

The Limnology of Kitlope Lake: a Cold, Glacially-Turbid, Sockeye Salmon (Oncorhynchus nerka) Nursery Lake

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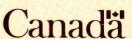
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THE LIMNOLOGY OF KITLOPE LAKE:

A COLD, GLACIALLY-TURBID, SOCKEYE

SALMON (Oncorhynchus nerka) NURSERY LAKE.

by

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ABSTRACT

Stockner, J. G., K. S. Shortreed, E. A. MacIsaac, and B. Nidle. 1992. The limnology of Kitlope Lake: a cold, glacially-turbid sockeye salmon (Oncorhynchus nerka) nursery lake. Can. Tech. Rep. Fish. Aquat. Sci. 1909: 35 p.

Limnological studies were conducted on Kitlope Lake from 1978-80 as part of the Salmonid Enhancement Program's (SEP) Lake Enrichment Program (LEP). lake is strongly influenced by the glacially turbid Tezwa River which delivers high flows to the lake during the growing season (April-November). As a result Kitlope Lake is fast flushing (0.5 yr water residence), glacially turbid (mean compensation depth 4 m, Secchi depth 3 m), cold and weakly stratified (mean epilimnetic depth 6 m), mildly acidic (mean pH 6.7) and of low alkalinity (mean TDS 25 mg·L¹). The lake has very low nutrient levels with total phosphorus (TP) concentrations of between 1-2 $\mu g \cdot L^{-1}$, and nitratenitrogen (NO₃-N) ranging from 50-60 μ g·L⁻¹ in May to < 10 μ g·L⁻¹ from July to September. The high turbidity, rapid surface layer flushing, low surface layer stability, low temperatures and low nutrient conditions result in low phytoplankton biomass (chlorophyll) and production levels. Chlorophyll ranged from 0.7-1.8 μ g·L¹, with lowest concentrations in May and highest in September. Primary production averaged 35 mg C·m²·d¹ in the second year of fertilization, giving an annual areal value of about 6 g C·m², with over 75% of the production attributable to cells <8 μm in size (nano- and picophytoplankton). The phytoplankton community was dominated by small coccoid cyanobacteria (picoplankton) and microflagellates (Chrysomonads and Cryptomonads), with larger diatoms, greens and blue-green algae either rare or absent. The zooplankton community contained few species and was dominated by the cladoceran Bosmina longispina and the cyclopoid copepod Acanthocyclops vernalis. Both phytoplankton and zooplankton communities showed elevated biomass levels in 1979 and 1980 after aerial fertilization with ammonium nitrate and ammonium phosphate. During treated years, peaks of rotifers in 1979 and Bosmina longispina in 1980 (5800 m⁻³) occurred. Rapid flushing, high turbidity, thermal instability and low biotic production are thought to be the principal factors limiting the production and survival of juvenile sockeye salmon in this ultra-oligotrophic nursery lake.

Key words: Limnology, glacial, turbidity, nutrients, ultra-oligotrophic, sockeye salmon, fast-flushing.

RÉSUMÉ

Stockner, J.G., K.S. Shortreed, E.A. MacIsaac, and B. Nidle. 1992. The limnology of Kitlope Lake: a cold, glacially-turbid sockeye salmon (Oncorhynchus nerka) nursery lake. Can. Tech. Rep. Fish. Aquat. Sci. 1909: 35 p.

Nous avons effectué de 1978 à 1980 des études limnologiques sur le lac Kitlope dans le cadre du programme d'enrichissement des lacs du Programme de mise en valeur des salmonidés. Le lac est fortement influencé par les eaux à turbidité glaciaire de la rivière Tezwa, qui apportent une grande quantité d'eau au lac pendant la saison de croissance (avril à novembre). En conséquence, le lac Kitlope présente une chasse rapids (0,5 an de séjour de l'eau), une turbidité glaciaire (profondeur de compensation moyenne de 4 m, profondeur au disque de Secchi de 3 m), des eaux froides et faiblement stratifiées (profondeur moyenne de l'épilimnion de 6 m), modérément acides (pH moyen de 6,7) et de faible alcalinité (MTD 25 mg L¹). Le lac présente des concentrations très basses de nutriants, le phosphore total se situant à 1-2 μ g·L·1, et le nitrate et l'azote (NO₃-N) de 50-60 μ g·L·1 en mai à <10 μ g·L·1 de juillet à septembre. La forte turbidité, la chasse rapide dans la couche superficielle, la faible stabilité de cette couche, les basses températures et les failbes concentrations de nutriants font que la biomasse phytoplanctonique (chlorophylle) et la production sont basses. La chlorophylle se situait à $0,7-1,8~\mu\mathrm{g}\cdot\mathrm{L}^{-1}$, les concentrations les plus basses étant notées en mai et les plus hautes en septembre. La production primaire était en moyenne de 35 mg C·m⁻²·j⁻¹ la deuxième année de fertilisation, ce qui donnait une valeur annuelle moyenne d'environ 6 g C·m², plus de 75 % de la production étant attribuable aux cellules de <8 μ m de taille (nano- et pico-phytoplancton). La communauté phytoplanctonique était dominée par de petites cyanobactéries coccoides (picoplancton) et par des microflagellés (Chrysomonades et Cryptomonades); les diatomées de plus grande taille, les algues vertes et bleues-vertes étaient soit rares soit absentes. La communauté zooplanctonique comptait un petit nombre d'espèces, et était dominée par le cladocère Bosmina longispina et par le copépode cyclopoide Acanthocyclops vernalis. Les communautés phytoplanctoniques et zooplanctoniques présentaient des niveaux élevés de biomasse en 1979 et 1980 après fertilisation aérienne au nitrate d'ammonium et au phosphate d'ammonium. Pendant les années de traitement, on a noté des pics chez les rotifères en 1979 et chez Bosmina longispina en 1980 (5800 · m⁻³). La chasse rapide, la forte turbidité, l'instabilité thermique et la faible production biotique semblent être les principaux facteurs qui limitent la production et la survie des saumons rouges juvéniles dans ce lac nourricerie ultra-oligotrophe.

Mots clés : limnologie, glaciaire, turbidité, nutriants, ultra-oligotrophe, saumon rouge, chasse rapide.

INTRODUCTION

Lakes that are seasonally turbid with silt from glacial runoff represent a relatively small subset of sockeye salmon (Oncorhynchus nerka) nursery lakes in British Columbia. Stockner (1981; 1987) described three types of sockeye nursery lakes on the British Columbia coast: 1. clear, 2. dystrophic, and 3. glacially-turbid. Clear and dystrophic lakes in British Columbia have been extensively studied (Stockner and Shortreed 1985, 1989; Shortreed and Stockner 1990), but less is known about the limnological characteristics of glacially-turbid systems. Despite the occurrence in most glacial systems of a cold thermal regime, shallow euphotic zone, and low plankton productivity, they often support large stocks of sockeye salmon important to both the commercial and native salmon fisheries (e.g. Owikeno, Meziadin, and Morice lakes).

An experimental nutrient fertilization program conducted on Great Central Lake in the early 1970's resulted in greatly enhanced plankton production, a doubling in growth and survival of juvenile sockeye and a seven-fold increase in adult returns (Parsons et al. 1972; LeBrasseur et al. 1978). Based on these results, a pilot-scale Lake Enrichment Program (LEP) was launched in 1977 by the Department of Fisheries and Oceans' (DFO) Salmonid Enhancement Program (SEP) (Stockner 1977; Stockner and Hyatt 1984). By 1980, 12 sockeye nursery lakes along the B.C. coast and on the Queen Charlotte Islands were being fertilized with inorganic nitrogen and phosphorus nutrients, including Kitlope Lake (Shortreed and Stockner 1981). Kitlope Lake was selected as a candidate for treatment after preliminary surveys showed the lake to be ultra-oligotrophic with very low levels of nitrogen (N) and phosphorus (P), low plankton biomass, and a depressed sockeye escapement (Stockner and Shortreed 1978; Simpson et al. 1981). Some of the earliest DFO escapement records from 1950-1980 suggested that the lake system at one time had supported annual runs of 50,000 adults.

The principal objective of this report was to consolidate and evaluate all of the limnological information on Kitlope Lake, some of which has previously been reported in miscellaneous DFO publications (Costella et al. 1982, 1983a, 1983b; MacIsaac et al. 1981; Nidle et al. 1984; Nidle and Shortreed 1985; Rankin et al. 1984, Rankin and Ashton 1980, Rankin and Radzuil 1986a, 1986b; Shortreed and Stockner 1981; Shortreed et al. 1984; Simpson et al. 1981; Stephens and Stockner 1983; Stockner 1981, 1987; Stockner and Shortreed 1979, 1985). Another objective was to evaluate the responses of the plankton community during the two years of nutrient additions to the lake. The Kitlope drainage basin is one of the largest remaining unlogged basins on the north central British Columbia coast and it has been proposed that the entire area be preserved as a wilderness reserve. This report is also intended to contribute to further studies of both the lake and drainage basin and may aid in the formulation of long-term plans for resource management within the Kitlope drainage basin.

DESCRIPTION OF STUDY LAKE

Kitlope Lake (Lat. 53°07'N and Long. 127°47'W) is located near the head of Gardner Canal on the north coast of British Columbia (Fig. 1). Gardner Canal is a long fjord extending about 30 km into the rugged terrain of the coast mountain range. The lake lies 10 km from salt water at an elevation <30 m. It is a considerable distance from the moderating influence of the Pacific Ocean and the climate has aspects of both the warm mediterranean coast and the colder continental climate of the interior coastal mountains. Farley (1979) placed the lake and its basin in the coastal western hemlock biogeoclimatic zone and estimated annual precipitation at >350 cm. Ice cover probably occurs

for a portion of most winters (in our study, surface temperatures were often <4°C in late April and early May) and a dimictic water circulation pattern is likely typical with monomictic circulation occurring only during milder winters.

Topography around Kitlope Lake is very steep, with mountains up to 1700 m in elevation rising directly from the lakeshore. As a result, the lake has a very narrow littoral zone with the exception of the wide, 3-km long outlet of the lake where depths average 3-5 m (Fig. 2). The lake has a surface area of 11.9 km² and a mean depth of 86 m, with a maximum depth of approximately 140 m in the centre of the lake. The main inflow to the lake is the Tezwa River, whose cold and glacially-turbid waters affect the clarity and thermal structure of Kitlope Lake during the summer months.

Sockeye salmon (Oncorhynchus nerka) spawn in the Tezwa River and along the shores of the lake. Recent escapements have ranged from 2,000-50,000 and averaged about 15,000 (Simpson et al. 1981). Seals that enter the lake in the autumn, together with a large bear population, likely account for most of the adult sockeye mortality in the Kitlope system. Planktivorous juvenile sockeye utilize the lake as a nursery area for 1-2 yr prior to seaward migration, but their growth rates are very low relative to other British Columbia sockeye stocks (Simpson et al. 1981). For this reason, Kitlope Lake was treated with nitrogen and phosphorus nutrients for six years (1979-83 and 1985) in an attempt to improve the abundance of plankton food and the growth rates of rearing juvenile sockeye. During the two treated years covered by this report, the southern half of the lake (Fig. 3) received 11.3 tonnes of ammonium nitrate (34-0-0) and 1.7 tonnes ammonium phosphate (11-55-0) fertilizers annually, divided into 18 weekly applications from May 7 to September 3, 1979 and June 1 to September 29, 1980 (Stephens and Stockner 1983). Fertilizers were applied as aqueous solutions by a DC6 water bomber.

METHODS

Float-equipped aircraft were used for the monthly sampling trips at the mid-lake station and inflatable boats were used during the detailed week-long surveys of the lake (Fig. 3).

Temperature profiles were obtained with a Montedoro-Whitney probe (Model TC-5C) or a bathythermograph, using surface temperature from a bucket thermometer for calibration. A Li-Cor light meter (Model 185A) with an underwater quantum sensor (400-700 nm, Model Li-192S) was used to determine compensation depths (1% of surface intensity) and extinction coefficients ($k_{\rm e}$). Water transparency was measured with a 22-cm white Secchi disk.

Van Dorn bottles rinsed with 95% ethanol were used for all water sampling. Pre-cleaned, screw-capped test tubes were rinsed and filled with sample water in the field for total phosphorus analyses. Water samples for the remaining analyses were collected in polyethylene bottles, stored in coolers, and filtered within 2-4 h. Pre-ashed (460°C for 4 h), 47-mm Whatman GF/F filters were washed with deionized distilled water (DDW) and sample water, and used to filter water for dissolved nutrient analyses. Nitrate and dissolved organic nitrogen samples were filtered and collected in borosilicate glass bottles, while ammonium, soluble reactive silicon and total dissolved solids samples were filtered into polyethylene bottles. A screw-capped test tube was filled with filtered sample water for total dissolved phosphorus (TDP) analysis. Samples were stored at 4°C in the dark. A 1-L water sample was filtered onto an ashed and washed 47-mm diameter Whatman GF/F filter and stored frozen for particulate carbon and nitrogen analysis on a Perkin-Elmer Model 240XA

elemental analyzer. All chemical analyses were carried out at the Pacific Biological Station in Nanaimo using the methods of Stephens and Brandstaetter (1983) and Stainton et al. (1977). Phosphorus data collected prior to 1980 are not reported because the modified seawater technique that was used (ascorbic acid reduction) gave erroneously high phosphorus values compared to the stannous chloride reduction technique adopted in 1980.

A 500-mL water sample was filtered onto a 47-mm diameter, 0.8-µm pore-size Millipore AA filter and a few drops of a saturated MgCO₃ suspension were added. The filter was desiccated overnight, and stored frozen for total chlorophyll analysis using a Turner Model 111 fluorometer (Strickland and Parsons 1972). Chlorophyll samples, size-fractionated with filters or Nitex screens, were processed in the same manner.

A Cole-Parmer Digi-Sense pH meter (Model 5986-10) was used in the field to determine the pH and total alkalinity of water samples, usually collected from depths of 2 and 7.5 m, using the standard potentiometric method (APHA 1975). Dissolved inorganic carbon (DIC) was calculated indirectly from pH, temperature, total dissolved solids, and bicarbonate alkalinity data. During the latter portion of the 1980 season, DIC analyses were also conducted in the field using the gas chromatography method of Stainton et al. (1977). Samples were collected in 50-cc plastic syringes, acidified with 0.5 mL of 0.5 N $_{\rm H_2SO_4}$, extracted with helium on ice for 10 min, and injected into a Carle gas chromatograph (Model 211M).

Vertical profiles of primary production and heterotrophic activity were measured using 125-mL light and dark borosilicate bottles incubated in situ as described by Costella et al. (1982) and MacIsaac et al. (1981). Methods used for primary production measurements in 1978 and 1979 (e.g. filters, scintillation methods) were significantly different from those used in 1980 and the data are not directly comparable among years. Only the methods and daily primary production estimates for 1980 are reported here, although some photosynthetic rate profiles from 1978 are used. Incubation bottles were inoculated with tracer levels of a sterile dual-labelled radioisotope stock containing 14C-bicarbonate and 3H-glucose and incubated at their respective depths for 1.5-2 h between 0900 and 1200 h. After incubation, 50-mL aliquots were filtered onto $0.2-\mu m$ Nuclepore polycarbonate filters and transferred to scintillation vials containing 14 mL of Aquasol-2 and 1 mL of phenethylamine as a scintillation cocktail. Where fractionated primary production was measured, additional aliquots were also filtered onto 8.0- μ m Nuclepore filters or 54- μm Nitex screens. Time-zero blanks were used to correct the glucose uptake data. Vials were counted with a Packard Tri-Carb 460C Liquid Scintillation Counter and corrected for quenching using the external standard method. Strickland's (1960) equation was used to convert carbon uptake to mg C·m³·h¹ and hourly volumetric production was converted to daily areal production (mg C·m⁻²·d⁻¹) using light data collected with a Li-Cor printing integrator (Model 550) and a Model 190S quantum sensor. Glucose turnover time was calculated and used as a measure of heterotrophic activity as described by MacIsaac et al. (1981).

Water samples were collected from a depth of 1 m in August, September, and October of 1979 in 1-L polyethylene bottles, stored on ice in the dark, and analyzed within 4-5 d using a Model TA Coulter Counter to determine the abundance and size of suspended particles (glacial silt, organic detritus, and plankton) in the surface waters. The Coulter Counter was used with both $100-\mu \mathrm{m}$ and $400-\mu \mathrm{m}$ apertures to determine particle abundance over the size range of 3-140 $\mu \mathrm{m}$. The electrolyte concentration of each sample was raised to 2% NaCl by dilution with $0.45-\mu \mathrm{m}$ filtered saline solution before analysis.

Bacteria were enumerated by filtering 5-mL water samples in the field onto 25-mm diameter, 0.2- μ m pore-size Nuclepore polycarbonate filters (Irgalan stained). Filters were air-dried at room temperature and stored for

transport. Bacteria numbers were enumerated using the acridine orange direct count method as described by MacIsaac et al. (1981). Eight random fields were counted on each filter using a Zeiss epifluorescence microscope and blue-band (450-490) excitation.

Phototrophic picoplankton (cyanobacteria and eukaryotic algae) were enumerated using the epifluorescence method described by MacIsaac and Stockner (1985). Fifteen-millilitre samples were filtered under subdued light onto stained Nuclepore filters as described for the bacteria method and air-dried and stored in the dark at room temperature. For enumeration, cells on the filter were rehydrated for 3-5 min with filtered DDW and filters were examined with a Zeiss epifluorescence microscope at 1250X oil immersion using wide-band excitation (397-560 nm). At least 30 random fields were counted. Phototrophic picoplankton were identified as cyanobacteria or eukaryotic algae and scored into size categories.

Water samples fixed with 1 mL of Lugol's iodine solution were used for identification and enumeration of phytoplankton >3 μ m in diameter. A subsample was settled overnight in a settling chamber of 7-, 12- or 27-mL volume and transects at 187.5X and 750X magnification were counted using a wild M40 inverted microscope equipped with phase contrast optics. Cells were identified to genus or species and assigned to size classes.

Methods used for zooplankton sampling and enumeration are described in detail by Rankin et al. (1984) and Rankin and Radziul (1986a, 1986b). Zooplankton were sampled by 0-25 m vertical hauls with a 100-μm mesh net (0.25-m² mouth area, 0.5 m·s¹ average haul speed). Filtration efficiency of the net was assumed to be 100%. Zooplankton were preserved in a 4% formaldehyde-sucrose solution (Haney and Hall 1973). One half of the sample was filtered onto a pre-dried and weighed Millipore HA filter (0.45-μm pore size) and dried at 90 C for 24 h to determine zooplankton dry weight. An aliquot of the remaining sample (usually 1/4) was diluted to 300 mL and 1 to 4 subsamples were enumerated. Zooplankton were identified to at least the genus level and 25-50 individuals of each of the major taxa were sized with an eyepiece micrometer or an electronic caliper system (Sprules et al. 1981). Only large rotifers or those with hard, spined exoskeletons are effectively collected by the zooplankton net, so the abundance of small soft-bodied rotifers is underestimated.

Daily flow data from the gauged Kemano River watershed (53°34'N, 127°56'W) was used to estimate daily runoff for the Kitlope Lake watershed. Kemano River daily flows for 1978-1980 were multiplied by the ratio of the areas of the two watersheds (1.5). Water residence time was calculated by dividing the volume of the lake by the mean total annual runoff estimated for each of the three study years. Daily surface layer (0-10 m) flushing was calculated by dividing the volume of the surface layer by the estimated daily runoff. Although they share similar climatic and seasonal precipitation patterns because of their relatively close proximity, the Kemano River watershed has a slightly higher elevational distribution than the Kitlope watershed (26% versus 9% of watershed area >1500 m). Thus annual areal runoffs are similar but the Kemano seasonal hydrograph is skewed, compared to the actual Kitlope hydrograph, towards higher snow and glacier melt runoff in mid-summer and lower fall runoff due to precipitation accumulating as snow at the higher elevations.

RESULTS AND DISCUSSION

HYDROLOGY AND PHYSICAL LIMNOLOGY

The large drainage basin area (872 km²) combined with the high precipitation of the coast mountains produces an exceptionally high annual runoff to Kitlope Lake. The net result is a fast flushing lake with a decidely riverine circulation pattern. Estimated total annual runoff ranged from 1.32-1.42·10° m³ during 1978-1980, yielding an average water residence time for the lake of 0.49 yr. Most of the runoff occurs from April through November with snow and glacier meltwater maintaining a high average runoff through the summer months. However, the seasonal hydrographs also exhibit numerous random spikes of high daily runoff caused by Pacific storms that frequent the coast mountains throughout the year. The outlet of Kitlope Lake is unusually wide, long, and shallow and outflow from the lake is entirely surface layer (0-10 m) water (Fig. 2). The result is very high daily surface layer flushing rates that ranged from 15% to >250% of the surface layer volume through the growing season (Fig. 4).

The high inflows from the Tezwa River also generate highly dynamic currents in the surface waters that affect all physical and biological characteristics of the lake. During weeklong studies, drogues placed to track surface water movements exhibited complex trajectories within the lake, sometimes circulating counterclockwise within a large river-driven surface water gyre but often swept up in the outflow of the lake. Surface temperatures also showed considerable spatial variation around the lake, differing on a given day by 1.5°C from east to west at several cross-lake transect locations. Coriolis effects on riverine circulation patterns in lakes have been well documented (Pharo and Carmack 1979) and are likely responsible for the large west-to-east variations in surface temperatures observed in Kitlope Lake.

Throughout our study Kitlope Lake exhibited weak thermal stratification (Fig. 5). The lake was always isothermal (\approx 4°C) in early May, with surface warming first detected by late May or early June. The lake remained weakly stratified with the epilimnion slowly warming through September. On a number of occasions in summer, a transitional thermocline or thin (<2 m) surface layer of warm (up to 15°C) water was observed, generally resulting from protracted periods of clear skies with little wind. Thermal stratification was strongest in August but the high volume of inflow from the cold, turbid Tezwa River and fast flushing of the surface waters maintained generally weak stratification.

Kitlope Lake exhibited large spatial and seasonal variations in water clarity with marked fluctuations in both Secchi transparency and compensation depths in response to changes in turbidity, circulation, and flushing conditions in the surface waters. Secchi depths ranged from 1-6 m, with highest values (4-6 m) always recorded in May and June (Table 1). This was followed by a decrease during the summer months (due to the increased flow and glacial turbidity of the Tezwa River), with lowest values (1-2 m) during late summer and early fall. Compensation depths (range: 3.7-11.4 m) also varied considerably in each year of the study.

WATER AND NUTRIENT CHEMISTRY

Kitlope Lake was mildly acidic, with pH values of 5.5-6.7 and total alkalinities of 0.7-2.3 mg $CaCO^3 \cdot L^{-1}$ (Table 1). Dissolved inorganic carbon concentrations were very low (range: 0.5-2.6 mg $C \cdot L^{-1}$), as were total dissolved solids (TDS) (range: 19-29 mg·L⁻¹). Concentrations of soluble reactive silicon (SRS) were <1 mg·L⁻¹ throughout the study, and ranged from 0.33-0.93 mg·L⁻¹

(1978 data are anomalously low). At no time did SRS concentrations reach levels thought to be limiting to diatom growth (Lund 1950).

The phosphorus and nitrogen nutrient data collected over the 3 yr of the study show variations that can not be attributed solely to the fertilization program. In 1980, the only year of reliable phosphorus data, total phosphorus (TP) concentrations at spring overturn were 1-2 μ g·L⁻¹. Total phosphorus remained at these levels until late summer when increases in the surface waters up to 8 μ g·L⁻¹ were detected. Total dissolved phosphorus (TDP) concentrations were almost always below the detection limit of 1 μ g·L¹. Although increased phosphorus levels in late summer would be expected after many weeks of fertilizer additions, the increased phosphorus levels also coincided with reduced water clarity from increased glacial turbidity in the Tezwa River. Analytical interference from turbidity (Koenings et al. 1987) and digestive extraction of mineral phosphorus from glacial silt could account for the higher phosphorus levels measured. Nitrate concentrations varied seasonally from 50-66 μ g N·L⁻¹ at spring overturn to about 5-10 μ g N·L⁻¹ through the summer, increasing to values of 15-25 μg N·L-1 by late October. Although the weekly applications of nitrate-based fertilizers could have short-term localized effects, most of the variations in nitrate levels can be attributed to seasonal shifts in the balance between flushing and nitrate replenishment by hydrologic processes and uptake by phytoplankton.

CHLOROPHYLL

Marked increases in chlorophyll levels during fertilization of Kitlope Lake were not apparent although levels were generally elevated through the summer and fall, particularly during the second year of fertilization. Mean epilimnetic chlorophyll concentrations ranged from 0.03-1.81 $\mu g \cdot L^{-1}$ with lowest (<0.20 $\mu g \cdot L^{-1}$) concentrations in May and early June (Table 2). In the unfertilized year (1978), chlorophyll levels gradually increased from June to a September peak, while in the two fertilized years, chlorophyll concentrations increased to seasonal maxima by early July and remained above 0.5 $\mu g \cdot L^{-1}$ for the rest of the season. Highest chlorophyll levels up to 1.81 $\mu g \cdot L^{-1}$ were recorded in the second year of fertilization.

On 3 occasions we sampled the lake for 5-6 consecutive days and chlorophyll concentrations fluctuated considerably at these times (Costella et al. 1982). In addition to the temporal heterogeneity, considerable spatial variation was also apparent. On July 28, 1980 we sampled 10 locations around Kitlope Lake and found surface chlorophyll concentrations ranging from 0.22-1.06 $\mu g \cdot L^{-1}$, with highest concentrations occurring on the east side of the lake. We also found considerable vertical heterogeneity, with subsurface chlorophyll maxima being frequently detected. Although we sampled sufficient depths to examine vertical heterogeneity on only two occasions (at all other times only 1, 3 and 5 m were sampled), on numerous occasions concentrations at 1 m were <0.5 $\mu g \cdot L^{-1}$, while 5 m concentrations were 3-9x higher. Detailed vertical profiles collected in September, 1979 and in July, 1980 provide an example of this persistent subsurface maximum (Fig. 6).

PHOTOSYNTHETIC RATES

Daily photosynthetic rates (primary production) in 1980 peaked in June and July at 60-90 mg C·m²·d¹, declining to less than half by late summer and early fall as surface flushing and glacial turbidity increased through the growing season (Table 2). As with all measured parameters, photosynthetic rates were highly variable, exhibiting up to a 3-fold change on consecutive days (Costella et al. 1982). Vertical profiles of photosynthetic rates show the effects on phytoplankton growth of decreasing water clarity and increasing

thermal stability (Fig. 7). In July rates were low, with significant photosynthesis extending down to 10 m (typical of clear, oligotrophic lakes) while in August individual photosythetic rates were higher with a distinct near-surface peak. Primary production results using size fractionation procedures showed that both in 1979 and 1980, about 75% of total carbon assimilation occurred in the <8 $\mu \rm m$ fraction with little seasonal variation in the proportions. The integrated annual production estimate for 1980 was 6 g C·m², considerably less than the 15-16 g C·m² estimated for Long and Morice lakes, two other lakes fertilized in 1980 (Costella et al. 1982).

PHYTOPLANKTON

The phytoplankton community of Kitlope Lake was indicative of highly oligotrophic conditions exhibiting low biomass, low numbers, and low species diversity. The picophytoplankton Synechococcus spp. (both unicellular and colonial forms) was most abundant, ranging from <1000·mL¹ to 5200·mL¹ (picophytoplankton were enumerated only from July to September of 1980). A coccoid eucaryotic picophytoplankton occasionally ranged up to 2000·mL¹. In a number of other oligotrophic British Columbia lakes, picophytoplankton numbers generally averaged >20,000·mL¹ (Stockner and Shortreed; 1989, 1991, 1992). We attribute the extremely low picoplankton numbers in Kitlope Lake relative to other highly oligotrophic lakes to its very high flushing rate, cold temperature regime, and weak water column stability.

Various flagellates such as Chrysochromulina sp., Ochromonas sp., and Mallomonas sp. were the most common nanophytoplankton, but numbers never exceeded 400°mL¹. Diatoms comprised a very minor component of the phytoplankton community with Cyclotella spp., Achnanthes minutissima and Navicula spp. occurring most frequently. Except for Cyclotella spp., most diatoms found in Kitlope Lake were periphytic in origin, further indicating the strong influence of the Tezwa River on the plankton community. Microphytoplankton were present in very low numbers, with the most common being Dinobryon spp..

BACTERIA

The low abundance and activity of heterotrophic bacteria in Kitlope Lake reflect the cold temperatures, low organic productivity, and active flushing of its surface waters (MacIsaac et al. 1981). Bacteria densities were only monitored during the 1979 and 1980 fertilized years but were usually low (<8.0X10⁵·mL¹) (Table 2). The glacial silt was not readily colonized by bacteria since less than 1% of bacteria appeared to be attached to particles. There were no strong seasonal patterns in abundance although highest levels were recorded in September of the second year of fertilization, coinciding with the highest levels of glacial turbidity, particulate organic carbon, and zooplankton biomass recorded in the lake. Glucose turnover times were usually >50 h throughout the season, with fastest turnover times associated with the warmer surface waters of late summer and fall.

PARTICULATES

Coulter Counter analyses found high concentrations of glacial silt particles in the 4-128 μm equivalent spherical diameter (ESD) size range in the surface waters in late summer and fall. Particles <10 μm ESD dominated numerically, however particles with 6-20 μm ESDs dominated the total particle volume (Fig. 8). Based on microscope counts, phytoplankton in the 4-128 μm size range were an insignificant component of total particle numbers and volume, contributing < 1% in any size-class. Although the quantity of suspended silt varied from August to October, overall particle size

distributions were similar.

Organic particulates in Kitlope Lake are diluted by high allochthonous loadings of inorganic glacial silt particles. For suspension feeding zooplankton, this can constrain their ability to feed on available concentrations of organic material, affecting both their productivity and the species composition of the zooplankton community (Koenings et al. 1990). Particulate organic carbon (PC) concentrations in 1980 were generally low, ranging from 158-400 $\mu \rm g~C \cdot L^1$ (Table 2). Particulate organic nitrogen levels were similarly low, ranging from 23-45 $\mu \rm g~N \cdot L^1$ (data not reported). PC concentrations did not track changes in chlorophyll levels and were highest in September when glacial turbidity and suspended silt levels were also highest. Using a 50:1 carbon to chlorophyll conversion factor, phytoplankton contributed up to 91 $\mu \rm g~C \cdot L^1$ and ranged from 17-46% of the total PC from June through October. Bacteria and allochthonous organic matter from the watershed contributed the bulk of the PC in Kitlope Lake.

ZOOPLANKTON

The zooplankton community of Kitlope Lake was unusual relative to those in other coastal sockeye nursery lakes. First, the community was relatively simple, being dominated by a small, herbivorous cladoceran (Bosmina longispina), an omnivorous cyclopoid copepod (Acanthocyclops vernalis), and very low numbers of rotifers (Rankin et al. 1984, Rankin and Radzuil 1986a, 1986b). Second, average crustacean zooplankton abundance in Kitlope Lake was among the lowest ever recorded for a sockeye nursery lake in British Columbia or Alaska (Rankin and Ashton 1980) (Table 3). Only Owikeno lake, another cold, glacially-turbid lake on the central British Columbia coast had equally low abundances of crustacean zooplankton. In the interior of British Columbia, Meziadin and Morice lakes also receive loadings of glacial silt during the summer months. However, their thermal structures, phytoplankton productivities, and zooplankton abundances more closely resemble clear water or humic-stained sockeye lakes. Glacially-turbid lakes encompass a wide range of plankton productivities and abundances determined by conditions other than the presence of suspended glacial silt.

Zooplankton abundances were generally low throughout the 3 yr of sampling with little indication of strong seasonal patterns, although two marked peaks in abundance occurred during the 2 fertilized years (Fig. 8). B. longispina abundances were always <500·m³ during 1978 and through the first year of fertilization in 1979. However, a high of 5800·m³ was recorded in September 1980, the second year of fertilization. Similarly, rotifer abundances were usually <400·m³ through the three years of study with the exception of a peak of 1780·m³ in June of 1979, shortly after the start of weekly fertilizer additions. In contrast, cyclopoid copepod abundance (largely A. vernalis) was always less then 500·m³ and there were no apparent seasonal patterns or increases during either of the fertilized years.

The extremely low numbers and lack of strong seasonal patterns in abundance common to warm-water lakes suggest that the combination of rapid flushing, cold temperatures, glacial silt, and low levels of organic particulates severely limit the productivity of the zooplankton community in Kitlope Lake. Zooplankton species in Kitlope must be opportunistic and able to exploit ephemeral periods of thermal stratification, reduced flushing, and increased phytoplankton food resources. They must also be able to feed on low densities of food particles diluted by abundant inorganic suspended glacial silt particles of similar sizes (Koenings et al. 1990). Of all cladoceran species, B. longispina has the ability to feed selectively and has one of the highest reproductive potentials of any crustacean zooplankton. It is not surprising that B. longispina was the only crustacean zooplankton showing a large, albeit

transient increase during the second year of fertilization.

FISH

Apart from two surveys conducted in June and September of 1978 (Simpson et al. 1981), little is known of the fish community of Kitlope Lake. Simpson et al. (1981) found that the predominant planktivores were juvenile sockeye, which generally occupied the 0-10 m surface layer of the lake at a relatively low average density of 250-275·ha⁻¹. Mean weight in mid-September, 1978 was slightly more than 1 g, and their mean length was 47 mm. Estimated densities of the pelagic stickleback (Gasterosteus aculeatus) were very low (<50·ha⁻¹), and of exceptionally small size. In 2 overnight (12 h) shore gillnet sets, only a single piscivorous dolly varden char (Salvelinus malma) (22 cm) was caught, suggesting very low predator densities in the lake. Between the June and September 1978 sampling dates juvenile sockeye mortality was low (Simpson et al. 1981) which is likely related to the reported low piscivore density. The 1 g weight for juvenile sockeye in September reported by Simpson et al. (1981) are among the lowest recorded for a B.C. coastal lake (Hyatt & Stockner 1985). Rankin and Ashton (1980) report that the fertilization of Kitlope Lake in 1979 led to a 60% increase in the weight of juvenile sockeye, but apart from this observation we are aware of no other data that documents the effects of fertilization on the juvenile fish populations.

Accounts of adult sockeye escapements to the Kitlope system (from aboriginal users and early fisheries officer records) suggest that historical escapements may have exceeded $50,000 \cdot \text{yr}^{-1}$ on some years (L. Bodie, DFO, Prince Rupert, B.C.). Current escapements are well below these early counts, now estimated at between $10-20,000 \cdot \text{yr}^{-1}$. Estimates of adult sockeye escapements for the 1979 and 1980 "treated" brood years ranged from 9-20,000 for return years 1982-85, values that are well within the normal range for sockeye escapements to the lake during the 1980-89 period.

SUMMARY AND CONCLUSIONS

Three predominant features of Kitlope Lake are its rapid hydrologic flushing rate, its cold temperature and weak thermal stratification, and the presence of turbidity gradients imparted by the glacially-turbid Tezwa River. Flushing and turbidity effects are most pronounced during summer when snowpack and glacial melt are highest and in early fall when the lake is warmest and most strongly stratified. Highest turbidity is associated with the river plume as it enters the lake. Because the glacial particles are small $(< 20 \mu m)$ and settle slowly, they impart a variable colour pattern to the entire lake surface. Increased light reflectivity (back-scatter) and reduced light penetration (attenuation) by glacial turbidity cause the light climate and temperature structure of Kitlope Lake and other glacially turbid lakes to be quite different from other coastal or interior B.C. lakes. These markedly affect the lake's biological production by reducing the depth and volume of the euphotic zone, and by producing cooler epilimnetic temperatures and weaker, less stable stratification. As a result, Kitlope's plankton communities are characterized by extremely low biomass, low production rates, and low species diversity.

Hydrologic processes, driven by high inflows from the Tezwa River, greatly affect the plankton community of Kitlope Lake, diluting and flushing the weakly stratified epilimnion. They also generate large spatial and temporal variations in all physical and biological parameters by maintaining dynamic circulation patterns in the surface waters. The degree of heterogeneity makes

obtaining representative samples and assessing effects of fertilization on plankton growth and abundance highly problematic. However, seasonal chlorophyll levels were higher during the two fertilized years relative to the unfertilized 1978 year (1978). Changes in the phytoplankton community were most apparent among smaller size classes (nano-flagellates and cyanobacteria). While the zooplankton populations also showed peaks in abundance during years of fertilization, notably rotifer populations in 1979 and the cladoceran Bosmina in 1980, their response was generally weaker and less pronounced than the phytoplankton.

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Date	Surface temp. (°C)	Secchi depth (m)	Compensation depth (m)	Нď	Total alk. (mg CaCO3·L ⁻¹)	Silicon (mg Si·L ⁻¹)	Nitrate (µg N·L ⁻¹)	Total P (µg·L ⁻¹⁾
1978								
May 9	3.8	4.0	11.4	6.3	2.3	ı	62.1	t .
Jun 9	9.5	3.5	7.7	6.2	1.4	ı	35.7	ı
Jul 20	14.4	3.0	9.5	6.4	1.1	ı	7.0	,
Aug 10	12.0	1.5	4.1	6.7	2.2	ı	23.3	ı
Sep 13	12.2	2.5	7.0	5.8	1.3	ı	8.7	1
Oct 17	11.1	2.5	0.9	5.9	1.3	ı	20.7	ı
1979								
May 4	4.3	3.0	6.4	5.7	7.0	0.52	52.0	ı
Jun 6	7.1	2.6	7.6	5.6	1.1	0.71	41.3	ı
Jul 13	8.8	2.5	8.2	5.6	1.2	0.53	8.3	1
Aug 8	15.5	2.3	8.3	6.5	1.6	0.48	5.0	1
Sep 4	12.7	2.1	8.0	6.4	1.5	0.43	5.2	ı
Oct 12	12.5	2.5	5.0	6.5	1.5	0.75	15.7	1
1980								
Apr 30	3.4	5.5	8.2	6.2	2.2	0.93	66.0	1.7
Мау 30	7.8	6.0	8.5	6.1	1.8	0.82	47.7	1.7
Jun 28	10.7	4.5	10.0	6.2	1.7	0.49	9.7	1.3
Jul 29	11.8	2.9	6.9	6.2	1.5	0.36	10.2	2.2
Aug 19	12.7	2.5	8.9	6.4	1.2	09.0	7.7	7.7
Sep 23	10.3	1.0	3.7	5.9	1.5	0.67	25.7	8.3
Oct 25	8.0	1.5	4.5	5.9	1.4	0.68	24.3	5.0

Table 2.	Variation in	in mean epilimnetic biological	c biological va	variables from Ki	from Kitlope Lake.	
		Photosyn. rate (mg C·m²·d¹)	Particulate Organic Carbon (μg C·L· ¹)	Bacteria $(10^6 \mathrm{mL}^4)$	Glucose turnover time (hr)	Zooplankton biomass (mg·m³)
May 9	0.03	i	ı	1	,	3.2
o unc	0.16	t	ı	1	ı	1.7
	0.46	1	ı	ı	ı	2.8
Aug 10	0.24	ı	1	ı	ı	1.6
Sep 13	1.60	1	•	ı	•	2.4
Oct 17	0.81	ŧ	I	1	1	1.1
1979					•	•
May 4	0.09	t	1	0.70	201	4.4
Jun 6	0.13	ı	1	0.50	138	2.0
Jul 13	1.13	ı	ı	0.64	296	2.4
Aug 8	0.83	ı	1	09.0	117	3.0
Sep 4	0.88	1	ı	0.74	83	S. S.
oct 12	0.55	ı	1	0.50	193	1.3
1980						1
Apr 30	0.12	ı	213	0.49	233	2.2
May 30	60.0	7	158	99.0	83	1.8
Jun 28	1.81	68	197	0.47	88	2.2
Jul 29	1.60	62	238	0.55	177	2.9
Aug 19	1.05	26	190	0.17	122	5.7
Sep 23	1.49	27	400	1.13	62	28.9
Oct 25	06.0	4	270	0.66	102	3.5

TABLE 3. Comparison of May-October averages of crustacean zooplankton abundance ($10^3 \cdot m^3$, geometric mean) and epilimnetic chlorophyll levels ($\mu g \cdot L^{-1}$) for glacial, clear, and humic-stained lakes in British Columbia (unpubl. data) and in Alaska (Koenings et al. 1990).

		Zooplankton Abundance	*
Lake	Year(s)	(10 ³ ·m ⁻³)	Chlorophyll (µg·L ⁻¹)
BRITISH COLUMBIA			
GLACIAL			
Kitlope	1978	6.3	0.56
	1979	3.4	0.60
	1980	10.2	1.10
Owikeno Stn.1	1978	9.4	1.89
Stn.2	1978	4.9	1.07
Stn.3	1978	5.2	0.86
Morice	1978	246.6	0.79
Meziadin	1978	491.0	1.39
STAINED			
Lowe	1978	73.5	1.22
Long	1978	99.1	2.22
CLEAR			
Great Central	1978	379.7	1.03
Nimpkish	1978	55.9	0.80
<u>ALASKA</u>			
Glacial	1979-1987	71.6	0.45
Clear	1979-1987	290.4	1.35
Stained	1979-1987	159.1	1.53

FIGURES

Fig. 1. Location of Kitlope Lake, British Columbia.



Fig. 2. Bathymetric map of Kitlope Lake.

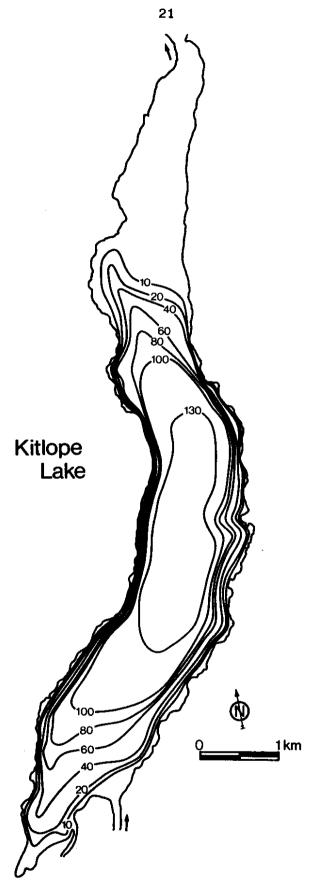


Fig. 3. Sampling station and fertilized zone of Kitlope Lake.

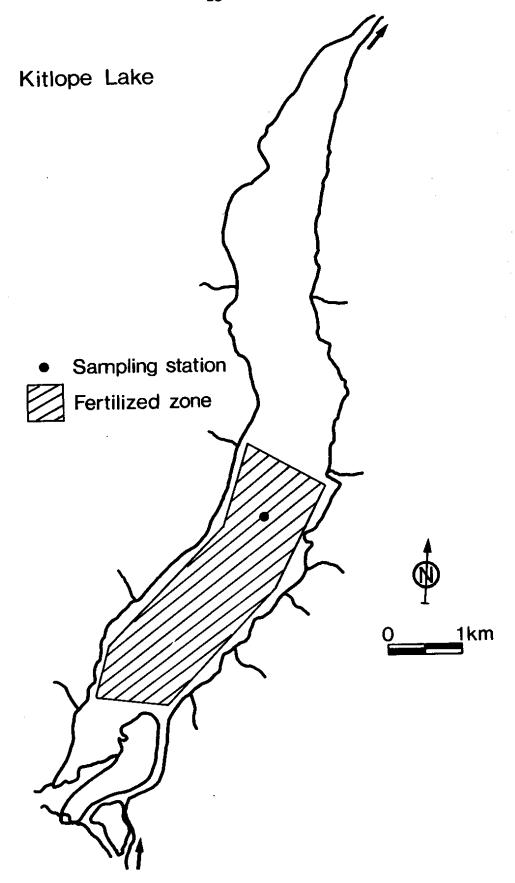


Fig. 4. Estimated daily flushing rates for 0-10 m surface layer of Kitlope Lake from 1978-1980.

% Daily Flushing of 0 - 10 m Surface Layer of Kitlope Lake

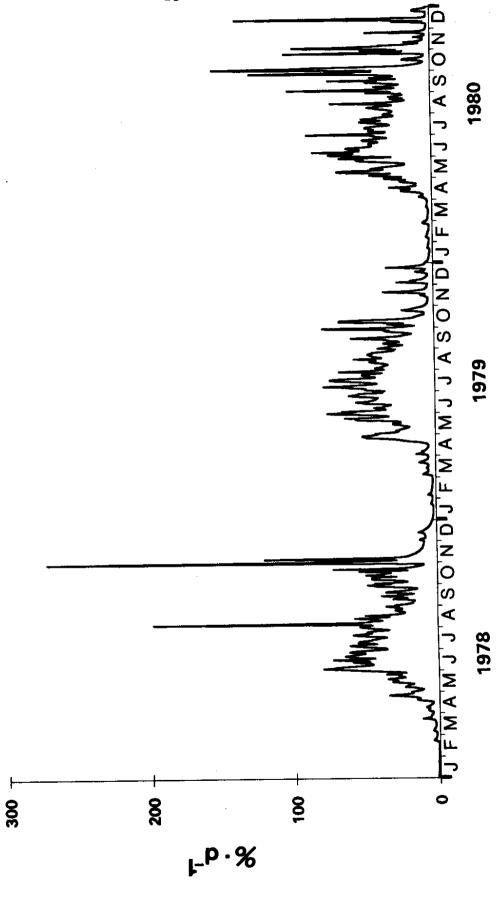


Fig. 5. Temperature isotherm plot for Kitlope Lake in 1978.

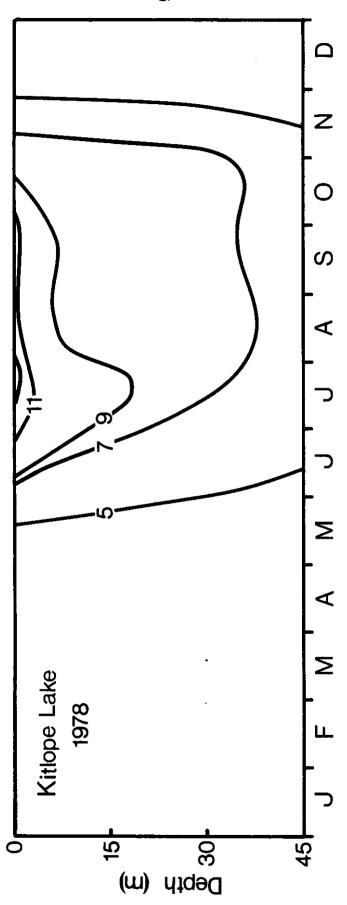


Fig. 6. Vertical profiles of chlorophyll from Station 1, September 3, 1979 and July 29, 1980.

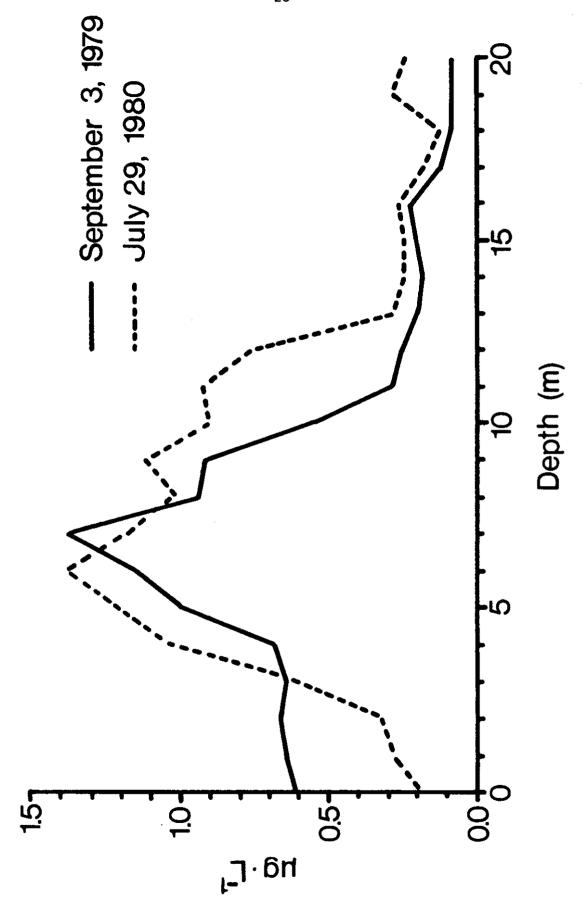


Fig. 7. Vertical profiles of primary production on July 20 and on August 10, 1978.

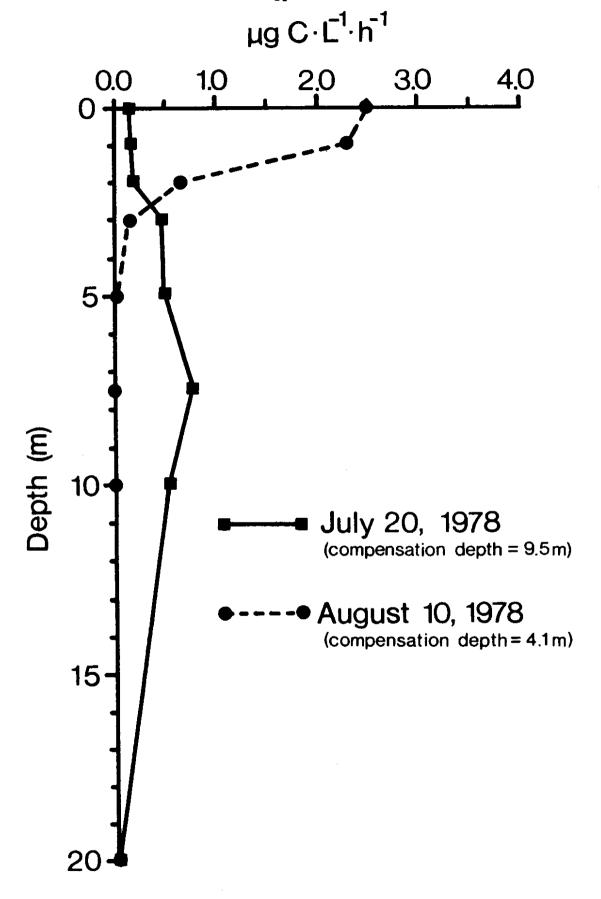


Fig. 8. Particle size spectra for the surface waters of Kitlope Lake in late summer and fall of 1979. Total particle number and volume distributions were measured with a Coulter Counter and phytoplankton volumes were estimated from microscope counts. Counts for particles <6 μm were only available for August.

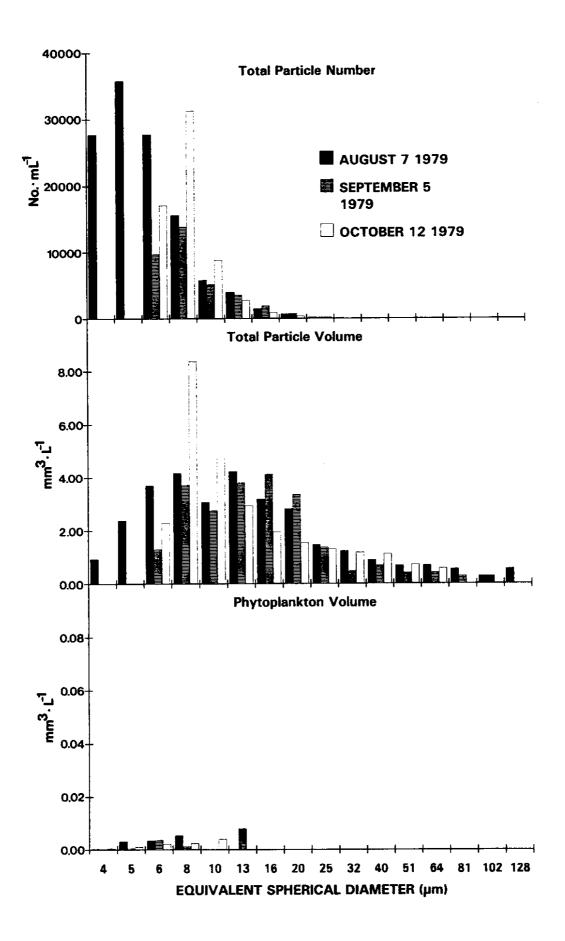
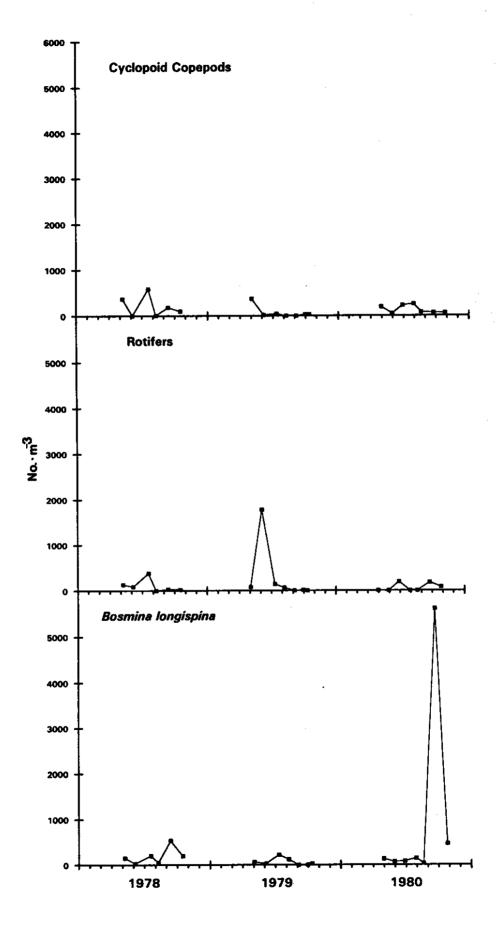


Fig. 9. Zooplankton abundances (no.·m³) determined from 0-25 m vertical hauls with a 100- μ m net.



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