Limnological Results from the 1979 British Columbia Lake Enrichment Program

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ABSTRACT

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Limnological investigations were conducted on 21 oligotrophic British Columbia lakes. At weekly intervals during the growing season, 12 of the lakes were fertilized with ammonium nitrate and ammonium phosphate. Phosphorus loads from fertilizer were from 24 to over 200% above annual natural loads. Annual production in the lakes averaged 31 g $C \cdot m^{-2}$ and ranged from 14 to 73. Mean epilimnetic chlorophyll concentrations in most lakes were between 1 and 2 $mg \cdot m^{-3}$ and the average of all lakes was 1.3 $mg \cdot m^{-3}$. Response of the lakes' phytoplankton communities to fertilization was quite variable, but production and biomass tended to be higher during fertilization. The response and variability are discussed with reference to annual variation in various physical, chemical and biological factors.

Key words: Limnology, oligotrophy, lake fertilization, primary production, chlorophyll, nutrients.

RÉSUMÉ

Shortreed, K. S., and J. G. Stockner. 1981. Limnological results from the 1979 British Columbia Lake Enrichment Program. Can. Tech. Rep. Fish. Aquat. Sci. 995: iii + 71 p.

Nous avons fait l'étude limnologique de 21 lacs de la Colombie-Britannique. A chaque semaine de la saison de croissance, 12 d'entre eux ont été fertilisés au nitrate et au phosphate d'ammonium. L'apport supplémentaire de phosphore était supérieur de 24 à 200% a l'apport naturel. La production annuelle des lacs, de 31 g de C/m^2 en moyenne, se situait entre 14 et 73 g/m^2. Dans l'épilimnion de la plupart de ces lacs, la concentration de chlorophylle, de 1,3 mg/m^3 en moyenne, se situait entre 1 et mg/m^3. La réaction du phytoplancton a été très variable, mais la production et la biomasse se sont accrues. Cette réaction et sa variabilité sont discutées, compte tenu des variations annuelles des divers facteurs physico-chimiques et biologiques.

Mots clés: Limnologie, oligotrophie, fertilisation, production primaire, chlorophylle, éléments nutritifs.

INTRODUCTION

This limnological investigation of 21 British Columbia lakes was part of the continuing Lake Enrichment Program (L.E.P.) of the joint federal-provincial Salmonid Enhancement Program (S.E.P.). Previous work in British Columbia (LeBrasseur et al. 1978) has demonstrated that growth and/or survival rates of juvenile sockeye salmon (Oncorhynchus nerka) may be increased if inorganic nitrogen and phosphorus fertilizer is added to the epilimnia of sockeye nursery lakes during the growing season. With this evidence, and with evidence from similar studies in other sockeye nursery lakes (Nelson and Edmondson 1955, Rogers 1977) the L.E.P. has expanded until 12 lakes were fertilized with ammonium nitrate and ammonium phosphate in 1979. An additional nine lakes were studied to determine their suitability for fertilization. Earlier work on many of these lakes and the rationale and objectives of these continuing studies have been previously reported by Stockner (1979), Stockner and Shortreed (1979) and Stockner et al. (1980). This report describes and discusses the limnological results of the 1979 L.E.P.

DESCRIPTION OF STUDY AREA

The study lakes range from near sea level to 580 m in elevation and from 49° to over 56° in latitude (Fig. 1). Consequently geographic, morphometric and hydrologic features vary widely (Table 1). Most south coastal lakes (Great Central, Henderson, Hobiton, Kennedy, Long, Nimpkish, and Woss) and all the Queen Charlotte Island lakes (Awun, Eden, Ian, and Mercer) are monomictic (although ice cover may occur for short periods during some winters). The remainder are dimictic; duration of ice cover is from 2-3 months on the coastal lakes and 5-6 months on the interior lakes (Bowser, Fred Wright, and Meziadin).

All Vancouver Island lakes studied are clear lakes (mean compensation depths >10 m), most mainland coastal and Queen Charlotte Islands lakes are dystrophic, and Bowser, Kitlope and Meziadin lakes are glacially turbid (Table 2). Detailed descriptions of climatic and morphometric features are given in Stockner and Shortreed (1978, 1979) and in Stockner et al. (1980).

METHODS

All lakes in this study were sampled from a float-equipped de Havilland Beaver aircraft, except Great Central and Mohun lakes, which were sampled by boat. Bowser, Damdochax, and Fred Wright lakes were sampled twice (in June and August); Awun, Eden, Ian, and Mercer lakes were sampled 4 times (in March, May, July, and September); Kitlope and Meziadin lakes were sampled 6 times (May to October); Bonilla, Curtis, Devon, and Lowe lakes were sampled 7 times (March to October); Nimpkish and Woss lakes were sampled 8 times (March to November); Hobiton, Henderson, Kennedy, and Mohun lakes were sampled 10 times; and Great Central Lake was sampled 11 times.

Temperature profiles to a depth of 50 m were obtained at each station using a bathythermograph (BT). A bucket thermometer was used to measure surface temperature for BT calibration. The extinction with depth of surface photosynthetically active radiation (PAR:400-700nm) was measured using a Li-Cor light meter (Model LI-185A) and vertical extinction coefficients were calculated.

A 4.5-L Van Dorn bottle was used to collect the samples. At each station 2-L water samples were collected in clean plastic bottles from depths of 1, 3, 5 and 20 m. Samples were stored in the dark and transported to the field laboratory within 4 hours. In the laboratory approximately 250 mL of water from each depth were filtered (after rinsing with sample) through an ashed and washed Whatman GFF filter. One half of each 250 mL of filtrate was placed in a glass bottle and the other half in a plastic bottle. All samples were then stored at 4°C in the dark. Samples placed in glass bottles were later analyzed for total dissolved phosphorus (TDP) and nitrate (NO_3-N). Samples in plastic bottles were analyzed for inorganic reactive silicon (IRS) and total dissolved solids (TDS). Ashed and washed GFF filters contributed no detectable silicon to the filtrate.

Unfiltered portions of each 2-L sample were placed in clean glass culture tubes, stored at 4°C in the dark, and analyzed for total phosphorus (TP). All chemical analyses were done according to Golterman's (1969) methods. An additional unfiltered portion was placed in a plastic bottle, fixed with Lugol's solution, and used for phytoplankton counts and identification using Utermöhl's (1958) method.

At each station glass jars were filled completely with water from depths of 2 and 7.5 m. These samples were used to measure pH and total alkalinity according to the standard potentiometric method of APHA (1975). Dissolved inorganic carbon was estimated indirectly from pH, bicarbonate alkalinity, TDS, and temperature (APHA 1975).

From each 2-L sample 500-mL subsamples were filtered through Millipore AA filters, to which a few drops of saturated $MgCO_3$ solution were added during filtration. Filters were frozen and later analyzed for total chlorophyll using the method of Strickland and Parsons (1972).

On lakes where phytoplankton fractionation studies were carried out (Bonilla, Great Central, Kitlope, Long, Lowe and Woss), additional 500-mL portions of the 2-L samples from 1, 3 and 5 m were filtered through 10 and 54-μm Nitex screens. These screens were stored and later analyzed for chlorophyll in the same manner as the Millipore AA filters. Chlorophyll concentrations in three size fractions (<10 μm, 10 to 54 μm and >54 μm) were then calculated.

Primary production was measured on all lakes except Awun, Bowser, Damdochax, Eden, Fred Wright, Ian, and Mercer. Depths of 0, 1, 2, 3, 5, 7.5, 10, and 20 m were sampled, except on Great Central, Hobiton, Henderson, Kennedy, Mohun, Nimpkish and Woss lakes, where 30 m was sampled and 2 m omitted. Two 125-mL light bottles were filled with water from each depth and one 125-mL dark bottle was filled from 1, 5, and 20 m. In addition, on lakes where phytoplankton fractionation studies were carried out, two 300-mL light bottles each were filled with water from depths of 1, 3, and 5 m and 300-mL dark bottles were filled with water from depths of 1 and 5 m.

The 125-mL bottles were inoculated with 1 mL of $NaH^{14}CO_3$ solution (approximately 75 $kBq \cdot mL^{-1}$), and the 300-mL bottles with 3 mL of the same solution. Activity of the radioisotope stock was determined by placing 1 mL of stock in each of 3 scintillation vials containing 15 mL of scintillation cocktail (toluene, 2-ethoxyethanol, and Amersham-Searle Spectrafluor). Samples were incubated for 2-3 hours and incubations normally commenced between 0900 and 1000 h (local time). After incubation samples were placed in light-tight boxes and transported to the laboratory, where filtration started within 2 h of the end of incubation.

Each 125-mL sample was filtered onto a 0.45-μm pore size Millipore filter at a vacuum pressure not exceeding 20 cm Hg. Each 300-mL sample was divided into 3 equal portions. One aliquot was filtered through a 0.45-μm pore size Millipore filter, another through a 10-μm mesh size Nitex screen, and the third through a 54-μm mesh size Nitex screen. Filters and screens were placed in scintillation vials containing 15 mL of the previously described cocktail and counted in either a Packard Tri-Carb Model 3375 or a Searle Isocap 300 liquid scintillation spectrometer. Quench series composed of the same cocktail and filters as that used for samples were used to calculate counting efficiencies and to convert $counts \cdot min^{-1}$ (CPM) to $disintegrations \cdot min^{-1}$ (DPM). Strickland's (1960) equation was used to calculate carbon uptake as $mg\ C \cdot m^{-3} \cdot h^{-1}$. Light data collected with Belfort pyrheliometers were used to convert hourly production rates to $mg\ C \cdot m^{-3} \cdot d^{-1}$ and integration of volumetric production rates gave $mg\ C \cdot m^{-2} \cdot d^{-1}$.

For those lakes for which bathymetric maps were available (all except Damdochax and Bowser), hydraulic loads and water residence times were calculated using methods described in Stockner et al. (1980). Annual phosphorus loads were calculated using Vollenweider's (1976) method and are reported in Table 4.

RESULTS

Although lake areas and mean depths varied widely, all but two of the lakes had residence times <2 years (Table 1). The exceptions were Woss Lake (3.0 yr) and Great Central Lake (7.3 yr). These high hydraulic loads resulted in areal phosphorus loading rates (Vollenweider 1976) ranging from 61 to 544 mg $P \cdot m^{-2} \cdot yr^{-1}$ despite low incipient concentrations of total phosphorus (Table 3).

Average pH values were <7 in the dystrophic lakes, circumneutral in the clear water lakes, and between 7 and 8 in Bowser, Damdochax, and Meziadin lakes (Table 3). The pH values were lowest in spring and tended to increase during the growing season. Average total inorganic carbon was lowest (0.7-1.2 $mg \cdot L^{-1}$) in the acidic north coast lakes (Bonilla, Curtis, Devon, and Lowe) and highest (6-9 $mg \cdot L^{-1}$) in glacial Bowser and Meziadin lakes.

Temperature profiles exhibited considerable variation among lakes (Fig. 2). The north coast lakes, Queen Charlotte Island lakes, and Fred Wright Lake stratified strongly with mixed layer depths <10 m. Vancouver Island lakes, with the exception of Nimpkish and Woss, stratified strongly but had mixed layer depths >10 m. Nimpkish, Meziadin, and Woss lakes developed weaker stratification and mixed layer depths >15 m. Kitlope lake was weakly stratified throughout the growing season and Bowser Lake was isothermal, even in August.

Seasonal variation in water transparency was not generally apparent, although compensation depths in both glacial and dystrophic lakes tended to be lower in late summer and early fall. Average compensation depth was lowest (2 m) in Bowser Lake, <5 m in humic Bonilla, Eden, and Ian lakes, and >15 m in Great Central, Mohun, and Woss lakes (Table 2).

Average nitrate concentrations ranged from 1 $\mu g \ N \cdot L^{-1}$ in Fred Wright Lake to 150 in Meziadin Lake (Table 3). Nitrate decreased in summer in all lakes investigated, and to concentrations below the detection limit of 1 $\mu g \cdot L^{-1}$ in all lakes except Bowser, Eden, Ian, Meziadin, Nimpkish, and Woss lakes (Fig. 3).

Total phosphorus concentrations in all lakes except Bowser were less than Vollenweider's (1976) "critical" level of 10 $\mu g \cdot L^{-1}$ (Table 3). Seasonal trends were not observed in either total or dissolved phosphorus concentrations.

Inorganic reactive silicate was lowest in early spring in most north coast and Queen Charlotte Island lakes and in late summer or early fall in the remainder. Concentrations of silicate (as silicon) decreased to <0.2 $mg \cdot L^{-1}$ in Bonilla, Curtis, Devon, Henderson, Lowe, and Mohun lakes only.

Annual primary production was lowest (14 g $C \cdot m^{-2}$) in Kitlope Lake and highest (73) at station 1 of Kennedy Lake (Table 2). Due to the considerable variability in weather conditions encountered on sampling trips, seasonal trends in production were generally not apparent. In all lakes except Great Central, Kennedy, Meziadin, Nimpkish and Woss, almost all carbon production occurred in the 0-5 m depth interval (Fig. 4). In lakes where phytoplankton fractionation studies were carried out, the <10-μm fraction comprised between 75 and 87% of total carbon assimilated. The sole exception was Woss Lake, where this fraction contributed 50% and the 10 to 54-μm fraction 33%. Most of the remainder of the production occurred in the 10 to 54-μm fraction except in Great Central Lake, where primary production in the >54-μm fraction was higher than that in the 10 to 54-μm category.

Chlorophyll concentrations averaged <0.2 mg $\cdot m^{-3}$ in Bowser Lake and ranged from 0.6 (Kitlope Lake) to 2.4 (Long Lake, station 2) in the remaining lakes (Table 2). In most lakes highest chlorophyll concentrations occurred in May or June and in no lakes did chlorophyll maxima exceed 4 mg $\cdot m^{-3}$ (Fig. 5). Autumnal peaks in chlorophyll were recorded in Henderson, Hobiton, Kennedy, and Great Central lakes only. However, infrequent sampling of the Queen Charlotte Islands lakes and of Bowser, Damdochax and Fred Wright lakes may have missed the occurrence of fall peaks. In the fractionation experiments, an average of 90% of the chlorophyll occurred in the <10-μm fraction in Bonilla, Lowe, and Meziadin lakes. In Long and Woss lakes this fraction averaged 80% of the chlorophyll, and in Great Central Lake only 62%. In all lakes most chlorophyll in the larger fractions (10 to 54-μm and >54-μm) occurred in early spring and decreased for the remainder of the growing season.

Mean annual algal numbers ranged from $2.80 \times 10^8 \cdot m^{-3}$ in Kitlope Lake to $6.07 \times 10^9 \cdot m^{-3}$ in Awun Lake (Table 2). The high numbers in Awun resulted from a September bloom of the small (<6 μm in diameter) coccoid blue-green alga Chroococcus sp. Mean epilimnetic algal numbers in most lakes were between $5.0 \times 10^8 \cdot m^{-3}$ and $3.0 \times 10^9 \cdot m^{-3}$. Algal volumes were also lowest (14 $mm^3 \cdot m^{-3}$) in Kitlope Lake and highest (750) at station 2 in Great Central Lake. Those lakes with average volumes >200 $mm^3 \cdot m^{-3}$ (Great Central, Henderson, Hobiton, Mercer, and Mohun lakes) were dominated by large diatoms. Phytoplankton species composition and seasonal succession were similar to that reported in Stockner and Shortreed (1979) and Stockner et al. (1980) for 1978 on the same lakes, and details will not be discussed in this report.

Bonilla, Curtis, and Devon lakes, sampled for the first time in 1979, had blooms in early May dominated volumetrically by Rhizosolenia sp. In Curtis and Devon lakes, Dinobryon sp. was also very common in spring. For the remainder of the growing season, unidentified coccoid algae <5 μm in diameter were dominant numerically in the three lakes. Chroococcus sp. in Devon Lake and Ankistrodesmus spp. in Bonilla and Curtis lakes were dominant numerically for much of the season. Volumetrically, the dinoflagellate Peridinium sp. was dominant in the three lakes in summer and fall.

DISCUSSION

PRIMARY PRODUCTION

The primary objective of the L.E.P. monitoring and research subprogram is to assess the impact of nitrogen and phosphorus additions on lake metabolism. Initially Rodhe (1969) and more recently Fee (1979) have discussed the advantages of using primary production estimates rather than chlorophyll concentrations as a variable to assess changes in a lake's trophic state. Primary production is affected by a range of physical, chemical, and biological factors (i.e. flushing, insolation, etc.) each subject to considerable daily, seasonal, and annual variation. When a lake is perturbed by relatively small weekly additions of nitrogen and phosphorus, phytoplankton response can easily be masked by variations induced by other factors, and hence interpretations are often difficult. Another major difficulty in interpreting data from this large limnological investigation is that manpower and financial constraints restricted sampling to once monthly. Results from Hobiton and Meziadin lakes provide examples of the problems which may be incurred by both these difficulties.

Annual primary production calculated from <u>in situ</u> estimates was 25 g $C \cdot m^{-2}$ (mean of two stations) in Meziadin Lake in 1978 (Stockner and Shortreed 1979), and 45 in 1979 (Table 3, Fig. 4). This 80% increase was accompanied by an increase of only 10% in total chlorophyll concentrations in the euphotic zone. Light conditions on sampling dates were similar in both years, as were measured nutrient concentrations and mean epilimnetic temperature. While water clarity was lower and stream discharge was higher in 1979 than in 1978, no differences are apparent which adequately explain the difference in production between years.

The fertilizer load to Hobiton Lake in 1979 was 50% higher than in previously treated years (Stockner et al. 1980). In 1979 average chlorophyll concentration was 40% higher than in 1978, and zooplankton biomass increased by almost 90% (P. Rankin, personal communication). However, estimated annual primary production was virtually the same in both years. Since higher algal biomass occurred in 1979 despite higher grazing pressure from the increased zooplankton population, primary production must have been higher than in 1978. The differences in primary production between the two years were not detected due to several factors, most important of which was the between year variation in light conditions (i.e. more cloud and rain on sampling dates in 1979).

These results from Hobiton and Meziadin lakes suggest that observations of increased primary production between years should be interpreted with caution and that recorded increases in lake metabolism during fertilized years may be either masked or enhanced by a variety of other factors.

After analysis of an 8 year production data set from ELA lakes in northwestern Ontario, Fee (1979, 1980) noted that annual <u>in situ</u> primary

production estimates among similar lakes varied by up to 100% and that use of an incubator could eliminate much of this variability. He also observed that the greatest variation in annual primary production was found in fast flushing systems; a finding which is germane to our B.C. coastal lakes which have far shorter residence times than the ELA lakes (Stockner et al. 1980, Schindler and Fee 1974). Calculation of annual primary production from incubator rather than in situ incubations and from simulation of cloudless weather as proposed by Fee (1978) would eliminate light as a variable and make production estimates more comparable among lakes and between years within lakes. However, in order to determine areal primary production this method requires either a complex incubator or the use of integrated samples, neither of which are feasible on most lakes in this study. In some study lakes thermal stratification is very weak, and temperatures decrease steadily from the surface with depth (Fig. 2). It would be extremely difficult to incubate samples taken from a temperature regime of this nature at in situ temperatures. In others, which do have stable stratification, light is attenuated very rapidly, and integrated samples of even 2 m would encompass large changes in light intensity. In the light of our present results and some of Fee's (1979, 1980) general conclusions, perhaps average chlorophyll and/or zooplankton biomass would be better variables for the assessment of the effects of fertilization than primary production. However, using average chlorophyll also has many inherent limitations as recently discussed by Fee (1979).

While annual estimates of production from in situ incubations are of limited use when comparing stations within or among lakes, a better understanding of the impact of weekly nutrient additions on autotrophic production in our study lakes is gained by measuring successive daily variations in carbon assimilation, for up to a week after a fertilizer application. In both Kitlope and Lowe lakes daily sampling after fertilization showed a marked increase in volumetric and areal production for several days, characterized by a production maximum in the surface layer (0-1 m) after the third day (Fig. 6). In an identical experiment on Great Central Lake in 1978 a similar response was noted 3 days following fertilization, but no change in production was noted at a control station several kilometers away (Costella et al. 1979 and Stockner et al. 1980).

Lake Classification

Annual production was estimated for 14 of the lakes in the investigation and 9 of the 14 were oligotrophic, based on Rodhe's (1969) classification (annual production ≤ 25 g $C \cdot m^{-2}$). The remainder were mesotrophic (annual production 26-74 g $C \cdot m^{-2}$). Meziadin Lake was the only unfertilized lake to be classified as mesotrophic. Closest to the eutrophic category was fertilized Kennedy Lake, with an annual production of 70 g $C \cdot m^{-2}$. In 1977, the first year of fertilization, primary production in Long Lake reached mesotrophic levels (57 g $C \cdot m^{-2} \cdot yr^{-1}$) and in 1978, its second year of treatment, eutrophic levels (106 g $C \cdot m^{-2} \cdot yr^{-1}$) (Stockner et al. 1980). In 1979 fertilizer loading was reduced by 40% and annual production was reduced to the mesotrophic category (33 g $C \cdot m^{-2}$).

Vollenweider's (1976) data set provided another means of assessing

the trophic state of our study lakes, using average epilimnetic chlorophyll concentration and total phosphorus loading characteristics. In 1979 all lakes in this study were in the oligotrophic category, with some overlap into mesotrophy (Fig. 7). The only lake considerably removed from Vollenweider's (1976) line of best fit was Bowser Lake. Although it had the highest total phosphorus concentrations of any lake in this study, the high light attenuation (average extinction coefficient = 2.75) and cold temperatures (mean surface temperature = 8.0°C) reduced chlorophyll concentrations to the lowest recorded. In both Rodhe's (1969) and Vollenweider's (1976) classification the lakes were at similar trophic levels. The data suggest that although variation in annual production and phosphorus loading may be considerable, it is not sufficient to prevent classification of the trophic condition of our study lakes.

Fertilization Response

Seven lakes (Awun, Eden, Ian, Kennedy-Main Arm, Kitlope, Lowe and Mercer) in this study were fertilized for the first time in 1979. Discussion of effects of fertilization will be confined to those (Kennedy-Main Arm, Kitlope, and Lowe lakes) for which pre-fertilization data are available. Fertilizer load to Kitlope and Lowe lakes increased natural phosphorus loads to each by approximately 40%, while the Kennedy-Main Arm load increased natural loading by approximately 150%. The increase in loading to Kitlope and Lowe lakes did not produce easily detectable increases in either annual production or average chlorophyll concentrations, but there were differences in seasonal chlorophyll concentrations. Chlorophyll concentrations were higher in both lakes during the fertilized period than during the same time in the unfertilized year (Fig. 5 and Stockner and Shortreed 1979). However, when the fertilization stopped on September 2nd, algal biomass decreased rapidly in both Kitlope and Lowe lakes, whereas in 1978 it increased in September to the highest levels of the year. By late August of 1979, zooplankton biomass was higher in both Lowe and Kitlope lakes than in the previous year (P. Rankin, personal communication). The higher zooplankton biomass and resulting increased grazing pressure, combined with the stoppage of fertilization and diminished primary production likely produced the rapid autumn decline in algal biomass.

The higher fertilizer load to Kennedy-Main Arm produced striking increases in both chlorophyll concentration and in primary production between years of comparison. Annual production increased from 29 g $C \cdot m^{-2}$ in 1978 to 73 in 1979, and average chlorophyll from 0.87 to 1.52 $mg \cdot m^{-3}$. This doubling of average chlorophyll did not result in detectable differences in transparency between years (Table 2 and Stockner et al. 1980). The increase in average chlorophyll concentration occurred despite a 75% increase in average zooplankton biomass (P. Rankin, personal communication). Unlike Kitlope and Lowe lakes, fertilization of Kennedy-Main Arm occurred over the entire growing season (April to October), and seasonal trends in 1979, despite the difference in magnitude, were similar to the unfertilized year (1978).

Diatom Succession and Silicon Concentration in Henderson Lake

Silicon concentration occasionally dropped to low levels in several lakes in this study, but only in Henderson Lake were levels <0.15 $mg \cdot L^{-1}$ for an extended period (June - October) (in this section IRS concentrations

are expressed as silicon). In Henderson Lake the initial decrease in silicon from the winter concentrations of 0.5 - 0.6 $mg \cdot L^{-1}$ was accompanied by a rapid increase in diatom numbers (mostly Tabellaria fenestrata). This bloom peaked in June and by July T. fenestrata had virtually disappeared from the epilimnetic phytoplankton population. In August, despite the low silicon concentrations, Asterionella formosa increased to 2.1×10^9 $cells \cdot m^{-3}$ (Fig. 8).

In 1977 in Henderson Lake Rhizosolenia sp. was the dominant diatom throughout the growing season, but in 1978 A. formosa succeeded Rhizosolenia sp. mid-way through the growing season (Stockner et al. 1980). In addition, overturn concentrations of silicon have declined from 0.8 mg $Si \cdot L^{-1}$ in 1977 to 0.6 $mg \cdot L^{-1}$ in 1979. It appears that the years of fertilization (1976 to the present) have increased silicon demand and that it is no longer being replaced at a sufficient rate to maintain pre-fertilized concentrations. This phenomena was observed in Lake Michigan by Schelske and Stoermer (1972), who predicted that continuing silica depletion would lead to dominance by blue-green or filamentous green algae. If silicon levels in Henderson Lake continue to decrease, it is likely that the spring bloom of T. fenestrata will be replaced by an A. formosa bloom (Kilham 1971), and that later in the growing season diatoms will be only of minor importance in the algal community. Because nitrogen and phosphorus concentrations even during fertilization were too low to permit development of nuisance algal blooms, replacement of diatoms by blue-green algae is unlikely to occur, but further silicon depletion could lead to dominance by filamentous green algae. Since zooplankton utilize mainly nanoplankton, μ algae, and bacteria (Gliwicz 1975), changes in dominance of the large, inaccessible algal species have little importance in the transfer of energy to the lake's higher trophic levels, most notably planktivorous juvenile sockeye salmon.

SUMMARY

All lakes in this investigation, with the exception of Bowser Lake, had low (< 8 $\mu g \cdot L^{-1}$) levels of total phosphorus. All lakes except Meziadin showed summer depletion of nitrate-nitrogen. Also, euphotic zone/epilimnion depth ratios were unfavorable (< 0.5) only in Bowser Lake, so during the growing season light limitation was not a serious factor to phytoplankton growth. Nutrient replenishment in the epilimnion by recycling from the sediments was not considered as important a source of nutrients for phytoplankton as the external nutrient load since the majority of the study lakes are deep and steep-sided (mean depths > 30 m) and had a calculated $A_e:V_e$ ratio (where: A_e = lake surface area - area at bottom of epilimnion, V_e = volume of epilimnion) (Fee 1979), with the exception of Lowe Lake, of less than 0.03. The weekly observations of areal and volumetric production following fertilization indicate that in all lakes both nitrate and phosphate are in short supply and required for growth. The majority of the study lakes were classed as oligotrophic with Long and Kennedy lakes in the mesotrophic category during years of fertilization. In Henderson Lake further lowering of silicon concentrations may cause a replacement of diatoms by filamentous

green algae. Increased zooplankton biomass during enrichment was recorded in those lakes on which data is available for both unfertilized and fertilized years (Rankin et al. 1979, Rankin and Ashton 1980, P. Rankin, personal communication) and it appears reasonable to assume that secondary production has been increased on application of fertilizer to most lakes. While increased growth of juvenile sockeye salmon as a result of an improved food supply would occur only if food was a limiting factor, available data indicates that this is the case in a number of coastal British Columbia lakes (T. Gjernes, personal communication, K. Simpson, personal communication).

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Table 1. Geographic, climatic, and hydrologic data from the 1979 study.

Lake	Latitude	Longitude	Elevation (m)	Lake area (km^2)	Mean depth (m)	Water residence time (yr)
Awun	53°36'	132°35'	51	4.9	47	0.9
Bonilla	53°31'	130°15'	10	2.3	34	1.0
Bowser	56°26'	129°30'	366	34	-	-
Curtis	53°30'	129°50'	10	3.0	34	0.6
Damdochax	56°30'	128°08'	580	2.0	-	-
Devon	53°27'	129°45'	10	1.8	29	1.3
Eden	53°51'	132°43'	70	5.9	43	0.9
Fred Wright	55°58'	128°47'	572	3.9	15	0.3
Great Central	49°22'	125°15'	82	51	212	7.3
Henderson[a]	49°05'	125°02'	15	15	109(43)	3.2(1.3)
Hobiton	48°45'	124°49'	15	3.6	36	1.0

Table 1. Cont'd.

Lake and Station	Latitude	Longitude	Elevation (m)	Lake area (km^2)	Mean depth (m)	Water residence time (yr)
Ian	53°45'	132°35'	116	20	50	1.1
Kennedy	49°06'	125°33'	12	64	33	1.1
Kitlope	53°07'	127°13'	15	12	86	0.4
Long	51°14'	127°10'	15	21	73	1.1
Lowe	53°34'	129°33'	10	3.7	25	0.2
Mercer	53°34'	132°53'	25	1.2	15	0.1
Meziadin	56°02'	129°15'	246	36	45	1.9
Mohun	50°07'	125°30'	200	9.9	13	1.5
Nimpkish	50°25'	126°57'	20	37	162	1.4
Woss	50°08'	126°38'	150	13	81	3.0

[a]Numbers in brackets are the result of calculating lake volume using only the mixolimnion.

Table 2. Physical and biological data from the 1979 study.

Lake and Station	Compensation depth (m)	Extinction coefficient (k_e)	Primary Production (g $C.m^{-2}.yr^{-1}$)	Total[a] Chlorophyll ($mg.m^{-3}$)	Algal[a] numbers ($No.x10^8.m^{-3}$)	Algal[a] volume ($mm^3.m^{-3}$)
Awun	5.2	0.80	-	1.54	60.7	100
Bonilla	4.2	1.02	25	1.04	11.2	134
Bowser-1	2.1	2.35	-	0.17	5.4	27
-2	1.8	3.15	-	<0.07	5.9	35
Curtis	6.0	0.77	21	1.24	21.0	113
Damdochax	7.5	0.65	-	1.63	13.9	192
Devon	5.8	0.78	21	1.79	11.9	180
Eden	4.8	0.92	-	1.24	7.3	37
Fred Wright	7.4	0.54	-	1.67	14.7	155
Great Central-1	18.5	0.25	22	0.90	15.8	705
-2	18.0	0.26	25	0.94	17.2	760
Henderson	11.7	0.38	51	1.76	17.7	534
Hobiton	10.4	0.44	24	1.54	25.4	298

Table 2. Cont'd.

Lake and Station	Compensation depth (m)	Extinction coefficient (k_e)	Primary Production ($g\ C.m^{-2}.yr^{-1}$)	Total[a] Chlorophyll ($mg.m^{-3}$)	Algal[a] numbers ($No.x10^{8}.m^{-3}$)	Algal[a] volume ($mm^{3}.m^{-3}$)
Ian-1	4.6	0.96	-	1.06	6.5	56
-2	3.9	1.12	-	0.89	5.0	28
Kennedy-1	13.3	0.37	73	1.52	21.8	180
-2	12.3	0.38	67	1.84	24.3	184
Kitlope	7.3	0.62	14	0.59	2.8	14
Long-1	9.3	0.51	37	2.02	17.3	119
-2	10.0	0.47	36	2.36	20.6	124
-3	10.0	0.43	26	1.69	17.9	87
Lowe	7.5	0.61	17	0.85	31.4	40
Mercer	6.4	0.70	-	1.66	15.7	309
Meziadin-1	10.9	0.40	53	1.68	13.1	99
-2	7.7	0.59	37	1.37	7.2	62
Mohun	16.3	0.30	39	1.31	26.6	444
Nimpkish	11.7	0.38	19	0.83	5.3	81
Woss	15.6	0.29	25	0.87	6.3	51

[a] Mean epilimnetic values

Table 3. Results of chemical analyses from the 1979 study (mean epilimnetic values).

Lake and Station	pH	Total alkalinity ($mg.L^{-1}$ $CaCO_3$)	Total dissolved solids ($mg.L^{-1}$)	Dissolved inorganic carbon ($mg.L^{-1}$)	Nitrate as N ($\mu g.L^{-1}$)	Total phosphate as P_1 ($\mu g.L^{-1}$)	Total dissolved phosphate as P_1 ($\mu g.L^{-1}$)	Inorganic reactive silicate as Si ($mg.L^{-1}$)
Awun	6.5	4.2	34	2.1	16	6	3	1.75
Bonilla	5.7	0.7	26	1.2	3	3	2	0.50
Bowser-1	7.8	32.1	104	8.2	45	18	4	0.70
-2	7.8	35.4	109	9.0	49	15	4	0.74
Curtis	5.8	0.8	22	1.1	10	4	3	0.45
Damdochax	7.4	25.9	61	7.3	17	5	5	2.11
Devon	5.6	0.6	25	1.1	5	4	3	0.47
Eden	6.6	4.7	41	2.1	27	5	4	1.81
Fred Wright	7.0	8.4	25	2.9	1	5	3	0.85
Great Central-1	7.0	12.7	28	4.4	9	3	2	0.74
-2	7.0	12.4	28	4.0	12	3	2	0.73
Henderson	7.0	7.9	78	2.6	14	5	3	0.31
Hobiton	6.8	5.2	28	1.9	13	6	3	1.12

Table 3. Cont'd.

Lake and Station	pH	Total alkalinity ($mg.L^{-1}$ $CaCO_3$)	Total dissolved solids ($mg.L^{-1}$)	Dissolved inorganic carbon ($mg.L^{-1}$)	Nitrate as N ($\mu g.L^{-1}$)	Total phosphate as P ($\mu g.L^{-1}$)	Total dissolved phosphate as P ($\mu g.L^{-1}$)	Inorganic reactive silicate as Si ($mg.L^{-1}$)
Ian-1	6.3	3.5	39	2.2	24	5	4	1.57
-2	6.2	2.5	40	1.7	24	5	5	1.44
Kennedy-1	7.0	10.1	34	3.3	12	4	2	0.77
-2	7.1	12.2	35	3.7	12	6	3	0.74
Kitlope	6.0	1.3	11	1.4	21	4	3	0.57
Long-1	6.4	2.8	16	1.6	20	5	2	0.74
-2	6.4	2.8	17	1.5	20	6	4	0.73
-3	6.7	8.3	1755	2.8	12	8	5	0.65
Lowe	5.7	0.4	13	0.7	10	4	3	0.42
Mercer	6.0	2.6	30	1.8	15	7	7	1.18
Meziadin-1	7.6	24.0	66	6.3	139	6	6	1.16
-2	7.5	24.7	70	6.7	150	5	5	1.27
Mohun	6.8	5.4	30	2.0	6	5	3	4.25
Nimpkish	7.0	10.5	41	3.2	37	3	2	1.76
Woss	6.8	8.5	25	3.0	16	3	3	1.24

Table 4. Phosphorus load to the fertilized lakes.

1979	Phosphorus load (Lp) (mg $P \cdot m^{-2} \cdot yr^{-1}$)	Fertilizer load (mg $P \cdot m^{-2} \cdot yr^{-1}$)	Critical load (mg $P \cdot m^{-2} \cdot yr^{-1}$)	% increase in P load from fertilizer	% P load of L_c
Awun	102	112	1018	110	21
Eden	186	99	931	53	31
Great Central	108	50	1075	46	15
Henderson	71	164	708	231	33
Hobiton	144	115	720	80	36
Ian	186	74	931	40	28
Kennedy	61	93	615	152	25
Kitlope	451	163	2256	36	27
Long	544	153	1360	28	51
Lowe	181	76	1809	42	14
Mercer	395	96	1974	24	25
Mohun	96	42	193	44	72

$$L_p = \frac{P \cdot \bar{Z} (1+\sqrt{T_w})}{T_w}$$

where: $\bar{Z}$ = mean depth (m)

T_w = water residence time (yr)

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

$$L_c = L_p$$

where: $P = 10\ mg \cdot m^{-3}$

(from Vollenweider 1976)

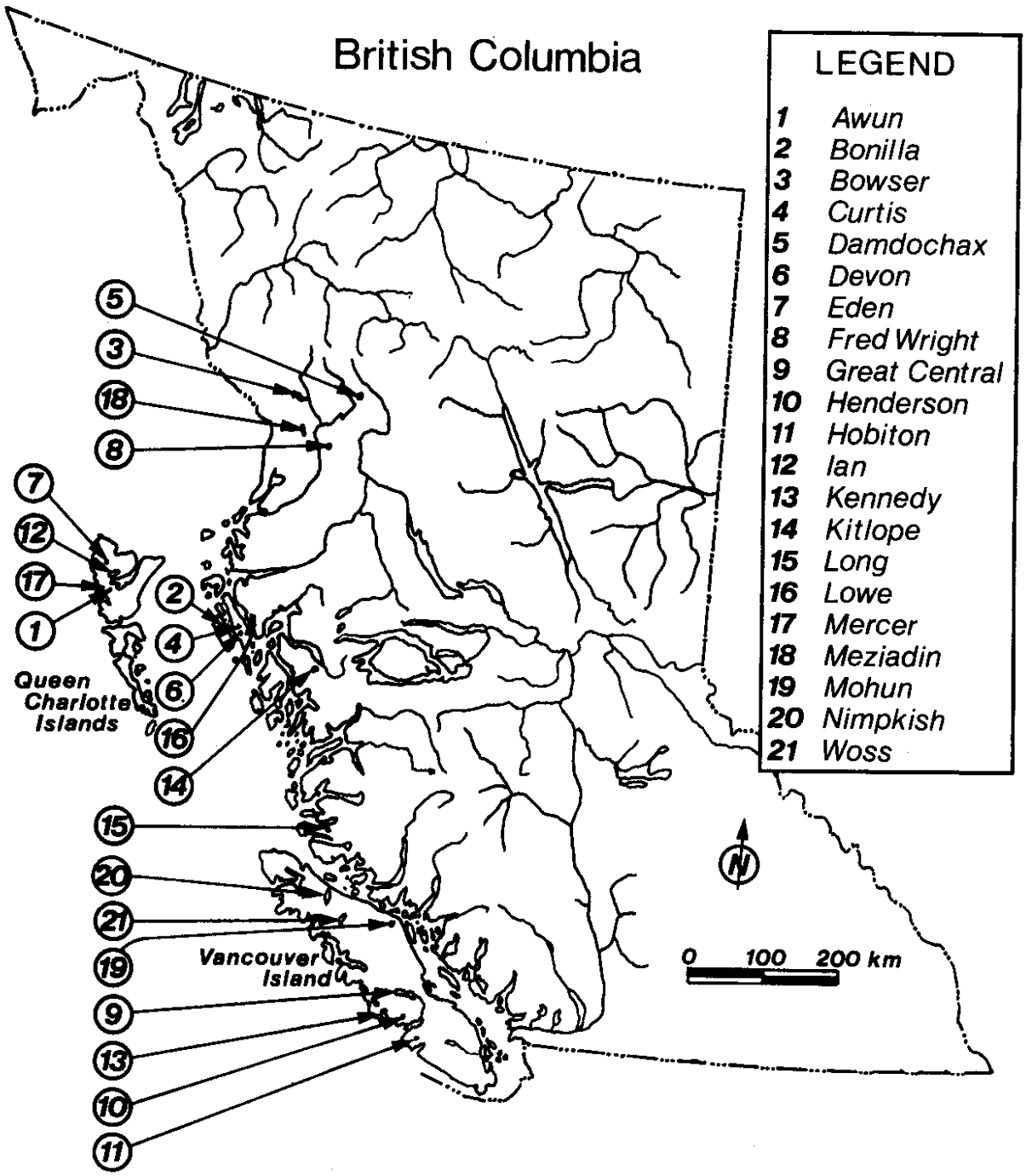

Fig. 1. Map of British Columbia with location of study lakes.

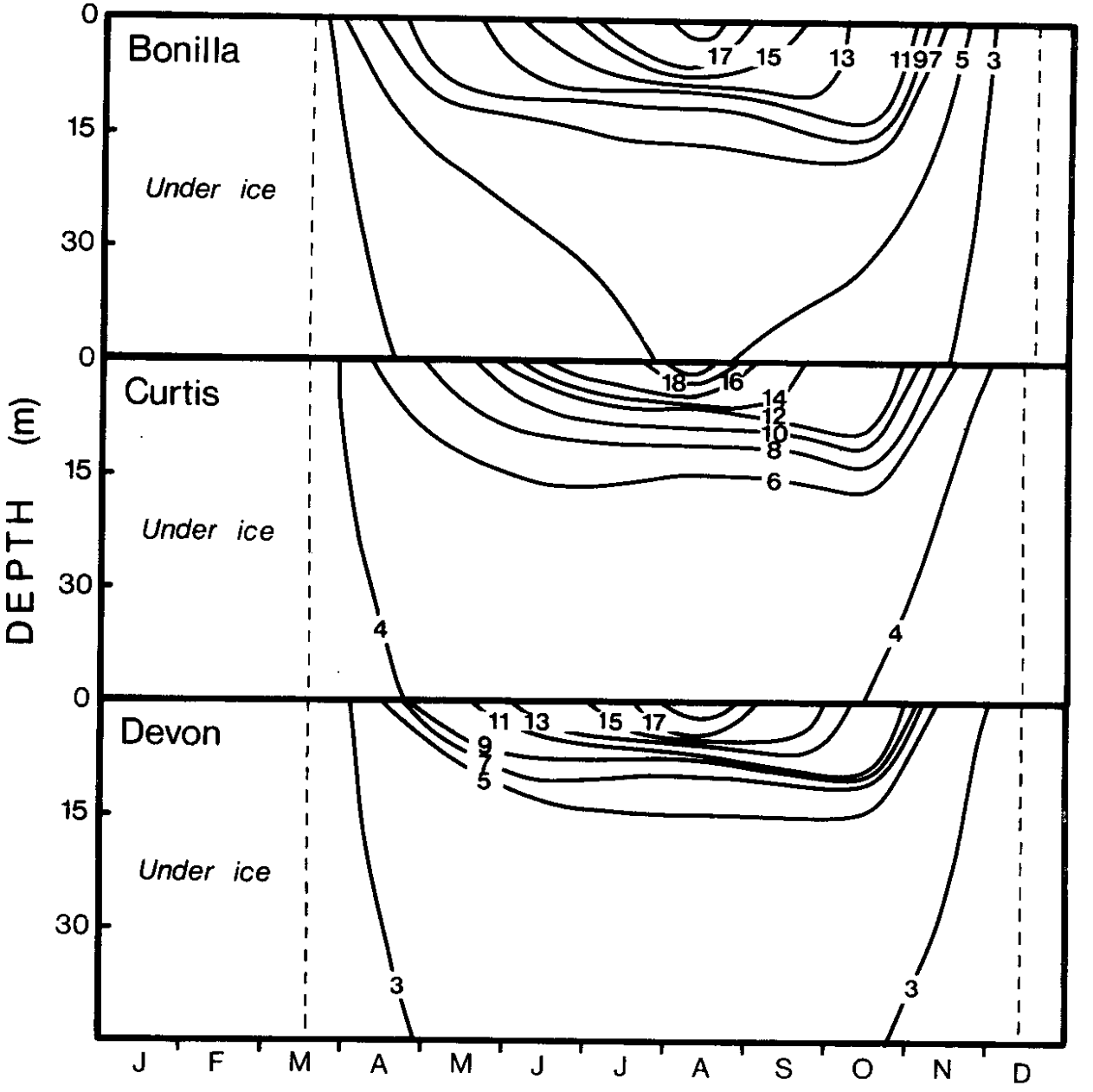

Fig. 2a. Seasonal isotherms of the study lakes.

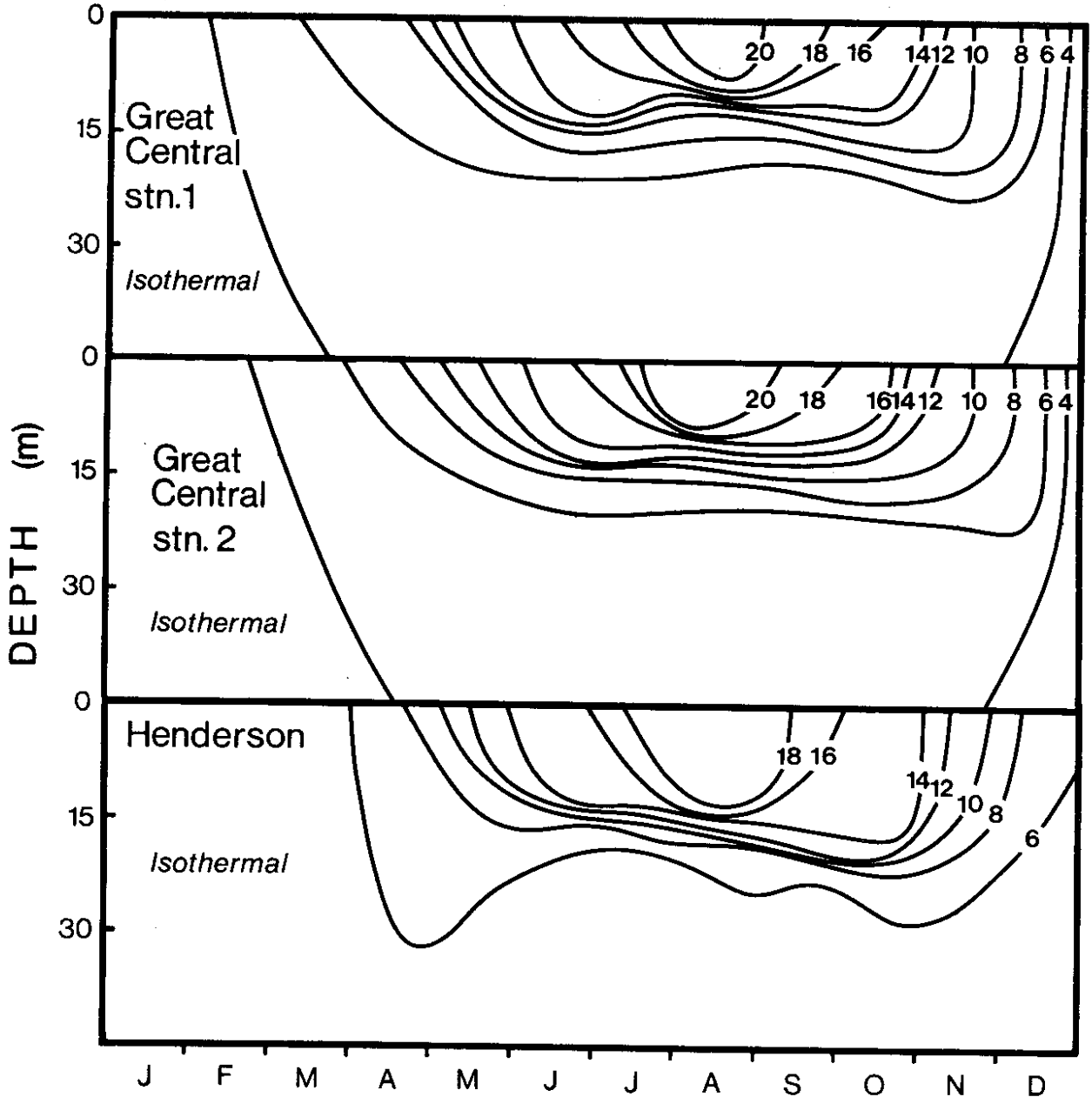

Fig. 2b. Seasonal isotherms of the study lakes.

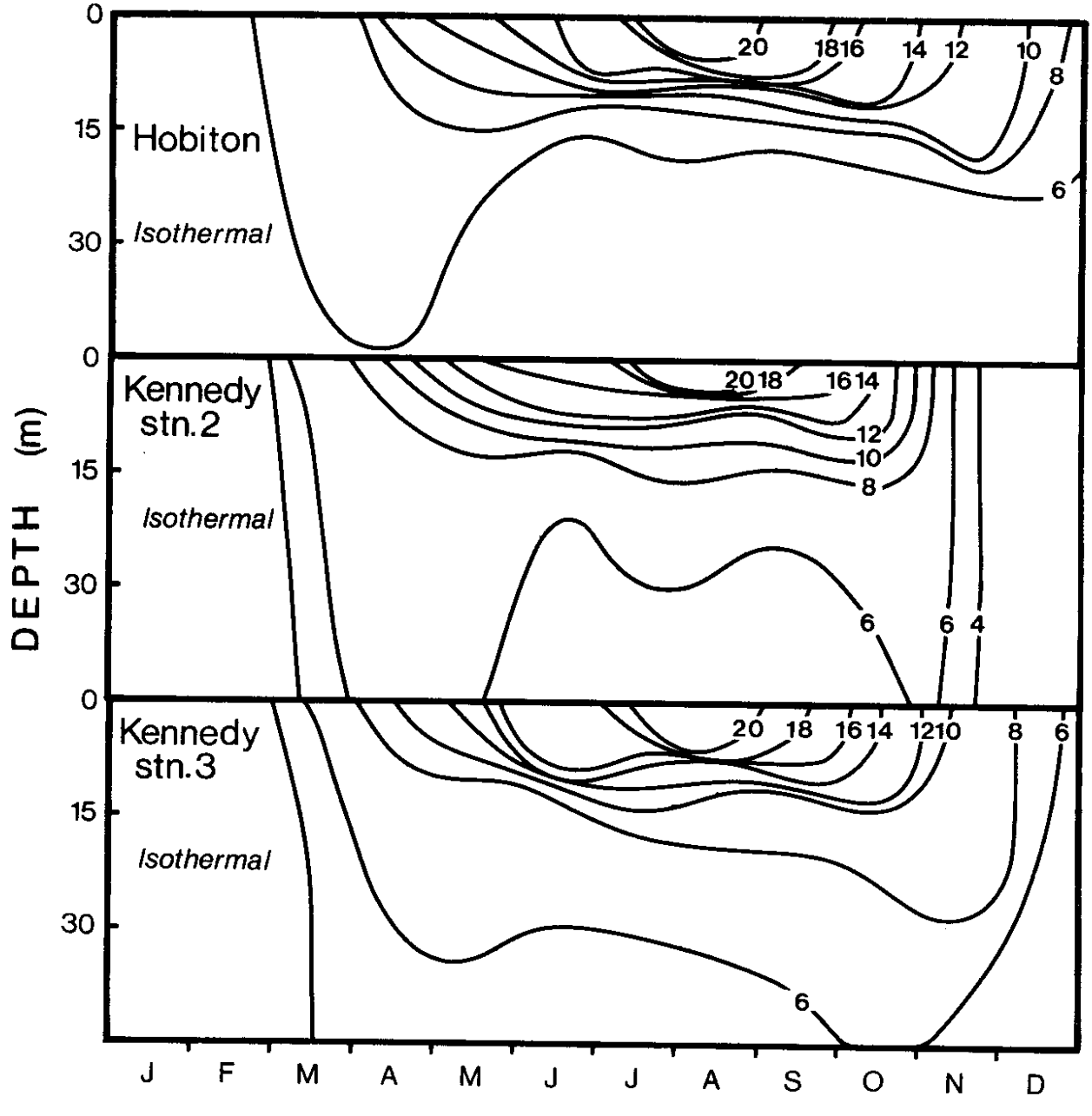

Fig. 2c. Seasonal isotherms of the study lakes.

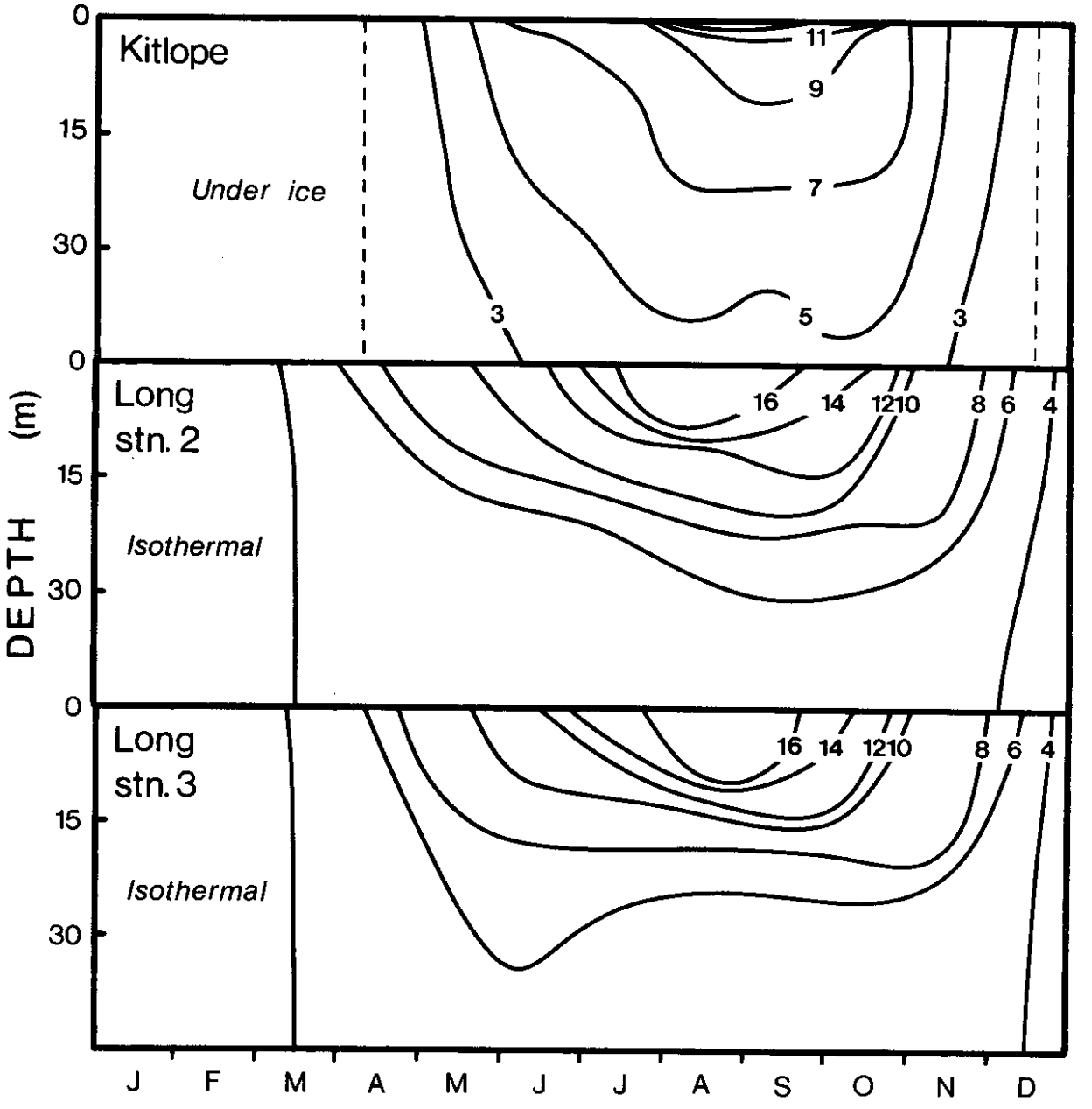

Fig. 2d. Seasonal isotherms of the study lakes.

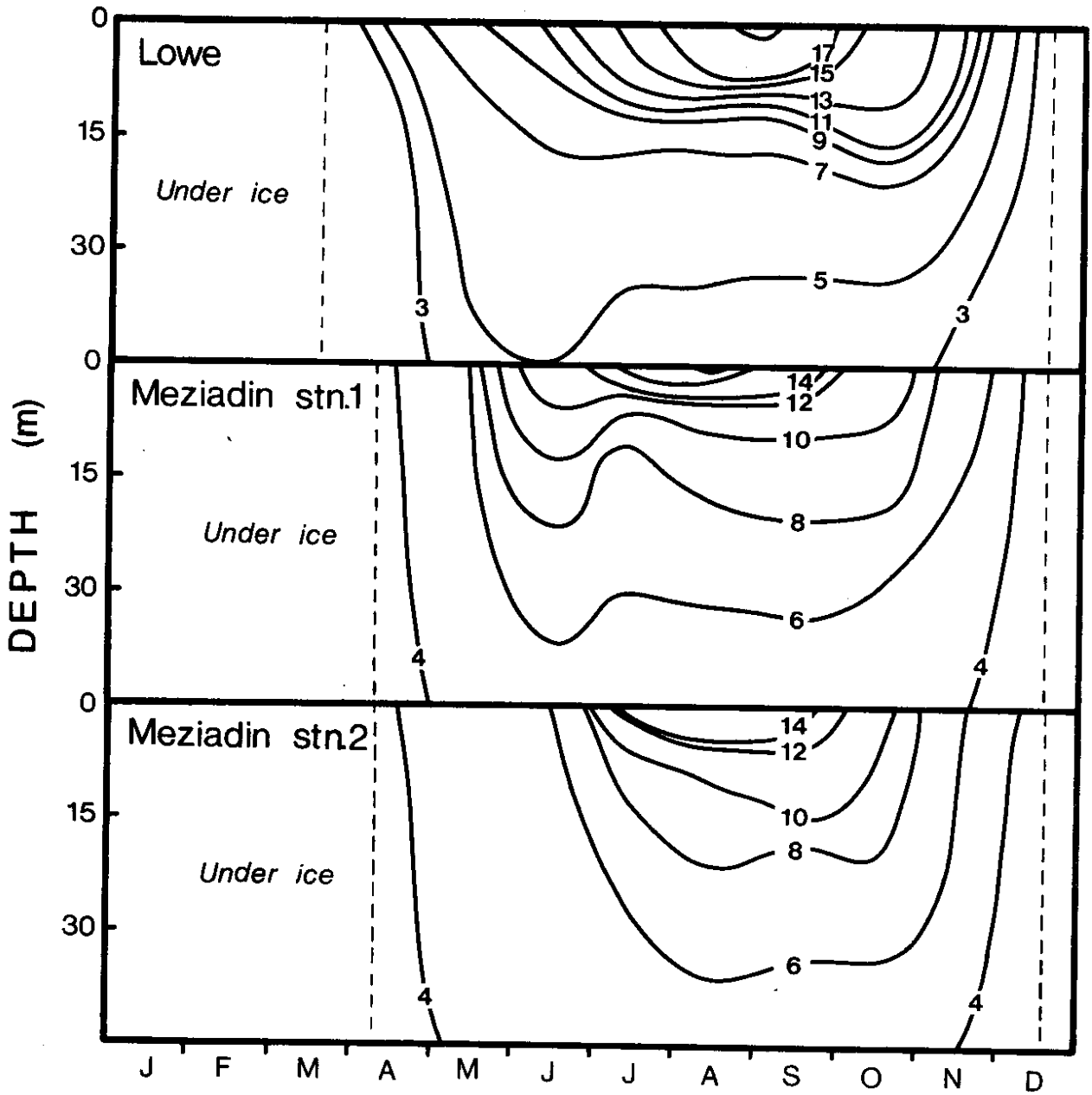

Fig. 2e. Seasonal isotherms of the study lakes.

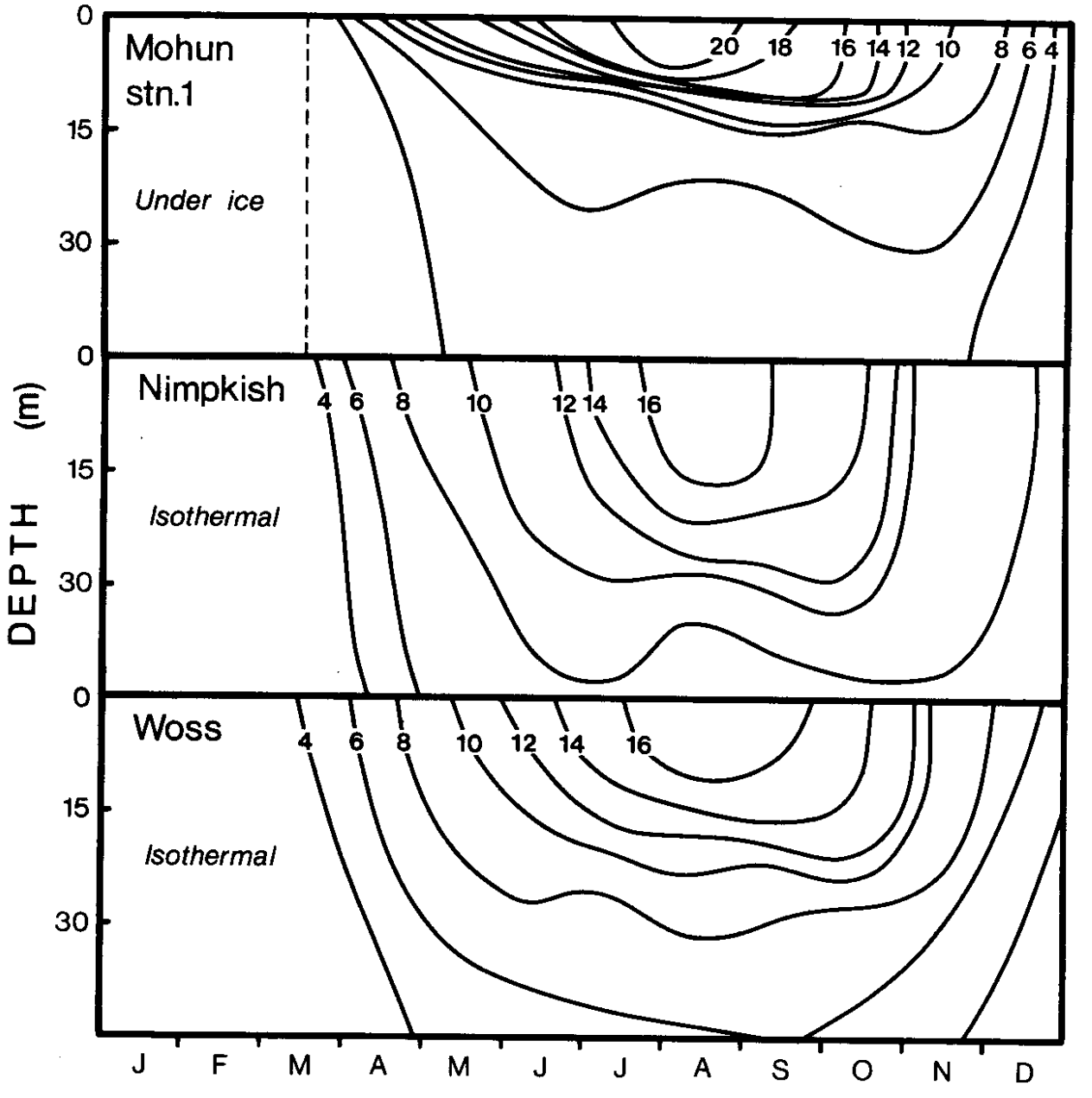

Fig. 2f. Seasonal isotherms of the study lakes.

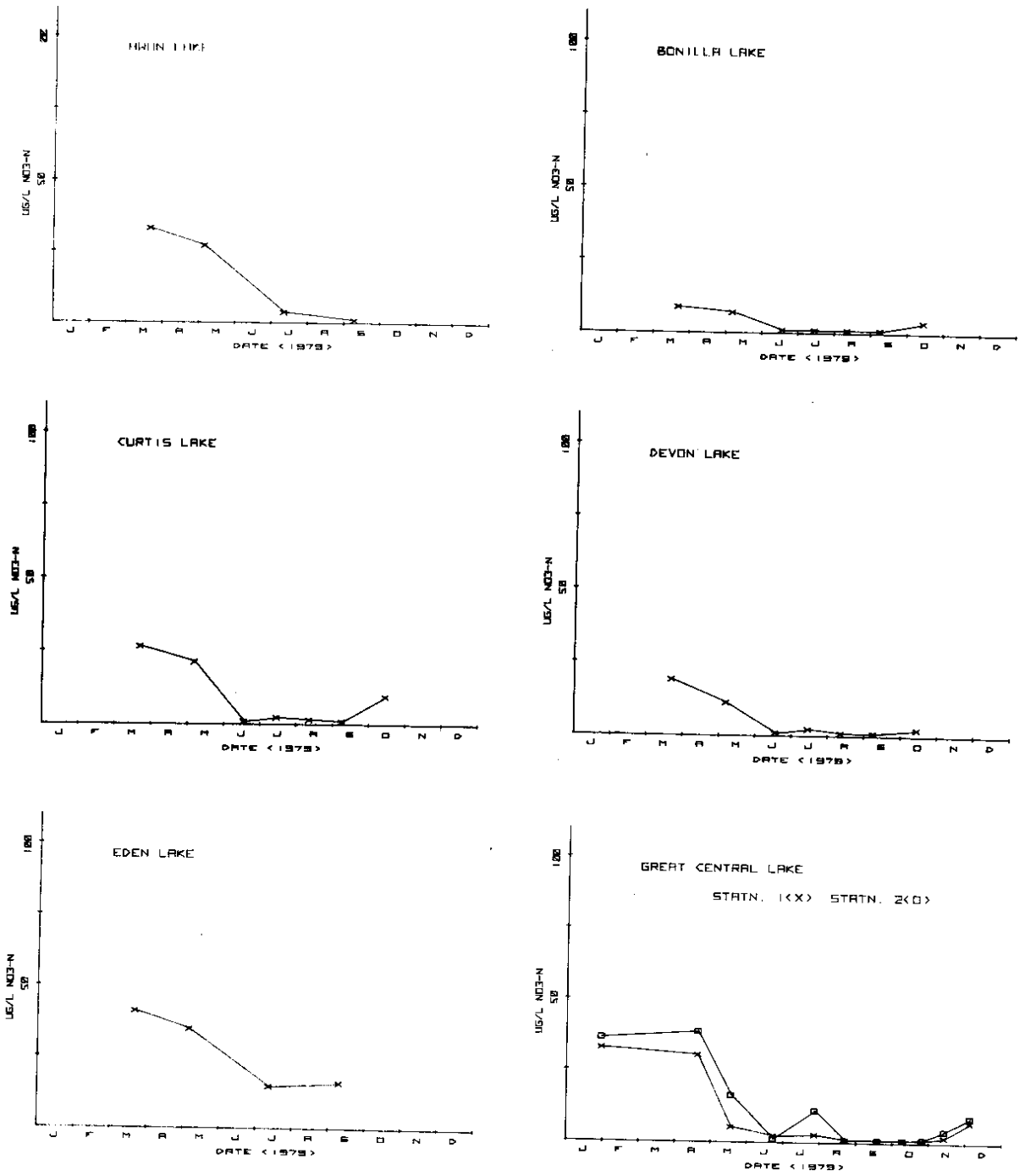

Fig. 3a. Temporal variation in epilimnetic nitrate-nitrogen concentration.

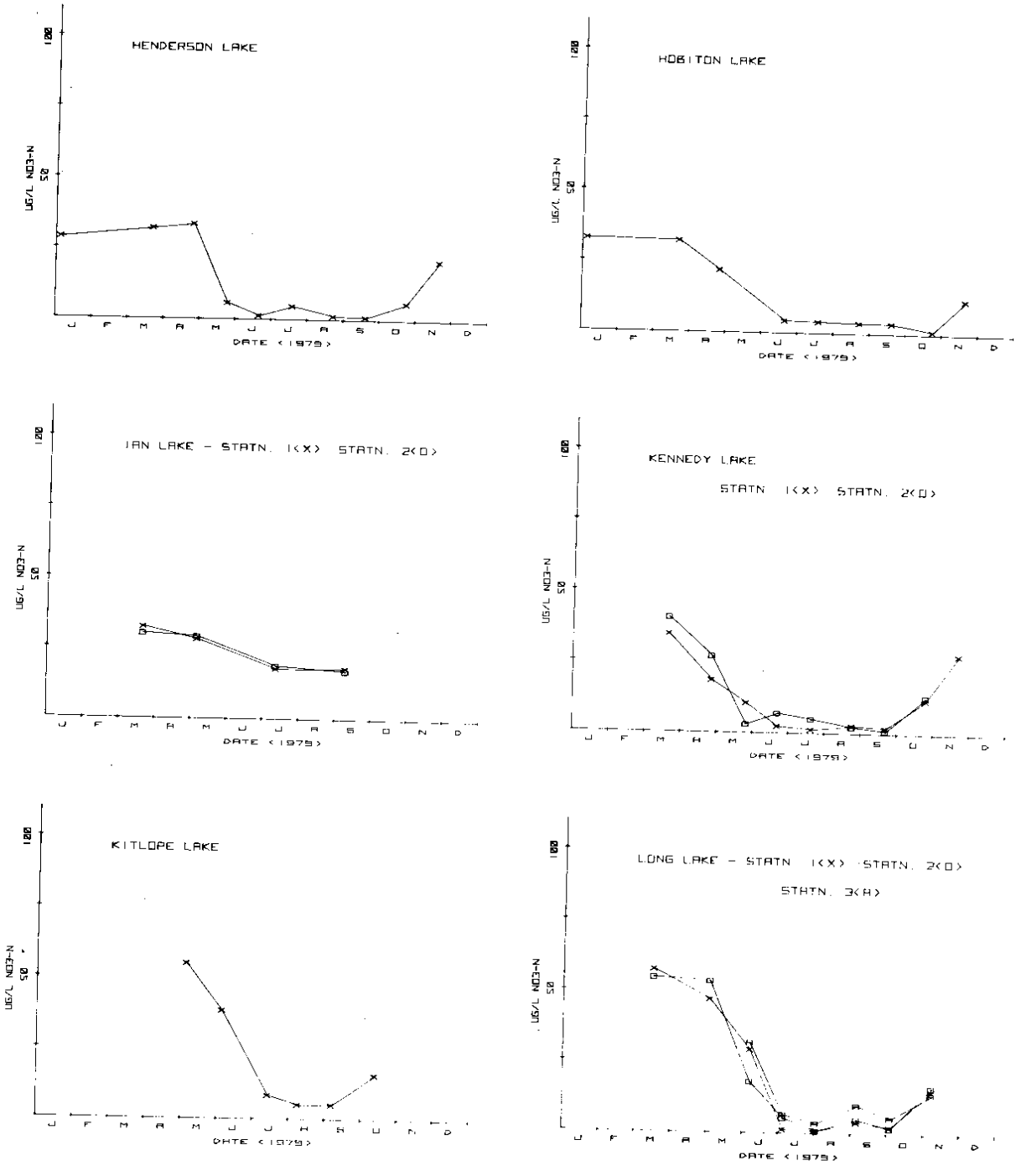

Fig. 3b. Temporal variation in epilimnetic nitrate-nitrogen concentration.

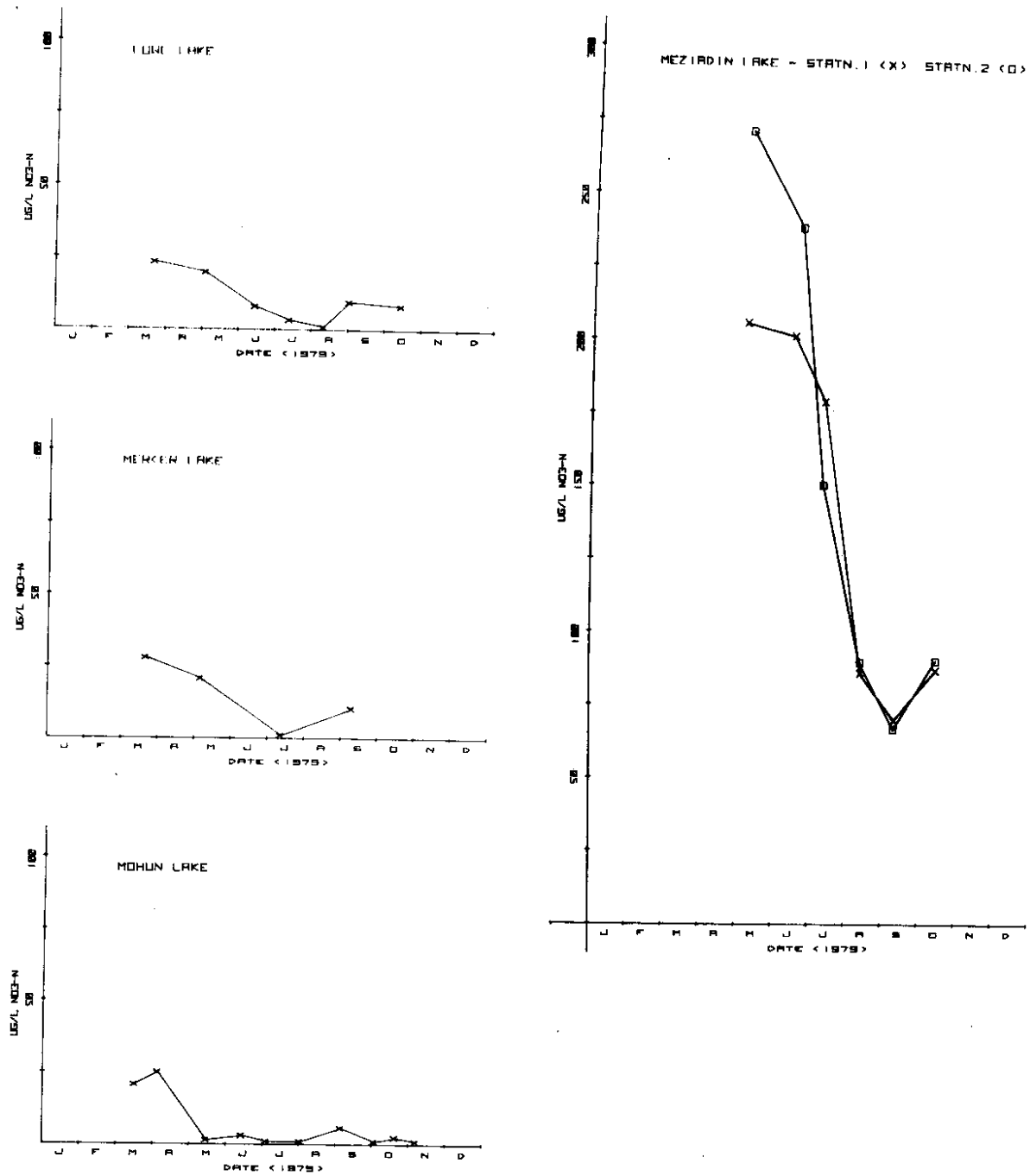

Fig. 3c. Temporal variation in epilimnetic nitrate-nitrogen concentration.

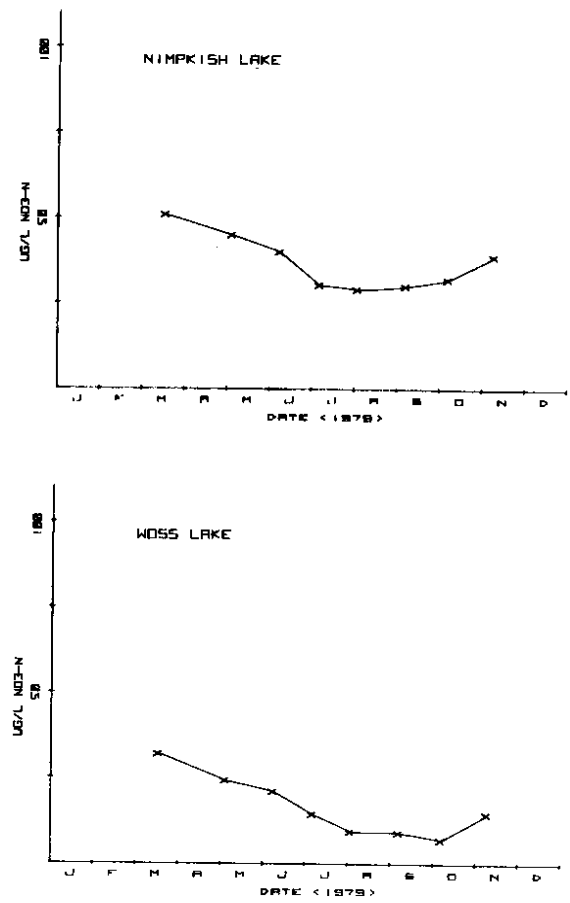

Fig. 3d. Temporal variation in epilimnetic nitrate-nitrogen concentration.

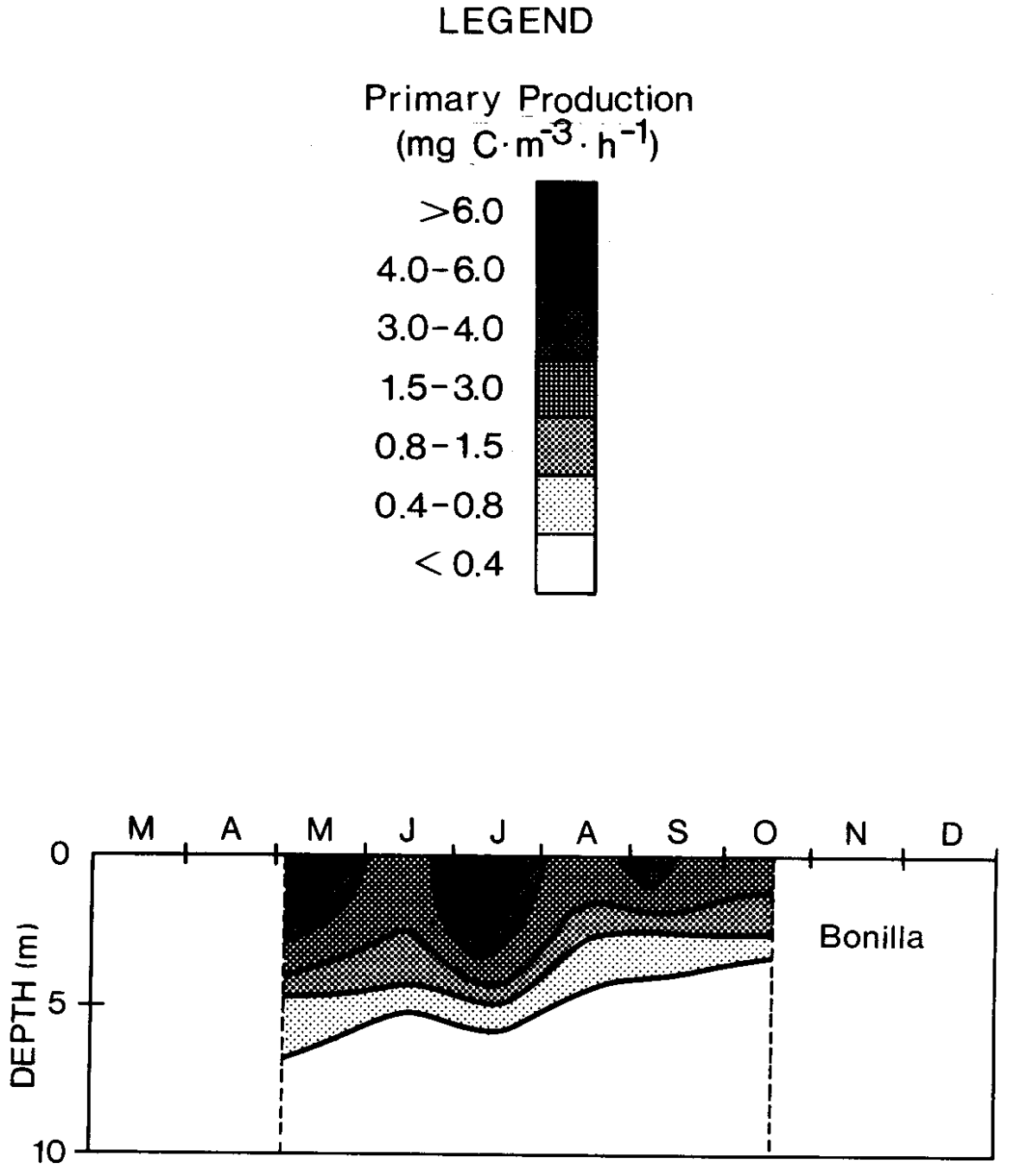

Fig. 4a. Primary production isopleths in the study lakes.

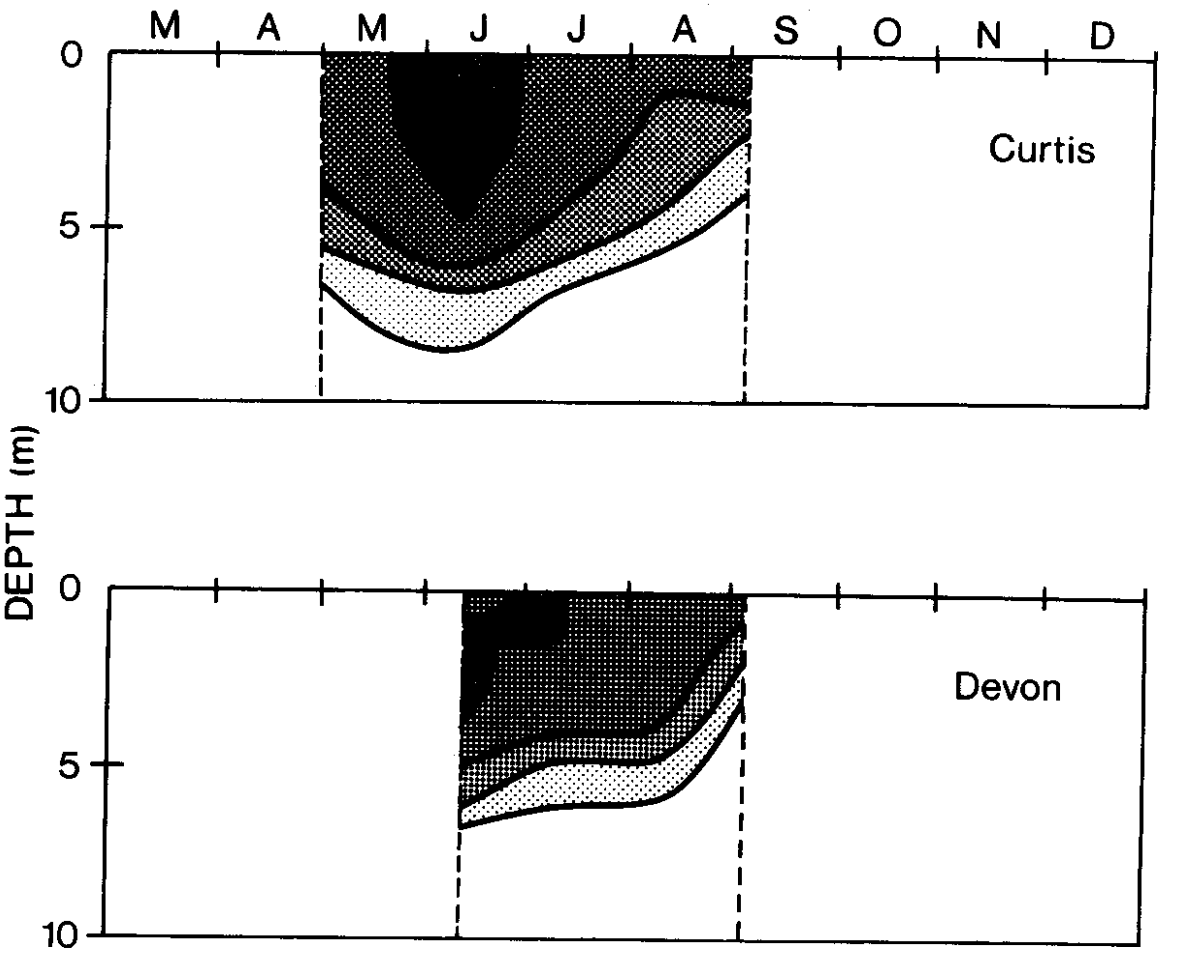

Fig. 4b. Primary production isopleths in the study lakes.

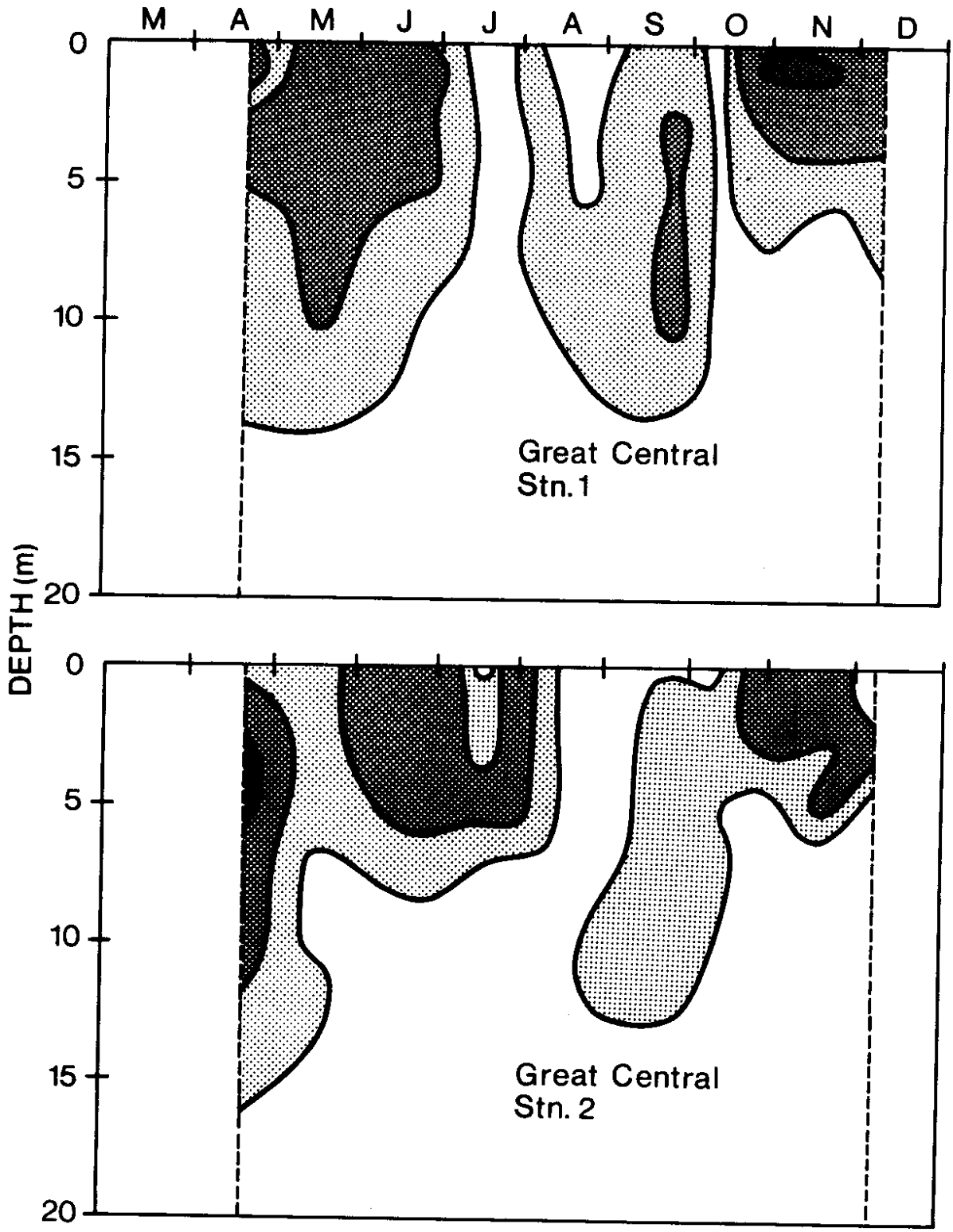

Fig. 4c. Primary production isopleths in the study lakes.

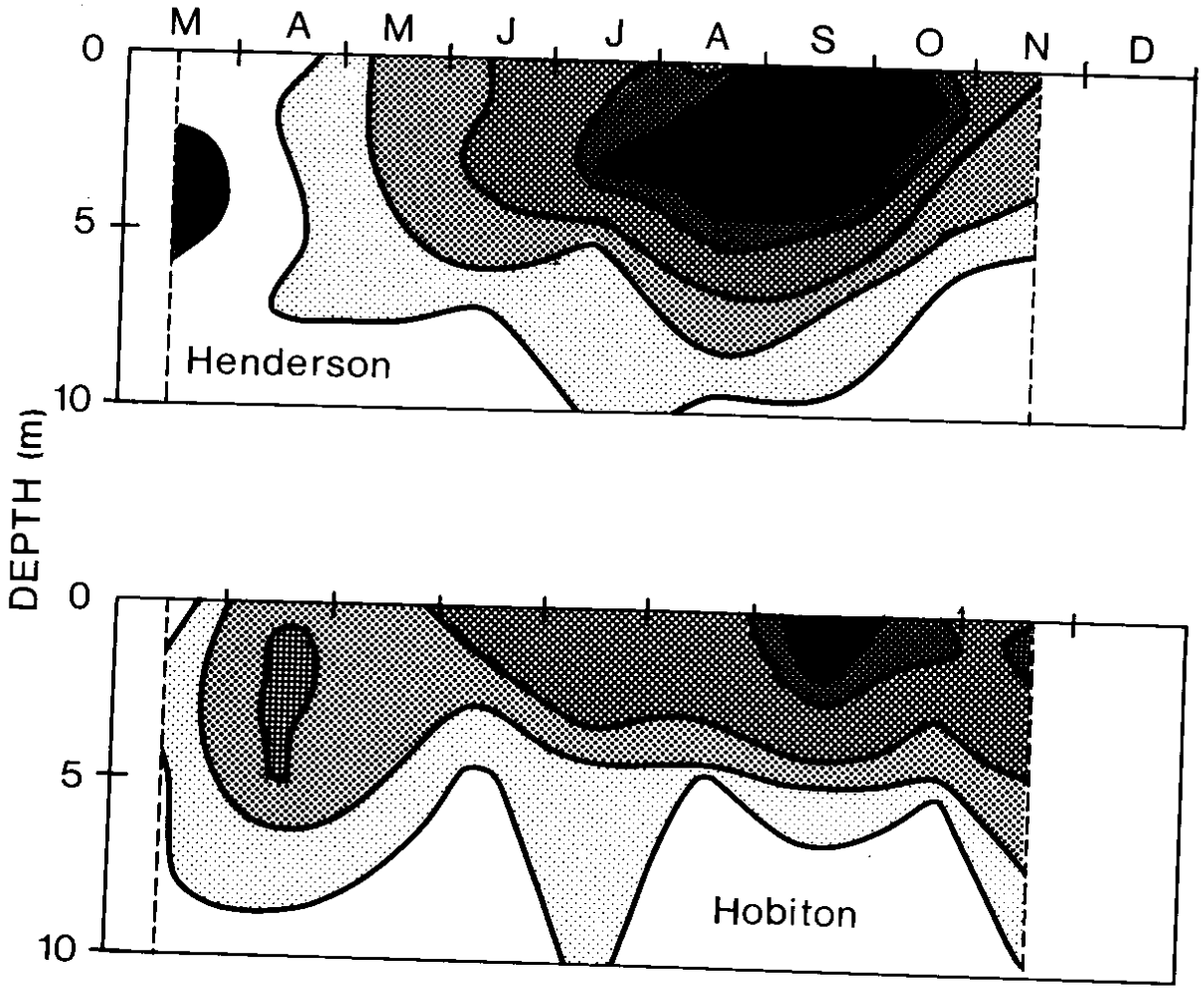

Fig. 4d. Primary production isopleths in the study lakes.

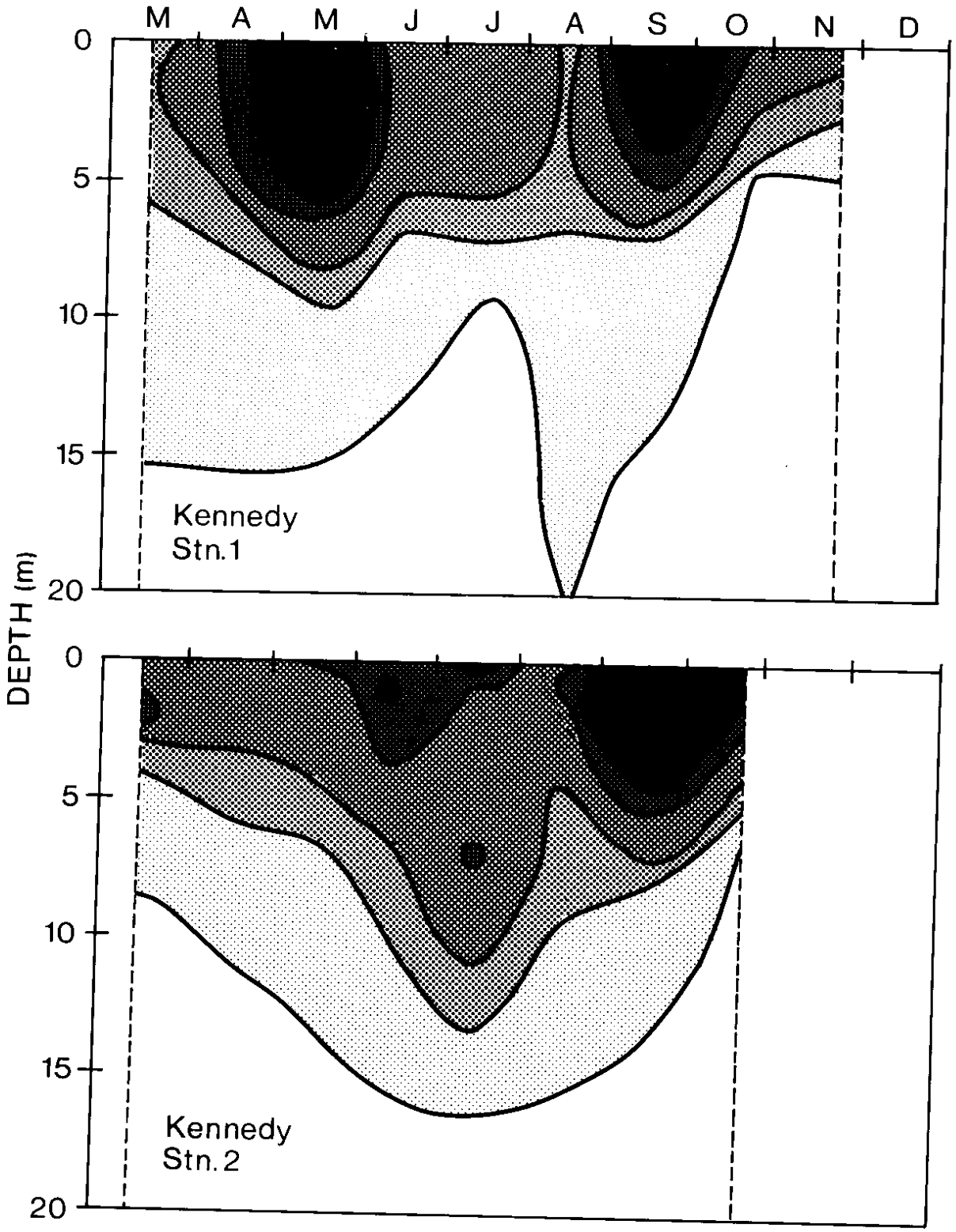

Fig. 4e. Primary production isopleths in the study lakes.

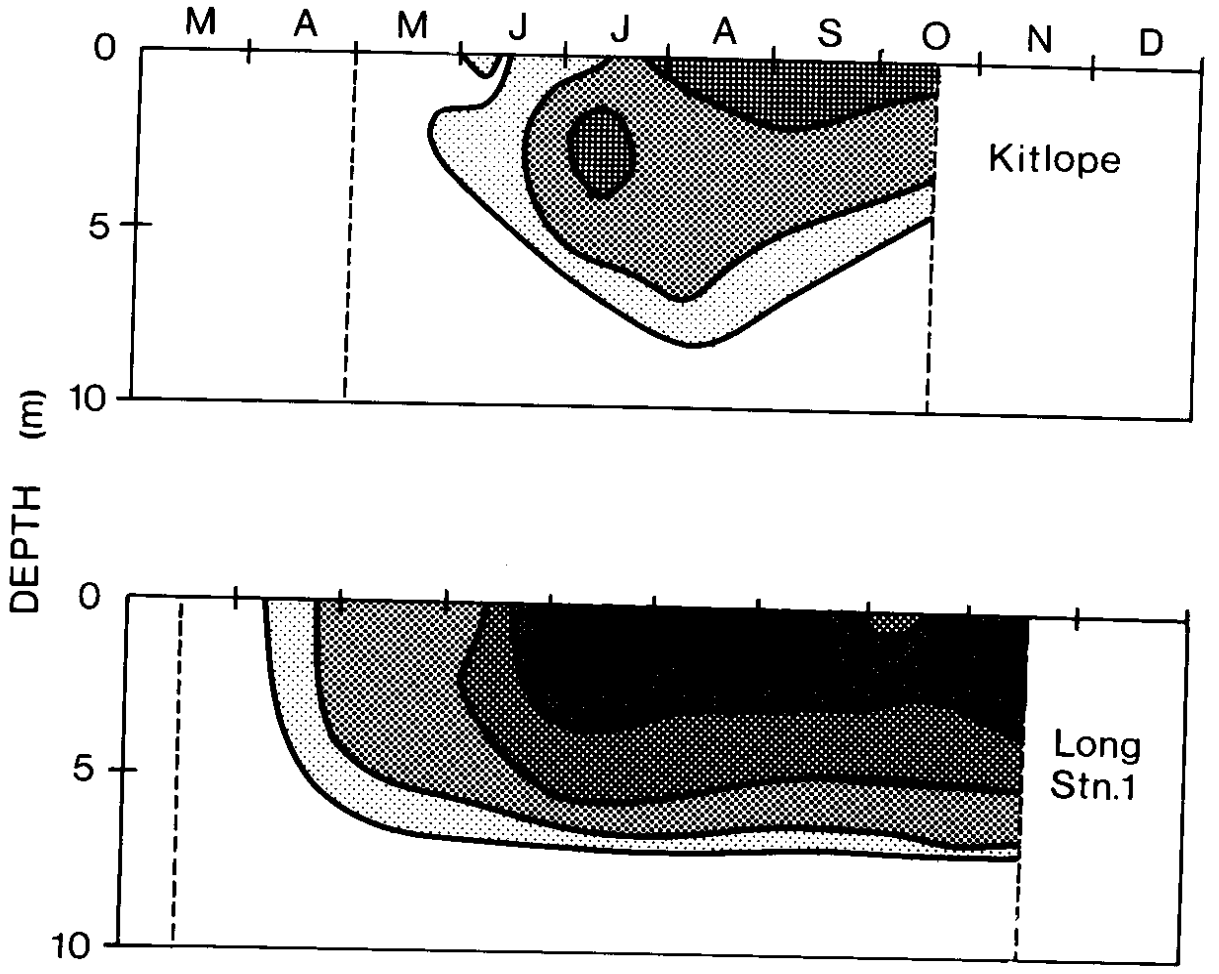

Fig. 4f. Primary production isopleths in the study lakes.

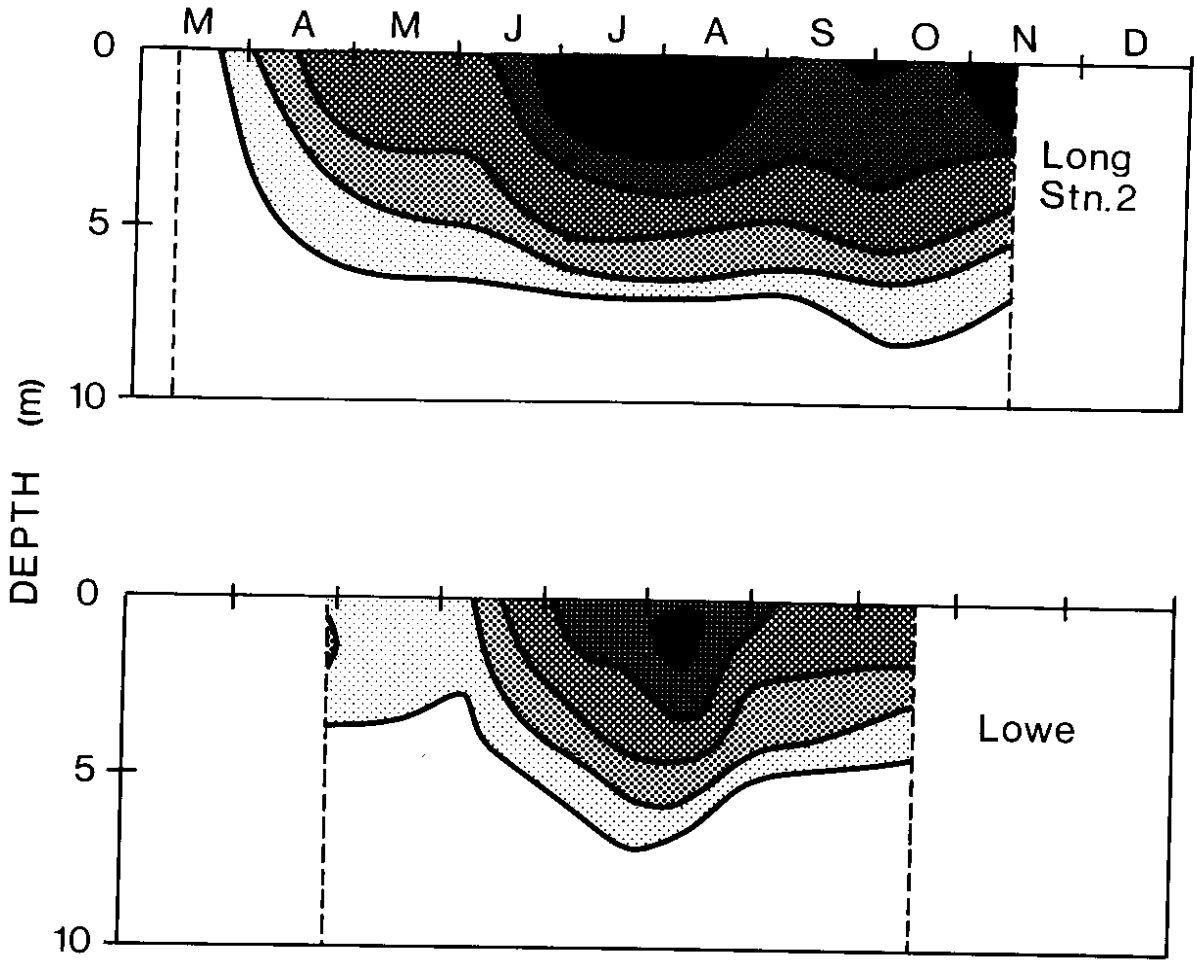

Fig. 4g. Primary production isopleths in the study lakes.

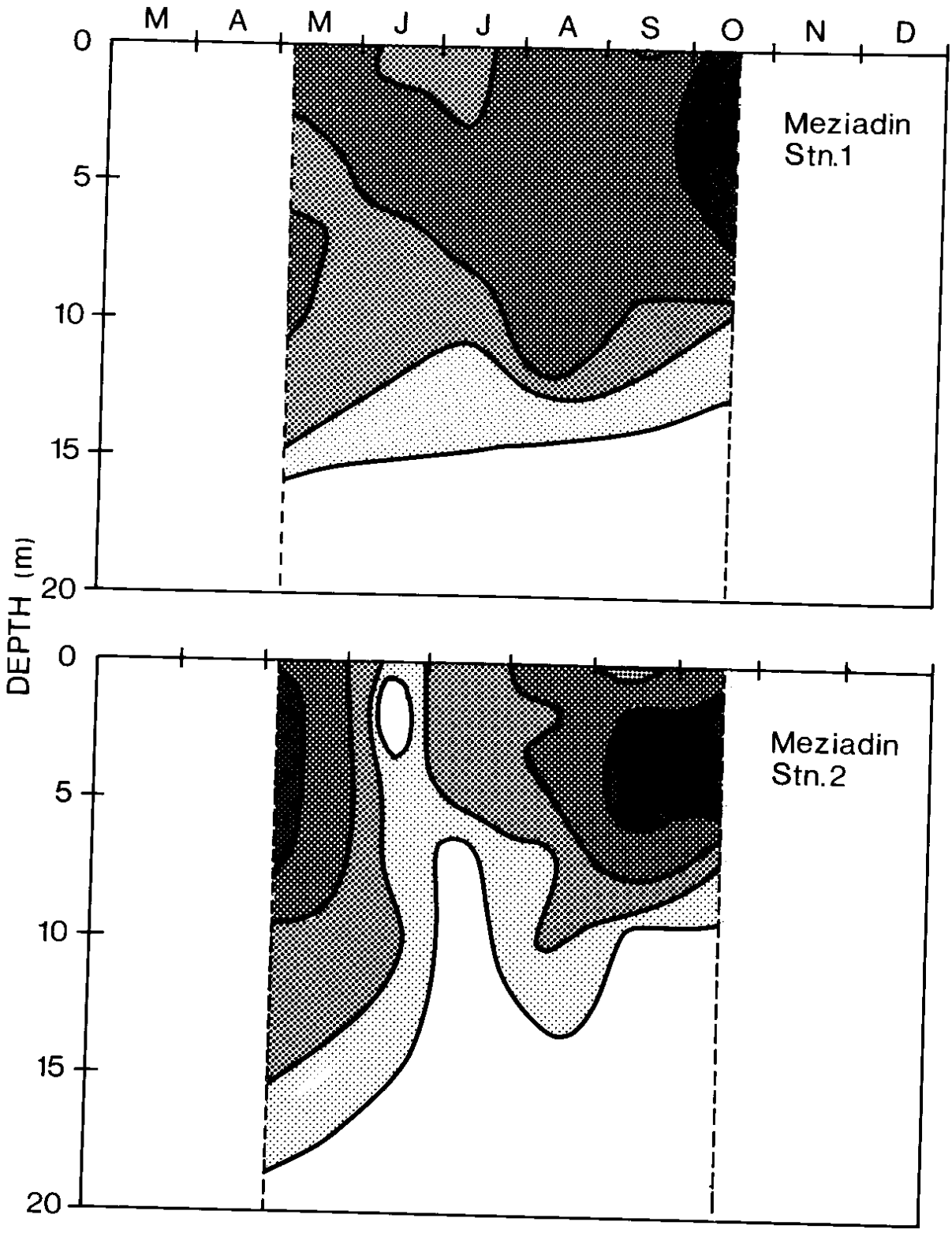

Fig. 4h. Primary production isopleths in the study lakes.

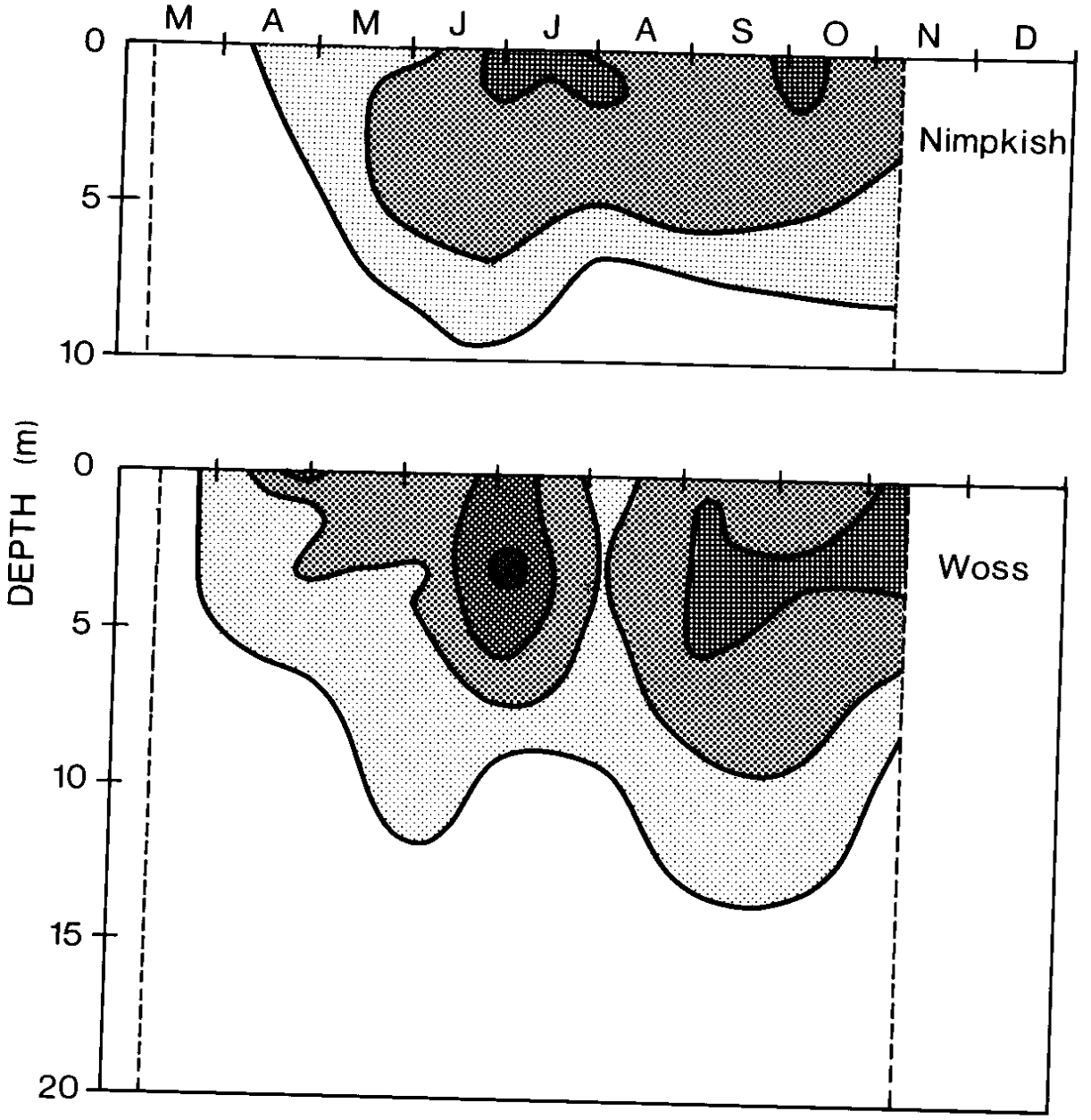

Fig. 4i. Primary production isopleths in the study lakes.

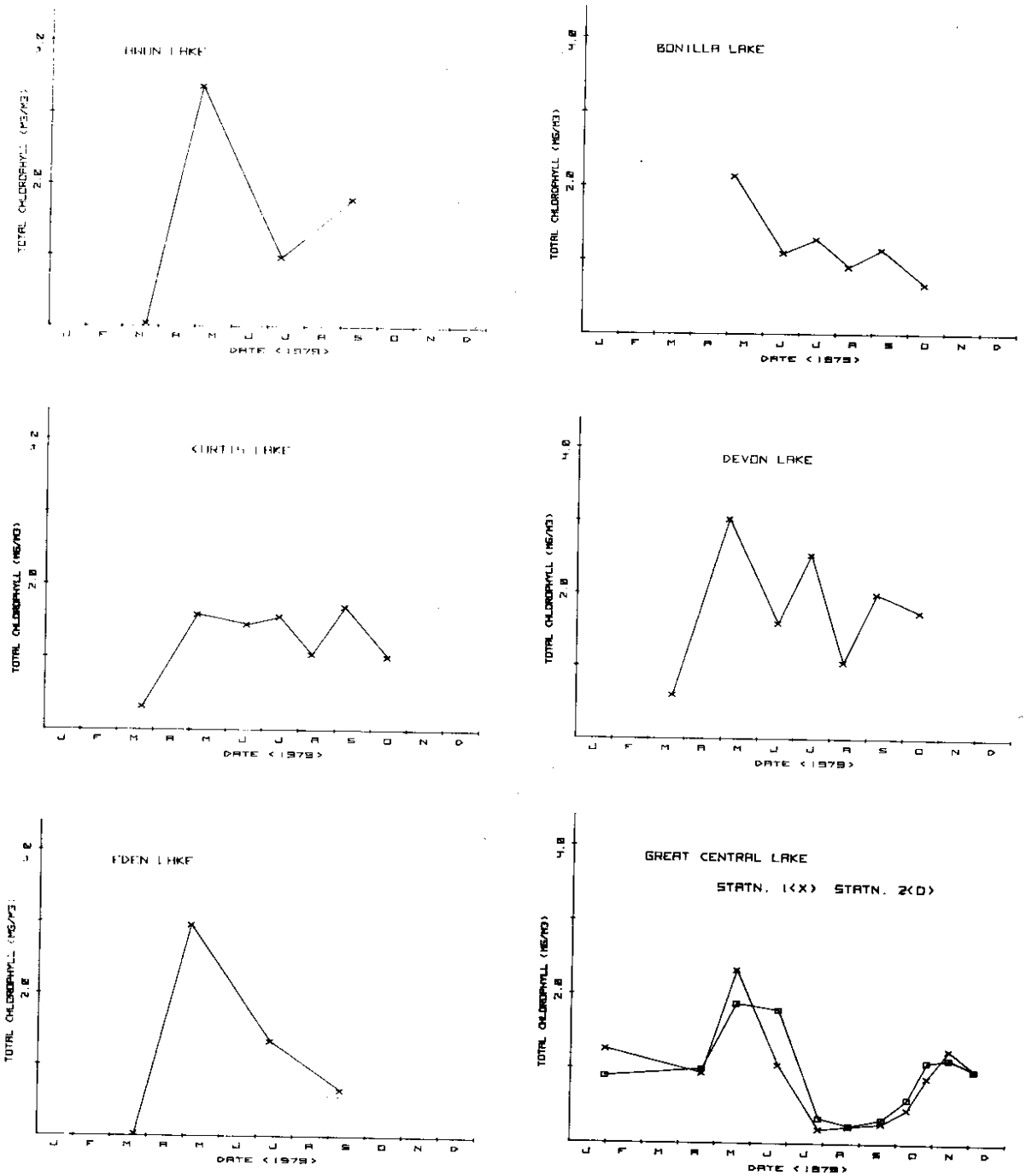

Fig. 5a. Temporal variation in epilimnetic chlorophyll concentration.

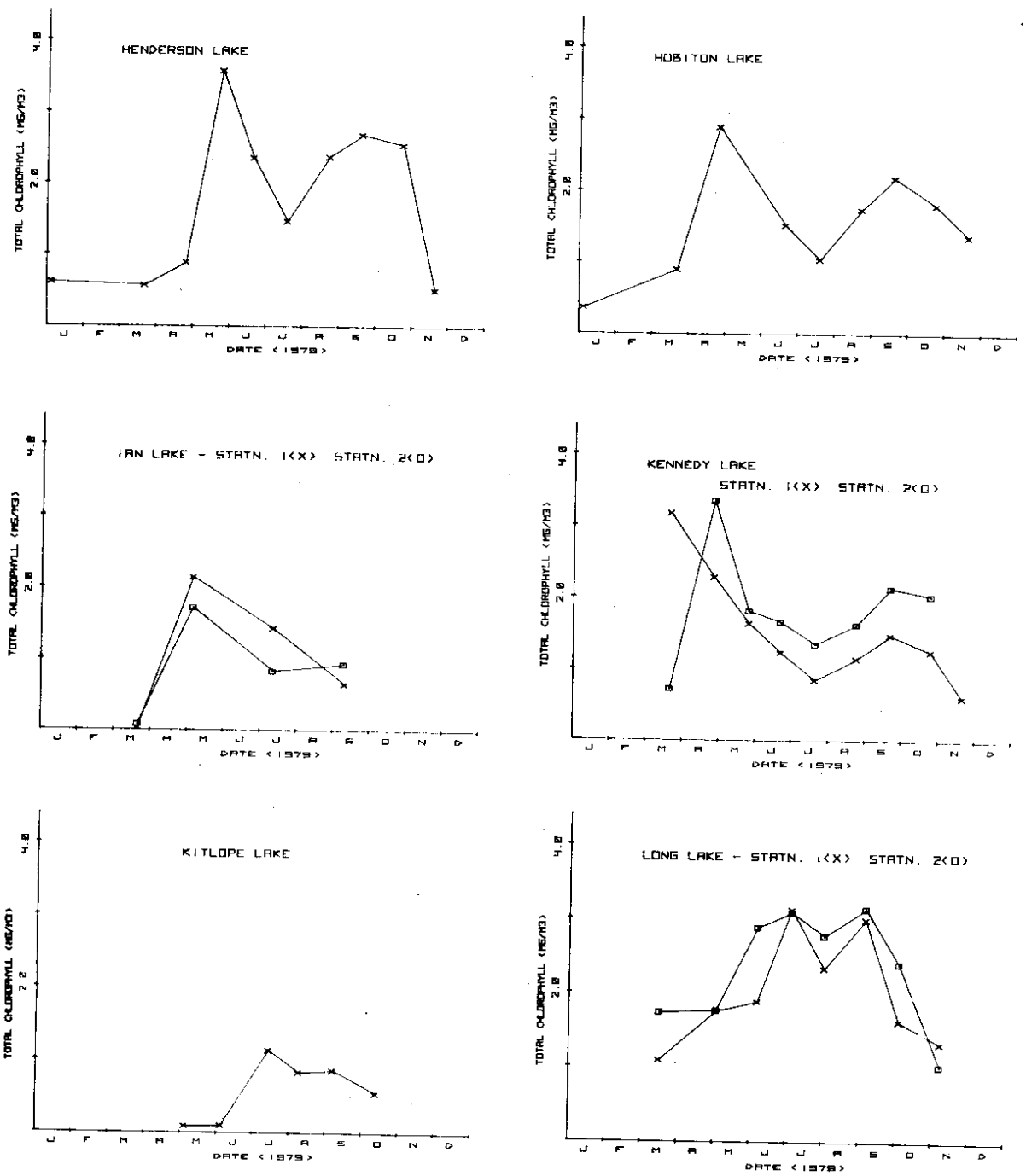

Fig. 5b. Temporal variation in epilimnetic chlorophyll concentration.

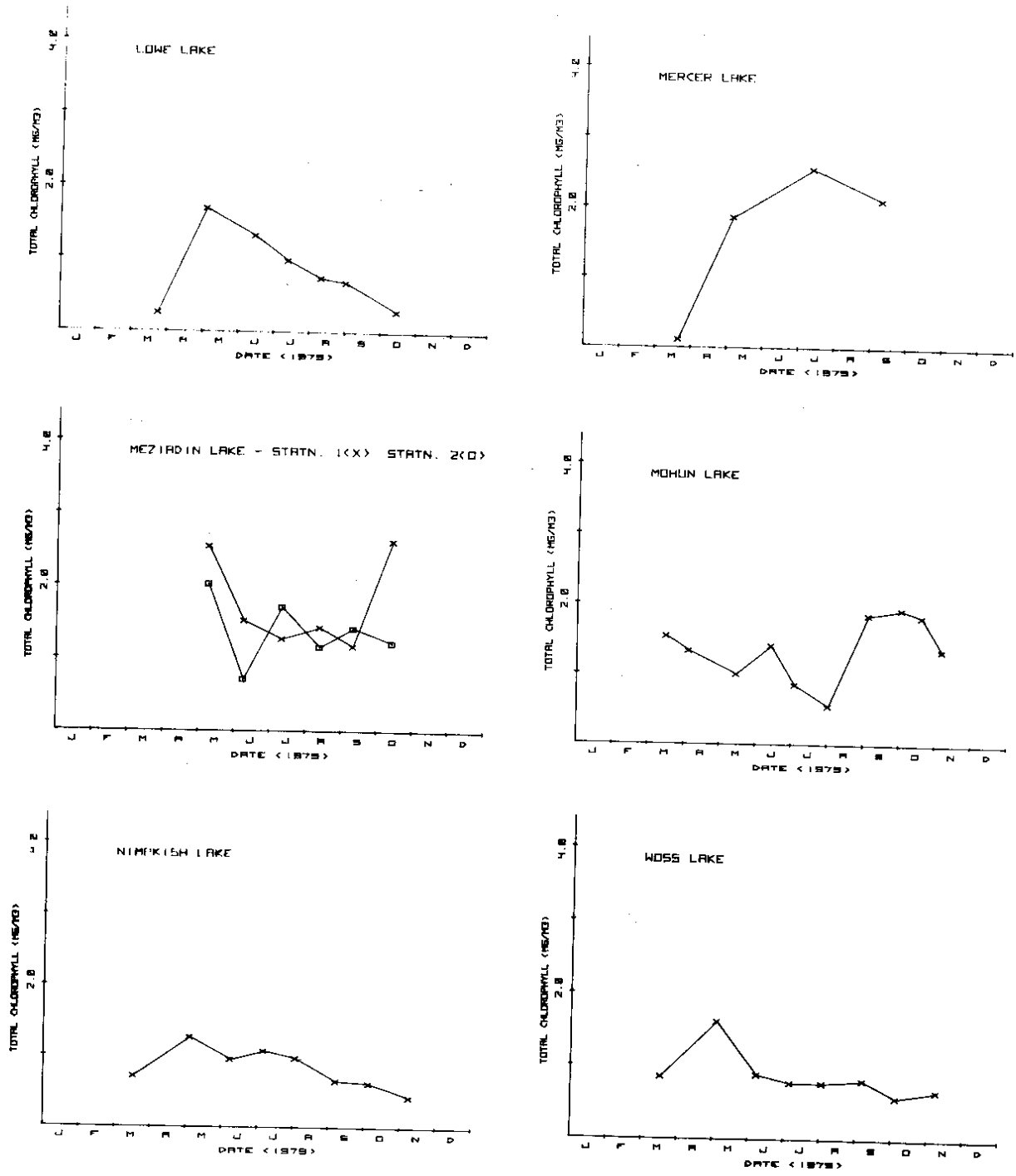

Fig. 5c. Temporal variation in epilimnetic chlorophyll concentration.

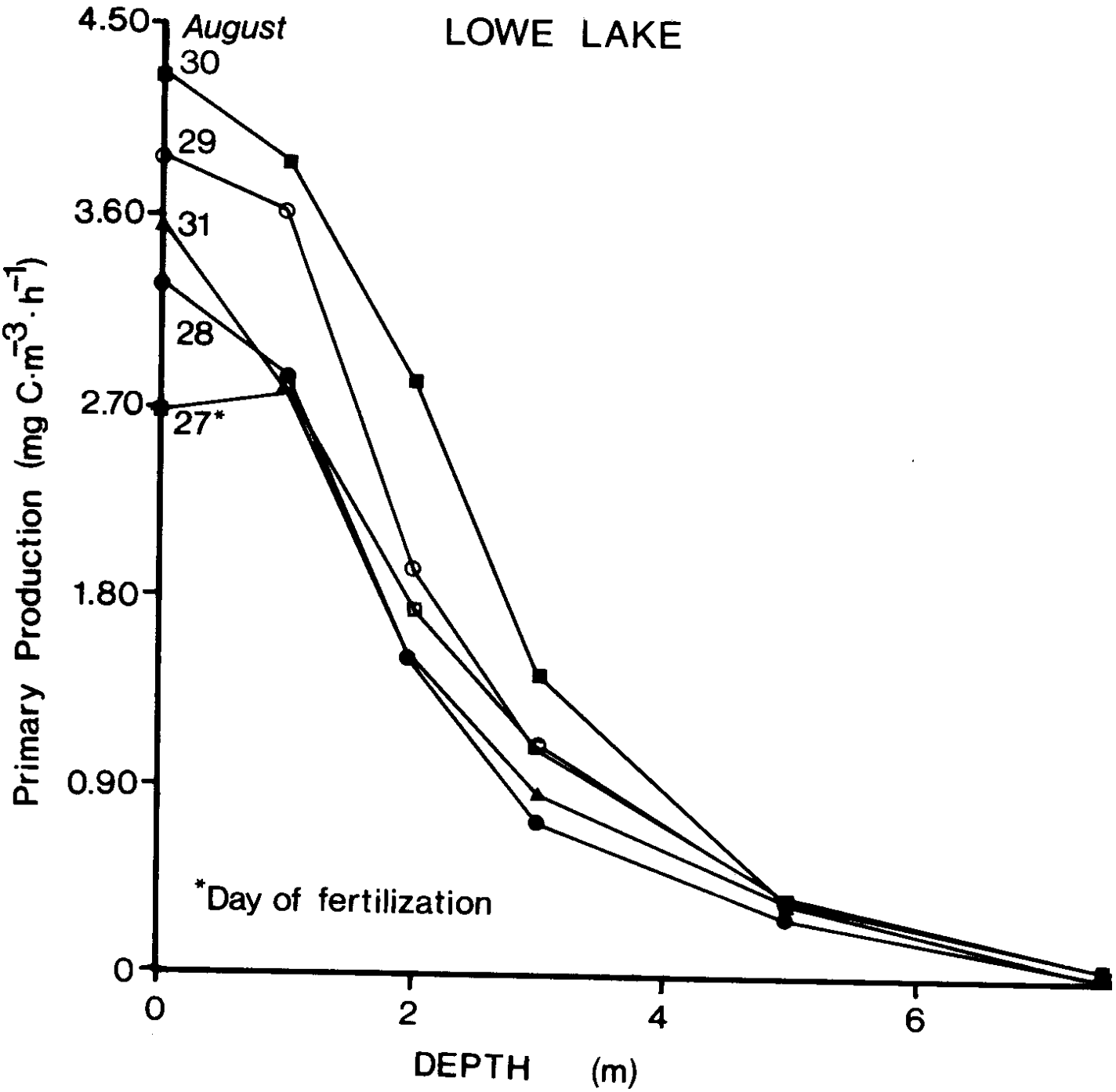

Fig. 6. Daily variation in carbon uptake following a fertilizer application.

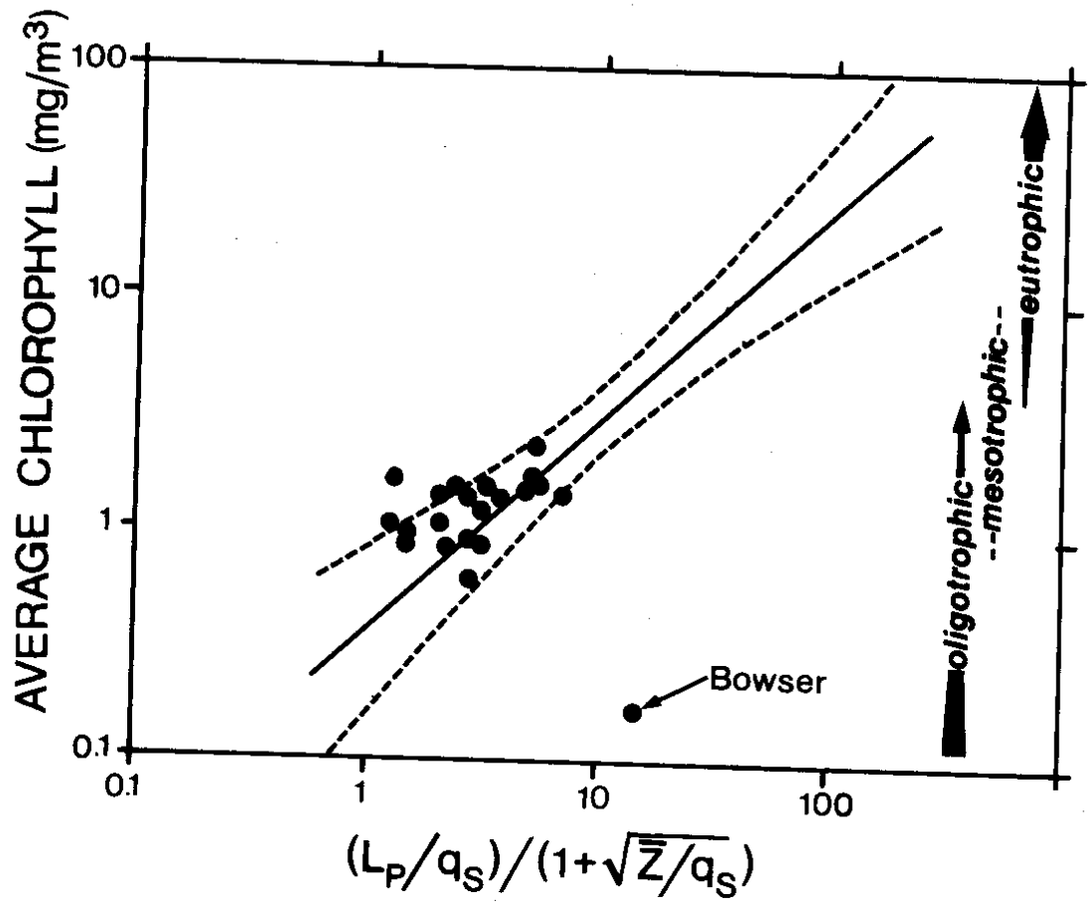

Fig. 7. Location of study lakes on Vollenweider's (1976) regression line of average chlorophyll vs. spring overturn total phosphorus concentration.

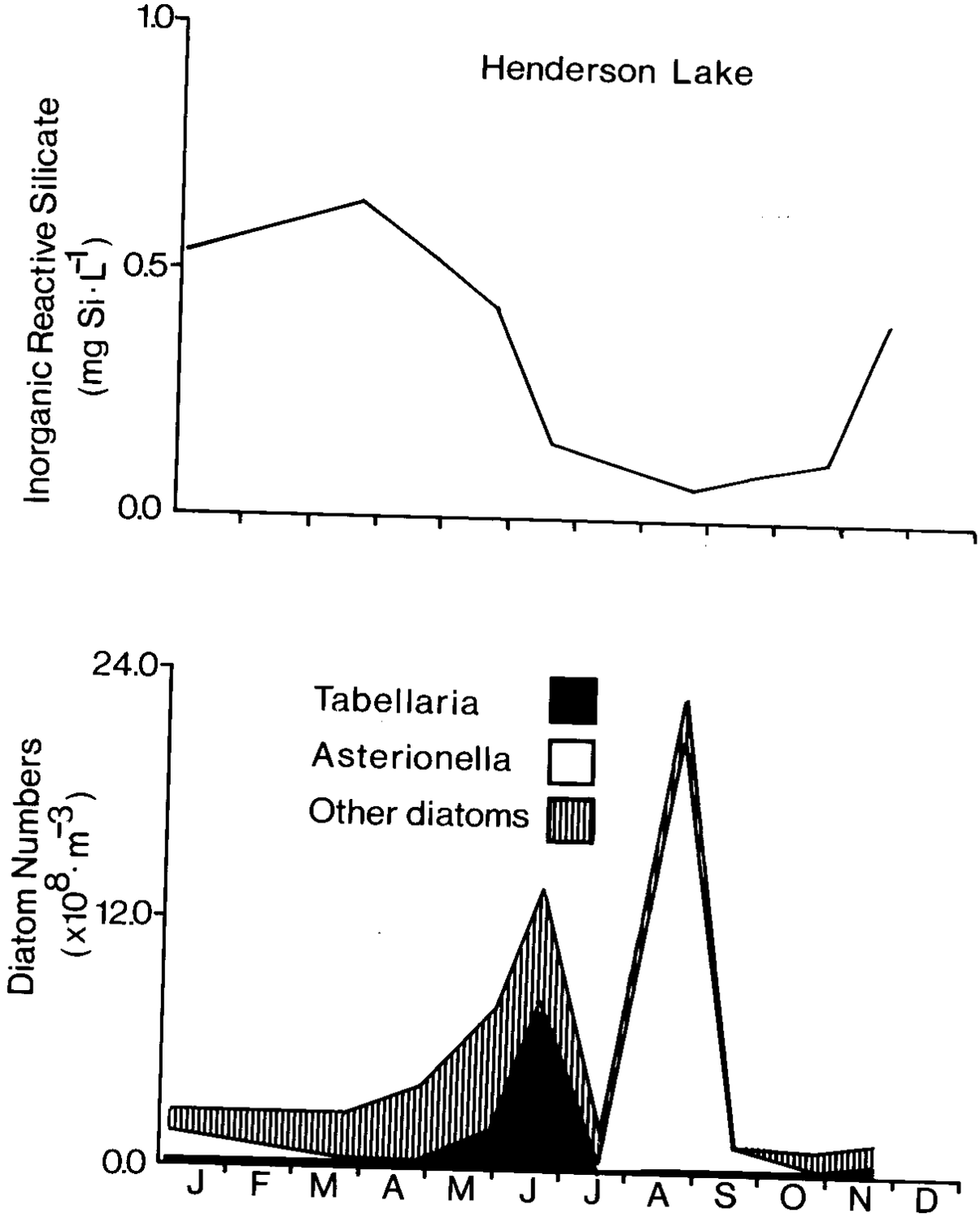

Fig. 8. Temporal changes in inorganic reactive silicate and diatom numbers in Henderson Lake.