Preliminary Categorization of the Productivity of 37 Coastal and Skeena River System Lakes in British Columbia

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PRELIMINARY CATEGORIZATION OF THE PRODUCTIVITY OF 37 COASTAL AND SKEENA RIVER SYSTEM LAKES IN BRITISH COLUMBIA

by

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We carried out limnological surveys of 37 lakes on British Columbia's north coast and Skeena River system. Limnological data collected on these surveys enabled us to make preliminary estimates of the lakes' trophic status and productive capacity for juvenile sockeye. Of the 37 lakes, one (Moore) was meromictic and one other (Tsimtack) was more properly termed a tidal lagoon than a lake. Thermal structure of the lakes ranged from warm monomictic (18 lakes) to dimictic (13 lakes) to cold polymictic (6 lakes). Euphotic zone depths ranging from 0.4-23 m. Total phosphorus concentrations ranged from 1.4-16.5 µg/L, indicating a wide range in trophic status in the surveyed lakes. Phytoplankton photosynthetic rates (PR) ranged from the lowest (8 mg $C \cdot m^{-2} \cdot d^{-1}$) to among the highest (387 mg $C \cdot m^{-2} \cdot d^{-1}$) yet recorded for a B.C. sockeye nursery lake. We categorized the lakes based on water type (glacial, organically stained, clear) and found significant differences in physical, chemical, and biological variables between the three lake types. In most cases, stained lakes had lower values for chemical variables and had less abundant plankton communities than clear lakes. Preliminary estimates of productive capacity indicate that sockeye escapements (normalized to lake area) needed to maximize sockeye smolt biomass ranged from 2-89 spawners/ha.

RÉSUMÉ

Shortreed, K.S., Hume, J.M.B., and Malange, K. 2007. Preliminary categorization of the productivity of 37 coastal and Skeena River system lakes in British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 2718: 91 p.

Nous avons effectué des études limnologiques dans 37 lacs de la côte Nord de la Colombie-Britannique et dans le réseau hydrographique de la rivière Skeena. Les données limnologiques recueillies lors de ces études nous ont permis d'effectuer des estimations préliminaires de l'état trophique et de la capacité de production de saumons rouges juvéniles des lacs. Parmi les 37 lacs étudiés, un était méromictique (Moore) et un autre a été classé parmi les lagunes à marée plutôt que parmi les lacs (Tsimtack). Sur le plan de la structure thermique, 18 lacs étudiés étaient monomictiques chauds, 13 étaient dimictiques et 6 étaient polymictiques froids. La profondeur de la zone euphotique a varié de 0,4 à 23 m. La concentration de phosphore total a varié de 1,4 à 16,5 µg/l, ce qui constitue un indice d'une gamme étendue d'états trophiques parmi les lacs étudiés. Le rendement photosynthétique du phytoplancton a varié d'une valeur minimale record (8 mg C/m^2 par jour) à des valeurs parmi les plus élevées jamais enregistrées (387 mg C/m^2 par jour) pour une alevinière du saumon rouge en C.-B. Nous avons classé les lacs dans diverses catégories en fonction du type d'eau (glaciaire, à charge élevée en matière organique et claire), et nous avons constaté des différences importantes sur le plan des paramètres physiques, chimiques et biologiques entre les trois types de lacs. Dans la plupart des cas, les paramètres chimiques étaient moins élevés dans les lacs à charge élevée en matière organique, et les communautés de plancton étaient moins abondantes dans ces lacs que dans les lacs à eau claire. Les estimations préliminaires de la capacité de production indiquent que les échappées de saumon rouge (normalisées à l'échelle des lacs) nécessaires pour maximiser la biomasse des smolts de saumon rouge ont varié de 2 à 89 reproducteurs par hectare.

INTRODUCTION

In British Columbia's central and northern regions there are >144 different sockeye populations (Riddell 2004), each associated with its own sockeye rearing area or lake. The current status of many, perhaps the majority, of these populations is unknown. The limnological status of some of these sockeye nursery lakes has been previously described (Shortreed et al. 1998; Shortreed and Morton 2000, 2003) but for the great majority, data are not available to document their trophic status, to estimate their productive capacity, or to determine the proportion of their rearing capacity that is currently utilized.

Since 1997, the Lakes Group of Fisheries and Oceans Canada's Salmon and Freshwater Ecosystems (SAFE) Division has been conducting synoptic limnological surveys of sockeye nursery lakes that are located in DFO's North Coast Area and that discharge into Pacific Fishery Management Areas 1, 4-6, and 8-9. In this report data from 37 lakes are presented. Most of these lakes are located near the coast, with the remainder in the Skeena River drainage basin. Most lakes were sampled on one occasion only in late summer (late August or early September). While caution must be used in interpreting a lake's limnological status based on only one sampling date, extant limnological data on any of these lakes were either extremely limited or non-existent, so even the single sampling date advanced our knowledge of the lakes' trophic status, productive capacity, and plankton community structure. In conjunction with these limnological surveys, hydroacoustic and trawl surveys were carried out on a subset of these lakes (J. Hume, DFO, Cultus Lake Salmon Research Laboratory, unpublished data). Together, data from these surveys provide the first approximation of the lakes' limnological status and of the current status of their sockeye stocks.

Specific objectives of this study were threefold. The first was to collect limnological data which could be used to describe the lakes' physical, chemical, and biological environments. This included the biomass, composition, and productivity of the plankton communities. Second, these data would be used to categorize the lakes' current trophic status. The third objective was to provide a first estimate of the lakes' rearing (productive) capacity for juvenile sockeye. To accomplish this objective, we used a sockeye rearing capacity model (the PR model). This model (Shortreed et al. 2000, Cox-Rogers et al. 2004) utilizes a lake's average photosynthetic rate to generate estimates of the maximum biomass of sockeye smolts a lake can produce and the escapement needed to produce that maximum biomass.

DESCRIPTION OF STUDY LAKES

The lakes surveyed for this report cover a wide geographic range (latitude - 51°40'-57°01'; longitude - 125°20'-132°33') or approximately 600 km in a north-south direction and 450 km east-west. Of the 37 lakes, almost half (18) are located near the coast and the remainder (19) are in the B.C. interior. Elevations range from near sea level (3 m) to 1,169 m (Table 1). All but one of the lakes are accessible to anadromous

sockeye salmon. The sole exception, Charlotte Lake, is located in the upper portion of the Atnarko River drainage basin above a series of rapids which are impassable to anadromous fish. Given the wide geographic distribution of the study lakes, climatic conditions vary considerably as well. Lakes near the coast are within the coastal western hemlock biogeoclimatic zone (Farley 1979). Based on the Koppen climate classification system (Kottek et al. 2006), the climate is maritime temperate, with cool summers and mild, wet winters. Most lakes in this zone are warm monomictic (no winter ice cover and continuous winter mixing). Most interior lakes are in the sub-boreal spruce biogeoclimatic zone and have a warm summer continental climate (warm summers, cold winters). Deeper lakes in the interior are dimictic, while several of the shallower lakes are either continuously or discontinuously cold polymictic (Wetzel 2001).

The lakes exhibit considerable morphometric variation as well (Table 1; Fig. 2-19). Surface areas range more than two orders of magnitude from 39 to 9,739 ha, although surface areas of the majority (19 out of 37) of the lakes are <200 ha (Table 1). Bathymetric maps are currently available for 27 of the 37 lakes, although on a number of lakes these maps were developed from relatively little data and are of poor quality. Bathymetric maps for some of these lakes were generated during recent acoustic surveys (J. Hume, unpublished data) and for others were available on the British Columbia Ministry of Environment's Habitat Wizard (http:/www.env.gov.bc.ca/habwiz). Based on the available data, mean depths range from 2.4 to 172 m, with the majority of lakes having mean depths <15 m. Several of the lakes are deep, fiord-type lakes with very limited littoral zones, while others have extensive littoral zones comprising a majority of the lake area. Tsimtack Lake is located at an elevation of only 3 m in an area where tidal heights regularly exceed 5 m. Consequently, it receives regular intrusions of salt water and is more properly termed a tidal lagoon than a lake.

Direct human influence on the lakes and their surrounding drainage basins is quite variable, ranging from heavy recreational/residential use (e.g. Lakelse Lake) to virtually pristine conditions (e.g. a number of coastal lakes). The drainage basins of a number of the lakes have been logged to varying degrees.

METHODS

We sampled most lakes in this study on one occasion only in late August or early September. Reported data were collected from August 20 to September 15. However, seasonal (monthly) data were collected from Kitwanga and Lakelse lakes in 2003 and from Morice Lake in 2002. Monthly data were collected from Owikeno Lake in 2001 and are reported by Shortreed and Morton (2003). To improve comparability between lakes, only data from late summer were used in this report. On most lakes only one central location was sampled, but if lakes were large or had multiple basins, we collected data from two to four locations. We used boats as sampling platforms on four of the lakes and on the remaining 33 lakes we used float-equipped Beaver aircraft. We determined surface area of each lake using Oziexplorer mapping software

(http:/www.oziexplorer.com) and digitized Natural Resources Canada 1:50,000 topographic maps (Spectrum Digital Imaging, http:/www.mapsdigital.com)

We used Applied Microsystems conductivity, temperature and depth meters (either models STD-12, STD-12 Plus, or Micro CTD Sensor) to obtain temperature and conductivity profiles from the surface to 100 m or the lake bottom, whichever was less. Thermocline depths were estimated by a visual inspection of plotted temperature and depth data. A Li-Cor data logger (model LI-1000) equipped with a spherical quantum sensor (model LI-193SA) was used to measure photosynthetically active radiation (400-700 nm) and determine euphotic zone depths (1% of surface light intensity). A 22-cm white Secchi disk was used to measure water clarity.

We used an opaque, 6-L Van Dorn bottle to collect all water samples. Sampling usually took place between 0800 and 1100 h (PST). At each station, water from 4-6 depths within the euphotic zone was collected and equal volumes mixed in 9-L Nalge Lowboy carboys to provide an integrated sample. If water depth was sufficient, a hypolimnetic water sample was collected from well below the thermocline. Replicate samples for analysis of turbidity, total dissolved solids, dissolved reactive silica, nitrogen (ammonia, nitrate), phosphorus (total, dissolved, soluble reactive, turbidity blank), bacteria, picoplankton, and phytoplankton were taken from each integrated sample. We also collected discrete water samples at 6-8 depths from the surface to 50 m or near bottom. These samples were collected in 1-L polyethylene bottles and later analyzed for turbidity, nitrate, and chlorophyll. At most lakes and stations, dissolved oxygen (DO) concentrations were determined at 6-8 depths from the surface to 50 m or near bottom using an Oxyguard Handy Alpha or Beta meter.

Chemical analyses were carried out according to methods given in Stephens and Brandstaetter (1983) and Stainton et al. (1977). For total phosphorus determination, clean screw-capped test tubes were rinsed with sample, filled, capped, stored at 4°C, and later analyzed using a molybdenum blue method after persulfate digestion. To correct total phosphorus concentrations for turbidity, a turbidity blank was run and these values were subtracted from total phosphorus (Koenings et al. 1987). Water for dissolved nutrient analyses was filtered through an ashed 47-mm diameter Micro Filtration Systems (MFS) borosilicate microfiber filter (equivalent to a Whatman GF/F filter). Each filter was placed in a 47-mm Swinnex filtering unit (Millipore Corp.), rinsed with 150 mL of distilled, deionized water (DDW), and then rinsed with approximately 50 mL of sample. For dissolved phosphorus determination, filtered water was treated as for total phosphorus, including the use of turbidity blanks. Other water samples for dissolved nutrients were kept cool and dark for 2-4 h, filtered into a clean, rinsed polyethylene bottle, and frozen. For chlorophyll analysis, we filtered 250-mL of water through a 47-mm diameter, 0.45-µm Millipore HA filter. Filters were folded in half, placed in aluminum foil dishes, and frozen. They were later analyzed using a Turner fluorometer (Model 112) after maceration in 90% acetone.

Water for bacterioplankton enumeration was collected in sterile scintillation vials and preserved with two drops of formaldehyde. Bacterioplankton were later counted

using the DAPI method (Robarts and Sephton 1981). Ten random fields were counted on each filter and the counts converted to numbers/mL.

For phytoplankton enumeration and identification, opaque 125-mL polyethylene bottles were rinsed with sample, filled, and fixed with 1-mL of Lugol's iodine solution. For analysis, each sample was gently mixed and a subsample was settled overnight in a 27-mL settling chamber. 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. Cells with a maximum dimension from 2-20 µm were classified as nanoplankton. All cells >20 µm were classified as microplankton. Phototrophic picoplankton (cyanobacteria and eukaryotic algae <2 µm in diameter) were enumerated using the method described by MacIsaac and Stockner (1985). Within several hours of sample collection, 15 mL of sample water was filtered through a 0.2-µm Nuclepore filter counter-stained with Irgalan black. Care was taken to minimize exposure of the sample to light during sampling and laboratory processing. Filters were placed in opaque petri dishes, air-dried and stored in the dark at room temperature until analyzed. During analysis, each filter was placed on a wet 40-µm mesh nylon screen in a filter holder, 1-2 mL of filtered distilled DDW were added to the filter column, and the cells on the filter were rehydrated for 3-5 min. Water was drawn through at a vacuum pressure of 20-cm Hg, and the moist filter was placed on a glass slide with a drop of immersion oil (Cargille Type B) and a coverslip. The Zeiss epifluorescence microscope used for picoplankton enumeration was equipped with a 397-nm longwave-pass exciter filter and a 560-nm shortwave-pass exciter filter, a 580-nm beam-splitter mirror and a 590-nm longwave-pass barrier filter. Filters were examined at 1250X magnification under oil immersion, and 30 random fields were counted. Phototrophic picoplankton were placed in categories based on morphological characteristics, fluorescence color, and size categories (Stockner and Shortreed 1991).

We determined *in situ* photosynthetic rates (PR) at each date and sampling location. PR was determined at 5-7 depths from the surface to below the euphotic zone. At each depth, two light and one dark glass bottles were filled, inoculated with approximately 137 kBq of a ^{14}C-bicarbonate stock solution, and incubated at the original sampling depth. To determine activity of the stock solution, at each station we inoculated three scintillation vials containing 0.5 mL of 0.2-N NaOH with the stock. Incubations lasted 1.5-2 h, usually between 1000 and 1300 h (PST).

After incubation, bottles were placed in light-proof boxes and transported to the field laboratory where filtration started <2 h after incubation stopped. We filtered the entire contents of each bottle through a 25-mm diameter MFS glass fibre filter at a vacuum not exceeding 20-cm Hg. Filters were placed in scintillation vials containing 0.5 mL of 0.5-N HCl and lids were left off the vials for 6-8 hr. All vials were stored cool and in the dark. Within a few days of the incubations, 10 mL of Scintiverse II (Fisher Scientific) (1997-2004) or Scintiverse II-BD (2005) was added to each scintillation vial and samples were counted in a Beckman Coulter LS6500 liquid scintillation counter. Quench series composed of the same scintillation cocktail and filters used for samples were used to determine counting efficiency and the equation of Strickland and Parsons

(1972) was used to calculate hourly PR. PR was converted from hourly to daily rates using methods described by Koenings et al. (1987).

Water for pH and alkalinity determinations was collected in 125-mL glass bottles from the same depths as for PR. Within 4 hr of collection, this water was combined into two integrated samples (top and bottom halves of the euphotic zone). From these integrated samples a Cole-Parmer Digi-Sense pH meter (Model 5986-10) and Ross combination electrode were used to determine pH and total alkalinity (mg $CaCO_3$/L) according to the standard potentiometric method of APHA (1998). In most lakes dissolved inorganic carbon (DIC) concentrations were calculated indirectly from pH, temperature, total dissolved solids and bicarbonate alkalinity. Starting in 2004, DIC in acidic lakes was determined using a UIC Inc. 5011 CO_2 coulometer (DOE 1994).

Replicate zooplankton samples were collected at every station with a 160-µm mesh Wisconsin net (mouth area = 0.05 m^2) hauled vertically to the surface from 30 m (vertical hauls from 50 m were done on Owikeno and Morice lakes) or near bottom, whichever was less. All samples were placed in 125-mL plastic bottles and preserved in a sucrose-buffered 4% formalin solution (Haney and Hall 1973). Zooplankton (all zooplankton except rotifers and nauplii, which were not counted) were later counted, identified to genus or species (Pennak 1978; Balcer et al. 1984; Dussart and Defaye (1983), and measured with a computerized video measuring system (MacLellan et al. 1993). Measurement of body length was carried out as described by Koenings et al. (1987). Zooplankton biomass (milligrams dry weight) was calculated with species-specific length-weight regressions adapted from Bird and Prairie (1985), Culver et al. (1985), Stemberger and Gilbert (1987), and Yan and Mackie (1987).

In all lakes sampled starting in 2004, net efficiencies were determined using a Rigosha and Co. Ltd. flowmeter mounted at the second ring of the Wisconsin net. Zooplankton numbers and biomass were corrected using the measured efficiencies. To improve comparability, samples collected prior to 2004 were adjusted by the average efficiency for all samples after 2004, which was 0.938±0.062 (2SE).

A number of surveyed lakes had populations of limnetic invertebrates (*Chaoborus*, *Leptodora*, or, in one lake, the mysid *Neomysis mercedis*) which have the potential to compete with juvenile sockeye for zooplankton prey items. For behavioural reasons (large diel migrations, fast swimming) and because of their lower densities, *Chaoborus* and mysids cannot be quantitatively sampled during the day or by the Wisconsin net we used. To sample these animals, on 8 lakes we did multiple night-time vertical hauls using a 350-µm mesh SCOR-type net with a mouth area of 0.25 m^2. In addition, they were captured by the midwater trawl we used during acoustic/trawl surveys (a total of 19 lakes). These data provided a qualitative estimate of abundance (none, low, moderate, high). Only on 2 lakes (Kitwanga and Lakelse) did we obtain quantitative seasonal estimates of the numbers of these invertebrates. When quantitative data were obtained, we estimated biomass (dry weight) of mysids using a length-weight regression equation from Chigbu and Sibley (1996). We determined biomass of *Chaoborus* using a length-weight relationship

(mg dry wt=0.0062xlength$^{1.9778}$) derived from *Chaoborus* collected from several of the study lakes. Several of the study lakes also contained *Leptodora*, a large predatory cladoceran. We assumed the Wisconsin net provided quantitative samples of these animals and we estimated their biomass using a length-dry weight regression from Culver (1985).

To compare correlations of selected variables between lake types and between data from this study with that of other studies, we used the SAS General Linear Models (GLM) procedure to examine heterogeneity of slopes and intercepts.

RESULTS

PHYSICAL

Thermal regimes exhibited by the lakes were highly variable (Fig. 20-25). Based on the thermal regime at the time of sampling, on the lake's morphometry, and on climate, we concluded that of the 37 lakes described in this report, 6 were cold polymictic (only intermittent stratification during the ice-free period), 13 were dimictic, and 18 were warm monomictic (Table 2). Several lakes could fall into more than one category, depending on the severity of the winter or on a specific lake basin. Epilimnion depths (EPZ) were also quite variable. EPZ was deepest (54 m) in the main basin of Owikeno Lake, but in the majority of stratified lakes EPZ was <10 m. Temperature profiles in saline Tsimtack Lake and meromictic Moore were quite unusual (Fig. 24,25). Tsimtack Lake had a surface lens of cooler water approximately 1 m in depth which likely resulted from freshwater discharge into this salt water lagoon. In Moore Lake, the top 10 m was typical of many smaller lakes, with an epilimnion, well-developed thermocline, and an upper hypolimnion. From 10-22 m, temperatures were higher than they were at 10 m. From 22-30 m temperatures decreased, and from 30-40 m they again increased slowly. Reasons for this will be discussed in a later section. Water clarity was also highly variable, with Secchi depths (SD) of <1 m in several of the glacial lakes. The maximum recorded SD of 14.5 m occurred in Charlotte Lake. Euphotic zone depths (EZD) ranged from 0.4 m in glacially turbid Kluayaz Lake to 23.0 m in Morice Lake. Turbidity of clear and stained lakes was uniformly low (<1 NTU), while that of glacial lakes ranged from 0.4 NTU in Morice Lake to 114 NTU in Kluayaz Lake (Table 2).

CHEMICAL

In most study lakes the conductivity was relatively low (<60 µS/cm) (Table 3, Fig. 26-31). With the exception of meromictic Moore and saline Tsimtack lakes, the highest conductivity of 102 µS/cm occurred in Kitwanga Lake. Tsimtack Lake was saline throughout its water column, with a conductivity of 7.6 mS/cm at 0 m and 26.7-30.5 mS/cm from 1 m and below (Table 3). This is equivalent to salinities of 3.9‰ at the surface and 16-18‰ in the rest of the water column. Moore Lake was meromictic, with conductivities of 71 µS/cm from the surface to 4 m and higher values

(189-243 µS/cm) from 4-11 m. Below 12 m, conductivities increased steadily and at 40 m were almost 5,000 µS/cm, or a salinity of app. 2.5 ‰.

Dissolved oxygen (DO) data were collected from 25 of the 37 lakes (Table 3, Fig. 32-35). In all cases epilimnetic DO was relatively high, ranging from 8.7-12.8 mg/L. The lakes exhibited a variety of DO profiles, with ten lakes exhibiting the orthograde profile (higher DO in the hypolimnion) typical of oligotrophic lakes in summer (Wetzel 2001). Ten lakes exhibited varying degrees of the clinograde profiles (lower DO in the hypolimnion) which are often seen in more productive lakes. Only Kitwanga Lake exhibited an extreme clinograde profile with an anoxic hypolimnion (DO data are not available for Slamgeesh Lake but nitrate profiles indicate it had a similar profile to Kitwanga). One lake only (Ecstall) exhibited a positive heterograde profile (metalimnetic DO maximum). Three shallow lakes (and an additional two shallow basins in other lakes) had no hypolimnia and therefore had similar DO profiles from the surface to the lake bottom. Two lakes had anoxic monimolimnia which commenced at depths of approximately 25 m in Moore Lake and 8 m in Tsimtack Lake.

Of the 37 lakes in this study, pH was acidic (<7.0) in 30 and alkaline in the remainder (Table 2). In only 4 lakes (Hartley Bay and the 3 Mikado lakes) was the pH<6.0. The highest pH of 7.9 occurred in saline Tsimtack Lake. Other than in Tsimtack Lake, total alkalinities were lowest (<0.25 mg/L $CaCO_3$) in the Mikado lakes and highest (62.2 mg/L $CaCO_3$) in Kitwanga Lake. With the exception of meromictic or saline lakes, DIC and TDS concentrations were lowest in the Mikado lakes (0.5 mg/L and 5 mg/L, respectively) and highest (18.4 mg/L and 77 mg/L, respectively) in Kitwanga Lake.

Nitrate concentrations were highly variable between lakes. Epilimnetic nitrate was depleted (<1 µg N/L) in 11 of the lakes and was >15 µg N/L in only 4 lakes (Table 4). In almost all lakes which had hypolimnia, concentrations below the thermocline were substantially higher than epilimnetic concentrations. Hypolimnetic concentrations were highest (146 µg N/L) in Evelyn Lake and lowest (1.0 µg N/L) in Kitwanga Lake (Table 4). Vertical profiles of nitrate concentration indicate that epilimnetic nitrate was reduced to low levels (<5 µg N/L) in most lakes (Fig. 37-39). Epilimnetic depletion was least pronounced in Canoona, Evelyn, Ian, Mikado, Morice, and Slamgeesh lakes. The nitrogen profile in Slamgeesh Lake was quite unusual (Fig. 39). Near-surface nitrate concentrations of approximately 15 µg N/L increased to 21 µg N/L at 2 m and then declined sharply to 1.9 µg N/L at a depth of 7 m (water depth at this location was 7.4 m). At the 7 m depth, ammonia concentration also increased sharply to 202 µg N/L (Table 4). The high ammonia indicates that substantial amounts of organic matter are accumulating in the deeper waters of Slamgeesh Lake. Further, the decline in nitrate at the same depth indicates a lack of oxygen, since nitrification ceases under anaerobic conditions. In the other lakes, ammonia was much lower, with epilimnetic concentrations <7 µg N/L in the majority of lakes (Table 4). In most lakes hypolimnetic concentrations were <15 µg N/L.

Total phosphorus (TP) concentrations ranged from 1.4 µg/L in Kooryet Lake to 16.5 µg/L in Slamgeesh Lake (Table 4). In the majority of lakes TP was <5 µg/L. We do not report TP from lakes with high glacial turbidity. Glacial flour can contain substantial amounts of P in the form of apatite, which is generally not available to phytoplankton. Consequently, TP values from these lakes can be anomalously high even after turbidity corrections, and does not reflect biologically available P or trophic status. However, the analysis of soluble reactive phosphorus (SRP) is not affected by apatite P, so this analysis provides some measure of the relative P load to all the lakes. In the majority of lakes SRP was <1.5 µg/L (Table 4). It was highest (6.7 µg/L) in Aldrich Lake and in Kitwanga, Kluayaz, and Motase lakes was substantially higher than in the other lakes. SRP data should be interpreted with caution, however, as high values can simply indicate that P is not the primary limiting factor, rather than indicate high P loading.

BIOLOGICAL

Bacterioplankton and phytoplankton

There was a 4.5-fold variation in bacterioplankton numbers in the study lakes, with lowest numbers (0.57 million/mL) occurring in saline Tsimtack Lake. In the freshwater lakes, numbers ranged from 0.62-2.56 million/mL (Table 5). Numbers were <1 million/mL in 12 of the 37 lakes in this study, between 1-2 million/mL in 17 lakes, and >2 million/mL in the remaining 8 lakes. Chlorophyll (CHL) concentrations also varied substantially, exhibiting a 7.8-fold variation, from 0.44 µg/L in lower Mikado Lake to 3.43 µg/L in Kitkiata Lake (Table 5). Epilimnetic CHL was <1 µg/L in 22 of the 37 lakes, between 1-2 µg/L in 11 lakes, and >2 µg/L in only four lakes. Vertical profiles of CHL also were quite variable. In most lakes, CHL was highest in the epilimnion and upper euphotic zone (Fig. 40-43). CHL was similar throughout the water column in Charlotte and Morice lakes, which is a pattern commonly seen in highly oligotrophic lakes with deep euphotic zones. In Johnston Lake, a subsurface CHL peak of 5.1 µg/L occurred at a depth of 11 m, which was the bottom of the euphotic zone. In two lakes (Kitwanga and Slamgeesh), CHL increased dramatically near the lake bottom. In both lakes this was also near the bottom of the euphotic zone. These accumulations of organic matter are relatively common in shallow lakes with high productivity. The highest CHL (18.9 µg/L) in the study occurred at a depth of 11 m in Tsimtack Lake. This was at the start of the anoxic layer.

Photosynthetic rates (PR) were highly variable, and covered the range from the lowest (8 mg $C \cdot m^{-2} \cdot d^{-1}$ in Kluayaz Lake) to among the highest (386 mg $C \cdot m^{-2} \cdot d^{-1}$ in Kitkiata Lake) ever recorded for B.C. sockeye nursery lakes (Table 5, Fig 44-51). Of the 37 lakes, 15 were highly unproductive, with PR values <75 mg $C \cdot m^{-2} \cdot d^{-1}$. Of the remaining lakes, 12 had low to moderate PR ranging from 75-150 mg $C \cdot m^{-2} \cdot d^{-1}$ and 10 had relatively high PR (>150 mg $C \cdot m^{-2} \cdot d^{-1}$). As in most lakes, the shape of vertical PR profiles in our study lakes was controlled by the light regime. Slowest attenuation occurred in lakes with the deepest euphotic zones (e.g. Charlotte, Morice, Swan) (Fig. 45,50,51). Fastest attenuation occurred in glacially turbid Kluayaz Lake, where highest PR occurred at the water surface, and was near zero at a depth of 1 m (Fig. 48).

Phytoplankton numbers and biomass varied substantially between the lakes, with total numbers ranging from 0.8-136 thousand/mL and volume from 112-15,666 mm^3/m^3 (Table 5). Picoplankton numbers ranged from only 300/mL in Rainbow Lake to 131 thousand/mL in Sicintine Lake (Table 5). Numbers of the phytoplankton size fraction most suitable for zooplankton grazing (nanoplankton, 2-20 µm maximum dimension) ranged widely from 400/mL to 20 thousand/mL, with a range in volumes from 24-654 mm^3/m^3. Microplankton volume ranged from 87 mm^3/m^3 in Rainbow Lake to a maximum of 15,650 mm^3/m^3 in Johnston Lake.

In all lakes, the picoplankton genus *Synechococcus* was numerically dominant. After *Synechococcus*, either a picoplankton-sized eukaryote or the chrysophyte *Chromulina* were most numerous in the majority of lakes. In almost all lakes, the genera *Cyclotella* and *Rhizosolenia* were the most numerically abundant diatoms. Exceptions were Bear and Azuklotz lakes, where *Asterionella* was more abundant than *Rhizosolenia*, and Keecha Lake, where *Cymbella* was more abundant than *Rhizosolenia*. *Rhizosolenia* was volumetrically dominant in all lakes but Azuklotz, Ecstall, Keecha, and Tsimtack. In these four lakes *Cyclotella* had the greatest biomass of all phytoplankton genera. In Johnston Lake, *Rhizosolenia* numbers (14 thousand/mL) were the highest we have yet recorded for a B.C. sockeye nursery lake and made up 99% of total phytoplankton volume.

Zooplankton

The zooplankton communities in the study lakes exhibited considerable variation in both biomass and species composition (Table 6). Total dry biomass was lowest 1.8 mg dry wt/m^3 in Johnston Lake and highest (332 mg dry wt/m^3) in Slamgeesh Lake. Daphnid biomass ranged from zero in several of the glacial and stained lakes to a maximum of 258 mg dry wt/m^3 in Slamgeesh Lake. Daphnids were comprised exclusively of the genus *Daphnia* in all lakes except Azuklotz, Bear, and Owikeno. In Owikeno Lake, *Ceriodaphnia* was more abundant than *Daphnia*. In Azuklotz and Bear lakes, low numbers of *Ceriodaphnia* were also present. *Daphnia* species identified in the study lakes included *D. galeata, longiremis, rosea,* and *thorata*. Bosminids were another group of cladocerans that were important contributors to total biomass in some lakes, with biomass ranging from 0 mg dry wt/m^3 in several glacially turbid lakes to 41 mg dry wt/m^3 in Slamgeesh Lake. Bosminids were comprised of *Bosmina longirostris* and *Eubosmina coregoni*. A number of other cladoceran genera occurred in the study lakes, but they were generally present in relatively low numbers. The sole exception was *Holopedium*, which was the dominant cladoceran in Morice Lake and was common in several stained lakes (Table 6).

Biomass of cyclopoid and calanoid copepods were roughly equal across the range of lakes in this study (Table 6). Cyclopoid biomass ranged from 0 mg dry wt/m^3 in several stained lakes to 41.9 mg dry wt/m^3 in Aldrich Lake. Cyclopoid biomass tended to be lower in stained and glacially turbid lakes than in clear lakes. The genus *Diacyclops* was the dominant cyclopoid by a substantial margin, followed by

Acanthocylops vernalis. Calanoid copepod biomass ranged from 0 mg dry wt/m^3 in a number of lakes to a maximum of 21 mg dry wt/m^3 at one location in Bear Lake. Calanoid biomass was more variable than that of the cyclopoids and ranged from 0 mg dry wt/m^3 to relatively high values in each of the three water types. *Leptodiaptomus* was the dominant calanoid copepod in a number of lakes, with highest biomass occurring in several clear lakes. *Epischura* and *Skistodiaptomus* were common or dominant in several other lakes and their highest biomasses occurred in stained lakes. *Hesperodiaptomus* was present in a few stained lakes but was dominant only in Owikeno Lake. *Heterocope* was abundant only in two clear lakes.

Macroinvertebrates

Large invertebrate planktivores such as the mysid *Neomysis mercedis* and the phantom midge *Chaoborus* may compete with juvenile sockeye for zooplankton prey and may also be a food source for some sockeye fry (Hyatt et al. 2005b). In this study, 25 of the 37 lakes were sampled with techniques that would determine the presence/absence and relative abundance of both these genera (Table 7). In only two lakes (Kitwanga and Lakelse) were we able to use techniques which enabled quantitative seasonal estimates of numbers and biomass to be made. Of the 25 lakes, *Neomysis mercedis* was observed in Lakelse Lake only. Its numbers ranged from a low of 4.7/m^2 (0.17/m^3) in May to a maximum of 365/m^2 (28/m^3)in August. Average seasonal (May-September) numbers and biomass of *N. mercedis* were 122/m^2 and 145 mg dry wt/m^2. *Chaoborus* was observed in 10 of the 25 lakes. In Kitwanga Lake, *Chaoborus* density ranged from 540-814/m^2 (August-October, n=3) and averaged 664/m^2 (51/m^3). *Chaoborus* biomass in Kitwanga Lake averaged 215 mg dry wt/m^2. Of the 10 lakes where *Chaoborus* was found, densities were categorized as low in four lakes, moderate in four lakes, and high in two lakes (Table 7).

The large predatory cladoceran *Leptodora kindtii* can also both be a food source for, and a competitor with, juvenile sockeye (Lunte and Luecke 1990). It is not known to undergo the large diel migrations commonly exhibited by *Chaoborus* and *Neomysis*, so we assumed the sampling method (daytime vertical hauls from 30 m with a Wisconsin net) used captured it adequately (Table 7). It was found in 7 of 36 lakes in this study with numbers ranging from 11-434/m^2. In Kitwanga Lake, *Leptodora* density ranged from 117-434/m^2 (August-October, n=3) and averaged 228/m^2, or 18/m^3.

DISCUSSION

COMPARISONS BETWEEN LAKE TYPES

To facilitate synthesis of data from this large suite of lakes, we grouped the lakes into three categories based on water type (glacial, organically stained, clear). Lakes were placed in one of these three categories based on qualitative assessment, with the result that 15 were clear, 6 were glacial, and 16 were stained. Although not a general rule for B.C. sockeye lakes, in this particular suite of lakes, all clear lakes were in the

interior and all stained lakes were near the coast. Of the glacial lakes, two were near the coast and the remaining four were in the interior.

Classification by water type is supported by statistical differences in the slopes of the correlations between euphotic zone depth (EZD) and Secchi depth (SD) in the three types of lakes (Fig. 52). In this study, slopes of EZD:SD were highest (2.63) in glacial lakes and lowest (0.92) in stained lakes (Fig. 52). In clear lakes the ratio was 1.47. Each of these slopes was significantly different from the other (SAS GLM procedure, $p<0.05$), but there was no significant difference in intercepts. Similar differences in EZD:SD ratios have been reported for a suite of 58 Alaskan lakes (Koenings and Edmundson 1991). Essentially, the most important factors affecting water transparency are light scattering in turbid (glacial) lakes and light absorption (color) in stained lakes. In glacial lakes there is less contrast between the white Secchi disk and water color than in stained (brown water) lakes, so SD's are shallower relative to EZD's (higher ratios) than in stained lakes.

However, as with any system of lake classification, caution should be used in applying these terms. While lakes near B.C.'s central and north coasts are often highly stained, lakes located near the south coast (e.g. Sproat, Great Central, Sakinaw, Nimpkish) are commonly quite clear (Stockner and Shortreed 1978, 1985). A number of interior lakes (e.g. Babine, Stuart, Takla, Trembleur) are stained, with EZD:SD ratios similar to those observed in coastal stained lakes (Shortreed and Morton 2000; Malange et al. 2005). Classification of lakes into these 3 types is useful not because of color or turbidity, but because color or turbidity reflect differences in hydrology, geology, climate, and forest cover.

We attempted to determine if there were any systematic differences in limnological variables between the 3 lake types. Consequently, we conducted ANOVA's on the averages of four physical, nine chemical, and 10 biological variables for the three lake types (Table 8,9). The analyses indicated a number of differences between lake types. Surface temperatures were significantly warmer in stained lakes than in either clear or glacial lakes. Previous research indicates that surface waters of stained lakes may be warmer than those of clear lakes because of increased absorption of infrared light (Wetzel 2001). Across all lake types, epilimnion depth was positively correlated with lake surface area ($n=32$, $r^2=0.54$, $Epil.=0.24 \times Area+5.82$). This correlation has been observed elsewhere (Fee et al. 1996) and is no doubt due to increasing fetch as lake area increases. Glacial lakes had the deepest average epilimnion depths, but these were significantly different only from depths in stained lakes (Table 8,9). Thermal stratification in glacially turbid lakes tended to be weaker as well as deeper, no doubt because glacial inflows are colder and because the location of glacially turbid lakes near to substantial mountains often results in windier conditions (catabatic winds). Water clarity (Secchi depth) was significantly lower in glacial lakes than in either clear or stained lakes. However, average euphotic zone depths were lowest in stained lakes and were significantly different only from those in clear lakes (Table 8).

Stained lakes were significantly more acidic than the other lake types. This was also the case in an analysis of data from over 600 humic and clear north temperate lakes (Nürnberg and Shaw 1999). In our study, stained lakes were also much more poorly buffered, with significantly lower conductivities, total dissolved solids, total alkalinities, and DIC concentrations than in glacial or clear lakes. Silica concentrations were also far lower in the stained lakes than in either of the other lake types. Neither epilimnetic nor hypolimnetic nitrate concentrations were significantly different among lake types, but total phosphorus concentrations were significantly higher in clear lakes than in stained lakes. In contrast, Nürnberg and Shaw (1999) found that both nitrogen and phosphorus concentrations were significantly higher in stained lakes than in clear lakes.

Bacteria numbers were significantly higher in clear lakes than in either glacial or stained lakes. Chlorophyll concentrations tended to be higher in glacial lakes, but differences between lakes were not significant. When daily PR was expressed on an areal basis, clear lake values appear substantially higher than those in glacial or stained lakes (Table 8). However, when expressed volumetrically, differences between lake types were much smaller and mean daily PR in glacial lakes was slightly higher. However, differences were not significant for either areal or volumetric PR (Table 9).

Of the major zooplankton groups, total, cyclopoid, and daphnid biomasses were significantly greater in clear lakes than in the other two lake categories, whether expressed volumetrically or areally (Table 7,8). Among lake categories, calanoid copepods varied the least, with no significant differences between lakes. Average areal bosminid biomass in stained lakes was significantly greater than bosminid biomass in glacial lakes. Expressed volumetrically, there were no significant differences in bosminid biomass between lake types.

Empirical relationships between various measures of phytoplankton biomass or productivity and chemical variables (primarily TP) have been widely reported in the limnological literature (e.g. Dillon and Rigler 1974; Vollenweider 1976; Stockner and Shortreed 1985; Nürnberg and Shaw 1999). We examined data from the suite of lakes in this study to see if similar correlations occurred. Chlorophyll (CHL) and TP (excluding that in glacial lakes) were positively correlated (Fig. 53, $n=29$, $r^2=0.42$, $p<0.01$). The slope of the relationship of the log-transformed data was not significantly different ($p>0.05$) than that reported for a number of coastal B.C. lakes (Stockner and Shortreed 1985) (Fig. 53). However, the intercepts were different ($p<0.05$), indicating the lakes in the earlier study had higher chlorophyll for a given TP concentration. On most lakes in the earlier study, whole-lake additions of inorganic nutrients (N and P) were taking place. Consequently, the proportion of the phosphorus pool that was biologically available may have been higher, leading to higher CHL per unit of TP. Also, data in our study come from a single sampling date in late summer (as opposed to seasonal averages in the earlier study), a time when epilimnetic nitrate depletion is usually at its seasonal maximum. Consequently, it is the time of year when co-limitation of nitrogen and phosphorus (Suttle and Harrison 1988; Stockner and Shortreed 1994) is most likely to be occurring. If this was taking place, a lower intercept in the CHL:TP relationship

would be expected. Other studies (Smith 1979; Prepas and Trew 1983) have reported CHL:TP correlations from lakes of much greater range in trophic status. When data from B.C. lakes were pooled with these data, there was a highly significant correlation (r^2=0.85, n=144, p<0.01) (Fig. 53).

We also found a significant correlation between volumetric daily PR and CHL in our study lakes (Fig. 54, n=37, r^2=0.62, p<0.01). Stockner and Shortreed (1985) also reported a significant correlation between PR and CHL for coastal B.C. lakes. There was no significant difference (p=0.32) in slopes between the log-transformed data from the two studies, but intercepts were different (p<0.01). Smith (1979) reported a relationship between PR and CHL in a suite of lakes comprising a much wider range in trophic status. As with the TP:CHL correlation, when log-transformed PR and CHL data from coastal B.C. lakes were pooled with these data, we found a highly robust relationship (r^2=0.89, n=141, p<0.01) (Fig. 54).

Both Smith (1979) and Stockner and Shortreed (1985) reported significant correlations between PR and TP, but in our study a significant relationship between PR and TP did not occur (n=31, r^2=0.12, NS). However, if data from all three studies were pooled, the relationship between PR and TP was highly significant (r^2=0.78, n=141, p<0.01) (Fig. 55).

ZOOPLANKTON

Total zooplankton biomass (expressed as mg dry wt/m^3) was significantly correlated with TP (n=29, r^2=0.41, p<0.01) (Fig. 55). Stockner and Shortreed (1986) reported a relationship between zooplankton biomass and TP for a suite of lakes in the Yukon. Neither slopes nor intercepts of the correlation between zooplankton and TP were significantly different (p>0.5) between the two suites of lakes. Hanson and Peters (1984) reported a relationship between zooplankton and TP for a much wider range of data (range in TP, 4-200 µg/L; range in zooplankton biomass, 11-786 mg dry wt/m^3). Data from our study appears to fit their regression line reasonably well (Fig. 55). In

Cladoceran numbers and biomass were quite variable between our study lakes and cladocerans were either absent or very sparse in glacially turbid lakes (Table 7). Plankton communities in these lakes had a simple population structure that was dominated by the copepod *Diacyclops* except in Owikeno Lake, where *Hesperodiaptomus* was dominant. Koenings et al. (1990) found similar zooplankton community composition in a number of glacially turbid Alaskan lakes and concluded that nondiscriminating filter feeders such as *Daphnia* ingest glacial silt along with phytoplankton, which can lower the energy extractable from ingested food below maintenance levels.

Several authors have stated that in coastal British Columbia lakes large-bodied cladocerans are usually either absent or present in very low numbers (Neill 1978; Stockner 1987). In our study, average *Daphnia* biomass was lower in stained lakes, but *Daphnia* biomass in the stained lakes was also quite variable, ranging from

0 mg dry wt/m^3 in several lakes to quite high (14-20 mg dry wt/m^3) in several others. Reasons for this variability do not appear related to trophic status, since one of these lakes (Ecstall) had very low *Daphnia* biomass despite a high PR of 190 mg C·m^{-2}·d^{-1}. It also does not appear to be related to *Chaoborus* abundance, since there appeared to be little relationship between our qualitative estimates of *Chaoborus* and *Daphnia* biomass (Table 6, 7). For example, some lakes with moderate to high populations of *Chaoborus* had relatively abundant *Daphnia* populations and other lakes with similar *Chaoborus* communities had very low *Daphnia* abundance. However, there was a negative trend between limnetic fish biomass (primarily age-0 sockeye and stickleback) and *Daphnia* biomass in stained lakes (standardized to surface area, Tables 6, 11). However, given the small sample size (n=5), the correlation for the log-transformed data was not significant (Fig. 56, r^2=0.62, p>0.05).

TROPHIC STATUS

A variety of limnological variables have been used to classify lakes from oligotrophic to eutrophic. These include TP (Vollenweider 1976), chlorophyll (Forsberg and Ryding (1980), bacteria (Bird and Kalff 1984), and Secchi depth (Carlson 1977). TP has been the most widely used variable to indicate trophic status, but its use is problematic in glacially turbid lakes. Secchi depth is useful only in lakes lacking organic stain or glacial turbidity (i.e. when variation in water clarity is caused solely by biological activity). Variables such as chlorophyll and bacteria are indicators of standing stock or biomass, while a lake's trophic status is a result of production rates. Based on TP in lakes which were not glacially turbid, four of the lakes in this study were mesotrophic and the remaining 25 were oligotrophic. When the CHL index was used, 36 lakes were oligotrophic and only one, Kitkiata Lake, was mesotrophic. Based on the bacteria index, eight lakes were mesotrophic and the remaining 29 were oligotrophic.

While biomass is often correlated with production rates, many biotic and abiotic factors can affect this relationship. While rate measurements are more difficult to obtain than biomass, they provide a direct indication of a lake's productivity and trophic status. We suggest a trophic state index based on PR would be a more accurate indicator of actual trophic status and would be applicable in a wider range of lakes. In our study lakes, daily PR ranged from 8.3-387 mg C·m^{-2}·d^{-1}, a 46-fold variation. Expressed volumetrically, the range in PR was less (an 18-fold variation from 3.4-60 mg C·m^{-3}·d^{-1}), but still greater than the range observed for other trophic indicators. TP (excluding glacial lakes) ranged 12-fold from 1.4-16.5 µg/L, CHL exhibited a lesser 8-fold variation (0.44-3.43 µg/L), and bacteria had only a 4-fold variation (0.57-2.56 million/mL) (Table 5). Based on the observed ranges, PR appears to be a more sensitive indicator of trophic status. The most widely used trophic classification is that proposed by Vollenweider (1976), where lakes with TP concentrations <10 µg/L were classified as oligotrophic, 10-20 µg/L as mesotrophic, and >20 µg/L as eutrophic. Using the relationship between PR and TP to set boundaries, we suggest that lakes with PR <270 mg C·m^{-2}·d^{-1} be considered oligotrophic, from 270-619 mg C·m^{-2}·d^{-1} as mesotrophic, and >619 mg C·m^{-2}·d^{-1} as eutrophic. Based on this classification, four lakes in this study were mesotrophic and the majority (33 lakes) were oligotrophic.

PRODUCTIVE CAPACITY

The PR model (Hume et al. 1996, Shortreed et al. 2000, Cox-Rogers et al. 2004) was developed primarily as a tool to predict a lake's sockeye productive capacity when sufficient data were not available to directly estimate capacity (e.g. fry/spawner over a wide range of escapements). The main input to the PR model is seasonal average daily integrated PR (mg $C \cdot m^{-2} \cdot d^{-1}$) ($PR_{mean}$). In shallow lakes, PR_{mean} is affected by the reduction of volume with depth, so for a number of lakes in this study PR_{mean} was adjusted downwards as described by Fee (1979) (Table 10). Although the PR model requires PR_{mean}, Cox-Rogers et al. (2004) showed that estimates of PR_{mean} could be derived from PR data collected on one occasion only in late summer (PR_{mean}=PRx0.748, r^2=0.60, n=113). In this study, seasonal average PR data were available for only four of the lakes. The remaining lakes were sampled only once in late August or early September and this adjustment to PR_{mean} was made (Table 10). Total seasonal phytoplankton carbon uptake (t C/lake/year) (PR_{total}) was then calculated by multiplying PR_{mean} by lake area and by growing season length (standardized as May 1-Oct 31). PR_{total} was then used to estimate maximum smolt biomass and the escapement needed to produce that biomass (Table 10).

In lakes where juvenile sockeye are the only limnetic planktivores, these PR model predictions are sufficient. However, in lakes where other limnetic planktivores are present and compete with sockeye fry, sockeye productive capacity is reduced. Consequently, initial PR model predictions needed to be adjusted downwards in some of our study lakes. Fish species which can compete with juvenile sockeye and which commonly occurred in the study lakes include kokanee (*O. nerka*), threespine stickleback (*Gasterosteus aculeatus*), redside shiners(*Richardsonius balteatus*), peamouth chub (*Mylocheilus caurinus*), and various whitefish species (*Coregonus* sp). Where successful acoustic and trawl surveys were carried out and enabled us to estimate biomass of limnetic planktivores other than sockeye (18 of the 37 lakes in this study), we reduced PR model predictions of maximum smolt biomass by a corresponding amount (Table 8) (Cox-Rogers et al. 2004; J. Hume, unpublished data). Using available data, we calculated average biomass of competitors in lakes of each type (clear, glacial, stained) and also calculated average PR from those same lakes. When no data were available on the limnetic fish community (19 lakes), we estimated competitor biomass by using the average biomass for that type of lake multiplied by the ratio of PR for that lake and the average PR for that lake type where fish data were available. We then reduced the productive capacity by this amount (Table 11).

Further adjustments to model predictions need to be made if the lake contains age-1 sockeye fry or if smolt weight at capacity are known to be <4.5 g (Cox-Rogers et al. 2004) (Table 11). In this study, age-1 sockeye fry were found in Morice, Motase, and both Banks lakes. Based on trawl survey data (J. Hume, unpublished data), average smolt weights (age-1 and age-2 combined) were estimated as 4.7 g in the Banks lakes (4.5 g age-1 smolts and 5% 9.0 g age-2 smolts) and 7.2 g in Motase Lake (4.5 g age-1 smolts and 40% age-2 smolts). Using available smolt data, average weight

of Morice Lake smolts was estimated as 5.6 g (Cox-Rogers et al. 2004). Estimated size of Owikeno Lake smolts at capacity was 2.3 g (Shortreed and Morton 2003).

Limnetic macroinvertebrates may also compete with juvenile sockeye for zooplankton prey and so further reduce a lake's productive capacity. However, their effect on the productive capacity of a sockeye lake is potentially much more difficult to estimate than that of planktivorous fish. Determining their abundance in a lake requires specialized sampling (large nets, night-time sampling, monthly intervals) that is not feasible on many of these remote lakes. If their abundance can be quantified, there are further difficulties in estimating the extent to which they compete with sockeye fry. For example, *Chaoborus* can effectively graze on *Daphnia* (Vanni 1988), but unlike sockeye fry, it frequently shows a preference for smaller bodied zooplankton (Swift and Fedorenko 1975; Campbell 1991). In contrast, *Neomysis* and *Leptodora* often selectively feed on *Daphnia* (Murtaugh 1981; Lunte and Luecke 1990; Chigbu 2004). Further, *Chaoborus* and *Neomysis* are often omnivorous and phytoplankton may constitute a portion of their diet (Swift 1992; Hyatt et al. 2005b). Finally, as well as competing with sockeye fry, all three of these macroinvertebrates may be prey items for the same fry. These "trophic triangles" (Lunte and Luecke 1990; Hyatt et al. 2005b) make it even more difficult to ascertain the extent to which macroinvertebrates reduce a lake's productive capacity for sockeye. In Kitwanga and Lakelse lakes, we have direct evidence from sockeye stomach contents and from stable isotope analyses that this trophic triangle is occurring (Shortreed and Hume, unpublished data). Given these uncertainties, we made no adjustments to PR model predictions when limnetic macroinvertebrates were present. Consequently, at present the model assumes that a reduction in food resources caused by macroinvertebrate grazing is balanced by benefits accruing to sockeye fry from grazing on macroinvertebrates (Table 10, 11).

Composition of the phytoplankton community also has the potential to affect a lake's productive capacity. Currently, the PR model assumes there is a linear relationship between phytoplankton carbon uptake and production of limnetic fish biomass, so it is implicit in the model that energy transfer efficiencies between trophic levels remain constant. In a given lake, if a greater than usual proportion of phytoplankton production is composed of species too large to be grazeable by zooplankton, then energy transfer efficiencies will be lower, and productive capacity will be reduced. Most grazeable phytoplankton fall into the nanoplankton size category (2-20 µm maximum dimension). However, smaller particles can also be consumed by some cladocerans (Wetzel 2001). Consequently, ultraplankton (0.2-20 µm maximum dimension) may also be considered the grazeable fraction.

In our study lakes, nanoplankton volume averaged 106 mm^3/m^3 (2 SE=37, range: 24-654 mm^3/m^3), or an average of 15% of total phytoplankton volume. Ultraplankton volume averaged 26% of total volume (161 mm^3/m^3, 2 SE=43, range: 26-671 mm^3/m^3). We obtained similar results in four large sockeye nursery lakes (Babine, Stuart, Takla, and Trembleur) in central British Columbia, where seasonal average nanoplankton volume was 98 mm^3/m^3 (17% of total phytoplankton volume) and average ultraplankton volume was 161 mm^3/m^3, or 30% of total volume (K. Shortreed, unpublished data). We

suggest that in the majority of these oligotrophic lakes, nanoplankton and ultraplankton biomass comprises a relatively constant proportion of the phytoplankton community.

However, using phytoplankton volume to assess the suitability of the phytoplankton community for zooplankton grazing can be misleading, since the importance of both nanoplankton and ultraplankton is usually substantially more than volume would indicate. For example, in the four large central B.C. lakes mentioned earlier, the relative proportion of nanoplankton biomass as chlorophyll was substantially greater than volume, averaging 36% of total phytoplankton chlorophyll (Shortreed and Morton 2000; Malange et al. 2005). Chlorophyll concentration of the ultraplankton averaged 83% of total chlorophyll, as compared to only 30% of total volume. In the same lakes, nanoplankton PR averaged 44% of total PR and ultraplankton PR was 83% of total PR. In contrast, microplankton (>20 µm maximum dimension) averaged 71% of total phytoplankton volume but only 17% of both total chlorophyll and total PR. In our study lakes, microplankton PR was not measured, but microplankton volume averaged a similar 74% of total phytoplankton volume. We suggest that if PR of both ultraplankton and microplankton were obtained, adjustments to PR model predictions could be made based on the proportion of the total PR represented by each fraction.

Poor quality grazing for zooplankton may result from several causes. In extremely unproductive lakes, there may be insufficient grazeable phytoplankton (nanoplankton) to support a zooplankton community of sufficient quantity and quality to be favourable to sockeye. In other lakes, despite adequate biomass and productivity of grazeable phytoplankton, mechanical interference by either abiotic or biotic particles may reduce filtration efficiencies. We previously suggested that interference by abiotic particles in several of the more glacially turbid lakes reduced cladoceran abundance. In other lakes, biotic particles may be of high enough density to reduce zooplankton grazing efficiency. For example, one of our study lakes (Johnston) had very little glacial turbidity (EZD of 10.7 m), but had extremely high (15,000/mL) numbers of the large diatom *Rhizosolenia* sp. So, although nanoplankton volume (83 mm^3/m^3) in Johnston Lake was near the average for all lakes, the high *Rhizosolenia* density resulted in nanoplankton making up only 0.5% of total phytoplankton volume. Because of this, it is most likely that carbon transfer efficiencies were lower in Johnston Lake than in the other study lakes, and may at least partially explain why Johnston Lake had the lowest volumetric zooplankton biomass (2.1 mg dry wt/m^3) of all study lakes. However, Johnston Lake also had very high numbers of limnetic fish (i.e. high grazing pressure on the plankton community) (Table 11,12).

The preceding paragraphs illustrate some of the challenges in applying the PR model to lakes which have complex limnetic planktivore communities and/or phytoplankton communities much different than the norm. To summarize, these include: other planktivorous fish species (including kokanee), more than one age class of sockeye fry, limnetic macroinvertebrates, and high abundances of non-grazeable phytoplankton. Estimates of planktivorous fish biomass may be obtained through acoustic and trawl surveys. We can then make the assumption that they are equal competitors with sockeye and correct for their presence. Biomass of invertebrate

planktivores can be determined with sufficiently intensive sampling, but further work is needed to determine to what extent, if any, these animals reduce a lake's sockeye productive capacity. In a small proportion of lakes we have studied to date, a high proportion of non-grazeable phytoplankton may reduce productive capacity. Estimating the PR of grazeable and non-grazeable phytoplankton appears to be the best way to ascertain differences from the norm and to make adjustments.

Once PR model predictions have been finalized, predicted maximum numbers or biomass can be compared with observed numbers or biomass (Table 12). This is a useful tool in determining current status of sockeye in a particular lake, including the amount of rebuilding that could potentially occur. Although PR model predictions are for smolt numbers and biomass, most available juvenile sockeye data from north coast lakes were collected during summer (August-September) acoustic and trawl surveys (J. Hume, unpublished data). Biomass of sockeye fry collected during these summer surveys is assumed to be equivalent to smolt biomass. In other words, mortality from summer to the following spring is assumed to be offset by growth during the same period.

However, for several reasons estimates of fry biomass collected in summer are likely to underestimate smolt biomass. First, efficiency of the small (2x2-m diameter) trawl used on the majority of these lakes declines as fry size increases, so on some lakes average fry size is underestimated, although we attempted to correct for this using formulas from (Hyatt et al. 2005a). Second, in most lakes sockeye fry mortality is highest early in lake residence and before the acoustic and trawl surveys took place. Conversely, most sockeye fry growth occurs between summer and the following spring, after the surveys take place. The net result of these factors is the likelihood that these summer fry biomass estimates underestimate smolt biomass, and so underestimate the proportion of the rearing capacity that is utilized (Table 12). An alternative to using summer fry biomass as a surrogate for smolt biomass is to assume that summer fry numbers are equivalent to smolt numbers. Since this assumes that mortality from summer to spring is zero, obviously it overestimates smolt numbers and the proportion of the rearing capacity that is utilized, but it does provide an upper boundary (Table 12).

Given that summer fry biomass and summer fry numbers provide underestimates and overestimates (respectively) of rearing capacity usage, in Table 12 we present both in order to provide a range that will contain the actual degree of utilization. Based on biomass, the amount of rearing capacity utilized ranged from 0-44% and averaged 12%. Using numbers, rearing capacity utilization averaged 31% and ranged from 0-161%.

The lakes in this study exhibited considerable variability in everything from physical and chemical characteristics, to plankton community structure and productivity, to composition of their limnetic fish communities, and finally to the proportion of their rearing capacity that is currently utilized. Even lakes that superficially appear very similar and are situated very close to each other may have substantially different limnological characteristics and equally different fish communities.

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Table 1. Morphometric and bathymetric data from the study lakes.

Water type	Location	Lake	Date sampled	Lat. (°N)	Long. (°W)	Elevation (m)	Surface area (ha)	Depth (m)		
								Mean	Max.	At sampling location
Clear	Interior	Aldrich	2-Sep-01	54°45'	127°22'	876	64	4.4	5.6	5.3
Clear	Interior	Azuklotz	9-Sep-03	56°05'	126°44'	783	165	4.1	9.5	8.7
Clear	Interior	Bear	9-Sep-03	56°07'	126°50'	780	1,884	14	75	37.8
Clear	Interior	Charlotte	4-Sep-97	52°11'	125°20'	1,169	6,597	41	101	79
Clear	Interior	Club	11-Sep-02	55°47'	128°34'	522	39	3.7	9.8	8.5
Clear	Interior	Dennis	2-Sep-01	54°46'	127°26'	841	90	2.6	5.5	5.6
Clear	Interior	Elbow	8-Sep-99	52°05'	125°42'	576	146	14	34	32
Clear	Interior	Kitwanga	12-Sep-03	55°22'	128°07'	376	774	5.0	9.5	9
Clear	Interior	Lakelse	14-Sep-03	54°23'	128°33'	77	1,372	8.5	32	28.5
Clear	Interior	Lonesome	8-Sep-99	52°14'	125°43'	482	408	14	41	35
Clear	Interior	McDonell	2-Sep-01	54°47'	127°36'	827	227	8.2	14.6	12.9
Clear	Interior	Rainbow	9-Sep-99	52°07'	125°43'	569	170	3.8	9	8
Clear	Interior	Slamgeesh	3-Sep-01	55°46'	128°26'	630	45	3.9	7.5	7.4
Clear	Interior	Stephens	11-Sep-02	55°45'	128°37'	518	188	11	26.9	24.8
Clear	Interior	Swan	11-Sep-02	55°46'	128°39'	525	1,736	36	68	67.5
Glacial	Coast	Johnston	20-Aug-05	53°53'	129°27'	25	187	47	80	82
Glacial	Interior	Kluayaz	25-Aug-04	57°01'	128°12'	1,012	139			20
Glacial	Interior	Morice	15-Sep-02	54°00'	127°40'	764	9,739	100		156
Glacial	Interior	Motase	10-Sep-03	56°02'	127°03'	1,021	397	13.4	31	32
Glacial	Coast	Owikeno	22-Aug-01	51°40'	126°53'	10	9,343	172	366	>100
Glacial	Interior	Sicintine	25-Aug-04	55°58'	127°23'	977	68	2.4	4	3.7
Stained	Coast	Banks E.	29-Aug-04	53°23'	130°08'	18	204	22	65	39.9
Stained	Coast	Banks W.	29-Aug-04	53°23'	130°12'	21	160	13	45	43
Stained	Coast	Canoona	31-Aug-04	53°03'	128°36'	37	345			60.4
Stained	Coast	Deer - north	31-Aug-04	53°14'	129°50'	37	323			49.8
Stained	Coast	Ecstall	20-Aug-05	53°45'	129°24'	35	90	7.0	20	20.2
Stained	Coast	Evelyn	5-Sep-01	53°36'	128°56'	33	59	15	23	20
Stained	Coast	Hartley Bay	21-Aug-05	53°26'	129°17'	18	93	3.5	9.5	10
Stained	Coast	Ian	23-Aug-05	53°46'	132°33'	39	1,878	47	165	>100
Stained	Coast	Keecha	30-Aug-04	53°18'	129°53'	11	339			67.3
Stained	Coast	Kitkiata	21-Aug-05	53°43'	129°17'	31	270	26	59	60.1
Stained	Coast	Kooryet	30-Aug-04	53°21'	129°59'	21	301			55
Stained	Coast	Mikado lower	6-Sep-01	53°26'	129°48'	19	74			51.9
Stained	Coast	Mikado middle	6-Sep-01	53°26'	129°45'	19	74			65.3
Stained	Coast	Mikado upper	6-Sep-01	53°26'	129°42'	44	119			59
Stained	Coast	Moore	28-Aug-04	53°25'	129°30'	4	283			41.5
Stained	Coast	Tsimtack	28-Aug-04	53°24'	129°28'	3	191			75

Table 2. Variation in thermal structure and water clarity in the study lakes (EPZ=epilimnion depth, SD=Secchi depth, EZD=euphotic zone depth).

Lake	Station	Surface temperature (°C)	EPZ (m)	Type of seasonal stratification	SD (m)	EZD (m)	Turbidity (NTU)
Aldrich	1	13.5		Polymictic	4.0	7.2	
Azuklotz	1	13.8	4.2	Polymictic	3.7	6.2	1.1
Club	1	13.6	5.0	Polymictic	7.5	8.5	
Dennis	1	12.6	4.8	Polymictic	4.0	8.7	
Kitwanga	1	15.5		Polymictic	4.2	9.4	
Lakelse	2	14.9		Polymictic	3.6	8.6	
McDonell	1	13.8		Polymictic	5.3	9.7	
Slamgeesh	1	11.9	2.4	Polymictic	3.4	4.9	
Bear	1	14.0	7.3	Dimictic	5.9	8.1	0.5
Bear	2	13.2	7.0	Dimictic	5.5	8.0	0.7
Charlotte	1	15.0	15.0	Dimictic	11.0	22.8	
Charlotte	2	14.7	15.3	Dimictic	14.5	21.4	
Elbow	1	13.5	13.0	Dimictic	5.0	7.9	
Kitwanga	2	15.3	8.6	Dimictic	9.2	15.1	
Lakelse	1	15.0	24.4	Dimictic	3.3	8.1	
Lonesome	1	14.8	14.0	Dimictic	7.5	11.7	
Rainbow	1	14.6		Dimictic	6.5	9.6	
Stephens	1	14.0	7.3	Dimictic	8.1	12.3	
Swan	1	13.6	8.6	Dimictic	10.3	15.4	
Kluayaz	1	11.9	1.9	Dimictic	0.1	0.4	114
Morice	2	9.7	17.9	Dimictic	8.3	19.3	0.4
Morice	5	10.8	19.7	Dimictic	11.0	23.0	0.4
Motase	1	9.6		Dimictic	0.2	1.7	30
Motase	2	9.5		Dimictic	0.2	1.8	26
Owikeno	1	13.9	27.0	Dimictic	1.8	8.0	2.8
Sicintine	1	13.2		Dimictic	0.5	2.1	11
Johnston	1	16.1	3.3	Monomictic	4.2	10.7	2.1
Owikeno	2	14.0	38.0	Monomictic	1.5	5.2	4.8
Owikeno	3	13.9	50.0	Monomictic	0.9	4.0	9.3
Owikeno	4	14.2	54.0	Monomictic	0.8	3.9	8.2
Banks E.	1	19.9	5.0	Monomictic	3.5	4.0	0.6
Banks W.	1	19.2	5.9	Monomictic	3.5	3.9	0.2
Canoona	1	18.3	5.0	Monomictic	5.2	6.4	0.5
Deer - north	1	19.7	4.9	Monomictic	3.5	4.6	0.1
Ecstall	1	19.2	3.2	Monomictic	10.1	9.0	0.5
Evelyn	1	12.3	8.5	Monomictic	3.7	5.4	
Hartley Bay	1	19.1	1.8	Monomictic	4.1	4.7	0.7
Ian	1	20.6	8.3	Monomictic	2.9	3.4	0.2
Ian	2	18.5	6.7	Monomictic	4.2	4.1	0.2
Keecha	1	19.6	5.0	Monomictic	4.2	5.8	0.1
Kitkiata	1	19.3	1.6	Monomictic	4.4	6.8	0.7
Kooryet	1	20.0	6.0	Monomictic	6.2	8.8	0.8
Mikado lower	1	11.9	13.6	Monomictic	4.7	5.9	
Mikado middle	1	11.6	12.0	Monomictic	4.7	5.7	
Mikado upper	1	11.5	9.5	Monomictic	4.3	6.1	
Moore	1	20.0	4.1	Monomictic	6.8	8.7	0.4
Tsimtack	1	17.5	1.4	Monomictic	7.4	9.5	0.2

Table 3. Variation in mean epilimnetic values of selected chemical variables.

Lake	Station	Conductivity (µS/cm)	DO (mg/L)	pH	T. Alk. (mg $CaCO_3$/L)	DIC (mg/L)	TDS (mg/L)	Diss. silica (mg Si/L)
Aldrich	1	31		6.29	12.8	6.53	32	1.31
Azuklotz	1	55	10.1	6.68	26.6	9.98	47	1.75
Bear	1	42	9.1	6.97			41	1.33
Bear	2	56	9.9	6.52	22.4	7.97	39	1.66
Charlotte	1	101		7.12			20	1.28
Charlotte	2	57		6.87	12.1	3.53	23	1.22
Club	1	55	9.5	6.60	17.4	5.41	29	0.60
Dennis	1	53		6.49	32.5	12.77	44	1.20
Elbow	1	48			12.6	4.58	28	1.20
Kitwanga	1	48	8.8	6.74	58.9	17.01	69	1.98
Kitwanga	2	47	8.8		62.2	18.44	77	2.25
Lakelse	1	46	9.7	7.55	24.7	8.18	33	1.87
Lakelse	2	27		6.67	24.5	7.92	43	1.86
Lonesome	1	102		7.09	14.4	4.75	28	0.49
McDonell	1	57		6.83	32.3	12.56	47	2.17
Rainbow	1	25		6.80	13.4	4.37	21	1.28
Slamgeesh	1	26		6.82	31.0	12.66	53	1.99
Stephens	1	42	9.5	7.00	17.8	5.52	29	0.58
Swan	1	41	9.8	7.03	17.1	5.14	31	0.71
Johnston	1	70	11.9	7.18	4.8	2.58	11	0.11
Kluayaz	1	43	9.5	7.04	31.8	8.79	79	1.14
Morice	2	43	11.0	6.98	16.4	4.97	24	1.02
Morice	5	22	10.5	6.46	15.7	4.85	27	1.09
Motase	1	22	12.2	6.44	4.2	1.97	15	0.24
Motase	2	18	11.8	5.94	4.0	1.93	11	0.17
Owikeno	1	42	12.4	6.95	4.1	3.46	12	0.12
Owikeno	2	20	11.6	6.29	6.6	4.04	16	0.66
Owikeno	3	21	12.8	6.14	9.8	5.32	23	0.45
Owikeno	4	23	11.6	6.23	9.4	4.95	25	0.34
Sicintine	1	25	9.9	6.29	16.6	5.06	33	0.76
Banks E.	1	19	8.9	6.26	2.2	1.22	27	0.01
Banks W.	1	21	8.7	6.22	1.7	0.96	21	0.01
Canoona	1	16	9.5	6.15	1.6	1.06	23	0.01
Deer	1	30	9.1	6.51	3.4	1.41	37	0.02
Ecstall	1	26	9.3	6.41	9.5	4.47	22	0.28
Evelyn	1	20		6.43	3.8	1.76	23	0.09
Hartley Bay	1	13	8.8	5.67	1.3	1.99	18	0.01
Ian	1	30	9.4	6.30	4.3	2.25	35	0.07
Ian	2	31	9.3	5.76	4.2	5.30	32	0.11
Keecha	1	24	9.1	6.28	2.1	1.11	36	0.00
Kitkiata	1	21	11.3	6.16	4.4	2.78	15	0.16
Kooryet	1	20	9.2	6.03	1.0	0.70	19	0.00
Mikado lower	1	16		5.56	0.2	0.61	7	0.10
Mikado middle	1	16		5.55	0.1	0.50	5	0.10
Mikado upper	1	16		5.42	0.0	0.52	5	0.10
Moore	1	71	8.9	6.05	1.5	1.10	136	
Tsimtack	1	7550	9.4	7.90	86.7	22.68	8395	

Table 4. Variation in epilimnetic and hypolimnetic values for nutrient data.

		Nitrate (µg N/L)		Ammonia (µg N/L)		Phosphorus (µg/L) (epil.)		
Lake	Station	Epil.	Hypol.	Epil.	Hypol.	Total	Dissolved	Soluble reactive
Aldrich	1	1.3		3.7		15.5	5.0	6.4
Azuklotz	1	2.0		3.3		11.6	7.2	1.6
Bear	1	1.4	103.5	3.6		9.0	6.9	1.3
Bear	2	2.4	78.8	5.3	4.7	7.5	5.8	1.1
Charlotte	1	14.2	11.9			3.9		
Charlotte	2	8.2	9.7			3.7		
Club	1	0.9		1.6		4.7	2.8	0.6
Dennis	1	0.6		4.3		6.0	5.2	1.4
Elbow	1	4.8	54.1	2.9	6.8	4.6	3.0	1.5
Kitwanga	1	1.3		3.5		15.1	10.1	3.1
Kitwanga	2	0.6	1.0	6.0		15.9	10.4	3.4
Lakelse	1	5.7	139.2	3.4	3.5	3.9	3.8	1.4
Lakelse	2	5.9		3.0		6.3	3.7	1.1
Lonesome	1	2.1	30.9	7.6	1.8	6.1	2.5	0.7
McDonell	1	0.3		3.9		7.3	5.7	1.3
Rainbow	1	2.4		4.8		4.4	2.7	2.0
Slamgeesh	1	14.5		40.9	202.3	16.5	9.9	2.1
Stephens	1	0.8		2.5		5.2	2.3	0.7
Swan	1	2.4	24.2	6.0	0.8	3.5	2.6	0.5
Johnston	1	2.5	131.7	4.0	4.8	6.0	1.4	0.5
Kluayaz	1	2.1	25.1	3.8	3.2			4.7
Morice	2	31.9	44.5	0.5		4.9	3.9	1.2
Morice	5	27.8	44.4	0.4	3.9	4.5	3.3	1.0
Motase	1	1.2	4.4	3.4				4.6
Motase	2	0.4	27.5	2.2	2.0			2.5
Owikeno	1	2.7	144.2	5.0	144.0	5.7	2.3	0.3
Owikeno	2	1.8	77.8	3.3	77.8			0.9
Owikeno	3	25.6	49.1	5.1	49.1			2.6
Owikeno	4	23.1	61.9	11.2	61.9			2.0
Sicintine	1	1.4		2.4	3.8			1.0
Banks E.	1	0.7	12.2	4.9	10.3	2.7	1.5	0.6
Banks W.	1	1.0	20.1	7.7	15.7	2.6	1.2	1.0
Canoona	1	8.2	79.5	4.6	7.0	2.7	2.1	0.8
Deer - north	1	0.8	22.4	4.4	10.2	1.9	1.0	0.8
Ecstall	1	2.6	16.5	4.3	18.1	3.8	2.1	1.0
Evelyn	1	60.7	146.2	13.3	5.7	5.3	2.7	0.3
Hartley Bay	1	0.5		5.2	2.7	4.2	2.2	0.6
Ian	1	17.4	41.9	6.2		3.2	2.6	2.1
Ian	2	20.5	51.1	7.1	19.9	3.5	2.3	1.2
Keecha	1	0.1	16.4	3.4		2.2	0.9	0.5
Kitkiata	1	1.2	76.1	4.7		6.7	2.5	0.3
Kooryet	1	0.1	27.8	1.6	10.4	1.4	0.7	0.4
Mikado lower	1	10.4	18.9	9.6	12.5	3.7	0.8	0.1
Mikado middle	1	10.1	19.8	12.4	9.5	3.2	0.9	0.1
Mikado upper	1	8.1	17.8	8.6	10.3	3.6	1.8	0.1
Moore	1							
Tsimtack	1							

Table 5. Variation in biological variables, including phytoplankton numbers and volume, with the exception of daily PR, data are mean epilimnetic.

					Phytoplankton					
		Bacteria	Chlorophyll	Daily PR	Numbers (thousands/mL)			Volume (mm^3/m^3)		
Lake	Station	(#x10^6/mL)	(µg/L)	(mg $C \cdot m^{-2} \cdot d^{-1}$)	Pico.	Nano.	Micro.	Pico.	Nano.	Micro.
Aldrich	1	1.06	1.70	154	4.9	1.1	1.38	15	56	731
Azuklotz	1	2.27	1.91	372	46.9	19.7	2.09	96	156	821
Bear	1		1.52							
Bear	2	2.08	1.77	231	33.2	10.0	2.71	65	176	2,059
Charlotte	1	1.88	0.49		36.4	7.3	0.38	80	45	173
Charlotte	2	1.38	0.47	76	39.9	14.5	0.43	90	57	124
Club	1	1.72	1.29	113	69.2	9.1	0.24	141	59	155
Dennis	1	1.08	0.74	69	7.0	0.6		17	33	385
Elbow	1	2.07	0.64	79	1.1	0.5	0.18	2	33	171
Kitwanga	1		2.19	274						
Kitwanga	2	2.44	2.66	301	41.5	16.2	0.94	85	93	443
Lakelse	1	1.25	1.51	144	36.2	11.7	2.05	80	193	1,795
Lakelse	2		1.34	108						
Lonesome	1	2.36	0.62	86	5.2	0.4	0.18	11	24	118
McDonell	1	0.80	0.78	80	15.0	2.0	0.52	28	49	681
Rainbow	1	1.64	0.61	103	0.3	0.4	0.14	1	25	87
Slamgeesh	1	2.10	1.52	92	2.1	0.7	0.82	5	40	890
Stephens	1	2.56	1.08	199	84.2	15.2	0.51	176	60	201
Swan	1	1.65	0.71	130	65.9	11.3	0.40	154	62	166
Johnston	1	1.18	2.79	283	15.3	1.3	14.96	33	83	15,650
Kluayaz	1	1.04	1.48	8	6.6	14.4	0.27	17	654	256
Morice	2		0.45	71						
Morice	5	1.23	0.54	89	44.6	8.2	0.13	91	43	131
Motase	1		0.88	17						
Motase	2	0.96	1.13	20	33.8	7.9	0.68	67	411	679
Owikeno	1		1.26	109						
Owikeno	2	0.65	2.73	148	1.2	2.8	0.98	4	180	1,163
Owikeno	3		2.18	131						
Owikeno	4	0.62	1.93	86	21.8	11.0	1.24	49	195	1,833
Sicintine	1	1.32	0.85	31	131.9	3.7	0.55	258	201	579
Banks E.	1	1.27	0.87	51	3.7	7.0	4.60	10	136	975
Banks W.	1	0.97	0.53	89	8.5	1.7	0.68	20	50	258
Canoona	1	1.15	0.63	97	13.6	1.0	1.61	37	34	224
Deer - north	1	0.88	0.61	66	9.5	4.8	1.89	26	48	140
Ecstall	1	1.38	1.54	190	26.8	7.6	2.57	56	72	772
Evelyn	1	1.48	1.56	85	6.7	3.5	0.49	19	84	525
Hartley Bay	1	1.91	0.61	69	11.0	2.8	0.42	29	56	238
Ian	1	1.61	1.02	63	6.1	3.7	0.31	15	117	279
Ian	2		0.69	74						
Keecha	1	0.93	0.85	76	14.5	8.2	1.95	51	76	388
Kitkiata	1	2.33	3.43	387	53.7	10.2	0.81	110	137	591
Kooryet	1	0.88	0.64	74	20.5	8.1	1.87	62	65	230
Mikado lower	1	0.95	0.44	20	3.9	0.9	0.53	11	52	734
Mikado middle	1	0.90	0.51	20	7.5	1.0	0.63	19	50	765
Mikado upper	1	0.80	0.63	32	3.9	0.9	0.61	11	38	614
Moore	1	0.86	0.66	68	9.3	2.0	1.60	28	49	530
Tsimtack	1	0.57	0.89	192	52.6	5.0	0.51	101	125	464

Table 6. Variation in dry biomass of the major zooplankton groups. To convert to areal biomass (mg dry wt/m2). data should be multiplied by haul depth.

		Haul	Zooplankton biomass (mg dry wt/m³)					
Lake	Station	depth (m)	Total	Daphnids	Bosminids	*Holopedium*	Cyclopoids	Calanoids
Aldrich	1	4.5	269.9	225.8	0.1	2.1	41.9	0.0
Azuklotz	1	9.0	33.1	17.5	0.3	0.0	14.6	0.6
Bear	1	30.0	29.7	0.2	0.8	0.0	5.1	21.0
Bear	2	30.0	15.4	1.9	0.8	0.1	6.0	6.6
Charlotte	1	30.0	49.2	23.2	2.0	0.1	5.6	18.3
Charlotte	2	30.0	54.6	24.2	2.0	0.0	8.2	20.0
Club	1	5.0	23.3	0.6	18.3	0.0	1.5	2.8
Dennis	1	4.5	256.3	223.3	2.8	0.0	30.3	0.0
Elbow	1	30.0	38.7	9.8	6.1	0.0	22.8	0.0
Kitwanga	1	8.0	74.1	67.5	0.0	0.0	0.9	4.7
Kitwanga	2	13.0	78.4	72.0	0.0	0.0	2.3	3.8
Lakelse	1	28.0	12.1	0.4	0.1	0.0	10.8	0.4
Lakelse	2	5.0	6.4	1.1	0.0	0.0	4.4	0.3
Lonesome	1	30.0	70.5	55.9	0.7	0.0	7.8	6.1
McDonell	1	11.0	47.0	29.1	1.8	0.0	15.7	0.4
Rainbow	1	8.0	89.9	85.8	0.3	0.0	3.3	0.0
Slamgeesh	1	6.5	331.9	258.3	41.0	0.0	25.8	4.2
Stephens	1	20.0	21.8	0.0	1.2	0.0	9.8	9.8
Swan	1	30.0	28.0	10.1	3.5	0.0	10.4	3.9
Johnston	1	30.0	1.8	0.3	1.2	0.0	0.2	0.0
Kluayaz	1	17.0	2.5	0.0	0.0	0.0	2.5	0.0
Morice	2	50.0	16.6	0.8	1.4	8.2	6.0	0.1
Morice	5	50.0	10.6	0.3	1.7	3.9	4.7	0.0
Motase	1	25.0	7.4	0.0	0.0	0.0	7.3	0.1
Motase	2	25.0	8.4	0.0	0.0	0.0	8.4	0.0
Owikeno	1	50.0	5.3	0.5	0.0	0.0	0.3	4.5
Owikeno	2	50.0	7.4	0.8	0.0	0.0	0.0	6.5
Owikeno	3	50.0	5.1	0.0	0.0	0.0	0.1	4.9
Owikeno	4	50.0	13.1	0.0	0.0	0.0	0.1	12.9
Sicintine	1	3.0	2.1	0.0	2.0	0.0	0.1	0.0
Banks E.	1	30.0	4.9	0.7	1.4	0.9	0.4	1.5
Banks W.	1	30.0	37.1	20.3	15.1	0.1	0.0	1.5
Canoona	1	30.0	9.3	0.9	7.4	0.0	0.2	0.8
Deer - north	1	30.0	13.9	4.7	0.5	0.0	0.0	8.6
Ecstall	1	15.0	4.5	0.1	3.4	0.1	0.9	0.0
Evelyn	1	20.0	33.8	17.5	4.4	0.2	0.2	11.3
Hartley Bay	1	7.0	12.1	0.2	4.7	0.1	0.2	6.8
Ian	1	30.0	14.1	9.1	1.1	1.0	1.9	1.1
Ian	2	30.0	22.2	14.0	0.4	0.7	6.5	0.5
Keecha	1	30.0	3.7	0.0	1.1	0.0	0.2	2.1
Kitkiata	1	30.0	2.7	0.1	1.7	0.0	0.7	0.0
Kooryet	1	30.0	4.8	0.0	1.2	0.0	0.0	3.5
Mikado lower	1	30.0	18.9	0.2	12.1	0.0	0.0	6.6
Mikado middle	1	30.0	7.6	0.5	4.5	0.0	0.0	2.6
Mikado upper	1	30.0	19.3	3.4	6.6	0.0	0.3	8.9
Moore	1	25.0	2.3	0.0	1.2	0.0	0.1	0.7
Tsimtack	1							

Table 7. Variation in macroinvertebrate abundance in the study lakes. Sampling methods were: 1. Wisconsin plankton net (160-µm mesh, daytime sampling); 2. SCOR plankton net (350-µm mesh, night time sampling); and 3. Acoustic and trawl survey. Quantitative seasonal estimates were obtained only in Kitwanga and Lakelse lakes.

Lake	Sampling methods	Macroinvertebrate number/m²		
		Chaoborus	*Neomysis*	*Leptodora*
Aldrich	1, 3	low	0	0
Azuklotz	1, 3	0	0	11
Bear	1, 3	0	0	0
Charlotte	1, 3	0	0	320
Club	1, ,2 ,3	0	0	0
Dennis	1	no data	no data	0
Elbow	1	no data	no data	0
Kitwanga	1, 2, 3	664	0	228
Lakelse	1, 2, 3	0	145	0
Lonesome	1	no data	no data	0
McDonell	1, 2, 3	0	0	0
Rainbow	1	no data	no data	400
Slamgeesh	1	0	0	0
Stephens	1, 2, 3	0	0	0
Swan	1, 2, 3	0	0	0
Johnston	1, 2, 3	0	0	0
Kluayaz	1	no data	no data	11
Morice	1, 3	0	0	0
Motase	1, 3	no data	no data	0
Owikeno	1	0	0	0
Sicintine	1	0	0	0
Banks E.	1, 2, 3	moderate	0	0
Banks W.	1, 2, 3	moderate	0	0
Canoona	1	no data	no data	0
Deer	1	no data	no data	0
Ecstall	1, 2, 3	0	0	0
Evelyn	1, 2, 3	high	0	0
Hartley Bay	1, 2, 3	high	0	0
Ian	1	no data	no data	0
Keecha	1	low	no data	398
Kitkiata	1, 2, 3	0	0	0
Kooryet	1	no data	no data	92
Mikado lower	1	low	no data	0
Mikado middle	1	low	no data	0
Mikado upper	1	moderate	no data	0
Moore	1	no data	no data	0
Tsimtack		no data	no data	no data

Table 8. Means of selected variables in lakes of different water types. The italicized numbers are 2 SE.

	Clear (n=15)		Stained (n=16)		Glacial (n=6)	
Surface temperature (°C)	13.9	*0.5*	17.4	*1.7*	12.6	*2.0*
Thermocline depth (m)	9.5	*3.6*	5.9	*1.8*	16.7	*18.8*
Secchi depth (m)	6.4	*1.4*	5.0	*0.9*	2.3	*2.4*
Euphotic zone depth (m)	10.4	*2.3*	6.2	*1.0*	6.8	*6.3*
Total dissolved solids (mg/L)	37	*8*	21	*6*	30	*21*
pH	6.80	*0.16*	6.16	*0.28*	6.67	*0.35*
Conductivity (µS/cm)	47	*10*	20	*3*	36	*16*
Total alkalinity (mg $CaCO_3$/L)	23.3	*6.7*	2.5	*1.3*	13.5	*8.6*
Dissolved inorganic carbon (mg/L)	8.16	*2.21*	1.63	*0.66*	4.62	*1.97*
Dissolved reactive silica (mg Si/L)	1.34	*0.30*	0.07	*0.04*	0.61	*0.36*
Nitrate (µg N/L)	3.4	*2.1*	8.8	*8.5*	8.3	*9.4*
Total phosphorus (µg/L)	7.8	*1.2*	3.4	*0.4*		
Bacteria (#x10^5/mL)	1.78	*0.14*	1.18	*0.12*	1.06	*0.10*
Chlorophyll (µg/L)	1.19	*0.32*	0.95	*0.37*	1.44	*0.69*
Photosynthetic rate (mg $C \cdot m^{-2} \cdot d^{-1}$)	137	*46*	99	*46*	108	*95*
Photosynthetic rate (mg $C \cdot m^{-3} \cdot d^{-1}$)	15.8	*7.3*	15.8	*6.3*	20.0	*11.7*
Zooplankton biomass (mg dry wt/m²)						
Total	895	*301*	351	*151*	215	*200*
Macrozooplankton	894	*302*	345	*153*	213	*201*
Daphnids	552	*279*	106	*93*	9	*9*
Bosminids	51	*38*	115	*68*	19	*24*
Cyclopoid copepods	185	*79*	13	*16*	81	*88*
Calanoid copepods	99	*84*	79	*46*	57	*113*

Table 9. Results of an ANOVA of selected physical, chemical, and biological variables from clear, stained, and glacial lakes. Underlined numbers are not significantly different (F test, p>0.05) from each other.

Variable	Lake type		
	Stained	**Clear**	**Glacial**
Surface temperature (°C)	17.4	13.9	12.6
Thermocline depth (m)	5.9	9.5	16.7
Secchi depth (m)	5.0	6.4	2.3
	Clear	**Glacial**	**Stained**
Euphotic zone depth (m)	10.4	6.8	6.2
pH	6.80	6.67	6.16
Conductivity (µS/cm at 25 °C)	47	36	20
Total dissolved solids (mg/L)	37	30	21
Total alkalinity (mg $CaCO_3$/L)	23.3	13.5	2.5
Dissolved inorganic carbon (mg/L)	8.16	4.62	1.63
Soluble reactive silica (mg Si/L)	1.34	0.61	0.07
Nitrate (µg N/L) – epilimnetic	3.4	8.8	8.3
Nitrate (µg N/L) – hypolimnetic	48	58	40
Total P (µg/L)	7.8		3.4
Bacteria (no.x10^6/mL)	1.78	1.06	1.18
Chorophyll (µg/L)	1.19	1.44	0.95
Daily PR (mg C·m^{-2}·d^{-1})	137	108	99
Daily PR (mg C·m^{-3}·d^{-1})	15.8	20.0	15.8
Zooplankton biomass (mg dry wt/m^2)	895	215	351
Cyclopoid copepods (mg dry wt/m^2)	185	81	13
Calanoid copepods (mg dry wt/m^2)	99	57	79
Daphnids (mg dry wt/m^2)	552	8.5	106
	Stained	**Clear**	**Glacial**
Bosminids (mg dry wt/m^2)	115	51	19

Table 10. PR model predictions for the study lakes. These are not adjusted for biomass of non-sockeye or for proportion of age-2 smolts.

		Average daily PR (mg/m²)				Unadjusted PR model predictions		
Lake	No. sampling dates	PR_{mean}	Adjusted for bathymetry	Converted to mean seasonal PR	PR_{total} (t C/lake/year)	Maximum smolt biomass (kg)	Total escapement (Smax)	Escapement density (spawners/ha)
Aidrich	1	154	138	103	12	543	2,231	35
Azuklotz	1	372	282	211	63	2,855	11,725	71
Bear	1	231	187	140	474	21,582	88,623	47
Charlotte	1	76	76	57	678	30,865	126,741	19
Club	1	113	59	44	3	139	571	15
Dennis	1	69	48	36	6	266	1,091	12
Elbow	1	79	65	49	13	581	2,387	16
Kitwanga	6	279	230	230	320	14,558	59,780	77
Lakelse	6	130	108	108	267	12,156	49,915	36
Lonesome	1	86	62	46	34	1,549	6,363	16
McDonell	1	80	70	52	21	972	3,990	18
Rainbow	1	103	53	40	12	556	2,283	13
Slamgeesh	1	92	76	57	5	207	852	19
Stephens	1	199	153	114	39	1,760	7,228	38
Swan	1	130	100	74	233	10,588	43,478	25
Johnston	1	283	283	212	71	3,243	13,316	71
Kluayaz	1	8	8	6	2	71	290	2
Morice	5	80	80	80	1,400	63,679	261,485	27
Motase	1	19	19	14	10	453	1,861	5
Owikeno	6	113	113	113	1,906	86,734	356,156	38
Sicintine	1	31	31	23	3	129	530	8
Banks E.	1	51	51	38	14	636	2,611	13
Banks W.	1	89	89	67	19	874	3,587	22
Canoona	1	97	97	73	45	2,061	8,462	25
Deer - north	1	66	66	49	29	1,303	5,352	17
Ecstall	1	190	190	142	23	1,043	4,283	48
Evelyn	1	85	85	63	7	304	1,249	21
Hartley Bay	1	69	50	37	6	285	1,170	13
Ian	1	71	71	53	179	8,160	33,508	18
Keecha	1	76	76	57	35	1,576	6,470	19
Kitkiata	1	387	387	289	141	6,393	26,251	97
Kooryet	1	74	74	55	30	1,364	5,600	19
Mikado lower	1	20	20	15	2	90	369	5
Mikado middle	1	20	20	15	2	90	369	5
Mikado upper	1	32	32	24	5	234	959	8
Moore	1	68	68	51	26	1,185	4,866	17
Tsimtack	1	192	192	143	49	2,243	9,211	48

Table 11. Adjusted PR model predictions for the study lakes. Predictions have been modified to account for limnetic biomass of non-sockeye fish planktivores and for lakes where average smolt size at capacity is known to differ from 4.5 g either due to known smaller smolts or to the presence of age-2 smolts.

Lake	Fish competitor biomass (kg/ha)	PR_{total} available to sockeye	Adjusted PR model predictions			
			Smolt biomass (kg) (R_{max})	Smolts (thousands)	Escapement (thousands) (S_{max})	Escapement (#/ha)
Aldrich	0.19	12	531	118	2.2	34
Azuklotz	3.96	48	2,201	489	9.0	55
Bear	0.75	443	20,166	4,481	82.8	44
Charlotte	0.00	678	30,865	6,859	126.7	19
Club	0.00	3	139	31	0.6	15
Dennis [1]	0.30	5	239	53	1.0	11
Elbow [1]	0.23	12	547	122	2.2	15
Kitwanga [1]	1.02	303	13,769	3,060	56.5	73
Lakelse	0.04	266	12,104	2,690	49.7	36
Lonesome [1]	0.24	32	1,452	323	6.0	15
McDonell	0.53	19	851	189	3.5	15
Rainbow [1]	0.34	11	498	111	2.0	12
Slamgeesh	0.19	4	199	44	0.8	18
Stephens	0.10	38	1,741	387	7.1	38
Swan	1.05	193	8,770	1,949	36.0	21
				0		
Johnston	0.39	70	3,170	704	13.0	70
Kluayaz [1]	0.01	2	69	15	0.3	2.0
Morice	0.10	1,377	62,671	11,191	206.8	21
Motase	0.01	10	450	62	1.2	3
Owikeno [2]	1.11	1,678	76,326	32,758	605.3	65
Sicintine [1]	0.04	3	126	28	0.5	8
Banks E.	1.34	8	363	77	1.4	7
Banks W.	0.54	17	787	167	3.1	19
Canoona [1]	0.72	40	1,811	402	7.4	22
Deer - north [1]	0.49	25	1,145	255	4.7	15
Ecstall	2.43	18	825	183	3.4	38
Evelyn [1]	0.63	6	267	59	1.1	19
Hartley Bay [1]	0.51	5	237	53	1.0	10
Ian [3]	0.06	177	8,040	1,787	33.0	18
Keecha [1]	0.57	30	1,382	307	5.7	17
Kitkiata	2.01	129	5,850	1,300	24.0	89
Kooryet [1]	0.55	26	1,198	266	4.9	16.3
Mikado lower [1]	0.15	2	79	17	0.3	4.4
Mikado middle [1]	0.15	2	79	18	0.3	4.4
Mikado upper [1]	0.24	5	205	46	0.8	7
Moore [1]	0.51	23	1,041	231	4.3	15
Tsimtack [1]	1.43	43	1,970	438	8.1	42

1 - Fish competitor biomass has not been measured in these lakes. We used the mean biomass measured in other lakes of the same water clarity type to estimate competitor biomass.
2 - Owikeno Lake competitor biomass was estimated at 12% of optimum smolt production (Shortreed and Morton 2003). It was not used in calculation of mean competitor biomass because it is an indirect estimate only.
3 - Fish competitor biomass in Ian Lake was provided by P. Rankin (DFO, Pacific Biological Station, Nanaimo, B.C.)

Table 12. Observed sockeye numbers and biomass in the study lakes and the proportional of potential production currently utilized.

	Observed age-0 sockeye biomass		Observed age-0 sockeye numbers		Observed/potential smolt production (%)	
Lake	kg/lake	kg/ha	000's/lake	000's/ha	Biomass	Numbers
Aldrich	0	0.00	0	0	0%	0%
Azuklotz	301	1.82	63,428	384	14%	13%
Bear	725	0.38	238,025	126	4%	5%
Charlotte	0	0.00	0	0	0%	0%
Club	4	0.11	2,224	58	3%	7%
Dennis						
Elbow						
Kitwanga						
Lakelse	1297	0.95	286,986	209	11%	11%
Lonesome						
McDonell	204	0.90	127,494	563	24%	67%
Rainbow						
Slamgeesh	88	1.96	20,382	455	44%	46%
Stephens	355	1.88	176,326	937	20%	46%
Swan	664	0.38	580,000	334	8%	30%
Johnston	569	3.04	1,137,068	6,081	18%	161%
Kluayaz						
Morice	1539	0.16	1,197,848	123	2%	11%
Motase	23	0.06	20,676	52	5%	33%
Owikeno						
Sicintine						
Banks E.	86	0.42	28,816	141	24%	37%
Banks W.	102	0.64	41,953	262	13%	25%
Canoona						
Deer - north						
Ecstall	6	0.07	5,798	65	1%	3%
Evelyn						
Hartley Bay	0	0.00			0%	0%
Ian [1]	747	0.40	319,260	170	9%	18%
Keecha						
Kitkiata	515	1.91	635,336	2,353	9%	49%
Kooryet						
Mikado lower						
Mikado middle						
Mikado upper						
Moore						
Tsimtack						

1 - Juvenile sockeye numbers and biomass in Ian Lake was provided by P. Rankin (DFO, Pacific Biological Station, Nanaimo, B.C.)

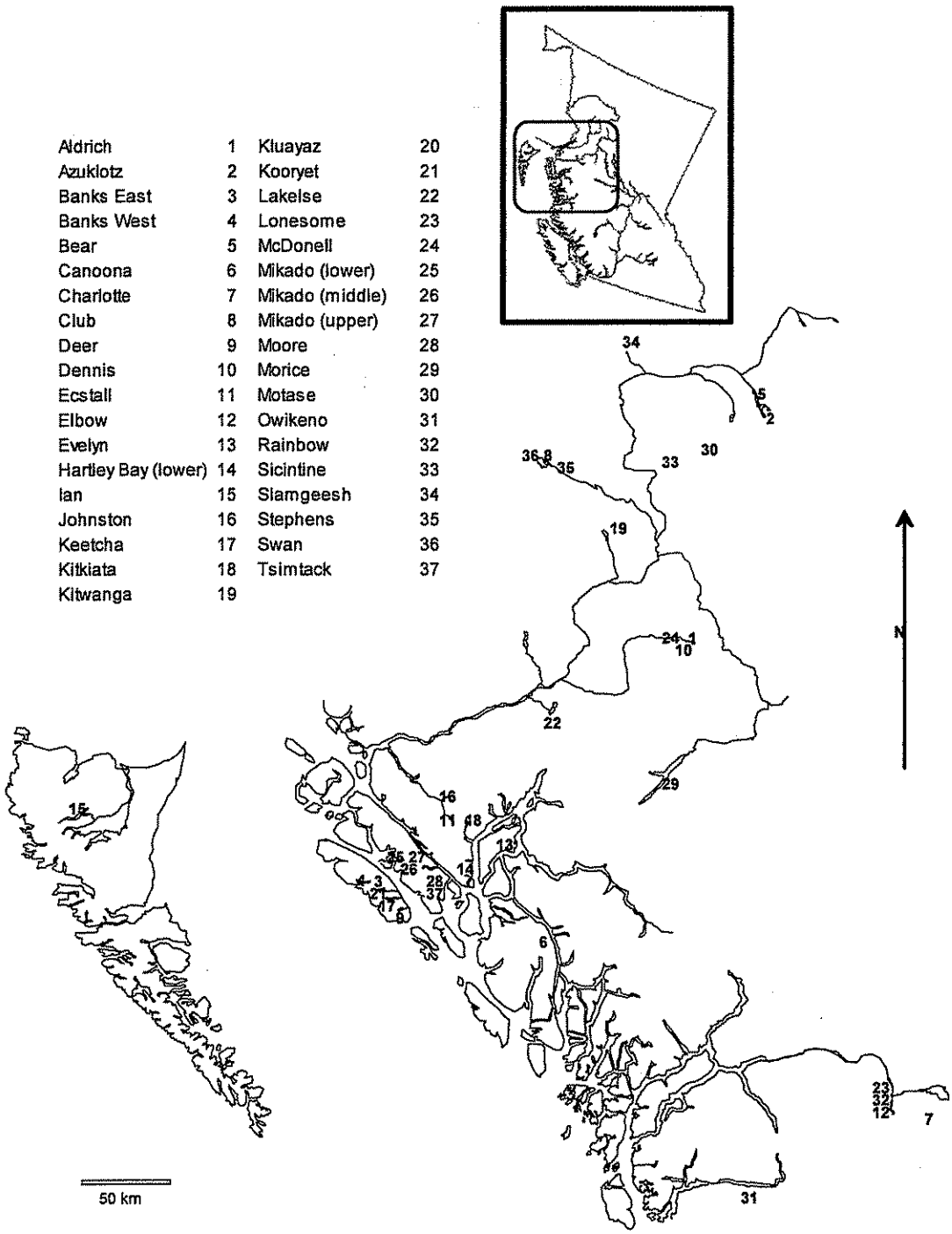

Fig 1. Map showing the location of the lakes surveyed for this report.

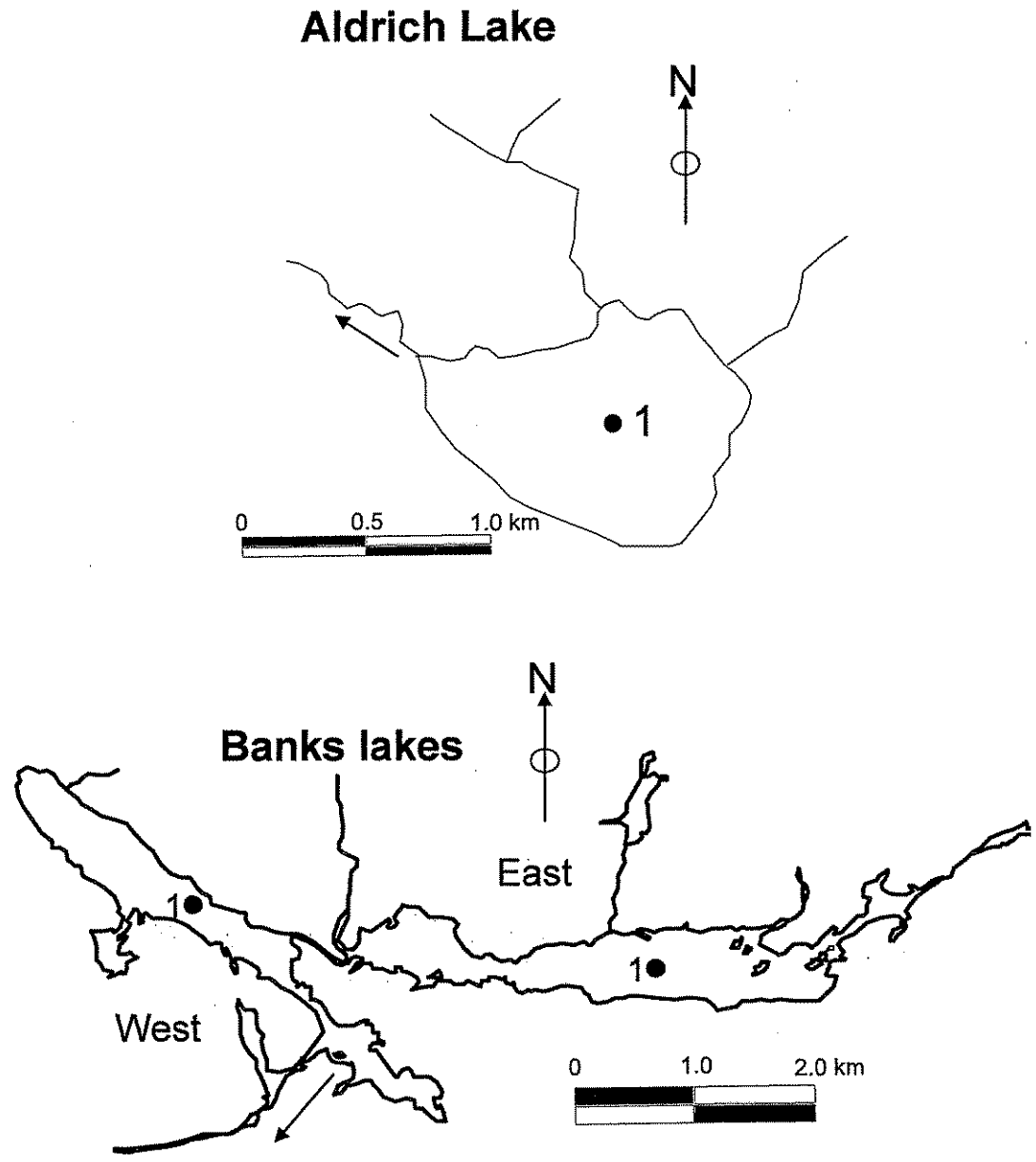

Fig. 2. Aldrich, East and West Banks lakes showing the limnological sampling stations.

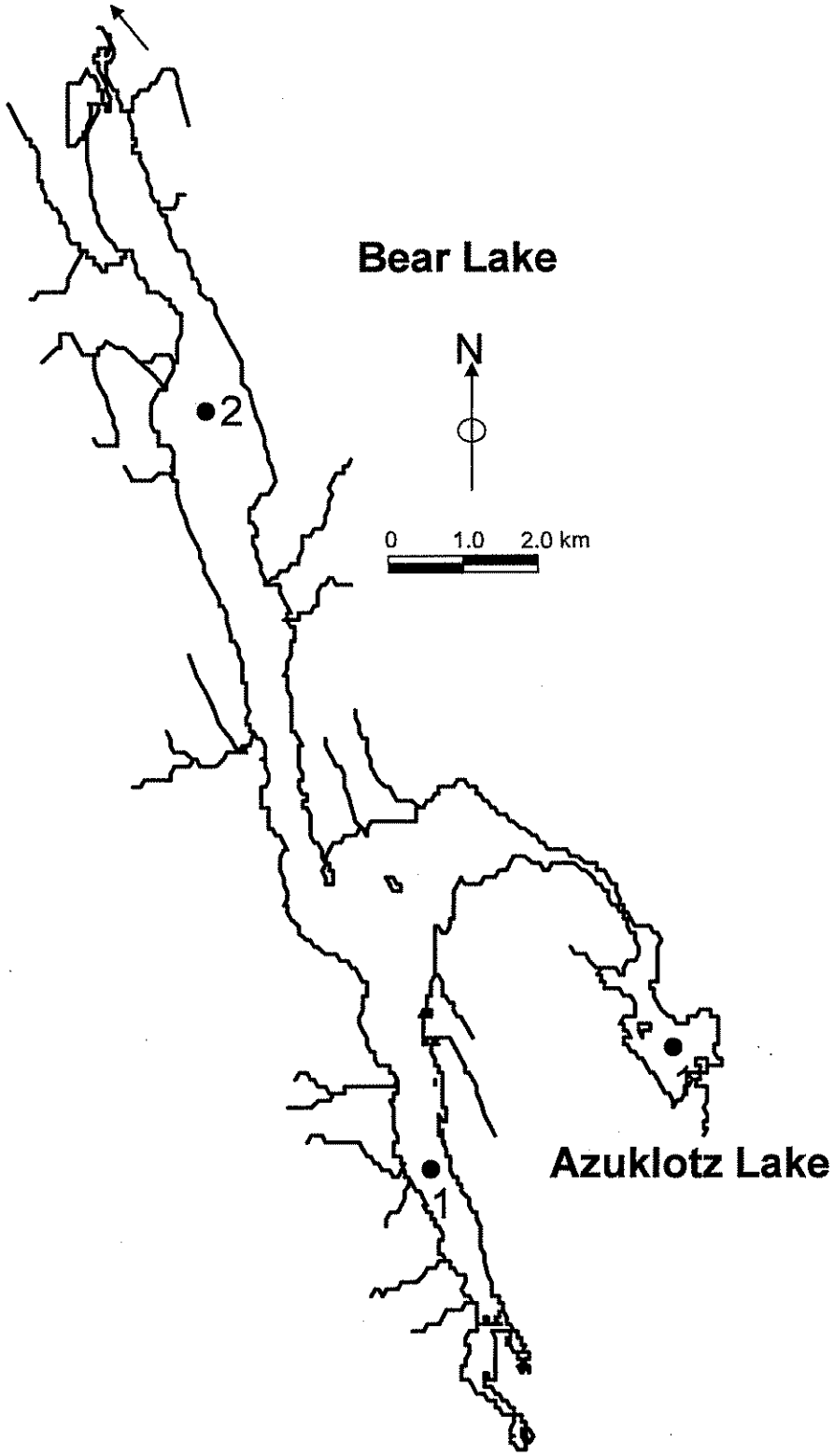

Fig. 3. Map of Azuklotz and Bear lakes and the location of the limnological sampling locations.

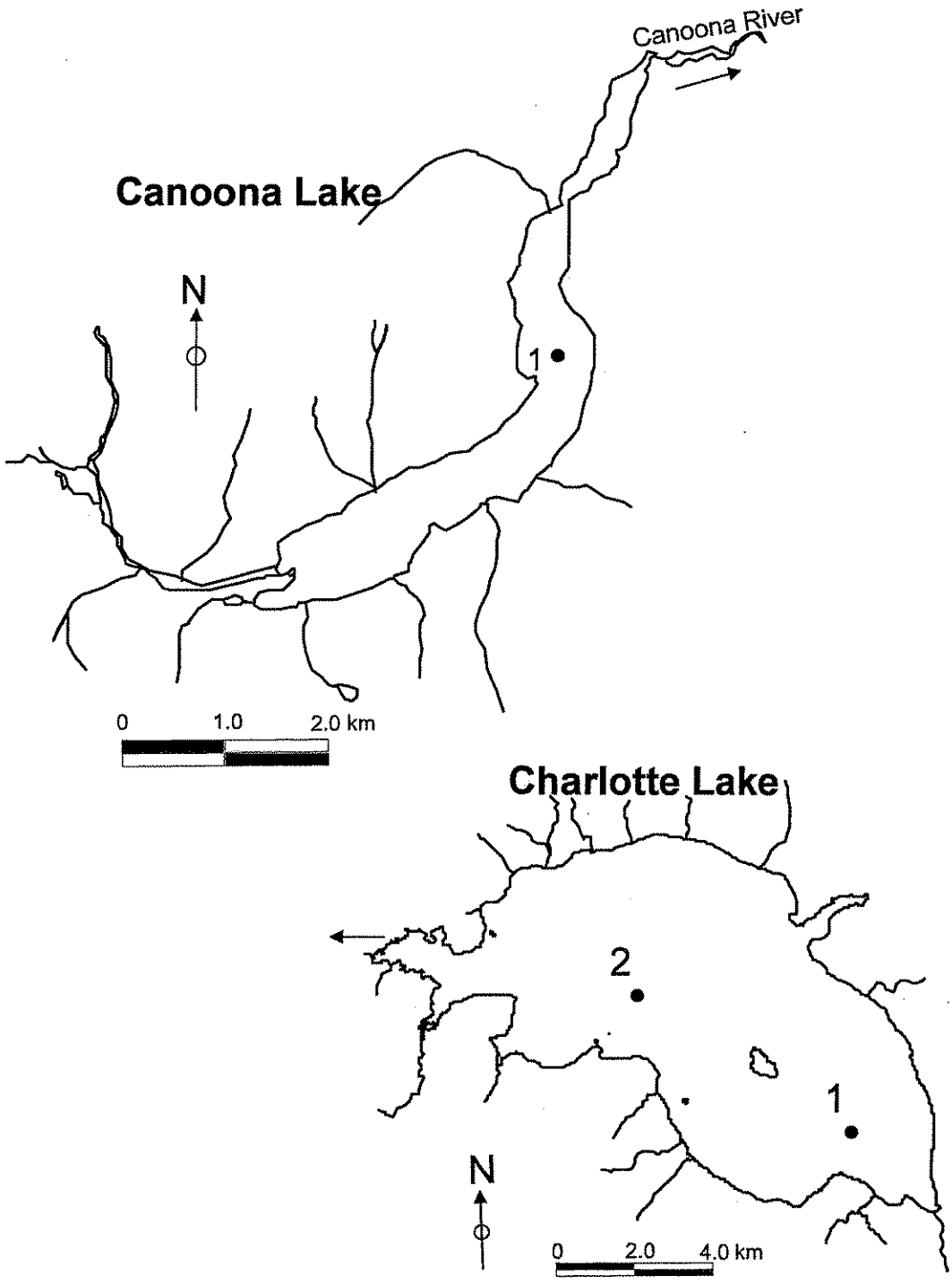

Fig. 4. Map of Canoona and Charlotte lakes and the location of the limnological sampling stations.

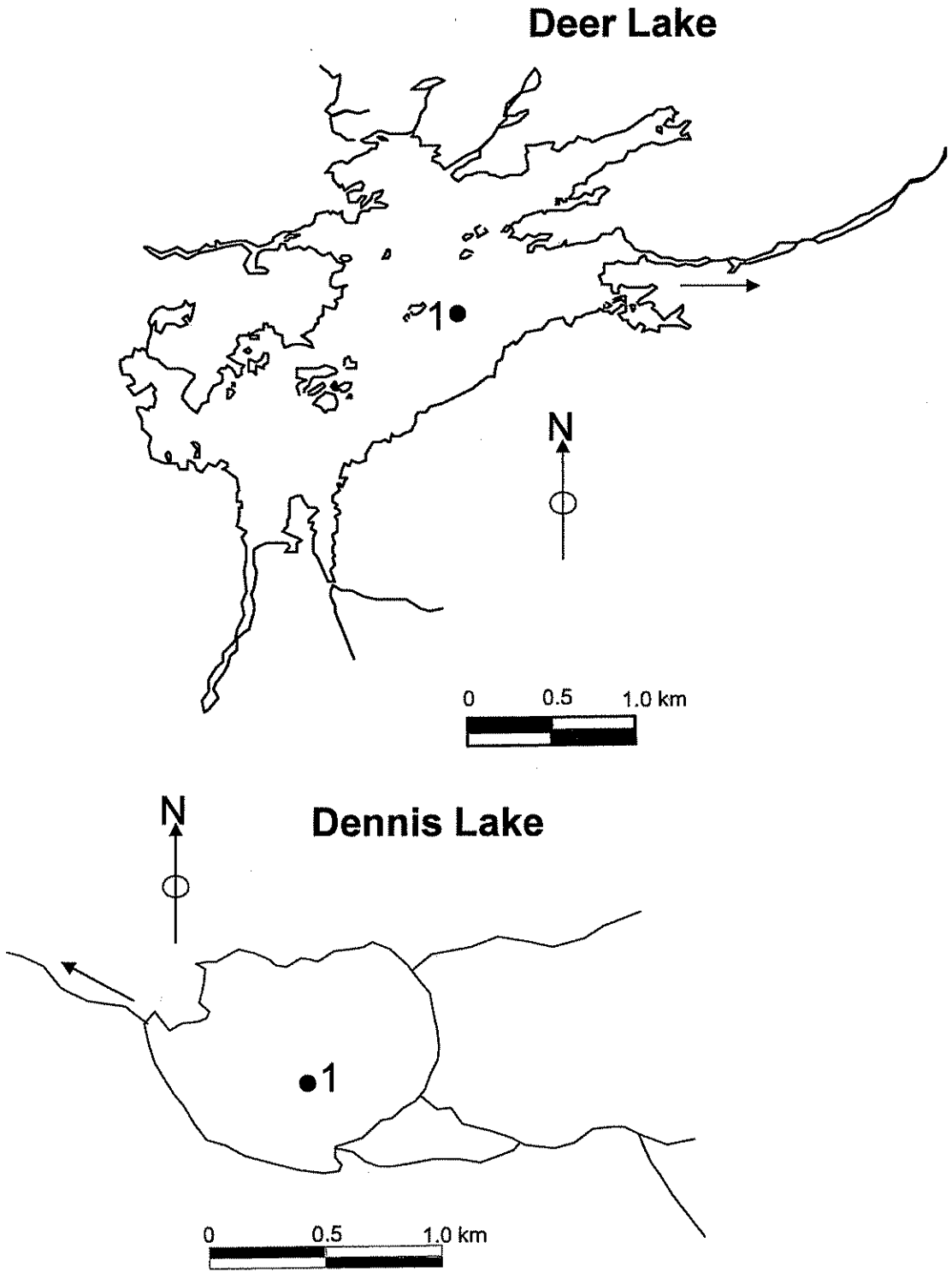

Fig. 5. Map of Deer (south end Banks Island) and Dennis lakes and the location of the limnological sampling stations.

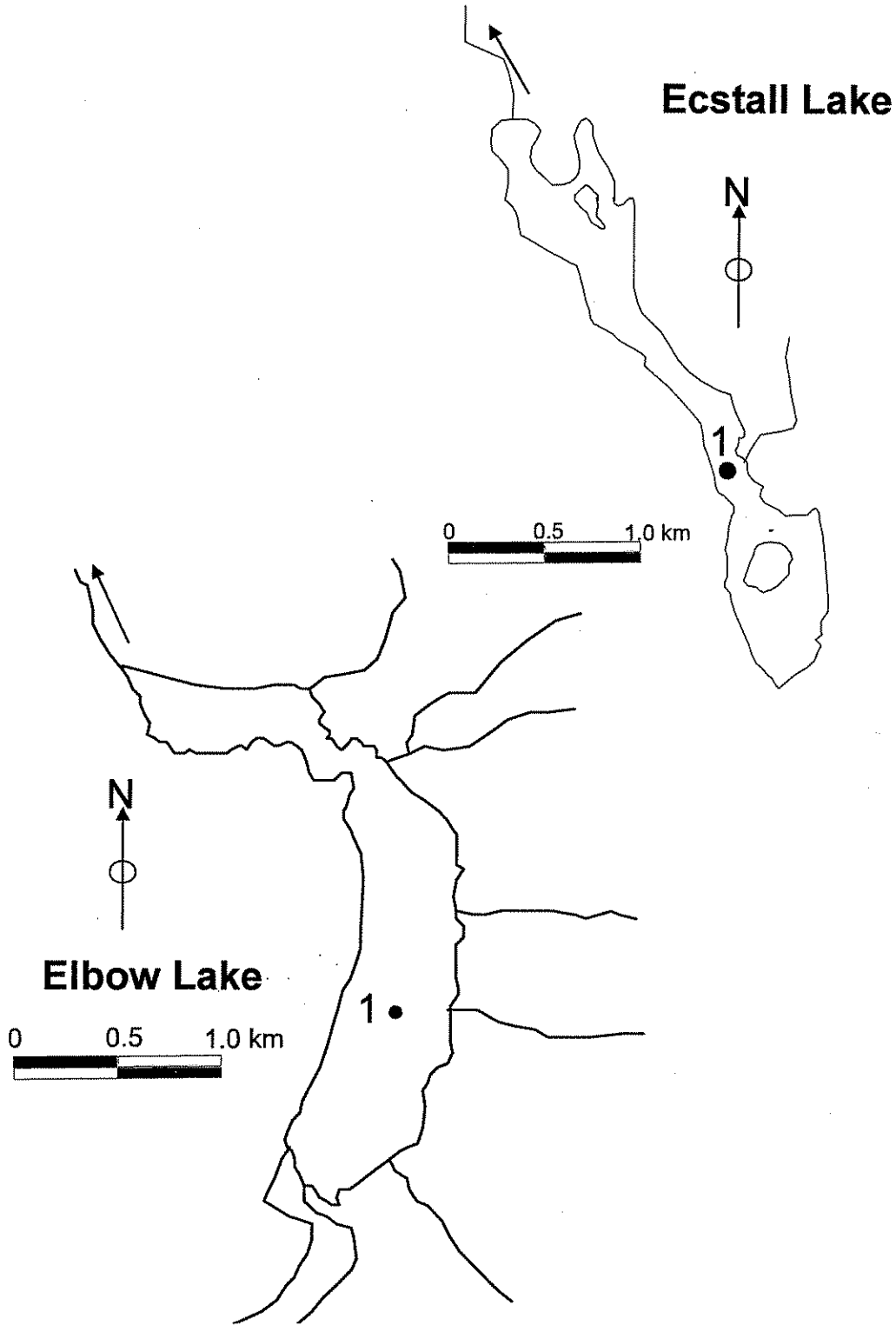

Fig. 6. Map of Ecstall and Elbow lakes and the location of the limnological sampling stations.

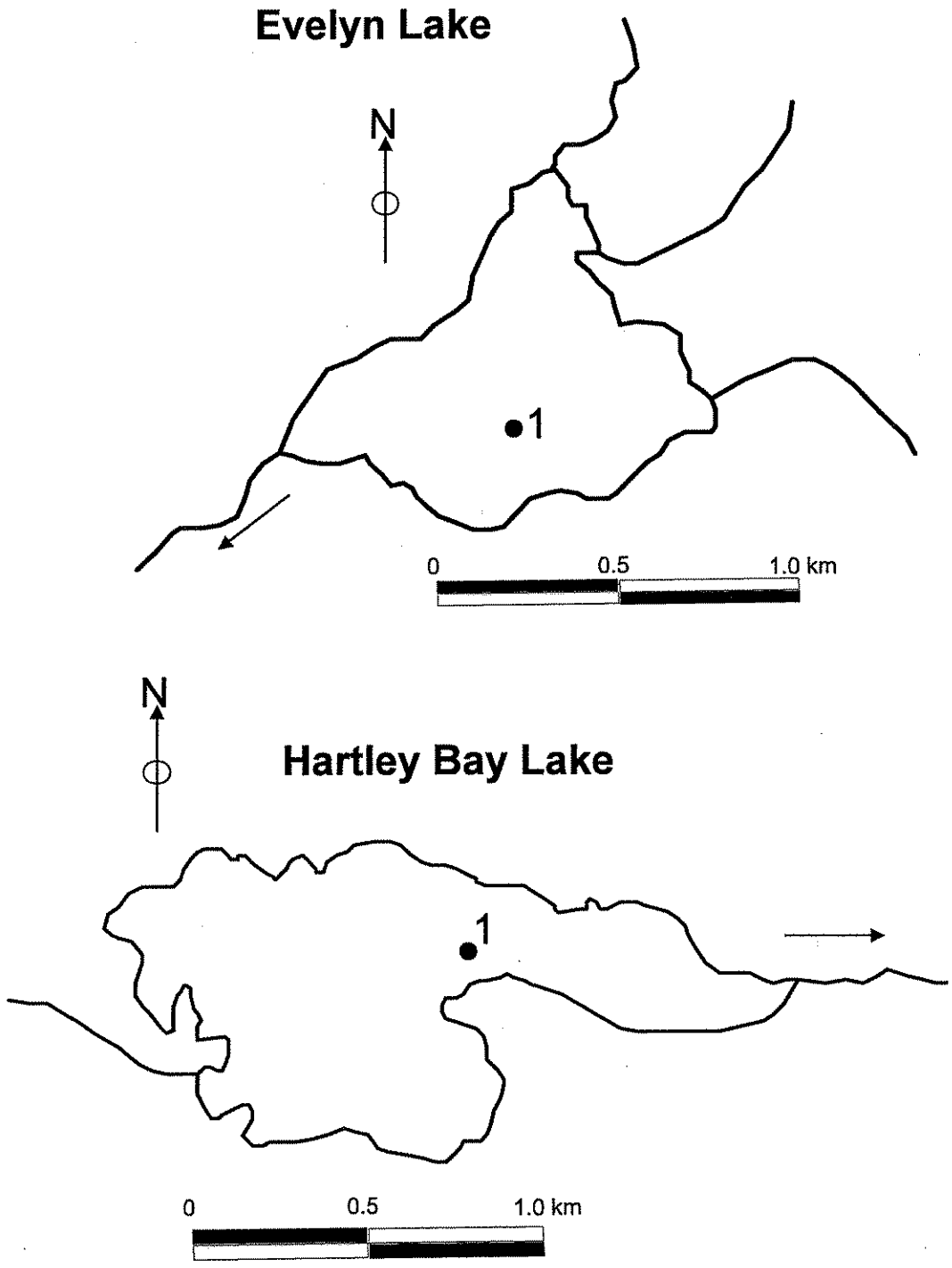

Fig. 7. Map of Evelyn and Hartley Bay (Lower) lakes and the location of the limnological sampling stations.

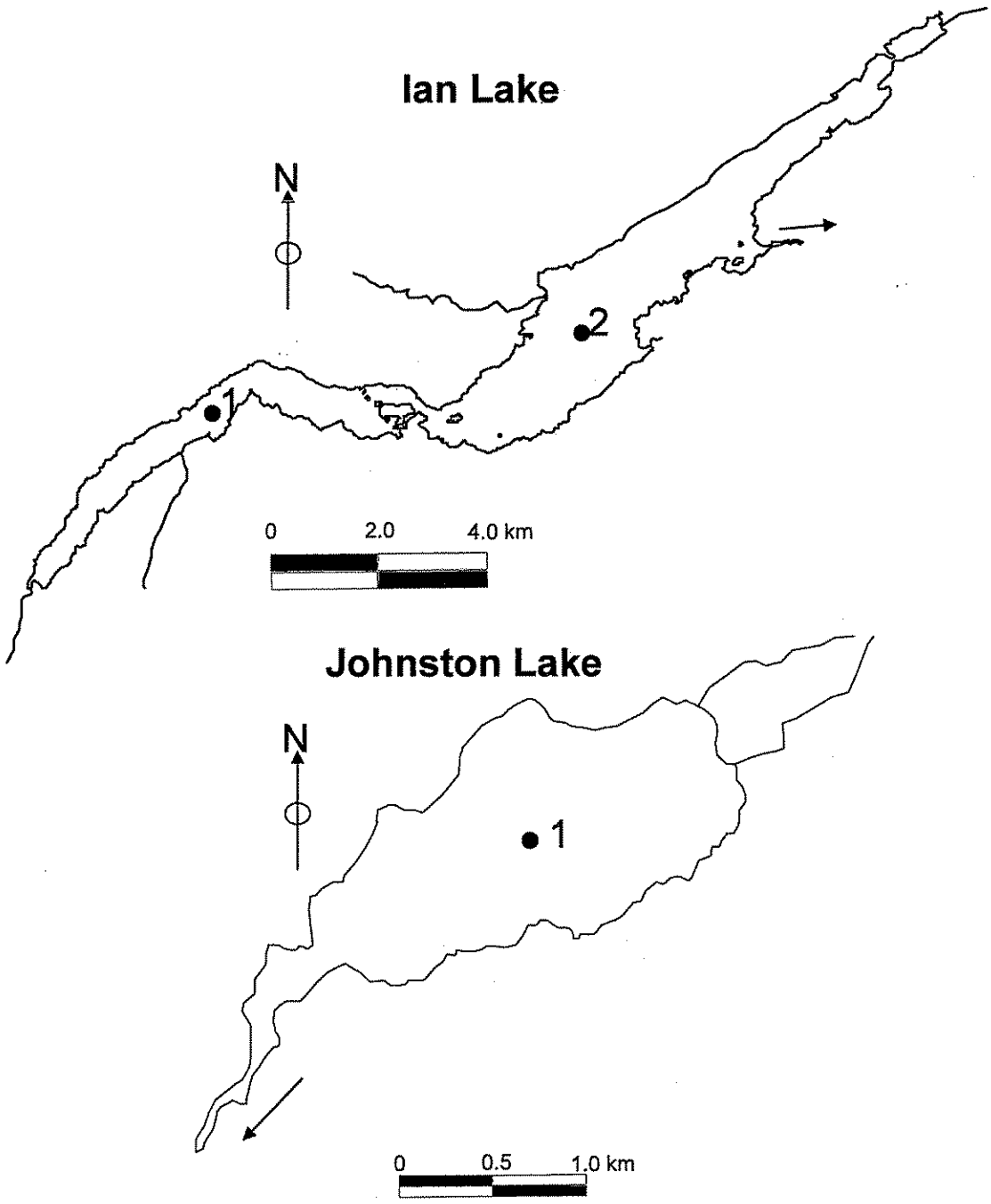

Fig. 8. Map of Ian and Johnston lakes and the location of the limnological sampling stations.

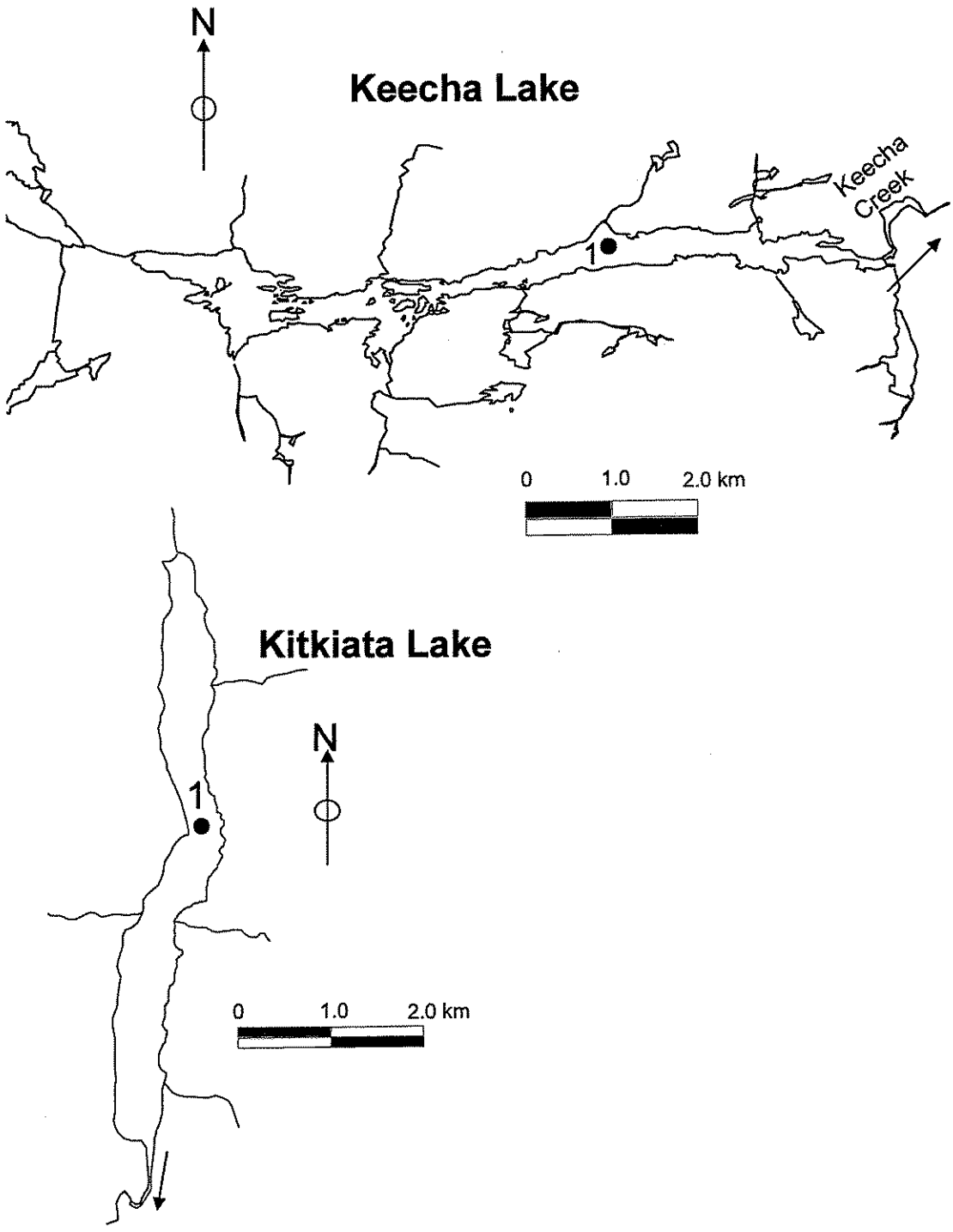

Fig. 9. Map of Keecha and Kitkiata lakes and the location of the limnological sampling stations.

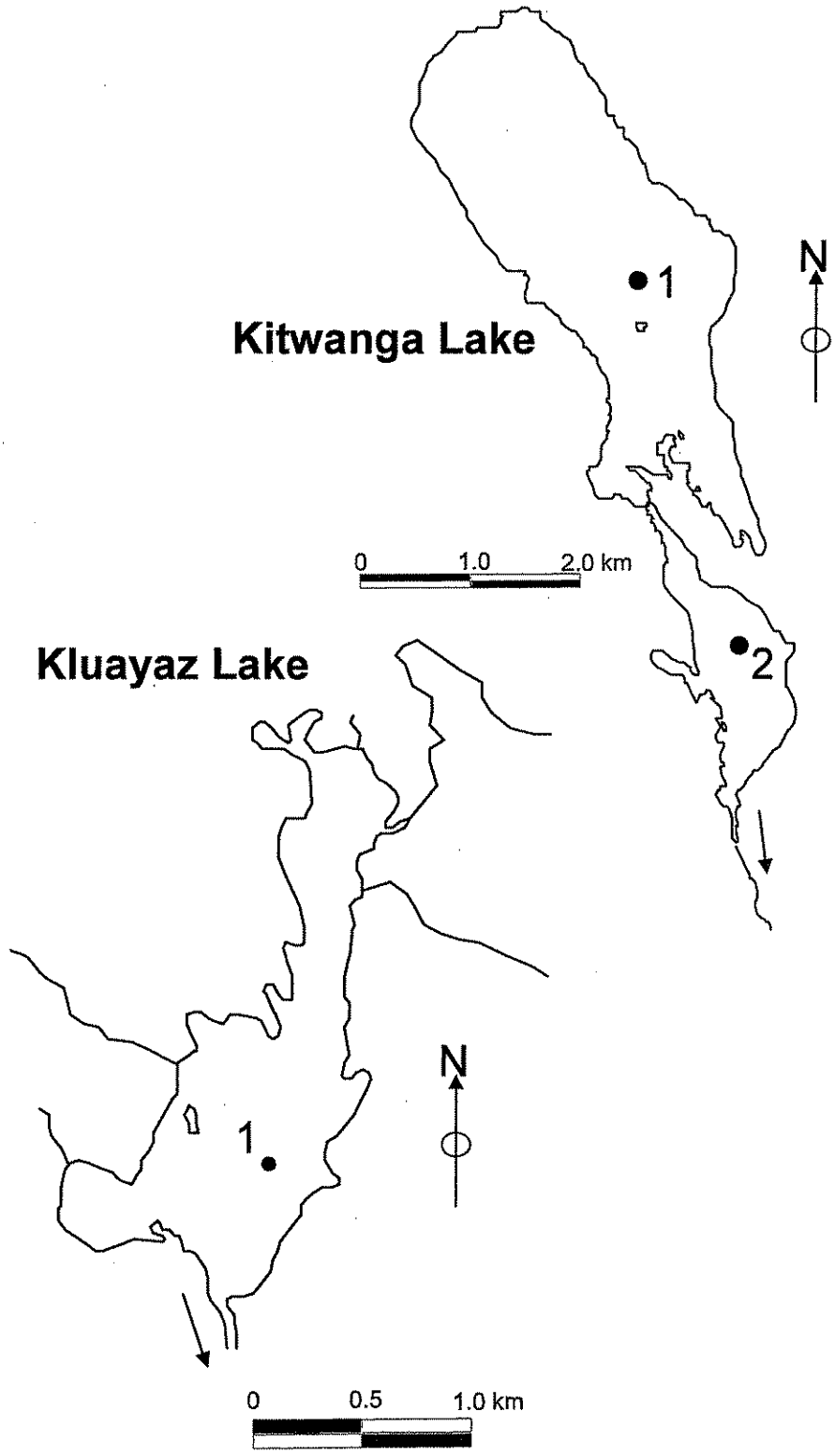

Fig. 10. Map of Kitwanga and Kluayaz lakes and the location of the limnological sampling locations.

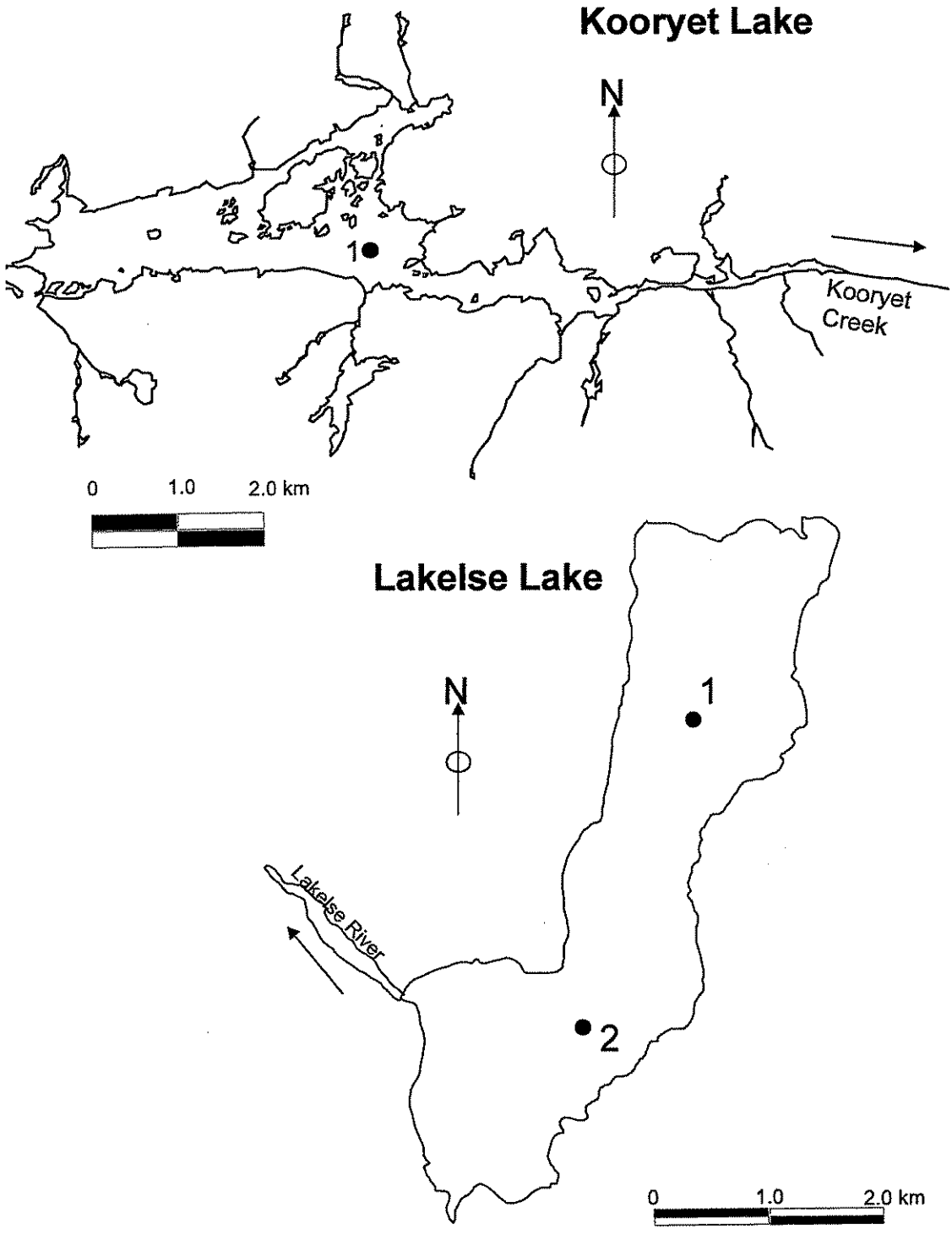

Fig. 11. Map of Kooryet and Lakelse lakes and the location of the limnological sampling stations.

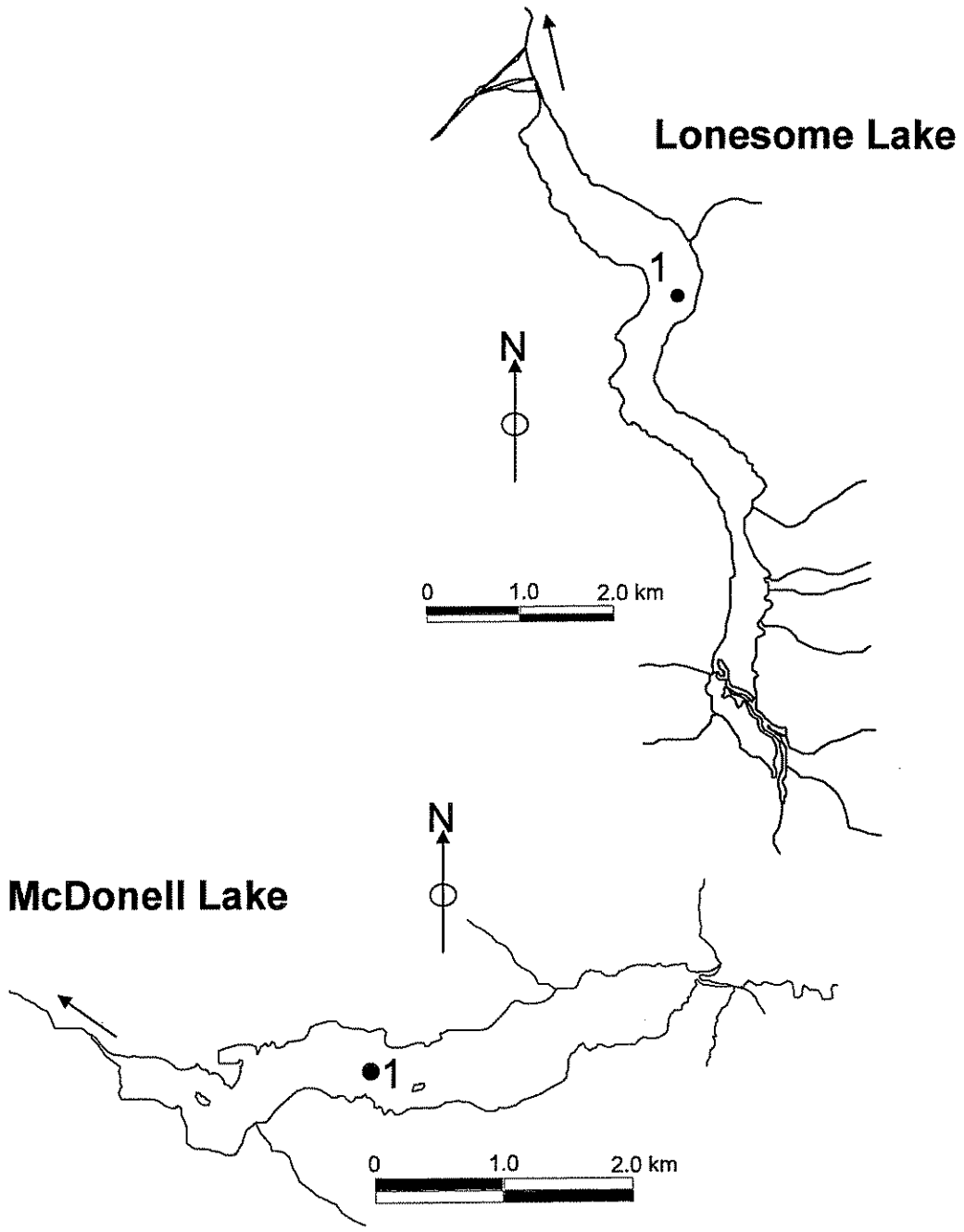

Fig. 12. Map of Lonesome and McDonell lakes and the location of the limnological sampling stations.

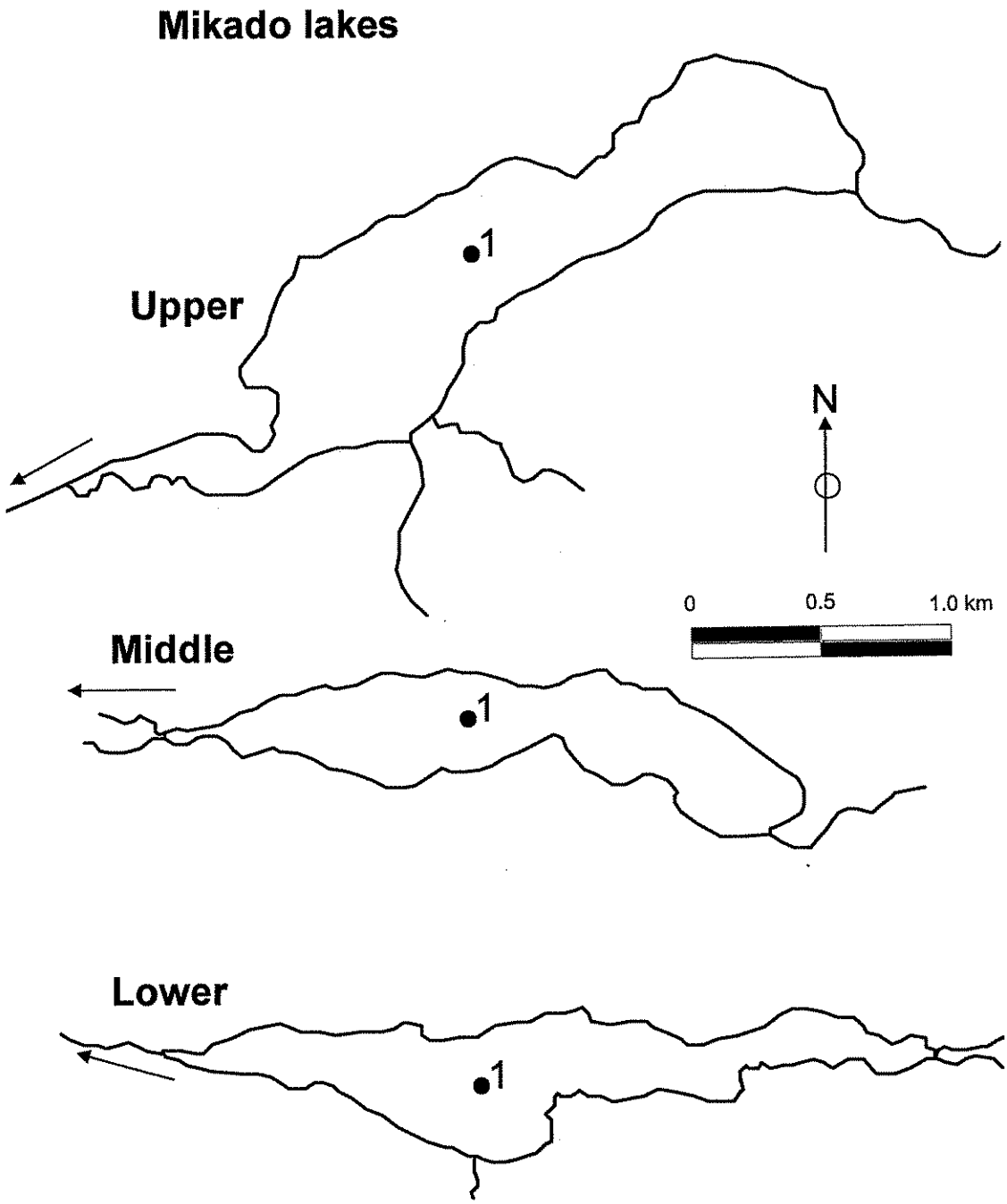

Fig. 13. Map of the Mikado lakes and the location of the limnological sampling stations.

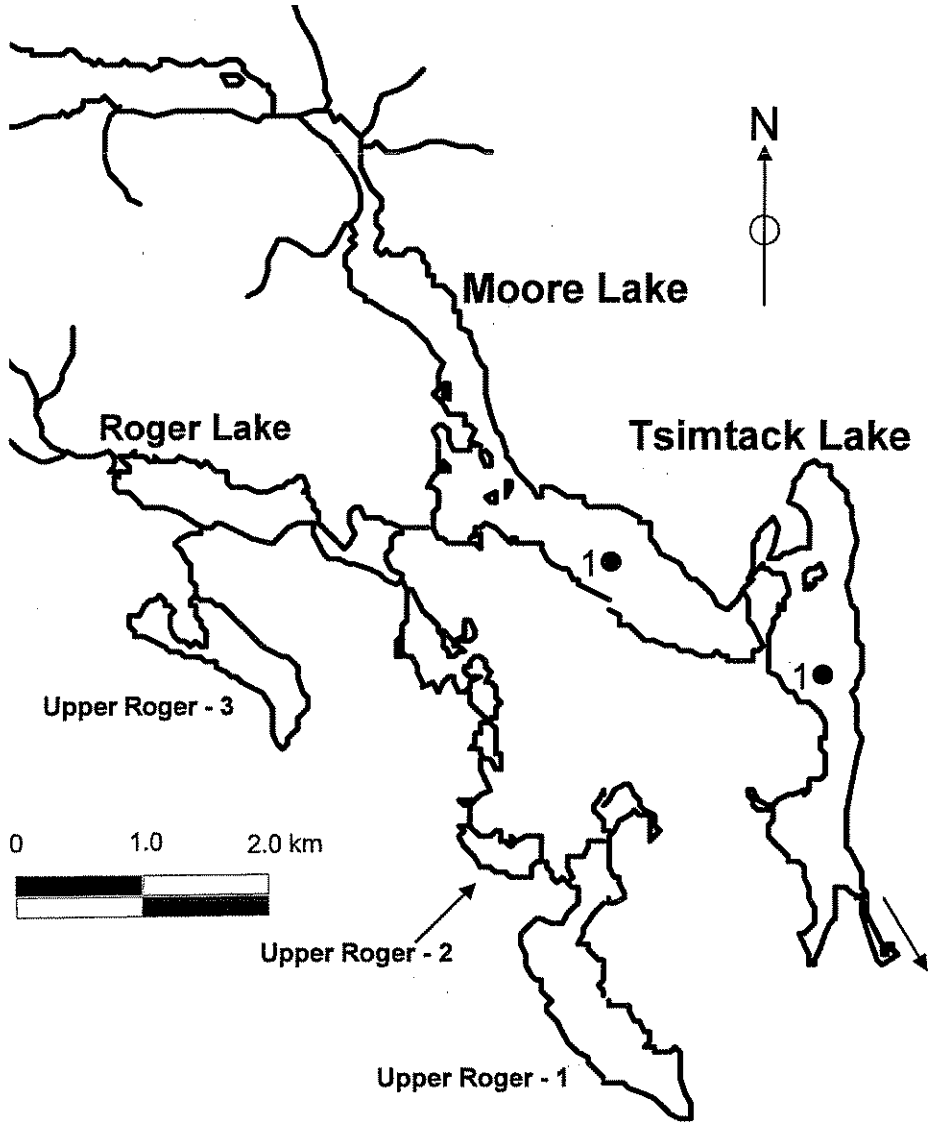

Fig. 14. Map of Moore and Tsimtack lakes and the location of the limnological sampling stations.

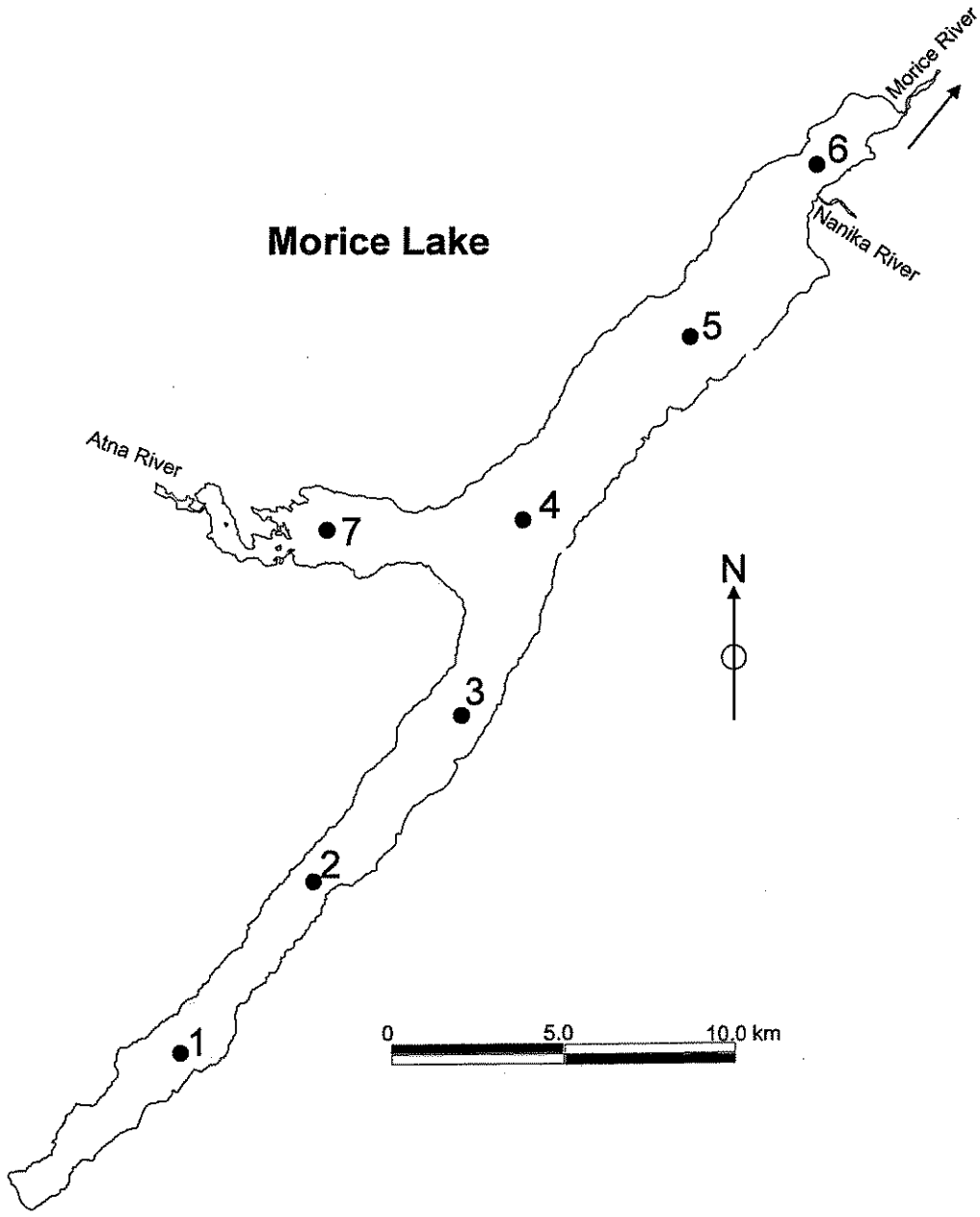

Fig. 15. Map of Morice Lake and the location of the limnological sampling stations.

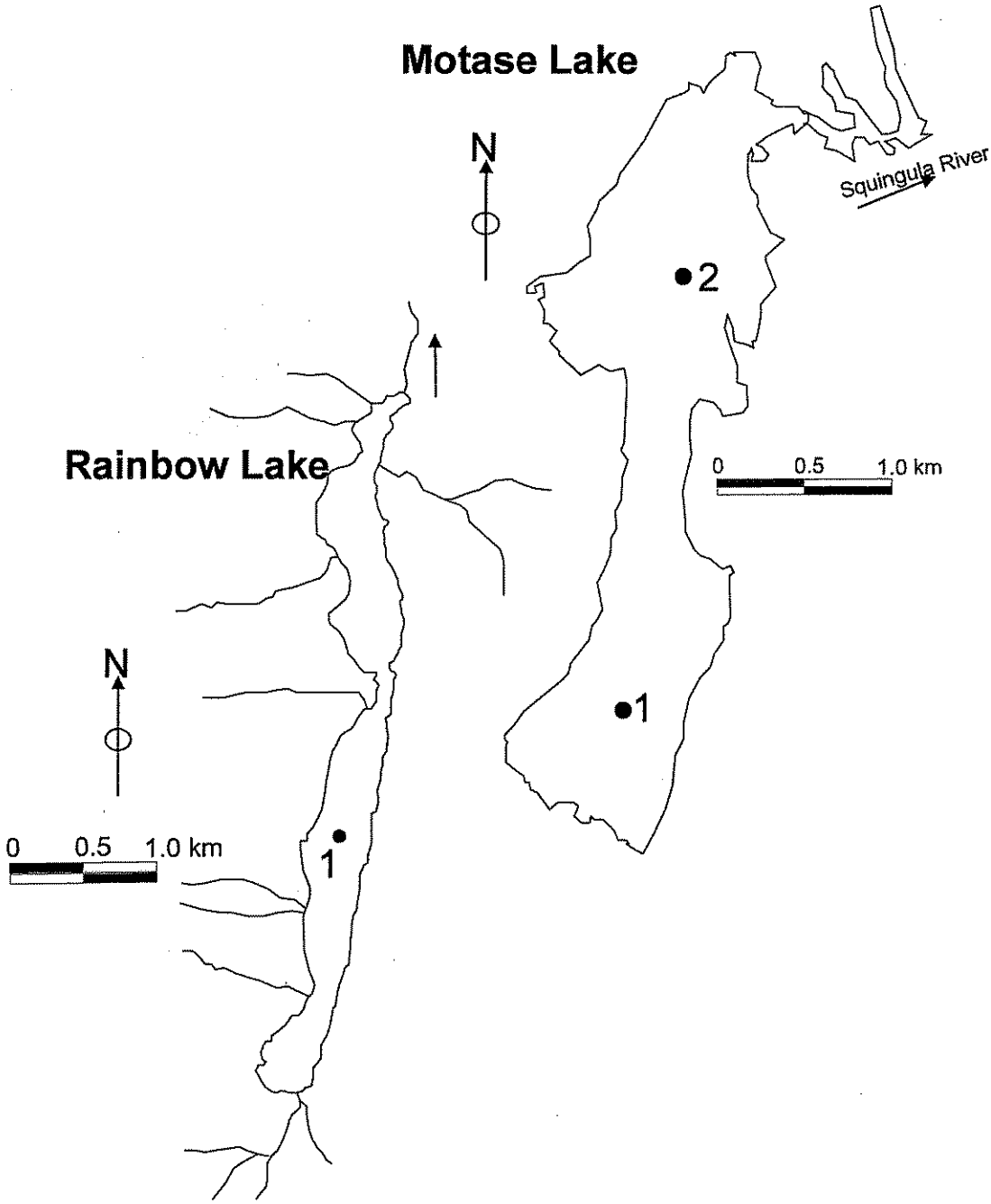

Fig. 16. Map of Motase and Rainbow lakes and the location of the limnological sampling stations.

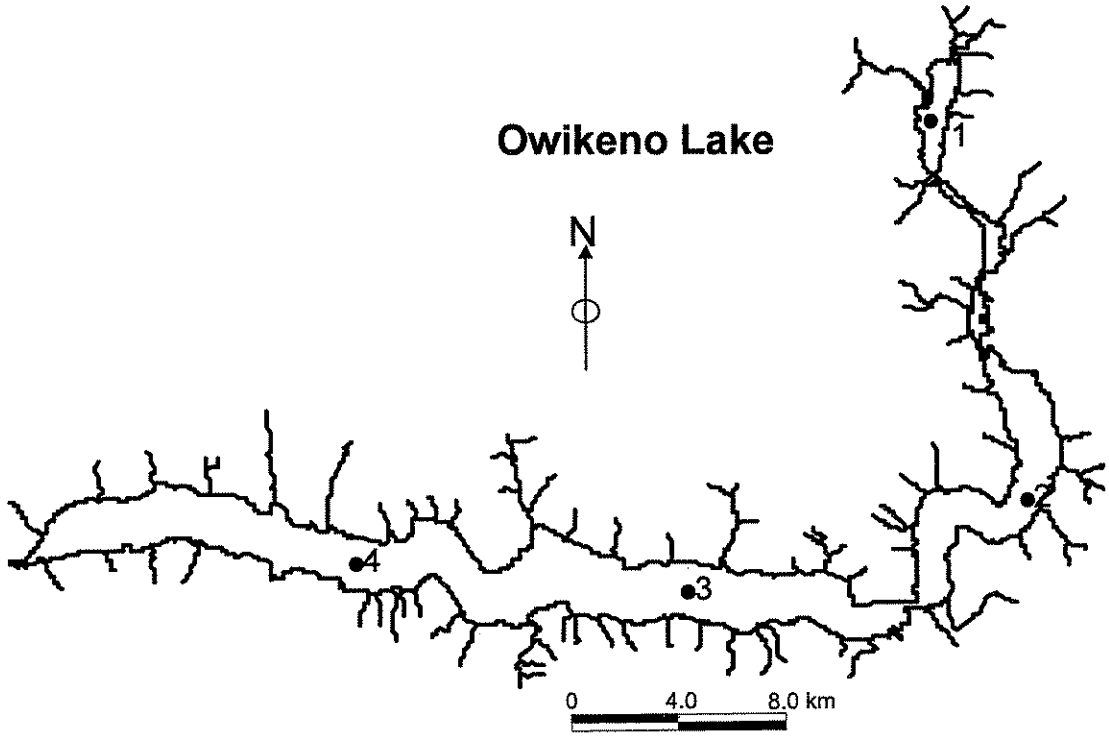

Fig. 17. Map of Owikeno lake and the location of the limnological sampling stations.

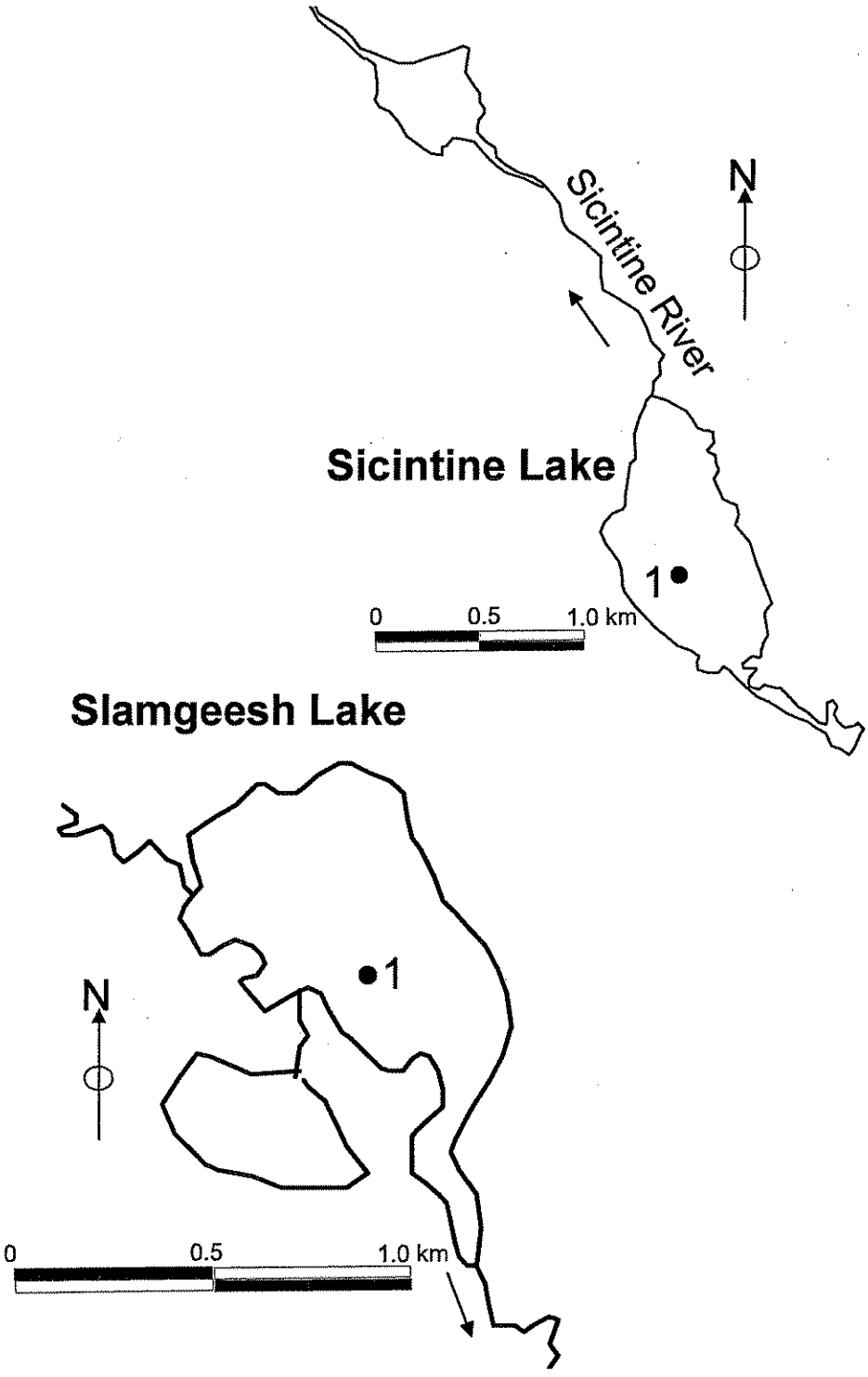

Fig. 18. Map of Sicintine and Slamgeesh lakes and the location of the limnological sampling stations.

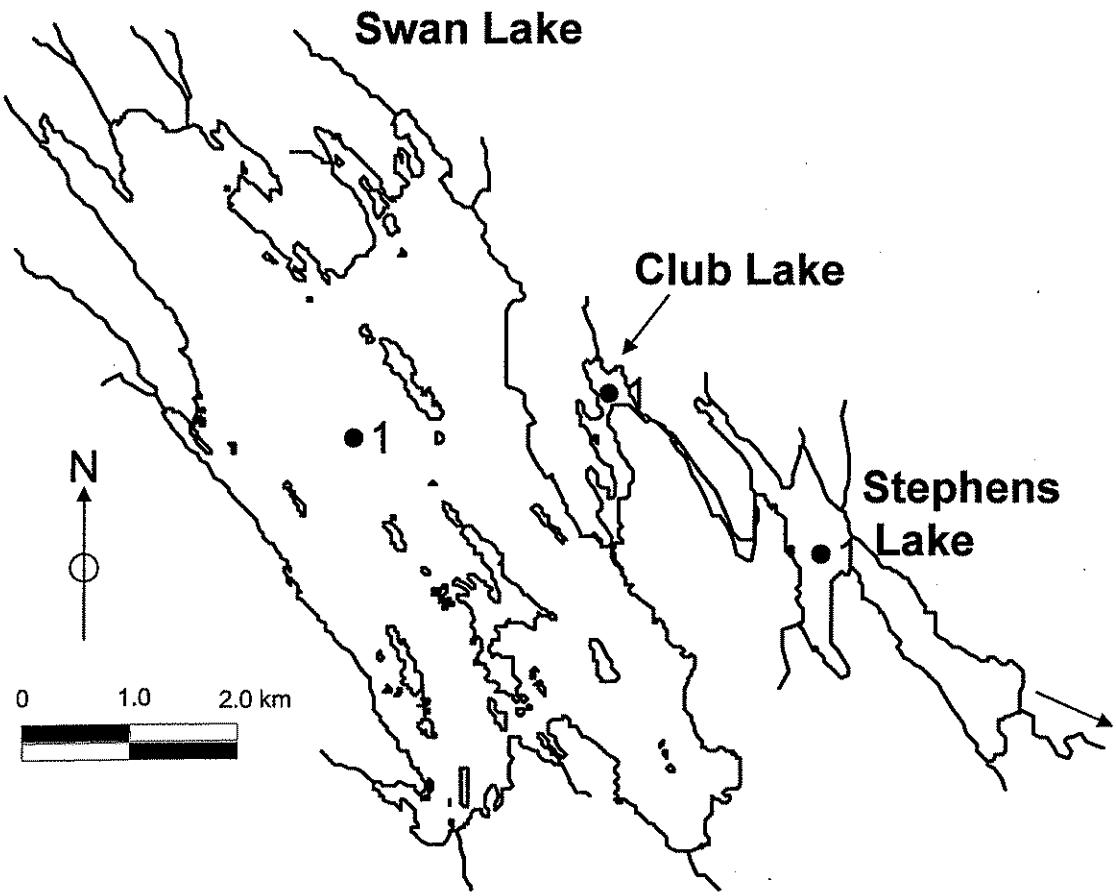

Fig. 19. Map of Swan, Club, and Stephens lakes and the location of the limnological sampling stations.

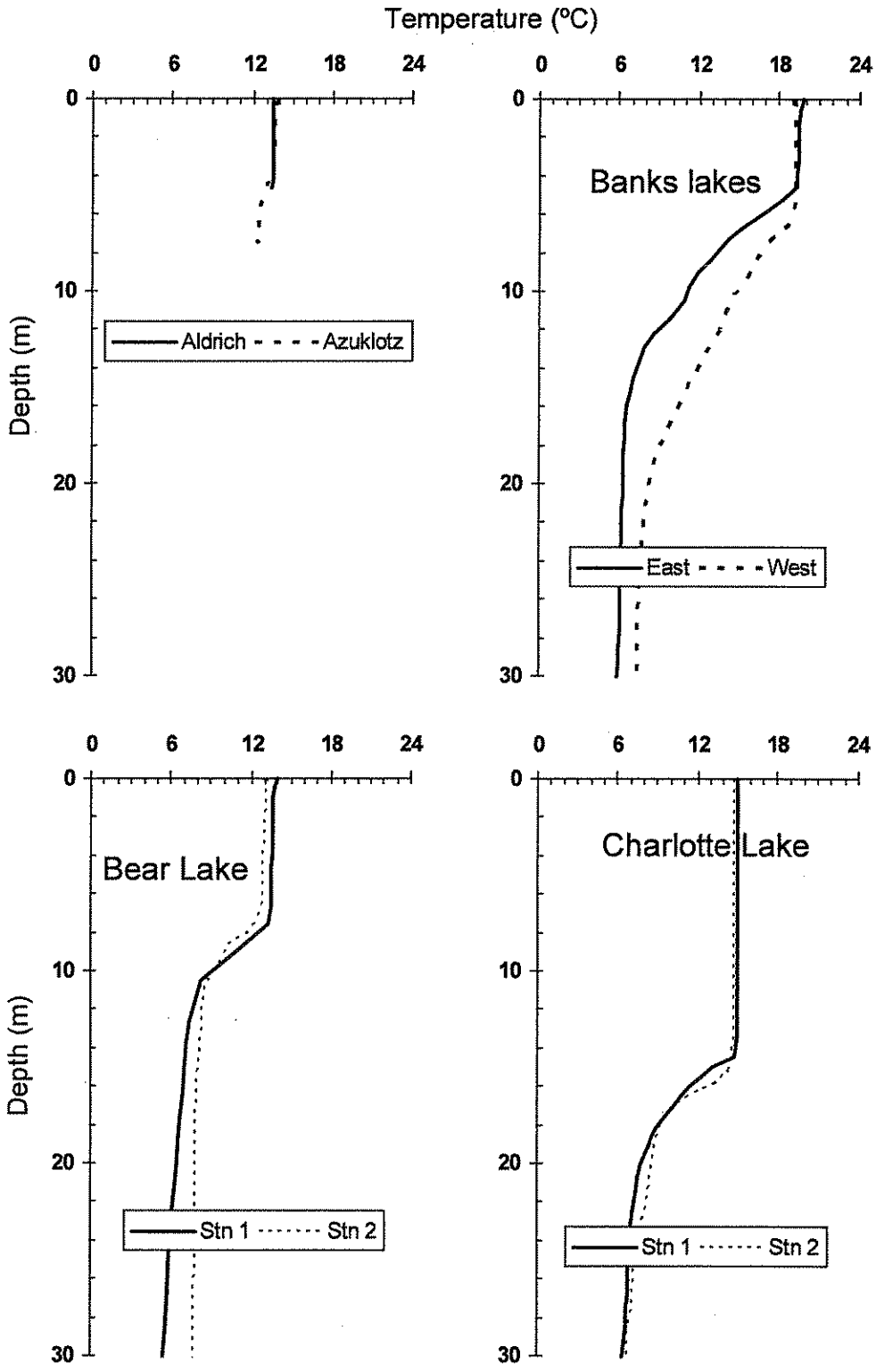

Fig. 20. Temperature profiles from the surveyed lakes.

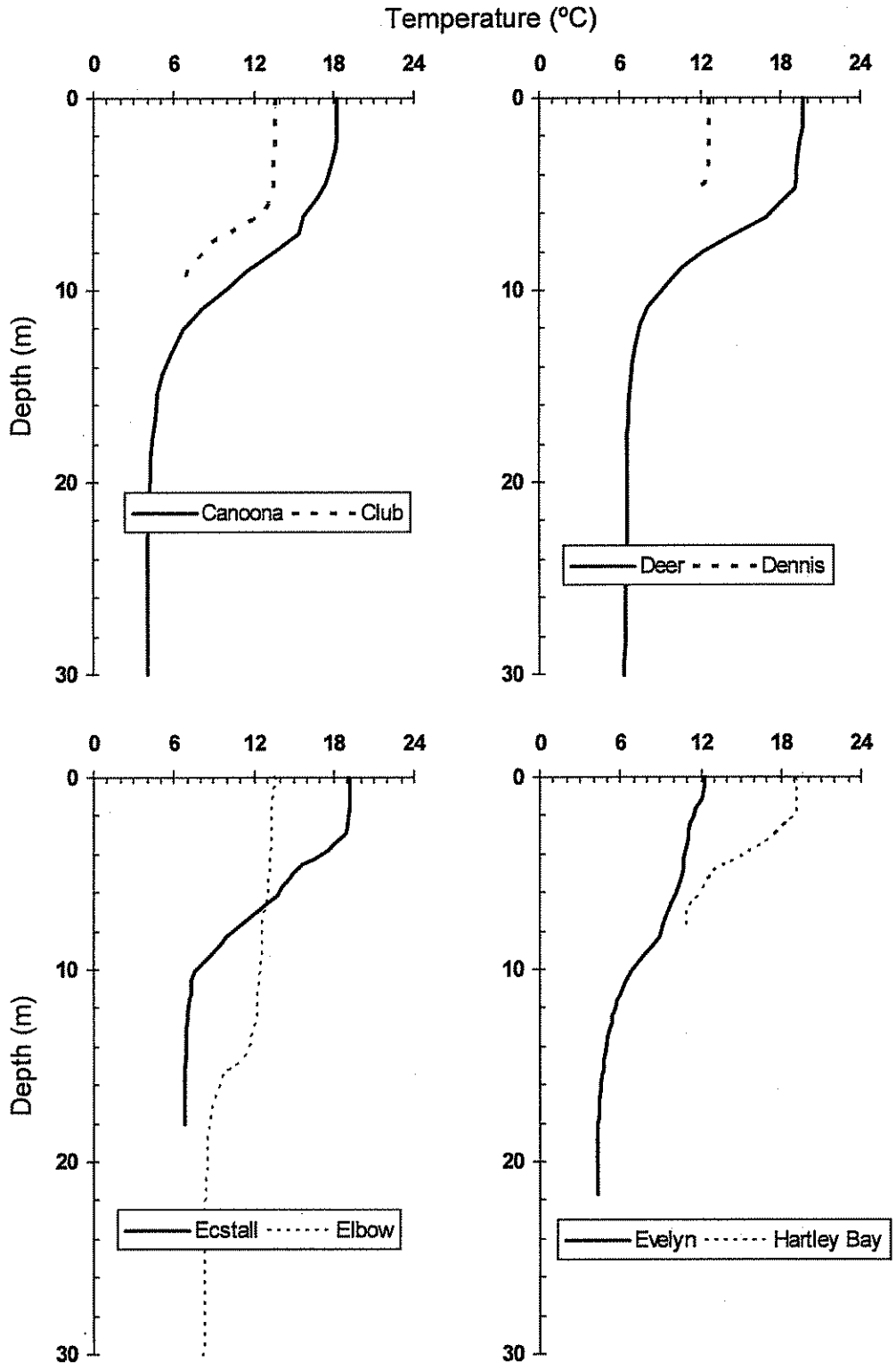

Fig. 21. Temperature profiles from the surveyed lakes.

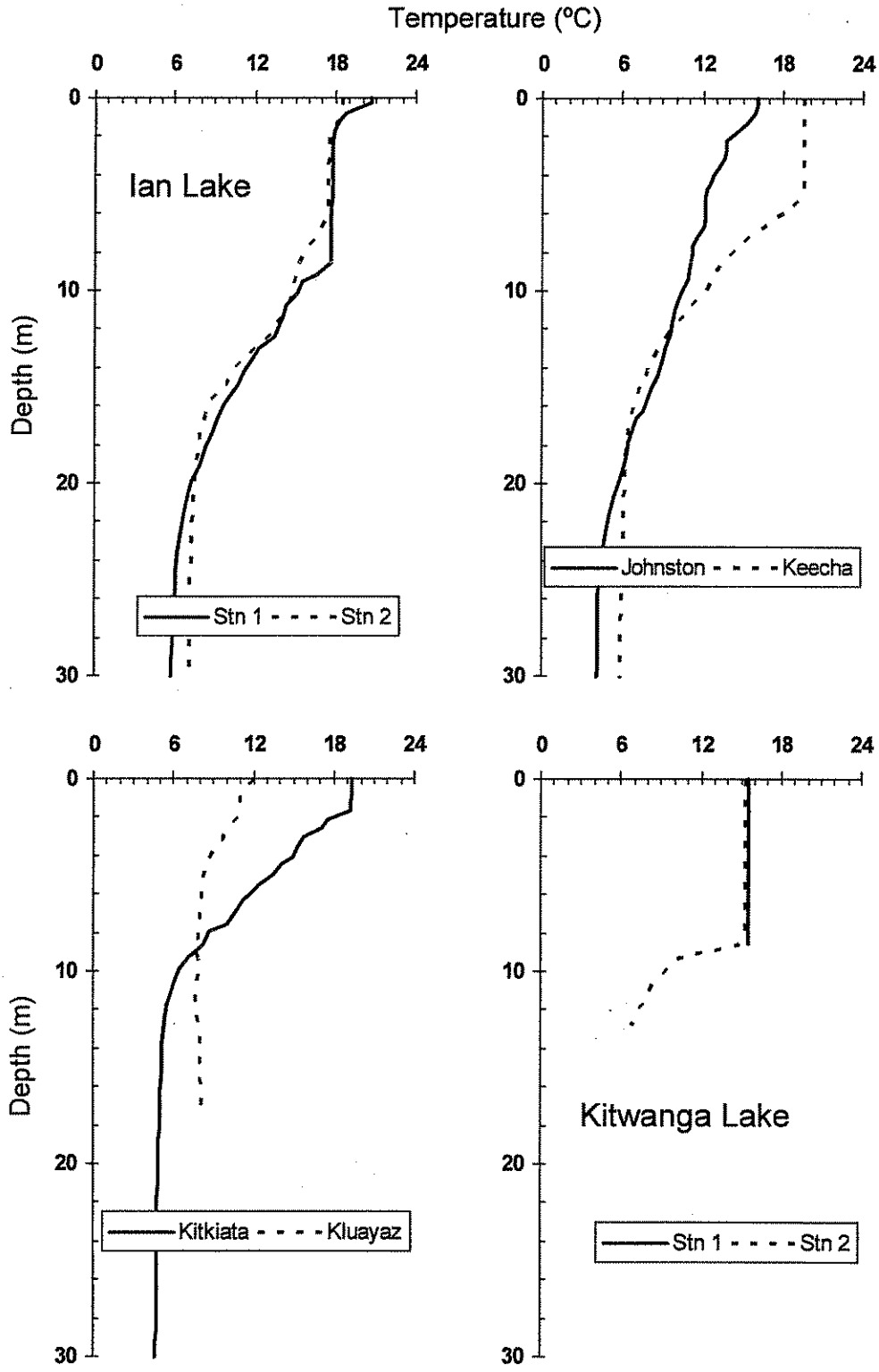

Fig. 22. Temperature profiles from the surveyed lakes.

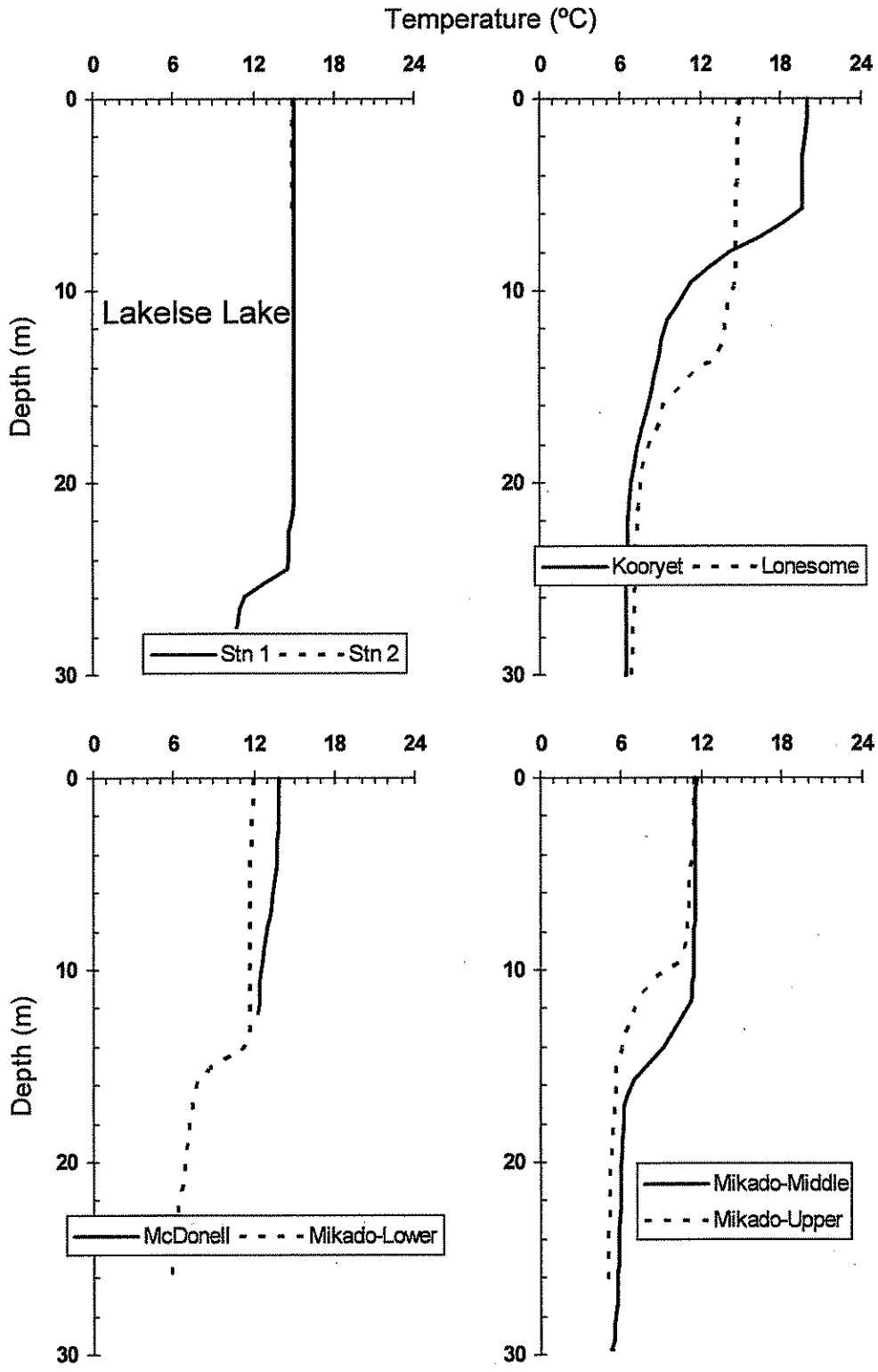

Fig. 23. Temperature profiles from the surveyed lakes.

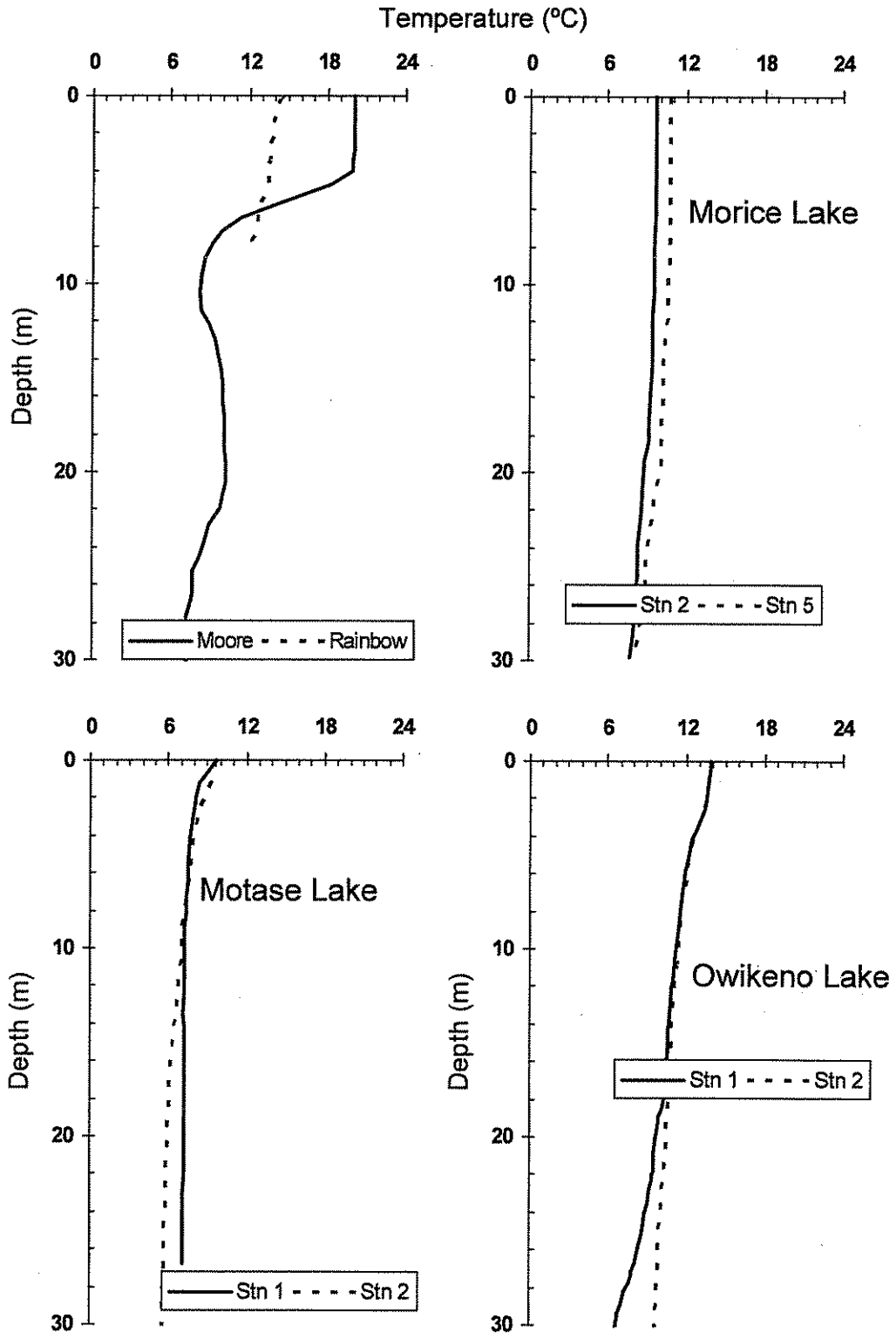

Fig. 24. Temperature profiles from the surveyed lakes.

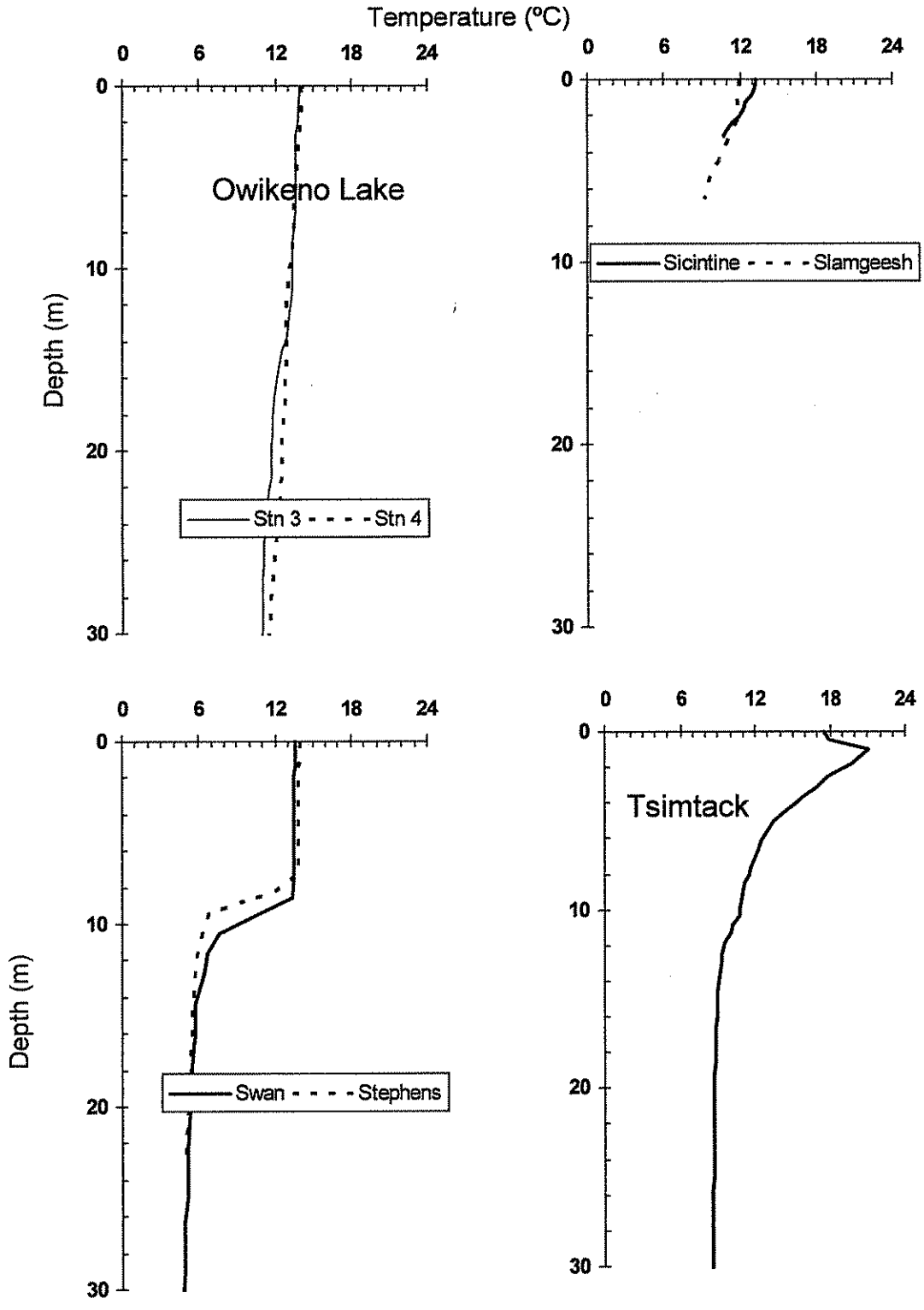

Fig. 25. Temperature profiles from the surveyed lakes.

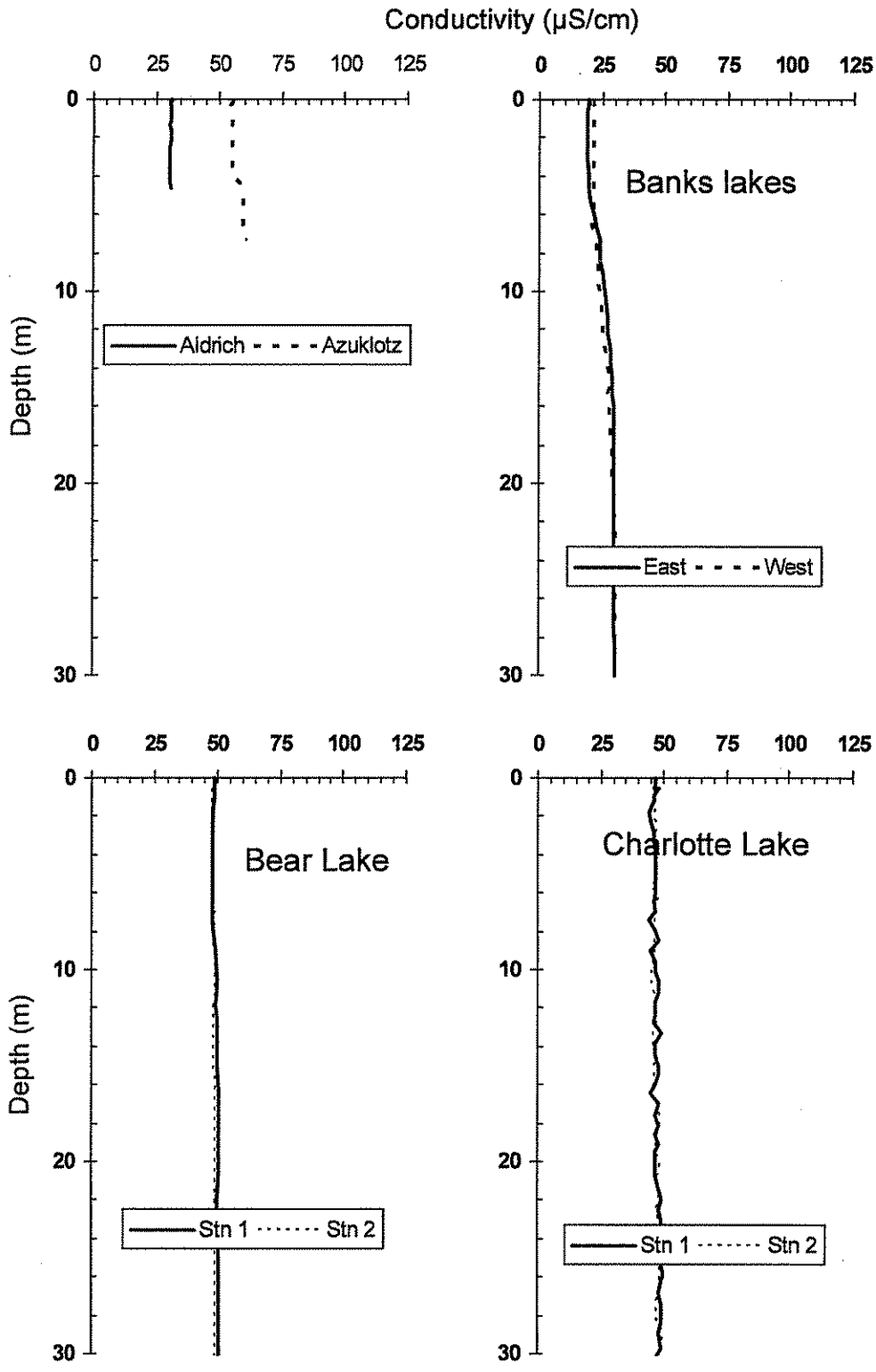

Fig. 26. Conductivity profiles from the surveyed lakes.

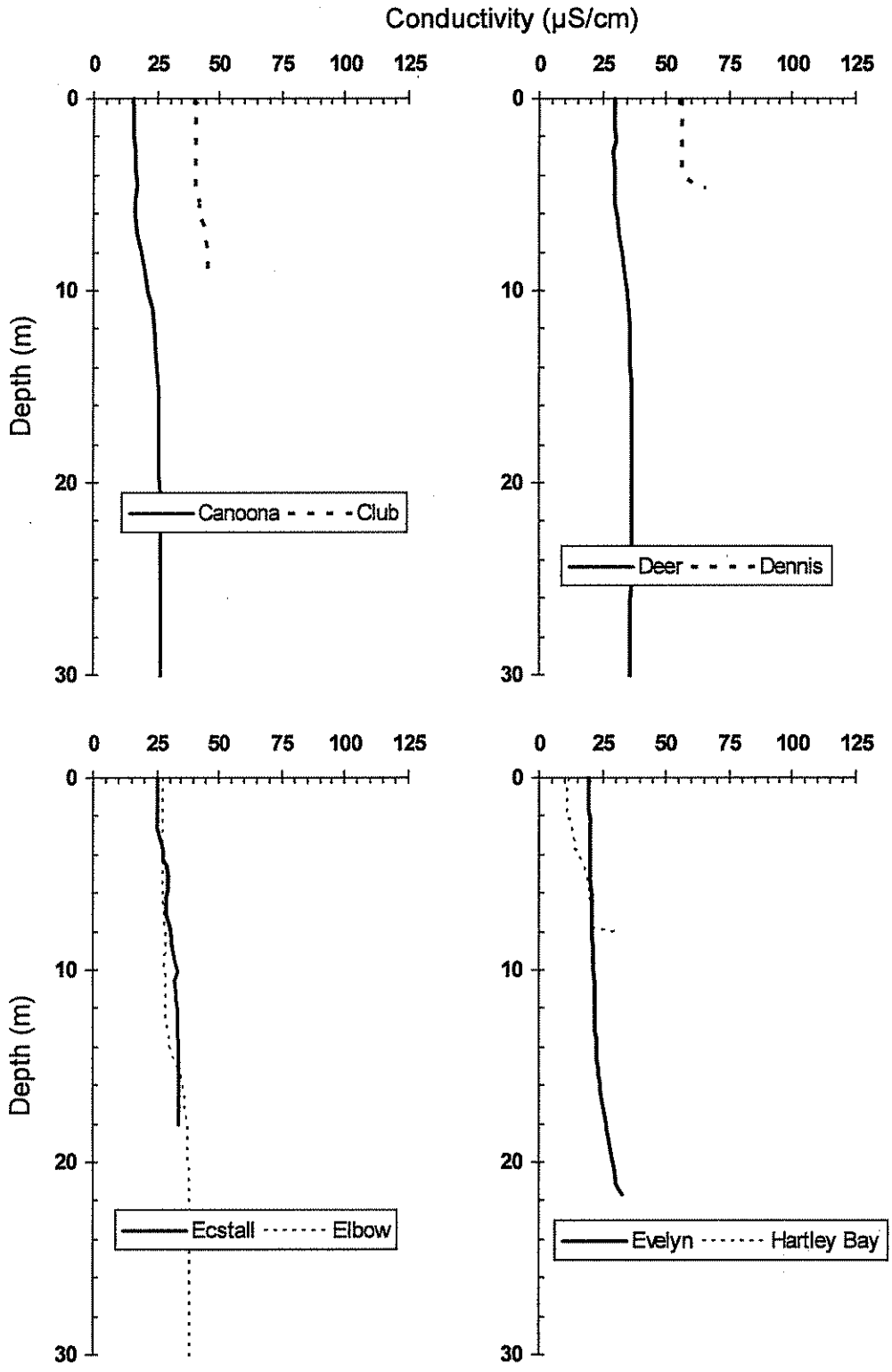

Fig. 27. Conductivity profiles from the surveyed lakes.

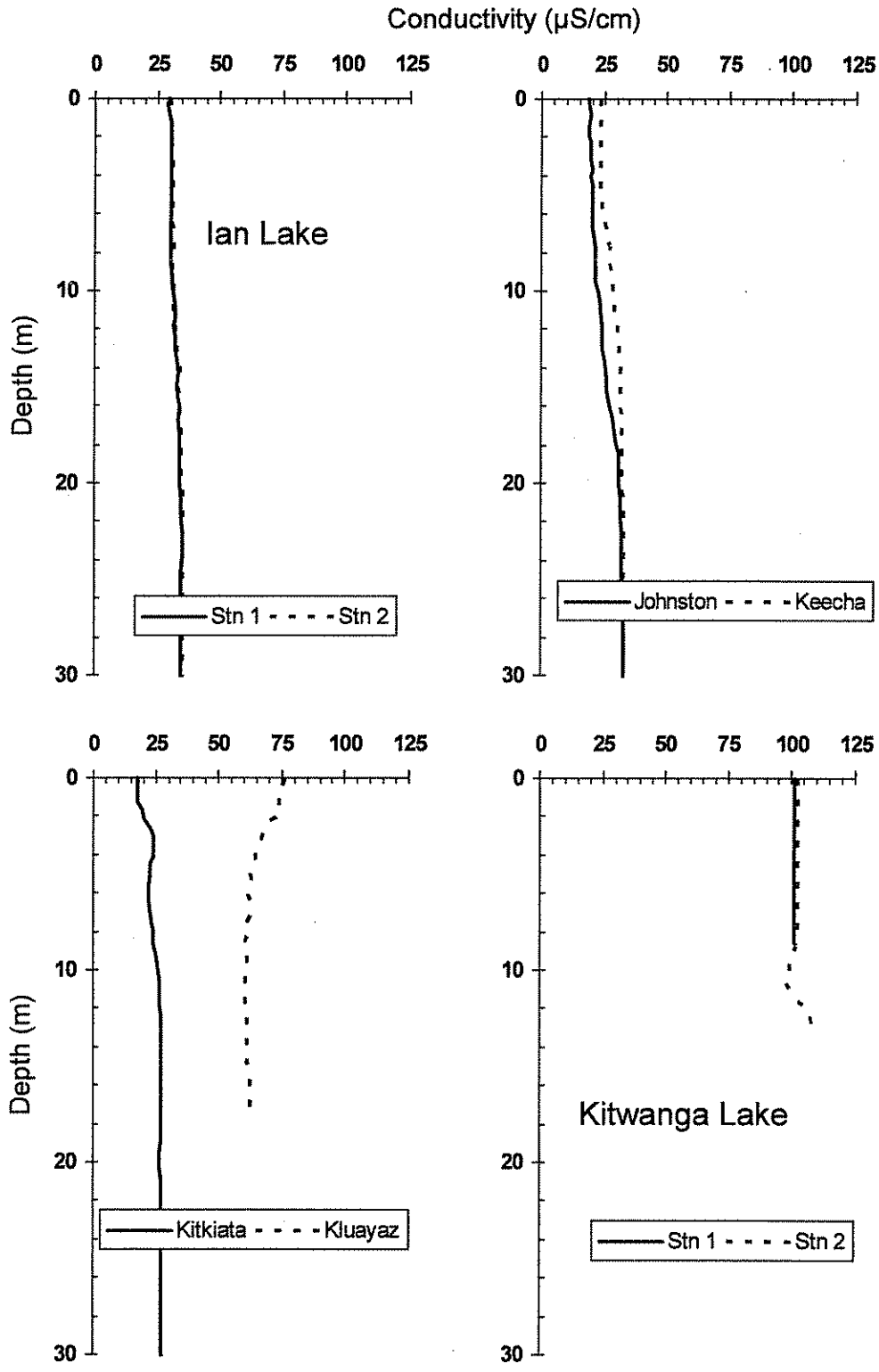

Fig. 28. Conductivity profiles from the surveyed lakes.

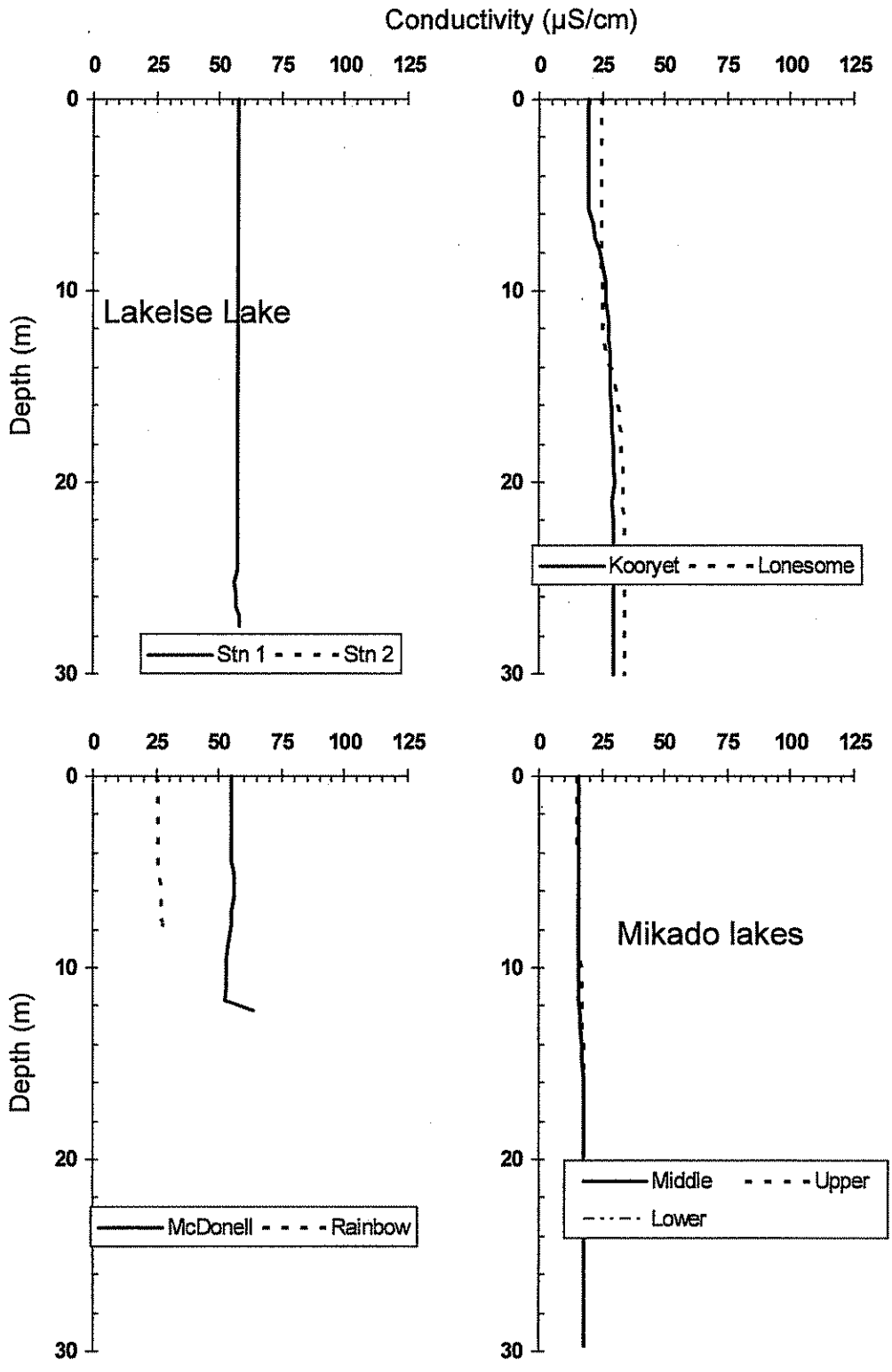

Fig. 29. Conductivity profiles from the surveyed lakes.

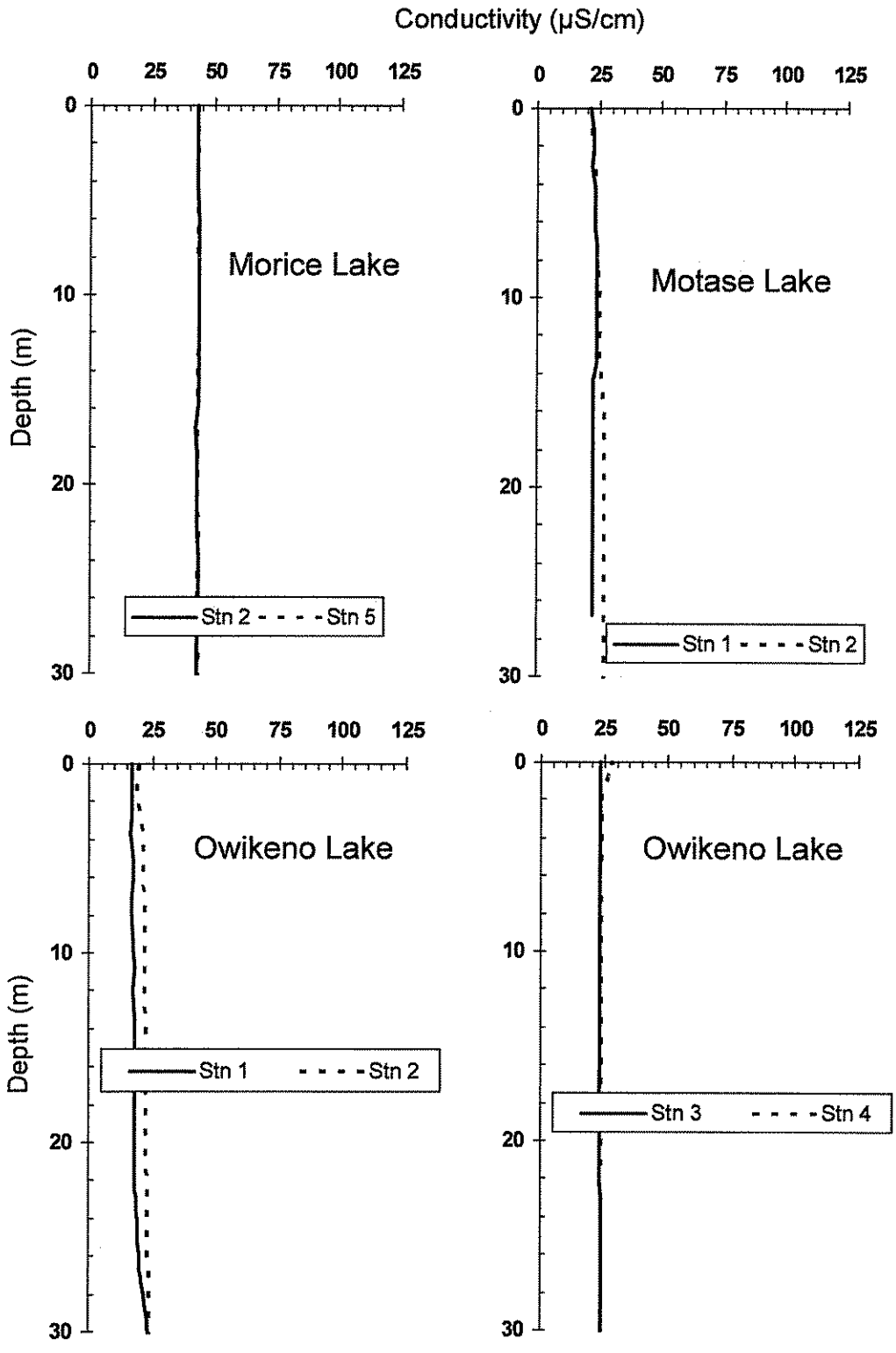

Fig. 30. Conductivity profiles from the surveyed lakes.

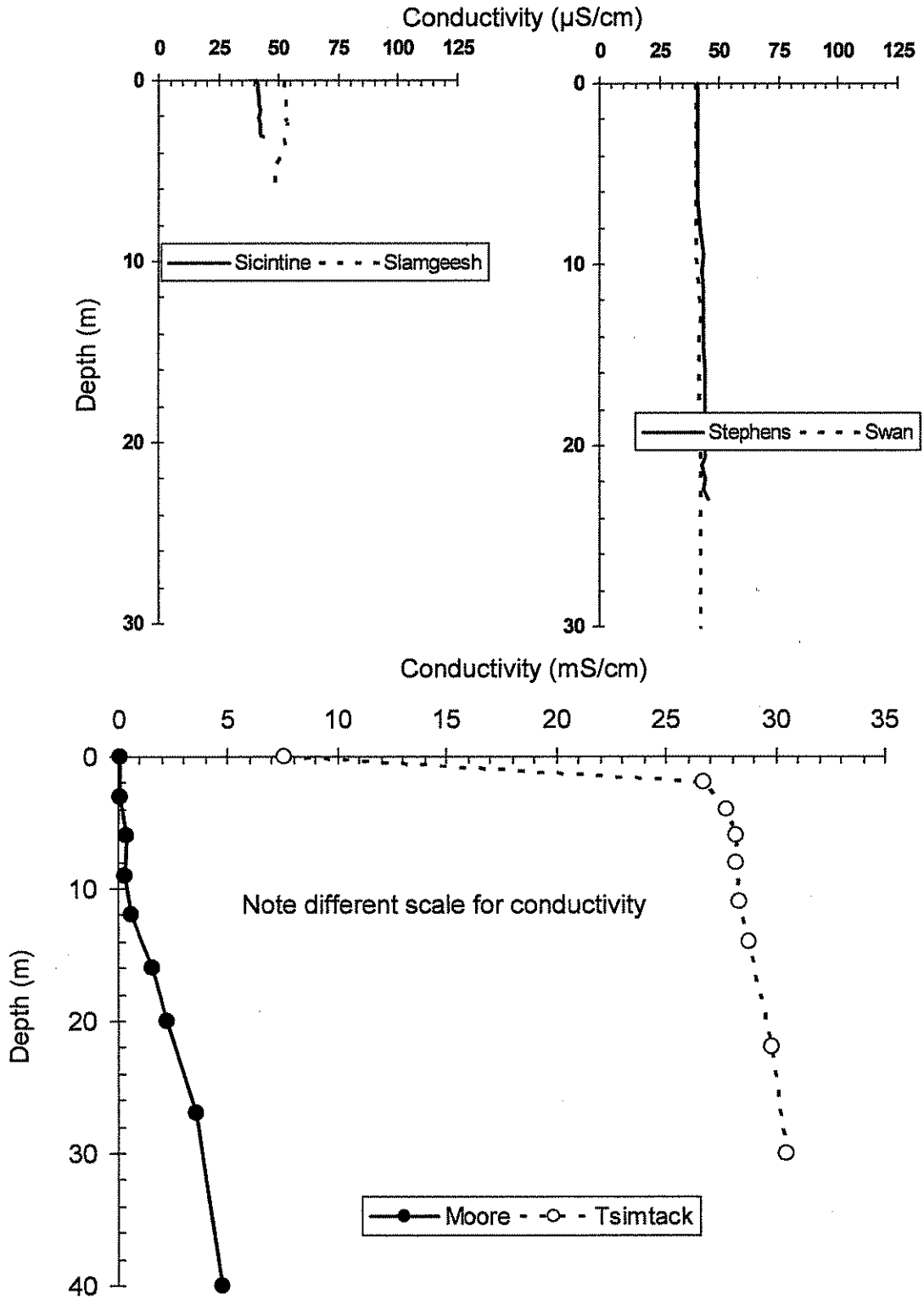

Fig. 31. Conductivity profiles from the surveyed lakes.

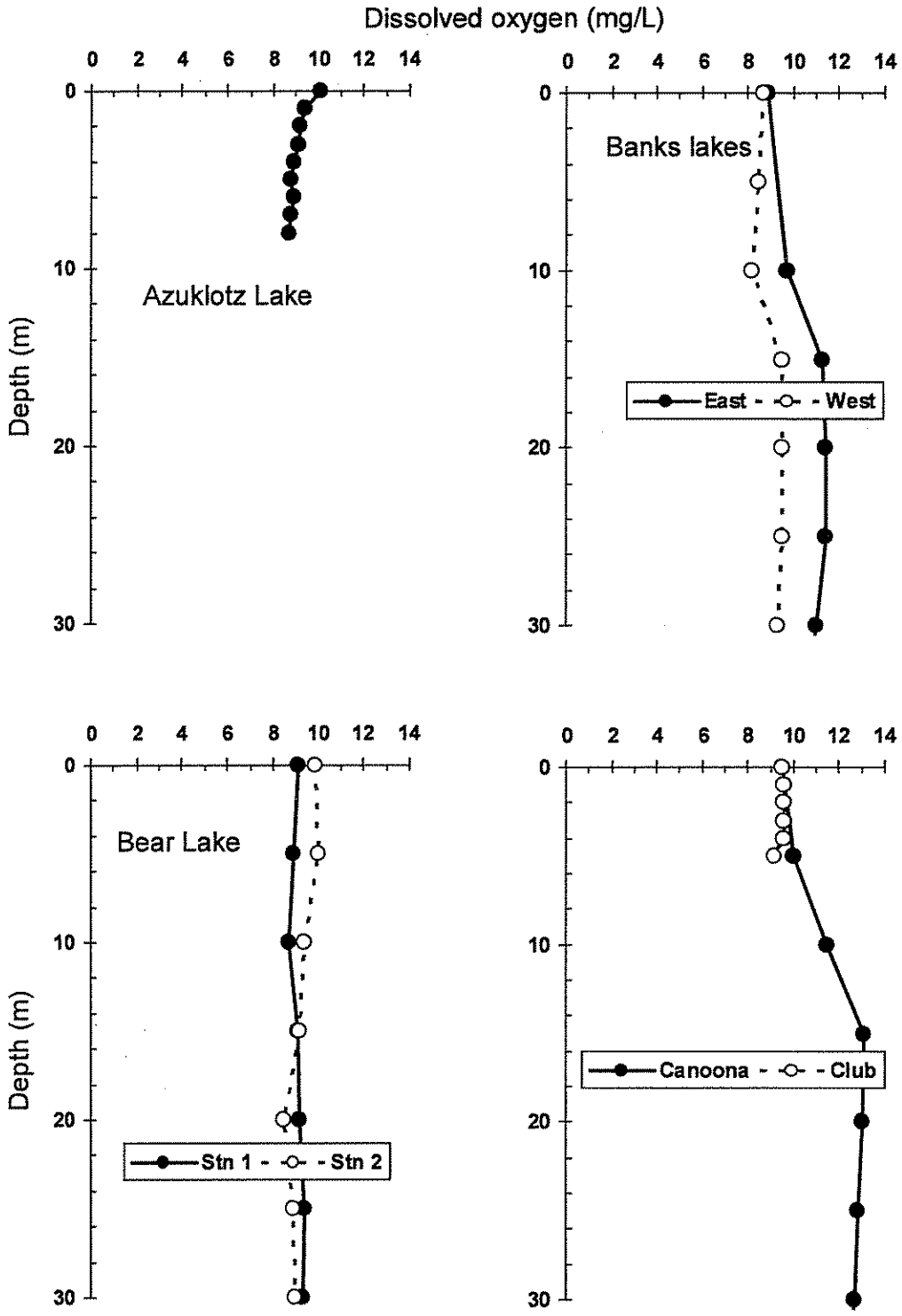

Fig. 32. Vertical profiles of dissolved oxygen concentration from the surveyed lakes.

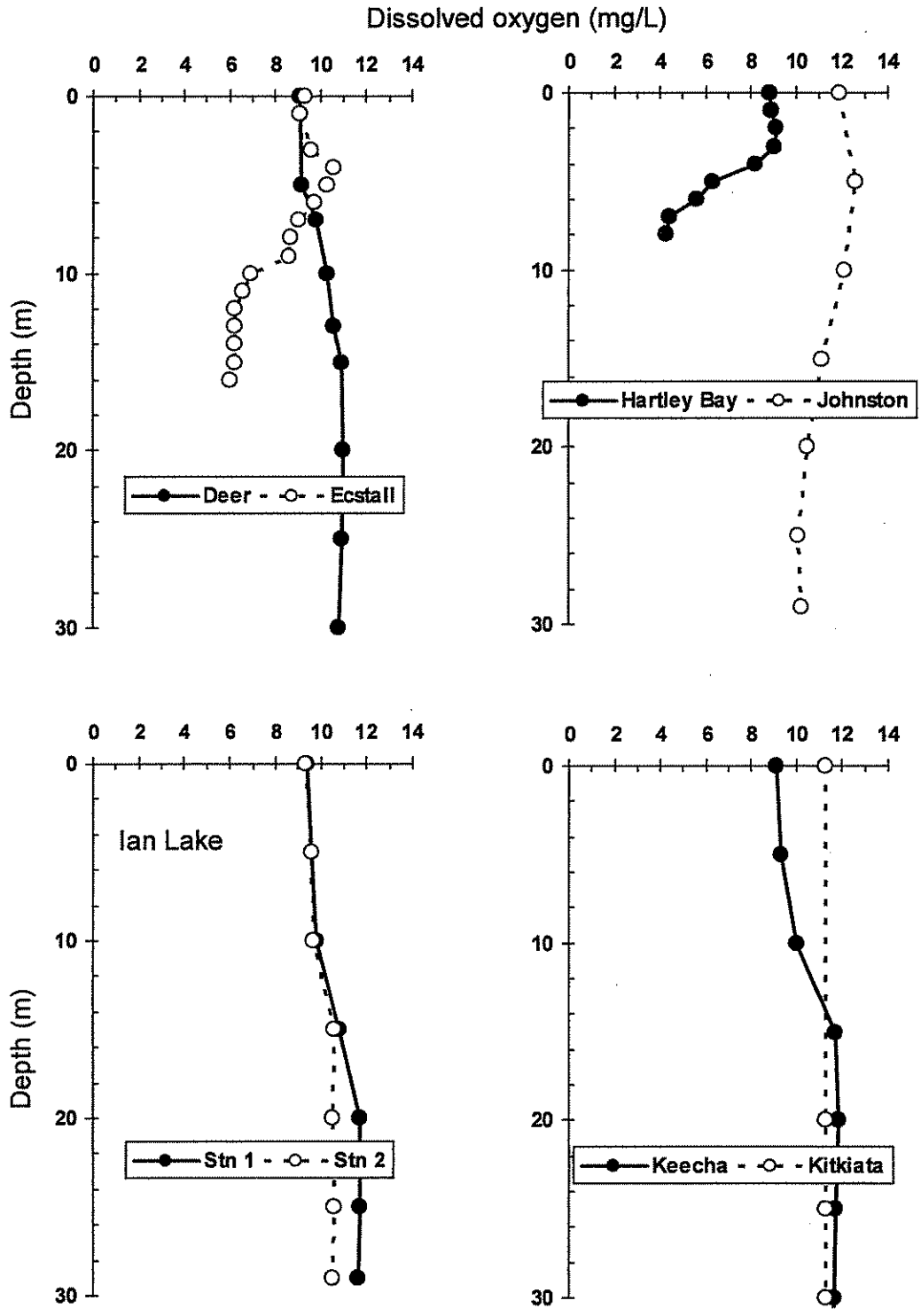

Fig. 33. Vertical profiles of dissolved oxygen concentration from the surveyed lakes.

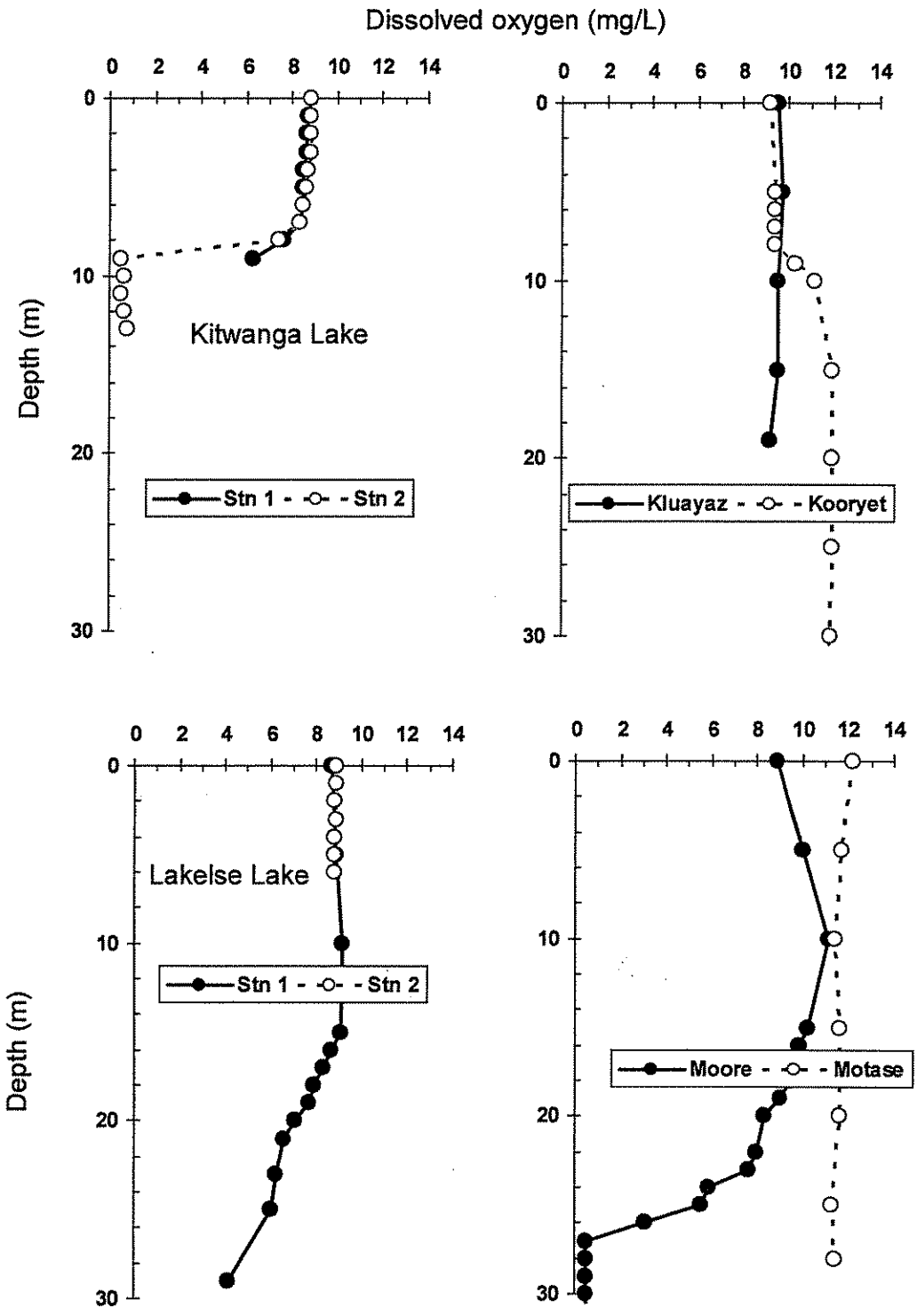

Fig. 34. Vertical profiles of dissolved oxygen concentration from the surveyed lakes.

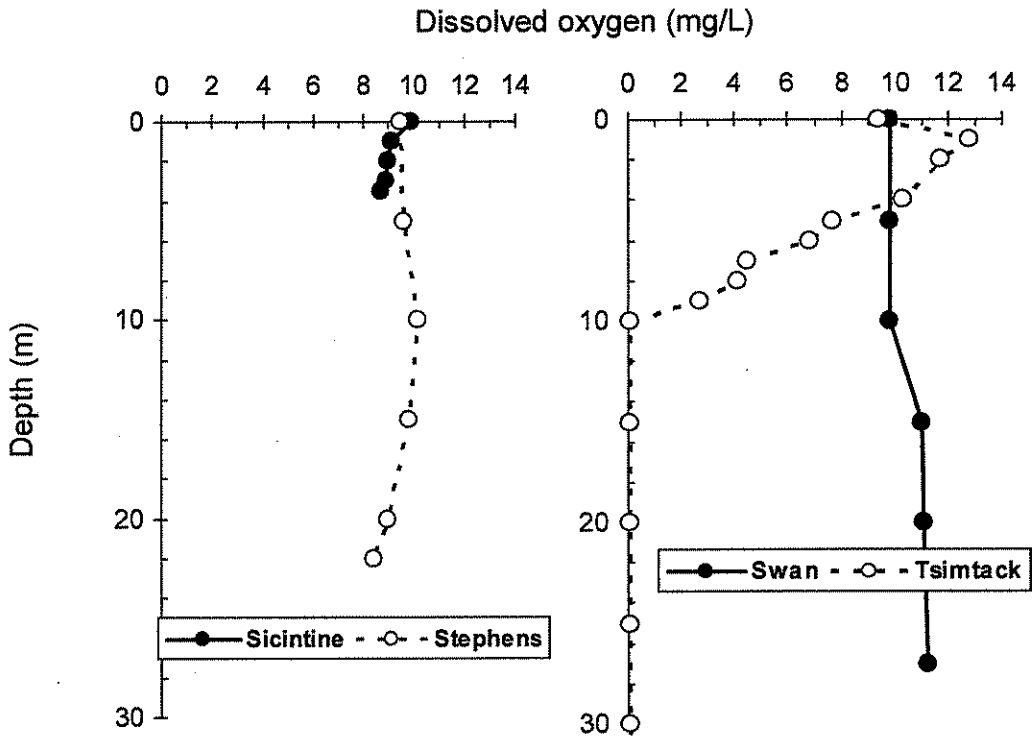

Fig. 35. Vertical profiles of dissolved oxygen concentration from the surveyed lakes.

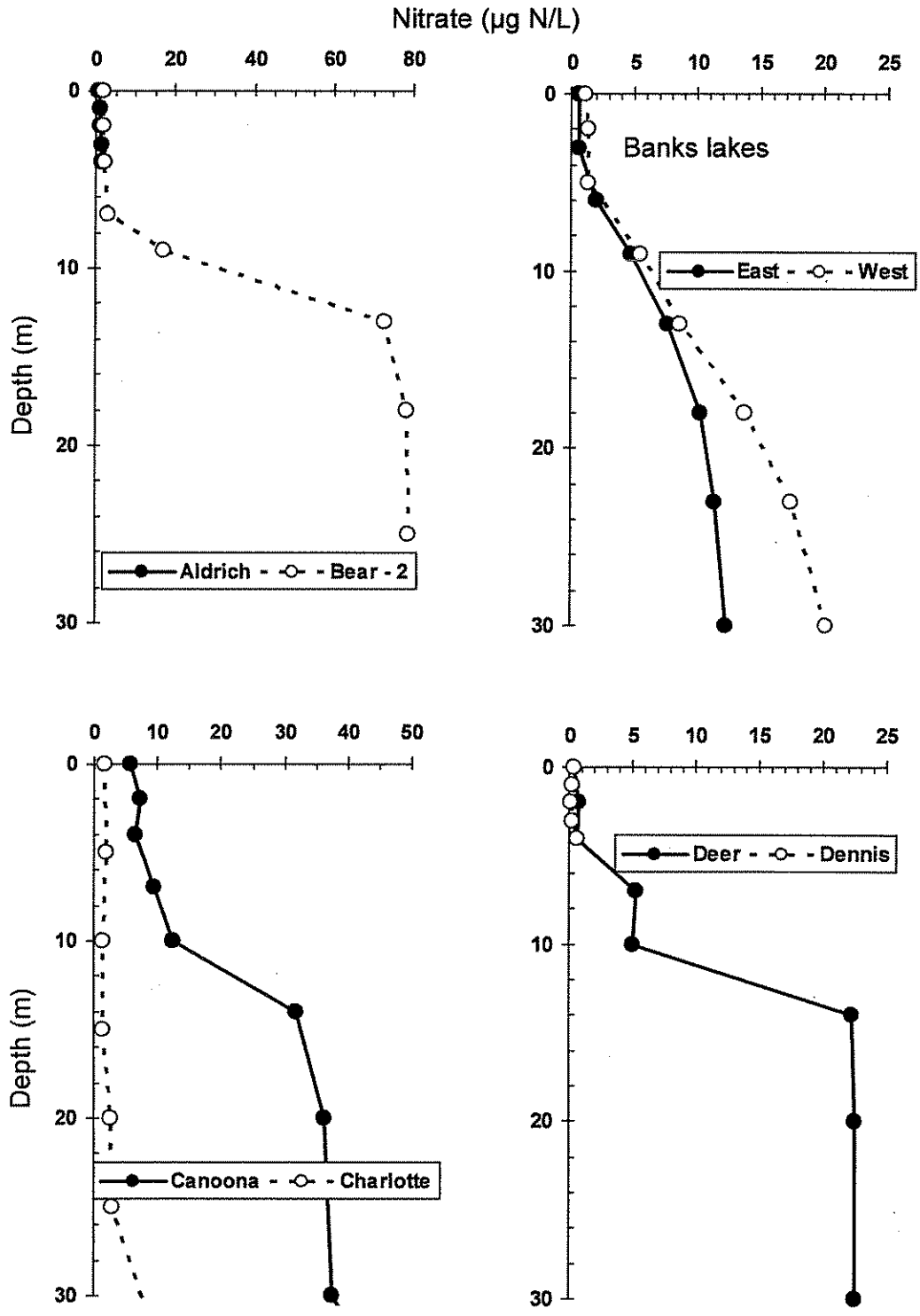

Fig. 36. Vertical profiles of nitrate concentration from the surveyed lakes. Note variable nitrate axes.

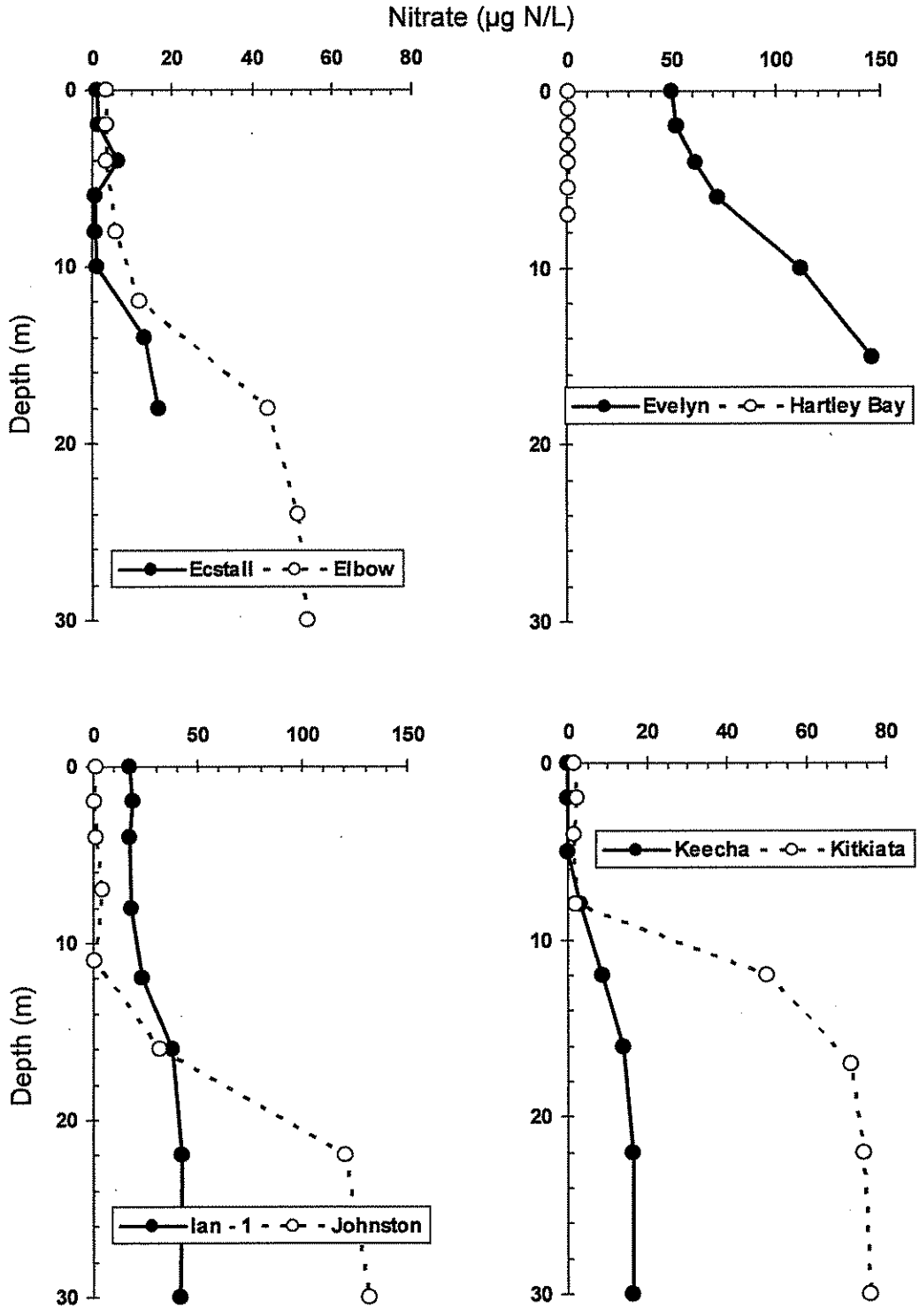

Fig. 37. Vertical profiles of nitrate concentration from the surveyed lakes. Note variable nitrate axes.

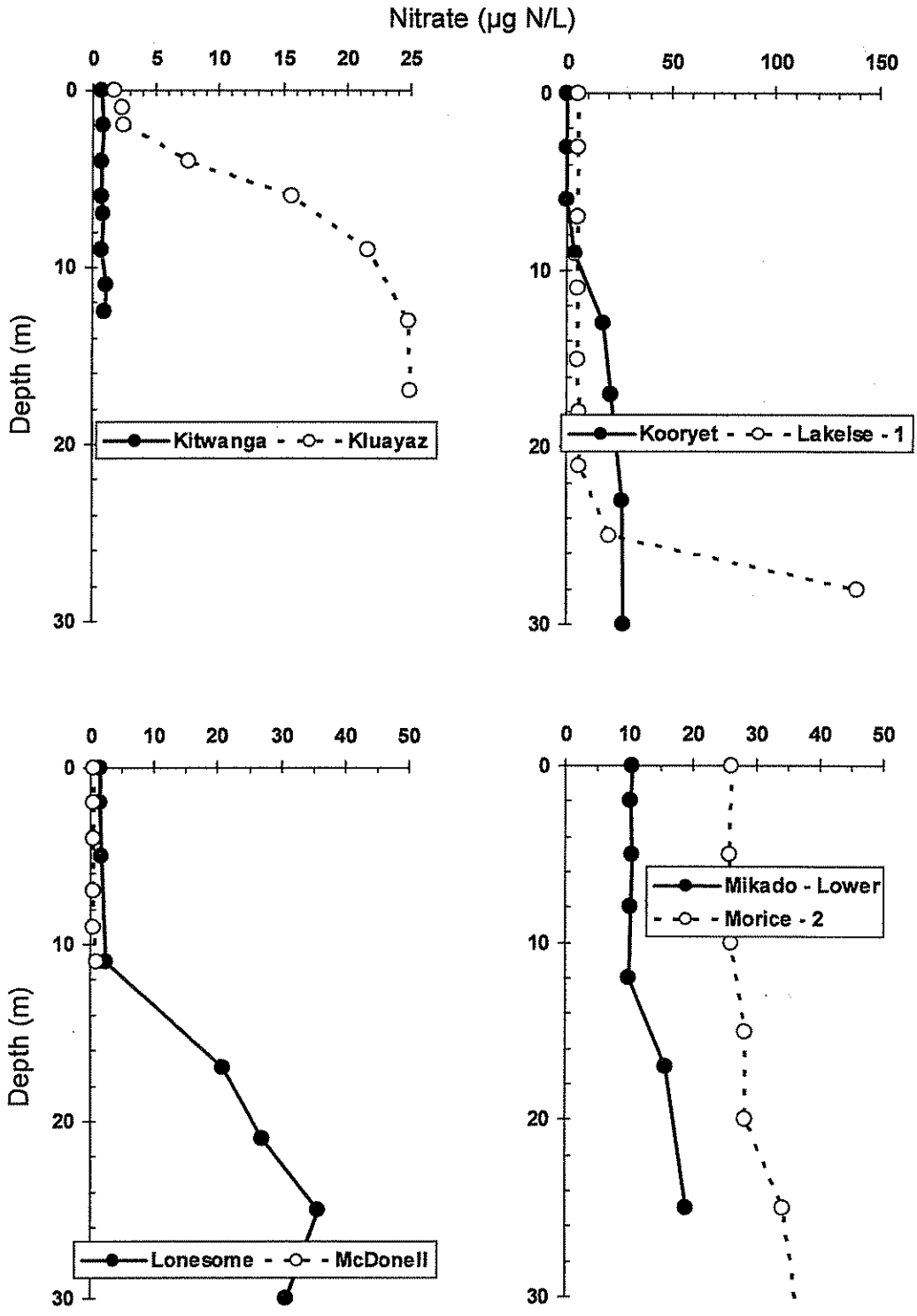

Fig. 38. Vertical profiles of nitrate concentration from the surveyed lakes. Note variable nitrate axes.

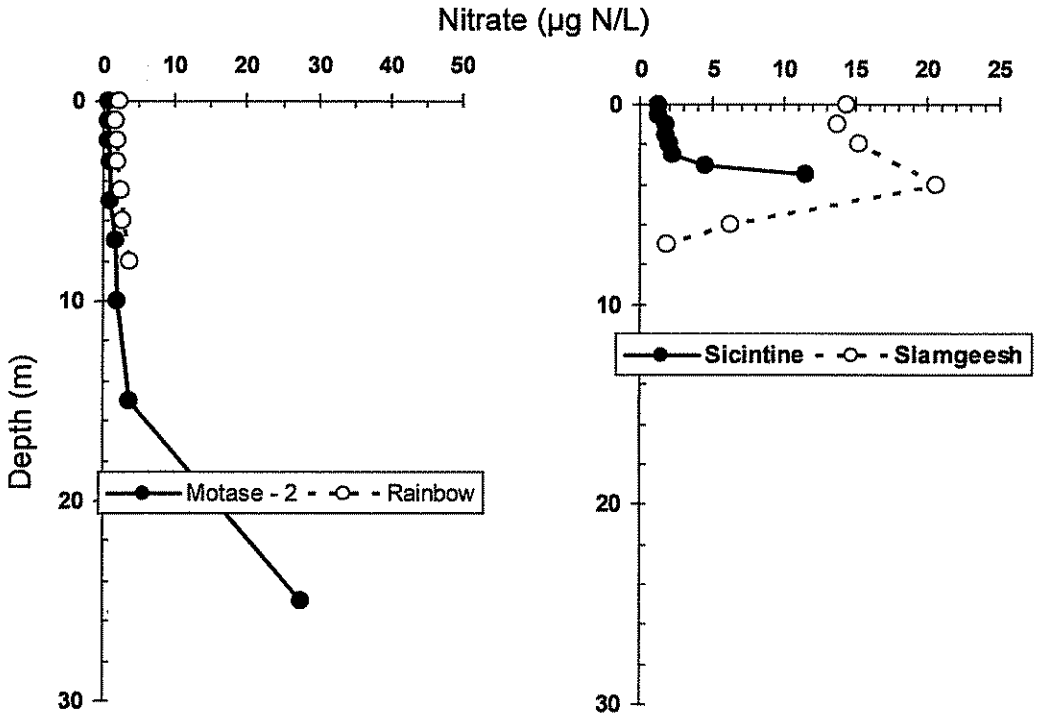

Fig. 39. Vertical profiles of nitrate concentration from the surveyed lakes. Note variable nitrate axes.

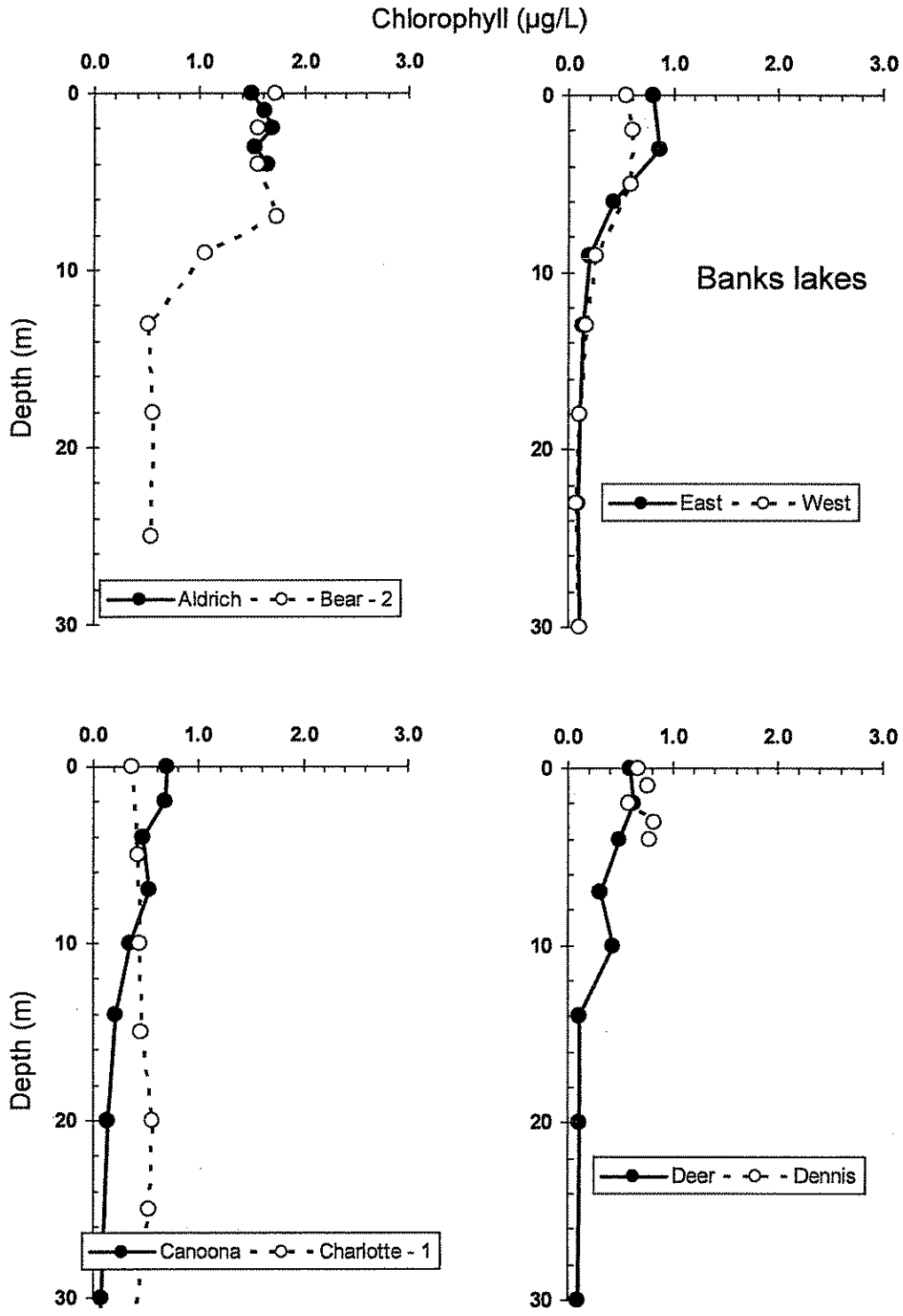

Fig. 40. Vertical profiles of chlorophyll concentration from the surveyed lakes.

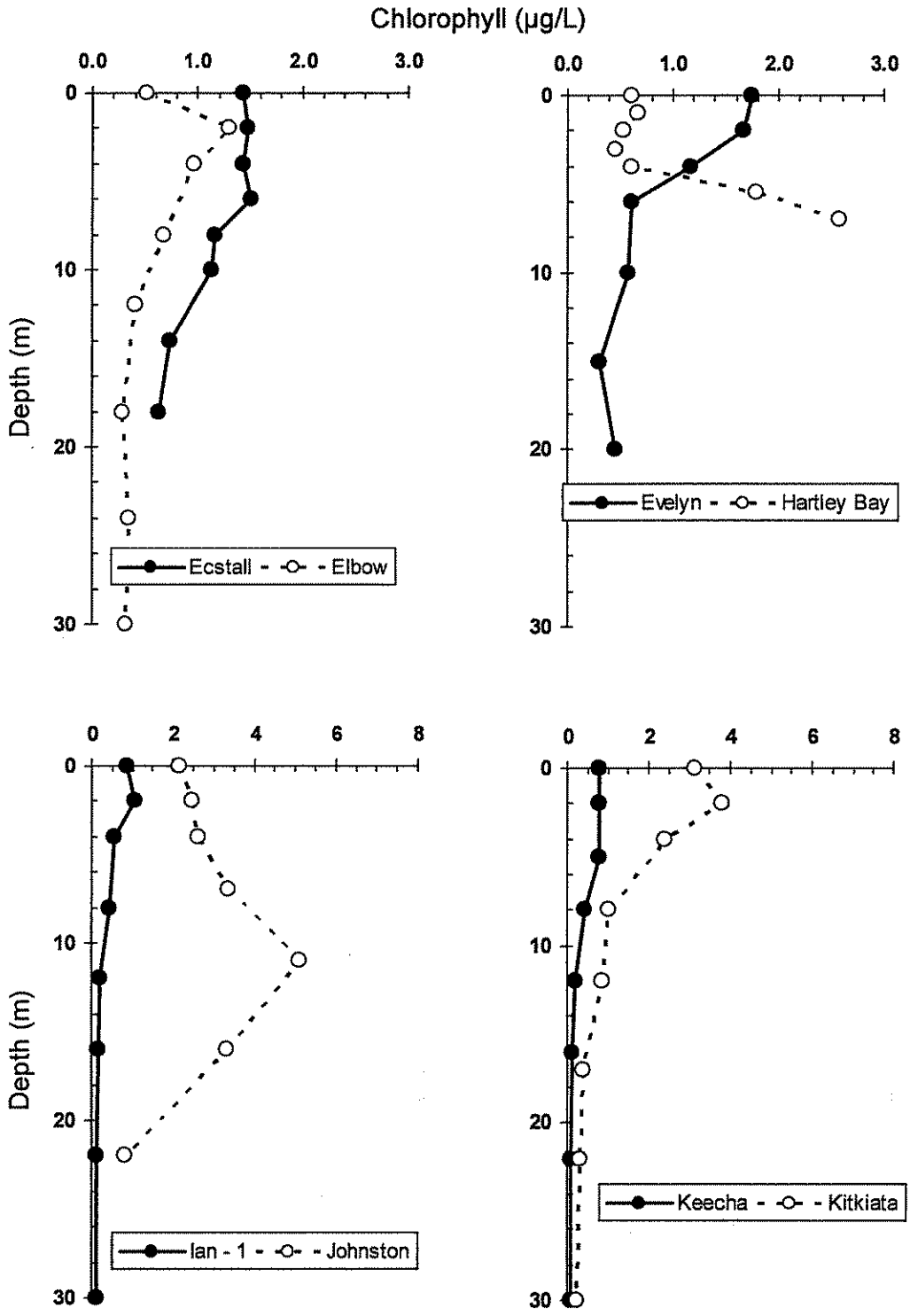

Fig. 41. Vertical profiles of chlorophyll concentration from the surveyed lakes. Note variable chlorophyll axes.

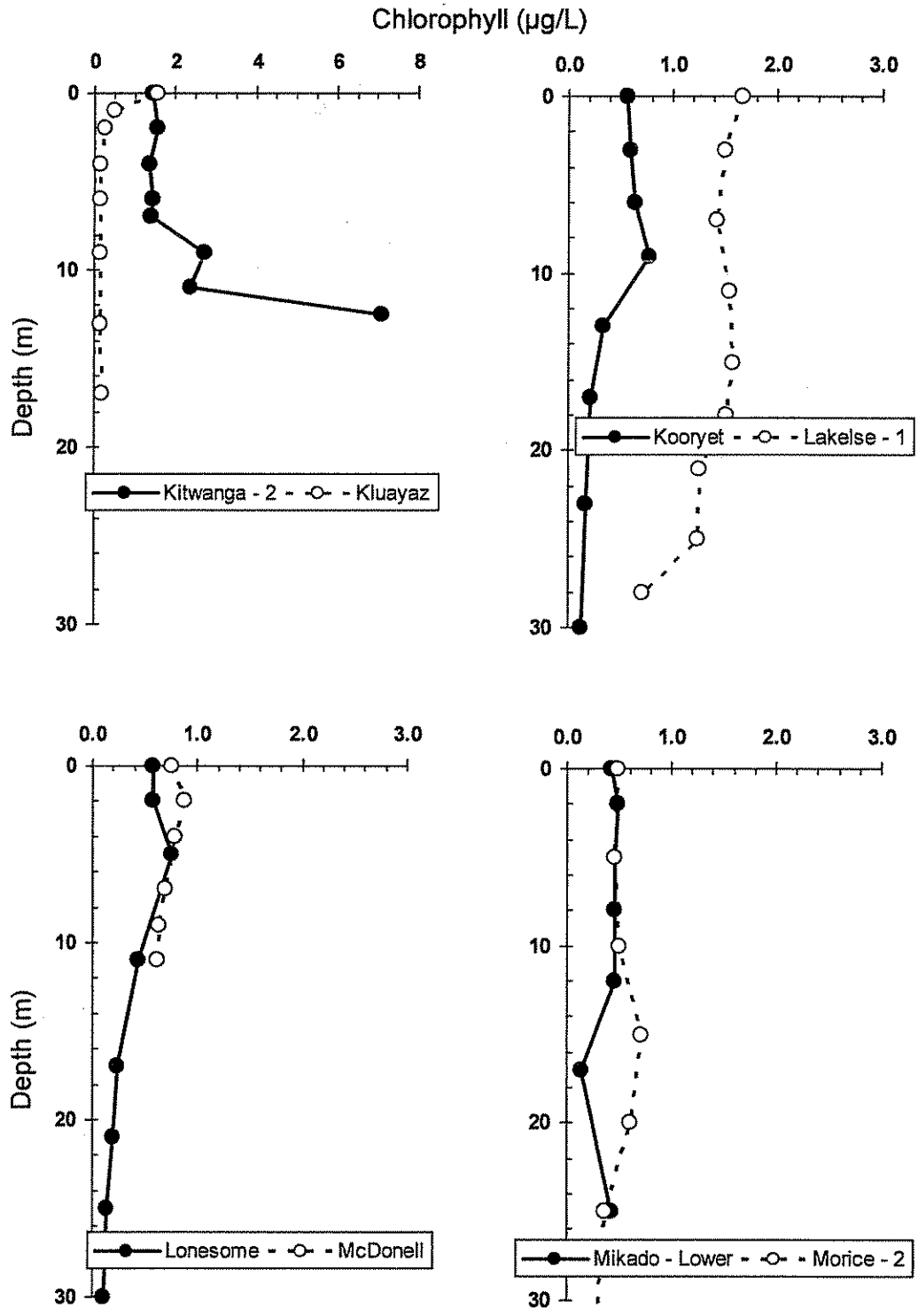

Fig. 42. Vertical profiles of chlorophyll concentration from the surveyed lakes. Note variable chlorophyll axes.

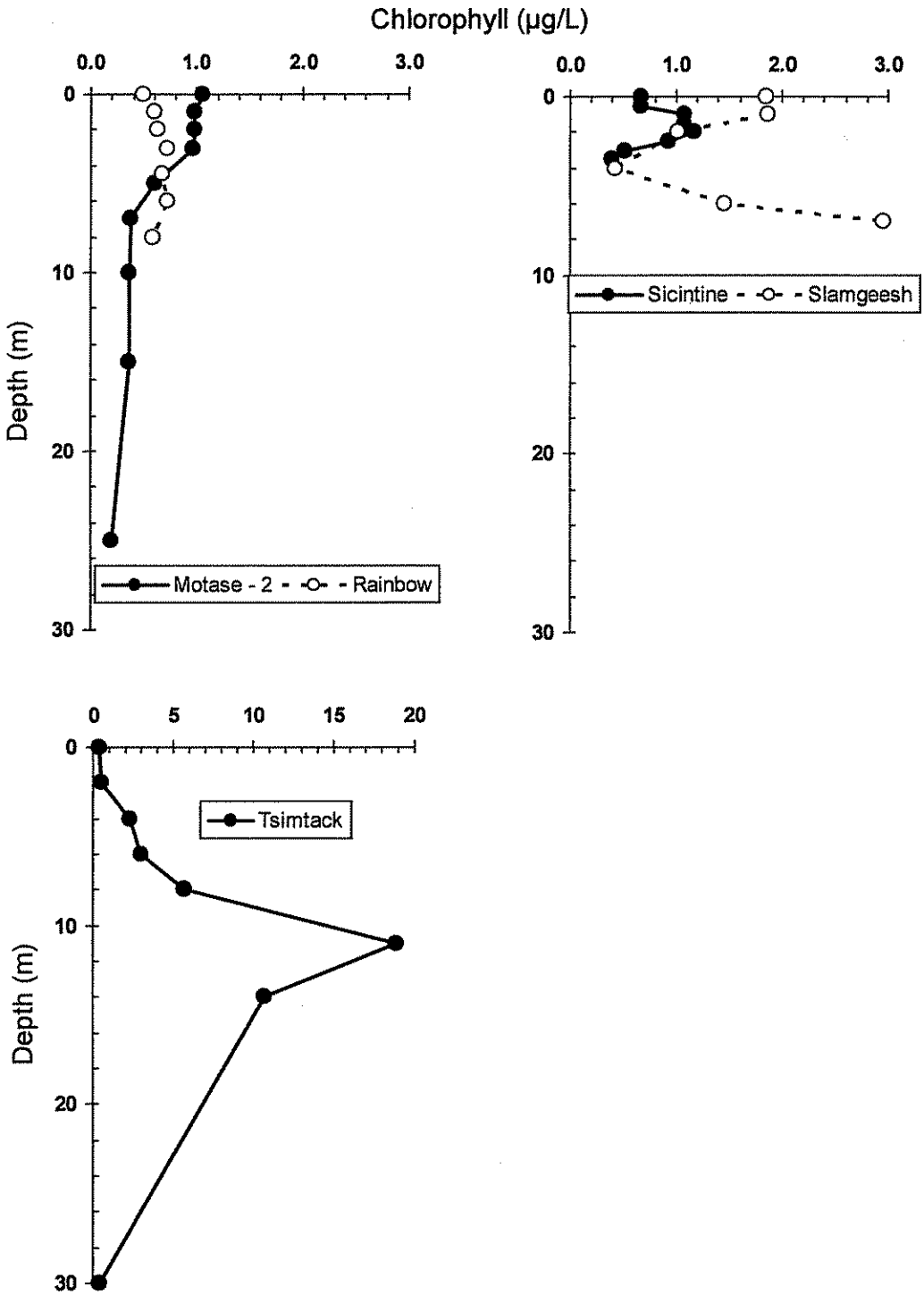

Fig. 43. Vertical profiles of chlorophyll concentration from the surveyed lakes. Note variable chlorophyll axes.

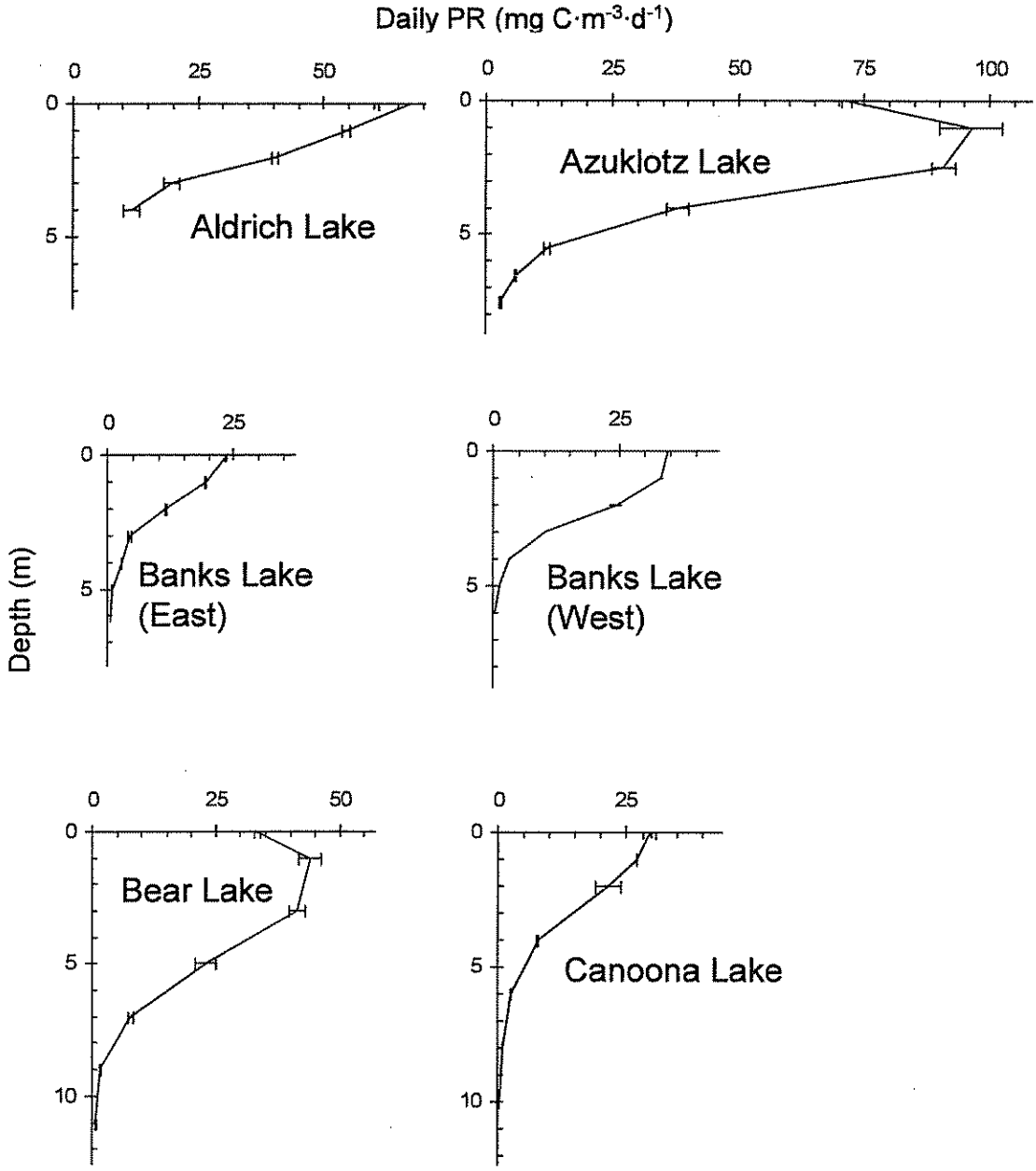

Fig. 44. Vertical PR profiles for the surveyed lakes.

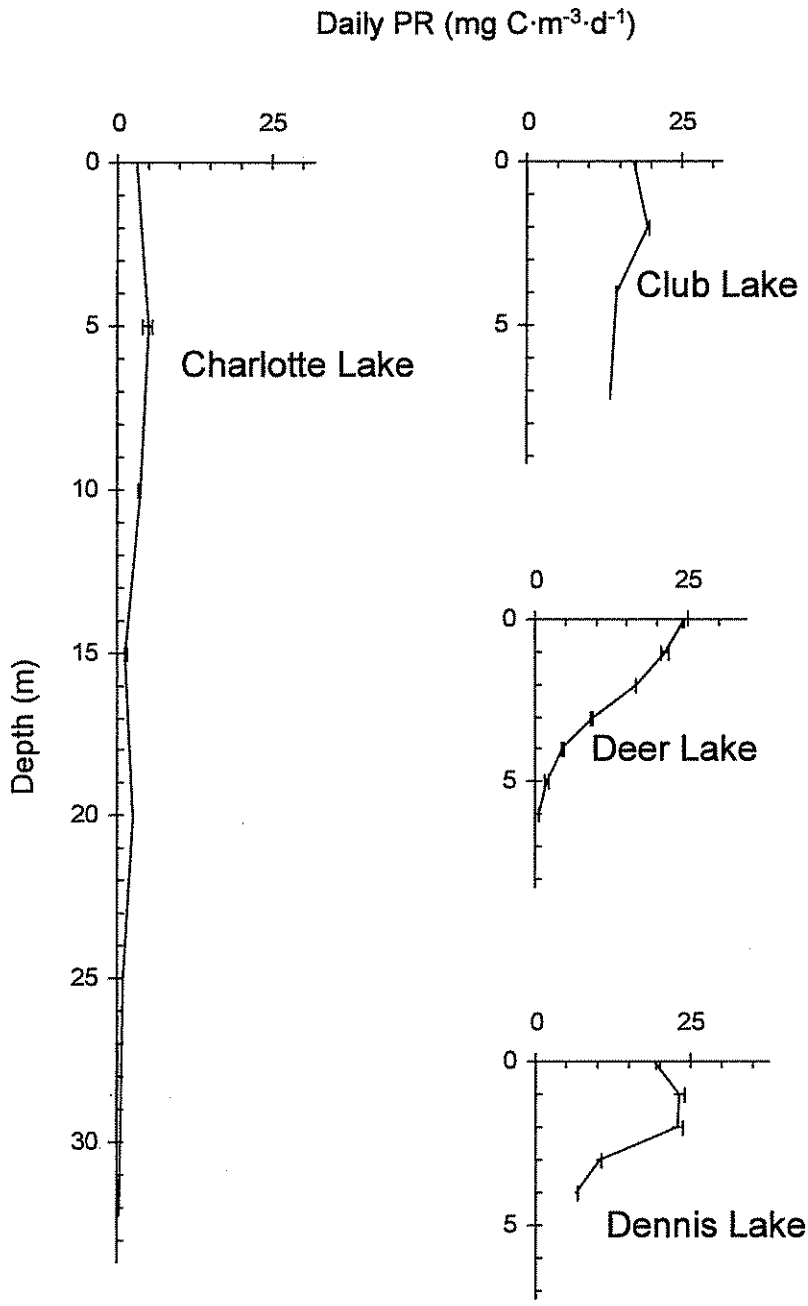

Fig. 45. Vertical PR profiles for the surveyed lakes.

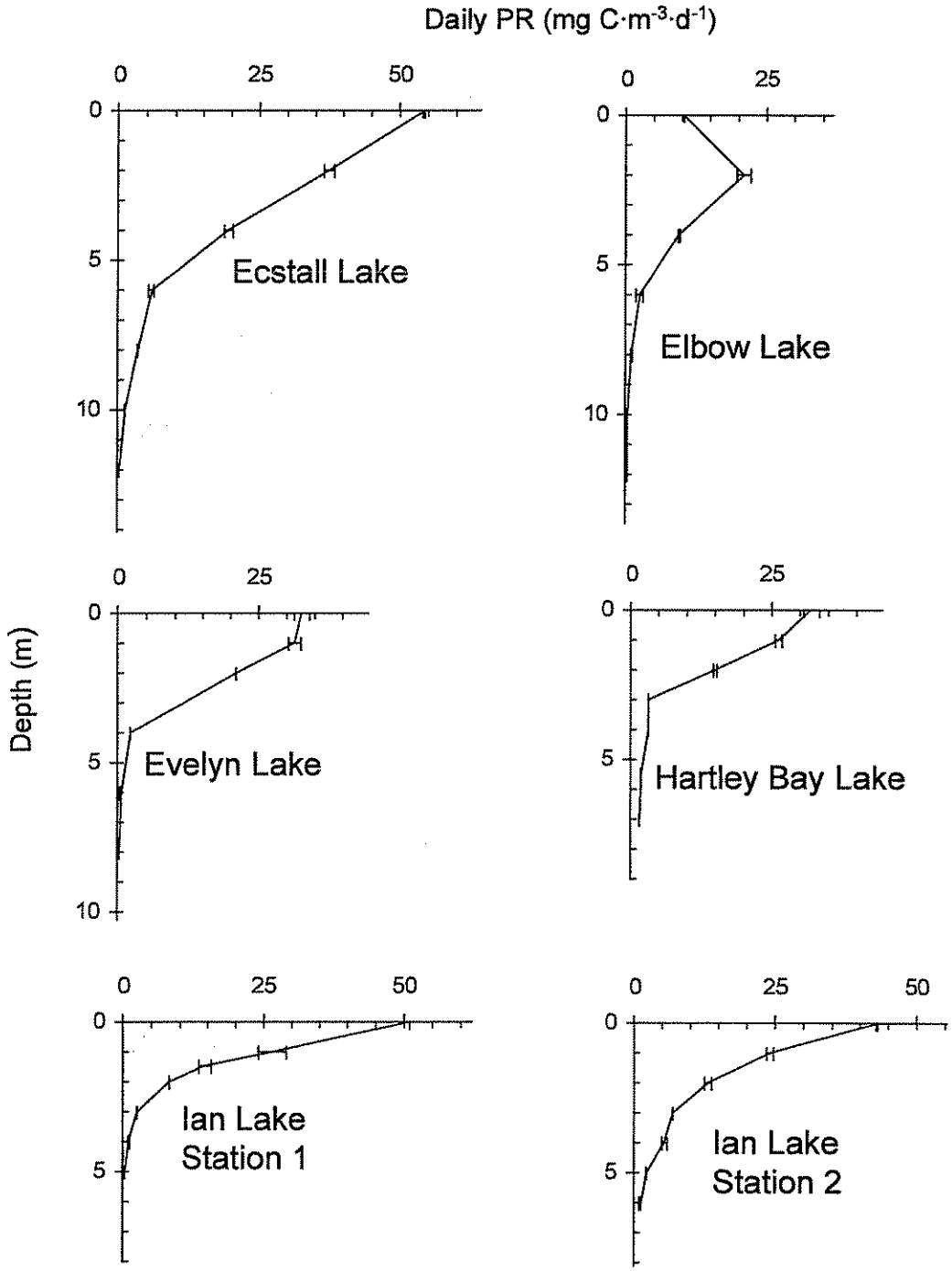

Fig. 46. Vertical PR profiles for the surveyed lakes.

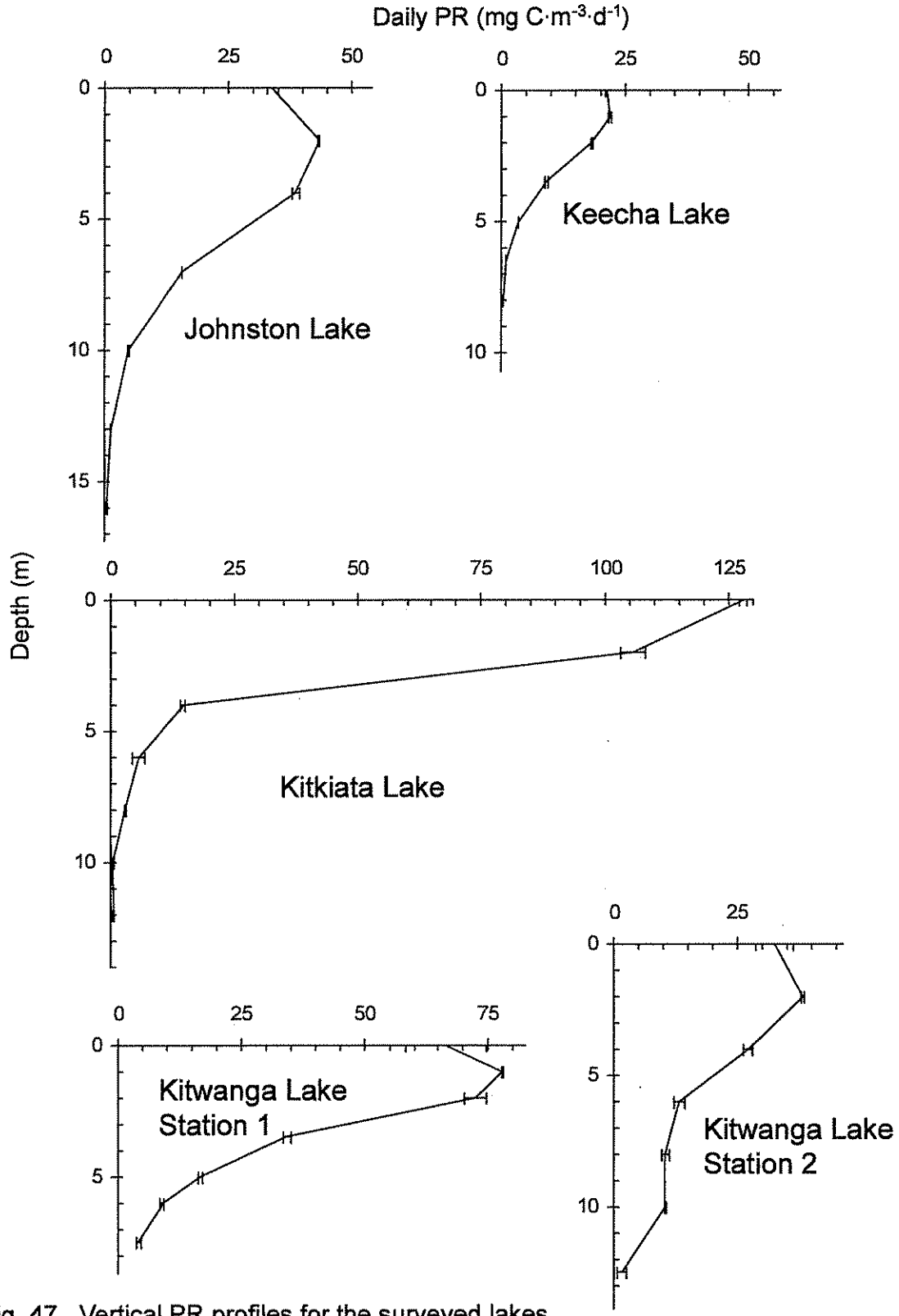

Fig. 47. Vertical PR profiles for the surveyed lakes.

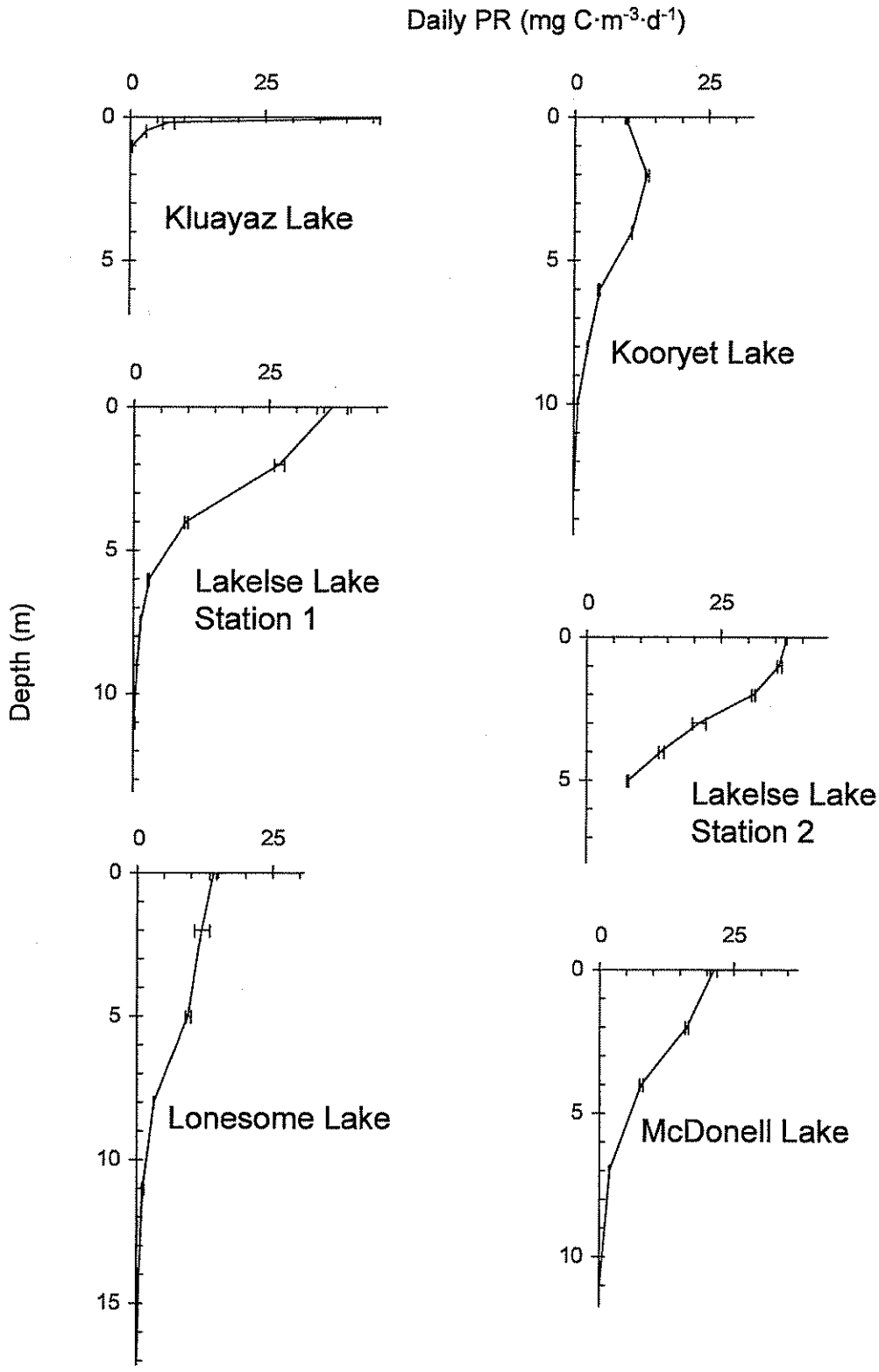

Fig. 48. Vertical PR profiles for the surveyed lakes.

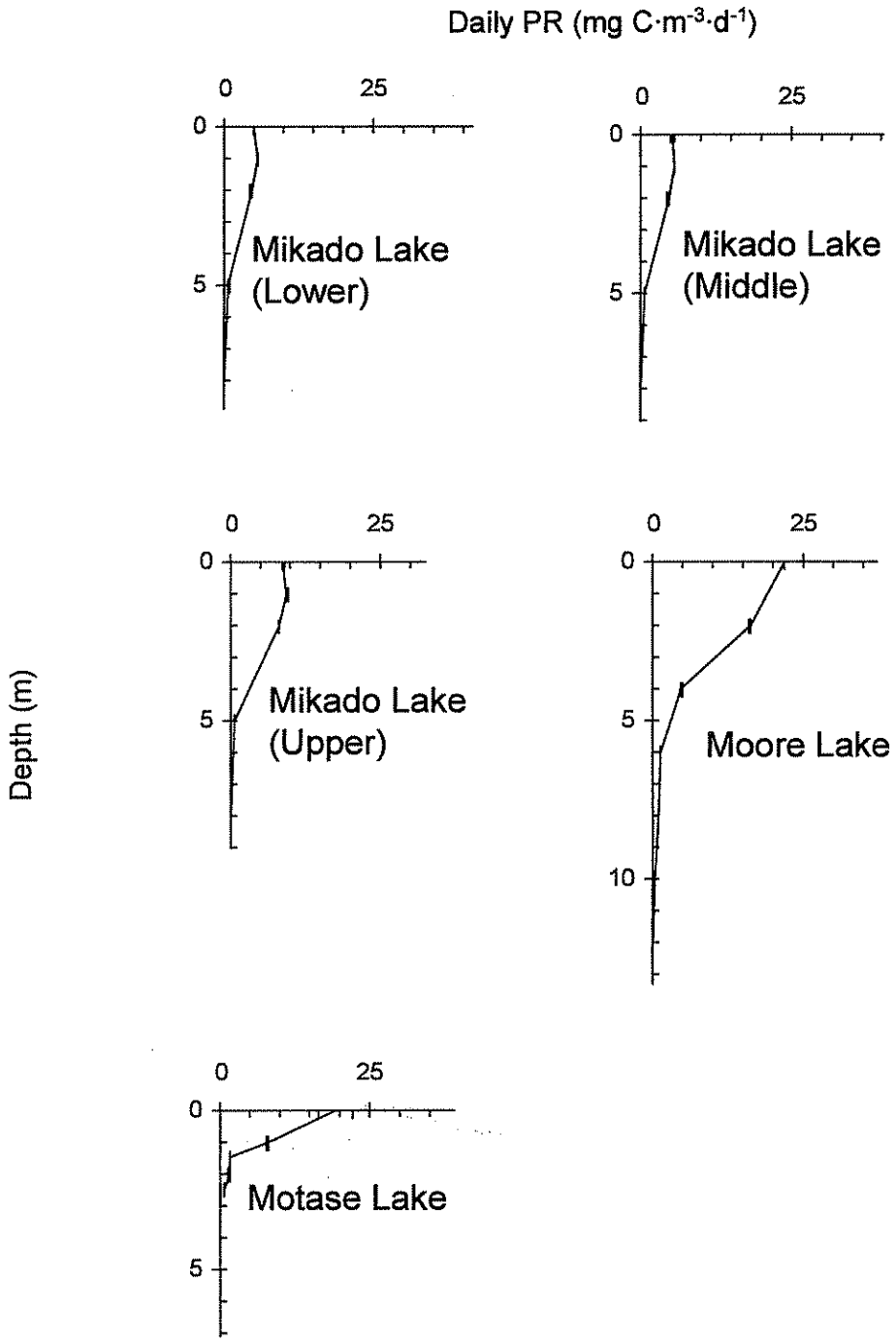

Fig. 49. Vertical PR profiles for the surveyed lakes.

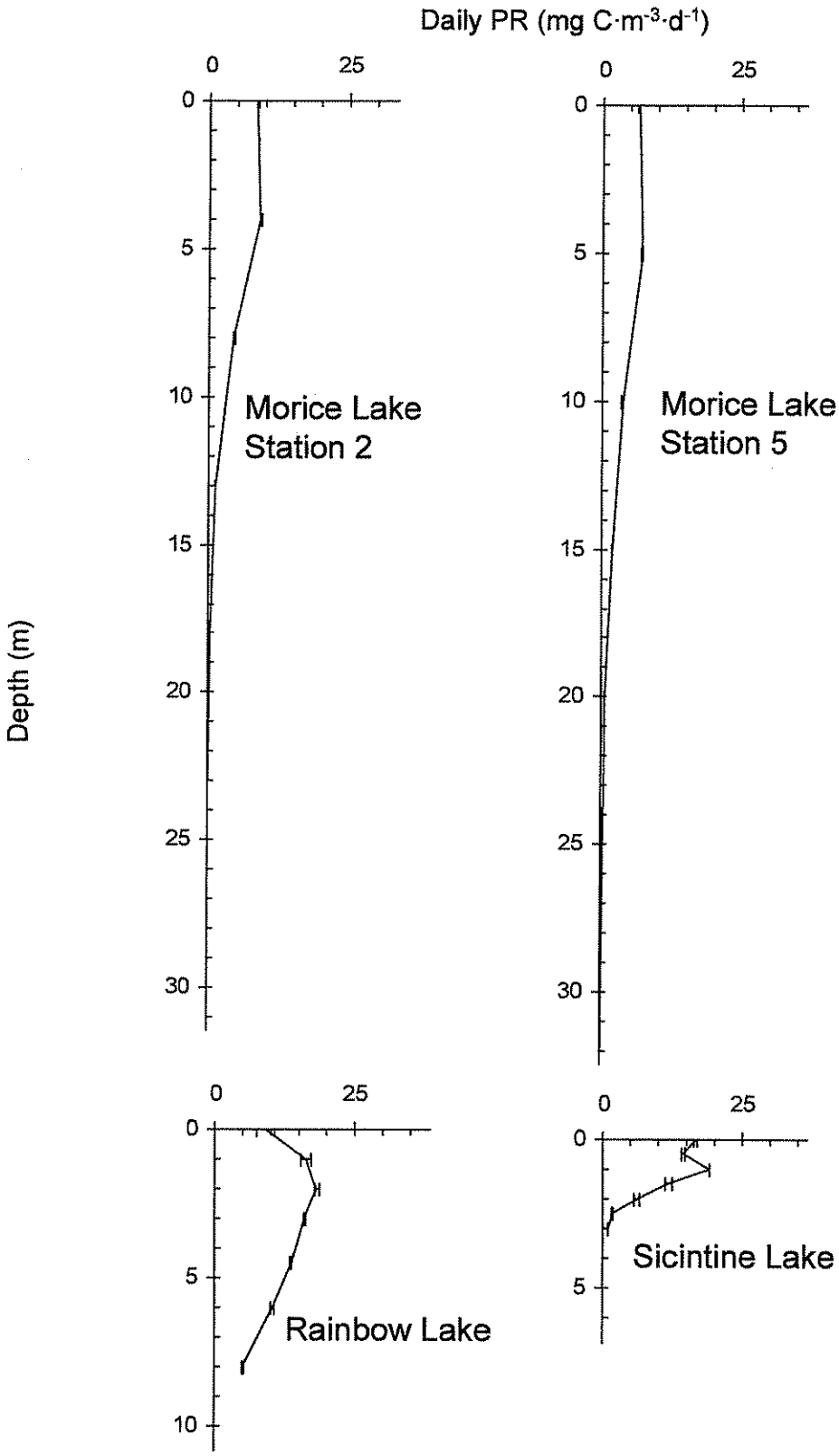

Fig. 50. Vertical PR profiles for the surveyed lakes.

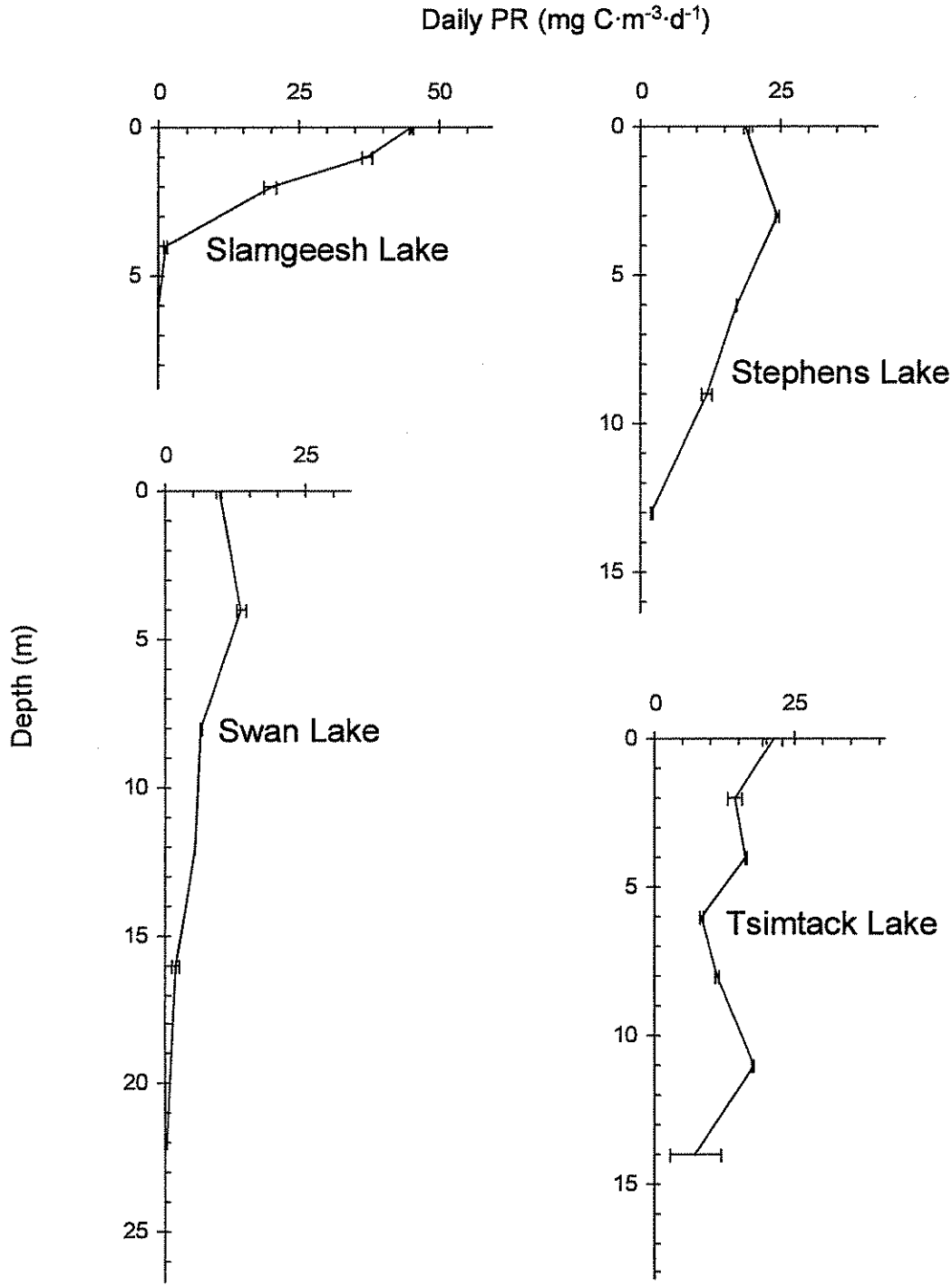

Fig. 51. Vertical PR profiles for the surveyed lakes.

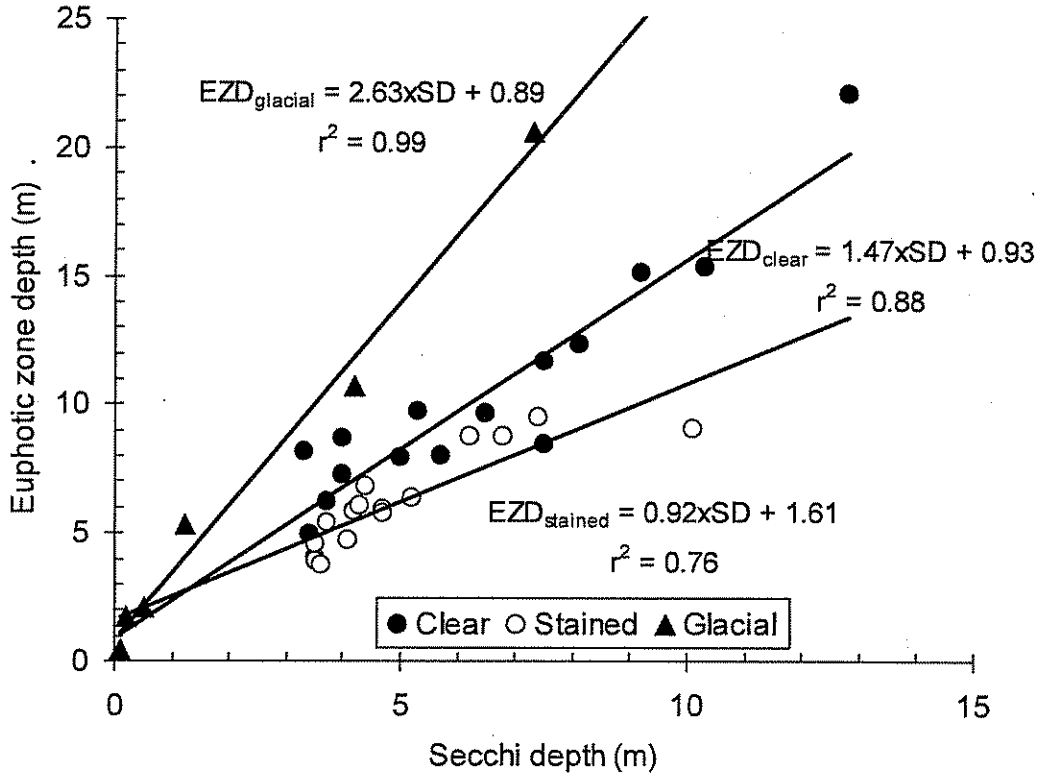

Fig. 52. Correlations between euphotic zone depth and secchi depth in the three lake types.

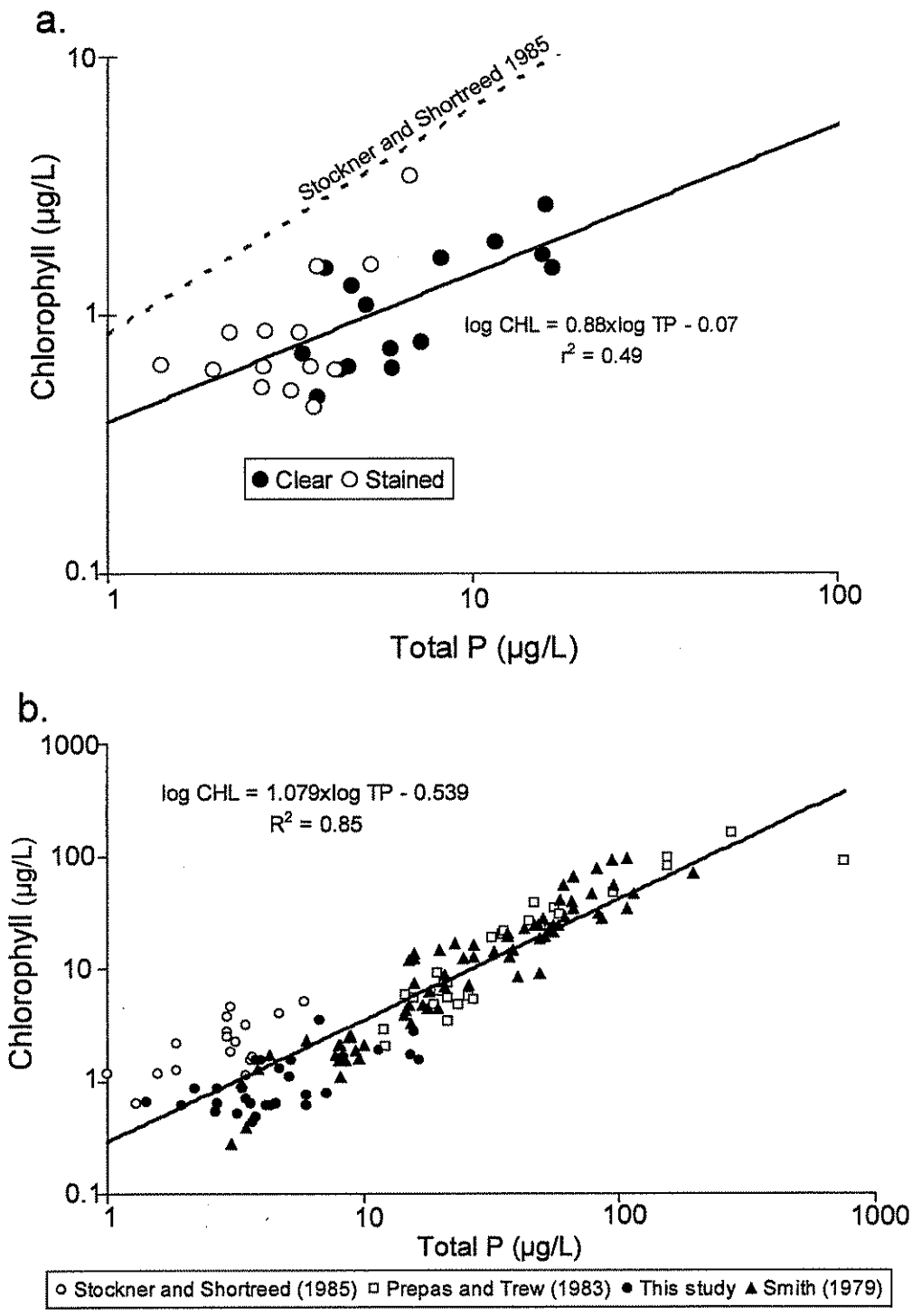

Fig. 53. Correlation between: a - CHL and TP for clear and stained lakes in this study, and b – CHL and TP from a number of studies on lakes covering a wide range in trophic status.

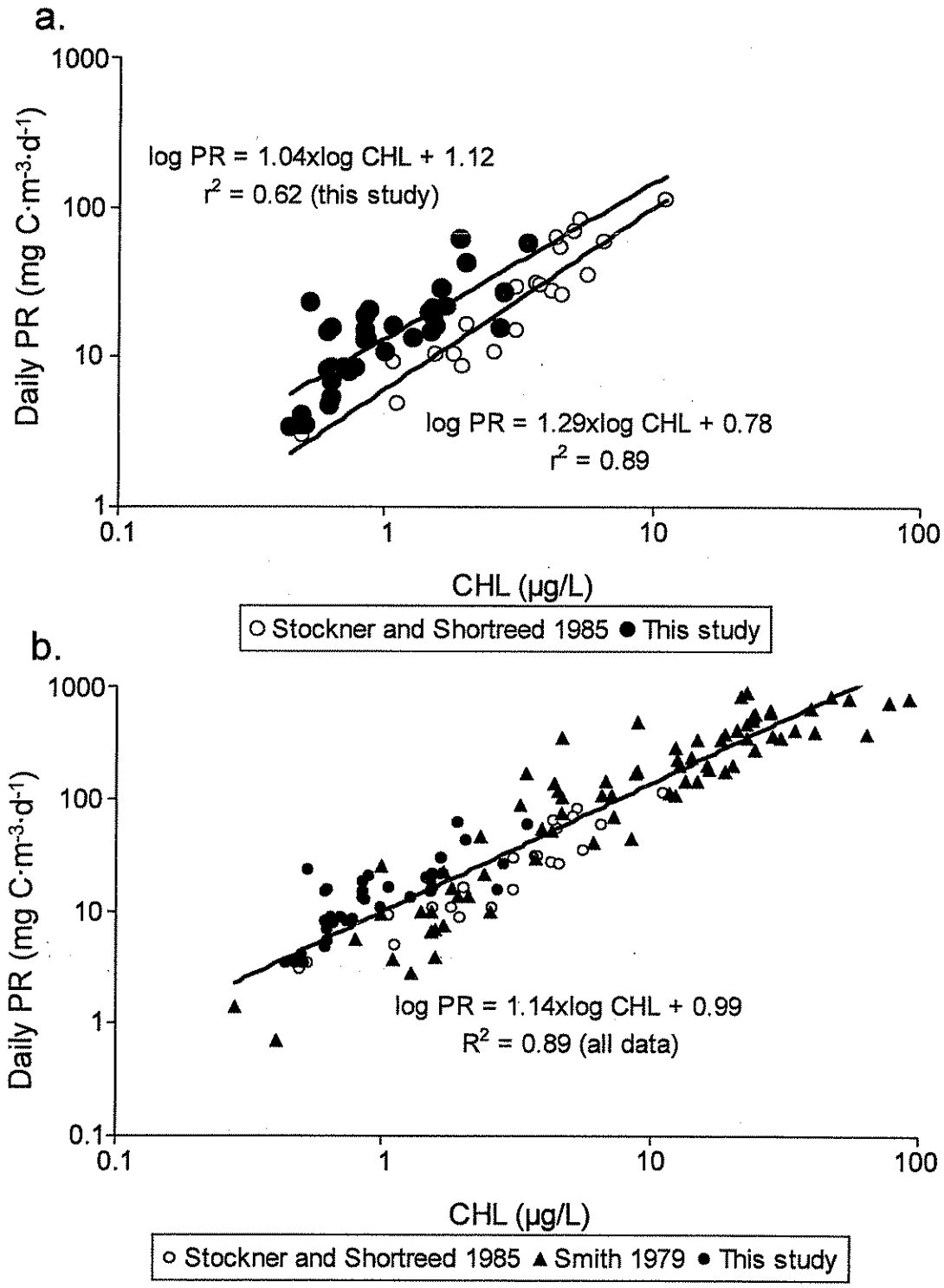

Fig. 54. Correlation between: a - Daily PR (mg C·m-3·d-1) and CHL in this study, and b - Daily PR and CHL from several studies covering a much wider range of trophic status.

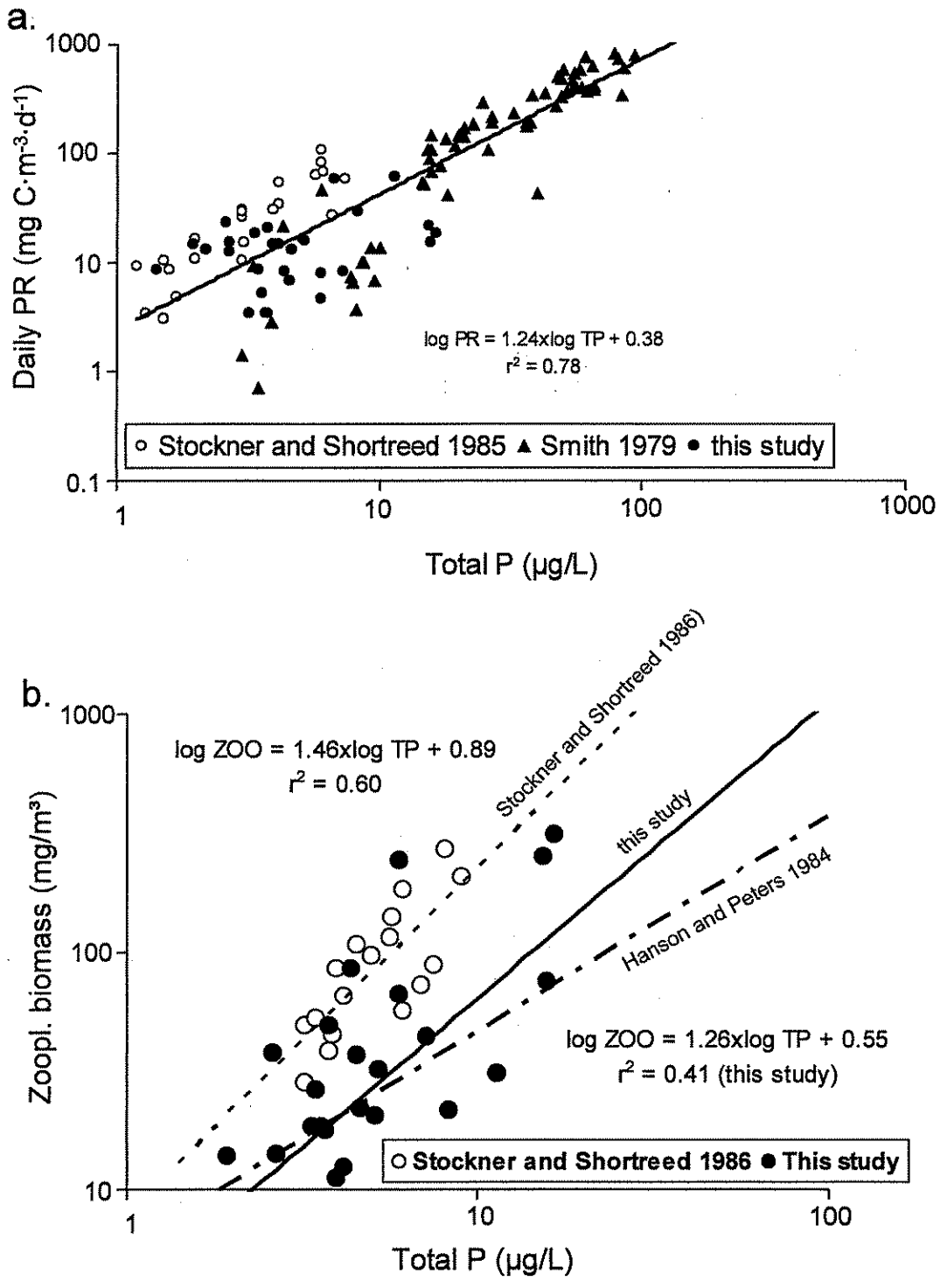

Fig. 55. Correlation between a - daily PR and TP using data from several studies covering a wide range in trophic status, and b - zooplankton biomass (mg dry wt/m³) and TP.

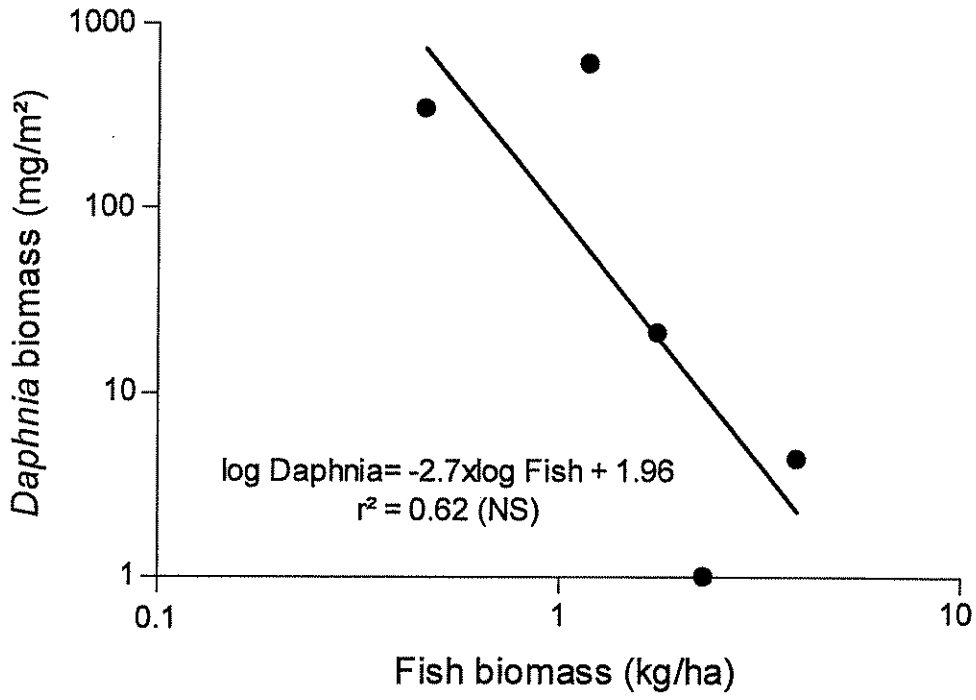

Fig. 56. Relationship between biomass of *Daphnia* and of limnetic fish in the study lakes.