the fish densities among the Alaskan and Canadian lakes. Production of smolts (indication of fry rearing density) from treated Canadian coastal lakes averaged 2,075 $fish{\cdot}hectare^{-1}$ (Hyatt and Stockner 1985), whereas in Leisure Lake smolt production during treated years averaged 2,400 and in Packers Lake 5,900 $fish{\cdot}hectare^{-1}$ (no smolt abundance is available for Frazer Lake). Thus, the use of zooplankton by high densities of planktivorous sockeye salmon fry in these lakes appears to have masked the increased production of zooplankton from higher phosphorus additions. A similar occurrence was suggested for the lack of increase in zooplankton density in fertilized Bear Lake in Alaska (Kyle 1994) and Lake Hecklan in Sweden (Olsson et al. 1992).

Finally, it is evident from the trophic level responses in these 3 lakes that nutrient treatment can sustain both zooplankton and smolt production at higher levels. In addition, the phosphorus loading rate in the 3 lakes benefited (i.e., number and/or size of smolts) rearing fry without jeopardizing the oligotrophic status of the lakes (i.e., sustained phosphorus concentrations below the upper level used to categorize oligotrophic lakes). However, trophic and sockeye smolt production responses to nutrient treatment did vary among the lakes, so extrapolation of these results to predict responses in other lakes is inappropriate. I concur with Stockner (1987) that no single lake process is responsible for the success of a nutrient treatment project, and that responses appear to be site-specific. The efficacy of nutrient treatment depends upon a number of biological and physical factors, such as food-web processes at all trophic levels, plankton and fish community structure, environmental factors, and lake morphometry.

LITERATURE CITED

Bechtol, W. R., and N. C. Dudiak. 1988. The development of the Leisure Lake sockeye salmon *Oncorhynchus nerka*: smolt and adult production summary, 1977–1984. Alaska Department of Fish and Game, FRED Division Report 83, Juneau.

Blackett, R. F. 1987. Development and performance of an Alaskan steeppass fishway for sockeye salmon *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 44:66–76.

Brooks, J. L. 1957. The systematics of North American *Daphnia*. Memoirs of the Connecticut Academy of Arts, New Haven.

Carlson, R. E. 1977. A trophic state index for lakes. Limnology and Oceanography 22:361–369.

Edmundson, J. M., G. B. Kyle, G. S. Carpenter, and T. M. Willette. 1993. Juvenile sockeye salmon *Oncorhynchus nerka* stocking into Pass and Esther Passage Lakes, and nutrient enrichment of Pass Lake: an experiment on changes of the forage base. Alaska Department of Fish and Game, FRED Division Report 125, Juneau.

Haney, J. F., and D. J. Hall. 1973. Sugar coated *Daphnia*: a preservation technique for Cladocera. Limnology and Oceanography 18:331–333.

Hyatt, K. D., and J. G. Stockner. 1985. Responses of sockeye salmon *Oncorhynchus nerka* to fertilization of British Columbia coastal lakes. Canadian Journal of Fisheries and Aquatic Sciences 42:320–331.

Koenings, J. P., and R. D. Burkett. 1987. The production patterns of sockeye salmon *Oncorhynchus nerka* smolts relative to temperature regimes, euphotic volume, fry density, and forage base within Alaskan lakes. Pages 216 to 234 *in* H. D. Smith, L. Margolis, and C. C. Woods, editors. Sockeye salmon *Oncorhynchus nerka* population biology and future management. Canadian Special Publication of Fisheries and Aquatic Sciences 96, Ottawa.

Koenings, J. P., and J. A. Edmundson. 1991. Secchi disk and photometer estimates of light regimes in Alaskan lakes: effects of yellow color and turbidity. Limnology and Oceanography 36(1):91–105.

Koenings, J. P., and G. B. Kyle. *In press*. Collapsed populations and delayed recovery of zooplankton due to intense foraging by juvenile sockeye salmon *Oncorhynchus nerka* foraging. *In* Proceedings of the international symposium on biological interactions of enhanced and wild salmonids. Special Publication of the Canadian Journal of Fisheries and Aquatic Sciences.

Koenings, J. P., R. D. Burkett, and J. M. Edmundson. 1990. The exclusion of limnetic cladocera from turbid glacier-meltwater lakes. Ecology 71(1):57–67.

Koenings, J. P., J. A. Edmundson, G. B. Kyle, and J. M. Edmundson. 1987. Limnology field and laboratory manual: methods for assessing aquatic production. Alaska Department of Fish and Game, FRED Division Report 71, Juneau.

Kyle, G. B. 1994. Assessment of trophic-level responses and coho salmon *Oncorhynchus kisutch* production following nutrient treatment (1981–1986) of Bear Lake, Alaska. Fisheries Research 20(2):243–261.

Kyle, G. B., J. P. Koenings, and B. M. Barrett. 1988. Density-dependent, trophic level responses to an introduced run of sockeye salmon *Oncorhynchus nerka* at Frazer Lake, Kodiak Island, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 45:856–867.

Kyle, G. B., J. P. Koenings, and J. A. Edmundson. *In press.* An overview of Alaska lake-rearing salmon enhancement strategy: nutrient enrichment and juvenile stocking. *In* A. Milner and M. Oswood, editors. Alaska freshwaters. Springer-Verlag, New York.

Lambou, V. W., S. C. Hern, W. D. Taylor, and L. R. Williams. 1982. Chlorophyll, phosphorus, secchi disk, and trophic state. Water Resource Bulletin 18:807–813.

LeBrasseur, R. J., C. D. McAllister, W. E. Barraclough, V. O. Kennedy, J. Manzer, D. Robinson, and K. Stephens. 1978. Enhancement of sockeye salmon *Oncorhynchus nerka* by lake fertilization in Great Central Lake: summary report. Journal of Fisheries Research Board of Canada 35:1580–1596.

Marcusen, P. 1988. Packers Lake annual progress report. Cook Inlet Aquaculture Association (unpublished report), Soldotna, Alaska.

Olsson, H., P. Blomqvist, and H. Olofsson. 1992. Phytoplankton and zooplankton community structure after nutrient additions to the oligotrophic Lake Hecklan, Sweden. Hydrobiology 243/244:147–155.

Pennak, R. W. 1978. Fresh-water invertebrates of the United States, 2nd edition. John Wiley and Sons, New York.

Reimann, B. 1978. Carotenoid interference in the spectrophotometric determination of chlorophyll degradation products from natural populations of phytoplankton. Limnology and Oceanography 23:1059–1066.

Reynolds, C. S. 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge, Massachusetts.

Rhee, G. Y. 1978. Effect of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. Limnology and Oceanography 23(1):10–25.

Schindler, D. E. 1992. Nutrient regeneration of sockeye salmon *Oncorhynchus nerka* fry and subsequent effects on zooplankton and phytoplankton. Canadian Journal of Fisheries and Aquatic Sciences 49:2498–2506.

Schindler, D. W. 1978. Factors regulating phytoplankton production and standing crops in the world's freshwaters. Limnology and Oceanography 24:478–486.

Smith, V. H. 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: an empirical and theoretical analysis. Limnology and Oceanography 27(6):1101–1112.

Smith, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 221(4611):669–671.

Stockner, J. G. 1987. Lake fertilization: the enrichment cycle and lake sockeye salmon *Oncorhynchus nerka* production. Pages 198 to 215 *in* H. D. Smith, L. Margolis, and C. C. Woods, editors. Sockeye salmon *Oncorhynchus nerka* population biology and future management. Canadian Special Publication of Fisheries and Aquatic Sciences 96, Ottawa.

Stockner, J. G., and K. S. Shortreed. 1985. Whole-lake fertilization experiments in coastal British Columbia lakes: empirical relationships between nutrient inputs and phytoplankton biomass and production. Canadian Journal of Fisheries and Aquatic Sciences 42:649–658.

Strickland, J. D. H., and T. R. Parsons. 1972. A practical handbook of seawater analyses. Journal of Fisheries Research Board of Canada 167, Ottawa.

Vollenweider, R. A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Memorie dell'Institute Italiano di Idrobiologia 33:53–83.

Wilson, M. S. 1959. Calanoida. Pages 738 to 794 *in* W. T. Edmondson, editor. Fresh-water biology, 2nd edition. John Wiley and Sons, New York.

Woods, P. F. 1986. Deep-lying chlorophyll maxima at Big Lake: implications for trophic state classification of Alaskan lakes. Pages 195 to 200 *in* D. L. Kane, editor. Proceedings: cold regions hydrology symposium. American Water Resources Association, Bethesda, Maryland.

Yeatman, H. C. 1959. Cyclopoida. Pages 795 to 815 *in* W. T. Edmondson, editor. Fresh-water biology, 2nd edition. John Wiley and Sons, New York.