

AN ABSTRACT OF THE THESIS OF

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Title: Responses to Fertilization and Fish Stocking in the
Pelagic Ecosystem of a Naturally Fishless Lake.

Abstract Approved :

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Gary L. Larson

Ecologists have studied the responses of pelagic ecosystems to varying levels of nutrient loading and fish predation on many different scales ranging from small experimental enclosures to whole lake systems. There are recurring patterns of response to these two variables, which are generally predictable on the basis of biogeographic, behavioral, morphological, and physio-environmental ecological principles applied to the life histories strategies of individual species. This study focused on the changes in pelagic trophic structure in response to varying levels of productivity (regulated by nutrient loading rates) and fish densities (determined by stocking densities). Zooplankton life history traits used to explain the community responses to these two variables included: body size at sexual maturity, generation time, reproductive potential, temperature dependant growth rates, morphological adaptations to vertebrate and invertebrate predation, and modes of food acquisition. A small naturally fishless lake in southeastern Alaska was the observational unit of this study conducted over a seven year period from 1980

through 1986. The objectives of this study were to 1) test whether additions of inorganic fertilizer to the lake would increase its capacity to produce coho (*Oncorhynchus kisutch*) smolts, and 2) describe the structural and functional changes in the pelagic ecosystem in response to varying rates of nutrient loading and zooplanktivore densities. The study design consisted of no treatments during four of the study years, and one year of each of the following treatments: 1) fertilization only, 2) no fertilization and low stocking densities (2,000 fry/ha), and 3) fertilization and high stocking densities (4,000 fry/ha). During nonfertilized years, rainfall was the driving force behind nutrient loading rates. Nutrient loading rates (exclusive of fertilizer additions) displayed a two to three fold magnitude in annual variation over the seven year study period. Changes in nutrient loading during nonfertilized years appeared to regulate pelagic productivity, but in a complex and counter intuitive manner. In contrast to the widely documented positive correlation between chlorophyll concentrations and nutrient loading rates, grazing pressure by zooplankton appeared to be the factor regulating standing crops of phytoplankton. During nonfertilized years, mean summer total chlorophyll was inversely correlated to total zooplankton biomass, and displayed a 2.5 fold magnitude in annual variation. *Diaptomus kenia* biomass (the primary component of total zooplankton biomass) was low in 1980 following a year with a low amount of summer rainfall (1979), then increased after each year (1980 and 1981) with relatively high amounts of summer rainfall. The positive response of *D. kenia* to conditions stimulated by high summer rainfall (and high nutrient loading rates) was delayed by their long generation time (one reproductive period per year). *D. kenia* and total zooplankton biomass peaked in 1982, the year that the least amount of summer rainfall was observed. In contrast to the intuitive perception that nutrient poor conditions are less productive, the highest zooplankton production occurred when

nutrient loading rates and phytoplankton concentrations were at their lowest levels. Accelerated nutrient regeneration rates and phytoplankton turnover times were the most probable factors which allowed the high zooplankton production to be maintained under these nutrient poor conditions. Fertilizer treatments increased the mean summer total chlorophyll concentrations four to six fold over the maximum observation (1.03 $\mu\text{g/l}$) for nonfertilized years. At high nutrient loading rates, the relationship between total chlorophyll and zooplankton biomass switched to a positive correlation. Rapid egg production and short maturation times allowed the cladocerans to most efficiently exploit the food resources stimulated by fertilization. *B. longirostris* dominated zooplankton biomass during the fertilized stocking period, but was only preyed upon by a small percentage of the fish when larger zooplankters (*Holopedium gibberum* and *Epischura nevadensis*) were abundant. Fertilization treatments increased the the coho smolt producing capacity of the lake by about 60 %.

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in the Pelagic Ecosystem of a
Naturally Fishless Lake

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RESPONSES TO FERTILIZATION AND FISH STOCKING IN THE PELAGIC ECOSYSTEM OF A NATURALLY FISHLESS LAKE

INTRODUCTION

Aquatic ecologists have devoted considerable effort to conducting observational and experimental studies to gain an understanding of the mechanisms and conditions which structure pelagic ecosystems. The use of small lakes and ponds as observational units in community level studies have the advantages that the pelagic ecosystems are relatively well defined, biotic migrations are usually insignificant, and the zooplankton and fish communities are typically composed of only a few species. However, even lakes and ponds in close proximity can differ quantitatively and qualitatively, posing both practical and theoretical problems to finding suitable "replicates" for experimental studies of whole lake systems (Hurlbert 1984).

Observational and experimental approaches have merit, depending on the scale and objectives of a study. On a small scale, enclosure experiments are relatively simple to conduct, but do not truly duplicate the dynamics of an open system. The intermediate scale of "replicate" ponds offer a compromise between the logistics of data collection and the heuristic value of the results. In addition, aquacultural pond studies provide an opportunity to manipulate fish stocking rates and, obtain an accurate measure of fish yield. Individual lakes are representative of whole-lake environments, but several years of baseline observation are usually required to identify and describe the relative influences of several key factors regulating an ecosystem. Finally, the most extensive approach calls for pooling data from many lakes sampled over a wide geographic area. This approach comes closest to meeting the objective of

identifying and quantifying generalized models, that have predictive value in a large number of lakes.

One of the most widely documented regulatory mechanisms is the affect of predation by vertebrate zooplanktivores on the size structure of zooplankton communities. Size selective feeding by zooplanktivores (Kerfoot 1980; Zaret 1980) shifts the zooplankton community structure towards smaller individuals and species in small enclosures (Lynch and Shapiro 1981; McQueen et al. 1986; Vanni 1986; 1987a, 1987b), "replicate" ponds (Hall et al. 1970; O'Brien and DeNoyelles 1974; Davidson and Boyd 1981), and individual lakes (Hutchinson 1971). Additional indirect effects on the size structure of phytoplankton communities (Sprules and Knoechel 1984; Shapiro 1980), algal productivity (Henrikson et al. 1980), and nutrient recycling rates (Lehman 1980) have been associated with the presence or absence of planktivores.

Based on food web interactions, the capacity for primary production in an ecosystem will eventually establish a limit on the population sizes of top level predators (Lindeman 1942). On a time scale of thousands of years, the capacity of most lakes for primary production follows an upward trend as the lake accumulates nutrients essential for algal growth and intralake nutrient cycling gains in importance as a regulating mechanisms (Henderson-Sellers and Markland 1987). On this long time scale, the trajectory for the carrying capacity of top predators will parallel the upward trend in algal production, within the constraints of environmental changes that occur as the lake shallows with age.

Thus, factors controlling the annual production of the basal components of a pelagic food web are important mechanisms to establishing limits on productivity of higher trophic levels. Based on an extensive data set collected from eighteen countries globally, Vollenweider (1976) derived a general mathematical model describing the effects of depth, water residence time, and

total phosphorus loading on mean concentrations of chlorophyll. Although tropical and temperate lakes possessed separate patterns of response, lake productivity was correlated to these factors within common geographic regions.

Whole-lake fertilization projects in British Columbia and Alaska (Nelson and Edmondson 1955; Schindler and Fee 1974; Le Brasseur et al. 1978; Kyle and Koenings 1983; Hyatt and Stockner 1985), have been almost exclusively conducted in sockeye salmon (*Onchorynchus nerka*) nursery lakes. The effectiveness of fertilization as a coho smolt enhancement technique has not been tested in a naturally fishless lake. The objectives of this study were to: 1) test whether the application of inorganic phosphorus and nitrogen fertilizer during summer months increases the coho smolt producing capacity of the lake, and 2) describe the qualitative and quantitative changes in pelagic community structure in response to variable nutrient loading rates and fish densities.

This study is a continuation of a project started in the late seventies by the Northern Southeast Regional Aquaculture Association (NSRAA), a private nonprofit salmon enhancement organization based in Sitka, Alaska. It was conducted in a nutrient-poor lake that was dramatically altered with the addition of inorganic fertilizer and variable fish stocking densities. The lake was the observational unit of this study, and in lieu of "replicate" lakes, the treatments are tested (using pseudoreplication) sequentially over the course of seven growing seasons. First, the low to moderate baseline productivity of the lake was studied for two years. During the third year, coho fry (mean length of 52 mm) were stocked at a density of 2,000 fry/ha under natural nutrient loading conditions. In year four, less than 10 % of the fish population remained in the lake following the spring migration of smolts. Inorganic phosphorus and nitrogen fertilizer was applied to the lake during summer of the fifth year at a rate of 1.6 mg P/m²/day and 14 mg

N/m²/day. When nitrogen depletion was observed in the surface waters of the lake during this first year of fertilizer treatment, the nitrogen loading rate was increased to 34 mg N/m²/day (Phosphorus: 1.8 mg P/m²/day) in year six. Coho fry (50 mm) were stocked at twice their previous density in year six to test whether fertilization increased coho smolt production. Fertilization treatments were discontinued during the seventh year of the study, when less than 10% of the fish population remained in the lake, following the spring migration of smolts.

Our current knowledge of pelagic ecosystem dynamics predicts that 1) nutrient additions will increase the productivity of the lake, 2) zooplanktivory will shift the size structure of the zooplankton community towards smaller species, and 3) smolt production will increase. Changes in zooplankton community structure in response to large changes in lake productivity has not been well documented, but is reasonably predicted from life histories strategies. Life history combined with morphological and physiological adaptations provide zooplankters with the capacity to most effectively exploit resources and reproduce under a specific range or combination of environmental conditions. Cladocerans and rotifers would be expected to be the first zooplankters to increase in population size in response to fertilizer treatments because they have short generation times. However, the cost of diverting much of their energy intake into reproduction, rather than lipid reserves, makes them less capable of surviving when food resources are scarce (Goulden and Henry 1984). The life history strategy of calanoid copepods is almost the complete reverse of the cladocerans and rotifers (McNaught 1975). Calanoid copepods are cold adapted (Wilson 1959), and invest much of their excess energy intake into lipid reserves, enabling them to grow during spring when food availability and temperatures are low. The application of fertilizer in summer will only affect the late instars of calanoid copepods. If calanoid copepods benefit from fertilizer treatments,

their annual mode of sexual reproduction should delay significant increases in population size by one year.

STUDY SITE

The study site is a small unnamed lake on the northern tip of Kruzof Island (57° 18.3' N, 135° 47.1' W) in southeastern Alaska. The lake is referred to as Sealion Cove Lake (Figure 1) because the outlet stream (Alaska Department of Fish and Game identification no. 113-61-005) enters the Pacific Ocean at Sealion Cove. The lake lies at an elevation of 67 m. The northern and southern portions of the watershed are steep slopes which rise precipitously to elevations near 800 m. A low gradient *Sphagnum* bog (muskeg) drains into the lake from the east. A dense canopied hemlock (*Tsuga sp.*), Sitka spruce (*Picea sitchensensis*), and yellow cedar (*Taxus brevifolia*) forest extends halfway up the hillslopes before the alpine zone is reached. Alder (*Alnus sitchensis*) borders two sides of the lake. Soils in these watersheds are poorly developed, about 80 % of which is bare rock either completely exposed, or covered with a 5-15 cm mat of *Sphagnum* moss. Patches of soil rich in organic matter can be found at the base of the forested slopes, but the remainder of the watershed consists primarily of a dense layer of *Sphagnum* moss (muskeg) up to a meter thick.

Sealion Cove Lake has a small surface area (7.5 ha) that accounts for approximately one seventh of the entire watershed. The shallow nature of the lake (mean depth: 4.3 m) combined with a high mean annual precipitation (290 cm/yr) result in a fast flushing rate for the lake (about 0.25 years). A littoral shelf of less than 2 m deep accounts for 45 % of the lake area. The maximum depth is 11.9 m (Figure 2).

The lake is slightly acidic (pH range: 6.3-6.8), low in alkalinity (range: 3-5 mg/l as CaCO₃) and hardness (Appendice I), and generally low in mineral content, with the exception of moderate concentrations of iron and reactive silicon (Appendix II).

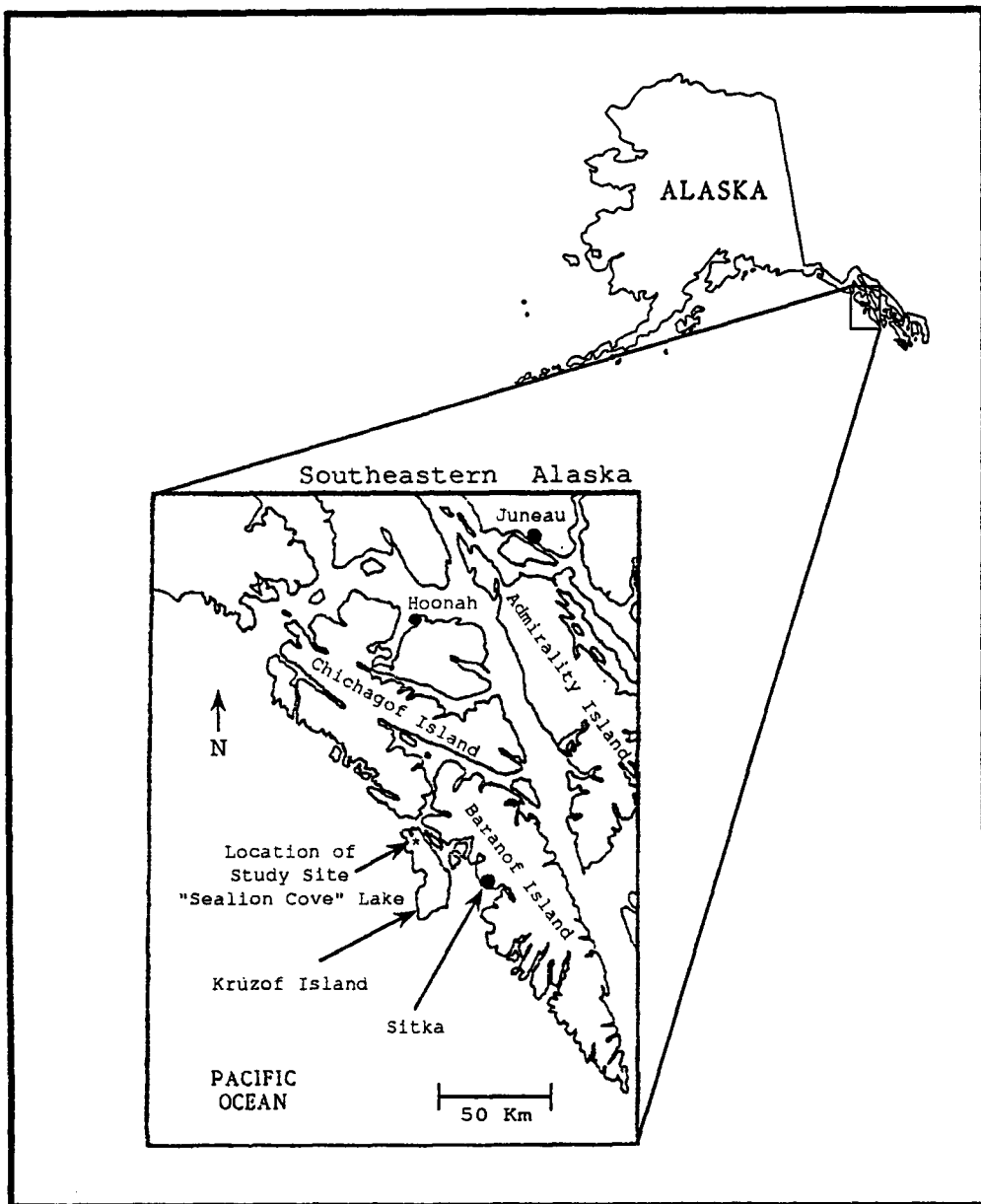


Figure 1. Southeastern Alaska and location of the study site Sealion Cove Lake.

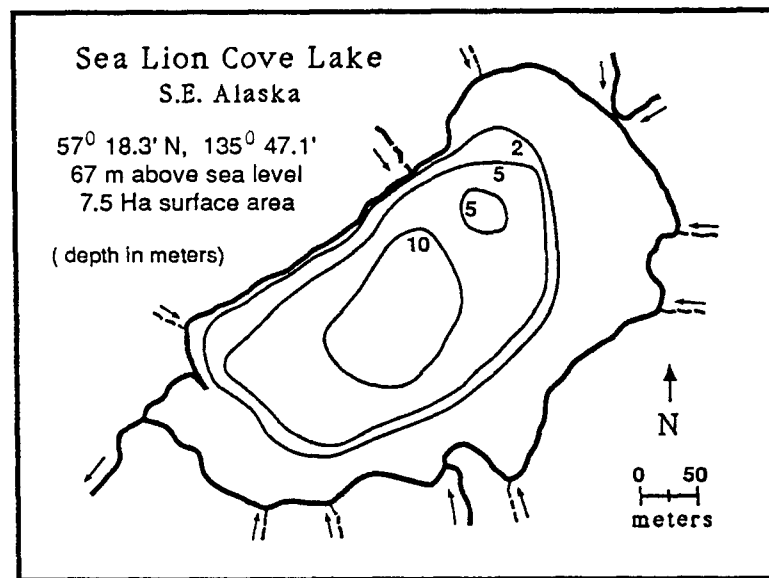


Figure 2. Bathymetric map of Sealion Cove Lake, Alaska.

Based mostly on climate data collected by the U.S. Geological Survey Magnetic Observatory in Sitka, Alaska, the weather at the study site is dominated by persistent cloud cover (Appendix III), with rainfall occurring in all months of the year (Appendix IV). The driest months (May-July) precede the wettest (August-October). At this high of a latitude the term dry season is something of a misnomer, since at least 4-6 inches of rain typically falls during each summer month, but occasionally summers (1982 and 1983) are much drier. Air temperatures are cooler on the north tip of Kruzof Island than at Sitka (Appendix V). Mean summer epilimnetic temperatures range between eleven and fourteen degrees centigrade (Appendix V). Thermal stratification begins to develop by mid-June, persists throughout the summer months, then it is destabilized by winds and rainstorms which cool and mix the lake in early-fall (Appendix VI).

Water quality parameters at Sealion Cove Lake were well within the oligotrophic range prior to fertilization treatments. Mean summer total chlorophyll concentrations were observed at or below 1.03 $\mu\text{g/l}$. Total phosphorus concentrations at spring overturn ranged between 2.7 and 6.0 $\mu\text{g/l}$, and mean summer total phosphorus never exceeded 9.2 $\mu\text{g/l}$.

The cold adapted calanoid copepod (*Diaptomus kenia* and *Epischura nevadensis*) and rotifer (*Kellicottia longispina* and *Chonochilus sp.*) components of the zooplankton community are abundant in the spring and early summer. The cladocerans (*Bosmina longirostris* and *Holopedium gibberum*) are dominant in late summer and early fall (Appendix VII). *Cyclops bicuspidatus* and early instars of *D. kenia* are at high densities during the winter months along with remnant populations of *B. longirostris* and *K. longispina*.

C. bicuspidatus, a raptorial feeder, is probably omnivorous in its early copepodid instars, until reaching a large enough size to become an efficient predator. *E. nevadensis* a potentially

voracious predator in some lake ecosystems (Mesner 1984; Wong and Sprules 1985), appears to be capable of functioning as a grazer at times in this lake. *E. nevadensis*, in combination with the largest grazer *D. kenia*, account for 1/2 to 2/3 of the total zooplankton biomass observed under unaltered conditions. The cladocerans (*B. logirostris* and *H. gibberum*) possess comb like appendages for filter feeding, and the rotifers (*K. longispina* and *Conochilus sp.*) a ciliated corona for collecting suspended particles (Goldman and Horne 1983).

MATERIALS AND METHODS

STUDY DESIGN

The study design is graphically illustrated by Figure 3. The primarily objective of the study was to test whether fertilizer applications during summer months would increase the lakes capacity to produce age 1+ coho smolts. To test this question, the lakes production of age 1+ coho smolts when stocked at a density of 2,000 fry/ha under unaltered conditions in 1982 was compared to the smolt production when the lake was stocked at twice this density of fry (4,000 fry/ha) under fertilizer conditions in 1985.

The stocking strategy of the coho lake rearing program emphasizes the production of age 1+ smolts, rather than stocking lakes with larger numbers of fry which may require several years of lake rearing before emigrating as smolts. Prior stocking experience by the NSRAA has determined that 2,000 coho fry/ha is near the maximum stocking density for a lake with the physical and biological characteristics of Sealion Cove Lake. Adjusting stocking densities so that a maximum number of smolts emigrate from the lake after one summer of rearing allows the populations of food organisms two summers with low amounts of fish predation (from the small numbers of age 1+ and 2+ fish that remain in the lake) before the lake is restocked with the progeny of the fish that emigrated as age 1+ smolts. This strategy is analogous to the agricultural practice of leaving fields fallow to reestablish soil fertility.

Secondary objectives of the study were to document and interpret the changes in pelagic ecosystem dynamics that occurred in response to fish introductions and fertilization. A descriptive analysis which compared pelagic community dynamics under a set of contrasting experimental conditions (Figure 4) was carried out to achieve these objectives. Lack of

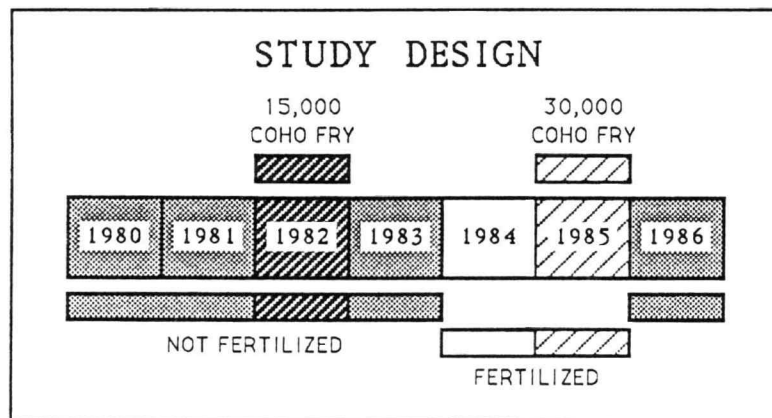


Figure 3. Study design illustrating fertilized (light), unfertilized (shaded), and fish stocking (striped) treatments over the seven year study period at Sealion Cove Lake, Alaska (1980-1986).

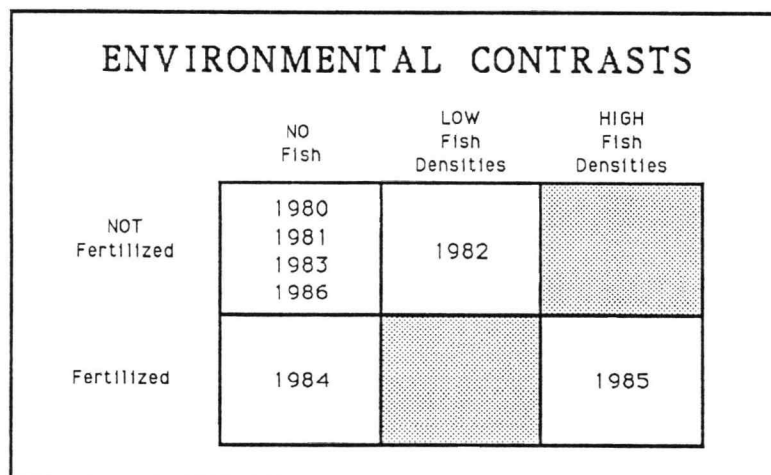


Figure 4. Contrasting environmental conditions tested at Sealion Cove Lake, Alaska (1980-1986).

replication for the fertilization and fish density manipulations precluded the use of inferential statistic in the analyses.

FERTILIZATION

Liquid and solid pellet fertilizers were employed to increase nutrient loading rates for the lake. Liquid agricultural products have been widely utilized in Alaska and British Columbia because they can be applied on the surface of deep lakes where the probability of diffusion into the (upper) trophogenic zone is maximized. Solid fertilizer has the potential to greatly reduce the costs associated with application, but broadcasting pellets into a deep lake would diffuse nutrients into the (lower) hypolimnion where they are not immediately available to phytoplankton. Methods can be devised to suspend the pellets within the epilimnion, but for a large lake this would require a tremendous investment of time and effort into an untested technology. Small shallow lakes in the coho lake stocking program with a complete baseline of limnological and fish data were considered as candidates for a pilot test of the nutrient dispersal properties of solid fertilizer. Sealion Cove Lake was chosen because it was the only lake which met all these criteria in 1984.

Liquid fertilizer (phosphate dissolved in an ammonium nitrate solution) with a ratio by weight of 27/7 nitrogen to phosphorus was applied from late-May to mid-August in 1984, and from late-May to late September in 1985. Fertilizer was diluted 1:1 with lake water and applied by 1) a hand pumped insecticide sprayer while rowing grid patterns across the lake, and 2) drip applicators while personnel were away from the site. The frequency of spray application varied due to logistical constraints. Spray applications were scheduled for every second day in 1984 and every third day in 1985, while drip applicators typically ran one week out of a month.

Slow leeching pellet fertilizer (27:7 N:P by weight) was broadcast on the littoral shelf (181 Kg) and suspended in burlap sacs (91 Kg) at a depth of 1.0 m in the pelagic zone in mid-August 1984. The sacs were removed from the lake at the end of the growing season (early October). Analysis of the nutrient content of the pellets (by weight) suggested that they did not release much of their nutrients over that time interval. Exceptionally high dissolved phosphorus concentrations were observed during a winter survey in 1985, then a return to normal concentrations in the late spring. This suggests that most of the remaining fertilizer leached from the pellets and was flushed from the lake. Assuming that the nutrient contributions from the remaining pellets was negligible, fertilizer was applied at a rate of 1.6 and 1.8 mg P/m²/day and 14 and 34 mg N/m²/day in 1984 and 1985 respectively. Nitrogen loading rates were increased in 1985 to eliminate the undesirable pattern of seasonal dissolved nitrogen depletion in the epilimnion that reoccurred in 1984.

LIMNOLOGICAL SAMPLING

The limnological lake survey outlined in Table 1 was conducted monthly in 1980, 1982, 1983 and 1986 and bimonthly in 1984 and 1985 (fertilizer treatment years) between early spring and late fall. Zooplankton tows were the only samples collected in 1981. During each monthly survey in 1980 only one sample was collected for chlorophyll (1.0 m), and zooplankton tows were not replicated.

With the exception of water samples collected at the mouths of inlet streams, all limnological sampling was conducted over the deepest portion of the lake (Figure 5). Collection, filtering, storage, transport, and chemical analyses of water samples were conducted according to Koenings et al. (1987).

Table 1. Limnological sampling conducted during lake surveys.

<u>Type of Sampling</u>	<u>Comments</u>
FIELD ANALYSES / MONITORING	Observed at mid-lake station
Light Intensity Profile Conductivity Profile Temperature Profile	Collected at surface and 0.5 m intervals
Secchi Depth	19 cm diameter disc
Alkalinity Hardness pH	Collected at 1.0 m and mid-hypolimnion depths
LABORATORY ANALYSES	
Filtered Water	0.45 μ m pore diameter glass fiber filters
Nitrate + Nitrite, Ammonium, Filterable Reactive Phosphorus, Total Filterable Phosphorus	Collected at 1.0 m and mid-hypolimnion depths
Total Chlorophyll	Collected at 1.0 m, mid-compensation, and compensation depths
Unfiltered Water	
Total Phosphorus, Total Kjeldahl Nitrogen, pH, Alkalinity, Calcium, Magnesium, Iron, Reactive Silicon	Collected at 1.0 m and mid-hypolimnion depths
BIOLOGICAL SAMPLING	
Periphyton	3 littoral stations
Zooplankton	Replicate vertical tows at the mid-lake station

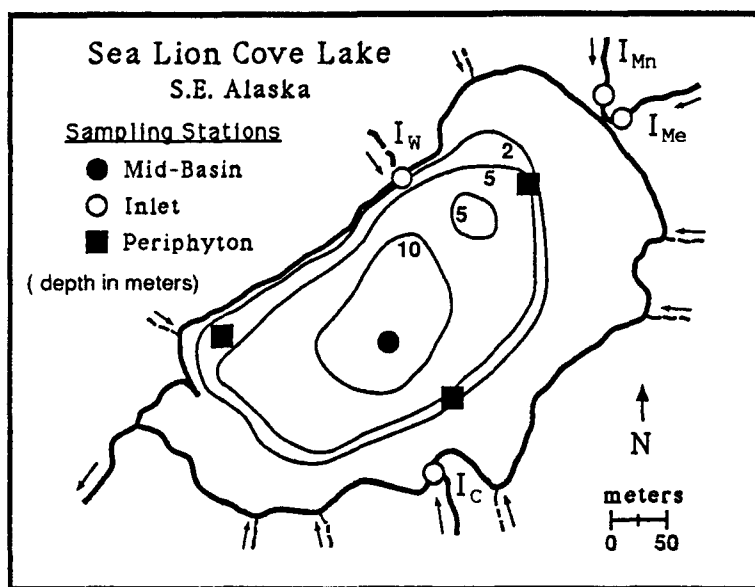


Figure 5. Locations of mid-basin (1980-1986), inlet (1984-1986), and periphyton (1982-1986) sampling stations at Sealion Cove Lake, Alaska.

Specific analyses consisted of a fluorometric procedure for total chlorophyll (Strickland and Parsons 1972) determined on 3-6 samples collected from depths distributed evenly throughout the photic zone. Filterable reactive phosphorus (FRP) was analyzed by the methods of Murphy and Riley (1962) as modified by Eisenreich et al. (1975). Total phosphorus was determined by the FRP method after persulfate digestion. Nitrate and nitrite analysis followed the methods of Stainton et al. (1977), nitrate being analyzed as nitrite after cadmium reduction. Ammonium analysis was according to the phenohypochlorite methodology of Stainton et al. (1977). Total Kjeldahl nitrogen was determined as nitrite (Stainton et al. 1977), following acid digestion.

Temperature was recorded with a Yellow Springs Instruments model 33 salinity-conductivity-temperature meter. A Protomatic photometer (no model number) with an upward facing probe was used to measure the photosynthetic usable wavelengths of light (400-700 μm). Lake discharge was determined with a staff gauge and pygmy current velocity meter following the procedures of Koenings et al. (1987).

Periphyton was collected at 1 month intervals from clear plexiglass plates suspended 1.0 m below the lake surface. Periphyton was scraped off a surface area of 200 cm^2 at each sampling, and analyzed for total chlorophyll content. Results were presented as the means of the three periphyton stations monitored (Figure 5).

Replicate vertical zooplankton tows were collected using a 0.5 m diameter conical net with a mesh size of 153 μm . Mean lengths and biomass for each zooplankton species was estimated following Koenings et al. (1987). Zooplankters were identified to species by John Edmundson (Alaska Department of Fish and Game, Soldotna, Alaska) according to Pennak (1978) for the cladocerans and rotifers, and Wilson (1959), Yeatman (1959), and Harding and Smith (1974) for the copepods.

FISH SAMPLING

Coho salmon fry were stocked in mid-summer (08 July) at mean lengths of 52 and 50 mm, and mean weights of 1.4 and 1.2 g in 1982 and 1985, respectively. Bimonthly sampling was conducted during both introductions to estimate the mean size and condition of the fish population. Fork lengths were measured to the nearest millimeter from samples of 600-1,200 fish collected with small (22 cm diameter) and large (60 cm diameter) funnel traps distributed throughout the lake. In addition, samples of 50 (in 1982) and 100 (in 1985) fish were measured individually for fork length (to the nearest mm) and damp weight (to the nearest 0.1 g) after being held in cages and deprived of food for about 24 hours. Emigrant smolts were collected in a 100% efficient inclined screen trap located at the outlet. All fish were counted, most were measured (except at peak run periods), and 100 fish subsampled for weights every three to four days during the outmigration period. Rick Oestman is currently conducting an analysis (at the University of Washington, in Seattle, Washington) of stomach samples collected using hypodermic syringes to the flush stomachs. Twenty-four afternoon feeding fish were collected for stomach contents in 1982, whereas in 1985 an additional set of 24 morning feeding fish were added to the sampling program.

NUTRIENT LOADING ESTIMATES

Total and dissolved phosphorus and nitrogen loading rates at Sealion Cove Lake for study years prior to 1984 were backcalculated by deriving their relationship to rainfall observed at Sitka, Alaska (rainfall data provided by the U.S. Geological Survey Magnetic Observatory). This analysis was performed 1) to provide an estimate of the possible annual variation in

nutrient loading rates during prefertilization study years, and 2) to provide a measure of the relative magnitude the nutrients contributed by fertilizer represent in comparison to natural loading rates.

The climate of Sitka is slightly drier than at the study site, but rainfall ($r^2=0.88$) and lake discharge ($r^2=0.64$) can be reasonably estimated from the Sitka data base (Appendix VIII). Sitka rainfall and lake discharge correlate the best during the drier summer months. During rainy summers (1985), both discharge and total nutrient concentrations are maintained at slightly higher levels (Appendix IX). Changes in nutrient concentrations affected by varying flow rates in the inlet streams were factored into the backcalculations of total phosphorus (Appendix X) and total Kjeldahl nitrogen (Appendix XI) loading rates using isopleth models.

It is difficult to define a meaningful error component for the nutrient loading estimates because of all the possible sources of error. As an alternative, monthly and bimonthly predictions of the model (based on estimated discharge and estimated nutrient concentrations in 1985) were compared to an independent estimate for nutrient loading calculated directly from measured parameters (Appendix XII). Although the predictions of the model are better on a bimonthly basis, only monthly weather summaries were available from years prior to 1984. Summer nutrient loading rates presented in the results will represent the mean loading rates for June, July, and August. Dissolved phosphorus and nitrogen loading rates were estimated, (based on inlet stream data collected in 1984 and 1985) as their ratios to total phosphorus and total Kjeldhal nitrogen, respectively (Appendix XIII).

RESULTS

NUTRIENT LOADING

Estimates of mean daily phosphorus and nitrogen loading rates to Sealion Cove Lake during the summer months of June through August are presented in Figure 6. Fertilizer inputs represent approximately 75% of dissolved phosphorus which entered the lake in the summers of 1984 and 1985. Fertilizer accounted for 26% and 53% of the dissolved nitrogen inputs in the summers of 1984 and 1985, respectively. The lowest summer phosphorus loading from watershed sources was estimated to have occurred in 1982 and 1983. Summer phosphorus inputs in 1982 and 1983 were $\leq 1/2$ of the phosphorus loads originating from the watershed during any other study year.

Dissolved nutrient concentrations in the surface waters of Sealion Cove Lake were generally low prior to fertilization treatments (Figure 7). Filterable reactive phosphorus (FRP) concentrations fluctuated erratically at times, but usually ranged between 2 and 4 $\mu\text{g/l}$. Nitrate + nitrite ($\text{NO}_3 + \text{NO}_2$) concentrations remained below 100 $\mu\text{g/l}$ prior to fertilization, and repeated a pattern of early summer depletion. This pattern of early summer $\text{NO}_3 + \text{NO}_2$ depletion persisted at a fertilization rate of 14 mg N/ m^2 /day in 1984, but was not observed when 34 mg N/ m^2 /day were added in 1985. Concentrations of FRP and $\text{NO}_3 + \text{NO}_2$ appeared to be inversely related during fertilized years. $\text{NO}_3 + \text{NO}_2$ concentrations were low when FRP concentrations were high in 1984, while FRP was low when $\text{NO}_3 + \text{NO}_2$ was high in 1985. Seasonal fluctuations in ammonia + ammonium concentrations varied between nonfertilized years, but were generally at a minimum in spring and summer.

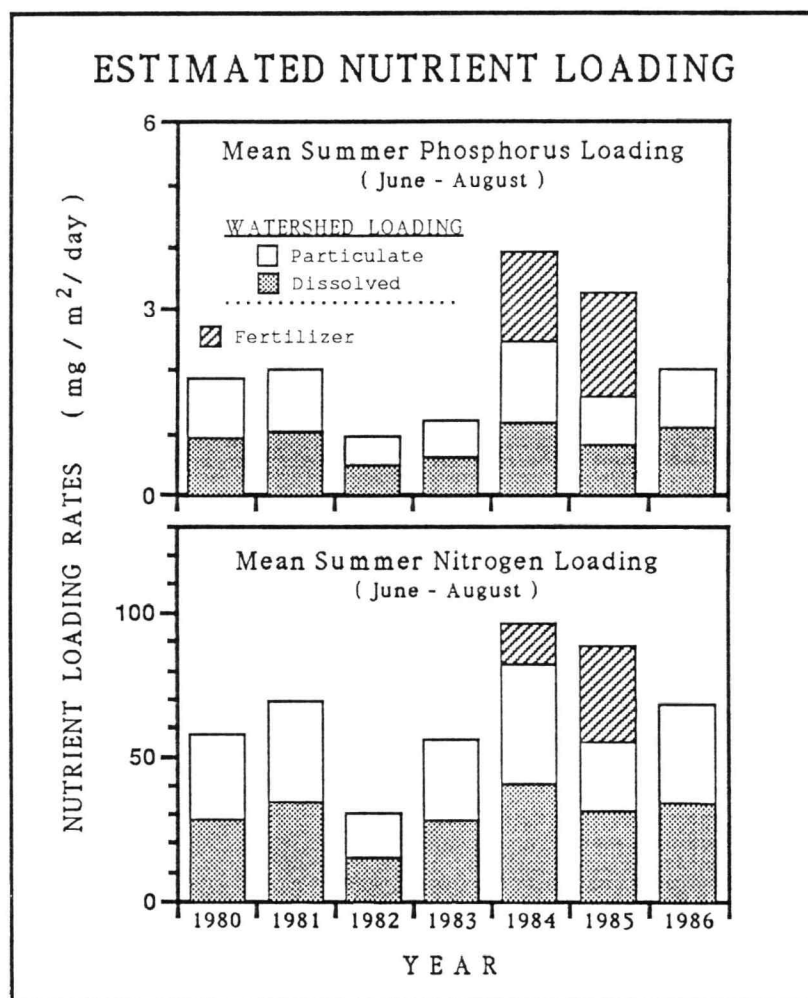


Figure 6. Estimated mean summer (June-August) phosphorus and nitrogen loading rates to Sealion Cove Lake, Alaska from 1980-1986.

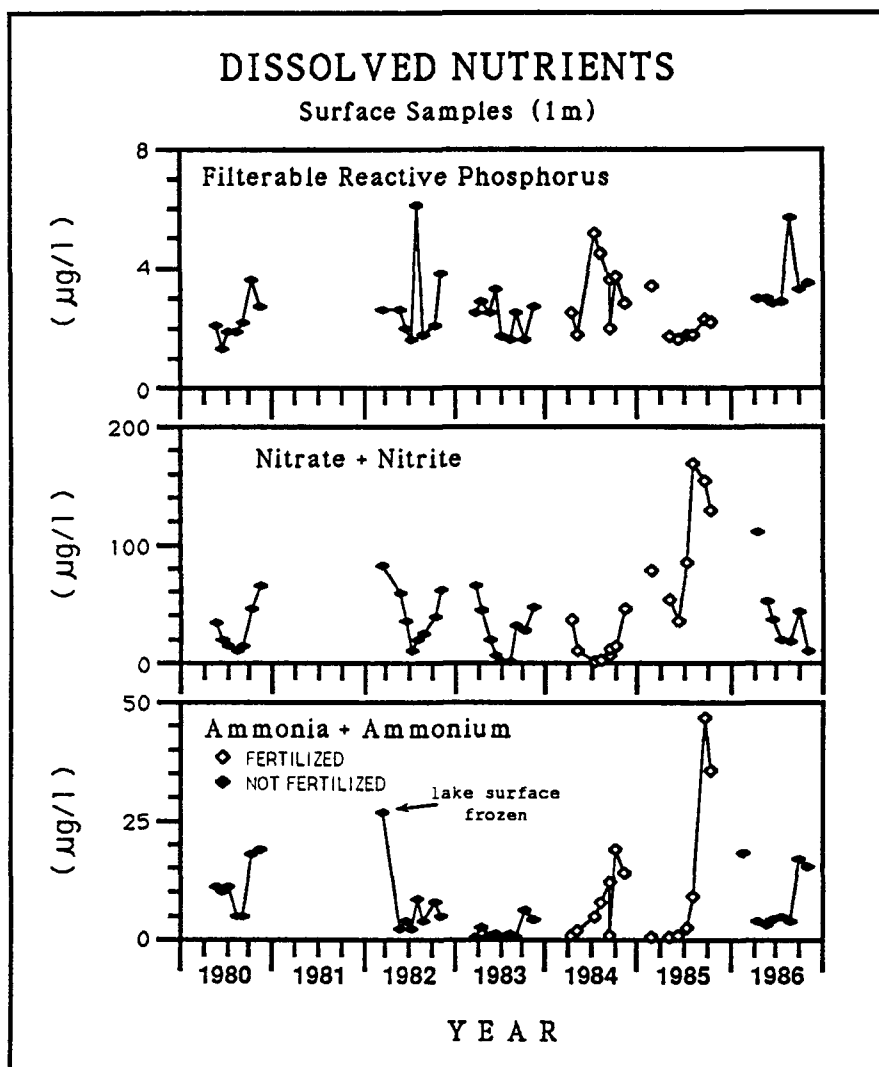


Figure 7. Filterable reactive phosphorus, nitrate+nitrite, and ammonia+ammonium concentrations in surface water of Sealion Cove Lake, Alaska (1980-1986).

Total phosphorus and total Kjeldahl nitrogen concentrations in the water column increased in both years when fertilizer was applied. Total phosphorus concentrations at one meter and midhypolimnion sampling depths exhibited erratic fluctuations in 1985, compared to the levels observed in 1984 (Figure 8). The buildup of total nutrients during fertilization roughly paralleled higher total chlorophyll concentrations. Peak total nutrient and total chlorophyll concentrations during fertilization were observed near the surface from early July to mid-August, 1985 (Figure 9).

PHYTOPLANKTON

Seasonal fluctuations in mean total chlorophyll concentrations varied considerably among unfertilized years. During the two unfertilized years with the highest levels of total chlorophyll (1980 and 1983), peak concentrations were observed during early summer in 1983, and in late summer in 1980. Total chlorophyll levels remained fairly stable during unfertilized conditions when concentrations were either moderate (1986) or low (1982).

Fertilization resulted in higher concentrations of total chlorophyll during both treatment years. Mean summer concentrations of total chlorophyll were about 3 and 5 times greater than the highest mean summer concentration observed during nonfertilized years in 1984 and 1985, respectively. Total chlorophyll concentrations were more stable in 1984 at a lower nitrogen fertilization rate (14 mg N/m²/day) compared to the erratic fluctuations observed in 1985 when 34 mg N/m²/day was applied (Figure 10).

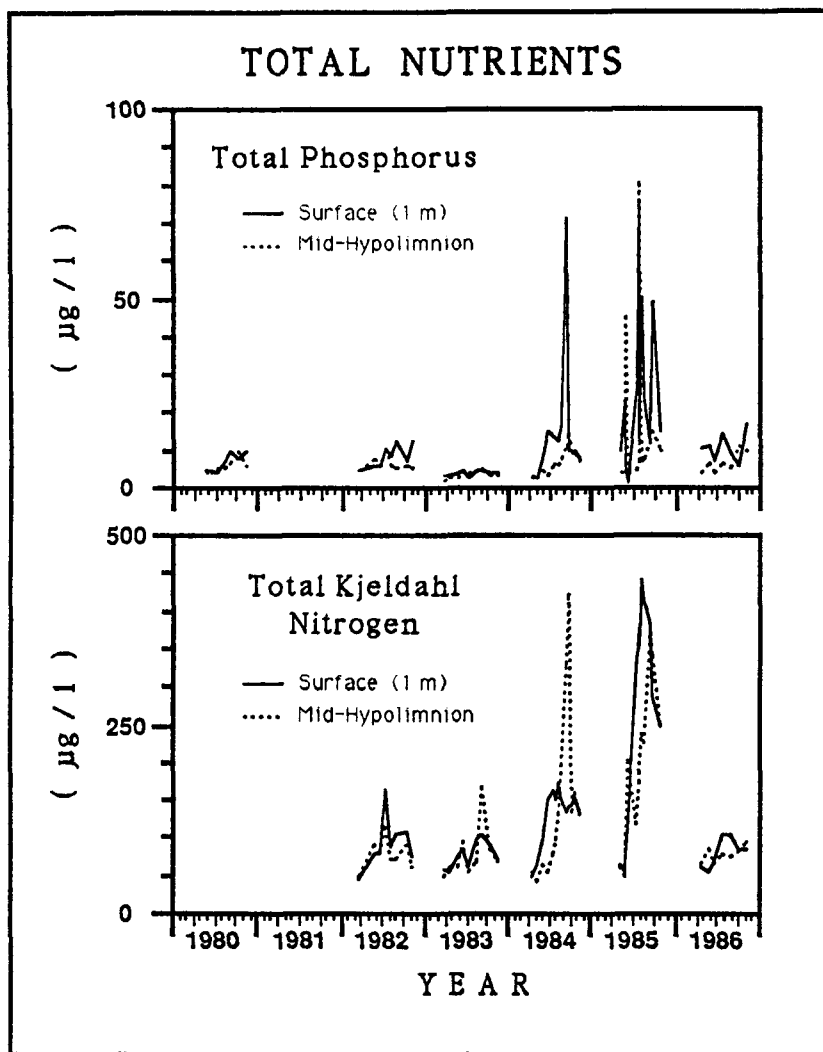


Figure 8. Total phosphorus and total Kjeldahl nitrogen concentrations at 1.0 m (solid lines) and mid-hypolimnion (broken lines) sampling depths at Sealion Cove Lake, Alaska (1980-1986).

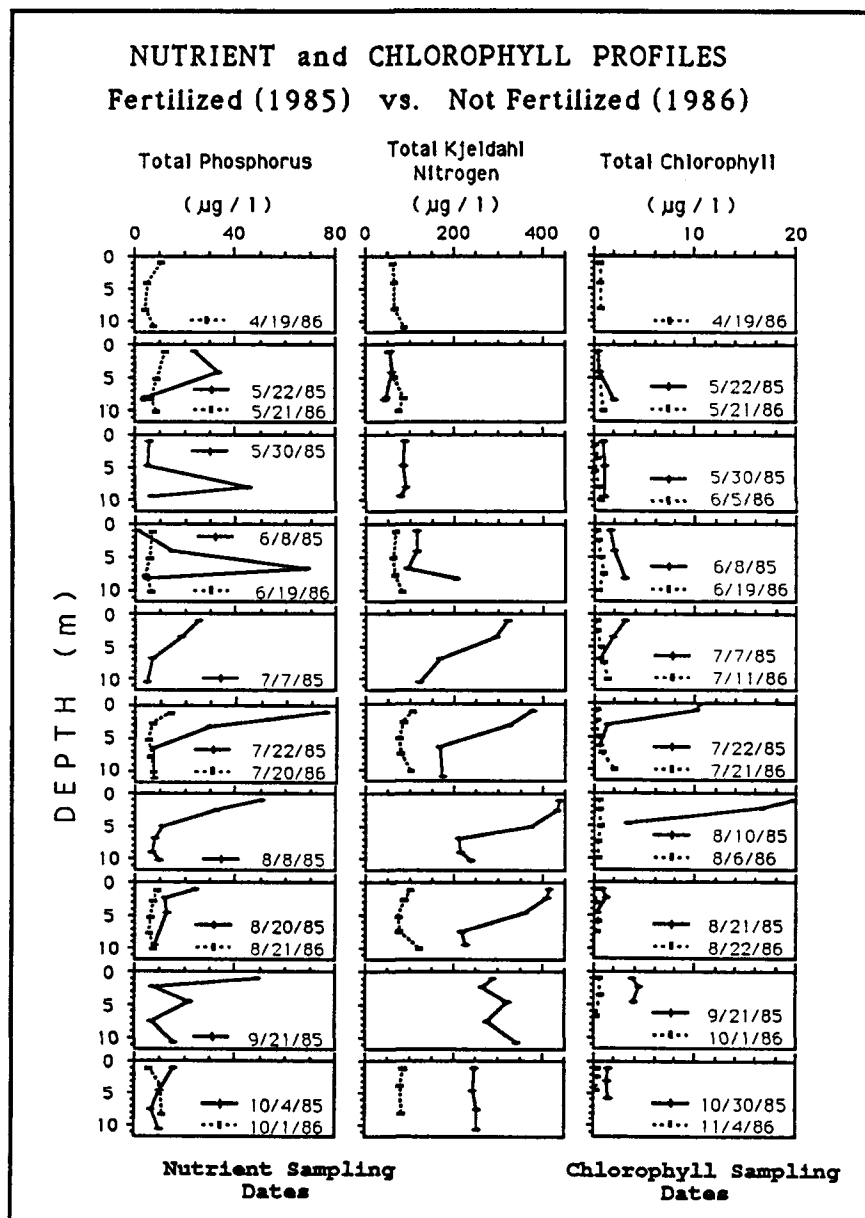


Figure 9. Total phosphorus, total Kjeldahl nitrogen, and total chlorophyll concentrations versus depth during fertilized treatments in 1985 (solid lines) and unfertilized conditions in 1986 (broken lines) at Sealion Cove Lake, Alaska.

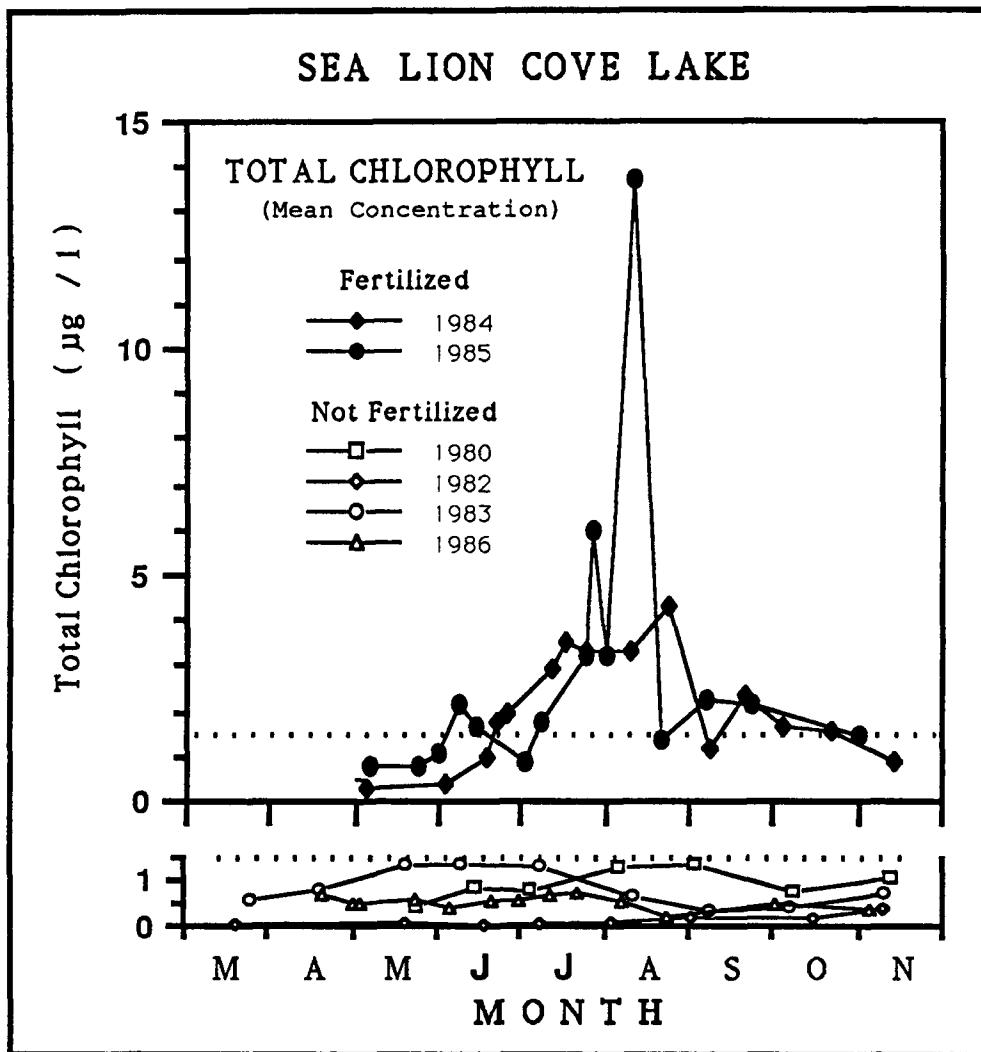


Figure 10. Seasonal variation in total chlorophyll concentrations contrasting fertilized treatments (solid symbols) and unfertilized conditions (open symbols) at Sealion Cove Lake, Alaska (1980-1986).

PERIPHYTON

Periphyton responses to fertilization treatments were of a higher magnitude and duration as compared to the responses of the phytoplankton. Fertilization resulted in increased monthly periphyton colonization and growth rates on plexiglass substrates by more than two orders of magnitude greater than prefertilization levels. One year after fertilization treatments were terminated, periphyton colonization and growth still remained one order of magnitude higher than the levels observed during unfertilized years (Figure 11).

ZOOPLANKTON

Determining cause and effect relationships that explain the annual variations in zooplankton abundances is often a problematic task, due to the complex nature of environmental and trophic interactions. In this study, the two environmental conditions (phytoplankton abundance, and intensity of planktivory) were altered to such a great extent that the effects of these changes on the abundance of zooplankton can be inferred with a reasonable degree of certainty. Changes in the abundance of macrozooplankton grazers were more reliably attributed to the manipulations imposed on the systems than the changes observed in the rotifer and predacious copepod populations. After the initial introduction of fish in 1982, *Diaptomus* declined to extremely low densities, and did not increase in abundance throughout the duration of the study (Figure 12). Prior to fertilization, *Holopedium* was observed only at low densities, but during fertilization (1984 and 1985) and the year following (1986) it maintained high densities throughout all of the summer months. During fertilization, densities of *Bosmina* peaked in late July at 484,400 organisms/m² in 1984 and 678,700 organisms/m² in 1985, but were exceptionally low

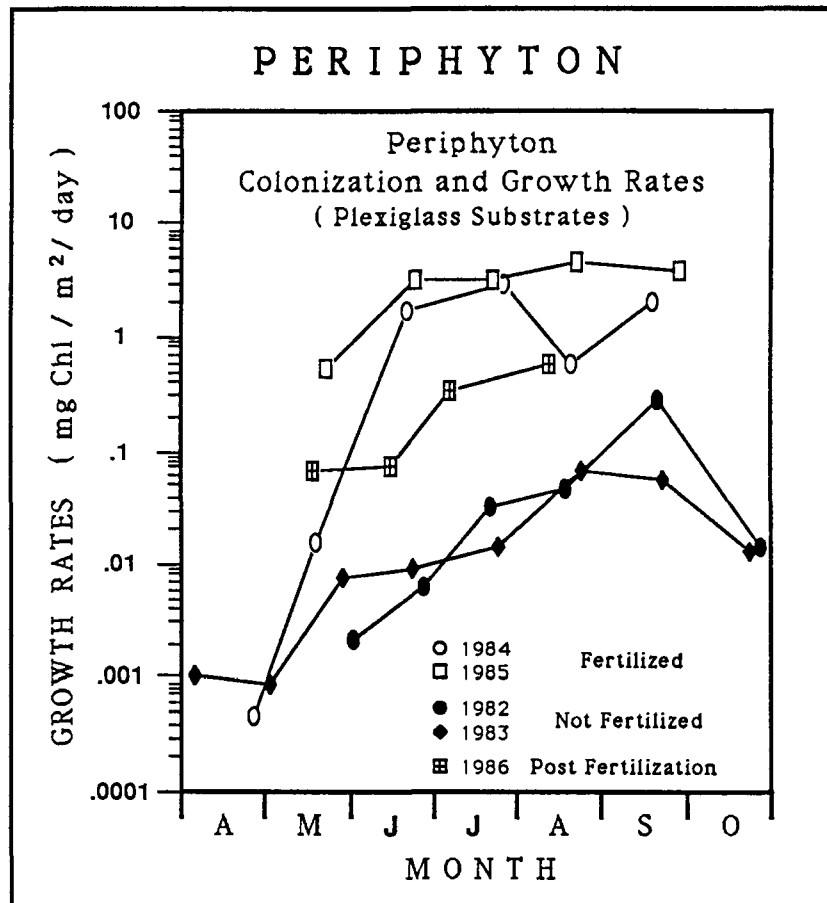


Figure 11. Periphyton colonization and growth rates estimated by changes in total chlorophyll during fertilized treatments (open symbols), unfertilized conditions (closed symbols), and one year after fertilization treatments (cross symbol) at Sealion Cove Lake, Alaska (1982-1986).

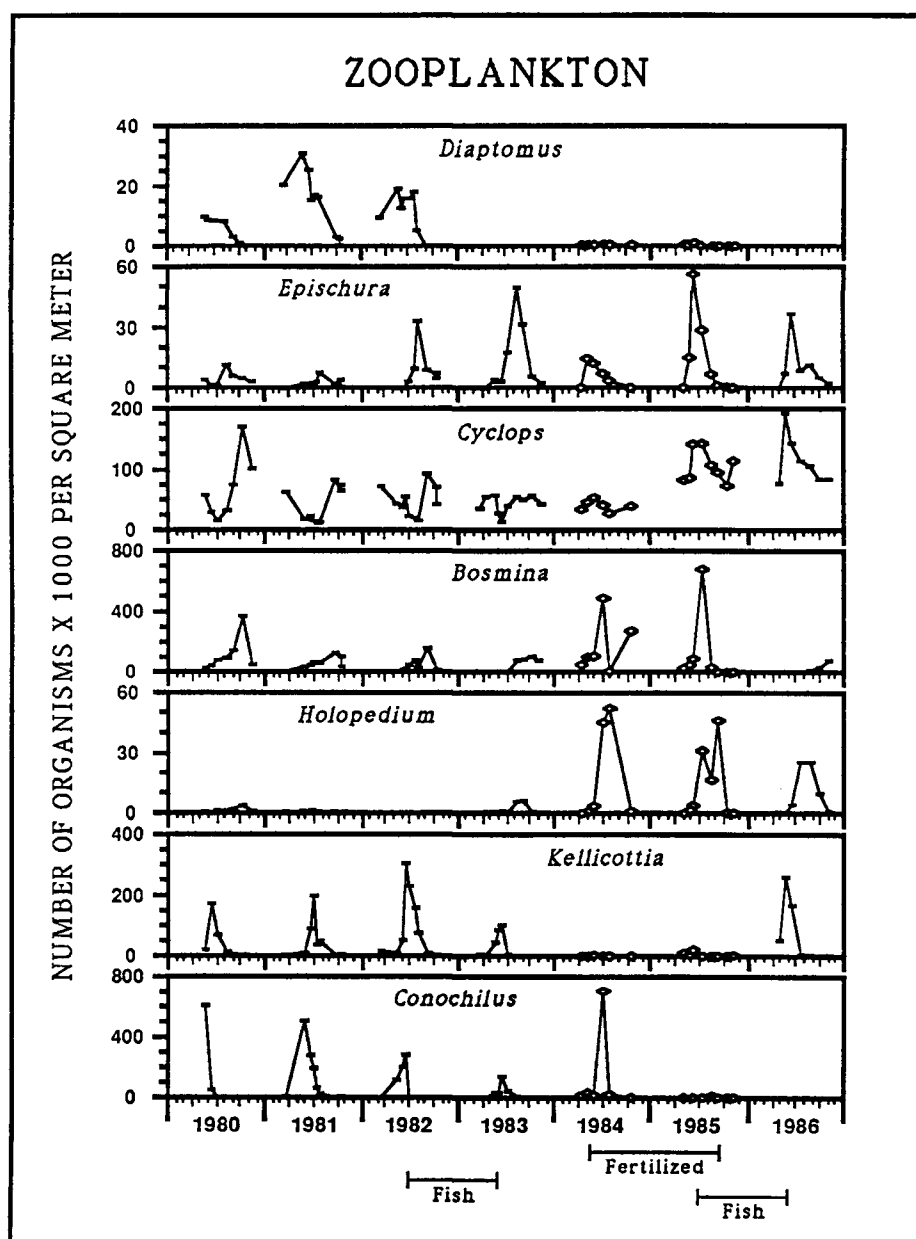


Figure 12. Seasonal variation in mid-lake zooplankton densities at Sealion Cove Lake, Alaska (1980-1986).

one year after fertilization treatments (1986). *Cyclops* increased in abundance following the high densities of *Bosmina* observed in 1980, 1984, and 1985, suggesting a predator-prey relationships between these two taxa. Densities of *Epischura* over the seven year study period show no discernable pattern of fluctuation, except a possible predator-prey relationship with *Conochilus* and *Bosmina*. Fertilization generally had a negative effect on the two rotifer taxa. High densities of *Conochilus* were observed for a short period of time during the first year of fertilization (1984), but remained extremely low throughout the next two years (1985 and 1986). *Kellicottia* densities were extremely low during both fertilization years. After fertilizer treatments were terminated (1986), the *Kellicottia* population increased to a size within the range observed prior to fertilization.

Calanoid copepods accounted for the majority of the zooplankton biomass produced prior to fertilization. The biomass of calanoid copepods followed an upward trajectory starting in 1980, reaching their peak in 1982, the first year fish were stocked (Figure 13). Cladocerans dominated the community biomass after phytoplankton densities increased in response to fertilization.

Zooplankton density can be an unreliable indicator of the amount of biomass present, due to temporal differences in mean body sizes for a population. This was the case for two of the zooplankters during the course of this study. High densities of *Bosmina* (1980) and *Epischura* (1983 and 1985) occurred during years when their biomasses were relatively low (Figures 12 and 13).

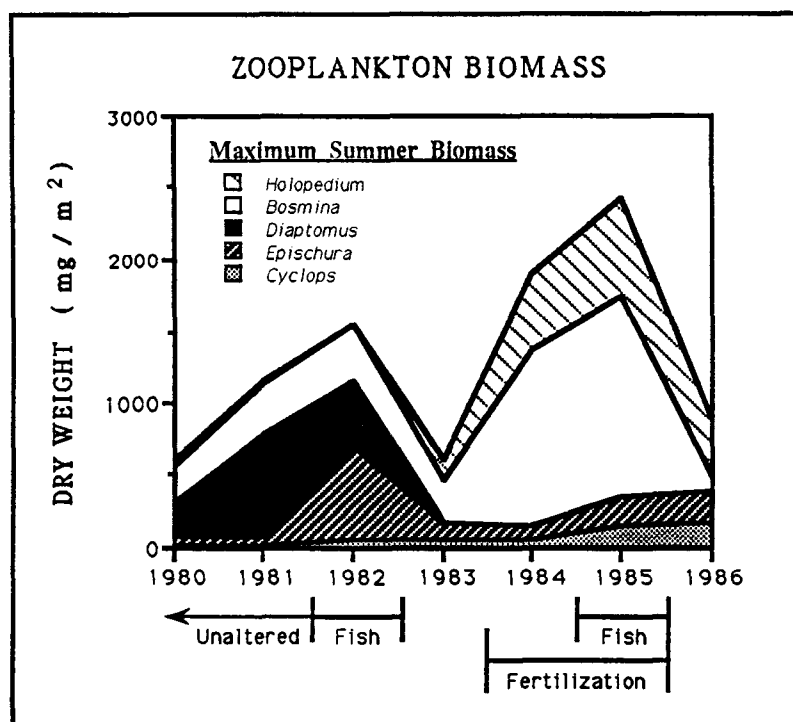


Figure 13. Maximum summer biomass estimated for each macrozooplankter found in Sealion Cove Lake, Alaska (1980-1986).

ZOOPLANKTON - CHLOROPHYLL RELATIONSHIPS

Two contrasting patterns of trophic interaction between zooplankton and phytoplankton were observed over the course of this study. Total zooplankton biomass had an inverse relationship with mean summer total chlorophyll during unfertilized years, and a positive relationship during fertilized years (Figure 14). Large zooplankters (calanoid copepods from 1980 to 1983, and *Holopedium* in 1986) dominated community biomass during unfertilized conditions, which at moderate to high standing crops exerted enough grazing pressure to depress standing crops of phytoplankton, and increase water clarity. During fertilized conditions, community biomass was dominated by the small cladoceran *Bosmina*, which did not exert enough grazing pressure to decrease mean summer concentrations of total chlorophyll.

COHO REARING CAPACITY

Coho growth, biomass, and numbers of smolts produced under fertilized conditions at a (high) stocking density of 4,000 fry/ha and unfertilized conditions at a (normal) stocking density of 2,000 fry/ha were compared to assess whether fertilization increased the coho rearing capacity of Sealion Cove Lake. The rate that fish grew in length was almost identical throughout both stocking periods. Under fertilized conditions, the total amount of coho biomass produced by the lake was about 60% greater than the amount produced at a lower stocking density without fertilizer treatments (Figure 15). On a per fish basis however, this represents a 20% decline in smolt biomass. The average weight and fork length for spring smolts produced under fertilized conditions was 10.5 g and 107 mm, compared to 13.5 g and 114 mm under unfertilized conditions. Fertilization

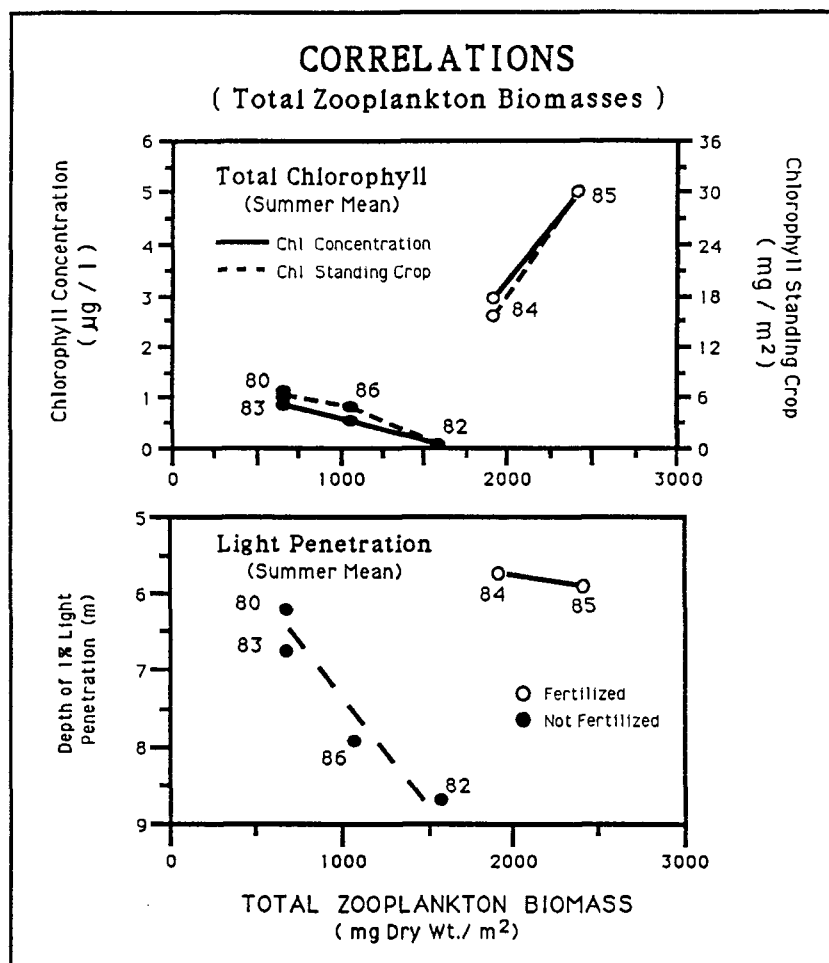


Figure 14. Mean summer total chlorophyll concentrations ($\mu\text{g/l}$) and standing crops (mg/m^2), and depth of one percent above surface light penetration versus total zooplankton biomass contrasting fertilized (open symbols) and unfertilized (solid symbols) conditions at Sealion Cove Lake, Alaska (1980-1986).

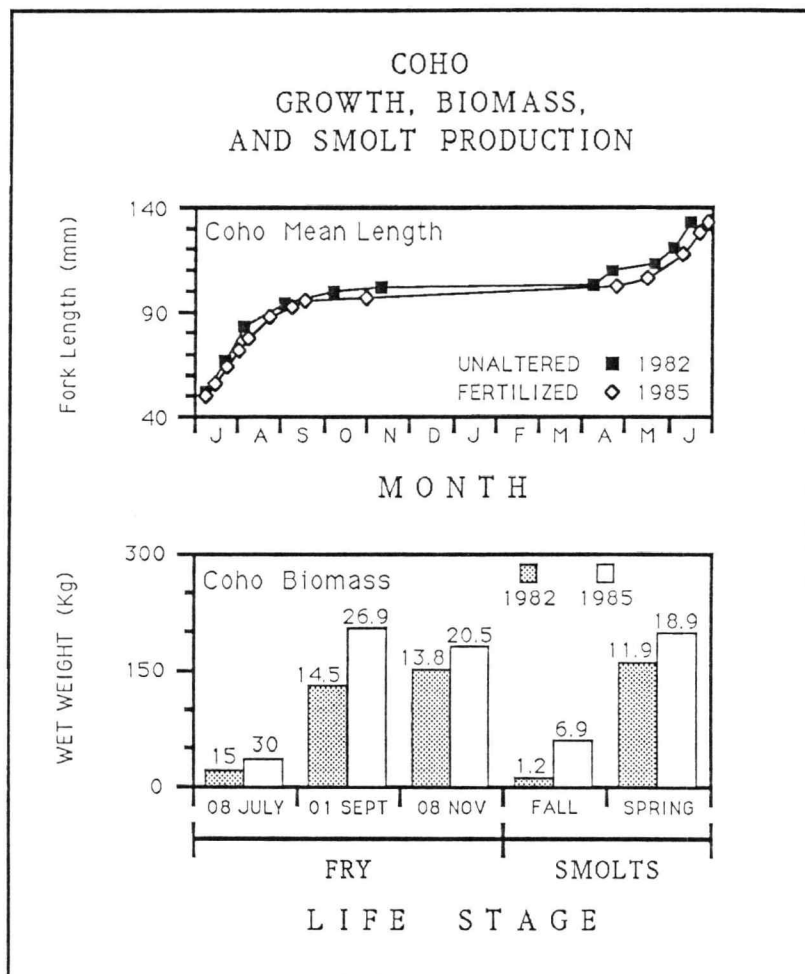


Figure 15. Coho (*Oncorhynchus kisutch*) growth and biomass contrasting fertilized conditions (open symbols) in 1985 and unfertilized conditions (closed symbols) in 1982 at Sealion Cove Lake, Alaska. Numbers above bar graphs represent the population size in thousands of fish.

was able to increase the numbers of spring smolts produced by 60%.

DISCUSSION

RESPONSES TO FISH INTRODUCTIONS

Many studies have documented the shifts in the size structure of zooplankton communities in response to planktivory at the scale of whole lake systems, ponds and experimental enclosures (see Kerfoot 1980 and Zaret 1980 for review). Fish introductions in this study represent a pulse type perturbation to the pelagic ecosystem of a small lake (Bender et al. 1984), due to the short amount of time the fish are present in the lake. The majority of fry stocked in early July leave the system as age 1+ smolts by late May of the following year. Gross examination of fish stomach samples collected in 1982 indicated the fry grew rapidly while feeding primarily on their pelagic resources which enabled them to reach the smolt stage after only one summer of freshwater rearing (figure 16). During the first stocking period (July, 1982 to June, 1983), fish predation reduced densities of the largest sized zooplankter (*Diaptomus*) to 2-4% of the population sizes observed from 1980 to 1982. The greatest decline in the *Diaptomus* population probably occurred during the spring when it was one of the few pelagic food items to supply a large biomass of presmolts. The second largest zooplankter in the community (*Epischura*) was a primary food resource for the fry in 1982, but was relatively unaffected by fish predation in the spring of 1983 because most of the population were either nauplii or early copepodids in spring.

High standing crops of phytoplankton might be expected following the disappearance of a large grazer component in the pelagic trophic structure. Standing crops of phytoplankton were high for unfertilized conditions in 1983, during the spring when *Diaptomus* would normally have occurred in the food web. Based on the theory of limiting similarity (Mac Arthur and Levins 1967) and the size-efficiency relationships for zooplankton

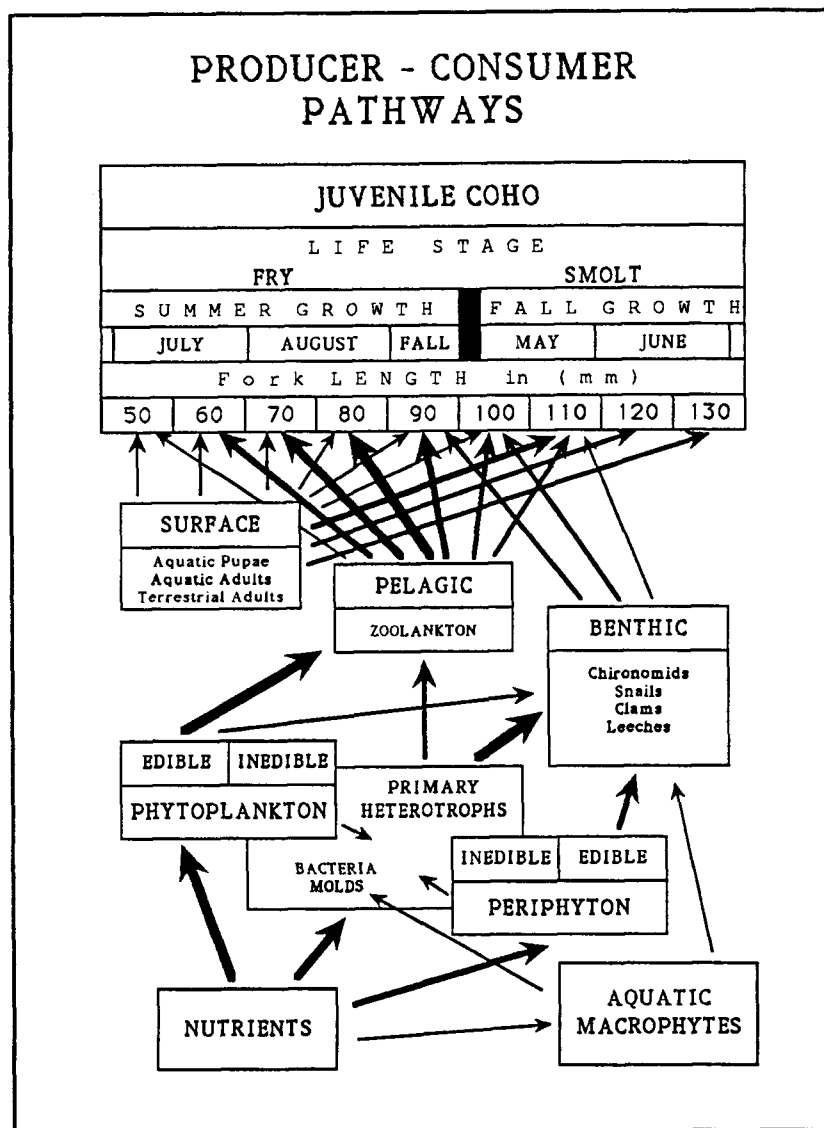


Figure 16. Significant producer-consumer pathways for coho (*Oncorhynchus kisutch*) food organisms throughout the time period fry (stocked at 50 mm in July) are reared to the smolt stage (110 mm by May and June), at Sealion Cove Lake, Alaska.

grazing potential (Stemberger and Gilbert 1987; Chow-Fraser and Knoechel 1985), other large grazers (*Epischura* and *Holopedium*) should have experienced a competitive release from a reduction in *Diaptomus* biomass. Nonetheless, neither appeared to have benefited from the disappearance of *Diaptomus* in 1983.

Epischura and *Holopedium*, the largest members of the zooplankton community during the second stocking period (1985), were the primary component of fish diets. Both were observed at moderate to high abundances in 1986, after being exposed to predation pressures exerted by a higher density and biomass of fish than were present during the first stocking. Several reasons can be hypothesized why neither of these two zooplankters abundances declined after the second fish stocking. Even though predator densities were twice as high during the second stocking, the predator - (large zooplankter) prey ratios did not increase twofold. Fertilization increased the abundance of *Holopedium* during the second stocking, which in combination with the high densities of *Epischura* observed that year, comprised a large zooplankton prey resource that was roughly twice (1.7 times) as abundant as the (*Diaptomus* and *Epischura*) prey resource observed during the first stocking. Different modes of reproduction among the zooplankters might account for some of the variation in survival rates. Diaptomids do not become sexually mature until they reach their maximum body size, and females carry their eggs for 2 to 3 weeks before releasing them. Diaptomids become more conspicuous to visual predator with the addition of large white egg masses, and their ability to avoid predators is probably reduced by the weight and drag of the eggs. Heavy predation on the later life stages of *Diaptomus* could potentially lead to a drastic reduction in recruitment of nauplii the following year. In contrast, *Epischura* and *Holopedium* reach sexual maturity at smaller sizes, and release eggs or embryos into the water column throughout their

adult life stage. Even if *Epischura* or *Holopedium* are preyed upon in the later stages of their life cycle, they still will have had an opportunity to lay some eggs (provided food is not scarce). *Epischura* and *Holopedium* hatched from eggs earlier in 1986 than most other years, but not early enough to be heavily preyed upon by the large smolt biomass present in spring.

This study did not conclusively explain why fish introductions drastically reduced the *Diaptomus* population and not the *Epischura* and *Holopedium* populations. I have presented two hypotheses I consider to be the most plausible explanations, but the relative importance of each factor is unknown. The major limitation to interpreting the results was due to the lack of data in the early spring of 1983. The first survey in 1983 was conducted from 23-25 March. Exceptionally low numbers of diaptomids were collected from the water column and fish stomachs during this survey, therefore it was not known whether significant numbers of *Diaptomus* had hatched prior to this time. Regardless of not knowing the precise timing of the decline in *Diaptomus*, the overall reduction in population size is indisputable.

RESPONSES TO FERTILIZATION

Increased concentrations of total phosphorus and mean summer total chlorophyll in Sealion Cove Lake was an anticipated response to increased nutrient loading (Sakamoto 1966; Dillon and Rigler 1974; Ostrofsky and Rigler 1987). Periphyton biomass generally displays a positive relationship with total phosphorus concentrations in the water column of lakes (Cattaneo 1987). This model predicts that colonization and growth of periphyton on our plexiglass samplers should increase during fertilized conditions, which was the case.

Although the work of Vollenweider (1976) documented that phosphorus limits seasonal production of phytoplankton in

many lakes, the nutrient-phytoplankton interactions in Sealion Cove Lake are almost certainly more complicated than just a simple link to phosphorus (Hutchinson 1944; Goldman 1972; Tilman et al. 1982; Tilman 1986). Under nonfertilized conditions, low dissolved nitrogen concentrations were observed at midsummer in the surface waters of Sealion Cove Lake. This is the time of year that high amounts of sunlight and warm water temperatures stimulate phytoplankton growth, which will result in greater rates of uptake and utilization of nutrients (Hutchinson 1957). Low phosphorus concentrations may limit phytoplankton production when high amounts of dissolved nitrogen are available in the spring and fall, but low dissolved nitrogen concentrations are more likely to limit algal growth in midsummer. When fertilizer was added to the lake in 1984 and 1985, the highest concentrations of total chlorophyll and zooplankton standing crops were observed in the midsummer. Moderate concentrations of dissolved nitrogen in the water column during midsummer, therefore, was a key to maintaining high levels of pelagic productivity with fertilizer treatments.

Viewed from this perspective, the first year of fertilizer treatments represented a small increase in the summer dissolved nitrogen loading rates ($14 \text{ mg N/m}^2/\text{day} = 26\%$ of the total inputs of dissolved N), and a moderate increase during the second year of fertilization ($34 \text{ mg N/m}^2/\text{day} = 53\%$ of the total inputs of dissolved N). The lower dissolved nitrogen loading rate in 1984 maintained total chlorophyll concentrations at moderate levels throughout the summer, whereas high nitrogen loading rates in 1985 resulted in large erratic fluctuations of total chlorophyll. When dissolved nitrogen loading rates were high in 1985, low phosphorus concentrations were observed in the surface waters of the lake. This suggests that phosphorus became limiting when phytoplankton reached high densities, and resulted in rapid phytoplankton dieoffs. Phosphorus did not

appear to be limiting in 1984 when lower amounts of dissolved nitrogen were added.

The purpose of the fertilizer additions were to stimulate the abundance of fish food organisms so that a greater number of coho smolts could be produced by the lake at a lower cost per fish. Both fertilization strategies resulted in high zooplankton abundances, but the costs associated with fertilization were roughly twice as much in 1985 compared to 1984. Maximum standing crops of zooplankton were only 25% greater in 1985 compared to 1984, but the relative amount of zooplankton production between the two years is not known because the numbers of zooplankton consumed by fish in 1985 has not been determined at this time. Regardless of this uncertainty, I would recommend that the fertilization strategy of 1984 be tested during a stocking year to determine whether an increase in smolt production could be achieved at the lower nitrogen loading rate. Furthermore, it is possible that only nitrogen fertilizer needs to be applied from early summer to midsummer because dissolved phosphorus appeared to be added in excess of algal demand in 1984. Inlet nitrogen concentrations at the study site are at a seasonal minimum from early to midsummer when the terrestrial vegetation and bacterial communities of the watershed are in rapid growth phases. Surface nitrogen loading rates increased at Sealion Cove Lake in mid-August when higher amounts of rainfall (~25 cm/month) increased stream flows. After mid-August the application of fertilizer did not appear necessary, provided the weather continued to be rainy. Fertilizer costs could be reduced by applying only nitrogen fertilizer between mid-June and mid-August.

As predicted on the basis of life history, strategies, the cladocerans (*Bosmina* and *Holopedium*) were the group of zooplankters to respond with the greatest increases in biomass during fertilized conditions. *Bosmina* populations underwent short periods of geometric growth during both treatment years

before crashing to low abundances. *Holopedium* maintained a more stable population size than the smaller cladoceran (*Bosmina*) in the presence (1985) or absence (1984) of heavy fish predation pressure. *Bosmina* appeared to be an important food resource for *Cyclops*, which typically doubled in population size after *Bosmina* was abundant. Any benefit *Epischura* may have had from fertilization would have been realized in 1985 due to their slow mode of reproduction. *Epischura* densities were high in 1985, but not much higher than the greatest densities observed during unfertilized conditions. Fish predation may have masked higher *Epischura* production in 1985, but this will not be known conclusively until the result of fish stomach contents are analyzed. The high reproductive potential of *Conochilus* allowed this species to become very abundant in 1984, but for unknown reasons it was virtually absent during the second year of fertilization. This could have been an indirect effect of the presence of large predator (*Epischura* or *Cyclops*) populations following the first year of fertilization, and/or changes in the species composition of the phytoplankton community.

COHO REARING CAPACITY

Several site specific characteristics that affect the coho rearing capacity of Sealion Cove Lake need to be recognized if the results of this study are to be used as a predictive model for lake stocking projects. This small, shallow lake, having an extensive unvegetated littoral zone (45 % by area), presents significant constraints for coho rearing. Small scale lake rearing projects are less cost effective, because the costs of administrating and monitoring projects remain fairly constant over a wide range of lake sizes. The lack of aquatic vegetation in the littoral zone significantly decreases the potential availability of coho food resources at Sealion Cove Lake. Coho can be stocked at densities as high as 4,000 fry/ha (twice the nonfertilized

stocking rate at Sealion Cove Lake) in small lakes with large vegetated littoral areas because adult insects resting on aquatic vegetation provide an abundant food resource (R.A. Crone, personal communication). Coho feeding opportunities at Sealion Cove Lake are more analogous to conditions which exist in large deep lakes, where pelagic zooplankton are the main food resource. However, the pelagic zone of Sealion Cove Lake accounts for only 55 % of the total lake area, whereas deep lakes are almost entirely pelagic water bodies (with respect to coho food resources). If the results of this study are to be applied to predicting the performance of coho in large deep lakes, it would be more appropriate to define stocking rates in terms of pelagic surface area, rather than total lake surface area. Stocking densities at Sealion Cove Lake based on pelagic surface area would nearly be twice the stocking density based on total surface area. Furthermore, the shallow depth of the pelagic zone at Sealion Cove Lake provides less opportunity for vertical separation of individuals in the water column than a deeper lake. The shallow depth of the pelagic zone in effect, results in even higher fish densities.

Fertilization was a successful aquacultural strategy for increasing the coho smolt producing capacity of Sealion Cove Lake. The number of coho smolts produced by the lake increased by 60%, but the largest portion of the zooplankton biomass stimulated by fertilization was not efficiently utilized as a food resource by the fry. The majority of fish fed (as expected) on larger sized zooplankters (*Holopedium* and *Epischura*). *Bosmina* accounted for (including a gross estimate of zooplankters consumed by fish) approximately 3/5 of the zooplankton biomass stimulated by the fertilizer treatments, but was only preyed upon by a small percentage of the fry when larger zooplankters were abundant. When the abundances of large zooplankters declined in early fall, *Bosmina* was no longer present in the water column as a potential food source. The

majority of the fertilizer that was transformed into zooplankton biomass, and potentially available as a food resource for the fry, did not contribute to the production of smolts.

These findings question whether the large food resource stimulated by fertilization (primarily *Bosmina*) can be more efficiently exploited to produce a greater number of coho smolts. The results of this study suggest that a higher number of coho smolts can be produced, and that a test of this hypothesis would be worth pursuing on a small scale. One possibility would be to gradually increase coho stocking densities in fertilized lakes. An important factor to consider is whether or not *Diaptomus* is a dominant member of the zooplankton community. Although *Diaptomus* was nearly eradicated after a relatively low density of coho were stocked at Sealion Cove Lake in 1982, *Diaptomus* populations have remained fairly stable in other lakes stocked at similar densities (R.A. Crone, personal communication). In these lakes, the benefit of producing more coho must be weighted against the increased chance of drastically reducing the *Diaptomus* population. *Diaptomus* was not a factor during the second stocking period at Sealion Cove Lake, and both *Epischura* and *Holopedium* were observed at moderate to high abundances in 1986 (the year after the lake was fertilized and stocked with 4,000 fry/ha). If coho densities had been higher in 1985, *Bosmina* probably would not have been preyed upon by a large percentage of the fry until the larger bodied *Epischura* and *Holopedium* populations were reduced to low abundances, because coho have selectively fed on the larger sized zooplankters during both stocking periods. Increasing coho stocking densities to more efficiently exploit a small sized food resource would not be an effective rearing strategy. It would probably reduce or eradicate the populations of large zooplankters, and little would be gained because *Bosmina* populations rise and crash over a relatively short period of time. An alternative approach to increasing coho smolt production

would be to fertilize and stock (about 4,000 fry/ha) lakes on an annual basis, rather than once every three years. Moderate to high abundances of *Epischura* and *Holopedium* observed at Sealion Cove Lake in 1986 probably could have been stimulated enough by fertilization to supported a stocking density of 4,000 coho fry/ha.

CONCEPTUAL FRAMEWORK

Schoener (1986) and McIntosh (1987) suggest that over the last decade there has been much "introspection" over the tradition ecological approaches of the past (MacArthur and Levins 1967), and an increasing tendency to use behavioral ecology, physiological ecology, and ecomorphology as theoretical bases for understanding community dynamics. The results obtained in this study were in agreement with these types of predictions based on fish behavior (size selective predation on zooplankters), zooplankton life history strategies (cladocerans will benefit from fertilization), and nutrient-chlorophyll relationships (fertilization will increase concentrations of chlorophyll). These are powerful inferential tools when an investigator is able to drastically alter environmental variables, but when observing smaller amounts of annual variation which occur naturally in lakes, these methods are often inadequate for providing definitive interpretations due to complex community interactions with the environment. Fortunately, meteorological conditions provided this study with a baseline of two pairs of dissimilar seasons (in terms of nutrient loading rates) prior to any fertilizer treatments, providing some hope of identifying responses to nutrient loading at this small scale.

A conceptual model of the functional changes in pelagic trophic structure that occurred at Sealion Cove Lake over the course of this study with respect to varying nutrient loading rates is shown in figure 17. The thickness of solid arrows

represents hypothetical measures of food web interaction strength in terms of biomass consumed in a given year, and the position of boxes enclosing the dates have been placed along a qualitative axis according to the relative amounts of summer phosphorus and nitrogen loading. During nonfertilized years, summer nutrient loading rates were largely determined by the amount of summer rainfall. At a moderate rate of nutrient loading in 1980, high concentrations of total chlorophyll (for nonfertilized conditions) were observed when total zooplankton biomass was low. Zooplankton populations may have initially been low in 1980 because the production of food resources required for reproduction was probably limited by low nutrient loading rates in 1979. In 1980, total chlorophyll concentrations reached a seasonal maximum in late summer, when a high amount of rainfall occurred during the period of time the terrestrial environment was releasing stored nitrogen. The high standing crop of phytoplankton was rapidly exploited by *Bosmina*, which subsequently stimulated the abundance of the small predator *Cyclops*. The abundance of *Diaptomus* increased in 1981, following a year with high total chlorophyll concentrations (1980). Although chlorophyll samples were not collected in 1981, moderate nutrient loading rates and successful reproduction of zooplankton suggest algal productivity was moderate to high this year. All three zooplankton grazers (*Diaptomus*, *Epischura*, and *Bosmina*) reached peak biomasses in 1982, following two years of relatively high nutrient loading rates and total chlorophyll concentrations. A high biomass of grazers during a year with low nutrient loading rates (1982) was associated with extremely low concentrations of total chlorophyll. Nutrient loading rates were low again in 1983, but total chlorophyll concentrations were high when total zooplankton biomass was low.

Total zooplankton biomass reached a prefertilization peak in 1982 (during the first fish stocking). Increased water clarity, and low standing crops of phytoplankton observed in 1982 were

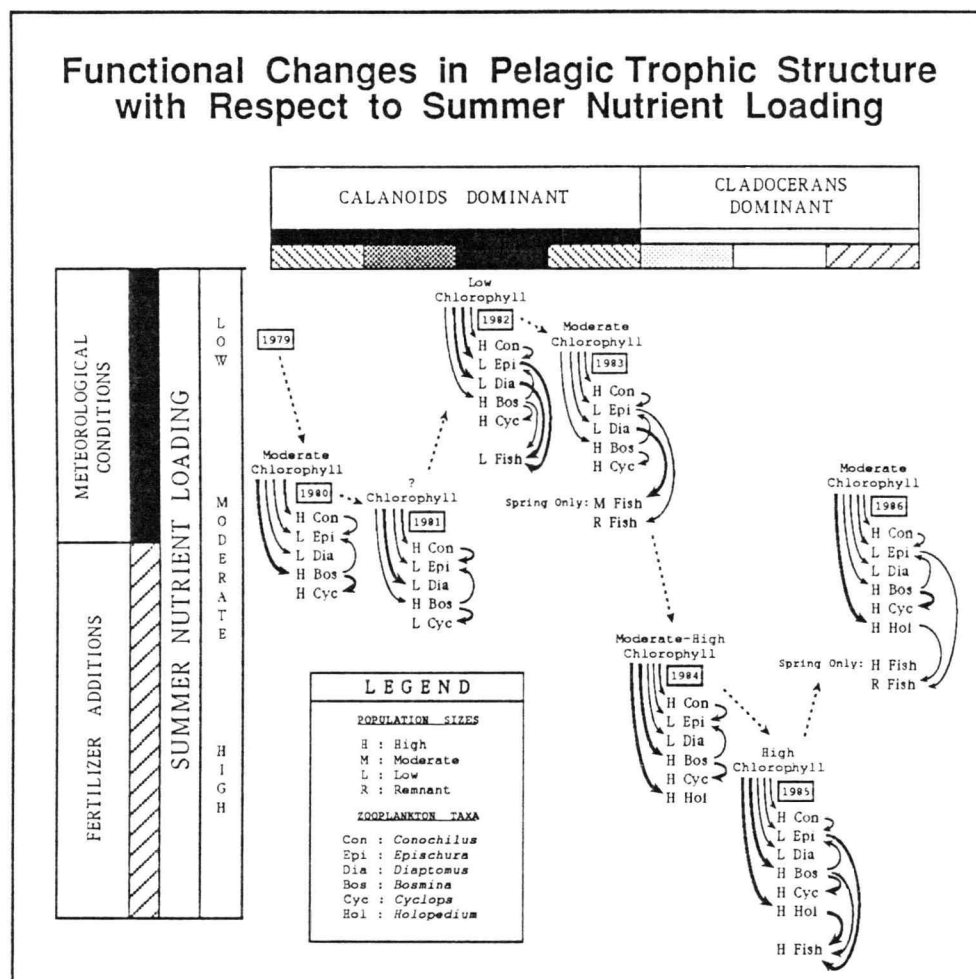


Figure 17. Changes in pelagic trophic structure relative to nutrient loading rates at Sealion Cove Lake, Alaska (1980-1986). Calanoid copepods dominated during prefertilization conditions, while cladocerans dominated during and after fertilization. Thickness of arrows represent hypothetical trophic linkage strengths estimated from the changes in density and biomass of each taxon.

initially associated with the large *Diaptomus* biomass that had built up over the previous two years. Exceptionally high biomasses of *Epischura* and *Bosmina* were developed following the seasonal decline in the *Diaptomus* population. Both *Epischura* and *Bosmina* appeared to exert enough grazing pressure to maintain the depressed standing crops of phytoplankton in 1982. This is fundamentally different than the functional interaction which occurred when *Bosmina* increased in abundance in response to higher standing crops of phytoplankton in 1980 and during the two fertilized years (1984 and 1985).

The zooplankton-chlorophyll interactions observed in 1982 may represent a situation where the grazing activities of zooplankton enhanced primary production by increasing the rate of nutrient regeneration in the water column (Lehman 1980; Taylor 1984). Although high biomasses were obtained by all the dominant zooplankton grazers in 1982, recruitment in 1983 was poor. The highest standing crops of phytoplankton over the four nonfertilized study years occurred during the late-spring and early summer of 1983, the period of time *Diaptomus* is typically the primary zooplankton grazer. Overall the standing crop of phytoplankton in 1983 cannot be considered out of the range of normal seasonal variation for nonfertilized years because high standing crops were also observed in 1980.

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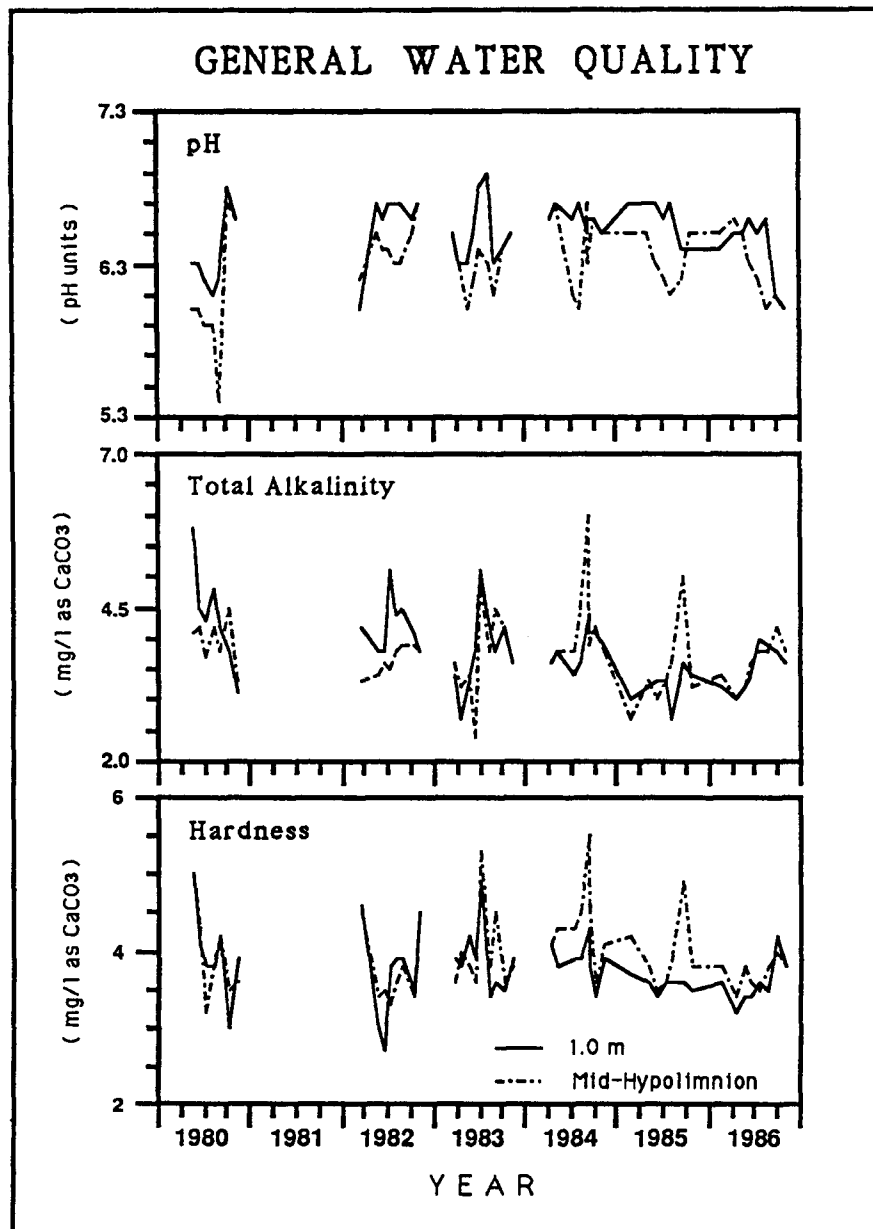
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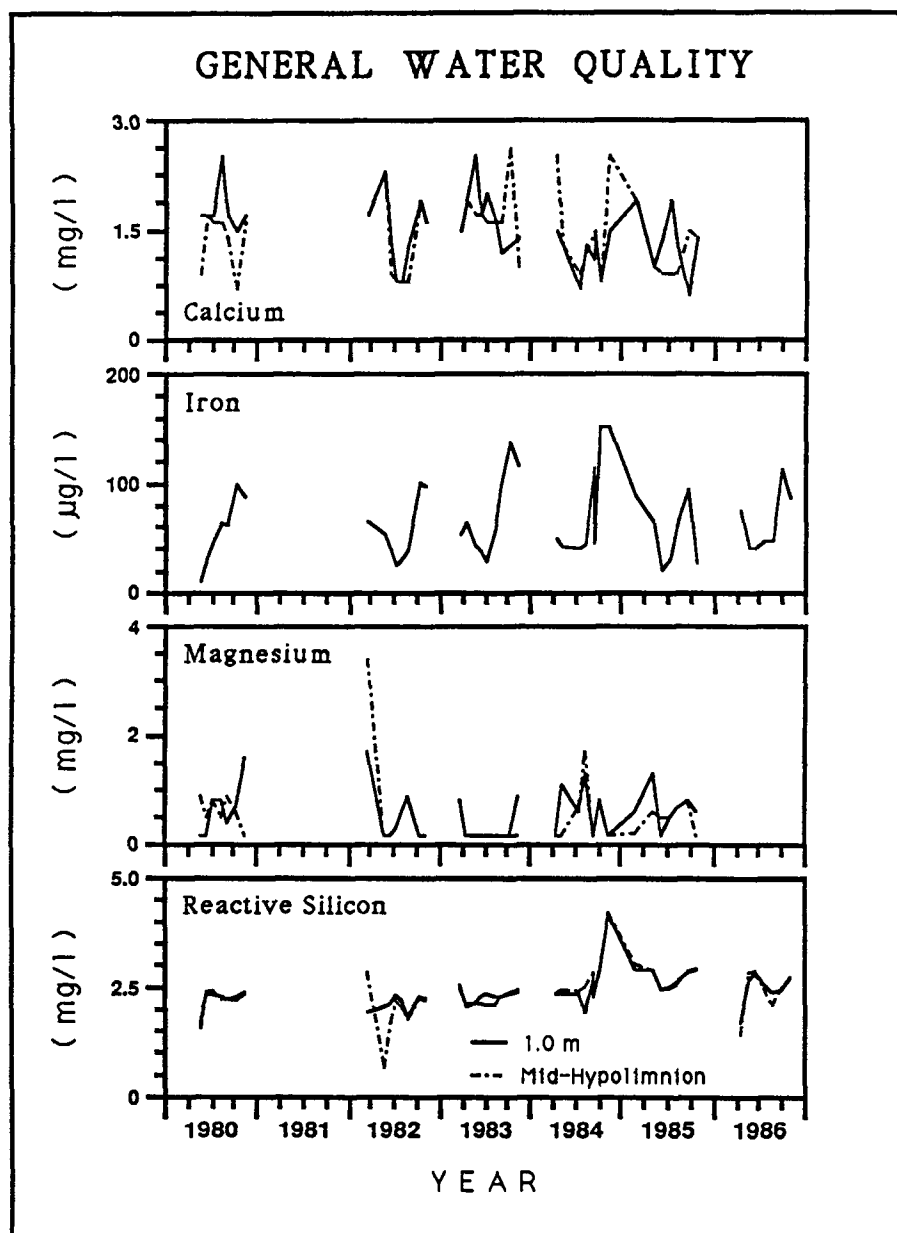
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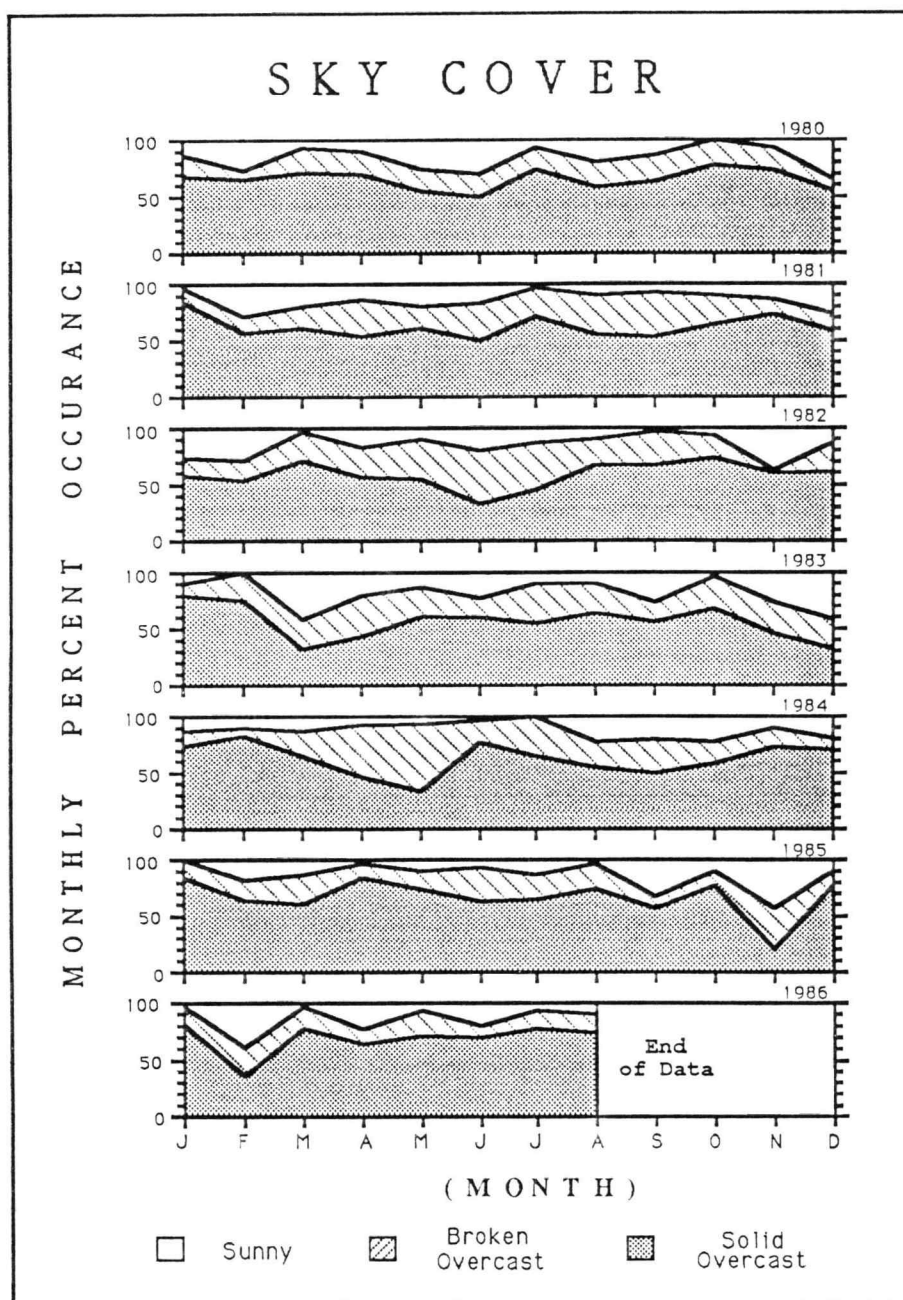
APPENDICES



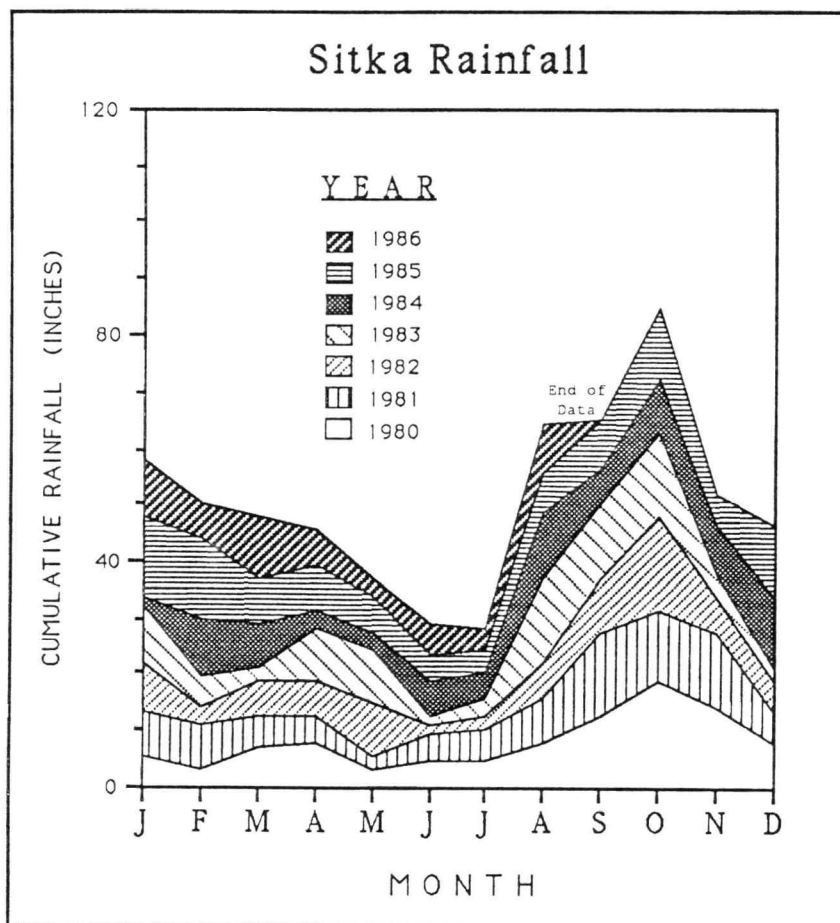
Appendix I. General water quality indicators: pH, total alkalinity and hardness measured at 1.0 m (solid lines), and mid-hypolimnion (broken lines) sampling depths at Sealion Cove Lake, Alaska (1980-1986).



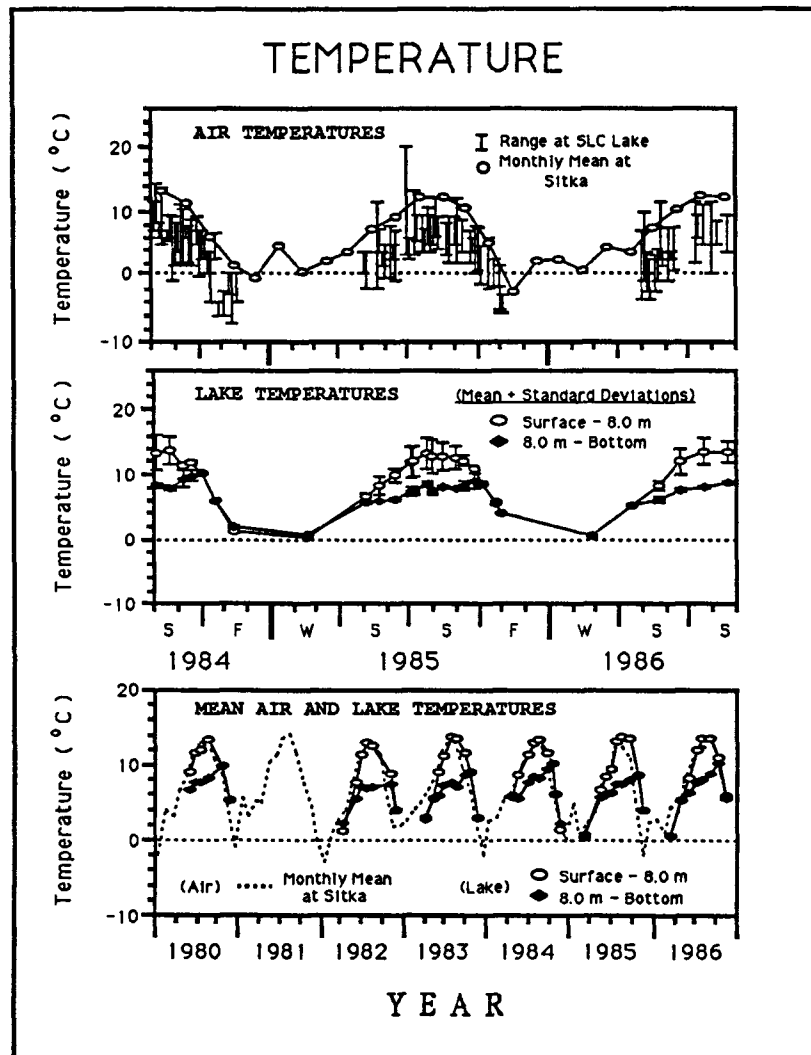
Appendix II. General water quality indicators: calcium, iron, magnesium, and reactive silicon measured at 1.0 m (solid lines), and mid-hypolimnion (broken lines) sampling depths at Sealion Cove Lake, Alaska (1980-1986).



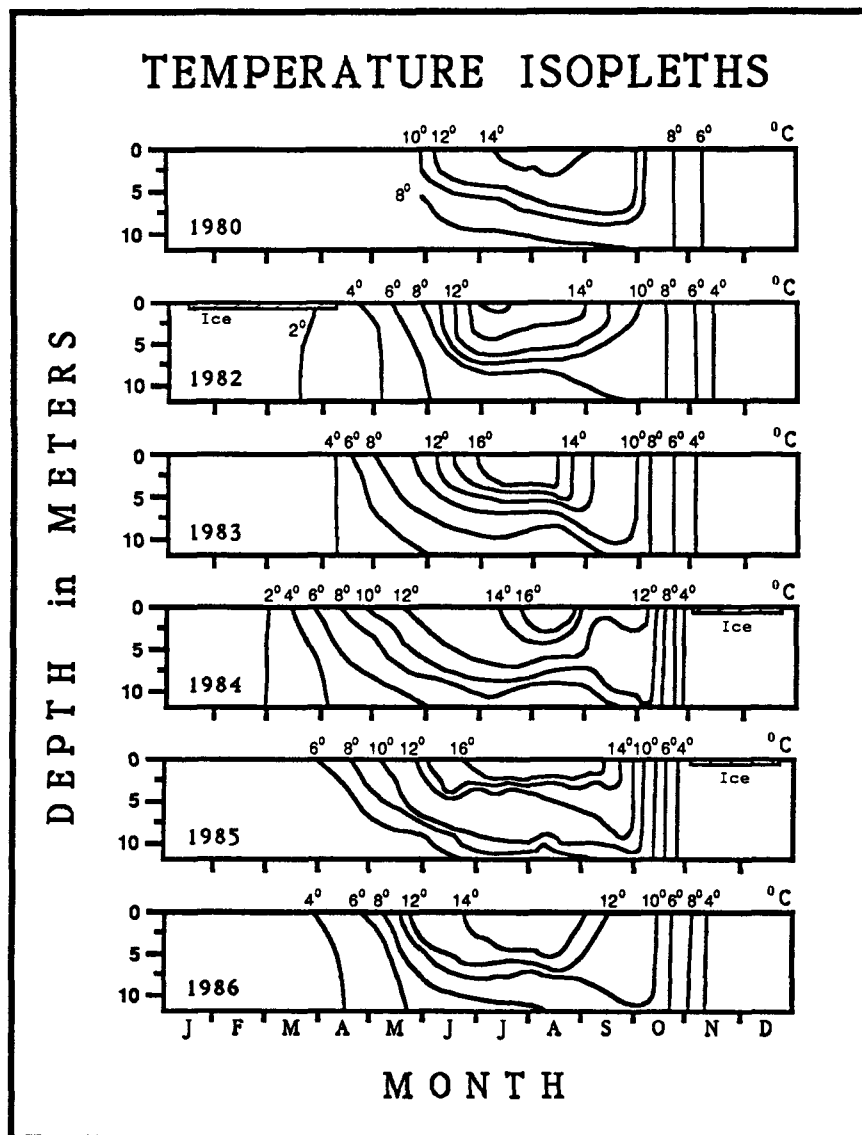
Appendix III. Sky cover observed at Sitka, Alaska as monthly percent occurrences of sunny, broken overcast, and solid overcast days (1980-1986).



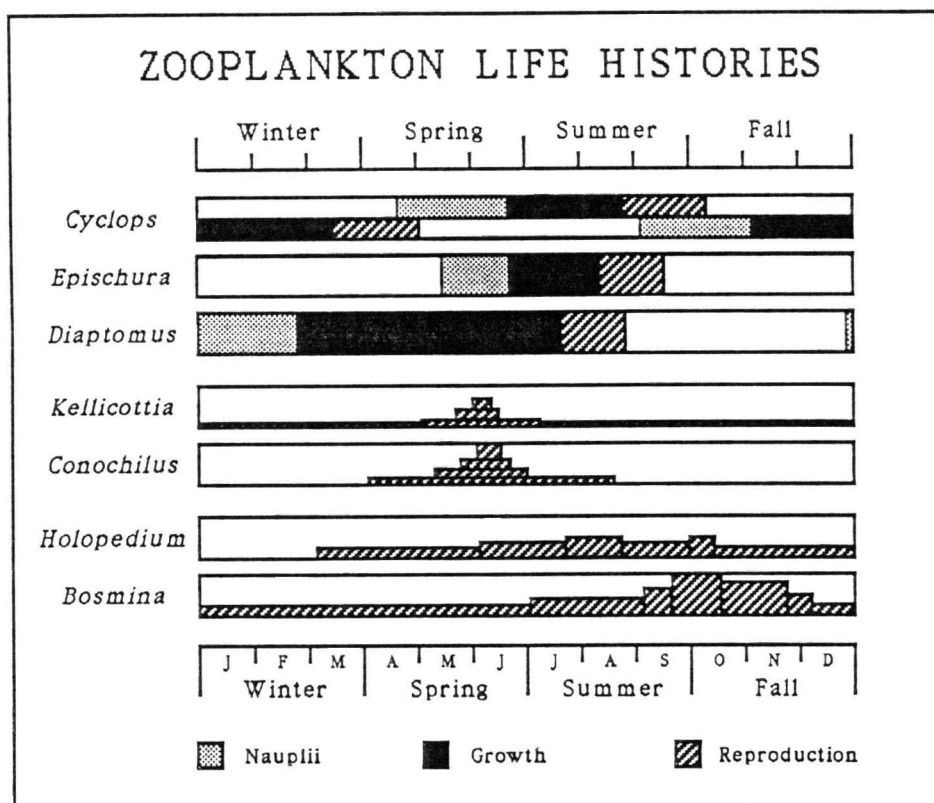
Appendix IV. Monthly rainfall at Sitka, Alaska presented as the cumulative total of seven individual years (1980-1986).



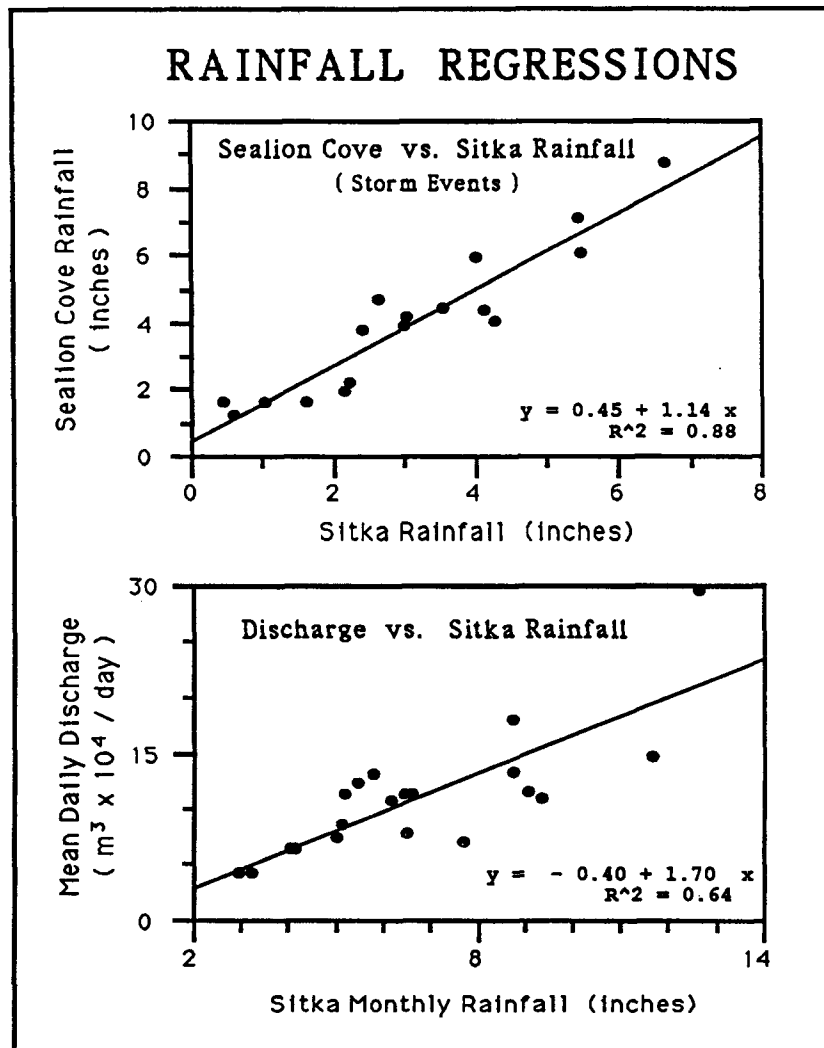
Appendix V. Air temperatures: range at study site (bars) and monthly mean for the highest and lowest daily observations at Sitka, Alaska; lake temperatures: surface (open symbol) and deep water (closed symbol) means recorded over 0.5 m intervals to a maximum depth of 11.7 m (summer 1984-summer 1986); and lake temperature overlayed on Sitka monthly mean air temperatures (broken line) for the entire study period (1980-1986).



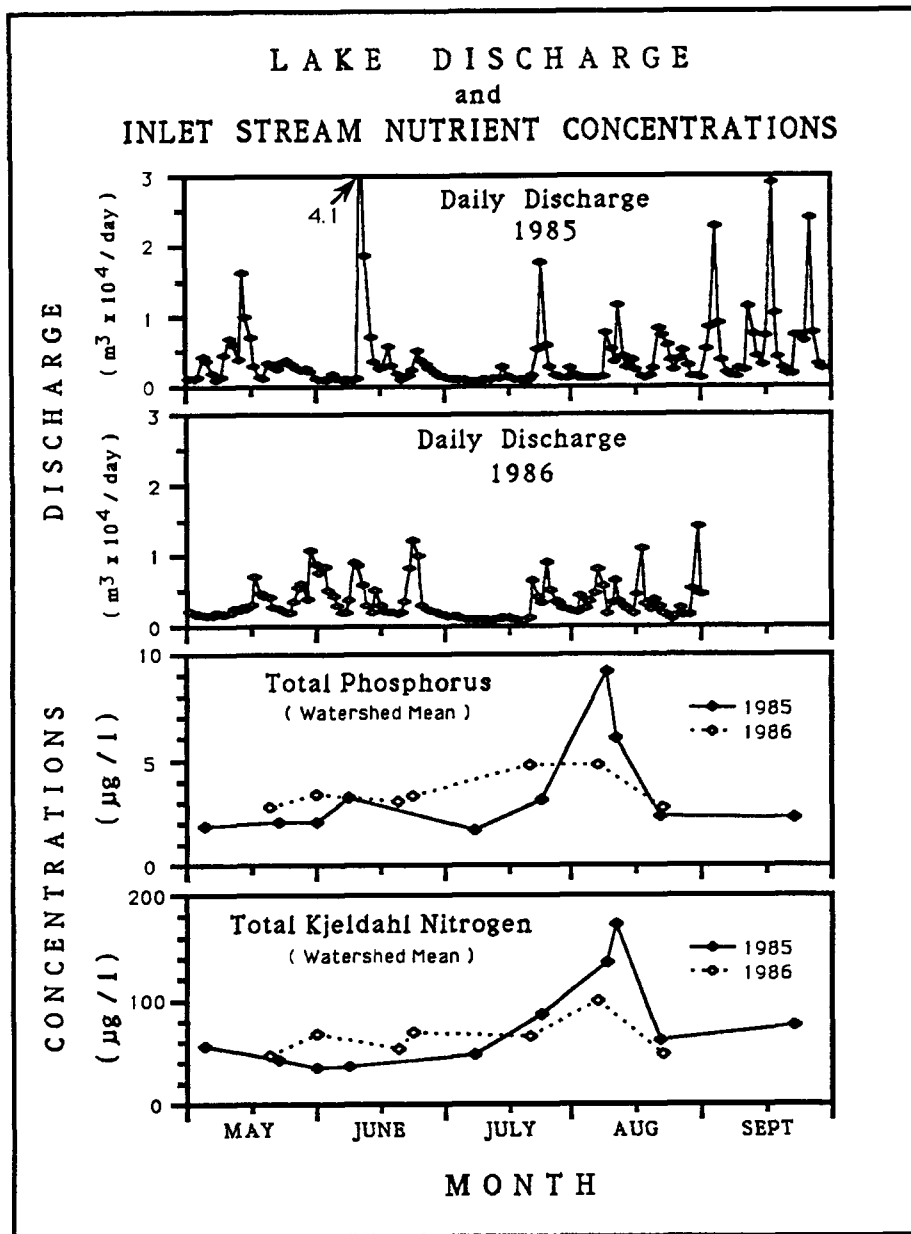
Appendix VI. Temperature profiles recorded over 0.5 m depth intervals at Sealion Cove Lake, Alaska (1980-1986).



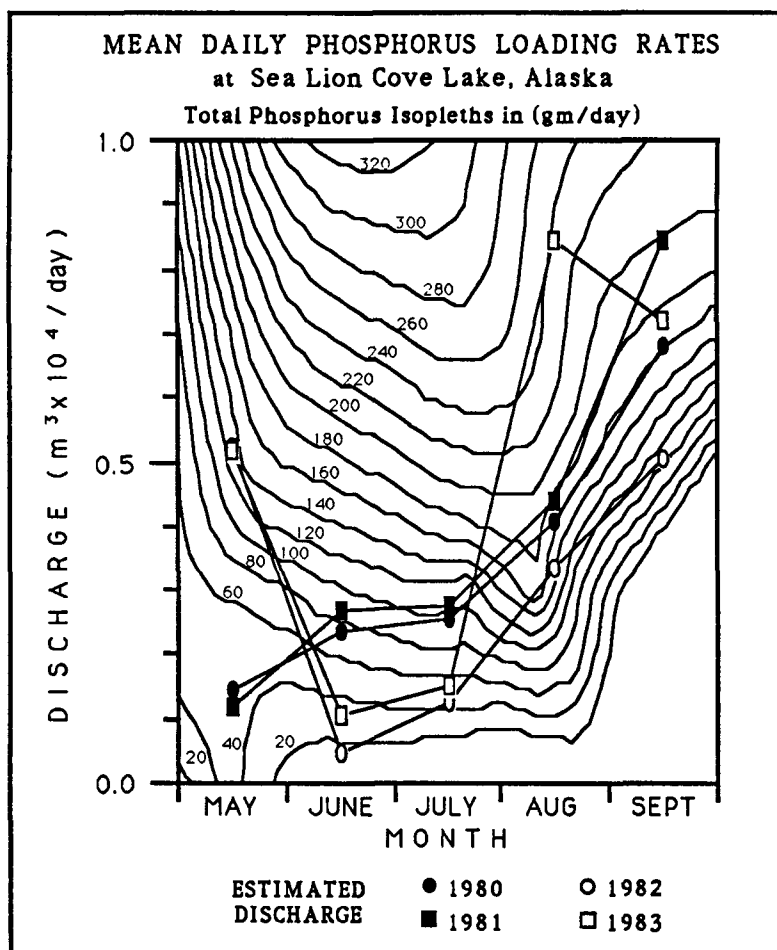
Appendix VII. Life history cycles of zooplankton occurring in Sealion Cove Lake, Alaska.



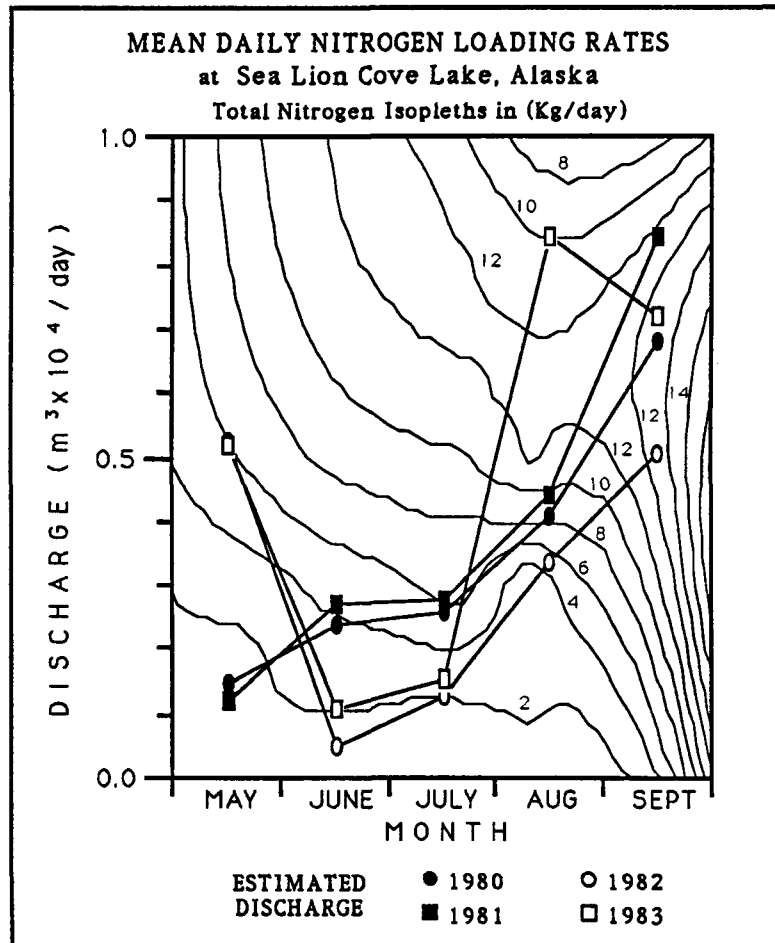
Appendix VIII. Relationships between rainfall at the study site and observations in Sitka, Alaska by storm event; and mean daily discharge versus Sitka monthly rainfall (1984-1986).



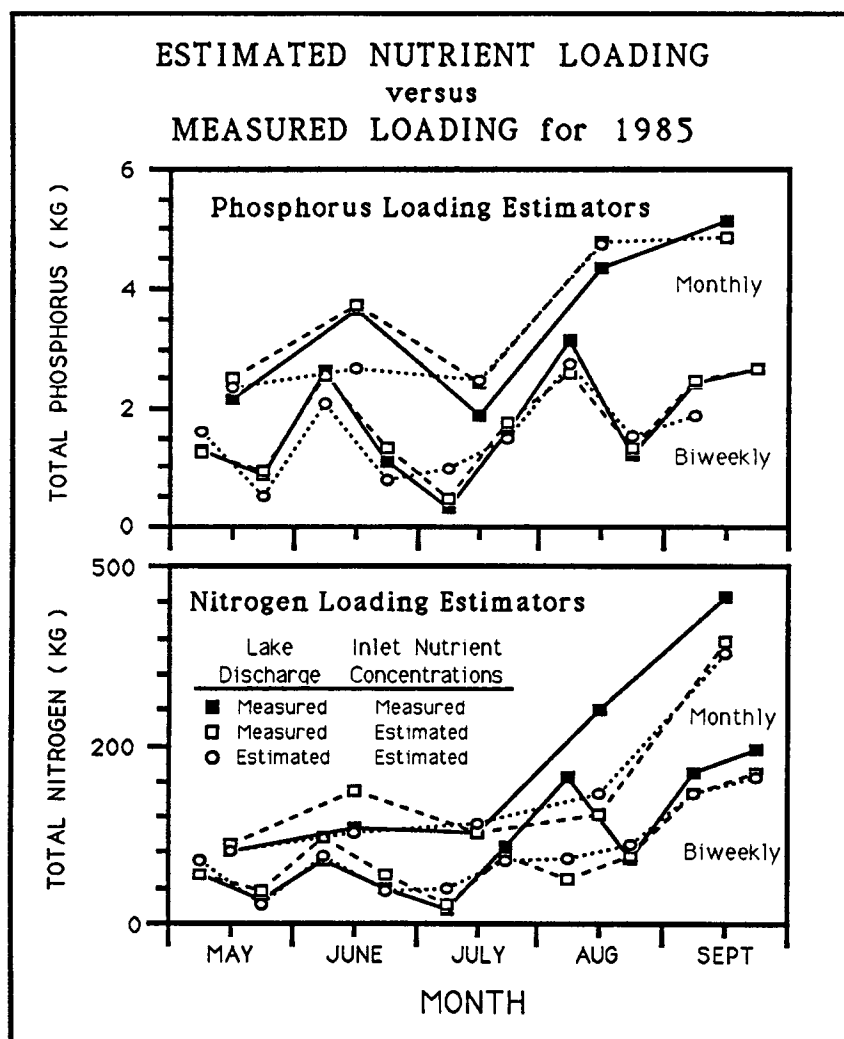
Appendix IX. Daily discharge, and watershed mean inlet total phosphorus and total Kjeldahl nitrogen concentrations at Sealion Cove Lake, Alaska in 1985 (open symbols) and 1986 (closed symbols).



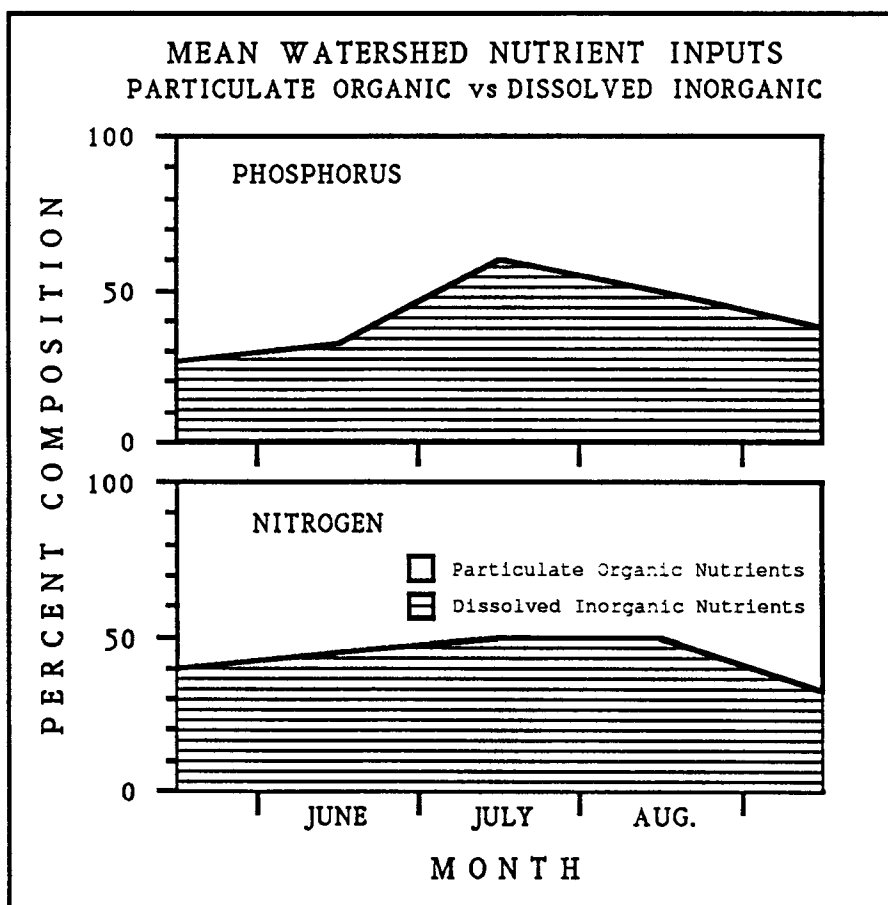
Appendix X. Mean daily total phosphorus loading (isopleths) with respect to mean monthly lake discharge and time of year. Monthly mean discharges estimated for summer months prior to 1984 were plotted on the isopleth model to calculate monthly total phosphorus loading rates for Sealion Cove Lake, Alaska.



Appendix XI. Mean daily total nitrogen loading (isopleths) with respect to mean monthly lake discharge and time of year. Monthly mean discharges estimated for summer months prior to 1984 were plotted on the isopleth model to calculate monthly total nitrogen loading rates for Sealion Cove Lake, Alaska.



Appendix XII. Test runs for the nutrient loading (isopleth-regression) model comparing results obtained with estimated parameters (open symbols) to an independent estimate calculated directly from measured parameters (closed symbols).



Appendix XIII. Percent composition of the total and dissolved fractions of phosphorus and nitrogen in the inlet streams of Sealion Cove Lake, Alaska.