Seasonal Distributions of Bacterioplankton Numbers and Activities in Eight Fertilized or Untreated Oligotrophic British Columbia Lakes

E. A. MacIsaac, K. S. Shortreed, and J. G. Stockner

Department of Fisheries and Oceans
Resource Services Branch
West Vancouver Laboratory
4160 Marine Drive
West Vancouver, British Columbia V7V 1N6

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SEASONAL DISTRIBUTIONS OF BACTERIOPLANKTON NUMBERS AND ACTIVITIES IN EIGHT FERTILIZED OR UNTREATED OLIGOTROPHIC BRITISH COLUMBIA LAKES

by

E. A. MacIsaac, K. S. Shortreed, and J. G. Stockner

Department of Fisheries and Oceans

Resource Services Branch

West Vancouver Laboratory

4160 Marine Drive

West Vancouver, British Columbia V7V 1N6

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ABSTRACT

MacIsaac, E.A., K.S. Shortreed, and J.G. Stockner. 1981. Seasonal distributions of bacterioplankton numbers and activities in eight fertilized or untreated oligotrophic British Columbia lakes. Can. Tech. Rep. Fish. Aquat. Sci. **994**: iii + 43 p.

Seasonal changes in the vertical distributions of total bacterioplankton numbers (AODC) and glucose (^3H) turnover-times are described for eight temperate, oligotrophic British Columbia lakes. This group included fertilized and untreated lakes, ranging in water clarity from clear to mildly dystrophic (humic stained) or glacially turbid. Mean annual bacteria numbers (0-10 m) ranged from 0.41 to $0.95 \cdot 10^6 \cdot mL^{-1}$ and mean annual glucose turnover-times ranged from 125 to 2200 h. The lakes are compared and monthly changes in bacteria numbers and activity are described in relation to flushing, stratification, fertilization, and various physical, chemical, and biological variables.

Key words: Bacteria, bacterioplankton, glucose turnover, heterotrophy, lake fertilization, microbiology.

RÉSUMÉ

MacIsaac, E. A., K. S. Shortreed, and J. G. Stockner. 1981. Seasonal distributions of bacterioplankton numbers and activities in eight fertilized or untreated oligotrophic British Columbia lakes. Can. Tech. Rep. Fish. Aquat. Sci. 994: iii + 43 p.

Les auteurs décrivent les variations saisonnières de la distribution verticale du nombre total de bactérioplanctontes (AODC) et du temps de renouvellement du glucose tritié dans 8 lacs oligotrophes tempérés de la Colombie-Britannique. Ces lacs comprenaient des lacs fertilisés ou non, où les eaux étaient limpides à légèrement dystrophes (colorées par les matières humiques) ou troubles du fait des glaces. Le nombre annuel moyen de bactéries (de 0 à 10 m) se situait entre 0,41 et 0,95 $\times 10^6 \times mL^{-1}$ et le temps de renouvellement moyen du glucose était de 125 à 2200 heures. Les auteurs établissent des comparaisons entre les lacs et décrivent les variations mensuelles du nombre et de l'activité des bactéries en relation avec le renouvellement des eaux, la stratification, la fertilisation et divers facteurs physico-chimiques et biologiques.

Mots clés: Bactéries, bactérioplancton, renouvellement du glucose, hétérotrophie, fertilisation, microbiologie.

INTRODUCTION

The pelagic zones of numerous British Columbia lakes are nursery areas for planktivorous juvenile sockeye salmon (Oncorhynchus nerka). The Lake Enrichment Program (LEP) of the Federal-Provincial Salmonid Enhancement Program (SEP) has been involved since 1977 in a pilot-scale study aimed at increasing the survival and/or growth of juvenile sockeye salmon through the addition of ammonium nitrate and ammonium phosphate fertilizers to sockeye nursery lakes. The objectives, methodologies,and various limnological studies of the program to date have been described in other reports (e.g. Stockner 1979; Stockner et al. 1980).

The trophic state of a lake is defined by the rate of input of allochthonous and autochthonous organic carbon and its rate of cycling within the lake ecosystem (Allen 1978). The primary objective of LEP is to stimulate autochthonous production and to increase the flow of carbon to higher trophic levels within the pelagic zone. Bacteria are an integral component of the carbon cycling processes in a lake (Saunders 1971) and may be a valuable measure of the success of inorganic nutrient enrichment in affecting an increase in the rates of carbon flux and transfer in an experimental lake.

Inorganic nutrient additions may directly and/or indirectly affect the activity and growth of the bacterioplankton community. Bacteria, in turn, can potentially affect energy transfer in the plankton community of an enriched lake in 3 ways:

1. In situ regeneration of added nutrients (Johannes 1968; Wright 1974; Saunders 1976; Hollibaugh 1978).
2. Competition with phytoplankton for added inorganic nutrients (Fuhs et al. 1972; Rhee 1972; Cavari 1977).
3. Food resource for zooplankton (Gliwicz 1969, 1975; Gophen et al. 1974; Pomeroy 1974; Peterson et al. 1978; Porter et al. 1979).

A great deal of information is available concerning experimental whole-lake fertilization and response of the phytoplankton, zooplankton,and fish communities (e.g. Schindler 1975; LeBrasseur et al. 1978; Stockner 1979; Stockner et al. 1980), but relatively little data exists on the response of the bacterioplankton community. Kerr et al. (1972) identified a bacterial response to inorganic nutrient additions in a small Georgia fishpond. Parsons et al. (1972) fertilized Great Central Lake in 1970 with inorganic fertilizers and an organic supplement (fish solubles) and used plate counts to monitor the bacteria population. Temporal changes in the heterotrophic utilization of sucrose were studied (Thompson and Hamilton 1973) in a small Canadian Shield lake fertilized to eutrophy with organic

(sucrose) and inorganic nutrients. Lehmusluoto and Ryhänen (1972), Hall (1975), and Jones (1977) studied the reponse of the bacteria community to nutrient enrichment in experimental lake enclosures and Martin and Bianchi (1980) investigated microbial changes in continuous culture, large volume, oligotrophic seawater tanks fertilized with inorganic nutrients. Seki et al. (1980, 1981) examined various substrate uptake kinetics in a number of fertilized and unfertilized lakes under study by LEP.

An investigation of the bacterioplankton ecology of fertilized and unfertilized lakes is a first step towards understanding the role of the microbial community in nutrient enrichment. Study of the total pelagic bacteria population and its heterotrophic activity commenced in 1979 and this report details the techniques and findings of the first year of study.

DESCRIPTION OF STUDY LAKES

An oligotrophic condition and a juvenile sockeye salmon population are the primary criteria for the selection of candidate lakes for study and/or fertilization (Stockner 1979). The eight temperate lakes in this investigation were fertilized or unfertilized lakes, with water clarities ranging from clear to mildly dystrophic (humic stained) or glacially turbid. Pertinent geographical, physical, and chemical parameters are summarized in Table 1 and lake maps and station locations are given in Stockner and Shortreed (1979), Stockner et al. (1980), and Appendix Figure 1. The lakes have relatively small littoral zones, low inorganic nutrient levels, low phytoplankton biomass (Stockner et al. 1980; Shortreed and Stockner 1981), and low zooplankton biomass (Rankin et al. 1979; Rankin and Ashton 1980).

Great Central and Woss lakes lie in central and north-central Vancouver Island, respectively, and are clear, warm monomictic lakes (Fig. 1). They had the longest flushing times ($\geq$3.0 yr), lowest mean annual extinction coefficients ($<$ 0.30), and warmest mean annual epilimnetic temperatures ($>$14°C) of the eight lakes. Summer mixed layer depths exceeded 15 m, pH values were neutral, and alkalinities were less than 13 mg·L^{-1}CaCO$_3$. Woss Lake was not fertilized in 1979 but Great Central Lake received weekly fertilizer additions during the first half of its growing season (April 16 to July 30; Table 3).

Long Lake is a mid-coastal, dystrophic, monomictic lake and Lowe and Bonilla lakes are north-coastal, dystrophic, dimictic lakes (Fig. 1). Bonilla had the highest concentration of humic substances with the highest mean annual extinction coefficient (1.02) of the 3 lakes. Lowe and Bonilla were the shallowest lakes studied ($\bar{z}<$ 35 m) with the lowest mean pH values (5.7) and alkalinities ($\leq$0.7 mg·L^{-1}CaCO$_3$) of any study lake. All three lakes were fast flushing ($\leq$1.1 yr) and Lowe had the shortest water residence time (0.2 yr) of the eight lakes. Bonilla Lake was not fertilized, however Long and Lowe lakes received weekly nutrient additions from April 16 to October 8 and May 7 to September 2, respectively (Table 3).

Kitlope, Meziadin, and Bowser lakes (Fig. 1) are glacially turbid, dimictic lakes with the coldest mean epilimnetic temperatures ($< 12^{\circ}C$) of the eight lakes. Bowser Lake was the coldest ($7.1^{\circ}C$) and most turbid ($k_e = 2.35$) of all eight lakes and Meziadin and Bowser lakes were the most alkaline ($pH \geq 7.6$; ≥ 24.0 mg·L^{-1} $CaCO_3$). Kitlope Lake was slightly turbid ($k_e = 0.62$) with a very short water residence time (0.4 yr). Meziadin Lake was slightly turbid ($k_e = 0.40$) and warmer ($11.8^{\circ}C$) than Bowser or Kitlope lakes, with a relatively long water residence time (1.8 yr). Bowser and Meziadin lakes were not fertilized but Kitlope Lake was fertilized from May 7 to September 2 (Table 3).

METHODS

Monthly sampling was conducted from a float-equipped de Havilland Beaver aircraft, except Great Central Lake, which was sampled by boat. Sampling continued from near-isothermal conditions in spring (April or May) until the onset of fall overturn (October or November). Bowser Lake was sampled in June and August only. Microbiological studies were an integral part of the ongoing limnological monitor program (Stockner et al. 1980; Shortreed and Stockner 1981).

Water samples were collected from depths of 0, 1, 2, 3, 5, 7.5, 10, and 20 m with a 4.5-L Van Dorn bottle sterilized with 95% ethanol. Thirty-meters depth was sampled in Great Central and Woss lakes (2-m depth omitted because of deeper mixed layers. Samples were usually collected between 1000 and 1300 h.

Relative heterotrophic activity was measured at each depth by dark uptake of a single tracer-level concentration of tritium-labelled glucose as described by Azam and Holm-Hansen (1973). More than 75% of the ethanol was aseptically removed from the glucose (D-6-^{3}H glucose, specific activity 30 Ci/mmol; Amersham/Searle Corp.) by room temperature evaporation with a small stream of compressed air. The glucose was diluted to 0.003 µg glucose·mL^{-1} with autoclaved, 0.2-µm filtered, distilled water and then filtered through a sterile, 0.2-µm membrane filter. Aliquots (10 mL) of this stock glucose solution were sealed in sterile glass ampoules and stored at $4^{\circ}C$ in the dark.

In the field, a 50-mL water sample from each depth was drawn into a sterile 50-mL plastic syringe and inoculated by needle through the syringe orifice with 0.5 mL (0.25 µCi) of stock glucose solution, enriching the sample by 0.03 µg glucose·L^{-1}. Syringes were capped, mixed, and incubated in the dark in styrofoam holders to minimize temperature changes. Controls (zero-time blanks) from 1-, 5-, and 20-m depths were inoculated, mixed, and immediately filtered by methods described later for the field laboratory. Three scintillation vials, each containing 15 mL of Biofluor scintillation cocktail (New England Nuclear Corp.), were also inoculated to determine the activity of the glucose added to each syringe. Samples incubated

for 3 to 4 h during transport to the field laboratory.

Each sample was mixed and filtered after incubation onto a wetted, 0.2-μm, 47-mm diameter Sartorius membrane filter at a vacuum head less than 20 cm Hg. The syringe was rinsed with 10 mL of filtered lake water which was then added to the filter column. The filter was rinsed with an additional 10 mL and placed in a scintillation vial containing 15 mL of Biofluor.

Vials were counted in a Packard Tri-Carb Model 3375 or Searle Isocap 300 liquid scintillation spectrometer. Counts per minute (CPM) were corrected for background in the controls and for quenching using the external standard or channels ratio methods. Quench series were constructed using Biofluor, Sartorius filters and tritiated toluene. The resulting disintegrations per minute (DPM) were converted to turnover-time (T) by the equation

$$T = At/U$$

where: t = incubation time (h)

A = DPM added to each sample

U = DPM taken up

Turnover-times represent the theoretical time necessary for complete removal of the naturally occurring substrate. Glucose turnover-times are "assimilated" turnover-times and do not include the respired fraction of the substrate (Wright and Burnison 1979).

Total numbers of bacteria were counted by the acridine orange direct count (AODC) epifluorescent technique as modified by Hobbie et al. (1977). Sterile culture tubes were filled in the field with sample water from each depth, stored in the dark and transported to the field laboratory within 2 h. A Nuclepore filter (0.2-μm, 25-mm diameter), previously stained in irgalan black solution (2 $g \cdot L^{-1}$ in 2% acetic acid), was rinsed in 0.2-μm filtered, distilled water and placed on a wetted, 100-μm, Nitex screen in a filter holder. One to 5 mL of sample water was added to the filter column and diluted to at least 5 mL total volume with autoclaved, 0.2-μm filtered, distilled water, then vacuum (< 20 cm Hg) filtered until just dry. Blanks were also filtered to correct for bacteria in the dilution water. Filters were placed in petrie dishes lined with Whatman (no. 1) filter paper, air-dried at room temperature (ca. 20°C), and stored for up to 3 weeks.

Counts were made with a Zeiss Model KLSM microscope equipped with a IV/FL epifluorescent condenser, HBO 50-W mercury lamp, 450-490 band-pass filter, 510 beam splitter, and LP 520 barrier filter. Each air-dried filter was placed on a wetted, 100-μm, Nitex screen in a filter holder, stained for 3 min with 1 mL of 0.2-μm filtered, acridine orange solution (0.05 $g \cdot L^{-1}$ in distilled water), filtered (< 20 cm Hg), and rinsed with 5 mL of 0.2-μm filtered, distilled water. The filter was placed on a glass slide with a drop of Cargille A immersion oil, a coverslip was added, and the bacteria were enumerated under oil immersion at 1250X magnification. Random fields were counted until more than 200 bacteria were enumerated and counts were converted to $no \cdot mL^{-1}$. Blanks for dilution water, acridine orange solution, and rinse water were counted and subtracted from the sample counts.

Fluorescing microalgae (ca. 1-μm diameter) were distinguished from bacteria by differences in morphology and fluorescent color (interference from autofluorescent photopigments) and were excluded from the total bacteria counts.

One-liter water samples (1-m depth) were collected from Kitlope (July 13), Great Central (August 20), and Lowe (August 29) lakes. They were stored in plastic bottles at 4°C in the dark and transported to the main laboratory to test the air-drying preservation method. There were no significant differences (t-test; $p \leq 0.05$) in total bacteria counts between samples stained, filtered, and counted immediately and samples air-dried and stored up to 3 weeks before counting (Table 4).

Clean 2-L plastic bottles were filled in the field with water from each of 1-, 3-, 5-, and 20-m depths and stored in the dark for transport (within 2 h) to the field laboratory. Each sample was mixed and 1 L was filtered onto an ashed, 55-mm diameter, Whatman GFF filter (0.7-μm mean pore size). Filters were stored frozen and one half of each filter was analyzed for particulate carbon (PC) by oxygen combustion using a Coleman Model 33 Carbon-Hydrogen Analyzer. The other filter half was analyzed for particulate nitrogen (PN) using a Coleman Model 29 Nitrogen Analyzer. Only mean annual PC and PN values are included in this report.

"Epilimnetic" values are means for the 0 to 10 m layer in each lak
Seasonal correlation coefficients (r) were calculated (Snedecor 1946) betwee
bacteria counts (square root transformed) or glucose turnover times ($\log_{10}$ transformed) and various untransformed physical, chemical, and biological variables (Shortreed and Stockner 1981).

RESULTS AND DISCUSSION

Small (< 0.5 μm), free-living, coccoid and rod-shaped bacteria were dominant in the study lakes. The bacteria fluoresced green in all air-dried samples examined. Concentrations of autofluorescent detritus (red) or glacial-silt particles (yellow-green) were never high enough (in 5 mL sample water) to notably interfere with bacteria counts. Bacteria were rarely observed attached to the glacial-silt particles.

MEAN ANNUAL VALUES

Mean annual epilimnetic bacteria numbers ranged from 0.41 to $0.98 \cdot 10^6 \cdot mL^{-1}$ with a mean of $0.68 \cdot 10^6 \cdot mL^{-1}$ for all eight lakes (Table 2). Annual means are within the range of values for oligotrophic waters (Spencer 1978; Hobbie 1979) and lower than comparable total bacteria numbers reported for various temperate mesotrophic and eutrophic lakes (Coveney et al. 1977; Jones 1977; Riemann 1978; Rao et al. 1979; Daley et al. 1980).

Mean annual epilimnetic glucose turnover-times varied among the lakes by more than an order of magnitude but were generally slower than those reported for temperate eutrophic lakes (Hobbie 1967; Wetzel 1967; Allan 1969; Hall 1975; Berman et al. 1979) (Table 2). Fastest mean annual turnover-times were in Kitlope, Long, Bonilla, Lowe, and Meziadin lakes (125 to 335 h) while the slowest were in Woss and Bowser lakes (2200 and 1060 h) with a mean of 415 h for all lakes.

Mean annual PC, and PN concentrations were low, less than 0.41 mg $C \cdot L^{-1}$ and 0.08 mg $N \cdot L^{-1}$, and typical of oligotrophic waters (Wetzel 1975; Allen 1978) (Table 2).

Very low mean annual values of bacteria numbers, glucose turnover, chlorophyll, PC, and PN reflect the ultra-oligotrophic conditions of unfertilized Bowser and Woss lakes (Table 2). Dystrophic Bonilla Lake had the highest mean annual number ($0.67 \cdot 10^6 \cdot mL^{-1}$) and fastest glucose turnover (250 h) of the unfertilized lakes. Dystrophy generally indicates high allochthonous organic inputs (Allen 1978) which may be partly responsible for the higher bacterial numbers and activity in Bonilla Lake.

Assessing the response of a lake to fertilization is difficult without data from unfertilized years, but comparisons of enriched and untreated lakes with similar physical and chemical characteristics can help to identify major changes in the bacterioplankton community. Fertilized lakes generally had higher mean annual bacteria numbers than unfertilized lakes, with means of 0.85 and $0.50 \cdot 10^6 \cdot mL^{-1}$, respectively (Table 2). The mean number in Great Central Lake ($0.85 \cdot 10^6 \cdot mL^{-1}$) was double that of untreated Woss Lake ($0.42 \cdot 10^6 \cdot mL^{-1}$) and glucose turnover was 3-fold faster in the former. They have very similar physical and chemical characteristics and the higher levels of bacterial numbers and activity in Great Central Lake are largely attributed to fertilization.

Among the dystrophic lakes, mean annual bacteria numbers in fertilized Long and Lowe lakes ($0.98 \cdot 10^6 \cdot mL^{-1}$) were 45% higher than untreated Bonilla Lake ($0.67 \cdot 10^6 \cdot mL^{-1}$). They were the highest recorded in this study, suggesting a bacterial response to nutrient enrichment (Table 2). Glucose turnover was similar in Lowe (275 h) and Bonilla (250 h) lakes but slightly faster in Long Lake (180 h). Substantial physical and chemical differences between Long and Bonilla lakes may negate a direct comparison. However, Lowe and Bonilla lakes are more comparable (Tables 1 and 2). Bacteria numbers in Bonilla Lake may be higher than pre-treatment years in Lowe Lake because of its longer water residence time and slightly higher concentrations of allochthonous (humic) organic matter.

The bacterial response of Kitlope Lake to fertilization is more difficult to assess by comparing annual means, in light of great dissimilarities in physical, chemical, and biological variables among the glacially-turbid lakes (Tables 1 and 2). Glucose turnover in Kitlope Lake (125 h) was the fastest recorded in this study while annual numbers ($0.60 \cdot 10^6 \cdot mL^{-1}$) were the lowest recorded for a fertilized lake, but were higher than untreated Bowser ($0.41 \cdot 10^6 \cdot mL^{-1}$) and Meziadin ($0.48 \cdot 10^6 \cdot mL^{-1}$) lakes. However, the higher annual number in Kitlope Lake cannot be readily identified as a fertilization

response.

Mean annual bacteria numbers and glucose turnover-times of the lakes were not significantly correlated, partly owing to the inability of a single substrate to represent the total spectrum of organic matter utilized by the various bacterioplankton communities. Correlations between annual numbers or turnover-times and various autotrophic or physico-chemical indices of trophic states were not significant.

SEASONAL VARIATIONS

Great Central Lake

Mean epilimnetic bacteria numbers and glucose turnover-times ranged from $0.24 \cdot 10^6 \cdot mL^{-1}$ and 5000 h to $1.77 \cdot 10^6 \cdot mL^{-1}$ and 135 h (Fig. 2). Glucose turnover in the fertilized zone (Station 2) increased more than an order of magnitude during fertilization as epilimnetic temperatures increased (7 to 19°C). However, bacteria numbers remained low ($< 0.50 \cdot 10^6 \cdot mL^{-1}$) during a spring bloom of the diatom Rhizosolenia sp. The rapid increase in bacteria in July (to $1.01 \cdot 10^6 \cdot mL^{-1}$) coincided with stronger temperature stratification and sinking of the diatoms out of the epilimnion to form an upper hypolimnetic plate (J.G. Stockner, unpubl.data). Similar conditions of high diatom and low bacteria numbers in the spring have been described in other temperate lakes (e.g. Menon et al. 1972; Rao et al. 1979), and diatom release of antibiotic substances during bloom conditions was suggested as inhibiting bacterial growth (Burkholder 1963; Sieburth 1968; Menon et al. 1972; Rao et al. 1979).

The fastest epilimnetic glucose turnover-time (135 h) recorded in Great Central Lake occurred just prior to the end of fertilization. Turnover-times were markedly slow (4800 h) 3 weeks after the cessation of fertilization despite the highest epilimnetic bacteria number ($1.77 \cdot 10^6 \cdot mL^{-1}$) and temperature (21°C) recorded in the lake. Bacteria numbers declined during the post-fertilization period to the lowest epilimnetic value ($0.24 \cdot 10^6 \cdot mL^{-1}$) recorded in this study, while glucose turnover-times remained slow (> 800 h). Rapid cooling of the epilimnion (14 to 8°C) and the breakdown of stratification in late fall coincided with faster turnover-times (300 to 400 h) and a small peak in bacteria number ($0.84 \cdot 10^6 \cdot mL^{-1}$) and epilimnetic chlorophyll (Shortreed and Stockner 1981).

A once monthly sampling scheme precludes stating exactly when glucose turnover and bacteria numbers reached maximum or minimum levels relative to the end of fertilization. However, increased bacterial biomass and activity during fertilization, with marked declines after cessation (lag response in bacteria numbers), clearly demonstrate enhancement of the flow of organic carbon to the heterotrophic community. Increased autotrophic production and associated organic release is the logical carbon source although a fertilization response was not as readily detected in the phytoplankton community from chlorophyll and in situ primary production measurements (Shortreed and Stockner 1981).

Bacteria numbers and glucose turnover-times in the upper hypolimnion

(20 and 30 m) exhibited temporal variations similar to those in the epilimnion, but the changes were less pronounced (Figs. 3a and 4a). Mean temperatures were between 5 and 6°C. Glucose turnover was slower in the epilimnion during fertilization, slightly faster in the post-fertilization period, and slower during the fall peak. Bacteria numbers were higher in the epilimnion after the initial increase in July, but numbers were slightly higher at 30 m in October when epilimnetic numbers reached minimal values. Apparently temporal variations in the upper hypolimnetic bacteria population of Great Central Lake were not entirely independent of the epilimnetic population.

Bacteria in the upper hypolimnetic diatom plate were free-living cells rarely associated with frustule surfaces (to indicate attachment). Numbers and glucose turnover-times were similar to those above and below the plate. Coupled with the lack of microbial attachment and the persistence of autofluorescent photopigments in the diatoms throughout the summer, this indicates that microbial decomposition of the hypolimnetic plate was not occurring.

Samples for bacteria counts only were taken at station 1 located between the fertilized zone (station 2) and the outlet of the lake (Fig. 3b). Although station 1 did not receive direct fertilizer additions, it received advected water from the fertilized regions of the lake (Parsons et al. 1972) and exhibited temporal variations in bacteria numbers similar to those of station 2. Bacteria numbers were lower than in the fertilized zone during summer when flushing and advective currents were minimal.

Woss Lake

Mean epilimnetic bacteria numbers and glucose turnover-times ranged from $0.37 \cdot 10^6 \cdot mL^{-1}$ and 5000 h to $0.50 \cdot 10^6 \cdot mL^{-1}$ and 775 h (Figs. 2 and 4b). Variations in the seasonal and vertical distributions of bacteria numbers were very minor (seasonal isopleth omitted), and in conjunction with low numbers and activities, illustrate the extreme oligotrophic condition of Woss Lake. This sharply contrasts with the temporal response to fertilization of the bacterioplankton in Great Central Lake (Fig. 2). The epilimnetic turnover of glucose was very slow in the spring and fall, slightly faster in the surface waters during summer stratification and significantly correlated with epilimnetic temperature ($r = 0.76; 1,5df; p \leq 0.05$). The seasonal pattern of microbial glucose activity was very similar to that of zooplankton biomass (D.P. Rankin, unpubl. data), but was not clearly related to changes in phytoplankton biomass (Shortreed and Stockner 1981). Heterotrophic activity was maximal in the epilimnion when inorganic nutrients were depleted and regenerated nutrients were most likely to be important in sustaining the phytoplankton community.

Long Lake

Mean epilimnetic bacteria numbers and glucose turnover-times for station 2 (fertilized zone) ranged from $0.47 \cdot 10^6 \cdot mL^{-1}$ and 950 h to $1.43 \cdot 10^6 \cdot mL^{-1}$ and 35 h (Figs. 2, 3b and 4b). Long Lake has a relatively short flushing time (1.1 yr) and receives the greatest portion of its total annual runoff during the spring from snowmelt and precipitation. This intense flushing

largely accounts for the marked decline in epilimnetic numbers to minimal levels ($0.47 \cdot 10^6 \cdot mL^{-1}$) during May and June despite relatively fast glucose turnover-times (185 to 110 h). The initial high bacteria concentration ($1.05 \cdot 10^6 \cdot mL^{-1}$) in the spring is believed to be an endogenously dormant population, overwintering from a fall-overturn peak in the previously fertilized year (1978) and maintained in the lake by low temperatures and minimal flushing during winter. Bacteria numbers after spring flushing were lowest in the 0 to 10 m layer, suggesting that flushing was more intense in the surface layers. Long Lake has three main basins, separated by shallow sills, with most of the spring runoff discharged to the unsampled basin furthest from the outlet. This may result in rapid flushing of the surface waters of the other two basins.

Epilimnetic numbers increased during the remainder of the fertilized period to maximum levels ($1.19 \cdot 10^6 \cdot mL^{-1}$) in the fall. After the onset of fertilization and stratification, glucose turnover was consistently faster in the epilimnion than the hypolimnion, and bacteria numbers were concentrated in the epilimnion. The mid-summer maximum of glucose turnover (35 h) coincided with warmest epilimnetic temperatures (16.2°C) and strongest stratification, and turnover-times slowed during autumn cooling of the epilimnion. After cessation of fertilization in early October, glucose turnover slowed markedly to its lowest recorded value (950 h), with a slight decline in numbers ($1.14 \cdot 10^6 \cdot mL^{-1}$). Seasonal epilimnetic glucose turnover was significantly correlated with chlorophyll ($r = 0.81; 1,5df; p \leq 0.05$) and temperature ($r = 0.78; 1,5df; p \leq 0.05$).

Samples were taken for bacteria numbers at station 3, situated between the fertilized zone (station 2) and the outlet of the lake. Numbers were slightly higher than the fertilized zone after spring flushing but slightly lower during summer and early fall when advection from the fertilized zone was minimal (Fig. 3c).

Lowe Lake

Lowe Lake has the shortest theoretical water residence time (0.2 yr) of the eight study lakes with periods of highest flushing in the spring and late fall. However, most of its water input is discharge from other nearby dystrophic lakes and its hydrology is complicated by the locations of its inlet and outlet rivers (Stockner and Shortreed 1979).

Mean epilimnetic bacteria numbers and glucose turnover-times ranged from $0.60 \cdot 10^6 \cdot mL^{-1}$ and 1710 h to $1.34 \cdot 10^6 \cdot mL^{-1}$ and 60 h (Fig. 2). Numbers were low (0.60 to $0.67 \cdot 10^6 \cdot mL^{-1}$) during spring flushing despite relatively fast glucose turnover-times (335 to 195 h) and numbers and turnover-times were homogeneously distributed throughout the water column. Low flushing and the development of strong temperature stratification in July (epilimnetic temperatures > 14°C) coincided with increased bacteria numbers ($1.01 \cdot 10^6 \cdot mL^{-1}$) and slower glucose turnover (555 h). During the remainder of the fertilized period flushing was minimal, epilimnetic temperatures were high (16 to 17°C), primary production was high (Shortreed and Stockner 1981), and bacteria numbers and glucose turnover increased to maximal values in the epilimnion ($1.34 \cdot 10^6 \cdot mL^{-1}$ and 60 h). Hypolimnetic numbers and glucose turnover-times

during stratification were consistently lower and slower than in the epilimnion (Figs. 3c and 4c). After the cessation of fertilization, glucose turnover declined markedly to minimal levels (1700 h) with a slight decline in numbers ($1.14 \cdot 10^6 \cdot mL^{-1}$). Epilimnetic bacteria numbers were positively correlated with temperature ($r = 0.90; 1,4df; p \leq 0.05$) but negatively correlated with chlorophyll ($r = 0.85; 1,4df; p \leq 0.05$). Glucose turnover was significantly correlated with zooplankton biomass ($r = 0.88; 1,4df; p \leq 0.05$).

Bonilla Lake

Bonilla Lake experiences spring and fall periods of flushing less intense than Lowe Lake. Epilimnetic bacteria numbers and glucose turnover-times ranged from $0.45 \cdot 10^6 \cdot mL^{-1}$ and 760 h to $1.05 \cdot 10^6 \cdot mL^{-1}$ and 60 h (Fig. 2). Numbers declined slightly and remained low (0.58 to $0.52 \cdot 10^6 \cdot mL^{-1}$) during spring flushing and a small bloom of the diatom Rhizosolenia sp., but glucose turnover increased (665 h to 145 h). Numbers doubled during the summer to a maximum of $1.05 \cdot 10^6 \cdot mL^{-1}$ coinciding with the fastest recorded glucose turnover-time (60 h). Numbers and glucose turnover declined sharply in the fall to spring levels with breakdown of stratification and increased flushing. Vertical zonation of bacteria numbers was not apparent during the growing season. However, the fastest glucose turnover-times occurred in the epilimnion during stratification (Figs. 3d and 4c).

Kitlope Lake

Kitlope Lake was rapidly flushed during the ice-free season. It received its greatest hydraulic load in the spring from snowmelt and precipitation. The influx of cold, turbid, glacial melt-waters was maximal during mid-summer. Stratification was very weak, with a shallow (< 2 m) warm surface layer during late summer. The distribution of bacteria numbers exhibited relatively little temporal or vertical variations (Figs. 2, 3d and 4d). Numbers in the 0-10 m layer declined slightly (to $0.50 \cdot 10^6 \cdot mL^{-1}$) during spring flushing, gradually increased during fertilization to a maximum of $0.73 \cdot 10^6 \cdot mL^{-1}$ in late summer, and declined ($0.50 \cdot 10^6 \cdot mL^{-1}$) in the fall post-fertilization period. However, concentrations exceeding $0.90 \cdot 10^6 \cdot mL^{-1}$ were found in the shallow warm surface layer in September.

Glucose turnover was fast (> 250 h) throughout the season, with a peak (105 h) during intense spring flushing, slower turnover in early summer (245 h) and fastest in late summer (55 h) when water temperatures and bacteria numbers were maximal. Bacteria numbers were only significantly correlated with zooplankton biomass ($r = 0.95; 1,4df; p \leq 0.05$).

Meziadin Lake

Mean epilimnetic (0-10 m) bacteria numbers and glucose turnover-times at station 1 ranged from $0.33 \cdot 10^6 \cdot mL^{-1}$ and 705 h to $0.69 \cdot 10^6 \cdot mL^{-1}$ and 100 h (Fig. 2). Numbers were low ($0.33 \cdot 10^6 \cdot mL^{-1}$) in the spring and gradually increased to a summer maximum ($0.69 \cdot 10^6 \cdot mL^{-1}$). Glucose turnover also increased from minimal spring levels to its fastest value (100 h) in late summer, just after the peak in numbers. Slower glucose turnover (345 h) and a slight increase in numbers accompanied the onset of fall-overturn and a chlorophyll peak

(Shortreed and Stockner 1981). Vertical stratification of bacteria numbers was not apparent; however, glucose turnover was faster in the epilimnion than the hypolimnion during late summer stratification (Figs. 3c and 4d).

Samples for total bacteria counts were taken at station 2. Epilimnetic numbers ranged from 0.44 to $0.74 \cdot 10^6 \cdot mL^{-1}$ and exhibited the same seasonal pattern as station 1, although concentrations were slightly higher (Fig. 3c).

Bowser Lake

Mean bacteria numbers and glucose turnover-times at station 1 were $0.38 \cdot 10^6 \cdot mL^{-1}$ and 4000 h under isothermal conditions in June and $0.44 \cdot 10^6 \cdot mL^{-1}$ and 280 h during near-isothermal conditions in August (Fig. 2). Numbers were similar at station 2. There was little variation in the vertical distributions of bacteria numbers or glucose turnover-times. High glacial turbidity coupled with a cold, near-isothermal temperature regime resulted in very low levels of phytoplankton productivity (Shortreed and Stockner 1981). Very low bacteria numbers and activity confirm the ultra-oligotrophic status of Bowser Lake.

SUMMARY

Small (< 0.5 μm), free-living, coccoid and rod-shaped bacteria were dominant in the lakes. Mean annual bacteria numbers (0-10 m) ranged from 0.41 to $0.98 \cdot 10^6 \cdot mL^{-1}$. Mean annual glucose turnover-times ranged from 125 to 2200 h. Bacteria numbers were higher in fertilized lakes ($0.85 \cdot 10^6 \cdot mL^{-1}$) than in unfertilized lakes ($0.50 \cdot 10^6 \cdot mL^{-1}$). Very low mean annual values of bacteria numbers ($\leq 0.41 \cdot 10^6 \cdot mL^{-1}$) and glucose turnover-times (> 1000 h) identified untreated Woss and Bowser lakes as ultra-oligotrophic.

Late summer (August-September) maxima of glucose turnover were observed in the **epilimnion** of each lake, with the exception of Great Central Lake. These seasonal peaks in bacterial activity generally coincided with higher water temperatures and strong stratification. Smaller peaks of glucose turnover were also observed during periods of spring flushing in Long, Lowe, Bonilla, and Kitlope lakes.

Bacteria numbers reached maximum concentrations in the epilimnia of the enriched lakes during or immediately following the last fertilizer applications. Epilimnetic glucose turnover slowed markedly after the cessation of fertilization in all treated lakes. However, in Long, Lowe, and Kitlope lakes, this also coincided with the onset of fall overturn. A positive response by bacterioplankton to inorganic nutrient additions could only be clearly identified during the half-season fertilization of Great Central Lake. Increased bacteria numbers and activity were attributed to the indirect effects of enhanced autotrophic production.

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Table 1. Geographic, hydrologic, morphometric, and mean annual (1979) physical/chemical parameters[c].

Lake and Station	Latitude	Longitude	Elevation (m)	Lake area (km^2)	Mean depth (m)	Water res. time (yr)	Temperature[a] (^oC)	pH[a]	Total[a] Alkalinity ($mg \cdot L^{-1} CaCO_3$)	Extinction coefficient (k_e)
Bonilla	53°31'	130°15'	10	2.3	34	1.0	13.6	5.7	0.7	1.02
Bowser-1[b]	56°26'	129°30'	366	34	-	-	7.1	7.8	32.1	2.35
Great Central-2	49°22'	125°15'	82	51	212	7.3	14.8	7.0	12.4	0.26
Kitlope	53°07'	127°13'	15	12	86	0.4	7.9	6.0	1.3	0.62
Long-2	51°14'	127°10'	15	21	73	1.1	13.0	6.4	2.8	0.47
Lowe	53°34'	129°33'	10	3.7	25	0.2	13.4	5.7	0.4	0.61
Meziadin-1	56°02'	129°15'	246	36	45	1.9	11.8	7.6	24.0	0.40
Woss	50°08'	126°38'	150	13	81	3.0	14.2	6.8	8.5	0.29

[a]Mean epilimnetic.

[b]Sampled June & August only.

[c]Shortreed and Stockner 1981.

Table 2. Mean annual (1979) biological and chemical parameters.

Lake and Station	Total[a] bacteria number ($\cdot 10^6 \cdot mL^{-1}$)	Glucose[a] turnover time (h)	Total[a,d] chlorophyll ($mg \cdot m^{-3}$)	Particulate[b] carbon ($mg\ C \cdot L^{-1}$)	Particulate[b] nitrogen ($mg\ N \cdot L^{-1}$)
Bonilla	0.67	250	1.04	0.35	0.08
Bowser-1[c]	0.41	1060	0.17	0.10	0.02
Great Central-2	0.85	740	0.94	0.28	0.04
Kitlope	0.60	125	0.59	0.35	0.05
Long-2	0.98	180	2.36	0.41	0.05
Lowe	0.98	275	0.85	0.25	0.05
Meziadin-1	0.49	335	1.68	0.25	0.04
Woss	0.42	2200	0.87	0.22	0.04

[a] Mean epilimnetic (0-10m).

[b] Mean of 1, 3, 5, and 20m samples.

[c] Sampled June & August only.

[d] Shortreed and Stockner 1981.

Table 3. Weekly areal fertilizer additions in 1979.

Lake	Number of Weeks	mg PO_4-P·m^{-2}·wk^{-1}	mg NO_3-N·m^{-2}·wk^{-1}	mg NH_4-N·m^{-2}·wk^{-1}
Great Central	16	2.8	8.5	9.8
Kitlope	18	8.1	24.3	28.0
Long	26	5.2	16.1	18.5
Lowe	18	3.8	12.3	14.1

Table 4. Comparison[a] of bacteria counts (mean[b] ± SE·10^6·mL^{-1}) between stained, wet-filtered samples counted immediately and air-dried samples stored (20°C) up to 20 days before counting.

	Kitlope Lake	Great Central Lake	Lowe Lake
Stained, wet-filtered	0.71 ± 0.06	1.82 ± 0.08	1.65 ± 0.06
Air-dried, stored(d)			
0	0.69 ± 0.07	1.79 ± 0.08	1.68 ± 0.05
7	0.73 ± 0.06	1.79 ± 0.07	1.71 ± 0.05
15	0.68 ± 0.08	1.83 ± 0.07	1.66 ± 0.06
20	0.71 ± 0.06	1.84 ± 0.08	1.64 ± 0.06

[a] tested for significant differences by t-test ($P \leq 0.05$).
[b] total of 60 random fields from 3 replicate filters.

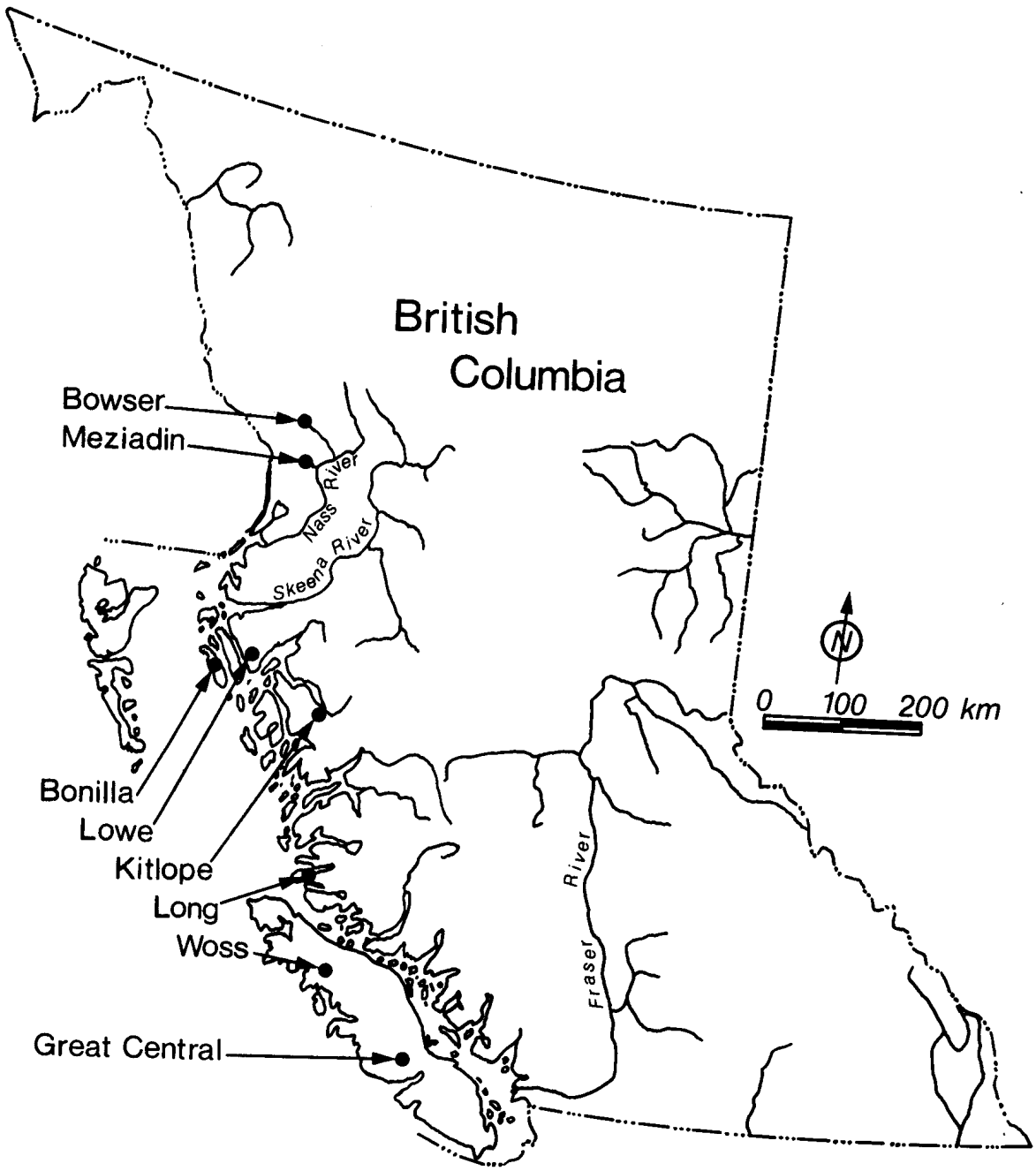


Fig. 1. Map of British Columbia and locations of study lakes.

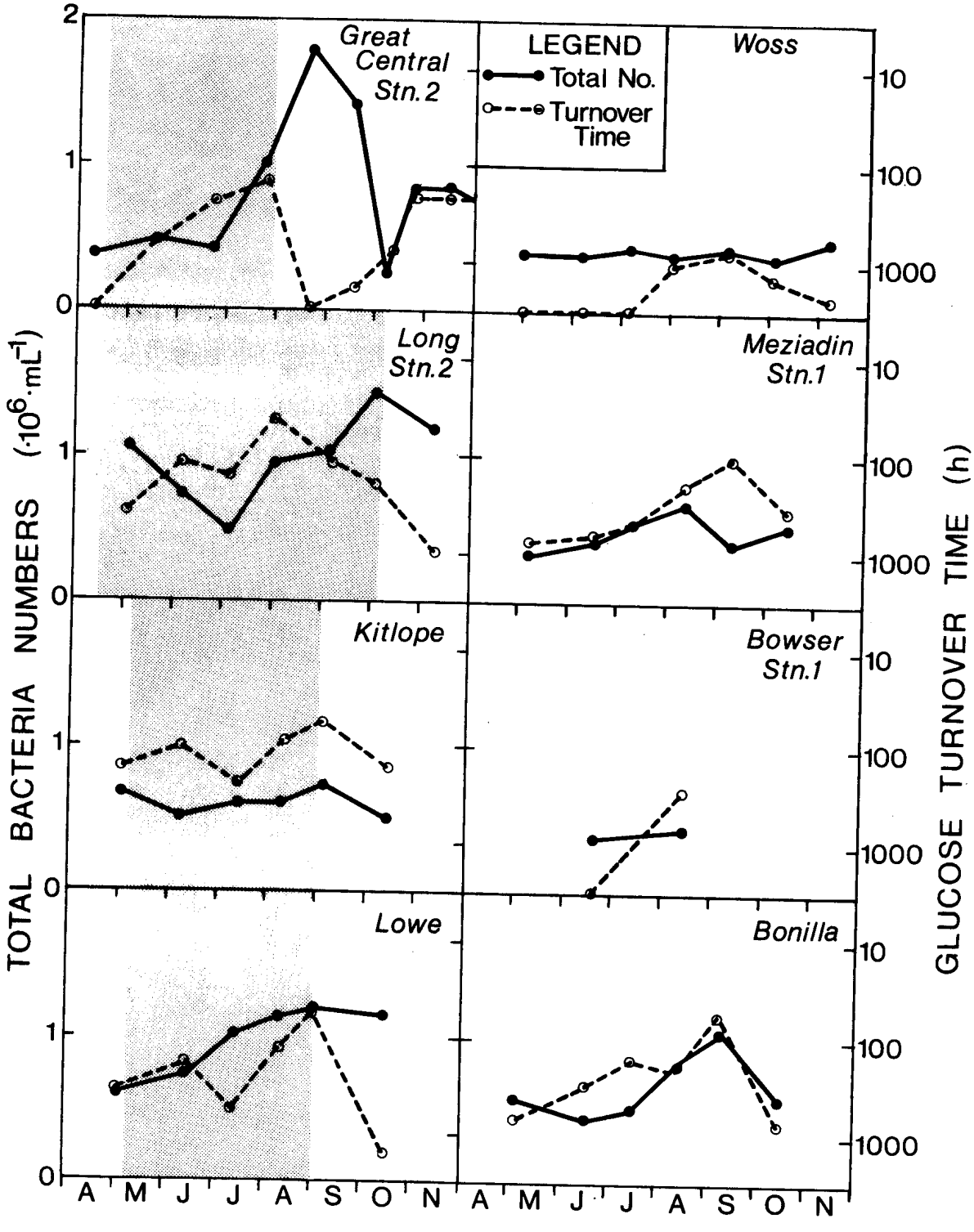


Fig. 2. Seasonal variations in epilimnetic (0-10 m) total bacteria numbers and glucose turnover times of the study lakes. Shaded areas indicate periods of fertilizer additions.

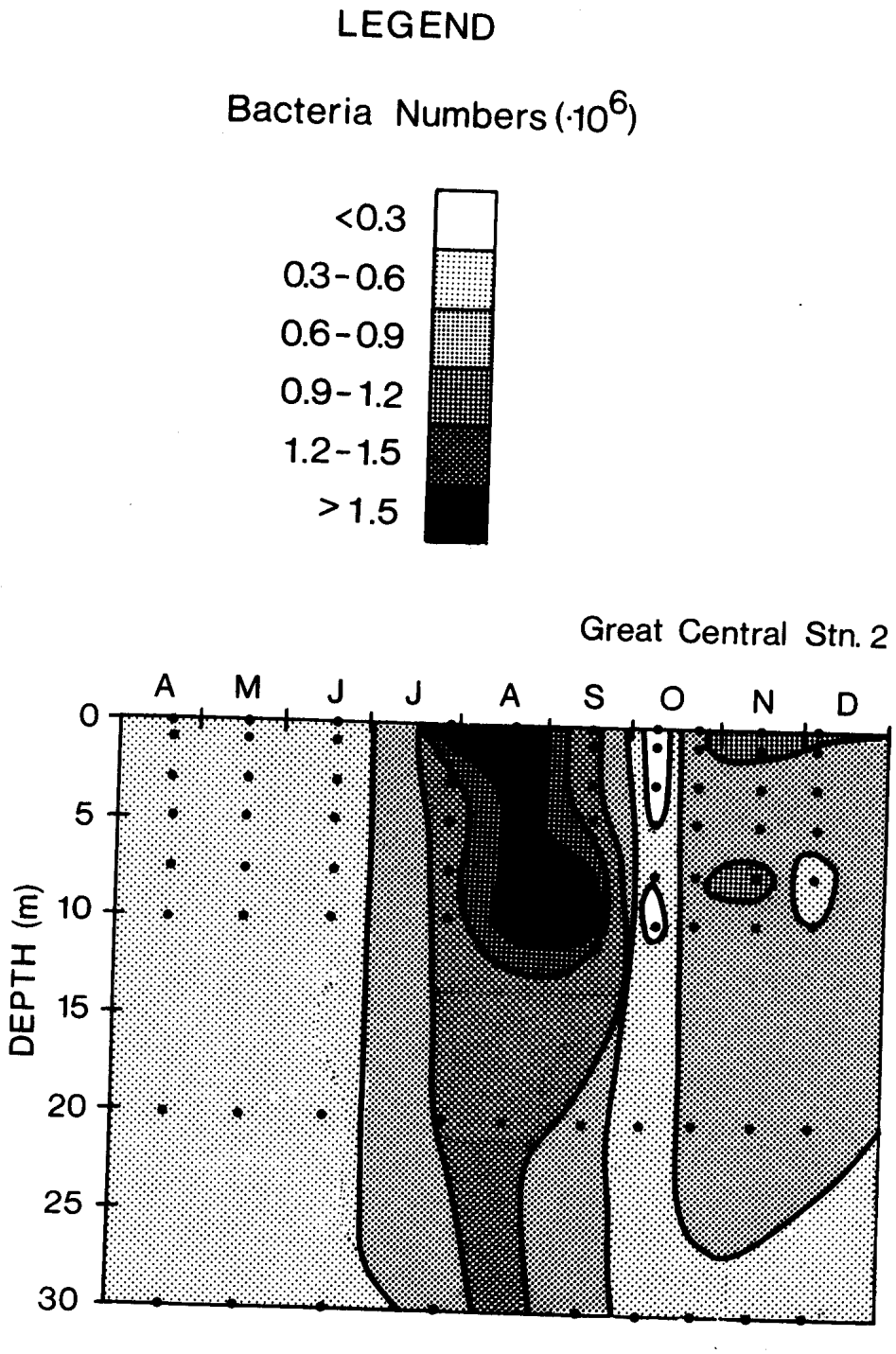


Fig. 3a. Seasonal isopleths of total bacteria numbers.

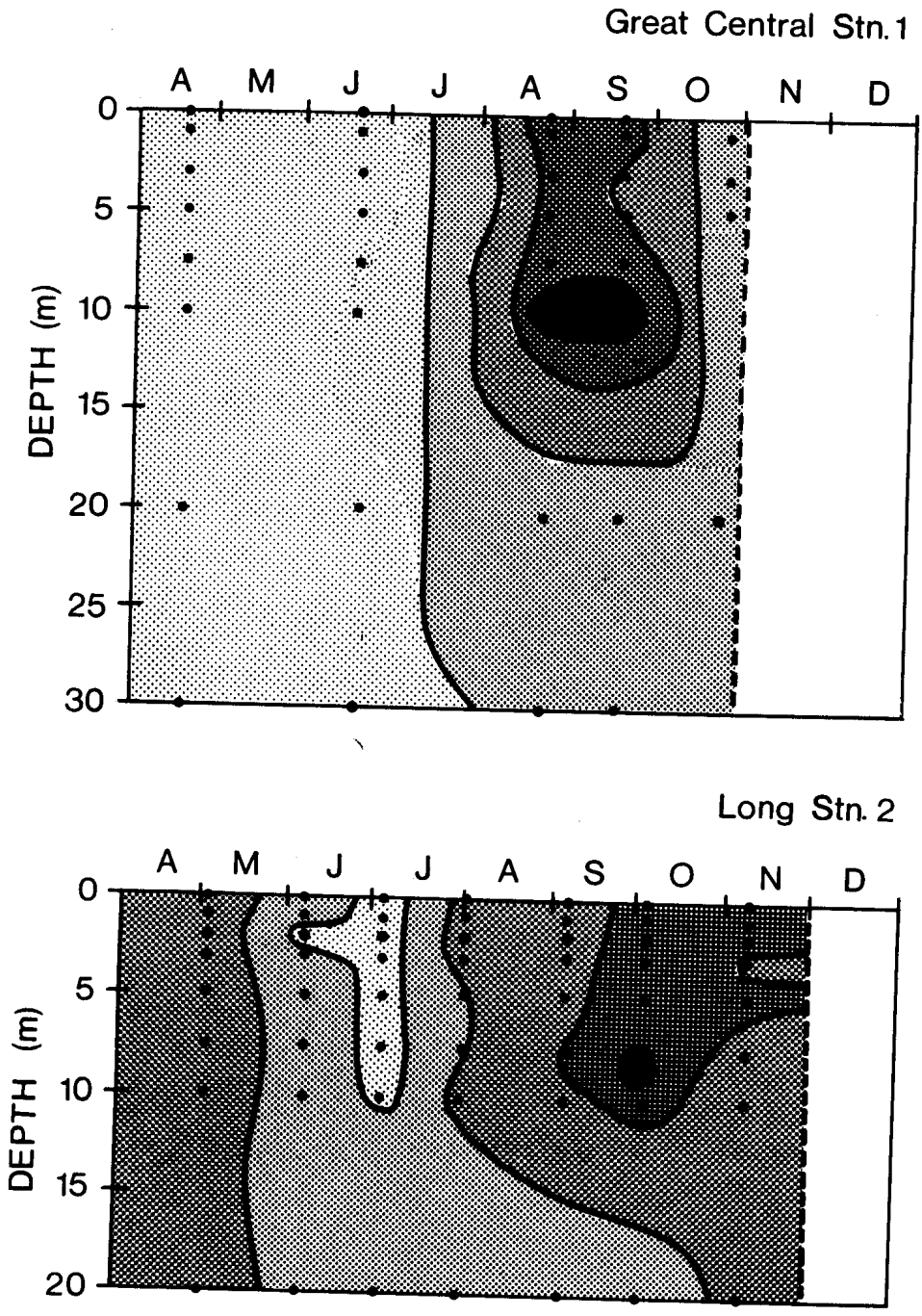


Fig. 3b. Seasonal isopleths of total bacteria numbers.

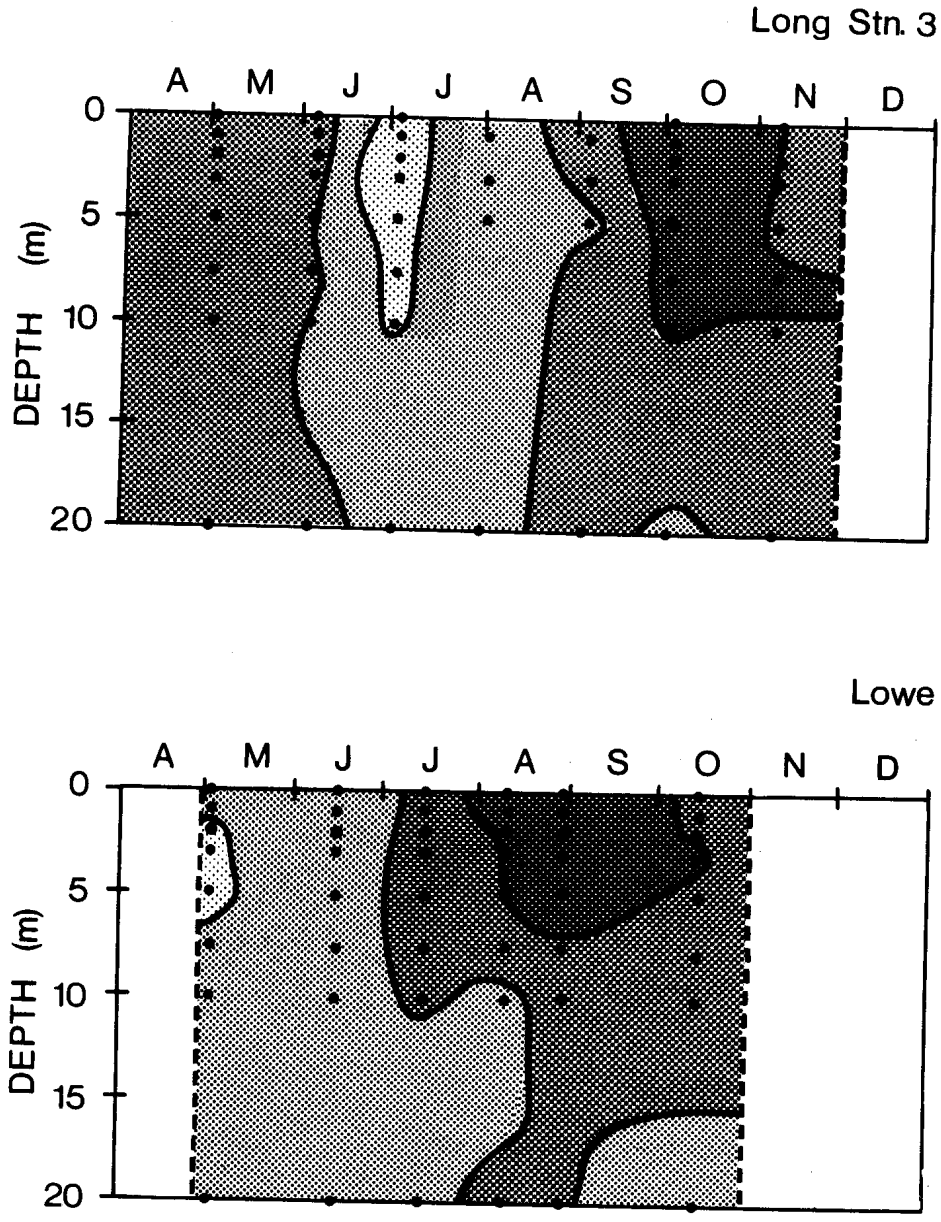


Fig. 3c. Seasonal isopleths of total bacteria numbers.

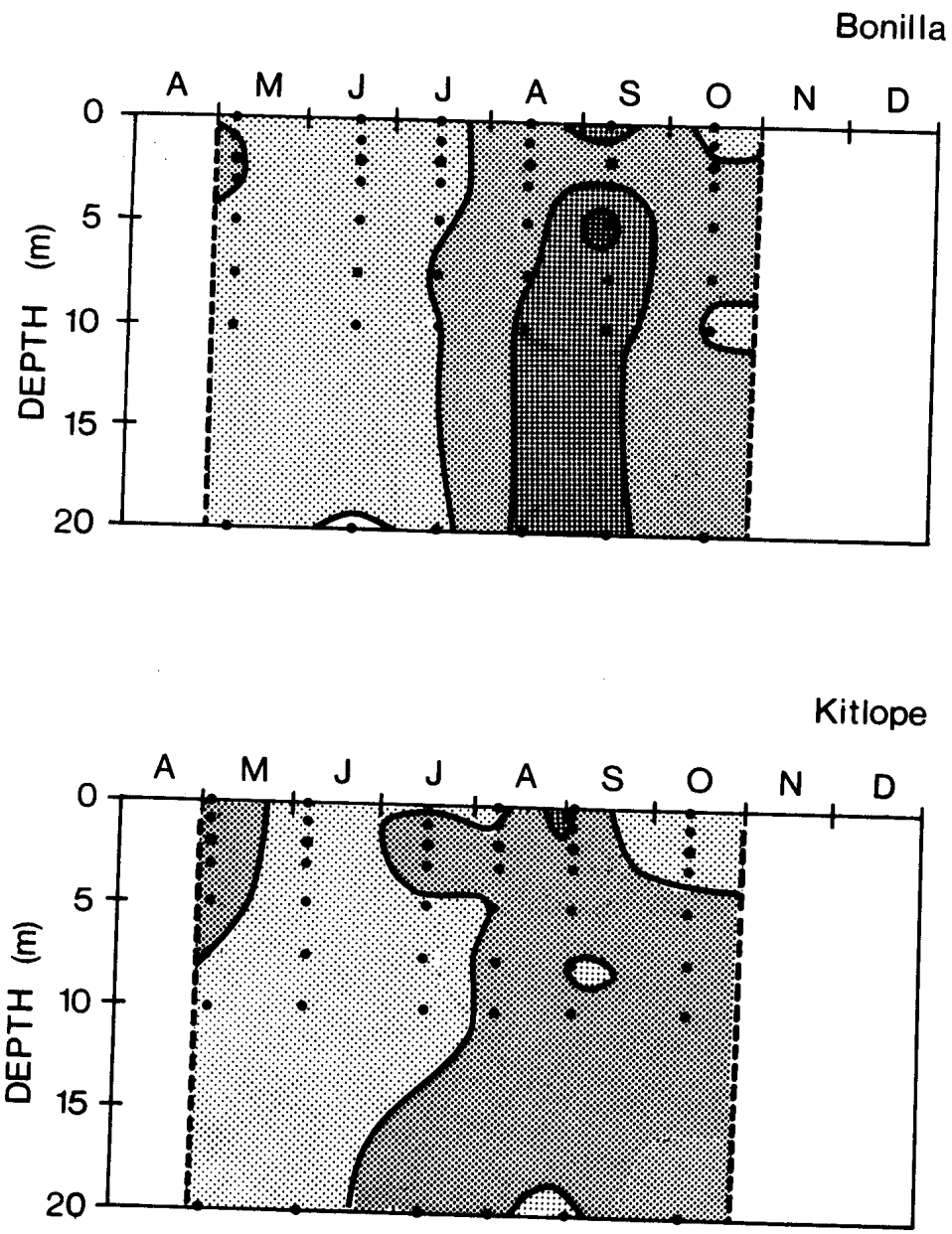


Fig. 3d. Seasonal isopleths of total bacteria numbers.

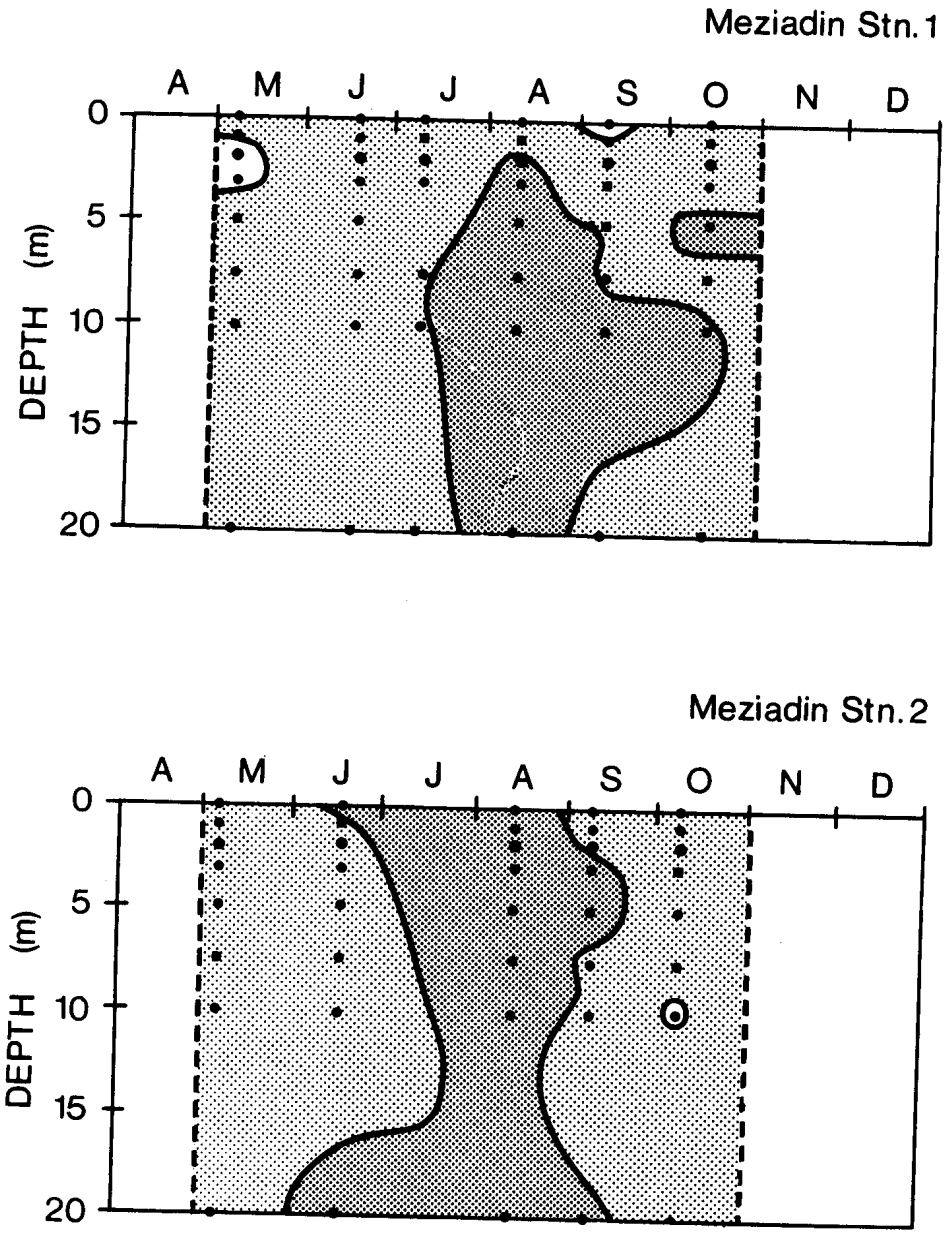


Fig. 3e. Seasonal isopleths of total bacteria numbers.

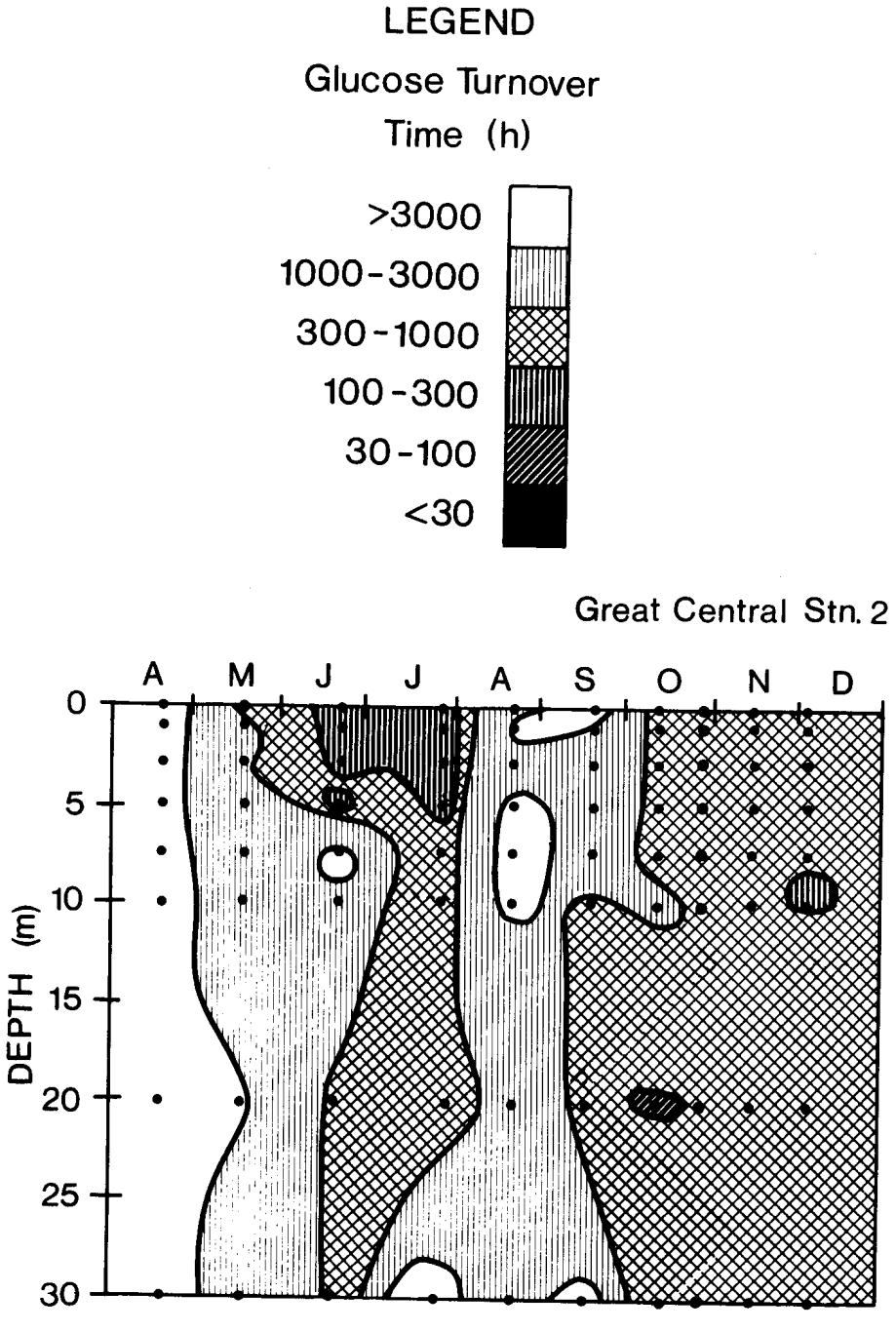


Fig. 4a. Seasonal isopleths of glucose turnover-times.

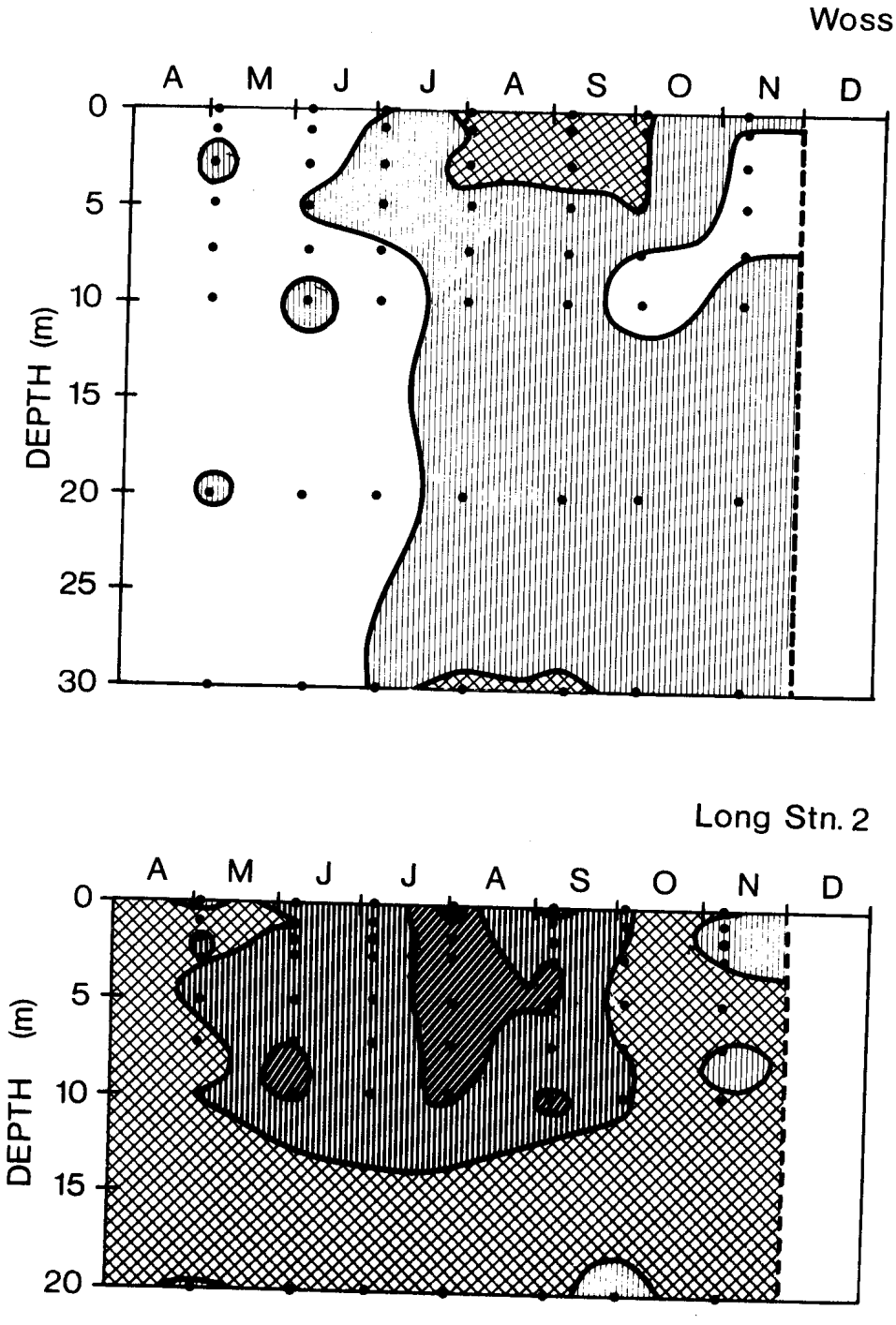


Fig. 4b. Seasonal isopleths of glucose turnover-times.

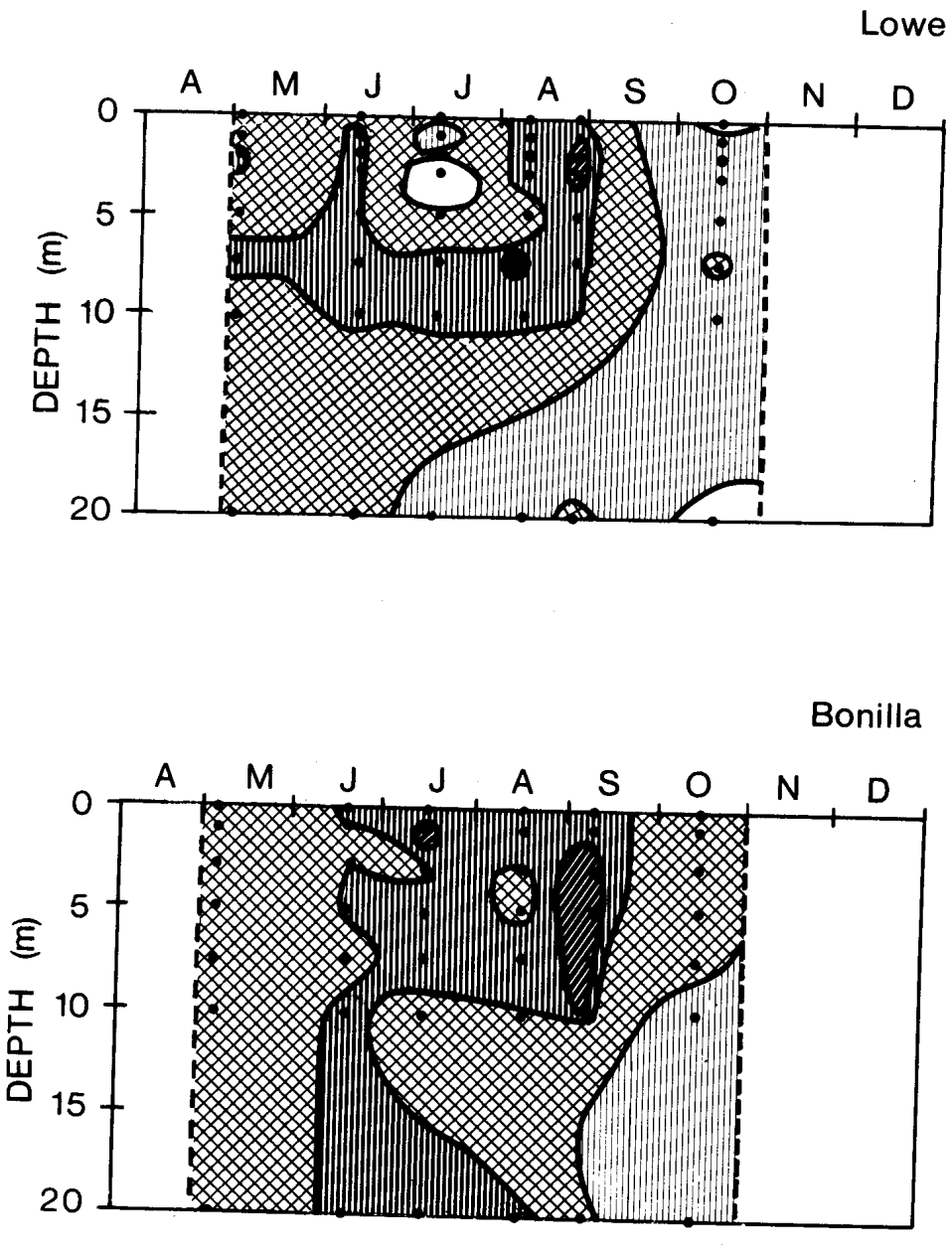


Fig. 4c. Seasonal isopleths of glucose turnover-times.

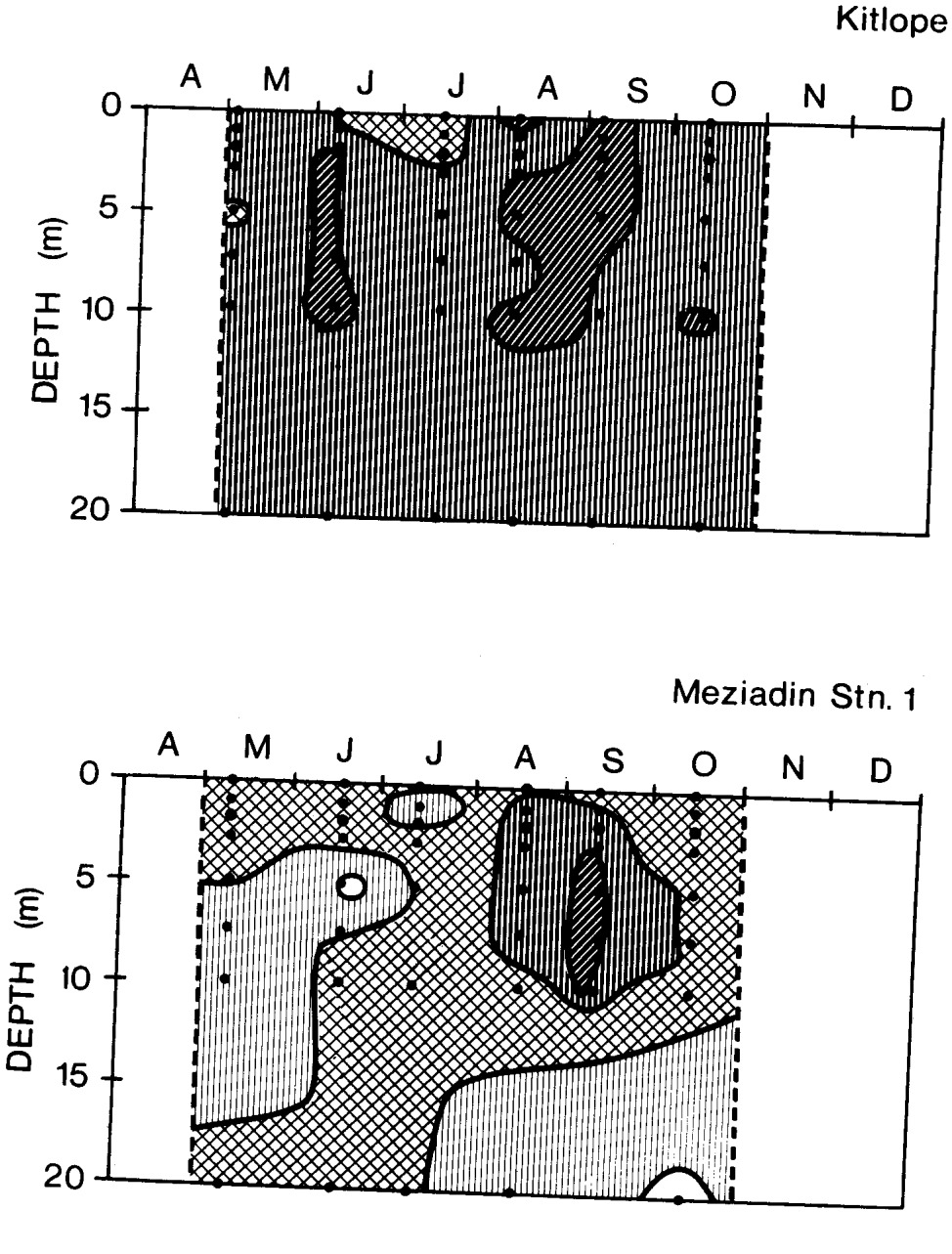
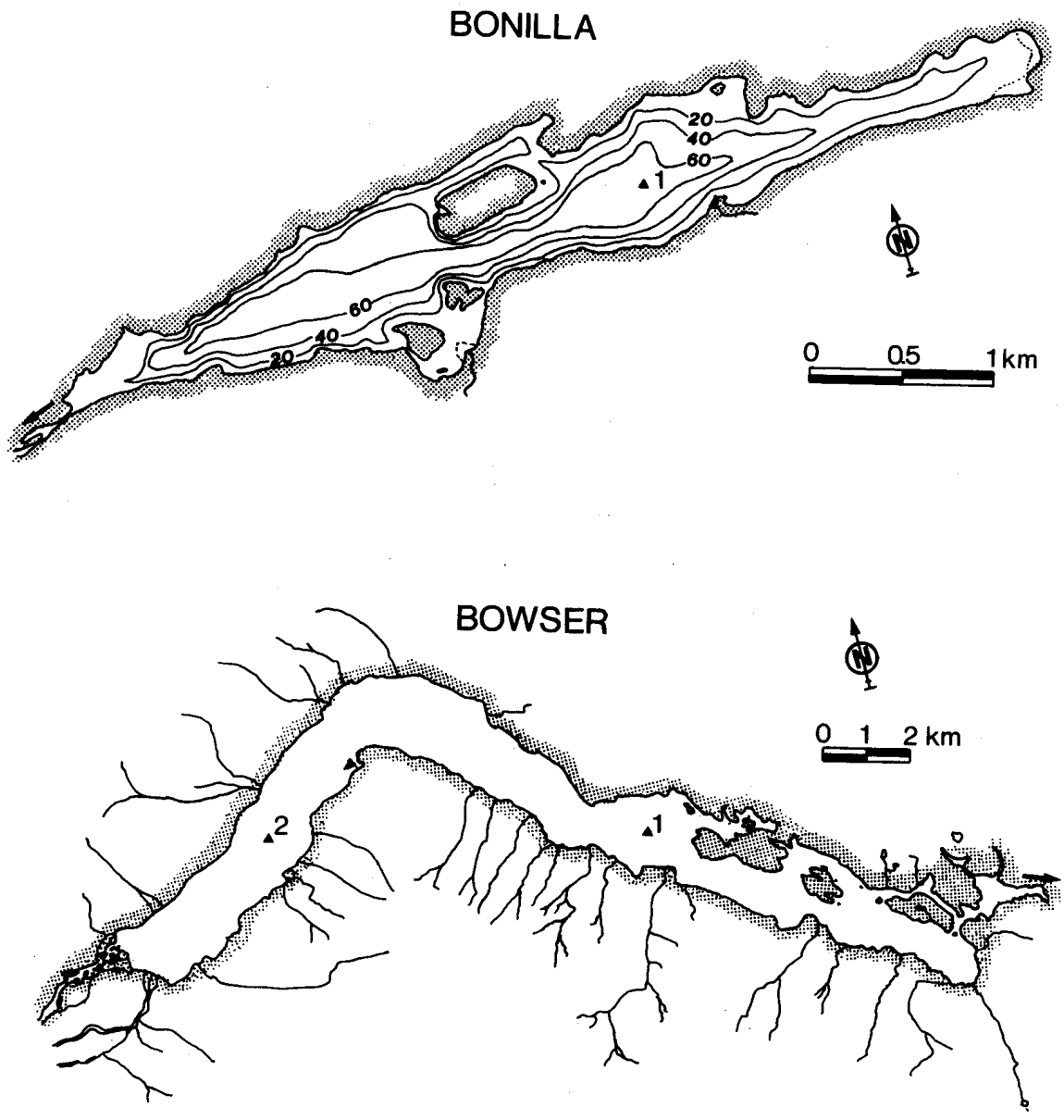


Fig. 4d. Seasonal isopleths of glucose turnover-times.



Appendix Figure 1. Maps and station locations of Bonilla and Bowser lakes.