The British Columbia Lake Fertilization Program: Limnological Results From the First 2 Years of Nutrient Enrichment

J. G. Stockner, K. S. Shortreed, and K. Stephens

Department of Fisheries and Oceans
Resource Services Branch
West Vancouver Laboratory
4160 Marine Drive
West Vancouver, British Columbia

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THE BRITISH COLUMBIA LAKE FERTILIZATION PROGRAM: LIMNOLOGICAL RESULTS FROM THE FIRST 2 YEARS OF NUTRIENT ENRICHMENT

by

J. G. Stockner[1], K. S. Shortreed[1], and K. Stephens[2]

[1]Department of Fisheries and Oceans

Resource Services Branch

West Vancouver Laboratory

4160 Marine Drive

West Vancouver, British Columbia

[2]Department of Fisheries and Oceans

Resource Services Branch

Pacific Biological Station

Nanaimo, British Columbia V9R 5K6

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ABSTRACT

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Limnological studies were conducted on five sockeye salmon (Oncorhynchus nerka) nursery lakes and on one lake containing landlocked sockeye (kokanee) but no anadromous fish. The lakes were fertilized with ammonium phosphate and ammonium nitrate at levels up to 505 greater than calculated annual base loads. Annual primary production ranged from 16 to 150 $gC \cdot m^{-2}$, and all but Long Lake were classed as oligotrophic. The phytoplankton populations were dominated by diatoms; blue-green algae did not increase significantly with fertilization. Annual primary production and mean annual total chlorophyll in Kennedy Lake-Clayoquot Arm were 2 times higher in 1978 (fertilized) than in 1977 (unfertilized). Algal production and biomass in the remaining 5 lakes tended to be higher in the second year of fertilization (1978) than in the first (1977). Limnological conditions in all 5 lakes are discussed, where possible, with reference to higher trophic levels.

Key words: Limonolgy, primary production, phytoplankton, lake fertilization, sockeye salmon, nursery lakes.

RÉSUMÉ

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Des études limnologiques ont été menées dans cinq lacs d'élevage du saumon rouge (Oncorhynchus nerka) et dans un lac contenant des saumons rouges landlockés (kokani), mais aucun poisson anadrome. On a fertilisé des lacs avec du phosphate et du nitrate d'ammonium à des concentrations pouvant être de 50% supérieures aux charges de base annuelles calculées. La production primaire annuelle allait de 16 à 150 gC/m^2, et tous les lacs, à l'exception du lac Long, ont été jugés oligotrophes. Les populations de phytoplancton étaient dominées par les diatomées; la fertilisation n'a pas fait augmenter de facon notable la présence des cyanophycées. La production primaire annuelle et la moyenne annuelle totale de la teneur en chlorophylle dans le lac Kennedy et le bras Clayoquot étaient deux fois plus élevées en 1978 (après fertilisation) qu'en 1977 (avant fertilisation). La production d'algues et la biomasse des cinq autres lacs semblaient plus élevées la deuxième année de fertilisation (1978) que la première (1977). Les conditions limnologiques des 5 lacs sont étudiées, autant que possible, au regard des niveaux trophiques supérieurs.

Mots clés: Limnologie, production primaire, phytoplancton, fertilisation des lacs, saumon rouge, lacs d'élevage.

INTRODUCTION

The practice of adding inorganic and organic substances to lakes and ponds to increase production has been an integral part of Asian fish culture for centuries. Its historical development in Europe has been reviewed by Nees (1946). In North America the fertilization of lakes to improve fish production was first attempted on a scientific basis by Juday and Schloemer (1938) in an oligotrophic Wisconsin lake and later by Swingle and Smith (1938), Surber (1943), Swingle (1947) and Ball (1949) in productive lakes and reservoirs in the Eastern and Southeastern United States. In Canada, Huntsman(1948),Smith (1945, 1948, 1955) and Langford (1950) attempted to increase salmonid production by additions of fertilizer to small lakes and streams. In Scotland, fertilization to improve trout production in tarns was intensively studied by Brook (1956), Brook and Holden (1957), Holden (1959, 1961) and Morgan (1966). Perhaps more relevant to the objectives of this report, however, was the work of Nelson and Edmondson (1955) on the fertilization of Bare Lake, Alaska. Juday et al. (1932) hypothesized that a paucity of nutrients in Karluk Lake, Alaska, was one of the primary factors influencing growth and survival of juvenile sockeye salmon. A more extensive examination of a similar hypothesis was begun in 1969 in Great Central Lake, Vancouver Island (LeBrasseur et al. 1978).

The lake enrichment program currently underway in British Columbia under the auspices of the Federal-Provincial Salmonid Enhancement Program (SEP), is an expansion of the Great Central Lake experiment to include a greater variety of morphometric and trophic lake types found in abundance along the mainland coast of British Columbia. Although considerable work has already been done on nutrient enriched lakes (Edmondson 1969, Lund 1969, Schindler 1975, Fee 1979), seldom has it been carried out on this scale in such large lakes or with the specific objective of increasing the growth and/or numbers of juvenile sockeye salmon.

To gain a better understanding of the impact of fertilizing these oligotrophic lakes a program was conducted concurrent with the fertilization to follow changes in lake physics, chemistry, and biology in 1977 and 1978. Five of the lakes had little or no pretreatment studies and results are strictly a documentation of limnological conditions during fertilization. The sixth lake (Kennedy) had a one-year intensive prefertilization study in 1977, and results of treatment of the Clayoquot Arm in 1978 are compared with findings from the pretreatment study. This report presents, discusses, and summarizes the autotrophic production response to nutrient addition in six sockeye salmon nursery lakes in British Columbia, and where possible refers to the impact of the perturbation on higher trophic levels.

DESCRIPTION OF STUDY AREA

Pertinent geographic and physical data for each lake are presented in Table 1 and Fig. 1. The lakes studied are oligotrophic and warm monomictic with the exception of Mohun Lake, which freezes over in winter and is dimictic. All lakes except Long Lake are located on Vancouver Island. The watersheds of the six lakes are exposed to the cool Mediterranean climate of the British Columbia coast, with wet winters and warm, dry summers. Kennedy, Henderson, and Hobiton lakes lie in the western hemlock (*Tsuga heterophylla*) biogeoclimatic subzone with high annual rainfall (>200 cm) and warm temperatures ($\bar{x}$ = 8°C). Great Central Lake lies in central Vancouver Island where drier winters and more extreme temperature conditions prevail (Table 1). Mohun Lake is located in the rainshadow of Vancouver Island mountains and has a drier climate. Douglas Fir (*Pseudotsuga menziesii*) is the dominant forest vegetation. Long Lake is situated on the central mainland coast and has higher annual rainfall and colder winter temperatures than the lakes on the west coast of Vancouver Island (Table 1).

The six lakes range in transparency from the very clear Great Central Lake to the dystrophic(humic stained) Long Lake (mean Secchi depths are 12.4 and 5.2 m, respectively). Mean depths range from 14 m in Mohun Lake to 200 m in Great Central Lake, and all lakes are fast flushing with water residence times ranging from 10 years for Great Central Lake to 1 year for Hobiton Lake (Table 1). Lake areas range from 50.6 km^2 for Great Central Lake to 3.6 km^2 for Hobiton Lake.

All lakes but Mohun support populations of anadromous sockeye salmon; in Mohun Lake a population of landlocked sockeye (kokanee) occurs. Of the six lakes only Mohun, Kennedy, and Great Central lakes are accessible by road and support limited amounts of recreational boating and sports fishing.

METHODS

Fertilization

Dissolved ammonium nitrate (NH_4NO_3) and ammonium phosphate ($(NH_4)_3PO_4$) in an atomic ratio of 10:1 (N:P) were added once weekly to surface waters of each lake in pre-selected areas using a DC-6B water bomber (Plate 1). The nutrient solution was released from the tail of the aircraft as a spray of raindrop consistency from an altitude of approximately 30 m. On Mohun Lake, fertilizer was added in the wake of a slowly moving boat. Details of nitrogen and phosphorus loading rates are presented in Table 2. In 1977, fertilization of all lakes began June 1 and ended October 29, but in 1978 it commenced 6 weeks earlier, April 19, and was terminated on October 9.

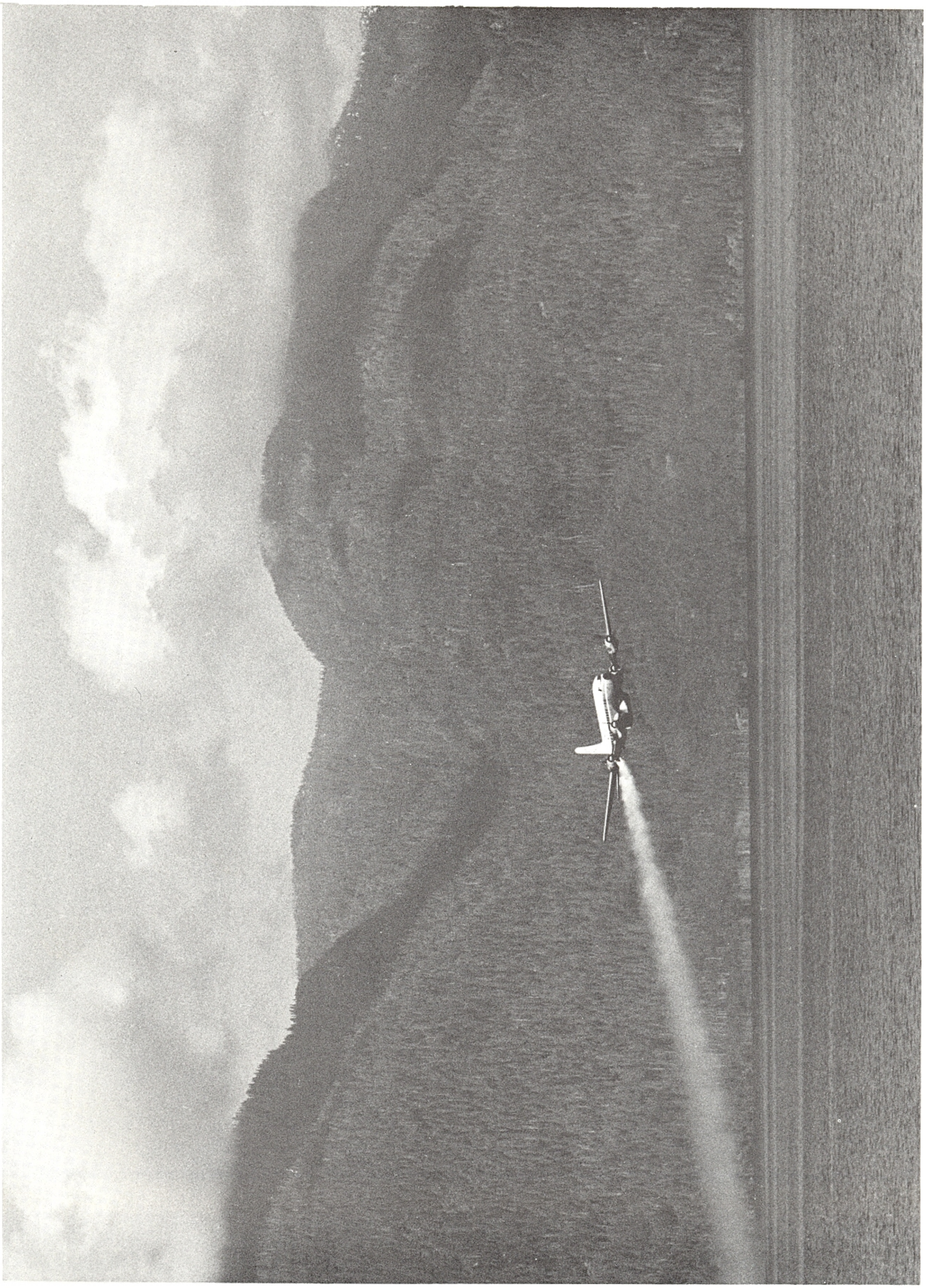

Plate 1. The DC-6B water bomber conducting the fertilization of Great Central Lake in August, 1978.

Sampling and analysis

On all lakes, except Great Central and Mohun, sampling was done from a float-equipped de Havilland Beaver aircraft. Great Central and Mohun lakes were accessible by road and were sampled from a boat.

Sampling stations were selected on the basis of lake morphometry. Only one station was sampled in the smaller lakes (Henderson, Hobiton and Mohun); two stations were selected in Long and Great Central lakes, and three in multibasin Kennedy Lake.

In 1977, all sampling stations, except those on Kennedy Lake and Station 1 on Great Central Lake, were situated within fertilized areas. In 1978, Station 3 on Kennedy Lake, Station 1 on Great Central, and Station 3 on Long Lake were located outside fertilized areas. In 1977, all lakes were sampled biweekly; in 1978 sampling was restricted to once monthly except on Kennedy Lake, where biweekly sampling was maintained.

Water clarity and light extinction with depth were measured with a standard 22-cm Secchi disk and a Montedoro-Whitney LMT-8A Illuminance meter. The natural logarithm of light intensity was plotted against depth. The slope of the line gave mean extinction coefficient (k).

A bathythermograph (BT) was lowered to 50 m to obtain a temperature-depth profile. Surface temperature for BT calibration was measured with a standard bucket thermometer.

A 3-L Van Dorn bottle was used to take water samples from 0, 1, 3, 5, 7.5, 10, 20, and 30 m, except on Long Lake, where a 2 m sample was substituted for the 30 m sample. A 2-L plastic bottle was filled from each sampling depth and transported to the laboratory in a light-tight cooler.

A portion of each sample was filtered through an ashed and washed Whatman GFC filter and used for analysis of soluble reactive phosphorus (SRP), using Golterman's (1969) method. Total carbonate alkalinity was determined using the standard potentiometric method as described by APHA (1975). Total phosphate-phosphorus (TPO_4-P), soluble reactive phosphorus (SRP), nitrate-nitrogen (NO_3-N) and inorganic reactive silicate (SiO_4-Si) were analyzed according to the methods of Golterman (1969) and Traversy (1971).

A 1-L sample was filtered onto a 47-mm diam., 0.8-μm pore size, Millipore AA filter at a vacuum pressure not greater than 20-cm Hg for total chlorophyll determination. Filters were frozen until analysis, which consisted of macerating the filter in 90% acetone and analyzing the filtrate in a Turner Model 111 fluorometer according to the method of Strickland and Parsons (1972).

Two 125-mL light bottles were filled at each sample depth and one 125-mL dark bottle each at 1, 5, and 20 m. A solution of bicarbonate carbon-14 was prepared with an activity of approximately 75 $kBq \cdot mL^{-1}$, and filtered 1-mL aliquots were injected into each bottle. Two scintillation vials containing 15 mL of a scintillation cocktail (1 part 2-ethoxyethanol, 1 part toluene, and 0.82 part Amersham-Searle Spectrafluor) were inoculated with the radioisotope solution for calibration purposes. After inoculation, the bottles were shaken and suspended horizontally from clear Plexiglass holders at the original sample depths. After a 2-to 4-h incubation, samples were placed in light-tight boxes and filtered within 2 h. Samples were filtered onto 47-mm diam., 0.45-μm pore size, Millipore HA filters at a vacuum pressure not exceeding 20-cm Hg and placed in scintillation vials containing the cocktail mentioned previously. Vials were counted in a Searle Analytic Isocap 300 Liquid Scintillation Spectrometer. Carbon uptake ($mg \cdot m^{-3} \cdot h^{-1}$) was calculated using the formula of Strickland and Parsons (1972) and converted to daily production ($mg\ C \cdot m^{-3} \cdot d^{-1}$) by calculating the proportion of total daily insolation available during the incubation period. Insolation data were obtained from a Belfort Pyrheliometer situated at the Pacific Biological Station in Nanaimo, B. C. Volumetric production rates were integrated over depth and over time to give $mg\ C \cdot m^{-2} \cdot d^{-1}$ and $g\ C \cdot m^{-2} \cdot yr^{-1}$, respectively.

A 100-mL aliquot was fixed with Lugol's acetate solution for use in phytoplankton enumeration and identification. Phytoplankton were counted and identified using a Wild M40 inverted microscope according to Utermöhl's (1958) settling method. Cell numbers were converted to volumes using values calculated by Stockner and Armstrong (1971) and Stockner and Shortreed (1975), although some direct estimates were made by converting cell dimensions to known geometric shapes.

On one occasion (July, 1978) carbon uptake, total chlorophyll, nutrient concentration, light and temperature were measured daily, from the day before a fertilizer application until three days after.

The paired "t" test statistic was used to compare values between stations within lakes and among the six lakes (Sokal and Rohlf 1969).

The nearest and most representative climatological station was selected for each lake, and Thornthwaite climatic water balance tabulations (Phillips 1976) and climatic normals (Atmospheric Environment Service 1971) were used with hydrologic maps of annual precipitation, small lake evaporation, evapotranspiration, and runoff (CNC/IHD 1978) to estimate these parameters for each lake and drainage area. Small-lake evaporation values were reduced 10% for extrapolation to a large deep lake (Spring and Schaefer 1974), and corrections for drainage area elevation as suggested by Schaefer (1976) were applied to runoff estimates. Annual runoff, lake precipitation, and lake evaporation were used to estimate annual lake outflow and, together with lake volume to estimate theoretical water residence time of each lake (Table 1).

Vollenweider's (1976) phosphorus loading equations were used to determine the critical specific loading L_c ($mg\ P \cdot m^{-2} \cdot yr^{-1}$) $= \frac{10 \cdot \bar{z}\ (1+\sqrt{Tw})}{Tw}$ and specific surface loading L_p ($mg\ P \cdot m^{-2} \cdot yr^{-1}$) $= \frac{P \cdot \bar{z}\ (1+\sqrt{Tw})}{Tw}$ for each lake where:

$\bar{z}$ = mean depth (m)

Tw = water residence time (yr)

P = spring overturn phosphorus concentration ($mg \cdot m^{-3}$).

RESULTS

Phosphorus loading

Calculated base loads of phosphorus (Lp) were higher in 1978 than in 1977 in all lakes except Kennedy Lake-Clayoquot Arm owing to a higher concentration of total phosphorus in the lakes (Table 2). The contribution of sockeye carcasses to the total load of phosphorus in each lake was quite variable among lakes and years. Highest contributions (10% of total load of phosphorus) by sockeye occurred in Great Central Lake and Kennedy Lake-Clayoquot Arm in 1978 and the lowest (1% of total load of phosphorus) in Henderson Lake in both 1977 and 1978. In all cases the phosphorus load from fertilizer was considerably greater than that from sockeye (Table 2). Phosphorus loads from fertilizer were 50 to 60% of the total load of phosphorus in Long Lake, Henderson Lake (1977 only), and Kennedy Lake-Clayoquot Arm (1978 only), but in other lakes and/or years, contribution by fertilizer to the total load of phosphorus ranged from a low of 15% in Hobiton (1978) to a high of 42% in Great Central Lake (1977). The critical phosphorus load (L_c) for each lake was computed (Vollenweider 1976); in no lake was the actual load near the critical value. Only in Henderson and Mohun Lakes in 1978 were phosphorus loads as high as 50% of estimated L_c. Natural phosphorus loads for each lake varied owing to annual differences, primarily in precipitation and secondarily in numbers of sockeye carcasses present in the lakes.

Physico-chemical

Mean Secchi depth ranged from 12.4 m at Station 1 in Great Central Lake in 1977 to 4.8 m in Long Lake in 1978 (Table 3A and B). Highest recorded value (>15.0 m) occurred in Great Central Lake in winter and the lowest (3.5 m) in Long Lake in summer. Mean extinction coefficients ranged from 0.19 at Station 2 in Great Central Lake to 0.69 at Station 1 in Long Lake (Table 3A and B). Distinct seasonal variation in water clarity was generally not apparent, although highest extinction coefficients (and lowest Secchi depth) were usually associated with bloom conditions found in May or June and in September.

All lakes developed a relatively stable summer stratification in both study years, although depth of mixing varied among lakes and years (Fig. 2-6). Mixed layer depth tended to be greater and stratification weaker in Long Lake than in other study lakes. The average mixing depth also tended to be greater in all lakes in 1978 than in 1977.

Highest NO_3-N (58 $\mu g.L^{-1}$) concentration was recorded at Station 1 in Long Lake in April of 1977. At all stations in all lakes NO_3-N concentrations below the detectable limit of 1 $\mu g.L^{-1}$ were recorded in summer, and the period of nitrate depletion tended to be longer in 1978 than in 1977 (Appendix Fig. 1 and 2). Mean annual NO_3-N concentrations ranged from a low of 5 $\mu g.L^{-1}$ at Station 1 in Great Central Lake in 1977 to a high of 25 at Station 2 in Long Lake in 1978 (Table 3A and B).

Mean concentrations of TPO_4-P ranged from 1.6 $\mu g \cdot L^{-1}$ at Station 2 in Kennedy Lake in 1977 to 5.2 in Henderson Lake in 1978. There was considerable seasonal TPO_4-P variation within lakes and mean annual concentrations were higher in 1978 than in 1977 in all lakes (Table 3A and B, Appendix Fig. 3 and 4). Soluble reactive phosphorus (SRP) concentration was measured in 1978 only and ranged from 3.1 $\mu g \cdot L^{-1}$ at Station 2 in Long Lake in August to <1.0 in the summer in most lakes (Table 3B). Mean SRP concentrations were 2.0 $\mu g \cdot L^{-1}$ in all lakes,but there was considerable variation with no clear seasonal trends apparent. Due to the rapid biological uptake of both nitrate and phosphate following each weekly fertilization, elevated concentrations of these nutrients were recorded only when sampling was carried out in the fertilized zone of a lake within 24 hours after a fertilizer application.

The highest recorded concentration of SiO_4-Si (1959 $\mu g \cdot L^{-1}$) was found in Hobiton Lake in April, 1978, and the lowest (155) at Station 2 in Long Lake in August, 1978. Mean concentrations of SiO_4-Si ranged from 1351 $\mu g \cdot L^{-1}$ in Hobiton Lake in 1977 to 616 in Henderson Lake in 1978 (Table 3A and B, Appendix Fig. 5 and 6).

Mean total dissolved solids (TDS) ranged from 82.5 $mg \cdot L^{-1}$ in Henderson Lake to 12.8 at Station 3 in Long Lake (1978) (Table 3A and B).

Biological

Epilimnetic total chlorophyll ranged from 6.0 $mg \cdot m^{-3}$ in Long Lake in August, 1978, to 0.1 at Station 2 in Kennedy Lake in January, 1978. Mean annual chlorophyll concentrations ranged from 0.7 in Kennedy Lake in 1977 to 2.3 in Long Lake in 1978, and were generally higher in 1978 than in 1977 (Table 4A and B). Although considerable seasonal variation in total chlorophyll occurred within lakes, sharp spring and fall peaks were generally not apparent (Appendix Fig. 7 and 8). Maximum values occurred most commonly in fall, and were significantly ($p<.05$) higher at fertilized stations than at unfertilized stations in Kennedy and Great Central Lakes, but this trend was not apparent in Long Lake. The lack of a significant difference in concentrations between stations in Long Lake was due to an exceptionally high chlorophyll value at the unfertilized station in August 1978 (6 $mg \cdot m^{-3}$).

Annual primary production ranged from 16 g $C \cdot m^{-2}$ at Station 1 in Great Central Lake in 1977 to 149 at Station 2 in Long Lake in 1978, and values tended to be higher in 1978 than in 1977 (Table 4A and B, Fig. 7 and 8). Mean hourly carbon uptake ($mg \cdot m^{-3} \cdot h^{-1}$) was highest at Station 2 in Long Lake (5.08) and lowest in Great Central (0.41). Mean assimilation number ranged from 0.54 at Station 1 in Great Central Lake in 1978 to 1.96 at Station 1 in Long Lake in 1977. As with chlorophyll, considerable seasonal variation in carbon uptake occurred within and among lakes, although distinct spring and fall maxima were not readily apparent (Fig. 7). Uptake rates within lakes during the fertilization period were significantly higher ($p<.05$) at fertilized stations than at unfertilized stations. Production-depth profiles in Henderson, Hobiton, Kennedy, Long, and Mohun Lakes showed pronounced maxima, varying in depth from 2 to 5 m. In Great Central Lake, there was seldom a distinct peak with depth except for 2 days immediately following fertilization when a sharp peak occurred at 3 m.

Mean annual phytoplankton numbers ranged from $9.06 \times 10^8 \cdot m^{-3}$ at Station 2 in Kennedy Lake (1977), to 23.6×10^8 at Station 2 in Great Central Lake (1978). Phytoplankton volumes ranged from 65 $mm^3 \cdot m^{-3}$ at Station 1 in Long Lake (1977) to 4414 at Station 2 in Great Central Lake in 1978 (Table 4A & B). Lowest algal numbers and volumes ($5.70 \times 10^7 \cdot m^{-3}$ and 3.0 $mm^3 \cdot m^{-3}$, respectively) were recorded at Station 2 in Long Lake in April of 1977. Highest numbers and volumes ($1.19 \times 10^{10} \cdot m^{-3}$ and $2.38 \times 10^4 mm^3 \cdot m^{-3}$) occurred in June, 1978, at Station 2 in Great Central Lake.

On a volume basis, diatoms were the dominant phytoplankton in both study years in all lakes except Long Lake in 1977, where small chrysophyceans were dominant. Common diatoms in the study lakes were Rhizosolenia spp., Fragilaria crotonensis, F. vaucheriae, Cyclotella stelligera and Achnanthes minutissima (Table 5). Non-diatom species that were common and on occasion numerically dominant were Rhodomonas sp., Ochroomonas sp., Dinobryon sp., the blue-green Merismopedia sp.; and an unidentified flagellated species of very small size (10 μm^3). In Long Lake Cosmarium sp. and the dinoflagellate Peridinium sp., and in Mohun Lake Asterococcus sp. were numerically dominant during the summer in 1978.

Vernal blooms in all lakes occurred several weeks earlier in 1978 than in 1977 and were dominated by the diatoms Rhizosolenia spp. and Cyclotella spp. In Long Lake, Fragilaria crotonensis, F. vaucheriae, and A. minutissima were most important (Fig. 9-11). Algal biomass was greater in 1978 than in 1977 in all but one of the lakes, due primarily to an increased diatom abundance. The exception was Henderson Lake, where Rhizosolenia spp. was much less numerous in 1978 and algal volume was consequently lower (Table 5, Fig. 9). Blue-green algae (mainly Merismopedia sp.) were common in summer in both study years, but in all lakes blue-greens were less numerous in 1978 than in 1977 (Fig. 9-11). Fall diatom blooms occurred in all lakes except Long Lake and dominant diatoms were: Cyclotella stelligera, Cyclotella spp., and Melosira italica in Hobiton Lake; Rhizosolenia spp. in Henderson Lake (1977) and Asterionella formosa (1978); and Rhizosolenia spp. in Great Central Lake, and at Station 2 in Kennedy Lake; Tabellaria fenestrata in Mohun Lake; and Cyclotella stelligera, Cyclotella spp. and Achnanthes minutissima at Station 3 in Kennedy Lake (Fig. 9-11). Algal species other than diatoms and blue-greens showed little seasonal variation or succession other than gradually becoming more numerous during the growing season. Although phytoplankton numbers and biomass in Kennedy Lake (Station 2) were greater in the fertilized than in the unfertilized year, species composition was similar between years.

Fertilization response

In the short-term experiment at Station 2 in Great Central Lake to determine changes in production rates for several days after a fertilizer application, light conditions were identical throughout the experiment: skies were uniformly clear, winds were light, and water transparency did not change (Secchi depth = 12.5 m). On the day of fertilization within 15 - 20 minutes after the fertilizer was applied, concentrations of SRP were 3 to 4 times above background levels at depths of 1 and 2 m only (epilimnion depth was 15 m), and concentrations of NO_3-N were 12 to 15 times control station levels at 1 and 2 m (Fig. 12). By mid-morning of the day following fertilization, SRP had returned to pre-fertilization levels, but NO_3-N did not return to pre-fertilization levels until two days following treatment. Nutrient concentrations at the untreated station (control) remained relatively constant throughout the 4 day period (Fig. 12).

Phytoplankton carbon assimilation profiles on the day of fertilization were similar to profiles and uptake rates on the day before fertilization. However, on the first day following fertilizer application, carbon uptake was 1.6x higher than on the day of fertilization, and on the second day uptake rates were almost twice those observed at the untreated control station (Fig. 13). These increases in carbon assimilation occurred only in the surface layers (0-5 m) of the fertilized region, while throughout the experimental period, daily carbon uptake in the unfertilized zone remained uniform and unchanged (Fig. 13). The response of the various phytoplankton size fractions to fertilization at the same station was monitored in 1978, and results showed that nannoplankton accounted for over 70% of the total daily carbon uptake and for over 75% of the annual carbon assimilated (Fig. 14) (Costella et al. 1979).

DISCUSSION

The large lakes of Vancouver Island and the central and south mainland coast of British Columbia are mainly oligotrophic (nutrient poor); and the majority of the watersheds are relatively undisturbed (some logging has occurred but its impact is short term). The oligotrophic condition has likely prevailed since recession of the last glaciation in the region, some 9 to 11,000 years B.P. (Armstrong et al. 1965). A state of trophic equilibrium has been sustained in each lake by several factors, the most notable being a high flushing rate caused by high annual rainfall on impervious bedrock watersheds with little overburden and poor water holding capacity. The oligotrophic nature of the six study lakes is best exemplified by their low ambient nutrient concentrations, low phytoplankton biomass (chlorophyll), and low rates of annual primary production. The doubling of annual base loads of nitrogen and phosphorus has not perceptibly altered the trophic state in those lakes in which comparisons are possible (i.e. pre-fertilization data available). This is in sharp contrast to other recent whole-lake fertilization studies where greater nutrient inputs to smaller, shallower lakes have led to striking changes in trophic state (Donaldson et al. 1971, Schindler 1975, Fee 1979). The addition of fertilizer to Kennedy and Great Central lakes, and possibly all treated lakes, increased phytoplankton production and zooplankton abundance (Rankin et al. 1979). Preliminary results from Kennedy Lake -Clayoquot Arm suggest that size of underyearling sockeye increased markedly in 1978, a fertilized year, (T. Gjernes, unpublished data).

Comparison between fertilized and unfertilized years – Kennedy Lake

The most valid interpretations of lake response to treatment come from comparisons of conditions before and after the fertilization of Kennedy Lake - Clayoquot Arm. An approximate doubling of the base phosphorus load (L_p) to Clayoquot Arm resulted in a more than twofold increase in annual primary production and a concomitant increase in all related biological variables (Table 6). Dissolved phosphorus remained at or below the detection limit throughout the growing season, but nitrate-nitrogen remained above 5 $\mu g.L^{-1}$ in 1978, while in 1977, the pre-treatment year, it was depleted for most of the summer period. Increased diatom abundance in 1978 resulted in lower silicon concentrations, but not to levels of potential limitation (Lund 1950, Schelske 1979). The fertilization in 1978 increased the magnitude of summer and especially autumn plankton biomass peaks, and the numbers of rotifers increased fivefold over 1977 values (Rankin et al. 1979) (Fig. 15), consistent with the observations of LeBrasseur and Kennedy (1972) on Great Central Lake after the first two years of treatment. The increase in rotifers, and to a lesser extent the abundance of the smaller Bosmina coregoni, was likely attributable to two factors: more intense selective grazing in 1978 by pelagic sockeye and sticklebacks, the latter being present in much greater numbers in 1978 (Table 7), and to markedly increased food supply in 1978. These observations are consistent with the recent studies by Lynch (1979) who showed that under strong vertebrate grazing pressure, small Bosmina and rotifers increase in abundance, and by Gliwicz (1969, 1975) and McCauley and Briand (1979) who documented a preference for ultra-and nannoplankton by most pelagic zooplankton. The standing stocks of juvenile sockeye in Clayoquot Arm were similar in both years; however, the average size of smolts was 1.98 g in 1978 (untreated) and 2.55 in 1979 (treated) (T. Gjernes, unpublished data). These data strongly suggest a significantly increased flow of energy to our target organism. The highly significant increases in phytoplankton in Kennedy-Clayoquot in 1978 are believed to be related to the fertilization and not to yearly climatic variations, for at Station 3 in the untreated Main Basin of Kennedy Lake, no significant differences were observed between years in all limnological variables measured (Table 8).

Comparisons between Great Central and Long lakes after two years of treatment

The limnology of the remaining four Vancouver Island lakes (Great Central, Henderson, Hobiton and Mohun) after two years of treatment was similar to that just described for Kennedy-Clayoquot in 1978, with some observed differences in timing of seasonal biomass peaks and in the relative abundance and species composition of plankton populations. These differences were attributable to local climatic differences (coastal fog and low cloud affecting Hobiton and Henderson, and less cloud and warmer temperatures influencing Great Central and Mohun), to basin morpho-edaphic variation, and to hydrologic differences.

The limnology of Long Lake after fertilization was markedly different than that seen in Vancouver Island lakes and a limnological comparison between Long and Great Central lakes is informative, because they represent the two extremes of responses observed to date (Table 9).

The most notable physico-chemical differences were related to the greater abundance of refractory organics (e.g. humics) in Long Lake and their paucity in Great Central Lake. Their presence markedly reduced the depth of the euphotic zone in Long Lake and led to a Findenegg (1964) Type I production-depth profile as contrasted with the Type II profile for Great Central Lake (Fig. 16). Concentrations of dissolved phosphorus were similar in both lakes, but at spring overturn nitrate-nitrogen levels were five times greater in Long Lake, while silicon levels were slightly higher in Great Central than in Long Lake. Bacterial biomass was twofold higher at spring overturn in Long Lake (E. MacIsaac, personal communication), but phytoplankton numbers were nearly identical (Table 9). Phytoplankton volume was almost 200 times greater in Great Central Lake owing to the presence of a large standing stock of Rhizosolenia eriensis in this lake and a paucity of large diatoms in Long Lake. The difference in phytoplankton volumes resulted in a much higher algal reproductive rate (Cushing 1976) in Long Lake than in Great Central Lake, as well as a greater phytoplankton turnover rate in the fertilized region of Long Lake than in the untreated region (Fig. 17). The differences between stations were not as large in Great Central Lake, except in the fall period, when Rhizosolenia spp. decreased in abundance at the treated station. Primary production was far higher in Long Lake than in Great Central Lake, and biomass (total chlorophyll) in Long Lake was twice Great Central Lake values (Table 9). Increased grazing by a large population of pelagic fish in 1978 ($7450 \cdot ha^{-1}$) reduced zooplankton to very low levels in Long Lake in 1978 (Rankin et al. 1979), and competition with a large stickleback population likely resulted in the smaller 1979 sockeye smolt which was less than half the weight of the 1978 smolt (Table 9). A similar pattern was observed in Great Central Lake which resulted in a smaller sockeye smolt in 1979.

Phosphorus loads and timing of first fertilization

In 1977 the first fertilization of the lakes occurred in early June just after the decline of the spring phytoplankton maximum. First treatment in 1978 began in early April coincident with the commencement of stratification, and just prior to the spring phytoplankton increase. In 1978 spring phytoplankton blooms occurred earlier, and were more sustained than in 1977 (Fig. 9 and 11). The earlier commencement of fertilization in 1978 was likely partially responsible for the striking differences seen within lakes between years, most notably in the greater abundance of phytoplankton and zooplankton, and in a twofold increase in annual primary production seen in all lakes except Hobiton in 1978. However, L_p (annual surface load of phosphorus) increased substantially in 1978 and was likely more important in causing the increases in these values than the timing of fertilizer additions (Fig. 18).

All lakes studied fit quite well on the regression line of Vollenweider's (1976) plot of average chlorophyll vs average total phosphorus concentration (Fig. 18). However, in summer, owing to the slower regeneration rate of nitrogen as opposed to that of phosphorus (Lean 1973), nitrate limitation in the euphotic zone is a feature common to all of our lakes. These observations underscore the importance of both nutrients as well as their ambient ratio in regulating phytoplankton growth and succession.

Schindler (1975) reported on the rapid uptake and sequestering of phosphorus by sediments following fertilization in some Ontario lakes in the Experimental Lakes Area (ELA), and noted that sediments were the major pathway of phosphorus loss from these lakes each year. The ELA lakes are oligotrophic, but are small and relatively shallow (Fee 1979), and extrapolation of their results to our fiord-type lakes is questionable. Total phosphorus in all our study lakes increased substantially in 1978, possibly owing to incomplete winter mixing in these very deep narrow lakes, but also due to an exceptionally dry and cold winter in 1977-78, which greatly reduced inflow and hence winter flushing. Preliminary analysis of 1979 data shows even higher average total phosphorus values than 1978, and this is coincident with identical fertilizer loads to previous years and an even colder-drier winter in 1978-79 (J. Stockner, unpublished data). Levels of solar radiation and air temperatures were generally similar in both years with nearly identical insolation from March to May; less light available in June and July,1977, but better light conditions in August,1977,than in 1978 (Fig. 19). These data suggest that the yearly variation in light was insufficient to cause the differences between years, and that timing of first fertilization had less effect on autotrophic production than annual variations in L_p.

Assessment of trophic state during fertilization

On the basis of mean daily rates of phytoplankton production, all treated lakes except Long Lake were in the oligotrophic range as defined by Winberg (1963) and Rodhe (1969) (75 to 100 mg $C.m^{-2}.d^{-1}$). Long Lake (Station 2) in 1978 was more productive with an average of about 300 mg $C.m^{-2}.d^{-1}$. Annual production estimates for Long Lake (Station 2) in 1978 lie within Rodhe's (1969) range of naturally eutrophic lakes. Annual production ranged from 20 to 40 g $C.m^{-2}.yr^{-1}$, and was similar to estimates for oligotrophic Precambrian Shield lakes reported by Fee (1979), but higher than estimates from 5 oligotrophic lakes studied by Kerekes (1972) in Newfoundland.

On the basis of the relation between average chlorophyll and total phosphorus, the majority of our lakes cluster in the oligotrophic position and are close to the line of best fit as predicted by Vollenweider (1976) from his extensive analysis of many lake systems throughout the world (Fig. 18).

Other indices of production or trophic state such as phytoplankton and zooplankton biomass clearly distinguish Great Central, Henderson, Kennedy and Hobiton lakes as oligotrophic, despite applications of fertilizer to each. Mohun Lake, a small shallow lake, lies on the upper end of Rodhe's oligotrophic category, while Long Lake, following the terminology of Jarnefelt (1925) can be considered mixotrophic as a productive humic-stained lake, similar in many characteristics to Babine Lake (Stockner and Shortreed 1975).

SUMMARY

The controlled enrichment of oligotrophic lakes for the purpose of enhancing survival and growth of juvenile sockeye salmon appears to be producing positive results. Preliminary results suggest that the target species is receiving the benefit of significantly increased production at the primary and secondary trophic levels. It is also apparent that the trophodynamics of treated lakes can differ markedly, as the responses of humic-stained Long Lake and clear Great Central Lake amply demonstrate. Ultimately, however, the production response of each lake must be measured in terms of adult sockeye salmon produced, which are available for harvest and increased escapement.

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Table 1. Salient physiographic, hydrologic and morphometric data for lakes investigated.

	Total Annual Precip. (cm)	Mean Annual Snowfall (cm)	Latitude	Longitude	Elevation (m)	Drainage Area (km^2)	Lake Area (km^2)	Mean Depth (m)	Water Residence Time (yr)
Great Central	192	81	49°22'	125°15'	82	393	51	212	9.7
Henderson	302	42	49°05'	125°02'	15	125	15	109	3.2
Hobiton	268	40	48°45'	124°49'	15	37	4	36	1.0
Kennedy-Clayoquot Arm	302	42	49°08'	125°35'	7	121	17	51	1.7
Kennedy Main Arm	302	42	49°04'	125°30'	7	336	47	27	0.9
Long	173	71	51°14'	127°10'	15	373	21	73	1.1
Mohun	154	104	50°07'	125°30'	200	48	10	13	1.5

Table 2. Phosphorus loads (mg $P \cdot m^{-2} \cdot yr^{-1}$) to the six lakes in 1977 and 1978 (after Vollenweider 1976).

	P load from sockeye[1]		P load from fertilizer		L_p		Total P load		L_c	% increase in total load due to fertilizer	
	1977	1978	1977	1978	1977	1978	1977	1978		1977	1978
Great Central	18	37	90	90	108	224	216	351	899	42	25
Henderson	2	3	121	121	114	370	237	494	950	51	24
Hobiton	15	8	40	40	147	218	202	266	720	20	15
Kennedy – Clayoquot Arm	3	25	-	122	108	95	111	242	691	0	50
Kennedy – Main Arm	2	1	-	-	115	163	117	164	585	0	0
Long	20	45	250	250	138	249	408	544	1360	61	45
Mohun	-	-	16	16	38	78	54	94	192	30	17

[1]Estimate of 9 g $P \cdot sockeye^{-1}$.

Table 3A. 1977 maximum-minimum and mean values of physico-chemical variables in study lakes.

Lake and	Station	Secchi Depth (m)	Extinction coefficient (k)	NO_3-N ($ug \cdot L^{-1}$)	TPO_4-P ($ug \cdot L^{-1}$)	SiO_4-Si ($ug \cdot L^{-1}$)	Total Alkalinity ($mgCaCO_3 \cdot L^{-1}$)	TDS ($mg \cdot L^{-1}$)
Great Central	1	15.0[a]	0.61	16.7	4.9	1201	14.0	29.3
		12.4[b]	0.27	5.2	2.3	1018	13.0	26.9
		7.0[c]	0.20	0.1	0.7	796	11.7	25.3
	2*	15.0		19.7	7.3	1201	15.5	28.1
		11.6		6.0	2.4	1018	12.9	25.8
		6.5		0.1	0.6	765	10.7	24.8
Henderson	1*	12.0	0.50	24.1	5.6	1420	8.2	101.2
		7.8	0.39	12.5	2.5	617	7.2	53.9
		5.5	0.31	0.1	0.5	326	6.5	22.8
Hobiton	1*	8.0	0.44	26.5	6.7	1453	8.9	54.9
		6.7	0.42	7.1	2.8	1301	5.9	30.9
		5.0	0.40	0.3	0.5	343	4.4	23.9
Kennedy	1	7.5	0.41	27.3	6.8	985	15.5	-
		6.9	0.37	16.5	2.2	934	14.4	28.2
		6.0	0.34	2.4	0.5	854	13.3	-
	2	10.0		34.3	3.3	1074	14.6	29.4
		7.9		13.9	1.6	945	13.0	28.0
		6.0		0.8	0.5	810	11.3	26.0
	3	8.0		26.2	3.1	1000	14.2	28.6
		6.9		9.8	2.0	914	11.4	27.3
		6.0		1.6	0.5	863	8.9	25.2
Long	1*	7.0	0.69	58.3	6.8	1114	4.4	32.4
		5.2	0.57	27.8	2.5	903	3.7	16.5
		3.5	0.27	1.6	0.5	647	3.0	10.9
	2*	7.0		48.5	12.7	1038	4.1	28.6
		5.2		24.3	3.0	859	3.4	16.1
		3.5		2.4	0.7	658	2.8	7.3
Mohun	1*	11.0		15.0	7.6	1359	6.5	22.1
		8.8		5.6	2.8	1057	6.1	18.5
		7.0		0.3	0.6	684	5.6	14.0

* denotes fertilized station   [a]-maximum value; [b]-mean value; [c]-minimum value.

Table 3B. 1978 maximum-minimum and mean values of physico-chemical variables in study lakes.

Lake and Station		Secchi Depth (m)	Extinction Coefficient (k)	NO_3-N (ug·L-1)	TPO_4-P (ug·L^{-1})	SRP (ug·L-1)	SiO_4-Si (ug·L^{-1})	Total Alkalinity (mg$CaCO_3$·L^{-1})	TDS (mg·L^{-1})
Great Central	1	15.0[a]	0.29	33.1	11.6	2.8	1400	14.3	47.7
		11.7[b]	0.24	12.5	4.7	1.4	966	12.9	32.2
		10.0[c]	0.20	0.4	1.0	1.0	610	11.5	19.3
	2*	14.0	0.33	34.7	6.1	2.7	1322	12.1	37.3
		11.2	0.25	12.5	3.9	1.3	942	11.6	27.5
		9.0	0.19	0.2	1.0	1.0	584	11.0	13.9
Henderson	1*	9.0	0.46	29.1	10.9	2.6	884	8.9	110.4
		7.1	0.41	12.5	5.2	1.5	616	7.0	82.5
		5.5	0.36	0.4	2.0	1.0	338	4.1	54.7
Hobiton	1*	8.0	0.47	29.7	5.7	2.8	1569	5.5	61.3
		6.6	0.45	10.9	3.7	1.2	1351	4.6	34.1
		6.0	0.42	0.6	1.3	1.0	1194	3.4	18.3
Kennedy	1*	8.0	0.56	43.9	10.3	1.9	1124	17.6	35.2
		6.2	0.42	10.2	4.2	1.1	811	13.4	27.2
		4.0	0.35	0.9	1.4	1.0	341	10.8	22.9
	2*	9.0	0.54	38.7	6.7	1.4	1131	13.5	70.8
		6.2	0.43	13.7	3.5	1.0	828	12.6	45.9
		4.0	0.38	0.6	1.3	1.0	297	11.2	28.5
	3	7.0	0.57	40.4	5.5	1.5	1051	11.8	53.5
		6.0	0.44	13.8	2.8	1.0	849	9.6	37.9
		5.0	0.36	0.7	1.5	1.0	278	8.8	26.8
Long	2*	6.0	0.59	56.3	7.7	3.1	1095	5.2	18.1
		4.8	0.50	25.4	4.6	1.3	822	3.4	15.2
		3.5	0.44	0.5	2.7	1.0	155	2.4	12.5
	3	5.3	0.60	55.3	5.4	1.3	1138	3.2	19.2
		4.8	0.51	20.6	4.0	1.0	814	3.0	12.8
		4.0	0.37	0.1	2.0	1.0	166	2.7	6.7
Mohun	1*	10.0	0.34	22.5	7.6	1.9	1475	17.9	30.5
		7.8	0.29	8.1	4.9	1.1	726	9.0	26.3
		6.5	0.26	0.4	3.1	1.0	244	4.7	23.2

* denotes fertilized station [a]-maximum value; [b]-mean value; [c]-minimum value.

Table 4A. 1977 maximum-minimum and mean values of biological variables in study lakes.

Lake and Station		Total Chlorophyll ($mg \cdot m^{-3}$)	Carbon Uptake ($mg \cdot m^{-3} \cdot h^{-1}$)	Assimilation No.	Annual Production ($gC \cdot m^{-2} \cdot yr^{-1}$)	Algal No's ($x10^8 \cdot m^{-3}$)	Algal Vol. ($mm^3 \cdot m^{-3}$)	Zooplankton biomass ($mg \cdot m^{-3}$)
Great Central	1	1.48[a]	0.91	2.30		22.2	4280	
		0.77[b]	0.41	0.67	16.5	14.9	2016	9.0
		0.31[c]	0.10	0.07		7.1	314	
	2*	1.47	1.32	2.53		21.1	2779	
		0.86	0.63	0.96	21.7	13.6	1555	15.6
		0.40	0.09	0.10		6.5	206	
Henderson	1*	2.93	1.89	3.64		36.9	9322	
		1.45	1.01	0.78	23.0	14.4	2185	7.5
		0.21	0.09	0.18		2.4	47	
Hobiton	1*	1.91	1.87	1.37		29.3	1903	
		1.30	0.99	0.73	28.7	13.5	433	11.0
		0.34	0.26	0.26		2.5	44	
Kennedy	1	1.30	1.60	1.36		14.4	537	
		0.96	0.64	0.58	-	10.9	281	-
		0.48	0.11	0.17		8.2	28	
	2	1.66	2.15	1.75		20.7	588	
		0.87	0.80	0.92	19.8	9.1	204	5.4
		0.17	0.10	0.07		1.8	30	
	3	1.22	2.19	2.35		16.2	568	
		0.71	1.25	1.50	-	10.1	219	-
		0.16	0.29	0.44		2.2	44	
Long	1*	3.17	9.98	4.97		18.6	165	
		1.55	3.26	1.96	59.2	11.3	65	20.5
		0.17	0.05	0.24		2.1	11	
	2*	3.30	9.23	4.20		26.5	353	
		1.67	3.25	1.78	55.2	13.3	91	19.9
		0.18	0.05	0.29		0.6	3	
Mohun	1*	2.10	2.27	2.11		57.2	1023	
		0.99	1.01	1.04	31.8	19.6	518	-
		0.39	0.14	0.30		5.6	250	

* denotes fertilized station [a]-maximum value; [b]-mean value; [c]-minimum value

Table 4B. 1978 maximum-minimum and mean values of biological variables in study lakes.

Lake and Station		Total Chlorophyll ($mg \cdot m^{-3}$)	Carbon Uptake ($mg \cdot m^{-3} \cdot h^{-1}$)	Assimilation No.	Annual Production ($gC \cdot m^{-2} \cdot m^{-3}$)	Algal No's ($x10^{8} \cdot m^{-3}$)	Algal Vol. ($mm^{3} \cdot m^{-3}$)	Zooplankton biomass ($mg \cdot m^{-3}$)
Great Central	1	1.78[a]	0.99	1.15		118.5	21280	
		0.99[b]	0.46	0.54	27.6	23.3	3873	6.7
		0.29[c]	0.17	0.06		6.8	310	
	2*	1.97	3.88	1.97		93.1	23790	
		1.06	0.85	0.75	34.9	23.6	4414	7.7
		0.50	0.14	0.14		6.1	593	
Henderson	1*	3.54	3.99	2.13		52.5	2052	
		1.69	1.38	0.83	56.2	17.7	546	8.0
		0.19	0.07	0.30		3.5	29	
Hobiton	1*	1.78	1.64	1.70		22.9	752	
		1.09	0.79	0.75	24.3	11.6	312	9.2
		0.32	0.07	0.23		2.6	43	
Kennedy	1*	5.49	17.68	1.25		30.5	2235	
		1.99	2.83	0.84	46.3	16.0	513	7.4
		0.33	0.01	0.02		3.5	40	
	2*	3.60	7.88	2.19		32.1	1547	
		1.53	1.68	0.98	41.2	13.7	393	10.4
		0.15	0.08	0.29		1.5	12	
	3	1.95	3.94	3.01		28.2	915	
		0.87	0.94	1.16	28.9	10,5	331	4.9
		0.20	0.13	0.41		2.1	48	
Long	2*	3.79	16.90	4.58		97.1	715	
		2.30	5.08	1.94	149.6	21.2	190	5.3
		0.22	0.20	0.22		1.3	9	
	3	5.79	4.59	2.45		70.8	441	
		2.14	2.64	1.35	61.8	18.2	165	9.7
		0.31	0.24	0.46		1.4	11	
Mohun	1*	5.48	3.47	3.41		43.4	1098	
		1.95	1.78	1.17	48.9	16.7	809	20.9
		0.67	0.27	0.27		1.4	416	

* denotes fertilized station   [a]-maximum value;   [b]-mean value;   [c]-minimum value.

Table 5. Phytoplankton species list and relative abundance in the six treated lakes.
(1 = rare, 2 = common, 3 = abundant)

	Volume u^3	Great Central 1	Great Central 2	Henderson	Hobiton	Kennedy 1	Kennedy 2	Kennedy 3	Long 2	Long 3	Mohun
Bacillariophyceae											
Achnanthes lanceolata (Breb.) Grun.	60	1						1		1	1
A. minutissima Kütz.	30	3	3	2	2	3	3	3	3	2	3
Amphora sp.	500								1		
Anomoeoneis serians (Breb. ex Kütz.) Cl.	60		1	1	1	1	1	2	1	1	2
Asterionella formosa Hass.	150	2	2	3		2	2	1	1	1	2
Cocconeis sp. 1	50	1				1	1	1		1	1
Cocconeis sp. 2	500							1			
Coscinodiscus sp.	6000										1
Cyclotella bodanica A. Cl.	4000							1			1
C. comta (Ehr.) Kütz.	500	2	2	2	2	2	2	2	2	2	2
C. stelligera Cl. & Grun.	50	2	2	3	3	3	3	3	3	3	3
Cyclotella sp.	100	1	1		1				1	1	1
Cymatopleura sp.	2000		1								
Cymbella sp. 1	100	1	1		1	1	1	1		1	
Cymbella sp. 2	3000					1	1	1	1		1
Diatoma elongatum (Lyngb.) Ag.	200	1	1		1						
D. hiemale (Roth.) Heib.	100	1						1			
Diploneis sp.	500										1
Eunotia pectinalis (O.F.Mull.) Rabh.	1000	1	1		1		1				1
Eunotia sp.	100			1	1	1	1	1	1		1

Table 5 (cont'd)

	Volume u^3	Great Central 1	Great Central 2	Henderson	Hobiton	Kennedy 1	Kennedy 2	Kennedy 3	Long 2	Long 3	Mohun
Fragilaria construens Grun.	60	1	1	1	1	1	1	1		1	1
F. crotonensis Kitton.	120	2	2	2	2	2	2	2	3	3	2
F. vaucheriae (Kütz.) Peters.	75	1	2	2	2	2	2	1	3	3	2
Frustulia rhomboides (Ehr.) Detoni.	2000	1	1		1				1		1
Gomphonema acuminatum var. coronatum (Ehr.) W. Sm.	1000							1			
G. parvulum (Kütz.) Grun.	50				1	1	1				
Gomphonema sp. 1	350	1	1	1	1	1	2	1		1	1
Gomphonema sp. 2	3000						1				1
Gyrosigma sp. 1	120		1								
Gyrosigma sp. 2	2000				1			1			1
Hannaea arcus (Ehr.) Patr.	100		1	1							
Melosira italica (Ehr.) Kütz. var. 1	120	2	2	1	3	1	1	1	1	1	3
M. italica (Ehr.) Kütz. var. 2	300	1	1					1		1	2
Meridion circulare (Greve.) Ag.	250				1	1			1		
Navicula sp. 1	100	1	1	1	1	1	1	1	1	1	1
Navicula sp. 2	500			1	1	1	1	1	1	1	1
Navicula Sp. 3	5000						1	1			1
Nedium sp.	300										1
Nitzschia acicularis (Kütz.) W.Sm.	60	1	1					1			

Table 5 (cont'd)

	Volume u^3	Great Central 1	Great Central 2	Henderson	Hobiton	Kennedy 1	Kennedy 2	Kennedy 3	Long 2	Long 3	Mohun
Nitzschia sp. 1	100		1					1			1
Nitzschia sp. 2	1000					1		1			1
Pinnularia gibba Hust.	25000										1
Pinnularia sp.	1500					1					
Rhizosolenia spp.	1500	3	3	3	3	3	3	3	1	2	3
Stephanodiscus sp.	3000						1	1			1
Surirella sp.	2000							1			1
Synedra ulna (Nitz.) Ehr.	1500	1	1	1		1	1	1	1	1	1
Synedra sp.	300			1							1
Tabellaria fenestrata (Lyngb.) Kütz.	3000	2	2	2	2	2	2	2	2	1	3
T. flocculosa (Roth.) Kütz.	1000	2	2	1	2	2	2	2	1	1	1
Chrysophyceae											
Chromulina sp.	20	1	1	1	1	1	1	1	1	1	1
Chrysidiastrum sp.	50			1							
Chrysochromulina sp.	50	3	3	2	2	2	2	3	3	2	2
Chrysolykos sp.	75				1	1	1	1		1	1
Chrysosphaerella sp.	90										2
Diceras sp.	60	2	1		1	1	1	1	1	2	1
Dinobryon borgeri Holm.	60	1	1	1	1	1	1	2		1	

Table 5 (cont'd)

	Volume u^3	Great Central 1	Great Central 2	Henderson	Hobiton	Kennedy 1	Kennedy 2	Kennedy 3	Long 2	Long 3	Mohun
Dinobryon sp.	350	2	2	2	2	2	2	2	3	3	2
Kephrion spp.	50	1	1					1			
Mallamonas sp. 1	250	1	2	1	1	2	2	1	2	1	2
Mallamonas sp. 2	500	2	1	2	2	2	2	2	1	1	1
Pseudokephyrion entzii Holm.	30	1	1	2	1	2	2	2	2	2	1
P. lactum Holm.	75	2	2		1	2	3	2	2	2	1
Cyanophyta											
Anabaena sp.	90	1	1		1	2	2				2
Aphanocapsa sp.	25[a]							1			1
Chroococcus sp.	20[a]			1	2	2	2	2			2
Coelosphaerium sp.	25[a]	1	1		1	1	1	3			2
Gloeocapsa sp.	5					1		1	1		2
Gloeothece sp.	6			1							
Gomphosphaeria sp.	8				1			2		2	1
Merismopedia sp.	3		1	3	3	3	3	3	2		3
Microcystis sp.	25[a]				2	2	1	2			1
Oscillatoria sp.	30[b]	1	1		1	2	2	1	1	1	1

Table 5 (cont'd)

	Volume u^3	Great Central 1	Great Central 2	Henderson	Hobiton	Kennedy 1	Kennedy 2	Kennedy 3	Long 2	Long 3	Mohun
Rhabododerma sp.	30				1						1
Synechocystis sp.	10			2							1
Others											
Ankistrodesmus sp. 1	30	1			3	1	1	1	1	1	
Ankistrodesmus sp. 2	75	1	1	1	2	1	1		1		1
Asterococcus sp.	100	1				1	1		1	1	3
Carteria sp.	60							1			
Ceratium spp.	75000	1	1		1	2		1			1
Chlamydomonas sp. 1	30			1		2	2	1	1	1	
Chlamydomonas sp. 2	100		1			1	1		1	1	1
Chroomonas sp.	150	1	1	1	1	2	2	2	1		1
Closteridium sp.	40	2	2	1	1	2	2	1			1
Cosmarium sp. 1	50					2	2	2	3	3	
Cosmarium sp. 2	200	1	2		1	2	1	2			2
Cosmarium sp. 3	1000	1				1	2	1			2
Crucigenia sp. 1	50	2	2	1	1	1	1	1			1
Crucigenia sp. 2	300		1		1						

Table 5 (cont'd)

	Volume u^3	Great Central 1	Great Central 2	Henderson	Hobiton	Kennedy 1	Kennedy 2	Kennedy 3	Long 2	Long 3	Mohun
Cryptomonas sp. 1	500	2	2	2	1	2	2	2	2	1	2
Cryptomonas sp. 2	1000	2	1	2	2	2	2	2	2	2	2
Desmatractum sp.	3500								1		
Desmococcus sp.	30	1									
Dictyosphaerium sp.	20				2	1		1			
Dispora sp.	40										1
Elakatothrix sp.	30										1
Gloeocystis sp.	10		1		2	1	1		1		1
Golenkinia sp.	40	1	1		1	2	2	2			
Gonium sp.	50			1		1	1	1			
Peridinium sp. 1	500	2	2	2	2	2	2	2	3	3	2
Peridinium sp. 2	1000	2	2	2	2	2	2	2	3	3	2
Peridinium sp. 3	4000			1	1	1	1	1	1		
Gymnodinium sp. 1	2000	1	1	1	1			1		1	
Gymnodinium sp. 2	8000	1	1		1	1					1
Heterogloea sp.	40							1			
Nephrocytium sp.	300	1	1								1
Oocystis sp. 1	80	1	1	1		2	2	1			2
Oocystis sp. 2	400				1						1

Table 5 (cont'd)

	Volume u^3	Great Central 1	Great Central 2	Henderson	Hobiton	Kennedy 1	Kennedy 2	Kennedy 3	Long 2	Long 3	Mohun
<u>Peridinium</u> sp. 4	3000			1	1	1	1	1			1
<u>Peridinium</u> sp. 5	20000	1					1				1
<u>Platydorina</u> sp.	25										1
<u>Pleodorina</u> sp.	50					1	1				
<u>Quadrigula</u> sp.	40	1	1		1			1			1
<u>Rhodomonas</u> sp.	50	2	2	2	2	3	3	2	3	3	3
<u>Roya</u> sp.	90		1	1				1			1
<u>Scenedesmus</u> sp. 1	50	2	2			2	2	2			1
<u>Scenedesmus</u> sp. 2	100	1	2	1		1	1	1			
<u>Staurastrum</u> sp. 1	500		1	1	1			1	1	2	
<u>Staurastrum</u> sp. 2	1500			1	2	2	2	1		1	2
<u>Teilingia</u> sp.	50				1	1	1		1	2	
<u>Treubaria</u> sp.	150								1		
Unidentified coccoid sp.	10	1	1	3				3			1
Unidentified Euglenoid sp.	50					1	1	1			2
Unidentified filament sp.	45	1			1						
Unidentified flagellate sp. 1	10	3	3	3	3	3	3	3	3	3	3
Unidentified flagellate sp. 2	40	3	3	2	3	3	3	2	2	2	3
Unidentified rod sp.	100								3	3	

a - per colony
b - per filament

Table 6. Comparisons of salient limnological variables between treated and untreated years in Kennedy Lake - Clayoquot Arm (values are annual means unless otherwise indicated).

Variable	1977 untreated	1978 treated
Phosphorus load (mg $P \cdot m^{-2} \cdot yr^{-1}$)	115	237
Algal volume ($mm^3 \cdot m^{-3}$)	204	393
Phytoplankton production ($mg\ C \cdot m^{-3} \cdot h^{-1}$)	0.80	1.63
($g\ C \cdot m^{-2} \cdot yr^{-1}$)	19.8	41.2
Total chlorophyll ($mg \cdot m^{-3}$)	0.87	1.53
Zooplankton biomass (mg d.w.$\cdot m^{-3}$)	5.4	10.4
Juvenile sockeye weight on August 15 (g)[1]	1.3	1.9
Sockeye population (x 10^6)	1.8	2.0
Stickleback population (x 10^6)	0.6	3.3

[1] Data from T. Gjernes (unpublished).

Table 7. Summary of sockeye and stickleback abundance and survival from potential eggs in fertilized lakes*.

	Lake area (ha)	Brood year	Fertilized	P.E.D. ($x10^6$)	Sockeye age "0" ($x10^6$)	Survival (% of eggs)	Age "0" sockeye·ha^{-1}	Other fish ($x10^6$)	Total fish·ha^{-1}
Great Central	5110	1976	yes	175	7.8	4.4	1500	0.9 (1^+ sockeye)	1700
		1977	yes	378	17.0	4.5	3200		3200
Henderson	1500	1976	yes	6.1	1.4	23.0	930	2.5 (stickleback)	2570
Hobiton	350	1976	yes	7.5	0.34	4.5	970	0.5 (stickleback)	2500
Kennedy	4940	1976	no	25.4	2.34	9.2	470	4.6 (stickleback)	1400
		1977	yes	92.7	2.39	2.6	485	14.1 (stickleback)	3340
Long	2140	1976	yes	105	1.7	1.6	668	4.2 (stickleback)	2760
		1977	yes	212	2.5	1.2	1170	17.3 (stickleback)	9250

* data from T. Gjernes (unpublished).

Table 8. Paired t-tests (one-way analysis) of mean epilimnetic values (0-10 m) of Stations 1, 2 and 3 of Kennedy Lake in 1977 (untreated) compared with 1978 (treated).[1]

	calc. t	tab. t	level of signif.		df
Station 1					
(Apr. 27 - July 13)					
Primary production (mgC·m^{-3}·h^{-1})	-3.120[2]	2.353	0.05	S[3]	3
Total chlorophyll (mg·m^{-3})	-8.615	8.610	0.005	S	4
Nitrate-nitrogen (ug·L^{-1})	+4.522	3.747	0.01	S	4
Total phosphorus (ug·L^{-1})	-3.739	2.776	0.025	S	4
Station 2					
(Apr. 27 - Sept. 28)					
Primary production (mgC·m^{-3}·h^{-1})	-2.187	1.895	0.05	S	7
Total chlorophyll (mg·m^{-3})	-2.792	2.306	0.025	S	8
Nitrate-nitrogen (ug·L^{-1})	+2.742	2.300	0.025	S	8
Total phosphorus (ug·L^{-1})	-4.597	3.499	0.005	S	7
Station 3					
(July 27 - Sept. 28)					
Primary production (mgC·m^{-3}·h^{-1})	+0.814	2.132	0.05	NS	4
Total chlorophyll (mg·m^{-3})	-0.623	2.353	0.05	NS	3
Nitrate-nitrogen (ug·L^{-1})	-1.667	1.638	0.70	NS	3
Total phosphorus (ug·L^{-1})	-1.674	2.920	0.05	NS	2

[1] Stations 1 and 2 were located in Clayoquot Arm and were both treated in 1978. Station 3 was in the Main basin and was untreated both years.

[2] + denotes 1977 $<$ 1978, - denotes 1978 $>$ 1977.

[3] S = significant, NS = not significant.

Table 9. Comparisons of salient limnological variables between Long and Great Central lakes (Station 2) in 1977 and 1978 (values are annual means unless otherwise indicated).

Variable	Long 1977	Long 1978	Great Central 1977	Great Central 1978
Phosphorus load ($mg\ P{\cdot}m^{-2}{\cdot}yr^{-1}$)	603	603	292	292
Phytoplankton volume ($mm^3{\cdot}m^{-3}$)	91	190	1555	4414
numbers ($x\ 10^8{\cdot}m^{-3}$)	13.31	21.20	13.62	23.60
Phytoplankton production ($mg\ C{\cdot}m^{-3}{\cdot}h^{-1}$)	3.25	5.08	0.63	0.85
($mg\ C{\cdot}m^{-2}{\cdot}yr^{-1}$)	55.2	149.6	21.7	34.9
Total chlorophyll ($mg{\cdot}m^{-3}$)	1.67	2.30	0.86	1.06
Zooplankton biomass ($mg{\cdot}d.w.{\cdot}m^{-3}$)	19.9	5.3	15.6	7.7
Juvenile sockeye weight smolts (g) [a] (for 1978-1979)	4.9±0.8	2.3±0.4	4.0±0.6	3.0±0.6
Sockeye population ($x\ 10^6$)	1.7	2.5	7.8	17.0
Stickleback population ($x\ 10^6$)	4.2	17.3	-	-
$Fish{\cdot}hectare^{-1}$	2760	9250	1700	3200

[a] Data from T. Gjernes (unpublished).

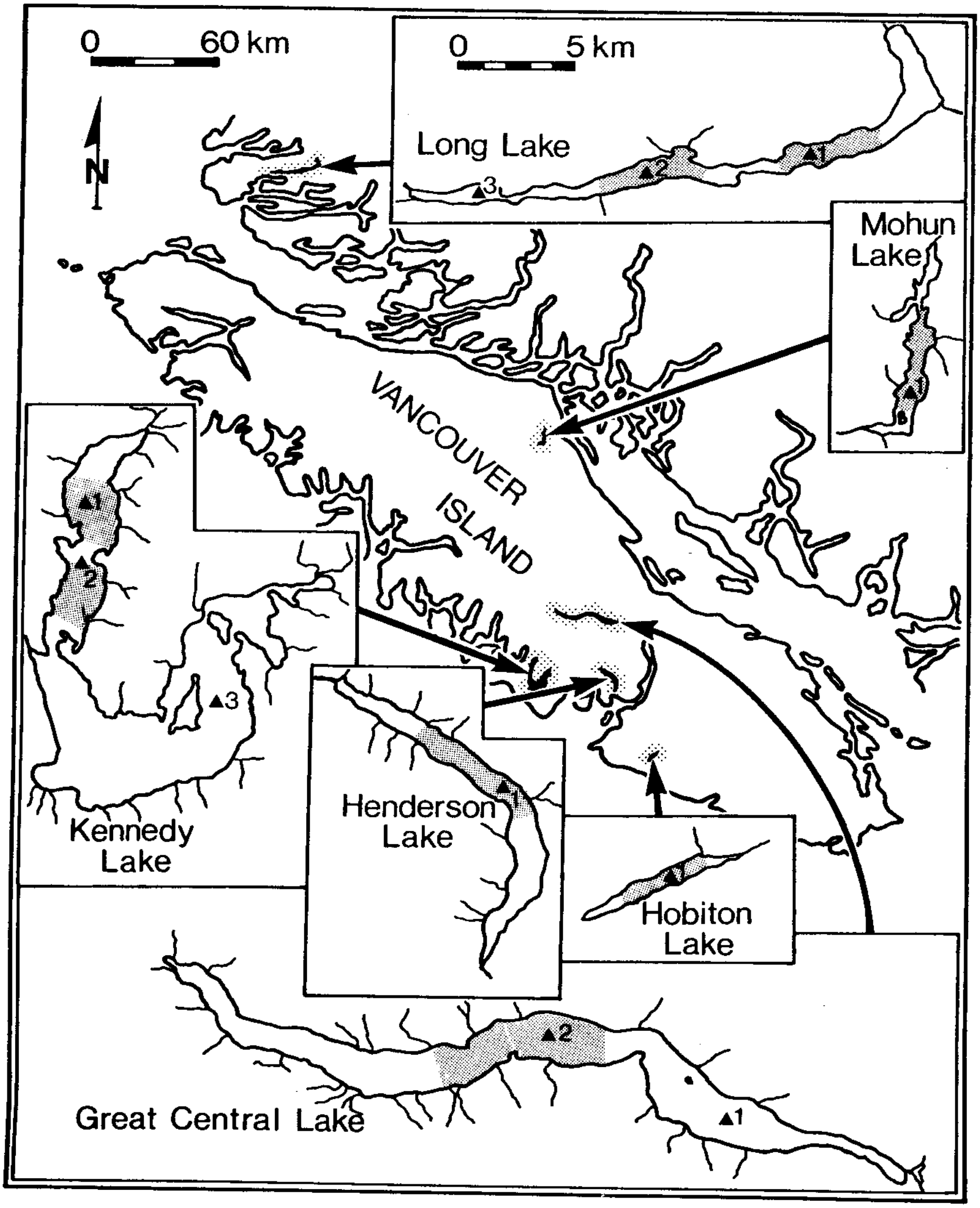


Figure 1. Map showing location of study lakes.

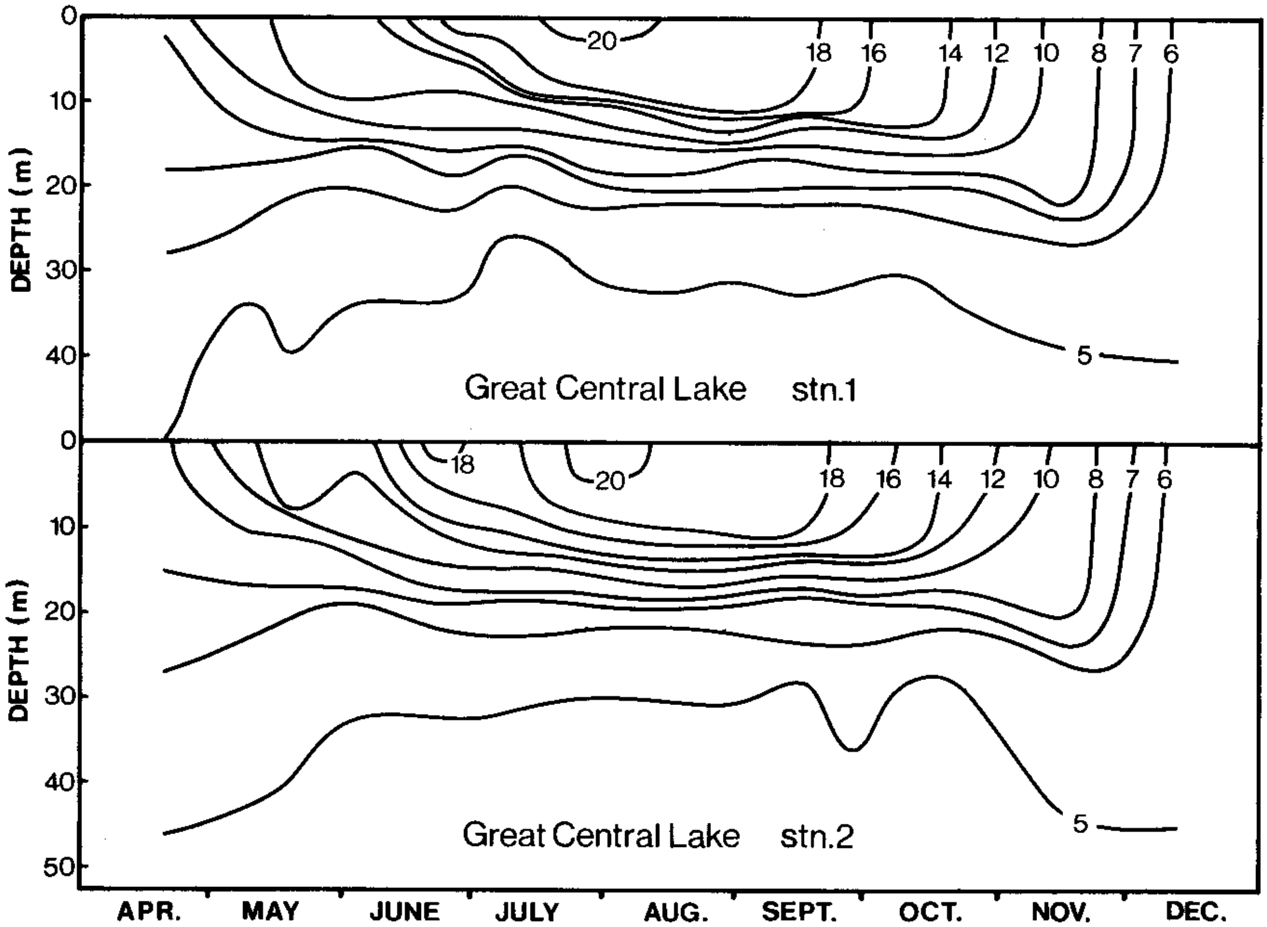


Figure 2. Annual temperature isopleths of each of the study lakes for 1977.

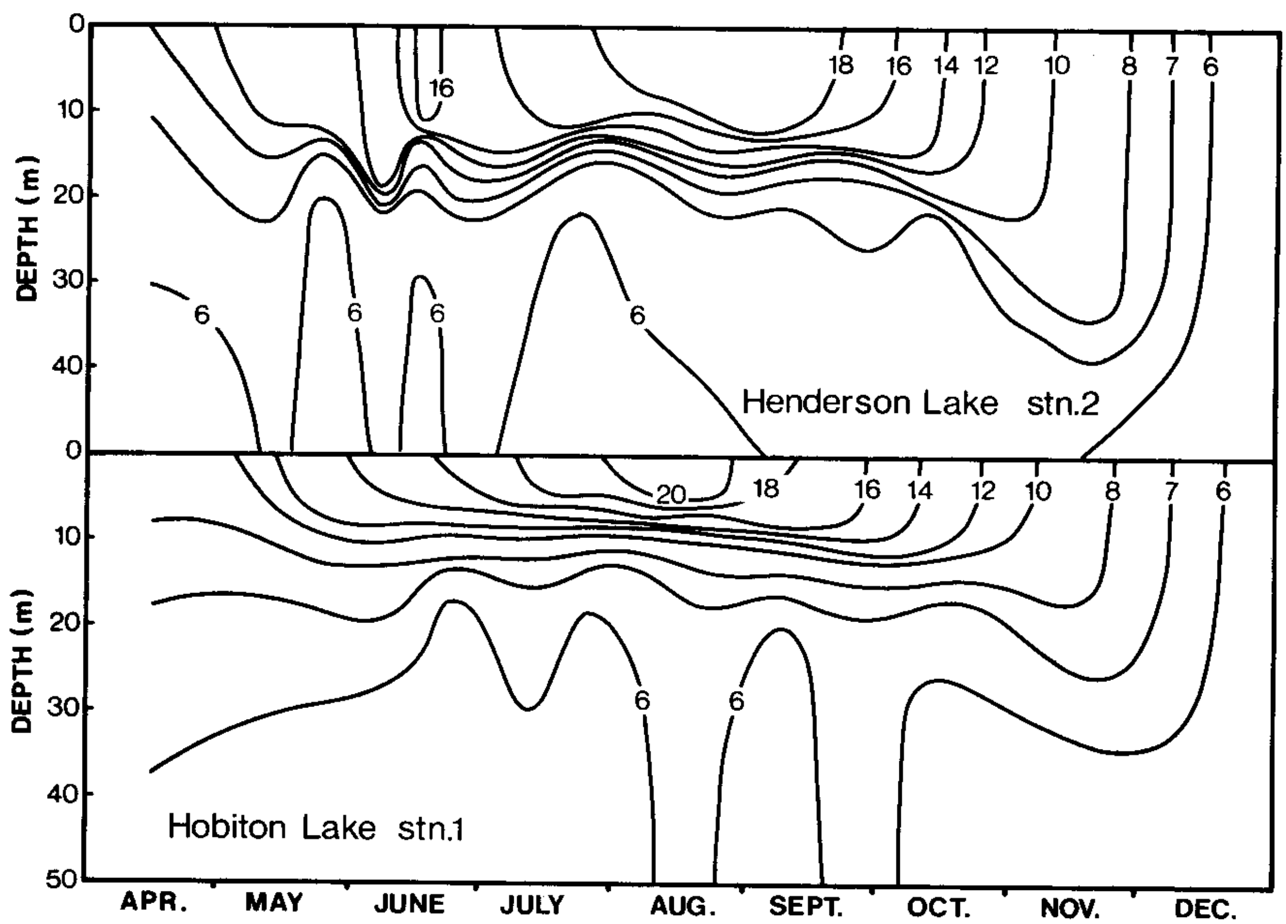


Figure 3. Annual temperature isopleths of each of the study lakes for 1977.

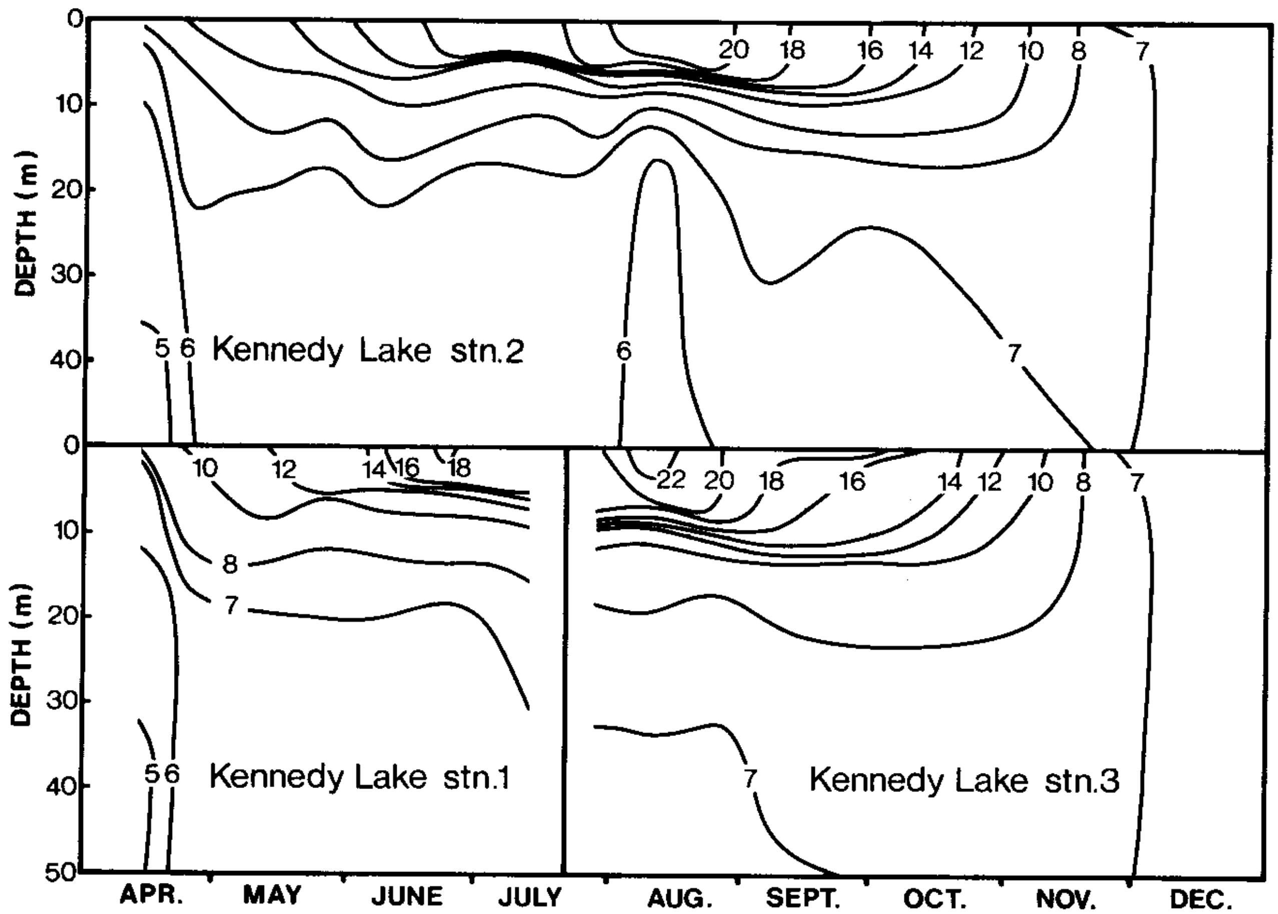


Figure 4. Annual temperature isopleths of each of the study lakes for 1977.

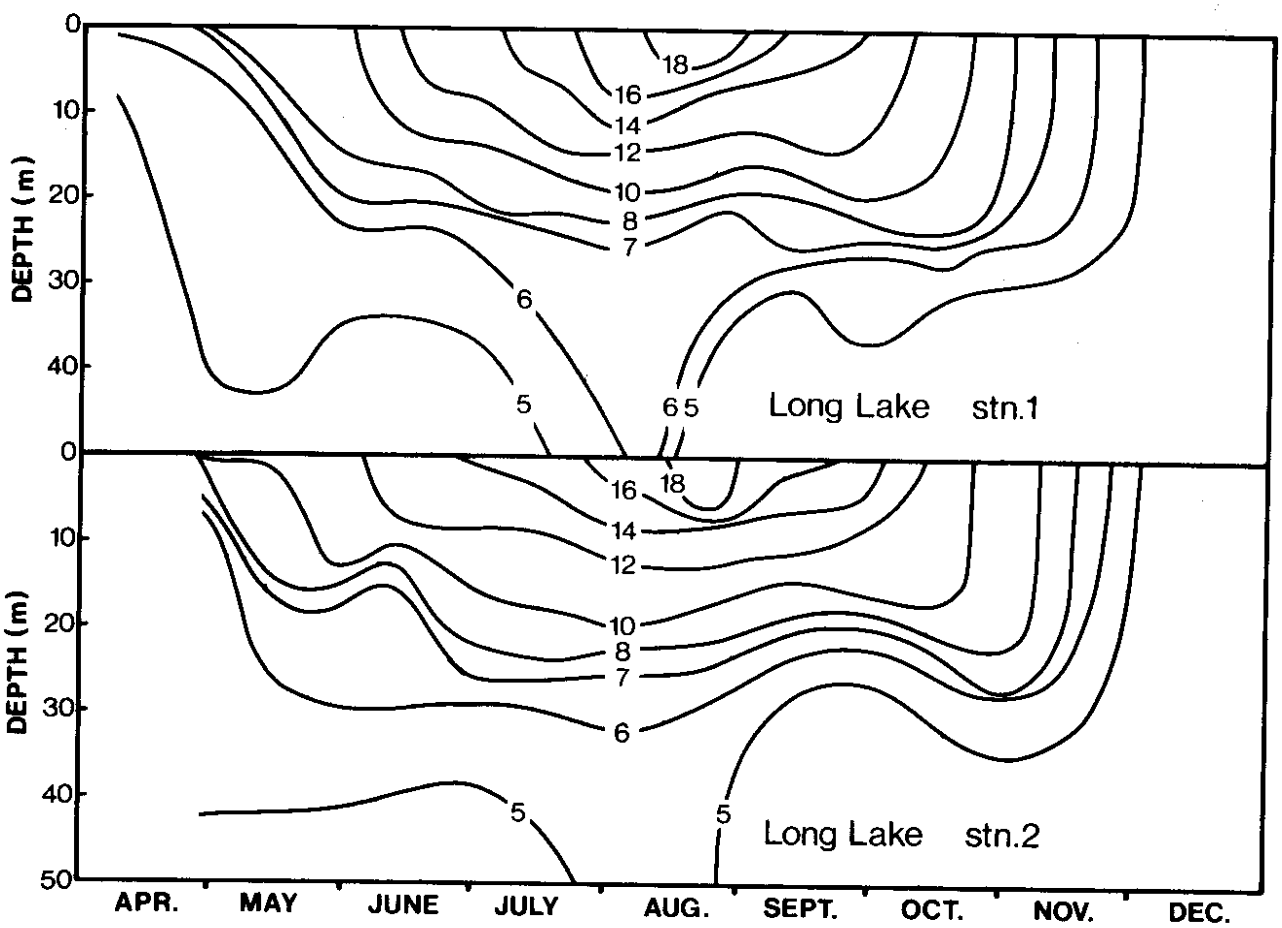


Figure 5. Annual temperature isopleths of each of the study lakes for 1977.

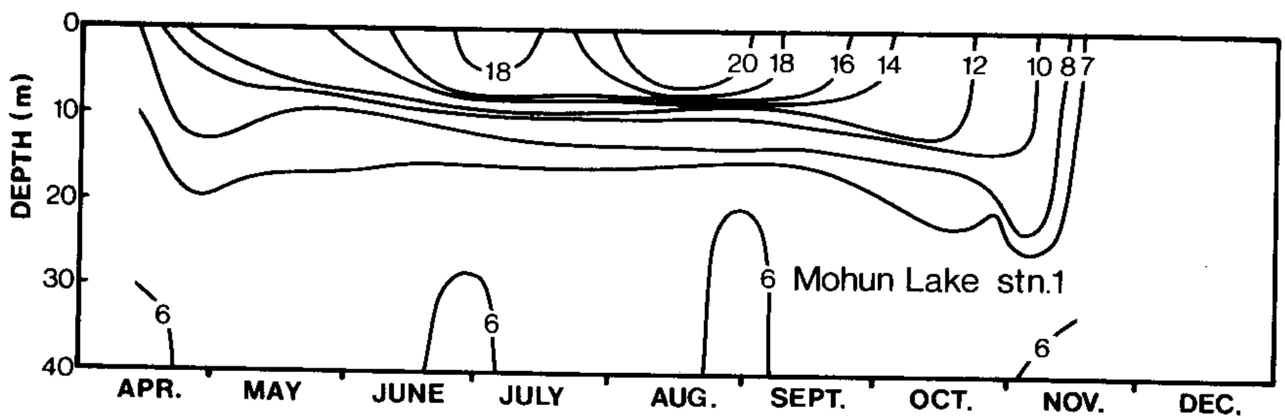


Figure 6. Annual temperature isopleths of each of the study lakes for 1977.

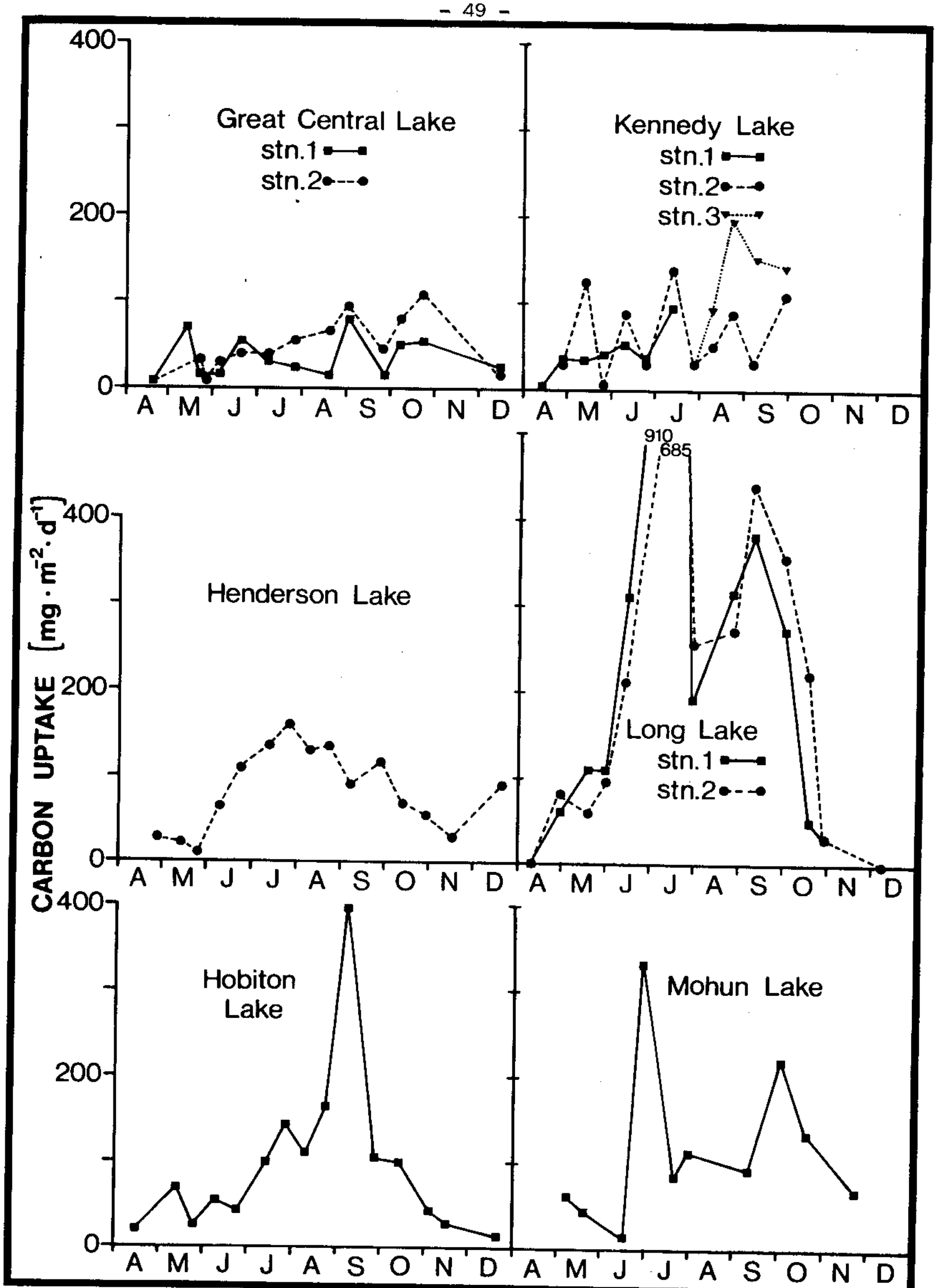


Figure 7. Annual carbon uptake profiles of each of the study lakes for 1977.

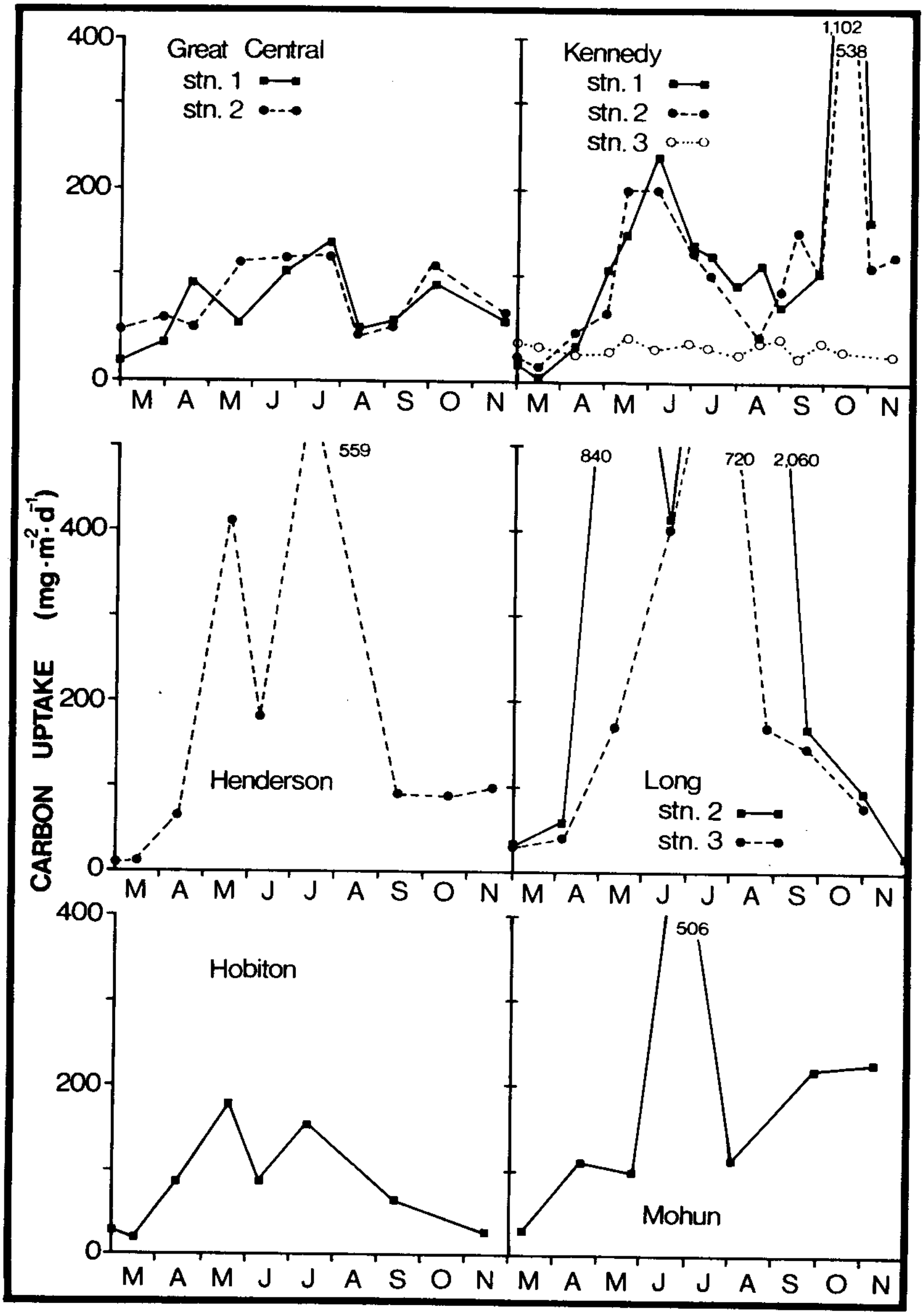


Figure 8. Annual carbon uptake profiles of each of the study lakes for 1978.

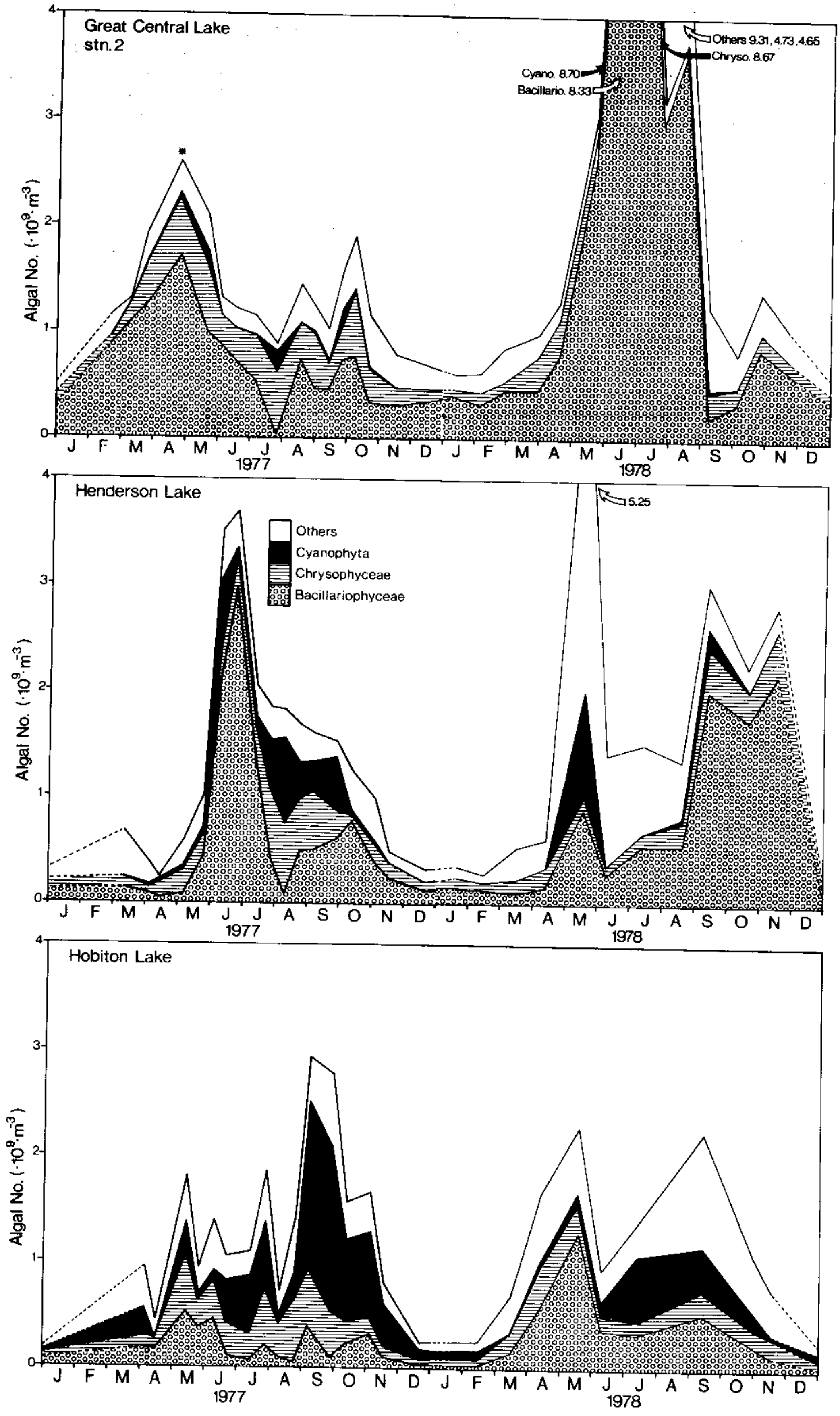


Figure 9. Phytoplankton numbers in each of the study lakes for 1977 and 1978.

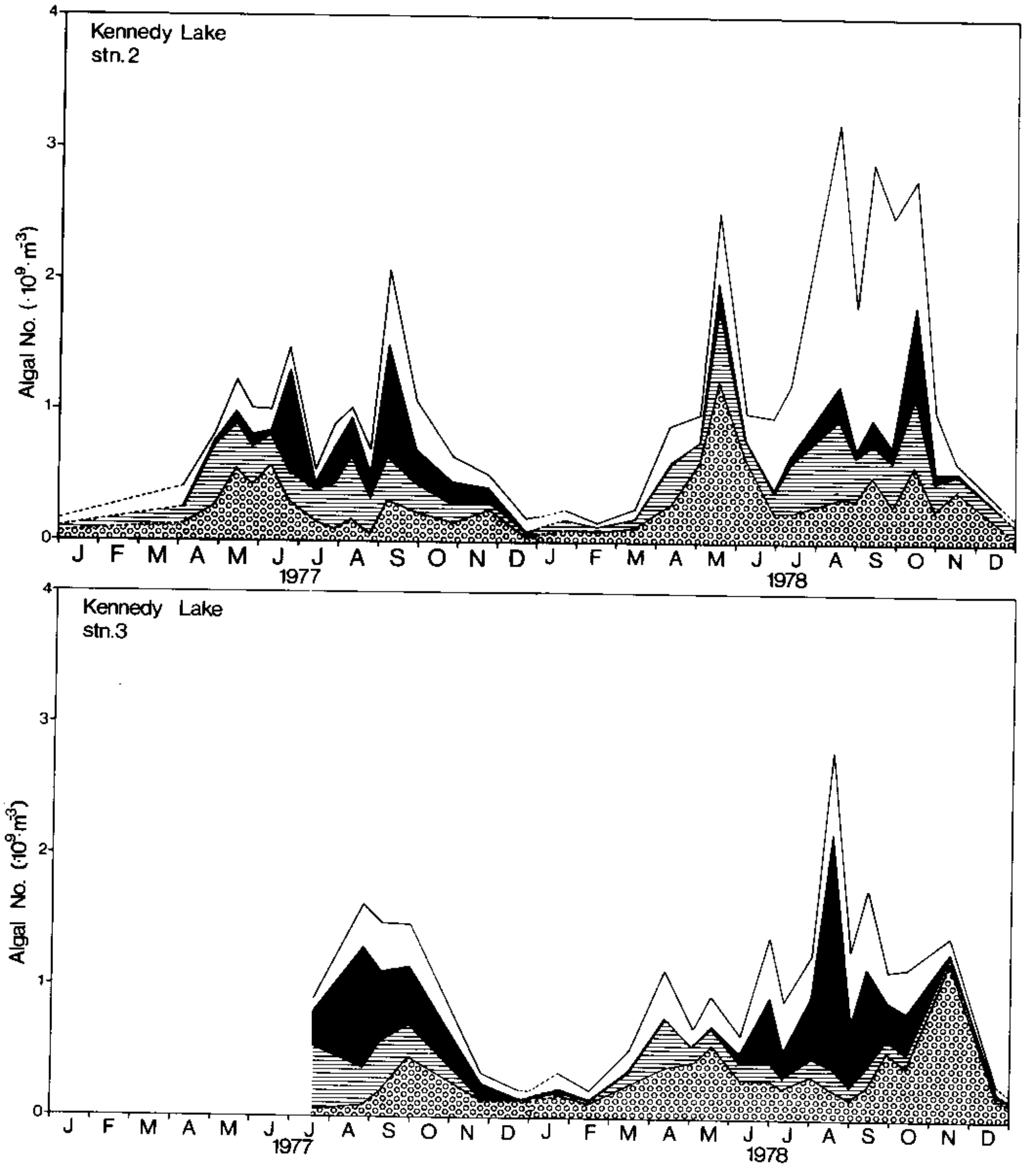


Figure 10. Phytoplankton numbers in each of the study lakes for 1977 and 1978.

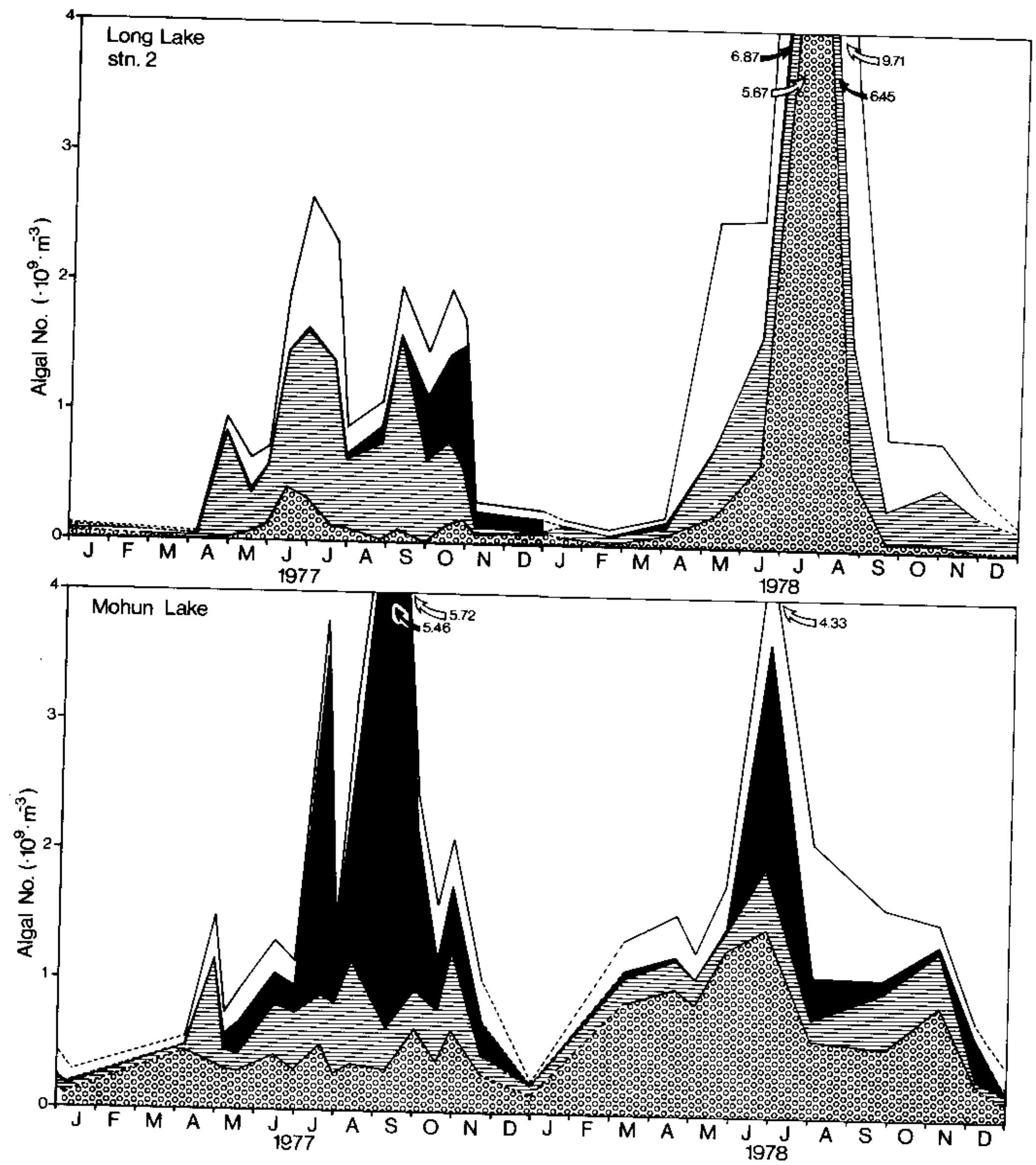


Figure 11. Phytoplankton numbers in each of the study lakes for 1977 and 1978.

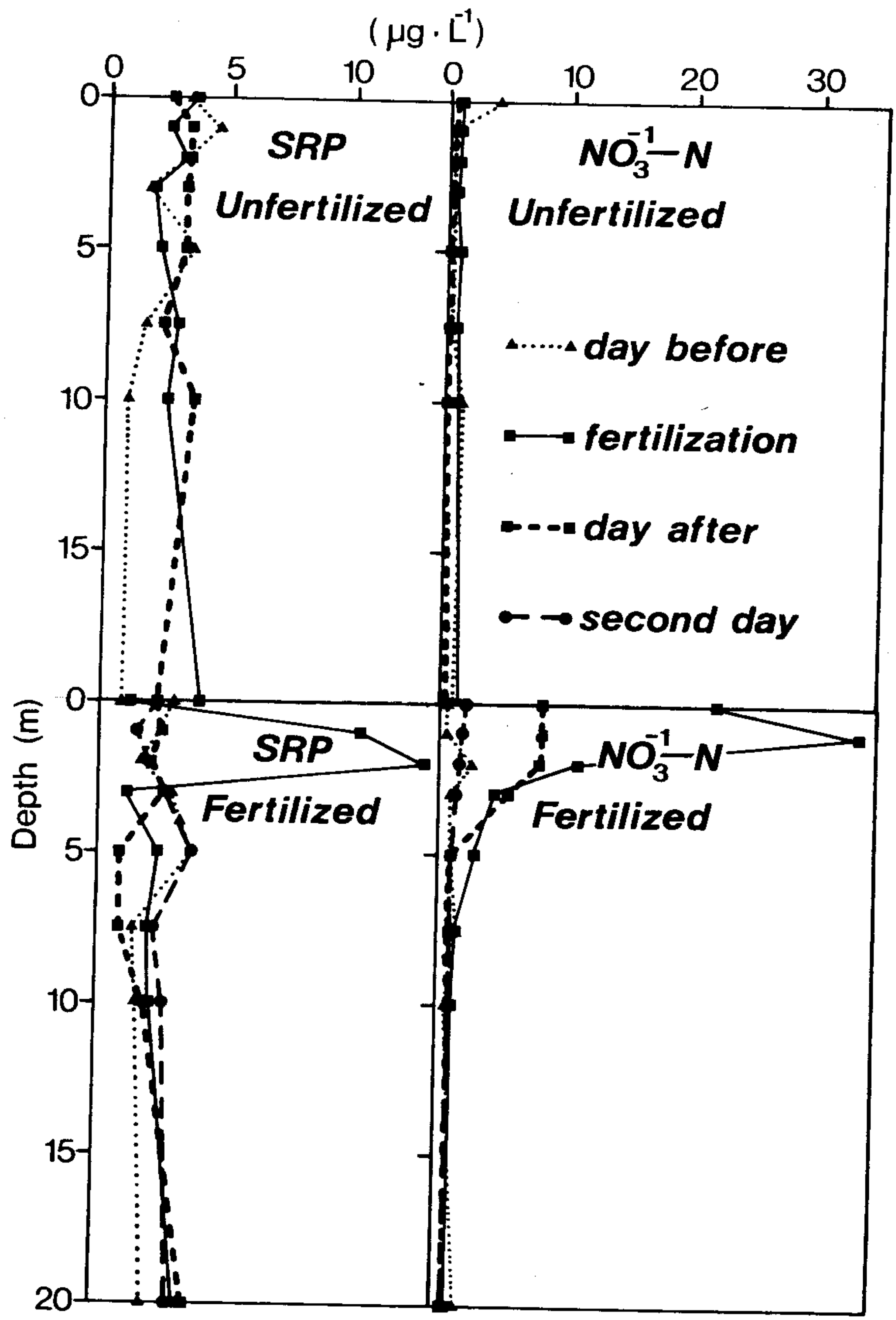


Figure 12. Soluble reactive phosphorus and nitrate concentrations in the fertilized and unfertilized zones of Great Central lake on the day before fertilization, day of fertilization and on the first and second days after fertilization.

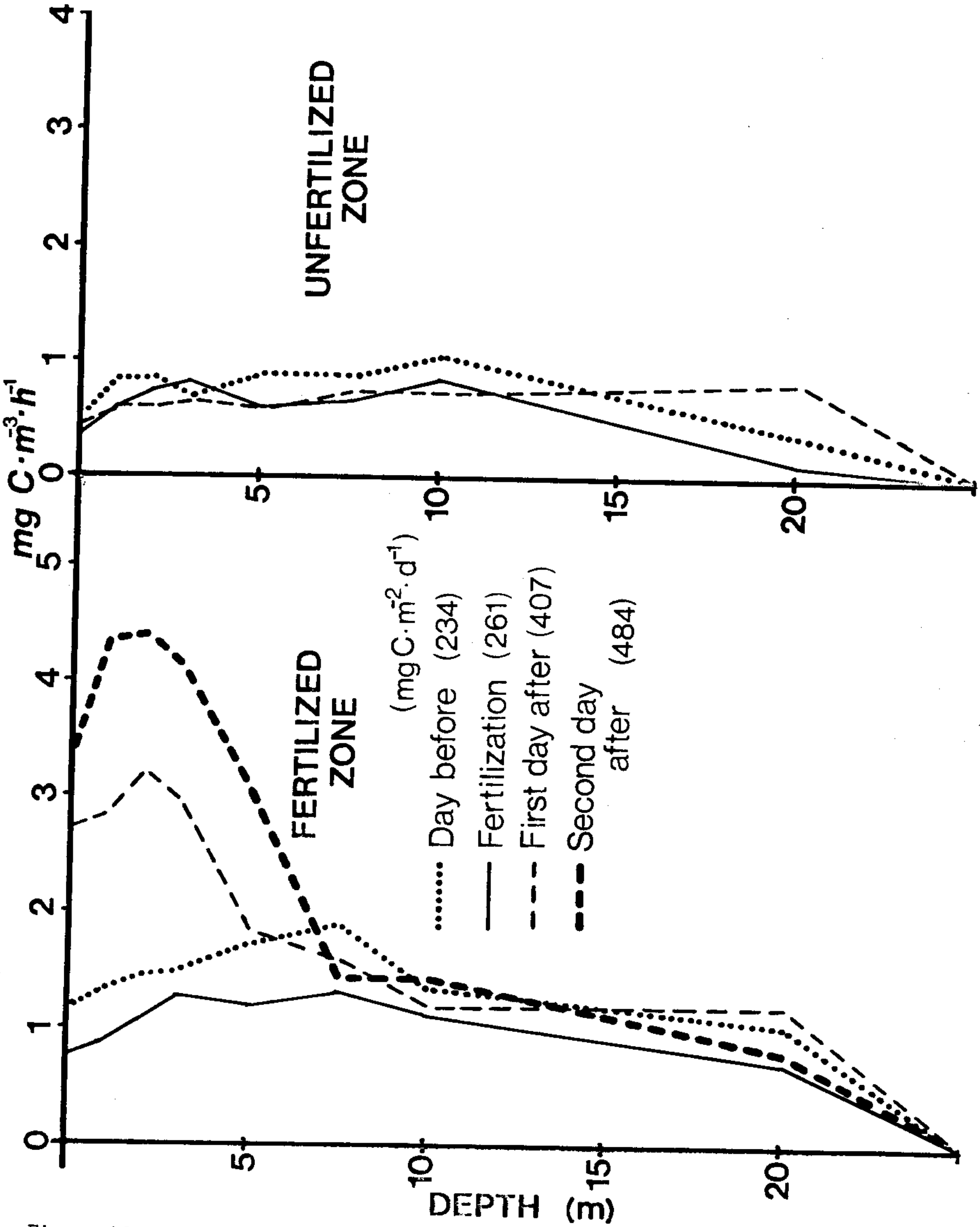


Figure 13. Carbon uptake vs depth profile in the fertilized and unfertilized zones of Great Central Lake on the day before fertilization, day of fertilization and on the first and second days after fertilization.

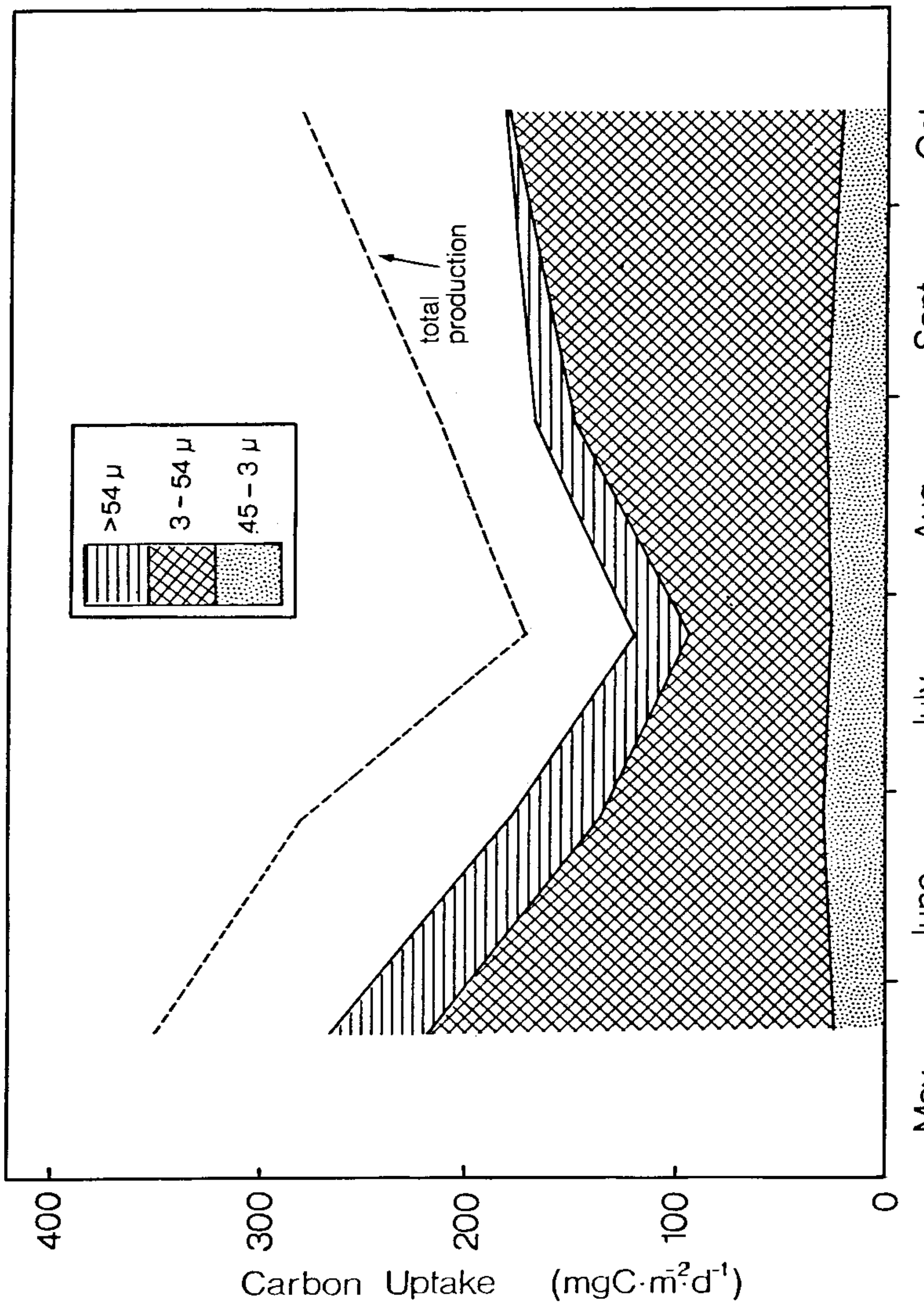


Figure 14. Mean carbon uptake values (mg $C.m^{-2}.d^{-1}$) of ultraplankton nannoplankton and net plankton. Total production measured separately (from Costella et al. 1979).

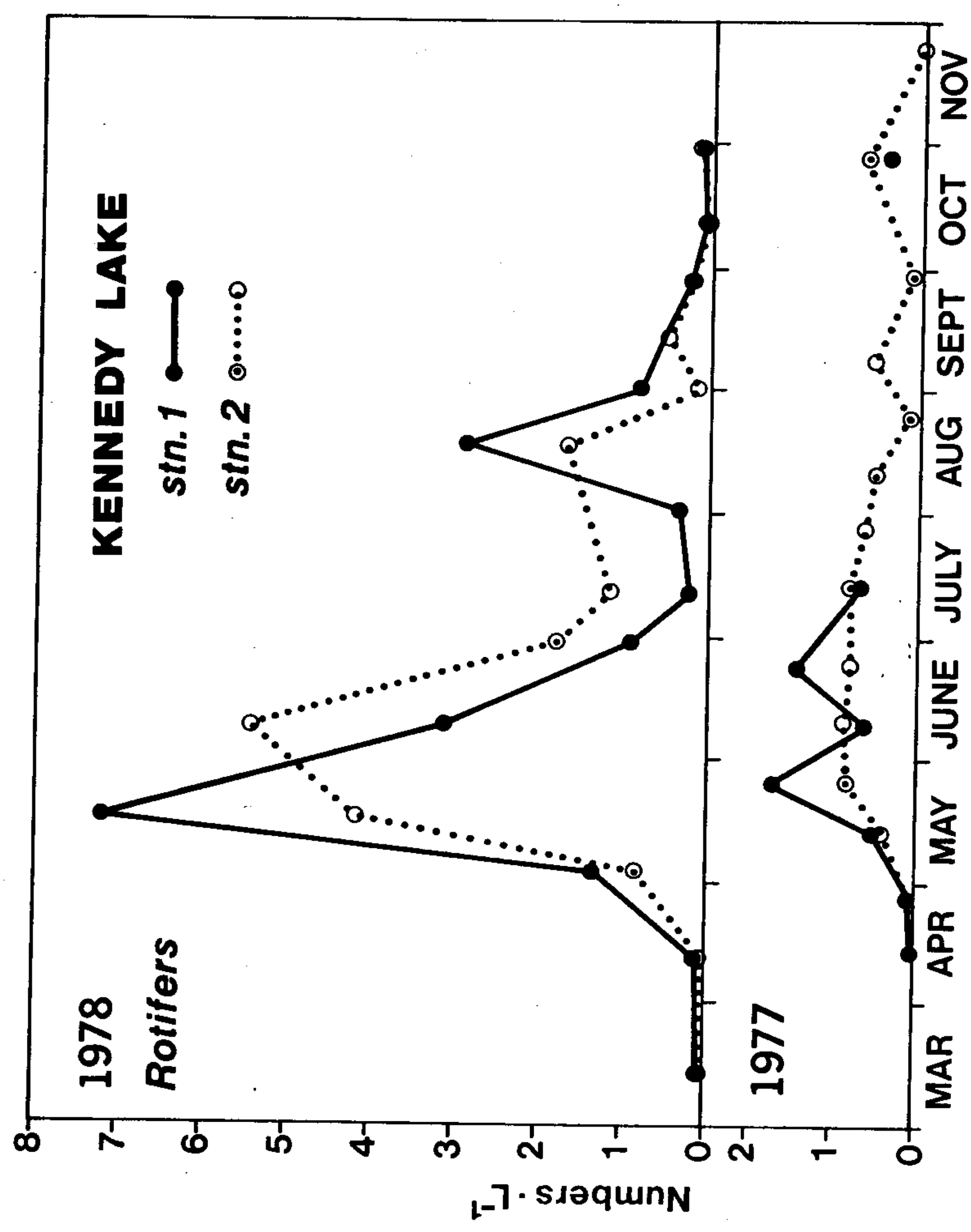


Figure 15. Annual profile of rotifer numbers in Kennedy Lake for 1977 and 1978.

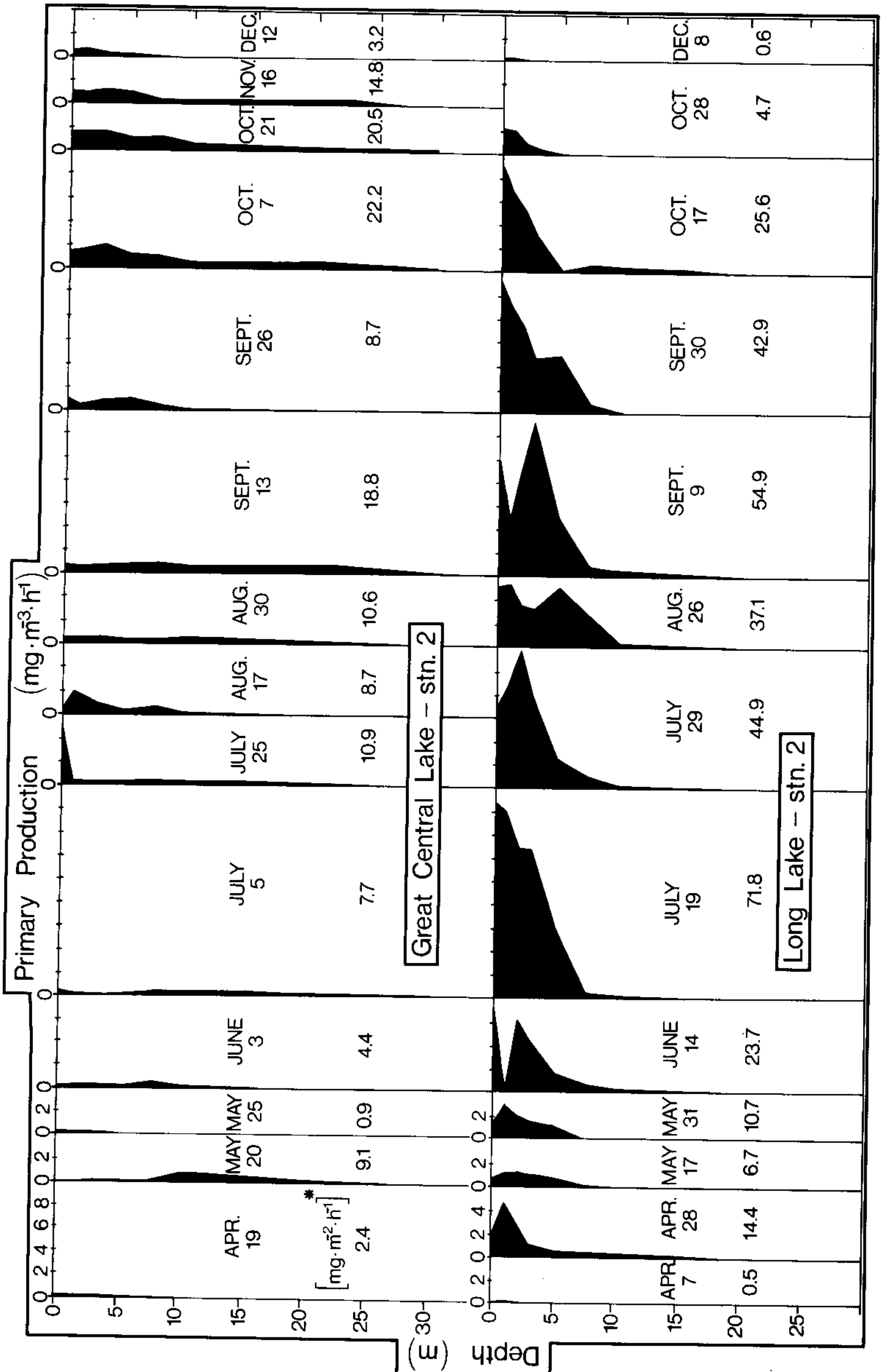


Figure 16. Annual primary production vs. depth profile and integrated values of production of Great Central Lake (Station 2) and Long Lake (Station 2) in 1978.

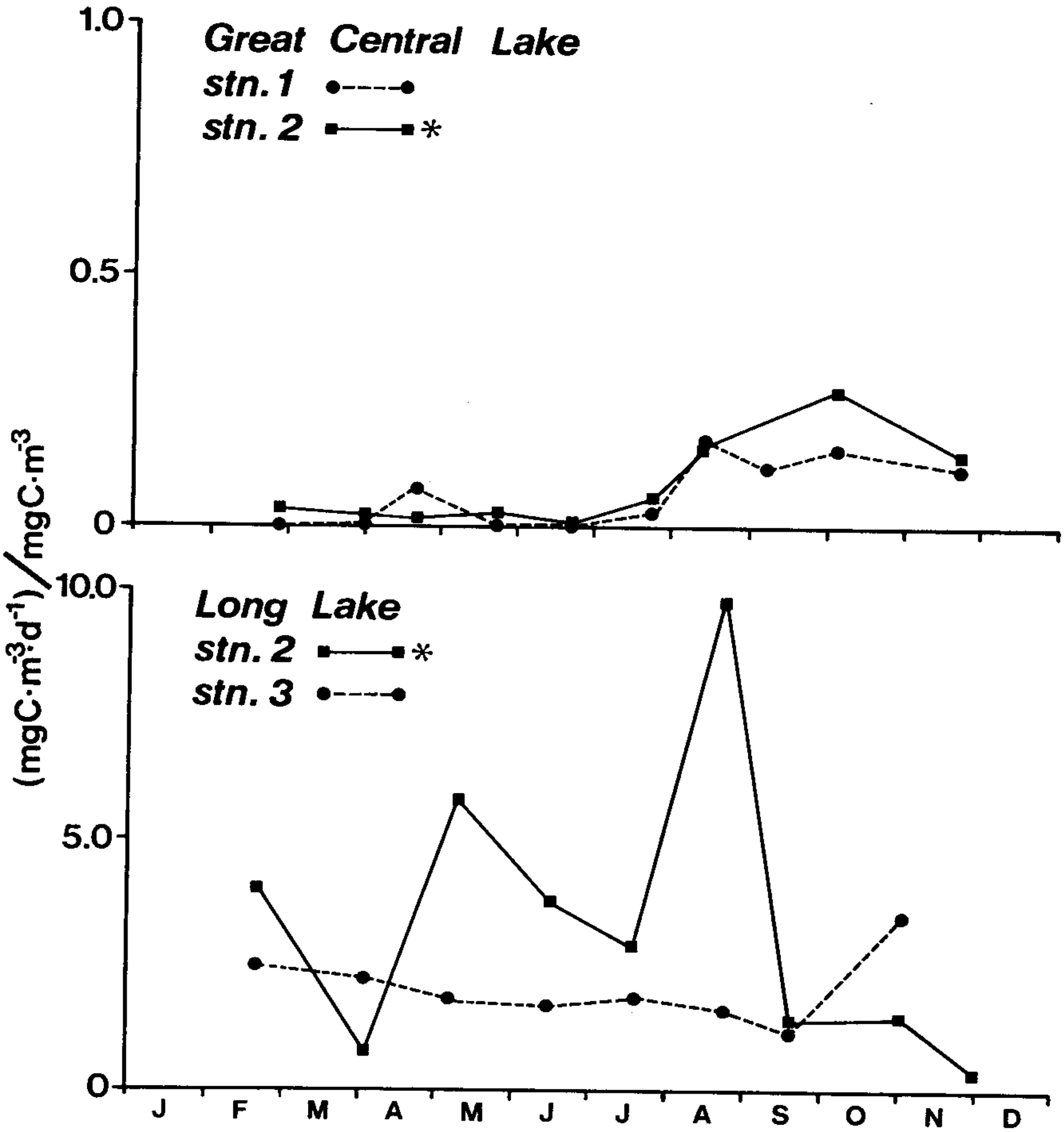


Figure 17. Annual phytoplankton reproduction rate (mgC.m^{-3}.d^{-1}/mgC.m^{-3}) of Great Central Lake and Long Lake. * denotes fertilized station.

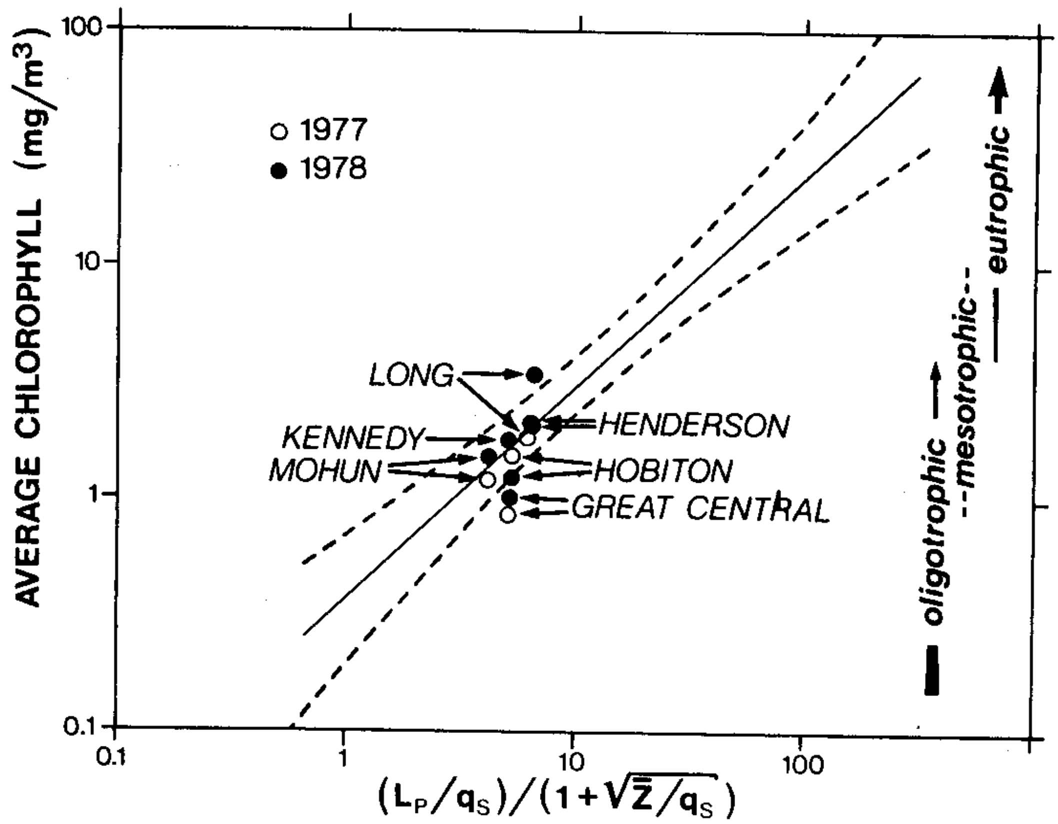


Figure 18. Relation between phosphorus load and average chlorophyll in study lakes in 1977 and 1978 (after Vollenweider 1976).

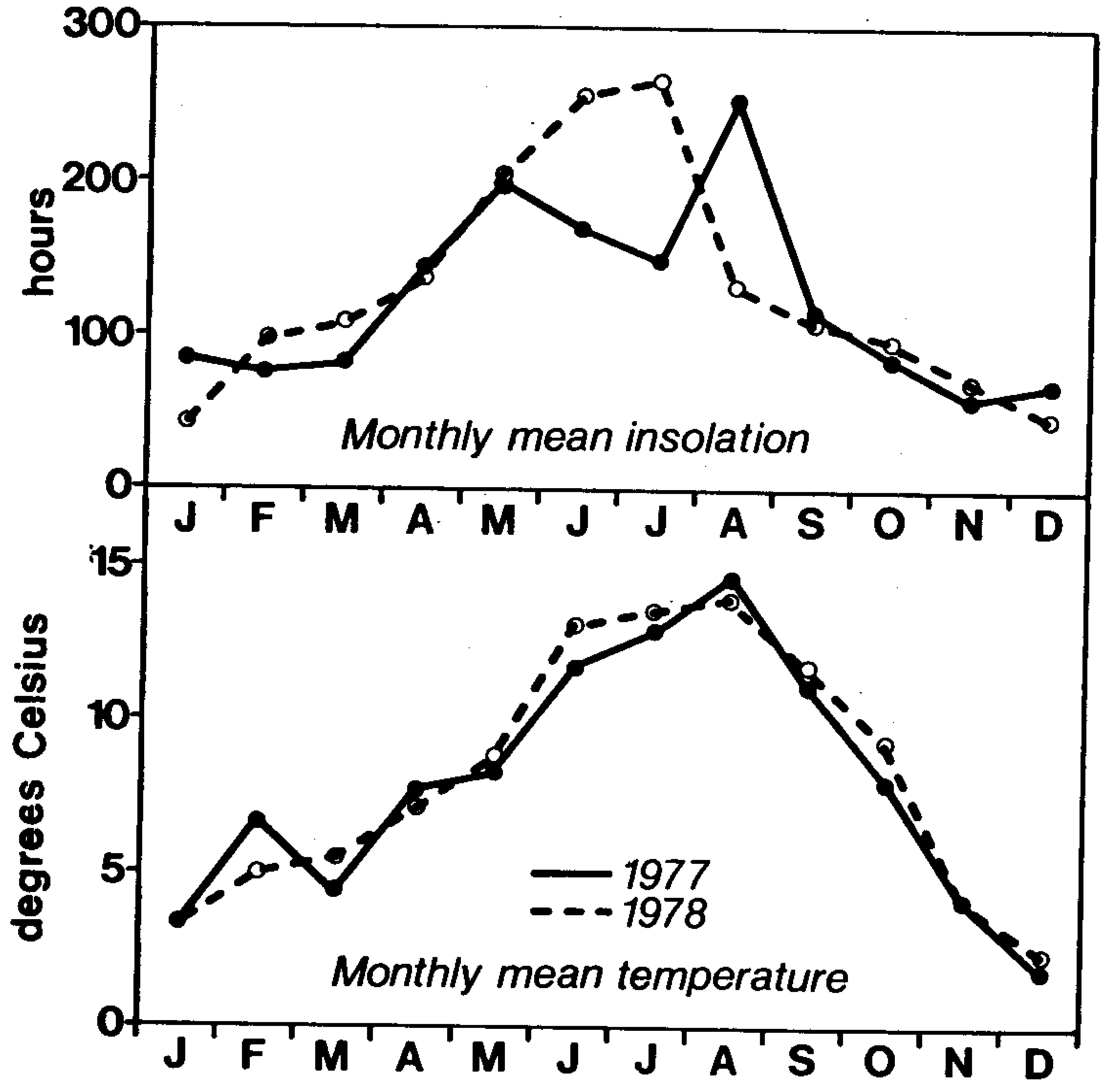
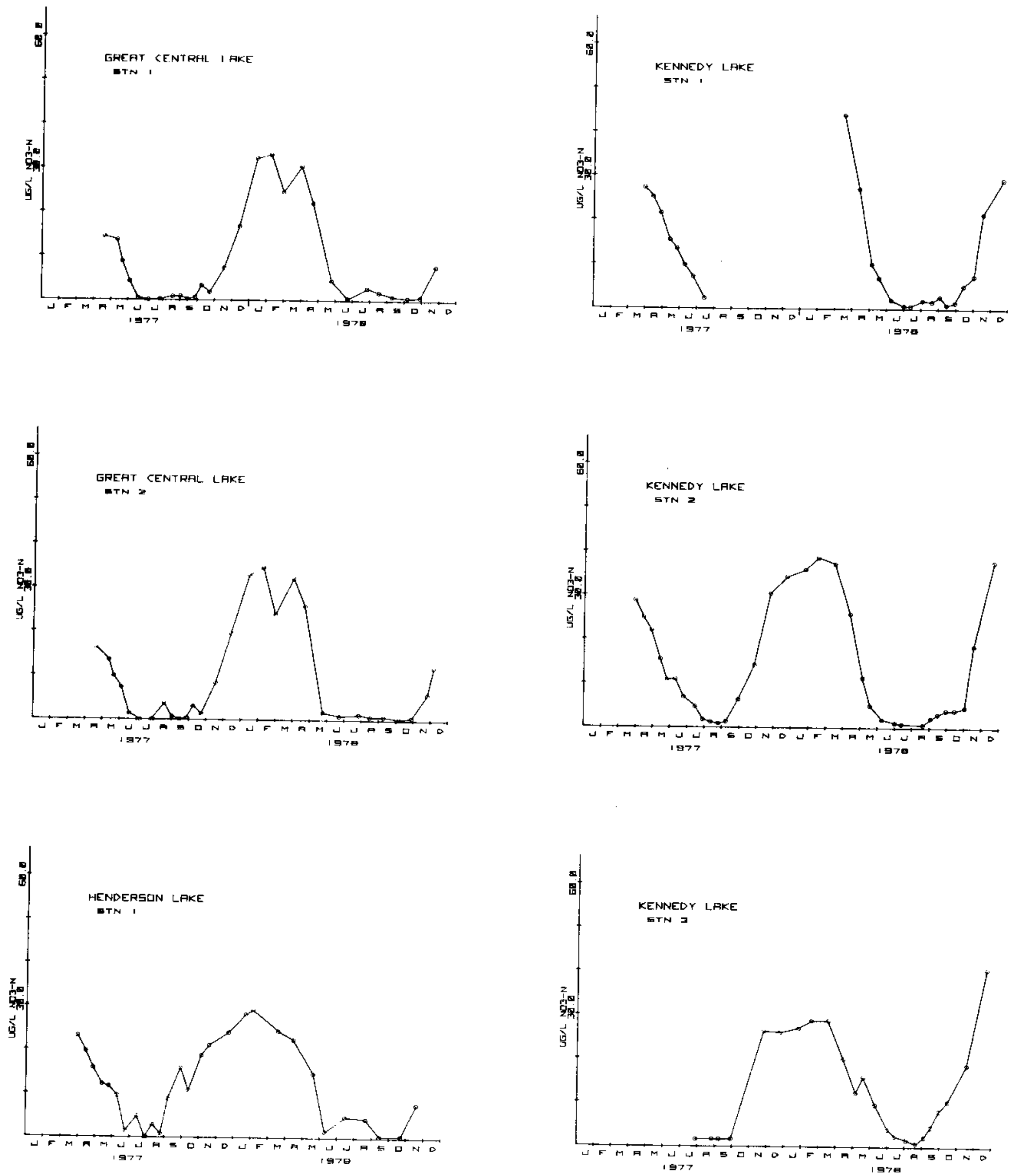
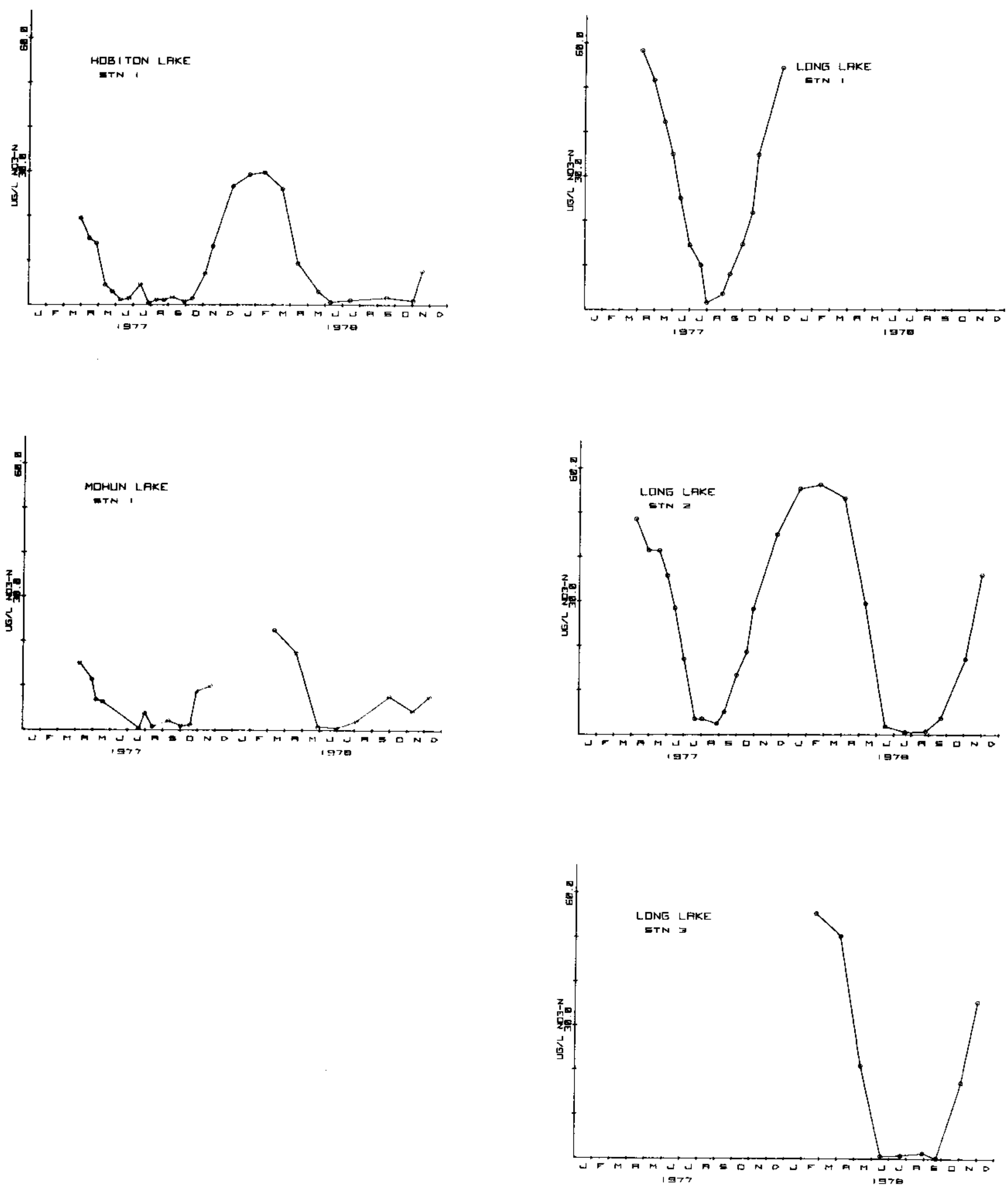


Figure 19. Profile showing monthly mean temperatures and monthly mean insolation values for 1977 and 1978 at Port Hardy Airport.

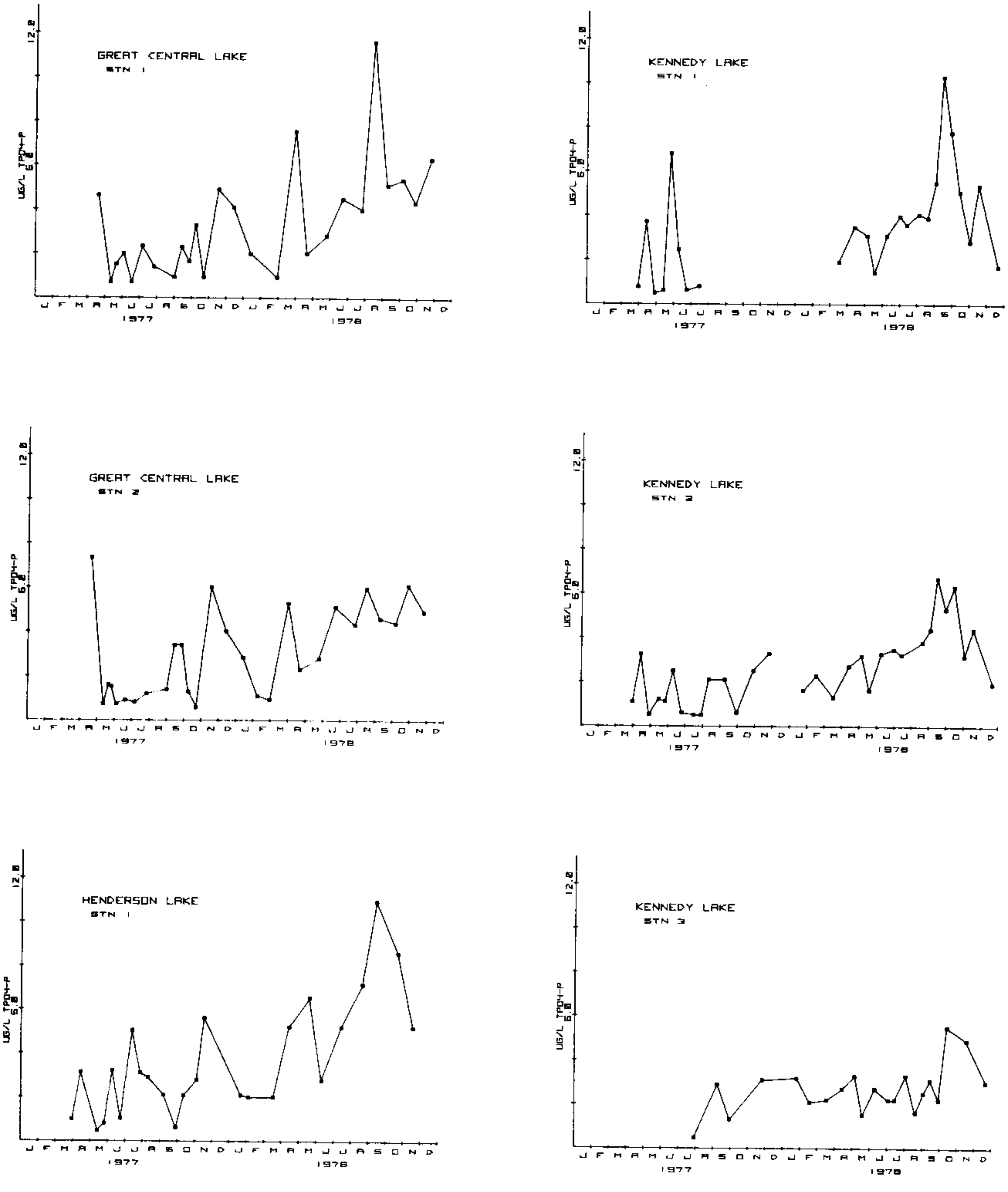
APPENDIX FIGURES



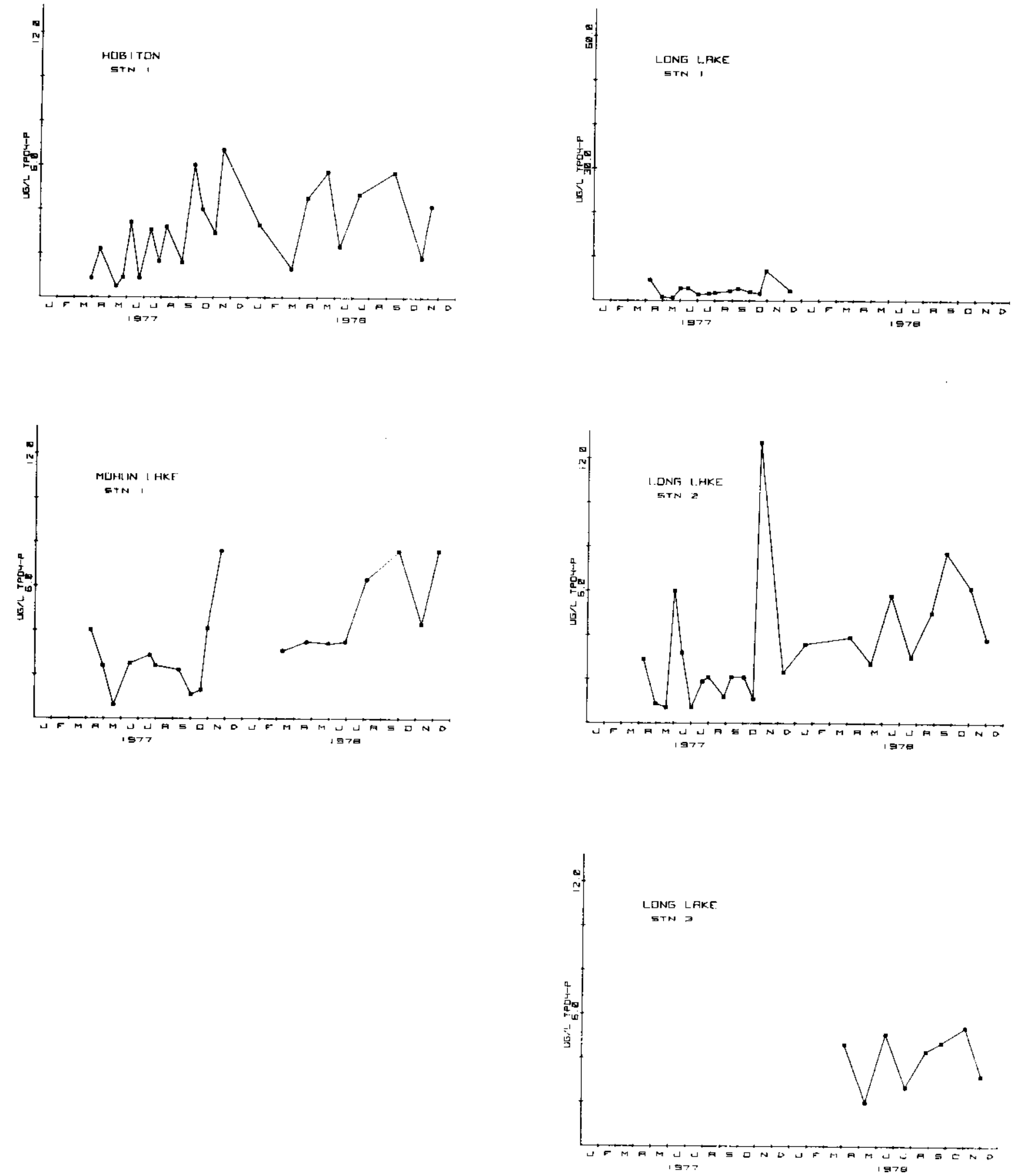
Appendix Figure 1. Mean epilimnetic values (0-10 m) of nitrate-nitrogen concentration ($\mu g.L^{-1}$) at each station in each of the study lakes.



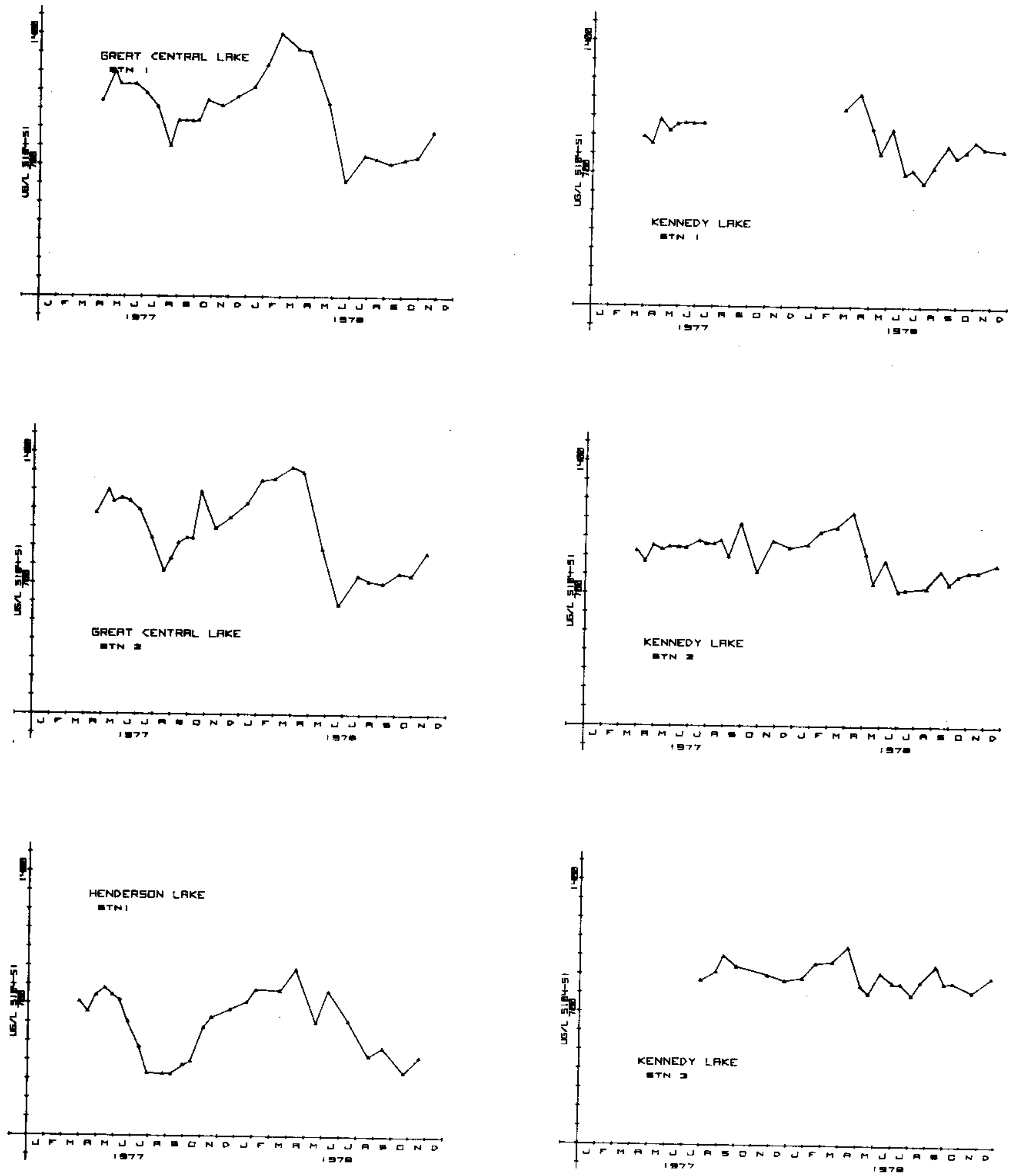
Appendix Figure 2. Mean epilimnetic values (0-10 m) of nitrate-nitrogen concentration ($\mu g.L^{-1}$) at each station in each of the study lakes.



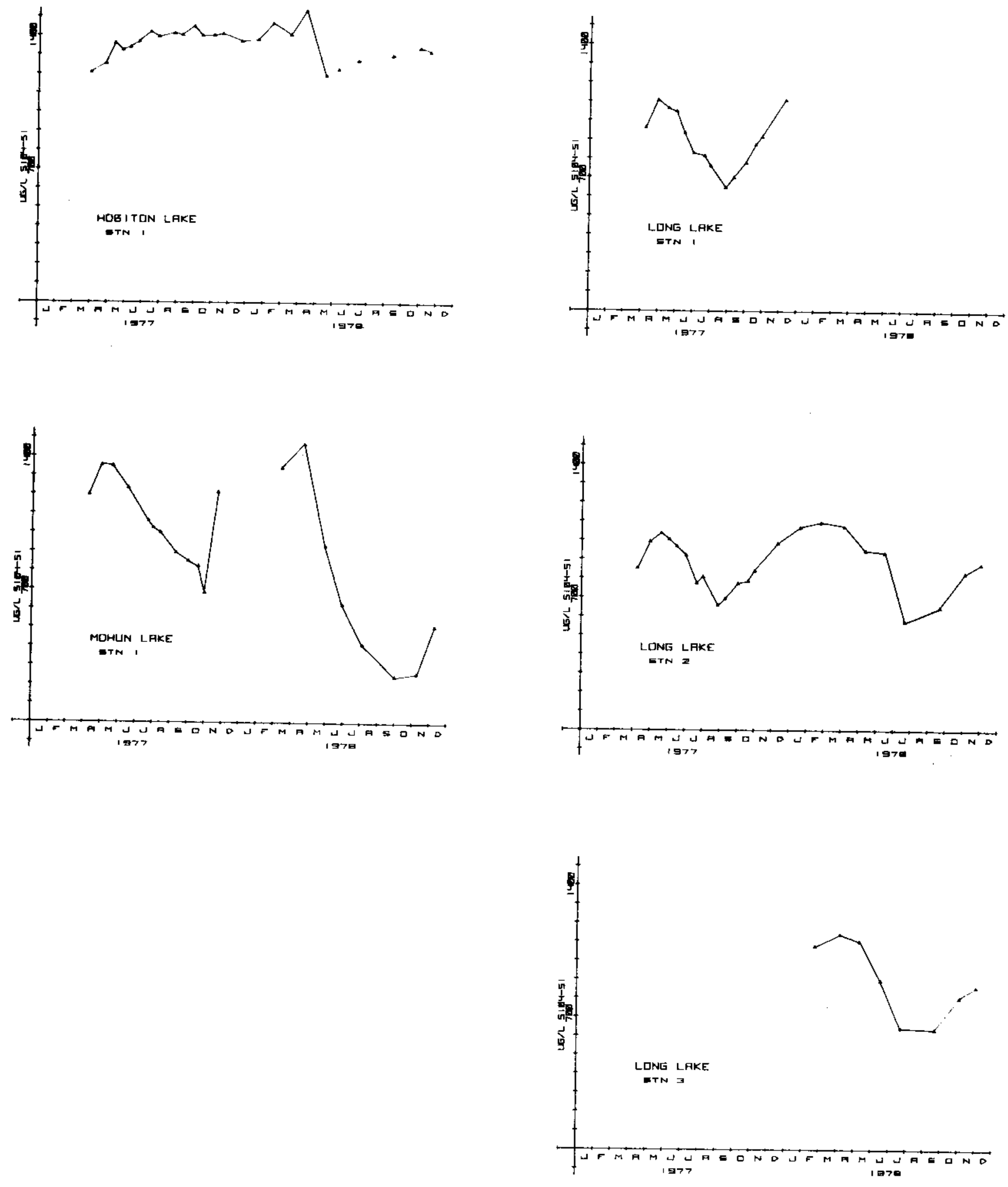
Appendix Figure 3. Mean epilimnetic values (0-10 m) of total phosphorus concentration (μg.L^{-1}) at each station in each of the study lakes.



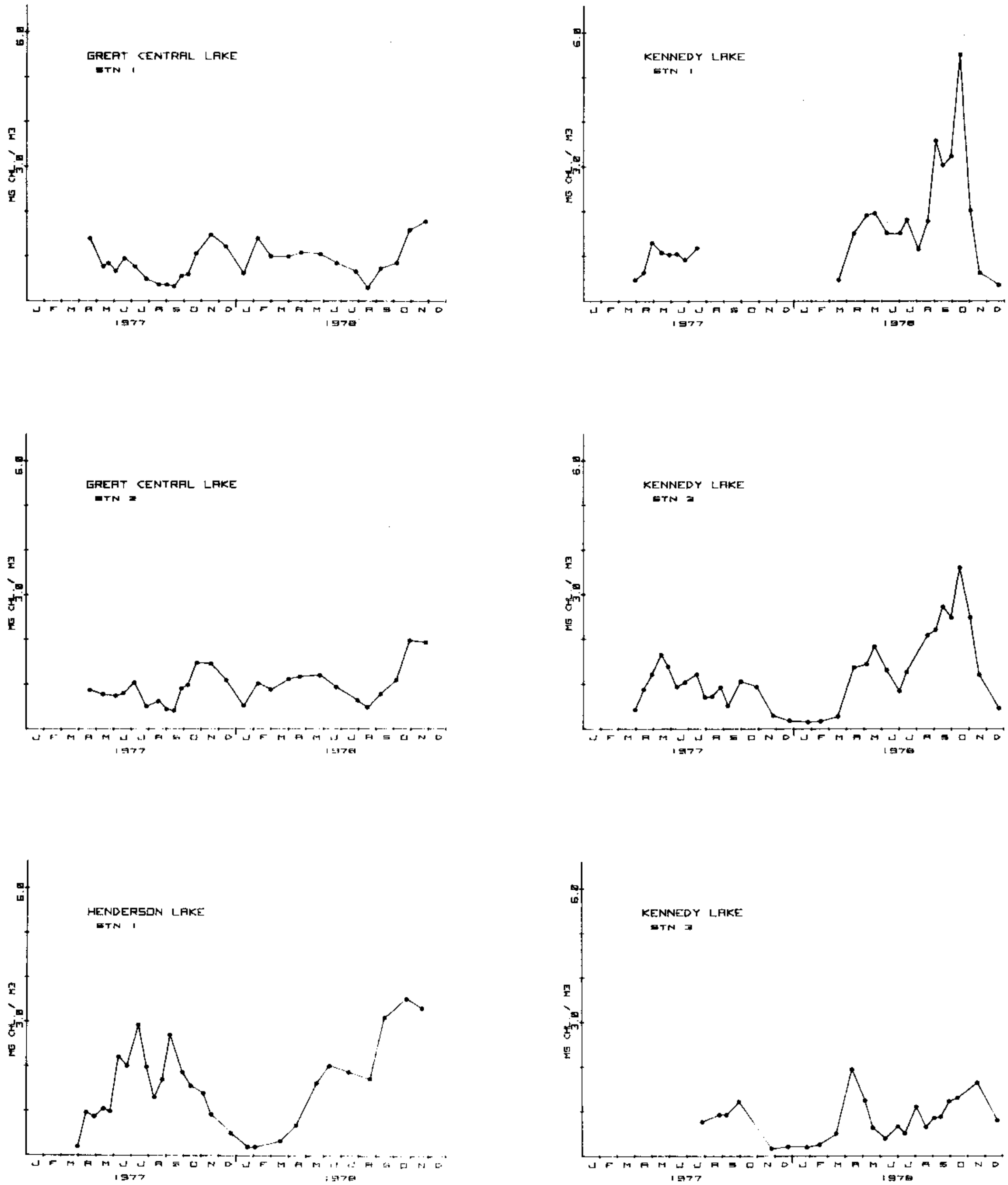
Appendix Figure 4. Mean epilimnetic values (0-10 m) of total phosphorus concentration ($\mu g.L^{-1}$) at each station in each of the study lakes.



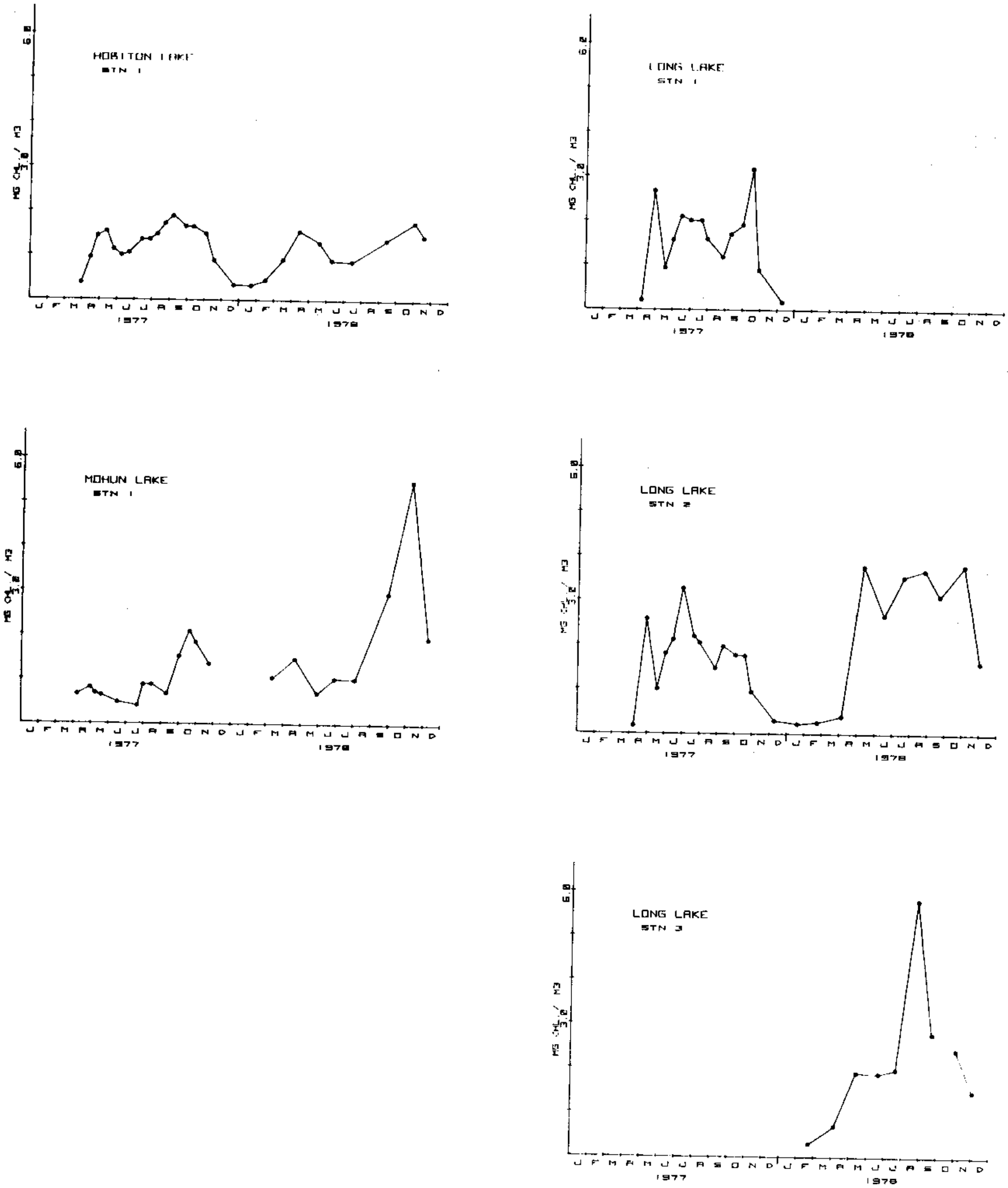
Appendix Figure 5. Mean epilimnetic values (0-10 m) of silicate concentration ($\mu g.L^{-1}$) at each station in each of the study lakes.



Appendix Figure 6. Mean epilimnetic values (0-10 m) of silicate concentration ($\mu g.L^{-1}$) at each station in each of the study lakes.



Appendix Figure 7. Mean epilimnetic values (0-10 m) of total chlorophyll concentration ($mg.m^{-3}$) at each station of each of the study lakes.



Appendix Figure 8. Mean epilimnetic values (0-10 m) of total chlorophyll concentration ($mg.m^{-3}$) at each station of each of the study lakes.