Limnology of Cultus Lake, British Columbia

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TABLE OF CONTENTS

LIST OF FIGURES

ABSTRACT

Shortreed, K.S. 2007. Limnology of Cultus Lake, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 2753: vi + 85 p.

From 2001 to 2003, we carried out a limnological investigation of Cultus Lake, B.C. The lake was warm monomictic and thermally stratified from May-November each year. Epilimnetic temperatures exceeded 20°C from June or July until September. Average euphotic zone depths were 15.8 m, 2.5x deeper than average epilimnion depths. Total phosphorus averaged 7.4 µg/L (8.9 µg/L at spring overturn) and average values of a number of chemical variables were the highest ever recorded in B.C. sockeye lakes. The seasonal average daily photosynthetic rate of 449 mg $C \cdot m^{-2} \cdot d^{-1}$ was also the highest ever recorded in these lakes. A range of chemical and biological variables indicated that Cultus Lake is mesotrophic and much more productive than most sockeye nursery lakes in B.C. The zooplankton community was abundant and dominated by *Daphnia* throughout the year. Data from this and from an earlier study indicate that Cultus Lake has warmed substantially in the last 75 yr and there are a number of indications that its productivity has increased as well.

RÉSUMÉ

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De 2001 à 2003, nous avons mené une étude limnologique dans le lac Cultus (Colombie-Britannique). Le lac était monomictique chaud et thermiquement stratifié de mai à novembre chaque année. La température de l'épilimnion dépassait les 20 °C de juin/juillet à septembre. La zone euphotique mesurait en moyenne 15,8 m de profondeur, soit 2,5 fois plus que l'épilimnion. La teneur en phosphore total était en moyenne de 7,4 µg/L (8,9 µg/L pendant le brassage printanier), et les valeurs moyennes de plusieurs variables chimiques étaient les plus élevées à avoir été enregistrées dans des lacs de séjour du saumon rouge de la Colombie-Britannique. Le rendement photosynthétique saisonnier moyen de 449 mg $C/m^2/j$ était également le plus élevé à avoir été répertorié dans ces lacs. D'après un éventail de variables chimiques et biologiques, le lac Cultus est mésotrophe et beaucoup plus productif que la plupart des lacs de séjour du saumon rouge de la Colombie-Britannique. La communauté zooplanctonique était abondante et dominée par les *Daphnia* toute l'année. Les données de cette étude ainsi que celles d'une étude antérieure montrent que le lac Cultus s'est considérablement réchauffé au cours des 75 dernières années, et plusieurs indices donnent à penser que la productivité a augmenté également.

INTRODUCTION

Cultus Lake is located in British Columbia's eastern Fraser Valley, approximately 10 km south of the city of Chilliwack. The lake and its surrounding drainage basin are heavily utilized residential/recreational areas. Developed areas with summer cottages, permanent homes, and businesses (including two golf courses) are located at the north and south ends of the lake. Most of the lake's shoreline is within either the Cultus Lake Provincial Park or the Cultus Lake Municipal Park. Both these parks are popular camping and day-use areas and receive about 1.5 million visitors annually. In summer, the lake is one of the most heavily utilized recreational areas in British Columbia.

Since Cultus Lake and the surrounding area have been heavily utilized since early in the 20th century, there have been extensive modifications to the riparian and littoral areas of the lake and its tributaries. These include channelization of tributary streams, removal of riparian vegetation, shoreline alteration, installation of wharves and piers, and placement of sand in riparian and littoral areas. Frosst Creek is the lake's largest tributary and approximately 10 km² of its drainage basin are used for agriculture (Chilliwack River Habitat Atlas, http://www.shim.bc.ca/atlases/Chilliwack/Index.cfm). Logging has occurred in portions of Cultus Lake's drainage basin at various times in the past century, and in the past 20 yr approximately 5 km² of the 75 km² drainage basin has been logged. Domestic use of fertilizers, agricultural runoff, and the extensive use of septic tanks all have the potential to affect the quality of the water entering Cultus Lake, but the magnitude of water quality changes, if any, is unknown.

In addition, a major change in the lake was the invasion of Eurasian watermilfoil (*Myriophyllum spicatum*). Milfoil may have direct deleterious effects on sockeye salmon by clogging spawning areas and may have indirect deleterious effects by contributing to increases in piscivore numbers (Schubert et al. 2002). It was first observed in Cultus Lake in 1977, and by 1988 it covered 22 ha of that portion of the lake's littoral zone <6 m in depth (Truelson 1988) (total littoral area <6 m in depth is 37 ha). In 2004, the survey was repeated and watermilfoil coverage was found to have increased to 27 ha (J. Hume, Fisheries and Oceans Canada, Cultus Lake Salmon Research Laboratory, Cultus Lake, B.C., pers. comm.).

Cultus Lake is the natal and freshwater rearing area for a genetically distinct stock of sockeye salmon (Schubert et al. 2002) which has several unusual characteristics. Unlike most sockeye stocks, Cultus sockeye are exclusively lake spawners. They also have a very protracted spawning migration, entering Cultus Lake from early August until early December, with spawning taking place from late November to December. Cultus sockeye are one of the most intensively studied sockeye stocks in the world, and their escapements (numbers of adults returning to spawn) have been monitored each year from 1925 until the present. As with most Fraser River sockeye stocks, for most of the 20th century escapements of Cultus sockeye were variable and cyclical, with numbers ranging from highs of >70 thousand for a few years in the 1920's and 1930's to lows of <100 spawners in 1997 and 2004. For a variety of reasons (Schubert et al. 2002), spawner numbers started to decline in the late 1960's and then declined precipitously in the late 1990's. As a result of this decline, in 2002 the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) gave Cultus sockeye an *Endangered* designation and recommended they be protected under Canada's Species at Risk Act (SARA). In 2005, the Government of Canada decided not to protect Cultus sockeye under SARA, citing significant social and economic costs if they were listed. Despite the lack of protection under SARA, a number of initiatives have occurred since then to try to better understand and reverse the decline in Cultus sockeye (Cultus Sockeye Recovery Team 2004).

Although major causes of the decline in Cultus sockeye were not thought to be attributable to freshwater habitat, it was recognized that this needed to be confirmed. Little was known of the current limnology of Cultus Lake and its continued suitability as a rearing area for juvenile sockeye. Available limnological data on Cultus Lake were not sufficient to adequately document the lake's status and, in any case, had been collected decades previously. Consequently, in 2001, DFO staff (Lakes Group, Salmon and Freshwater Ecosystems Division) commenced a limnological investigation of Cultus Lake. Objectives of the study were to document the lake's current limnological status, including productivity, limiting factors, phyto- and zooplankton biomass and community structure, and the quality of the lake's rearing habitat for juvenile sockeye. Further, where possible, we would compare current limnological conditions in the lake with previous studies. We carried out data collection from April of 2001 to March of 2003, and results of the investigation are reported here.

DESCRIPTION OF STUDY LAKE

Cultus Lake lies at an elevation of 46 m approximately 10 km south of the city of Chilliwack (Table 1). It lies in the coastal western hemlock biogeoclimatic zone – dry maritime subzone (Meidinger and Pojar 1991). Based on the Koppen climate classification system (Kottek et al. 2006), the climate is maritime temperate, with warm summers and cool, wet winters. Total annual precipitation averages 1.57 m and daily average temperatures range from 2.4°C in December and January to 18.3°C in August (Environment Canada, Canadian Climate Normals 1971-2000, http://www.climate.weatheroffice.ec.gc.ca/index.html). The lake's drainage basin has an area of 75 km^2, of which 16 km^2 lies in the United States.

Surface area of Cultus Lake is 6.3 km^2 and based on the most recent bathymetric data (J. Hume, Fisheries and Oceans Canada, Cultus Lake Salmon Research Laboratory, Cultus Lake, B.C., pers. comm.), it has a mean depth of 31 m. Maximum recorded depth is 44 m. Cultus Lake is steep-sided, with a littoral zone area (based on an average euphotic zone depth of 15.8 m) of only 0.9 km^2 and an area <6 m in depth of only 0.4 km^2 (Fig. 1). The lake discharges into Sweltzer Creek, which travels 2.9 km before emptying into the Chilliwack River. Downstream distance from Cultus Lake to the Fraser River is 19 km, and it is a further 99 km to the mouth of the Fraser River.

Average annual daily flow in Sweltzer Creek is 3.54 m^3/sec (Water Survey of Canada, Hydat data base, http://www.wsc.ec.gc.ca). Seasonally, maximum flows occur in late fall or winter after periods of intense rainfall (Fig. 2). Lesser peaks attributable to spring snowmelt occur in May or June and lowest annual flows occur in August or September. The lake's major tributary is Frosst Creek, which enters the lake at the northern end of Lindell Beach (Fig. 1). Frosst Creek discharge averages 32% of the total lake discharge at Sweltzer Creek. Annual water residence time of Cultus Lake averages 1.8 yr (Table 1).

In the 1940's, a number of aquatic macrophytes were reported to occur in Cultus Lake (Ricker 1952). These included *Chara* sp., several species of pondweed (*Potamogeton* spp.), coontail (*Ceratophyllum demersum*), a native milfoil species (*Myriophyllum* sp.), and water buttercup (*Ranunculus aquatalis* var. *capillaceus).* However, since Eurasian watermilfoil became established and dominant in the 1970's and 1980's, the abundance and species composition of the native macrophyte community has not been documented.

Cultus Lake has a diverse fish community and in addition to sockeye salmon, a total of 19 fish species have been observed in the lake (Schubert et al. 2002). These include six species of Pacific salmon and trout: chinook (*O. tshawytscha*), coho (*O. kisutch*), chum (*O. keta*), pink (*O. gorbuscha*), cutthroat trout (*O. clarki clarki*), and rainbow trout (*O. mykiss*). Other species include Dolly Varden (*Salvelinus malma*), northern pikeminnow (*Ptychocheilus oregonensis*), threespine stickleback (*Gasterosteus aculeatus*), redside shiner (*Richardsonius balteatus*), largescale sucker (*Catostomus macrocheilus*), longnose dace (*Rhinichthys cataractae*), and peamouth chub (*Mylocheilus caurinus*). Two species of lamprey (western brook – *Lampetra richardsoni* and river - *L. ayresi*) have been observed in the lake, as well as three sculpin species (prickly sculpin – *Cottus asper*, coastrange sculpin – *C. aleuticus* and Cultus pygmy sculpin – *Cottus* sp.). Cultus pygmy sculpin are a very small (<52 mm) limnetic form of *C. aleuticus* and have been listed as threatened by COSEWIC and SARA, primarily because they are thought to be genetically distinct from the normal form of *C. aleuticus* and because they are thought to occur only in Cultus Lake. On one occasion, a white sturgeon (*Acipenser transmontanus*) was captured in Cultus Lake, but that species is not thought to naturally occur or reproduce in the lake.

METHODS

We collected limnological data once monthly from April to November of 2001 (n=8) and from January to December of 2002 (n=12). In 2003, we sampled the lake four times (January to March and August). On each sampling date, we sampled one mid-lake location (station 1, Fig. 1). In addition, from January to December of 2002 we sampled Frosst, Spring, and Sweltzer creeks for a number of chemical variables. At every sampling date we used an Applied Microsystems Micro CTD 7079 to obtain temperature and conductivity profiles from the surface to the bottom (approximately 40 m). Depths of the epilimnion and metalimnion were estimated by a visual inspection of plotted temperature and depth data. We estimated water column stability with a modified Schmidt stability function (Costella et al. 1983) using temperature and conductivity data to a depth of 40 m.

We used a standard, white, 20-cm diameter, Secchi disk to measure water clarity. A Li-Cor data logger (model LI-1000) equipped with a model LI-193SA spherical quantum sensor was used to measure photosynthetic photon flux density (PPFD) (400-700 nm) and determine euphotic zone depths (1% of surface light intensity). We measured dissolved oxygen (DO) concentrations from the surface and 30 m with an Oxyguard Handy Beta meter. In addition, on one occasion on August 21, 2003, DO concentrations were measured at 11 depths from the surface to 30 m.

We carried out all water sampling between 0800 and 1100 h (PST). We used an opaque, 6-L Van Dorn bottle to collect all water samples. Water was collected from 8 discrete depths from the surface to 30 m and later analyzed for nitrate and chlorophyll concentrations. On most occasions, we collected replicate integrated samples consisting of water from six depths within the euphotic (trophogenic) zone. On a few occasions when thermal stratification was most pronounced (July-October of 2003), we collected replicate integrated samples from within the epilimnion and from the bottom of the epilimnion to the bottom of the euphotic zone. At all stations, we also collected a hypolimnetic sample from a depth of 30 m. All collected water was kept cool and dark until it was processed (filtered, frozen, or preserved), no more than 3 hr after collection. Subsequent replicate analyses from the integrated samples included total dissolved solids, chlorophyll, dissolved silica, phosphorus (total, dissolved, particulate, soluble reactive, and turbidity blank), nitrogen (nitrate and ammonia), bacteria, and phytoplankton. A single sample for total dissolved solids was also collected from each integrated sample. In addition, on two dates in April and May of 2001, samples were collected for later analysis of particulate carbon and particulate nitrogen.

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. Water for dissolved nitrate analyses was filtered through an ashed 47-mm diameter Advantec 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. Other water samples for dissolved nutrient were kept cool and dark for 2-4 h, filtered into clean, rinsed polyethylene bottles, and frozen. For dissolved phosphorus determination, filtered water was treated as for total phosphorus, including the use of turbidity blanks.

For determination of particulate phosphorus concentration, we filtered 1-L of water through an ashed 47-mm diameter MFS filter, placed the filter in a clean scintillation vial, and later analyzed it using the method of Stainton et al. (1977). For determination of particulate carbon and particulate nitrogen concentrations, we filtered

200 mL of water through an ashed 25-mm diameter GFF filter, folded the filter in half, place it in aluminum foil dishes and froze it. Later, PC and PN concentrations were determined on a Perkin Elmer Model 240XA Elemental Analyzer. For chlorophyll analysis, we filtered water through 47-mm diameter, 0.45-µm Millipore HA filters, which were then frozen. Filters were later macerated in 90% acetone and chlorophyll concentration was determined using a Turner Designs Model 10-AU fluorometer.

Water for alkalinity determinations was placed in glass bottles that were filled completely (one bottle from each sampling depth) and sealed. Within four hours of collection, a Cole-Parmer Digi-Sense pH meter (Model 5986-10) and Ross combination electrode were used to determine the pH and total alkalinity (mg $CaCO_3$/L) of these samples according to the standard potentiometric method of APHA (1998). Dissolved inorganic carbon (DIC) concentrations were calculated indirectly from pH, temperature, total dissolved solids, and bicarbonate alkalinity.

Water for bacterioplankton enumeration was collected in sterile scintillation vials and preserved with two drops of formaldehyde. Bacterioplankton were later counted with a Zeiss epifluorescent microscope using the DAPI method described by Robarts and Sephton (1981). Ten random fields were counted on each filter and the counts converted to numbers/mL.

For nano- and microphytoplankton enumeration and identification opaque 125-mL polyethylene bottles were rinsed with sample, filled, and fixed with 2 mL of Lugol's iodine solution. Each sample was gently mixed and a subsample was settled overnight in a settling chamber of 7-, 12-, or 27-mL capacity. Transects at 187.5x and 750x magnification were counted using a Wild M40 inverted microscope equipped with phase contrast optics. Cells were identified as to genus or species, and assigned to size classes.

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. 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 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 20 random fields were counted.

At every sampling date, we measured *in situ* photosynthetic rates (PR) at 7 depths from the surface to below the euphotic zone. At each depth, two light and one dark 147-mL glass bottles were filled, inoculated with approximately 137 kBq of a ^{14}C-bicarbonate stock solution, and incubated at the original sampling depth. Incubations lasted 1.5-2 hr and were started between 0900 and 1100 h (PST). To determine activity of the stock solution, we inoculated three scintillation vials containing 0.5 mL of 0.2 N NaOH with the ^{14}C-bicarbonate solution for later determination of its activity. After incubation, bottles were placed in light-proof boxes and transported to the field laboratory where filtration started <1 hr after incubation stopped. We filtered the entire contents of each bottle through a 25-mm diameter MFS glass fiber filter (equivalent to a Whatman GF/F) 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 hours. All vials were stored cool and in the dark. Within a few days of the incubations, 10 mL of Scintiverse II (Fisher Scientific) were added to each scintillation vial. Activity in each vial was determined using 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 Strickland's (1960) equation was used to calculate hourly PR. PR was converted from hourly to daily rates using light data collected with a Li-Cor Model LI-1000 data logger and Li-Cor 190SA quantum sensors.

Replicate zooplankton samples were collected at every station with a 160-µm mesh Wisconsin net (mouth area = 0.05 m^2) hauled vertically from 30 m to the surface. All samples were placed in 125-mL plastic bottles and preserved in a sucrose-buffered 4% formalin solution (Haney and Hall 1973). Zooplankton were counted, identified to family or species using Balcer et al. (1984) and Pennak (1978), 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 (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). We defined macrozooplankton as animals >250 µm in length. Nauplii and rotifers were not counted.

Growing season averages of data collected at each station (with the exception of PR) were calculated as time-weighted means of all sampling dates from May to October, inclusive. Total seasonal PR at each station was calculated by integrating daily PR over time, with the growing season defined as May 1 to October 31 (we assumed that PR was zero on the first and last days of the growing season). Seasonal average daily PR (PR_{mean}) was calculated by dividing total seasonal PR for each station by the length of the growing season (180 days).

We determined areas of the lake and its drainage basin using Oziexplorer mapping software (http:/www.oziexplorer.com) and digitized topographic maps (1:50,000 in Canada and 1:100,000 in the United States).

RESULTS AND DISCUSSION

PHYSICS

Cultus Lake is warm monomictic and is thermally stratified for an extended period each year. In our study, surface temperatures were lowest (5-6°C) in February or March and highest (23°C) in July or August (Table 2, Fig. 3). They exceeded 18°C for 3-4 months each year. Water column stability was greatest in August and lowest from January to March (Table 2, Fig. 3). The lake became thermally stratified in late April or early May and remained stratified until late November (Fig. 4-6). Epilimnion depths were seasonally variable, but during the period of strongest stratification (July-September) they averaged a relatively shallow 6.4 m (Table 2). The depth of the bottom of the metalimnion varied relatively little (range: 14-22 m) and averaged 16 m in both 2001 and 2002. Hypolimnetic (20-40 m) temperatures varied relatively little, ranging from 4.3°C in March of 2002 to 7.0°C in November of 2001.

Ricker (1937) carried out extensive temperature profiling in Cultus Lake from the late 1920's to the mid-1930's. Comparison of his data with ours indicates the lake is warmer now than it was 70 yr previously. With the exception of fall samples, mean monthly surface and mean 0-10 m temperatures were warmer in our study (Fig. 7). Average monthly temperatures of deep (20-40 m) water were also warmer in our study, again with the exception of the late fall (Fig. 8). Average monthly water column stability (Schmidt index, kg/s^2) was similar for much of the year, but in our study it tended to be higher in spring and summer (Fig. 8). Goodlad et al. (1974) reported on temperature data collected in the 1960's and early 1970's. In 1971, summer epilimnion temperatures did not exceed 20°C (Goodlad et al. 1974; their Fig. 2) and were slightly cooler then than in the 1930's or in our study. Goodlad et al. (1974) reported that seasonal (May-October) temperature averages (n=12) for the 0-9 m depth integral were 15.5°C, almost identical to the 0-9 m average of 15.8°C in our study. They also reported that the average temperature of the 12-27 m depth integral was 7.5°C, which was similar to the 12-27 m average of 7.0°C in our study. The data indicate that there is relatively little change in temperature regimes in the past 30 yr, but that there has been substantial warming in the approximately 70 yr since the Ricker (1937) study. This warming is likely due to climate change, since for the past 100 yr average annual minimum and maximum air temperatures in the eastern Fraser Valley have been increasing (Taylor and Langlois, 2000).

Cultus Lake has clear water, with seasonal average (May-October) Secchi depths during our study ranging from 9.2-10.6 m (Table 2). Secchi depths tended to be lowest in January-February and highest in fall or early winter (October-December) (Fig. 9). Ricker (1937) reported Secchi disk values collected on two occasions only in the fall of 1936, or 65 yr prior to our study. His Secchi depths were substantially deeper than any recorded in our study, but there are insufficient data to categorically state there have been actual changes in Cultus Lake water clarity (Fig. 9). Goodlad et al. (1974) reported a multi-year (May-October, n=6) average Secchi depth of 10.5 m, virtually the same as found in our study. They did not report the years in which their Secchi data were collected, but it is most likely from the 1960's, approximately 35 yr prior to our study.

Average euphotic zone depth was 16.6 m in 2001 and 15.0 m in 2002. It had a seasonal pattern similar to Secchi depth, with lowest values occurring early in the year (January-March) and highest values in summer or fall (August-October) (Fig. 9). During the period of stable thermal stratification (May-October), euphotic zones depths averaged 2.5x deeper than epilimnion depths (Table 2). On average, euphotic zone depths were 10 m deeper than epilimnion depths.

CHEMISTRY

Seasonal average trophogenic zone conductivities in Cultus Lake were 152-154 µS/cm, which are the highest yet recorded in a British Columbia sockeye nursery lake (K. Shortreed, unpublished data) (Table 3). A similar average conductivity of 167 µS/cm was reported in the early 1970's by Goodlad et al. (1974). Conductivity varied seasonally, with lowest values occurring in winter (January-March) and highest values occurring in summer (August-September) (Fig. 10). Epilimnetic conductivities were usually higher than those in the hypolimnion.

Cultus Lake had relatively high dissolved oxygen (DO) concentrations which were well within the range required by aquatic life (Davis 1975). Surface DO averaged 9.9 mg/L (108% saturation) and average hypolimnetic DO was somewhat lower (8.9 mg/L, or 71% saturation). Surface DO was highest in spring, declined somewhat in the summer months, and increased again in fall (Fig. 10). From January to September, epilimnetic and hypolimnetic DO concentrations were similar. However, in fall hypolimnetic DO began to decline and was reduced to 6.1 mg/L by late December. This was equivalent to only 50% saturation. However, only a few weeks later (mid-January) overturn had occurred and DO was again >10 mg/L throughout the water column. Progressive loss of hypolimnetic DO during the stratified period is a common phenomenon in many lakes (Wetzel 2001) and is primarily due to biological oxidation of organic matter.

Ricker (1937) collected detailed DO profiles in Cultus Lake from 1927-1935. To make comparisons between those data and the less intensive DO data collected during our study, we used data from 0 m and 30 m only. Seasonal surface DO concentrations were virtually identical between the two studies, except that late winter (January-February) concentrations were somewhat higher in the earlier study (Fig. 11). However, hypolimnetic (30 m) DO was substantially lower in our study than in the Ricker (1937) study (Fig. 11). These differences indicate that the intensity of oxidative processes in the hypolimnion have increased substantially since the 1930's. The most plausible explanation for this increase is that the amount of organic matter reaching the hypolimnion has increased. While increased phytoplankton biomass may account for some of the increase, an additional source of organic matter reaching the hypolimnion is Eurasian watermilfoil, which did not occur in Cultus Lake until the 1970's and which now occupies major portions of the lake's littoral zone. (Schubert et al. 2002). While hypolimnetic DO concentrations have not declined to levels which would deleteriously affect fish (Brett and Blackburn 1981), we suggest that DO should be regularly monitored to determine if the decline is continuing.

On one occasion (August 21 2003), we collected a detailed vertical DO profile (Fig. 12). On this date, epilimnetic DO was 9.2 mg/L, there was a pronounced metalimnetic DO peak (16.3 mg/L), and hypolimnetic DO declined to 7.2 mg/L at 30 m. This was 108% oxygen saturation at the surface, 160% at the metalimnetic peak, and 58% at 30 m. This type of DO profile is termed positive heterograde (Wetzel 2001) and is common in lakes where the euphotic zone is substantially deeper than the epilimnion, allowing sometimes substantial photosynthesis to occur in the cooler metalimnion. In the 1920's and 1930's, a metalimnetic DO peak also occurred in Cultus Lake (Ricker 1937), but DO concentrations at the peak were much lower (11.9 mg/L) (Fig. 12). This suggests that metalimnetic photosynthetic rates were higher in our study than in the 1930's.

Cultus Lake was alkaline on most sampling dates in our study and seasonal average pH was 7.6 in 2001 and 7.8 in 2002 (Table 3). Seasonal variation was not pronounced, but pH was highest (>8) in summer. In 1932, the May-October average was 7.7 (Ricker 1937), almost the same as the average in our study. However, the maximum recorded summer pH of 7.8 in the earlier study was lower than the maximum in our study. The increase (from 7.8-8.1) in maximum summer pH between the two studies could be a result of increased phytoplankton productivity. As with conductivity, we found average concentrations of total dissolved solids (TDS) (101-106 mg/L), total alkalinity (62-64 mg $CaCO_3$/L), and dissolved inorganic carbon (15.7-16.8 mg/L) were the highest ever seen in B.C. sockeye lakes (K. Shortreed, unpublished data) (Table 3).

Concentrations of soluble reactive silica (SRS) averaged 1.8-2.0 mg Si/L (Table 4). This is within the range commonly observed in B.C. sockeye lakes (K. Shortreed, unpublished data) and within the range reported for Cultus Lake by Ricker (1937). SRS exhibited some seasonality, with maximum annual concentrations occurring in January or February and seasonal minima occurring in September or October (Fig. 13). Seasonal minima were 1.7-1.8 mg Si/L, well above the concentration (0.5 mg Si/L) at which silicon availability becomes limiting to diatom growth (Wetzel 2001).

Nitrate concentrations in Cultus Lake were unusually high for a B.C. sockeye lake, with winter (January-February) values of >150 µg N/L and seasonal averages in the euphotic (trophogenic) zone of 39-45 µg N/L (Table 4, Fig. 14). Euphotic zone averages declined steadily from the winter peaks until seasonal minima of 12-14 µg N/L were reached in August or September, after which they began to increase. We collected vertical profiles of nitrate concentration on every sampling date (Fig. 15-17). Nitrate concentrations were similar throughout the water column from January to April, when epilimnetic concentrations started to decline. From August to October, a pronounced nitracline occurred. In summer, nitrate became depleted (<1 µg N/L) for more than half of the euphotic zone, with the result that the depth of depletion extended below the epilimnion, usually to near the bottom of the metalimnion (Fig. 17). The rapid temperature change over the depth of the metalimnion in summer acts as a physical barrier to vertical transport of hypolimnetic nitrate to the nutrient-depleted epilimnion. Photosynthetic activity and subsequent nitrate depletion in the metalimnion strengthens this barrier and reduces vertical transport even more. In the August-October period, hypolimnetic nitrate concentrations usually increased (Table 4). The most likely cause of this increase was water from Frosst and Spring creeks, which was colder (i.e. denser) than Cultus Lake's epilimnion and had much higher nitrate concentrations (see later section on stream chemistry). Trophogenic zone ammonia concentrations exhibited little seasonality and seasonal (May-October) averages were 6.6 µg N/L in 2001 and 5.3 µg N/L in 2002 (Table 4). Hypolimnetic averages were slightly lower (4.8 and 2.3 µg N/L in 2001 and 2002, respectively).

Spring (March-April) overturn total phosphorus (TP) was quite variable, with concentrations over the whole water column of 6.3 µg/L in 2001, 11.7 µg/L in 2002, and 8.3 µg/L in 2003 (Table 4). Reasons for these annual differences are not known, but these concentrations place the lake in the upper oligotrophic or lower mesotrophic range (Vollenweider 1976). TP exhibited little seasonality, but tended to be higher in 2002 than in 2001 (Table 4, Fig. 18). Concentrations of total dissolved (TDP) and soluble reactive (SRP) phosphorus were also higher early in 2002 than early in 2001 or 2003. For most of the study (April 2001- March 2003), SRP was <2 µg/L. Only in the early part (February-April) of 2002 did higher concentrations occur (Table 4, Fig. 18). Although there was some month-to-month variability, in both 2001 and 2002 average TDP was 71% of TP. SRP averaged 16% of TP in 2001 and 21% in 2002.

In 37 lakes from B.C.'s north and central coasts (Shortreed et al. 2007), SRP averaged 21% of TP, very similar to Cultus Lake, but average TDP was a lower 58% of TP. However, data presented in that study were from single sampling dates in late summer, rather than seasonal averages. Consequently, it is likely that nutrient data would suggest more pronounced nutrient limitation than the seasonal averages for Cultus Lake. Late summer data from Cultus Lake were more similar, with TDP averaging 60% of TP. In a data set consisting of multiple years of seasonal data from a suite of 28 B.C. sockeye lakes (K. Shortreed, unpublished data), TDP averaged 69% of TP, very similar to the proportion found in Cultus Lake. Average SRP concentration in this suite of lakes was 21% of TP, also very similar to that found in Cultus and the same as that reported by Shortreed et al. (2007). In general, summer concentrations of both SRP and nitrate were very low and suggest co-limitation of both nitrogen and phosphorus (Suttle and Harrison 1988) for a portion of each growing season. However, since spring concentrations of nitrate, TP, and SRP are higher than commonly seen in other B.C. sockeye lakes (K. Shortreed, unpublished data), the degree of nutrient limitation is likely somewhat less in Cultus Lake.

Particulate ratios of carbon, nitrogen, and phosphorus have been widely used to estimate the magnitude of nutrient limitation in lakes or oceans (Redfield et al. 1963; Hassett et al. 1997). Average C:N:P ratio of marine phytoplankton has been found to be 103:16:1, while C:N:P ratios in lakes tend to be more variable but much higher (Elser and Hassett 1994; Shortreed and Morton 2000). In this study, we measured particulate C and N on only two occasions (April and May of 2001), so particulate ratios cannot be used to estimate the extent of seasonal nutrient limitation in Cultus Lake. However, on these dates, when it would be expected that nutrient limitation would be at or near a seasonal low, C:N:P ratios ranged from 245:21:1 to 300:32:1. These were very similar to the average ratio of 314:31:1 found in Babine Lake (Shortreed and Morton 2000) and to the average ratio of 304:25:1 found in the suite of 28 lakes mentioned previously (K. Shortreed, unpublished data). These ratios are all indicative of severe P limitation (Hecky et al. 1993), although the degree of limitation is much less than was observed in a number of coastal B.C. lakes, where the ratio was 473:45:1 (Stockner and Shortreed 1985).

STREAM CHEMISTRY

In addition to the mid-lake station, in 2002 we sampled Frosst, Spring, and Sweltzer creeks for a variety of chemical variables (Table 5). Sweltzer Creek is the outlet of Cultus Lake. Frosst Creek is the lake's major tributary and its drainage basin of approximately 40 km² includes a portion of the Columbia Valley, which is an active agricultural area. Spring Creek is a small groundwater-fed stream which starts approximately 0.8 km from Cultus Lake. It passes through a golf course and a residential area before discharging into the lake. Seasonal (May-October) average temperatures ranged from 9.2°C in Frosst Creek to 20.9°C in Sweltzer Creek (Table 5). Cultus Lake and Sweltzer Creek had similar temperatures for much of the year (range: 5.2-24.9°C), but Sweltzer became slightly warmer in the summer months (Table 5; Fig. 19). Spring Creek exhibited little seasonal variation in temperature, ranging only from 8.2-10.4°C. Frosst Creek exhibited some seasonal variation, but for most of the year it was substantially cooler than Sweltzer Creek or Cultus Lake.

None of the sampling locations exhibited much seasonal variation in conductivity, although in Frosst Creek highest conductivities occurred in summer (Fig. 19). Average conductivity was lowest (100 µS/cm) in Frosst Creek and highest (238 µg/L) in Spring Creek (Table 5). TDS also exhibited little seasonal variability except in Frosst Creek, where lowest values occurred in spring and in late fall, most likely at times of higher discharge (Fig. 2, 20). Average TDS ranged from 84 mg/L in Frosst Creek to 184 mg/L in Spring Creek. DO exhibited little seasonal variation at any of the sampling locations, although in Spring Creek there was a slight decline in DO through the year (Table 5, Fig. 20). Average DO was relatively high (range: 10.8-13.3 mg/L) at all locations except for Spring Creek, where the average was only 4.9 mg/L. SRS did not vary seasonally except that Spring Creek concentrations increased in late fall (Table 5). Averages were similar at all locations, ranging only from 2.0-2.6 mg/L.

Nitrate concentrations exhibited considerable variation both seasonally and between stations. Sweltzer Creek and Cultus Lake had similar concentrations for much of the year, although Sweltzer concentrations were lower in summer (Fig. 21). Frosst Creek concentrations varied substantially, but were >500 µg N/L for much of the year. Lowest nitrate concentrations in Frosst Creek occurred in late May and in late

November, when seasonal peaks in discharge most likely occurred (Fig. 2). Spring Creek nitrate did not vary seasonally. Average nitrate was lowest (26 µg N/L) in Sweltzer Creek and highest (526 µg N/L) in Frosst Creek (Table 5). Unlike nitrate, ammonia exhibited little seasonal variation and concentrations were similar at all locations (Fig. 22). Average ammonia ranged from 3.6-6.7 µg N/L. Seasonal variation in TP concentration was minimal, except that highest concentrations occurred in summer in Spring Creek (Fig. 22). Average TP was highest in Spring Creek (13.1 µg/L) and was similar (7.6-8.6 µg/L) at the other three locations (Table 5). TDP also exhibited little seasonal variation and as with TP, average concentrations was higher (9.4 µg/L) at Spring Creek than elsewhere, where the average was 6.0-6.4 µg/L. Highest concentrations of SRP occurred in late winter in Cultus Lake and in Sweltzer Creek (Fig. 23). Concentrations at these locations then declined slowly for the rest of the year. The other two locations exhibited little seasonal variability. Seasonal (May-October) average SRP was highest (4.5 µg/L) in Spring Creek and ranged from 1.8-2.5 µg/L at the other locations (Table 5).

Nitrate concentrations in Frosst and Spring creeks were much higher than those in Cultus Lake and much higher than in any B.C. sockeye lake. Sources of the unusually high nitrate concentrations in Frosst and Spring creeks are unknown. While it is possible that they are due to natural geologic features of the drainage basin, it is more likely that anthropogenic inputs account for much of the high concentrations. Approximately 10 km² of the Frosst Creek drainage basin is used for agriculture. As for Spring Creek, in its short (0.8 km) length, it passes through both a golf course and a residential area serviced by septic tanks. Nitrate concentrations in both creeks were lower than those found in groundwater exposed to agriculture activities in the Fraser Valley (Sylvestre et al. 2004), but they were much higher than the average groundwater concentrations at a number of reference sites (i.e. those unaffected by agriculture) also in the Fraser Valley.

For the entire growing season, water from both Frosst and Spring creeks was much colder and had higher ion concentrations than the surface waters of Cultus Lake, so it was substantially denser. Consequently, their inflows would sink rapidly on entering Cultus Lake and likely contributed little to epilimnetic nitrogen loading during the period of thermal stratification. The summer and fall increases in Cultus Lake's hypolimnetic nitrate concentrations was likely due to input from Frosst, and to a lesser extent, Spring creeks (Tables 4 and 5).

METALS

On one occasion in January of 2004, we collected a water sample for metals analysis from one location approximately 350 m east of the mouth of Spring Creek. The sampling location was 21 m from shore and the water depth at this location was 3.8 m. The water sample was collected from 1 m above the bottom. Total metals were analysed by Elemental Research (now Cantest) of North Vancouver, B.C. Although this one sample is not likely to be representative of Cultus Lake as a whole, it constitutes the only available data on metals content of Cultus Lake water, and so is presented here

(Table 6). All measured metals were well below Health Canada's maximum allowable concentrations for Canadian drinking water quality, when given (http://hc-sc.gc.ca/). For comparative purposes, we plotted Cultus Lake metals data against data from a number of other B.C. lakes (E. MacIsaac, Fisheries and Oceans Canada, Simon Fraser University, Burnaby, B.C., pers. comm.; K. Shortreed, unpublished data) (Fig. 24-25). With two exceptions, concentrations of metals in Cultus Lake were within the range seen in the other lakes. In Cultus Lake, magnesium concentration was slightly higher than in the other lakes and strontium was substantially higher. Reasons for these differences are unknown, but in these forms neither metal is thought to have any health risks.

BACTERIA AND PHYTOPLANKTON

Seasonal variation in bacteria numbers was not pronounced, but highest numbers generally occurred in summer (Fig. 26). Average numbers were 1.97 million/mL in 2001 and somewhat higher (2.93 million/mL) in 2002 (Table 7). The 2002 numbers are the highest ever recorded for a B.C. sockeye lake. The overall average for data from 28 B.C. lakes (K. Shortreed, unpublished data) was far lower (1.02 million/mL), as was the average (1.39 million/mL) for 37 central and north coast lakes sampled once in late summer, when bacteria numbers were likely at their seasonal peak (Shortreed et al. 2007). Based on a bacteria-based trophic classification (Bird and Kalff 1984), average bacteria numbers in Cultus Lake place it in the lower range of mesotrophy (1.7-6.5 million/mL).

Seasonal average concentrations of trophogenic zone chlorophyll were 2.32 µg/L in 2001 and 2.01 µg/L in 2002 (Table 7). Distinct seasonal patterns were not apparent, but lowest values generally occurred in winter and highest in summer and fall (Fig. 26). These concentrations are well within the range that has been observed in many B.C. sockeye lakes (Shortreed et al. 2001). Based on the chlorophyll-based trophic classification of Forsberg and Ryding (1980), these concentrations place Cultus Lake in the oligotrophic category (<3 µg/L). We found that a deep chlorophyll maximum (DCM) persisted throughout the period of stable thermal stratification (June-July to October) (Fig. 27-29). In 2001, the DCM occurred near the bottom of the euphotic zone and concentrations at its peak were 6-8 µg/L from August to October. In 2002, the DCM was shallower than in 2001 and peaks were not as high (4-6 µg/L). In August of 2003, the DCM was again very similar to that observed in 2001 (Fig. 27-29). Summer euphotic zone depths were shallower in 2002 than in 2001, which may account for the shallower DCM in that year. Reasons for the difference in magnitude between 2002 and the other years are not clear. DCMs are relatively common in lakes and a number of hypotheses have been put forward to explain their development and maintenance (Pick et al. 1984; Shortreed and Stockner 1990). Given that in Cultus Lake the DCM occurred at depths well below that of maximum photosynthetic rate (PR), it is apparent that development and maintenance of the DCM was not entirely due to active photosynthesis at depth. Its formation must have been partially due to passive processes (i.e. accumulation of cells that were produced in shallower waters) (Jackson et al. 1990).

Seasonal patterns in PR were similar in both years, with highest values occurring in summer and lowest in winter (Fig. 30). Average daily (May-October) photosynthetic rates (PR) were 424 mg $C \cdot m^{-2} \cdot d^{-1}$ in 2001 and 473 mg $C \cdot m^{-2} \cdot d^{-1}$ in 2002 (Table 7). These are the highest average PR values ever recorded for a B.C. sockeye lake (Shortreed et al. 2001, 2007; K. Shortreed, unpublished data). Based on the PR-based trophic classifications proposed either by Wetzel (2001) or Shortreed (2007), these PR values place Cultus Lake well within the mesotrophic category. The shape of vertical PR profiles was variable, but in most cases highest PR occurred at depths >5 m (Fig. 31-35). This was no doubt due to the relatively deep euphotic zone and the presence of a DCM for a portion of the year (Fig. 27-29). Average assimilation ratios ($\mu g\ C \cdot \mu g\ Chl^{-1} \cdot d^{-1}$) in Cultus Lake were 14 and 20 in 2001 and 2002, respectively. This was higher than the average of 9.2 for a number of B.C. sockeye lakes (K. Shortreed, unpublished data) and indicates a high turnover rate (high trophic efficiency) within the Cultus phytoplankton community (Wetzel 2001).

Cultus Lake phytoplankton exhibited considerable seasonal and annual variability (Table 7, Fig. 36). Highest picoplankton numbers occurred in summer (up to 142 thousand/mL in August of 2002) and lowest in winter or spring (only 3.2 thousand/mL in May of 2001). Average picoplankton numbers in the trophogenic zone were substantially higher in 2002 (81 thousand/mL) than in 2001 (48 thousand/mL) (Table 7). These averages are within the range commonly observed for British Columbia and Yukon lakes (Stockner and Shortreed 1991). In late summer, picoplankton numbers were near the top of the range found in a suite of B.C. lakes located near the north and central coasts (Shortreed et al. 2007). Average nanoplankton numbers were far lower than picoplankton numbers, ranging from 1,000/mL in 2002 to 1,500/mL in 2001. Seasonal variation in nanoplankton numbers was much less pronounced than for picoplankton, but highest numbers also occurred in summer (Table 7). Seasonal variation in microplankton numbers was unusual, with highest volume occurring on the first sampling date each year (January of 2001 and April of 2002) and highest numbers occurring in summer and early fall (Table 7). Average microplankton volume was 69% of total phytoplankton volume. This was similar to the average of 77% for a number of interior B.C. sockeye lakes (K. Shortreed, unpublished data) and to the average of 74% reported by Shortreed et al. (2007) for 37 north and central coast lakes.

As in most B.C. sockeye lakes (Stockner and Shortreed 1991), the cyanobacteria *Synechococcus* sp. was the dominant picoplankton. In Cultus Lake, it comprised an average of 99% of total picoplankton numbers, with the remainder made up by a small eukaryote. Of total *Synechococcus* numbers, 59% were unicellular, with a colonial form making up the remainder. Stockner and Shortreed (1991) reported that colonial *Synechococcus* made up a greater proportion of the total as lake productivity increased (e.g. 10% in ultraoligotrophic Chilko Lake and 44% in more productive Shuswap Lake). Colonial *Synechococcus* made up 40% of the total in Cultus Lake, providing a further indication of Cultus Lake's relatively high productivity. The dominant nanoplankton on almost all sampling dates were the flagellates *Chromulina* sp. and *Chroomonas acuta*.

Also common or abundant on some occasions were other flagellates (*Chrysochromulina* and *Ochromonas*), a small diatom (*Cyclotella glomerata*), and the chlorophyceans *Crucigenia tetrapedia* and *Scenedesmus* sp.

A number of larger diatom genera made up the bulk of the microplankton size fraction. Prominent among these at various times were *Urosolenia* (formerly *Rhizosolenia*), *Cyclotella* spp., *Melosira* spp. (primarily *M. islandica*), and to a lesser extent, *Asterionella formosa.* Seasonal variation in diatom species composition was similar in both study years, although numbers varied (Fig. 37). Maximum numbers of *Melosira* occurred in winter or early spring. *Melosira* was the major contributor to the seasonal peak in phytoplankton volume. In the mid-1930's, Ricker (1938) found that *Melosira* numbers peaked in March or April. It is unclear whether seasonal peak in *Melosira* occurs earlier now than in the 1930's, or whether the difference is simply a matter of annual variability. However, in 2002, when we sampled throughout the year, the seasonal peak in *M. islandica* occurred in January. A lesser peak in *A. formosa* abundance occurred later in spring (April-June), at the same time as observed by Ricker (1938) in the mid-1930's. Highest numbers of *Cyclotella* spp. occurred in summer or early fall. *Urosolenia* did not exhibit much seasonal variation but was abundant throughout the year (Fig. 37).

On occasion, other taxonomic groups made up substantial, but lesser (by volume) portions of the microplankton community. These included *Dinobryon* spp. and gelatinous colonies of small cells which we placed in the microplankton category because of their large colony size. Highest numbers of these colonial forms occurred in summer and early fall, and included *Chrysosphaerella* and the cyanobacteria *Aphanocapsa*, *Aphanothece*, *Coelosphaerium*, and *Gloeocystis.* While not heterocystous, some of these cyanobacteria are capable of fixing nitrogen (Wetzel 2001) and under some conditions can produce deleterious blooms. They are also a less favorable food source for herbivorous zooplankton than many other phytoplankton species (Porter 1973).

From July to October of 2002, we examined phytoplankton community structure in both the epilimnion and in the DCM. Considerable differences in epilimnetic and DCM phytoplankton species composition have been recorded in other lakes (Pick et al. 1984; Shortreed and Stockner 1990). However, in Cultus Lake phytoplankton species composition in the epilimnion and at the DCM was similar. Higher chlorophyll concentrations at the DCM were the result of increased abundance of the entire community. This suggests that in Cultus Lake the DCM was caused primarily by metalimnetic photosynthesis. If it was caused by more passive processes (i.e. sinking of epilimnetic phytoplankton), faster-sinking species (i.e. diatoms) would likely have predominated at the DCM (Shortreed and Stockner 1990).

ZOOPLANKTON

Cultus Lake had an abundant zooplankton community, with seasonal average macrozooplankton biomasses of 1,457 mg dry wt/m² in 2001 and 1,396 mg dry wt/m² in 2002 (Table 8). This was substantially higher than average zooplankton biomass in the great majority of B.C. sockeye lakes (Shortreed et al. 2001, 2007; K. Shortreed, unpublished data), although higher biomass has been recorded in a few of these lakes. Highest seasonal biomass occurred in May, after which values generally declined until fall (Table 8, Fig. 39). The large cladoceran *Daphnia* is the preferred prey item of juvenile sockeye (Hume et al. 1996; Hampton et al. 2006), and in Cultus Lake it comprised the majority of the community biomass on most sampling dates (Fig. 39). In Lake Washington, Scheuerell et al. (2005) determined that juvenile sockeye fed almost exclusively on *Daphnia* as soon as *Daphnia* numbers exceeded 0.4/L. In Cultus Lake, *Daphnia* numbers substantially exceeded this threshold throughout our study, except on one occasion in March of 2002 (Table 9). In Cultus Lake, *Daphnia* comprised >90% of sockeye stomach contents on all dates for which we have data (five surveys carried out from June-November in 1996, 2004, and 2005) (S. MacLellan, Fisheries and Oceans Canada, Cultus Lake, B.C., pers. comm.). Seasonal average *Daphnia* biomass was 72% of total biomass, which is a higher proportion than in the majority of B.C. sockeye lakes (Shortreed et al. 2001, 2007; K. Shortreed, unpublished data) (Table 8). The copepod *Diacyclops* had the next highest biomass, making up an average of 14% of the total in 2001 and 22% in 2002. In both study years, highest *Diacyclops* biomass occurred in April. The calanoid copepod *Epischura nevadensis,* the cladoceran *Holopedium gibberum*, and bosminid cladocerans (mostly *Eubosmina coregoni* with smaller numbers of *Bosmina longirostris*) each had average biomasses of 5% or less of the total (Table 8).

Expressed numerically, *Diacyclops* was the most abundant genera in Cultus Lake, followed by *Daphnia* (Table 9). In the 1930's (Ricker 1938) and the 1960's (Goodlad et al. 1974), *Diacyclops* (then called *Cyclops*) was also the most abundant genus, with *Daphnia* the second most abundant. Timing of the seasonal maxima appear to have been slightly different in the 1930's. In our study, the *Daphnia* peak occurred in May, while in the 1930's the peak was in June. Similarly, in our study maximum numbers of both *Eubosmina* and *Diacyclops* occurred in April, but in the 1930's their peaks were in May. These difference in timing could have been due the warmer spring water temperatures in our study (i.e. climate differences). In both studies, highest *Epischura* numbers occurred in May (Table 8) (Ricker 1938). The large predatory cladoceran *Leptodora kindtii* occurred in relatively small numbers in Cultus Lake, with seasonal peaks of up to 750/m² or 20 mg dry wt/m² occurring in September or October. *L. kindtii* was not observed in the 1930's (Ricker 1938), but was noted in the 1960's (Goodlad et al. 1974).

Life-history strategies of *Daphnia* are variable, with some species or populations overwintering as adult females and others producing diapausing eggs (ephippia) after sexual reproduction in the fall (Gliwicz et al. 2001; Wetzel 2001). While little data have been collected in winter from B.C. lakes, in almost all B.C. sockeye lakes for which we have growing season data (April-May to October-November), *Daphnia* numbers are at their seasonal minima in spring (April-May) (e.g. Morton and Shortreed 1996; Malange et al. 2005; K. Shortreed, unpublished data). In addition, numbers often rapidly decline in fall. This strongly suggests that in these lakes *Daphnia* enter diapause in the fall and spend the winter as ephippia. However, in Cultus Lake, *Daphnia* maintains a relatively large overwinter population (as much as 975 mg dry wt/m² in late December of 2002). This suggests that Cultus Lake may be a better rearing environment for juvenile sockeye than the majority of B.C. sockeye lakes, since the preferred prey item is available throughout the year. Further confirmation of the favourable winter/early spring rearing environment in Cultus Lake is that growth of juvenile sockeye from fall to the following spring (fall fry to smolts) is substantially greater in Cultus than in other lakes at equivalent fish densities. At similar low densities, overwinter growth in Quesnel and Shuswap lakes ranged from 1-3 g, while overwinter growth in Cultus Lake was 4.5-9 g (J. Hume, Fisheries and Oceans Canada, Cultus Lake, B.C., pers. comm.).

Frequency histograms of *Daphnia* length indicate that on a number of our sampling dates there was a distinct bimodal distribution in length. This was most pronounced in winter and early spring (Fig. 40-47). One explanation for this would be the presence of more than one *Daphnia* species. Goodlad et al. (1974) reported that Cultus Lake contained both *D. longiremis* and *D. rosea*. Since *D. rosea* is larger than *D. longiremis* (Goodlad et al. 1974; Gillooly and Dodson 2000), the presence of both these species could explain the bimodal length distribution. *D. longiremis* prefers cold water and often is restricted to hypolimnetic waters (Bertilsson et al. 1995; Lindstrom 2001), while *D. rosea* can reproduce successfully in warmer water (Burns and Rigler 1967). Consequently, in Cultus Lake these two species could co-exist and be spatially separated for much of the year. However, recent examinations of Cultus Lake plankton samples indicate that the only abundant *Daphnia* species is *D. thorata* (G. Green, Royal B.C. Museum, Victoria, B.C., pers. comm.; S. MacLellan, Fisheries and Oceans Canada, Cultus Lake, B.C., pers. comm.). The switch from multiple *Daphnia* species to a single species could be due to increased competition because of reduced predation on *Daphnia* (Gliwicz 2001). In Cultus Lake, predation pressure (i.e. densities of planktivorous fish) was far higher in the 1960's and 1970's than in our study (Schubert et al. 2002). In the 1920's, *D. pulex* was the only *Daphnia* species identified from Cultus Lake (Foerster 1925), but given that this species is common in small ponds and rarely dominant in large lakes, this identification is uncertain.

In Lake Washington, Edmondson and Litt (1982) found that *D. thorata* was the most common *Daphnia* species when *Epischura* was abundant, and suggested that *D. thorata* may be less susceptible to *Epischura* predation than other *Daphnia* species. In our study, seasonal maximum numbers of *Epischura* were up to 33,000/m² (1.1/L), whereas Goodlad et al. (1974) listed it as rare. Increases in *Epischura* numbers could potentially be a contributing factor to a change in Cultus Lake's *Daphnia* community. With regard to the bimodal length distribution, Gliwicz et al. (2001) found a similar bimodal *Daphnia* length distribution in a Polish lake. They found that some *Daphnia* overwintered as adult (i.e. relatively large) females that reproduced throughout the winter. This could explain the presence of two cohorts in Cultus Lake. The rapid increase in *Daphnia* numbers in April-May would be due to reproduction from this population as well as from hatching ephippia.

REARING CAPACITY

The PR model (Hume et al. 1996, Shortreed et al. 2000, Cox-Rogers et al. 2004) was developed 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 $C \cdot m^{-2} \cdot d^{-1}$) ($PR_{mean}$). The May-October seasonal average is computed with PR assumed to be 0 on May 1 and October 31. In 2001 and 2002, PR_{mean} was 424 and 473 mg dry wt/m², respectively. This was an average PR of 449 mg $C \cdot m^{-2} \cdot d^{-1}$ ± 48(2SE). Total seasonal phytoplankton carbon uptake (t $C \cdot lake^{-1} \cdot yr^{-1}$) ($PR_{total}$) was calculated by multiplying PR_{mean} by lake area and by growing season length (standardized as May 1-Oct 31). Given the longer growing season in Cultus Lake, it may be appropriate to use a longer growing season than May 1-Oct 31. However, the extent to which a longer growing season affects rearing capacity is not known, so at present we have not made any adjustments to PR predictions. Average PR_{total} in Cultus Lake was 507 t C.

Several adjustments to PR model predictions may be required if the limnetic community contains planktivores other than juvenile sockeye, or if a portion of the sockeye population emigrates as age-2 smolts (Cox-Rogers et al. 2004; Shortreed et al. 2007). In Cultus Lake, we reduced PR_{total} applicable to model predictions from 507 to 463 t $C \cdot lake^{-1} \cdot yr^{-1}$, based on the biomass of limnetic planktivores other than juvenile sockeye, and based on approximately 1% of smolts emigrating as age-2's (J. Hume, Fisheries and Oceans Canada, Cultus Lake, B.C., pers. comm.). Non-sockeye planktivores in Cultus Lake were primarily threespine sticklebacks (*Gasterosteus aculeatus*), with periodic occurrences of redside shiners (*Richardsonius balteatus*) and pygmy sculpins (*Cottus* sp.). Kokanee were present but rare. After these adjustments, PR_{total} was used in the model to estimate maximum potential smolt biomass and the escapement needed to produce that biomass (Cox-Rogers et al. 2004).

In addition to planktivorous fish, limnetic macroinvertebrates may compete with juvenile sockeye for zooplankton prey and further reduce a lake's productive capacity. Low numbers (maximum observed density was 25/m³) of the large predatory cladoceran *Leptodora kindtii* occurred in Cultus Lake. *Leptodora* are exclusively carnivorous (Branstrator 1998) and as adults eat a broad range of prey, including *Daphnia* (Branstrator and Lehman 1991). Consequently, at some life-history stages they can be at least partial competitors with juvenile sockeye. However, in Cultus Lake *Leptodora* are also frequently found in the stomachs of juvenile sockeye (S. MacLellan, Fisheries and Oceans Canada, Cultus Lake, B.C., pers. comm.). This constitutes a "trophic triangle" where *Leptodora* is both a competitor and a prey item for the same species (Lunte and Luecke 1990; Hyatt et al. 2005). Consequently, it is extremely difficult to ascertain the extent to which macroinvertebrates affect Cultus Lake's sockeye rearing capacity. Given these difficulties, and given the generally low density of *Leptodora* in

Cultus Lake, we made no adjustments to rearing capacity estimates because of its presence.

The resulting PR model prediction for Cultus Lake, including weighting the prediction by the long-term average sex ratio of 57% female spawners, (Schubert et al. 2002) is that an optimum escapement of 75,000 spawners would produce up to 4.6 million smolts. This is similar to the maximum observed escapement and to the maximum observed smolt output (4 million smolts from 71 thousand spawners). A direct estimate of rearing capacity provided by the relationship between smolt biomass and female spawner numbers suggests that the optimum escapement to Cultus Lake is somewhat lower (50,000 spawners) (Cox-Rogers et al. 2004). In that study, it was suggested that the discrepancy between the two predictions of optimum escapement could be due to other constraints on fish production. In Cultus Lake, that could be the large number of piscivores (predominantly *Ptychocheilus oregonensis*) present in the lake. Another factor contributing to lower fish production could be the parasitic copepod *Salmincola californiensis*, which is known to cause mortality in juvenile sockeye salmon (Kabata and Cousens 1977). It is rare in B.C. sockeye lakes, but does occur in Cultus Lake. The amount of mortality it causes in Cultus Lake is unknown, but it is frequently observed on juvenile sockeye (J. Hume, Fisheries and Oceans Canada, Cultus Lake, B.C., pers. comm.).

QUALITY OF CULTUS LAKE REARING ENVIRONMENT

Since sockeye fry tend to avoid temperatures >18°C (Lebrasseur et al. 1978), for much of the growing season (app. mid-June to mid-October), Cultus Lake's epilimnion is not favorable sockeye habitat. However, temperatures in the meta- and hypolimnion are within sockeye temperature preferences. The lake's deep euphotic zone enables substantial phytoplankton production to occur below the epilimnion, which in turn contributes to the development of a metalimnetic chlorophyll maximum. As a result, zooplankton can find a suitable food supply below the warm epilimnion. Consequently, sockeye fry can graze effectively below the epilimnion, ameliorating the effect of the warm surface waters.

Photosynthetic rates and a number of chemical variables indicate Cultus Lake has the highest productivity yet recorded in a B.C. sockeye lake. Variables commonly used to categorize trophic status (e.g. PR, chlorophyll, TP, bacteria) place the lake either at the upper end of oligotrophy or lower end of mesotrophy. The widely used trophic state index (TSI) developed by Carlson (1977) has a scale of 0 to 100, and oligotrophic lakes have a value <30. The TSI value for Cultus Lake was 34, placing the lake near the boundary between oligotrophy and mesotrophy.

Phytoplankton community composition in Cultus Lake is favorable for grazing herbivores (i.e. abundant pico- and nanoplankton). There is an abundant zooplankton community made up of an unusually high proportion of *Daphnia*, the preferred prey item of juvenile sockeye. Further, unlike most B.C. lakes, in Cultus Lake *Daphnia* is present throughout the year, enabling substantial overwinter growth to occur. While planktivore numbers were low during our study, earlier studies (Foerster 1924, Ricker 1937, Goodlad et al. 1974) found that *Daphnia* remained abundant even when planktivore densities were far higher, providing further confirmation Cultus Lake *Daphnia* are highly productive. The favorable conditions are reflected in the large size of Cultus Lake sockeye smolts. In recent years, when fish densities and grazing pressure have been low, average smolt weight has been 13.4 g (n=6) (J. Hume, Fisheries and Oceans Canada, Cultus Lake, B.C., pers. comm.). Even in the 1950's and 1960's, when grazing pressure was much higher, smolts tended to be relatively large (5.2 g, n=8) (Schubert et al. 2002).

While there is legitimate concern about the extensive and increasing societal use of Cultus Lake and its drainage basin, the lake currently provides a suitable environment for juvenile sockeye. This is not to say there are not a number of habitat-related issues which have the potential to, or currently are, deleteriously affecting the lake's spawning or rearing environments. Most of these were listed by Schubert et al. (2002) and include increasing abundance of Eurasian watermilfoil (destruction of spawning habitat, increased pikeminnow numbers), predation by northern pikeminnow, mortality from parasite (*S. californiensis*) infestation, and pollutants in sediments, groundwater, and the lake itself (septic tanks, fertilizer use, outboard motors). The decline in hypolimnetic DO concentrations merits close attention, since the rate of decline could accelerate if nutrient loading increases further (i.e. increasing human activity) and the growing season lengthens (i.e. climate change). However, at present the limnetic zone of Cultus Lake provides a favorable nursery area for juvenile sockeye.

CURRENT AND PAST PRODUCTIVITY

Cultus Lake is unique among B.C. lakes in that there were detailed limnological investigations (Foerster 1925; Ricker 1937, 1938) carried out early in the 20th century, 70-80 yr prior to our study. Further, fish counting fences have provided accurate escapement numbers for most years from the 1920's to the present. In addition, accurate smolt numbers are available for many of the same years (Schubert et al. 2002). While some of the methods used in the early limnological investigations resulted in data that are not comparable with results from our study, there are still a number of variables which are directly comparable with those from our 2001-2002 study.

Temperature data from the earlier investigations were highly detailed and are readily comparable to our data. They indicate that for most of the year, both the shallow and deep waters of Cultus Lake are warmer now than they were early in the 20th century (Figs. 7 and 8). Combined with long-term increases in air temperatures in the Fraser Valley (Taylor and Langlois, 2000), there is convincing evidence that climate change has affected the physical environment of Cultus Lake. This is in agreement with trends for northern hemisphere lakes for which long-term observations are available (Magnuson et al. 2000).

Water clarity (as Secchi depth) was recorded on only two occasions in the earlier study (Ricker 1937), but it was substantially greater (by 24%, or 3.2 m) than Secchi depths recorded at comparable times of the year in 2001 and 2002 (Fig. 9). While only two measurements do not allow any definitive conclusions to be drawn, the data do suggest that the lake is less clear now than in the past, which is indicative of higher algal productivity and biomass.

Ricker (1937) also carried out extensive DO profiling in the years 1927-1935. Surface DO concentrations from those years were quite similar to those in our study, which indicates that methods were comparable (Fig. 11). However, for most of the year deep (30 m) DO was much lower in our study, indicating that the amount of organic matter reaching the hypolimnion is greater now than in the past. This could indicate greater phytoplankton biomass and productivity, but is no doubt at least partially due to the large increase in macrophyte biomass since the earlier study. Summer DO profiles exhibited a distinct metalimnetic peak in both our study and that of Ricker (1937). However, the magnitude of the peak was much greater in our study, indicating increased phytoplankton productivity (Fig. 12). Summer pH levels were also slightly higher in our study, further suggesting increased phytoplankton activity.

While differences in methods make it impossible to make quantitative comparisons in zooplankton numbers, seasonal changes in relative abundances indicate that timing of spring peaks in the dominant genera (*Daphnia*, *Diacyclops*, and *Epischura*) is approximately one month earlier now than in the 1930's (Fig. 39; Ricker 1938). The increased lake temperatures in the early part of the year (i.e. climate change) could be the explanation for the change in timing.

Finally, mean weight of Cultus smolts from years of comparable escapements (a range of 800-7000 female spawners) were 40% larger from 1990-2003 (n=4, mean=10.6 g) than from 1925-1937 (n=8 mean=7.5 g) (Fig. 48). These differences were significant (t-test, $p<0.05$; J. Hume, Fisheries and Oceans Canada, Cultus Lake, B.C., pers. comm.) and further suggest an increase in productivity since the 1930's.

Since sockeye escapements were far lower during our study and in the years preceding it than they were in most years of the earlier studies, input from marine-derived nutrients was lower before and during our study. This decrease in the annual nutrient load to Cultus Lake should have resulted in lower productivity (i.e. oligotrophication). However, the data indicate that productivity is now greater than it was during the 1920's and 1930's. It is probable that nutrient loading from anthropogenic sources (septic tanks, agriculture, and domestic fertilizer) is much higher than it was during the earlier study, more than making up for reduced loading of marine nutrients. Climate change (i.e. warming) has no doubt also played a role in the apparent increase in productivity over the last 70 years.

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Table 1. Salient morphometric and bathymetric data from Cultus Lake.

Variable	
1:50,000 map number	92H4, 92G1
Latitude (°N)	49°03.3'
Longitude (°W)	121°59.0'
Elevation (m)	46
Surface area (km²)	6.3
Shoreline length (km)	13.3
Shoreline development	1.5
Drainage basin area (km²)	75
Distance from Cultus Lake to the Chilliwack River (km)	2.9
Distance from Cultus Lake to the Fraser River (km)	19
Distance from Cultus Lake to the mouth of the Fraser River (km)	118
Mean depth (m)	31
Maximum depth (m)	44
Total annual precipitation (cm)[a]	157
Water residence time (yr)	1.8

[a] - Environment Canada, 1971-2000 Canadian climate normals

Table 2. Selected physical data from the Cultus Lake investigation. Means are time-weighted growing season (May-October) averages.

Date	Schmidt stability index	Epilimnion depth (m)	Surface temperature (°C)	Turbidity (NTU)	Secchi depth (m)	Euphotic zone depth (m)
18-Apr-01	244	iso	8.2	0.49	6.9	17.9
24-May-01	1,020	3.6	15.8		9.9	17.6
19-Jun-01	1,405	7.0	17.2		9.5	16.0
18-Jul-01	2,176	7.3	19.9		7.9	17.2
16-Aug-01	2,683	3.5	22.5		14.5	16.7
4-Sep-01	2,341	7.9	20.1		9.9	16.2
2-Oct-01	1,923	9.8	17.8		13.1	16.6
6-Nov-01	563	16.0	10.6		10.6	18.1
Mean	1,995	6.5	19.2		10.6	16.6
22-Jan-02	168	iso	5.9	1.12	3.3	10.0
26-Feb-02	179	iso	5.2	3.08	4.0	9.3
25-Mar-02	180	iso	6.3	0.86	7.2	14.6
30-Apr-02	379	5.0	10.0	0.39	6.2	13.3
30-May-02	819	2.0	15.1		11.0	17.3
27-Jun-02	1,920	2.6	21.8		6.0	16.4
23-Jul-02	2,422	4.2	23.0		6.1	12.5
28-Aug-02	2,695	5.8	22.2		8.5	13.3
25-Sep-02	1,924	9.4	18.1		13.6	15.3
24-Oct-02	1,178	10.9	14.2		12.6	19.2
20-Nov-02	513	20.3	10.5		11.4	15.0
19-Dec-02	227	iso	7.6		8.1	19.4
Mean	2,017	5.7	20.0		9.2	15.0
15-Jan-03	168	iso	6.2		8.1	14.2
12-Feb-03	171	iso	6.2		8.3	11.9
13-Mar-03	176	iso	5.8		6.5	14.4
21-Aug-03						15.2

Table 3.. Selected chemical data from the Cultus Lake investigation. Data are euphotic zone averages except where otherwise specified. Means are time-weighted growing season (May-October) euphotic zone averages.

Date	Conductivity (µS/cm)	Diss. oxygen (mg/L)		Diss. oxygen (% saturation)		pH	Total dissolved solids (mg/L)	Total alkalinity (mg $CaCO_3$/L)	Diss. inorganic carbon (mg/L)
		Surface	at 30 m	Surface	at 30 m				
18-Apr-01	134	12.5	11.4	105	91	6.97	101	64.4	19.3
24-May-01	146	10.7	9.4	108	76	6.95	112	64.7	19.3
19-Jun-01	147	10.6	9.4	110	76	7.29	105	64.5	17.3
18-Jul-01	158	9.2	8.3	101	67	8.17	105	59.7	14.7
16-Aug-01	167	9.4	7.4	109	60	7.63	111	66.4	17.0
4-Sep-01	163					7.87	96	65.4	16.5
2-Oct-01	159					7.84	111	65.3	16.7
6-Nov-01	140	10.4	6.4	93	52	7.70	112	65.2	16.6
Mean	154	9.9	8.7	106	70	7.63	106	64.2	16.8
22-Jan-02	125	10.9	10.8	87	86		101		
26-Feb-02	110	11.7	11.6	91	90		107		
25-Mar-02	123	12.9	12.3	104	94		104		
30-Apr-02	136	13.5	12.4	119	98	7.77	105	62.7	15.6
30-May-02	140	10.5	10.4	104	83	7.75	104	62.6	15.7
27-Jun-02	149	9.4	9.4	108	75	7.58	101	60.5	15.4
23-Jul-02	155	9.5	9.1	111	73	7.50	97	60.8	15.9
28-Aug-02	156	9.1	8.8	105	71	8.05	107	63.6	15.7
25-Sep-02	156	10.1	8.0	107	65	8.04	97	63.4	15.7
24-Oct-02	148	11.2	7.6	109	61	7.93	105	63.3	15.8
20-Nov-02	139	10.7	6.3	96	51	7.77	115	62.4	15.6
19-Dec-02	133	10.8	6.1	90	50	7.56	108	63.9	16.5
Mean	152	9.8	8.9	108	71	7.81	101	62.3	15.7
15-Jan-03	130	10.5	10.4	84	84	7.64	108	63.4	16.1
12-Feb-03	129	11.1	11.0	89	88	7.68	101	62.6	15.8
13-Mar-03	129	11.8	11.6	94	92	7.86	111	30.7	7.6
21-Aug-03		9.2	7.2	108	58				

Table 4. Selected chemical data from the Cultus Lake investigation. Data are euphotic zone averages except where otherwise specified. Means are time-weighted growing season (May-October) averages.

Date	Soluble reactive Si (mg/L)	Nitrogen (µg N/L)				Phosphorus (µg/L)				Particulates (µg/L)			Atomic ratios		
		Nitrate	Hypol. nitrate	Ammonia	Hypol. ammonia	Total	Hypol. total	Dissolved	Soluble reactive	C	N	P	C:N	N:P	C:P
18-Apr-01	2.05	103	117	5.7	7.1	6.0	6.6	3.6	0.8	331	42	2.9	9	32	300
24-May-01	2.03	120	161	7.5	4.1	5.4	9.5	6.3	2.0	152	15	1.6	12	21	245
19-Jun-01	1.94	65	139	6.3	4.4	7.3	6.0	4.9	1.2			1.3			
18-Jul-01	1.84	33	140	9.2	7.5	5.8		4.7	1.0			3.0			
16-Aug-01	1.69	12	152	6.3	5.0	6.2	5.2	3.6	1.1			3.8			
4-Sep-01	1.70	15	168	5.7	3.9	5.8	4.4	3.4	0.7			2.9			
2-Oct-01	1.55	14	170	3.1	2.0	5.6	6.4	4.0	0.2			4.1			
6-Nov-01	1.77	42	199	6.6	3.0	6.5	6.3	4.4	0.7			2.8			
Mean	1.80	39	153	6.6	4.8	6.1	5.9	4.4	1.0			2.7			
22-Jan-02	2.44	172	176	4.1	2.4	7.8	9.0	5.6	1.8			3.9			
26-Feb-02	2.34	130	136	7.6	5.7	11.5	14.4	8.3	7.3			3.7			
25-Mar-02	2.03	137	147	8.3	6.4	12.1	11.0	11.4	4.8			5.1			
30-Apr-02	2.39	109	144	4.5	12.0	11.8	11.8	5.5	3.0			5.1			
30-May-02	2.10	94	156	12.1	3.7	6.7	7.6	6.3	1.9			3.8			
27-Jun-02	2.08	89	161	8.1	2.0	9.8	8.7	8.8	2.1			3.3			
23-Jul-02	1.94	41	154	5.8	2.9	8.1	8.7	5.2	2.1			4.0			
28-Aug-02	2.06	16	232	2.8	3.0	9.6	8.7	6.6	1.6			3.2			
25-Sep-02	1.83	14	221	2.4	1.0	8.3	6.9	4.6	1.6			2.8			
24-Oct-02	2.10	56	229	3.5	1.6	7.6	6.8	5.0	1.2			4.1			
20-Nov-02	2.23	48	241	7.5	1.7	6.9	6.4	3.7	0.8			2.2			
19-Dec-02	2.28	103	227	10.9	7.1	7.3	7.1	4.7	1.1			2.9			
Mean	2.00	45	193	5.3	2.3	8.6	8.1	6.1	1.8			3.5			
15-Jan-03	2.57	160	161	4.7	2.7	7.6	7.8	4.1	2.0			3.1			
12-Feb-03	2.66	163	163	4.9	4.0	8.4	6.9	4.0	1.5						
13-Mar-03	2.43	155	159	5.3	4.6	8.8	7.9	5.3	1.2			3.5			

Table 5. Monthly variation in chemical variables from Frosst, Spring, and Sweltzer creeks. For comparative purposes, data from the mid-lake station are included. Station numbers are: 1- mid-lake, 2- Frosst, 3- Sweltzer, and 4- Spring. Means are May-October time-weighted averages.

	Temperature (ºC)				Conductivity (µS/cm)				Total diss. solids (mg/L)				Diss. oxygen (mg/L)				Sol. reactive Si (mg/L)			
Date	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
22-Jan-02	5.9	3.9	5.7	8.5	125	125	124	.	101	109	105	.	10.9	13.4	11.1	.	2.44	2.42	3.38	.
26-Feb-02	5.2	6.7	5.5	8.9	110	141	124	.	107	121	107	172	11.7	12.6	11.7	7.2	2.34	2.63	1.62	1.29
25-Mar-02	6.3	7.6	6.9	8.5	123	151	127	218	104	129	109	187	12.9	12.5	13.3	7.5	2.03	2.91	1.96	1.85
30-Apr-02	10.0	6.0	10.4	9.2	136	.	.	219	105	76	111	184	13.5	12.7	13.7	7.9	2.39	2.13	2.33	2.75
30-May-02	15.1	7.2	15.7	9.8	140	.	150	214	104	51	105	185	10.5	12.6	11.1	6.9	2.10	1.33	2.06	3.19
27-Jun-02	21.8	12.0	21.9	10.4	149	120	159	242	101	92	107	185	9.4	11.1	9.4	6.4	2.08	2.15	2.03	2.18
23-Jul-02	23.0	15.1	24.9	9.3	155	206	169	240	97	136	97	181	9.5	10.5	9.5	6.0	1.94	2.61	2.03	2.33
28-Aug-02	22.2	12.3	23.7	8.8	156	209	162	256	107	163	112	189	9.1	10.9	8.9	5.2	2.06	2.77	2.21	2.55
25-Sep-02	18.1	10.4	18.6	8.2	156	210	158	214	97	160	108	183	10.1	11.4	10.3	4.9	1.83	2.72	2.07	2.80
24-Oct-02	14.2	7.2	14.1	8.7	148	188	149	238	105	144	103	184	11.2	12.8	10.9	4.4	2.10	3.04	2.08	2.92
20-Nov-02	10.5	7.8	10.3	8.2	139	.	138	235	115	56	113	189	10.7	12.2	10.9	5.3	2.23	1.51	2.06	3.69
19-Dec-02	7.6	4.3	7.6		133	100	130	238	108	84	105	184	10.8	13.3	10.9	4.9	2.28	2.59	2.30	4.66
Mean	20.0	11.5	20.9	9.2	152	182	160	236	101	131	106	185	9.8	11.3	9.8	5.6	2.00	2.50	2.09	2.58

	Nitrate (µg N/L)				Ammonia (µg N/L)				Total P (µg/L)				Total diss. P (µg/L)				Soluble reactive P (µg/L)			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
22-Jan-02	172	528	174	.	4.1	5.6	7.6	.	7.8	4.5	8.2	.	5.6	4.6	5.2	.	1.8	1.5	2.1	.
26-Feb-02	130	766	133	490	7.6	5.2	5.6	11.5	11.5	7.7	10.4	10.6	8.3	6.8	8.5	9.0	7.3	3.3	3.8	3.9
25-Mar-02	137	832	132	468	8.3	6.6	9.7	8.6	12.1	7.7	9.8	10.6	11.4	8.3	7.3	11.2	4.8	7.1	3.3	5.4
30-Apr-02	109	302	111	441	4.5	2.7	4.0	8.0	11.8	6.2	9.0	11.3	5.5	6.0	6.3	11.1	3.0	3.3	3.1	4.7
30-May-02	94	144	91	435	12.1	1.5	9.1	7.1	6.7	10.5	6.9	8.6	6.3	5.0	6.0	7.8	1.9	2.1	1.9	4.3
27-Jun-02	89	319	71	416	8.1	4.1	9.2	10.8	9.8	7.1	8.4	14.5	8.8	6.8	6.6	10.5	2.1	2.5	2.4	5.6
23-Jul-02	41	503	17	381	5.8	4.1	9.4	8.0	8.1	7.4	11.0	17.5	5.2	5.6	6.4	8.3	2.1	2.6	2.3	4.7
28-Aug-02	16	713	2	433	2.8	4.1	3.7	6.5	9.6	8.0	9.7	13.3	6.6	8.2	6.4	11.1	1.6	2.6	1.7	4.0
25-Sep-02	14	680	1	431	2.4	3.9	1.8	3.9	8.3	6.7	6.9	10.6	4.6	6.0	5.0	8.3	1.6	2.8	1.4	3.9
24-Oct-02	56	610	2	447	3.5	2.4	5.0	2.0	7.6	6.9	7.0	9.6	5.0	5.9	4.7	9.7	1.2	2.3	1.4	4.4
20-Nov-02	48	60	40	468	7.5	2.6	10.0	8.9	6.9	32.9	8.5	12.9	3.7	8.3	5.4	10.4	0.8	3.1	1.1	4.8
19-Dec-02	103	263	107	472	10.9	1.1	8.5	22.7	7.3	6.1	8.9	11.7	4.7	4.9	5.0	10.7	1.1	2.3	1.4	5.1
Mean	45	526	26	420	5.3	3.6	6.2	6.7	8.6	7.6	8.6	13.1	6.1	6.4	6.0	9.4	1.8	2.5	1.9	4.5

Table 6. Concentration (μg/L) of selected metals in unfiltered Cultus Lake water. Standards are for Canadian drinking water quality.

Element (ug/L)	Cultus Lake	Canadian drinking water guidelines
Aluminium	25	100
Arsenic	<1	10
Cadmium	<0.01	5
Calcium	30,300	
Chromium	0.5	50
Cobalt	0.05	
Copper	1.9	1,000
Iron	170	300
Lead	<0.01	10
Lutetium	<0.01	
Magnesium	3,310	
Manganese	4.2	50
Nickel	<0.1	
Potassium	410	
Selenium	<1	10
Sodium	3,630	200,000
Strontium	215	
Zinc	<1	5,000

Table 7. Salient biological data from the Cultus Lake investigation. Means are time-weighted growing season (May-October) euphotic zone averages except for mean PR, which was calculated as described in the methods.

				Phytoplankton number (thousands/mL)				Phytoplankton volume (mm³/m³)			
	Bacteria (millions/mL)	Chlorophyll (µg/L)	Daily PR (mg C·m^{-2}·d^{-1})	Total	Picopl.	Nanopl.	Micropl.	Total	Picopl.	Nanopl.	Micropl.
18-Apr-01	1.50	1.28	230	11.1	9.1	1.05	0.89	1,016	17	73	925
24-May-01	1.48	0.99	430	5.5	3.2	1.11	1.16	502	8	72	422
19-Jun-01	1.87	2.32	625	11.4	9.1	1.12	1.22	703	20	78	605
18-Jul-01	1.92	2.22	503	43.2	40.6	1.82	0.82	810	102	110	598
16-Aug-01	1.85	2.58	707	74.6	66.5	1.96	6.12	894	166	123	606
4-Sep-01	2.47	2.58	358	85.7	81.2	1.30	3.19	779	194	80	506
2-Oct-01	2.06	2.84	350	97.5	91.0	1.21	5.27	930	213	86	631
6-Nov-01	2.27	1.06	178	25.1	24.1	0.53	0.46	245	46	38	160
Mean	1.97	2.32	424	52.0	47.7	1.47	2.81	780	115	94	570
22-Jan-02	1.51	0.51		42.6	40.3	0.85	1.45	2,120	80	53	1,987
26-Feb-02	1.06	0.83		57.4	56.4	0.65	0.38	737	111	53	573
25-Mar-02	1.41	2.72		37.1	35.6	0.85	0.62	866	69	73	724
30-Apr-02	2.38	2.13	599	92.8	91.4	0.91	0.44	776	168	83	526
30-May-02	2.38	1.02	374	13.7	12.5	0.97	0.24	384	25	75	285
27-Jun-02	3.24	1.14	515	19.8	18.6	0.63	0.59	240	38	46	156
23-Jul-02	3.11	3.56	937	114.3	106.9	1.42	6.07	1,340	272	108	960
28-Aug-02	3.17	1.61	545	145.8	142.1	0.83	2.90	900	398	48	454
25-Sep-02	2.56	2.15	310	93.3	88.8	1.13	3.37	826	253	78	495
24-Oct-02	2.67	1.89	369	62.6	61.1	0.89	0.62	692	140	65	487
20-Nov-02	3.05	1.12	445	30.1	29.1	0.69	0.36	403	59	45	299
19-Dec-02	2.77	1.11	114	11.5	10.0	1.18	0.34	472	22	70	380
Mean	2.93	2.01	473	85.1	81.3	1.0	2.8	788	216	70	501
15-Jan-03	1.33	0.73	66								
12-Feb-03	1.60	0.96	135								
13-Mar-03	1.92	1.44	83								
21-Aug-03						0.72	7.02			48	957

Table 8. Variation in biomass (mg dry wt/m²) of the zooplankton community. Data are from 30 m vertical hauls. Means are time-weighted growing season (May-October) averages.

	Total	Macrozoopl.	*Daphnia*	Bosminids[a]	*Diacyclops*	*Epischura*	*Holopedium*	Others
18-Apr-01	920	919	355	200	364	0	0	0
24-May-01	2,544	2,542	2,130	94	149	163	6	0
19-Jun-01	2,040	2,040	1,737	75	161	42	22	3
18-Jul-01	1,359	1,359	783	88	309	6	172	2
16-Aug-01	981	981	736	57	137	19	25	6
4-Sep-01	1,006	1,006	710	48	114	55	59	20
2-Oct-01	1,079	1,078	783	28	205	5	55	1
6-Nov-01	570	570	364	7	136	15	35	13
Mean	1,457	1,457	1,095	67	184	40	64	6
22-Jan-02	457	457	307	6	136	8	0	0
26-Feb-02	380	380	241	12	123	5	0	0
25-Mar-02	129	129	42	8	78	2	0	0
30-Apr-02	1,538	1,538	351	53	1,050	63	22	0
30-May-02	3,272	3,272	2,313	21	499	438	2	0
27-Jun-02	1,048	1,048	578	17	346	93	14	0
23-Jul-02	1,874	1,874	1,392	1	351	114	11	5
28-Aug-02	1,139	1,139	764	2	329	19	9	16
25-Sep-02	776	776	629	5	113	7	6	17
24-Oct-02	982	982	777	13	108	23	27	34
20-Nov-02	444	443	344	18	70	6	6	0
19-Dec-02	1,106	1,105	975	30	93	9	0	0
Mean	1,395	1,394	985	8	289	91	11	11
15-Jan-03	756	756	639	42	68	7	0	0
12-Feb-03	710	710	622	26	58	1	0	4
13-Mar-03	1,460	1,458	1,189	108	160	2	1	0

[a] - predominantly *Eubosmina coregoni* with smaller numbers of *Bosmina longirostris*

Table 9. Variation in numbers/m³ of the major zooplankton genera. Data are from 30 m vertical hauls. Means are time-weighted growing season (May-October) averages.

	Total	Macrozoopl.	*Daphnia*	Bosminids[a]	*Diacyclops*	*Epischura*	*Holopedium*	Others
18-Apr-01	11,898	11,848	1,506	2,176	8,210	0	0	6
24-May-01	12,540	12,440	7,140	1,260	3,560	520	20	40
19-Jun-01	7,697	7,687	3,809	557	3,114	131	66	20
18-Jul-01	8,585	8,585	2,300	650	4,704	104	821	6
16-Aug-01	5,068	5,031	1,770	535	2,588	75	67	33
4-Sep-01	5,326	5,314	1,940	444	2,640	126	144	31
2-Oct-01	6,538	6,513	2,075	288	3,975	13	163	25
6-Nov-01	4,253	4,253	1,116	63	2,956	53	56	9
Mean	7,343	7,320	2,912	594	3,421	140	253	24
22-Jan-02	3,295	3,295	855	54	2,358	28	0	0
26-Feb-02	2,568	2,568	599	110	1,850	10	0	0
25-Mar-02	1,797	1,792	213	91	1,459	30	0	5
30-Apr-02	20,424	20,424	1,160	400	18,067	598	200	0
30-May-02	15,300	15,300	5,700	250	8,200	1,100	50	0
27-Jun-02	8,827	8,827	1,331	113	6,800	546	38	0
23-Jul-02	10,433	10,433	3,137	17	6,592	629	29	29
28-Aug-02	8,443	8,418	1,875	42	6,300	165	42	21
25-Sep-02	4,064	4,042	1,462	103	2,354	79	34	33
24-Oct-02	4,463	4,454	1,901	164	2,264	56	65	13
20-Nov-02	2,853	2,833	1,148	275	1,405	18	8	0
19-Dec-02	6,022	5,992	3,394	478	2,133	17	0	0
Mean	8,345	8,334	2,328	93	5,471	394	40	18
15-Jan-03	4,150	4,115	2,050	690	1,390	20	0	0
12-Feb-03	3,023	3,008	1,423	408	1,183	5	0	5
13-Mar-03	9,467	9,342	3,750	1,208	4,475	8	17	8

[a] - predominantly *Eubosmina coregoni* with smaller numbers of *Bosmina longirostris*

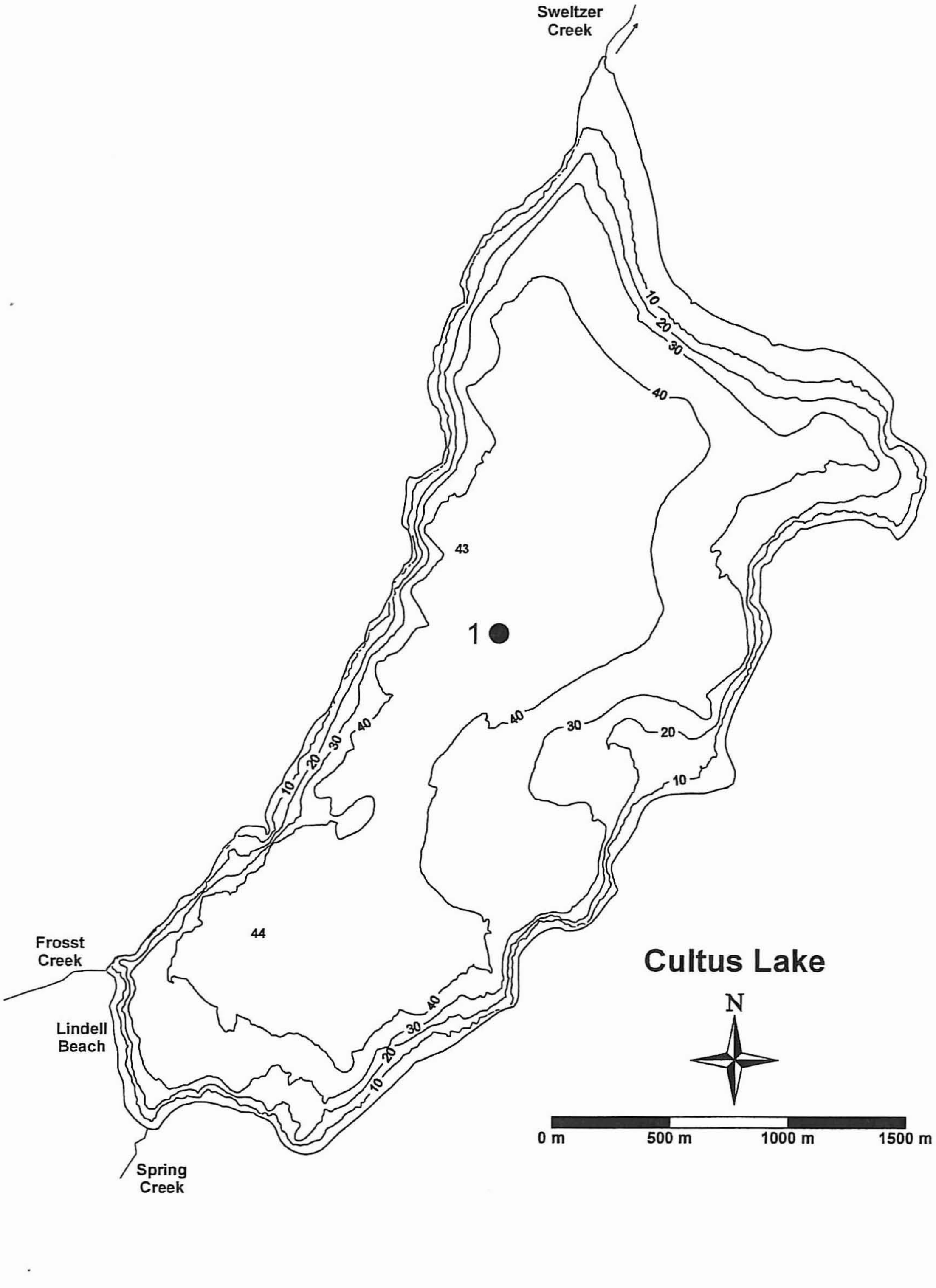


Fig. 1. Bathymetric map of Cultus Lake showing the limnological sampling station and the location of the three streams sampled in 2002.

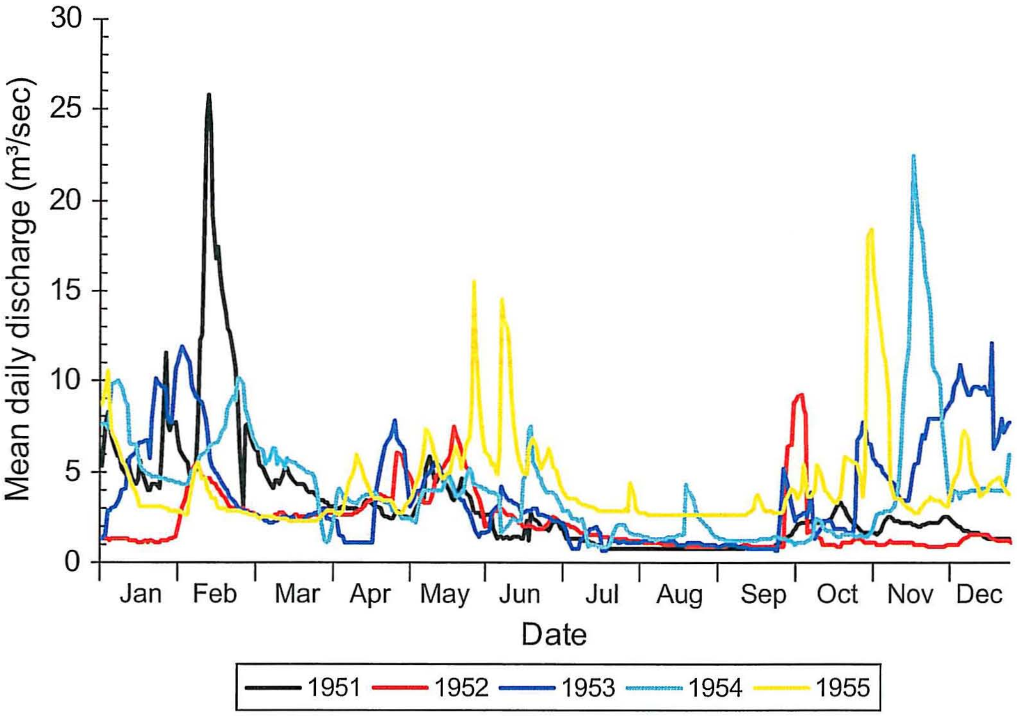


Fig. 2. Mean daily discharge of Sweltzer Creek measured near Cultus Lake. Discharge data were collected by Water Survey of Canada from 1947-1964, but annual data are complete for these years only.

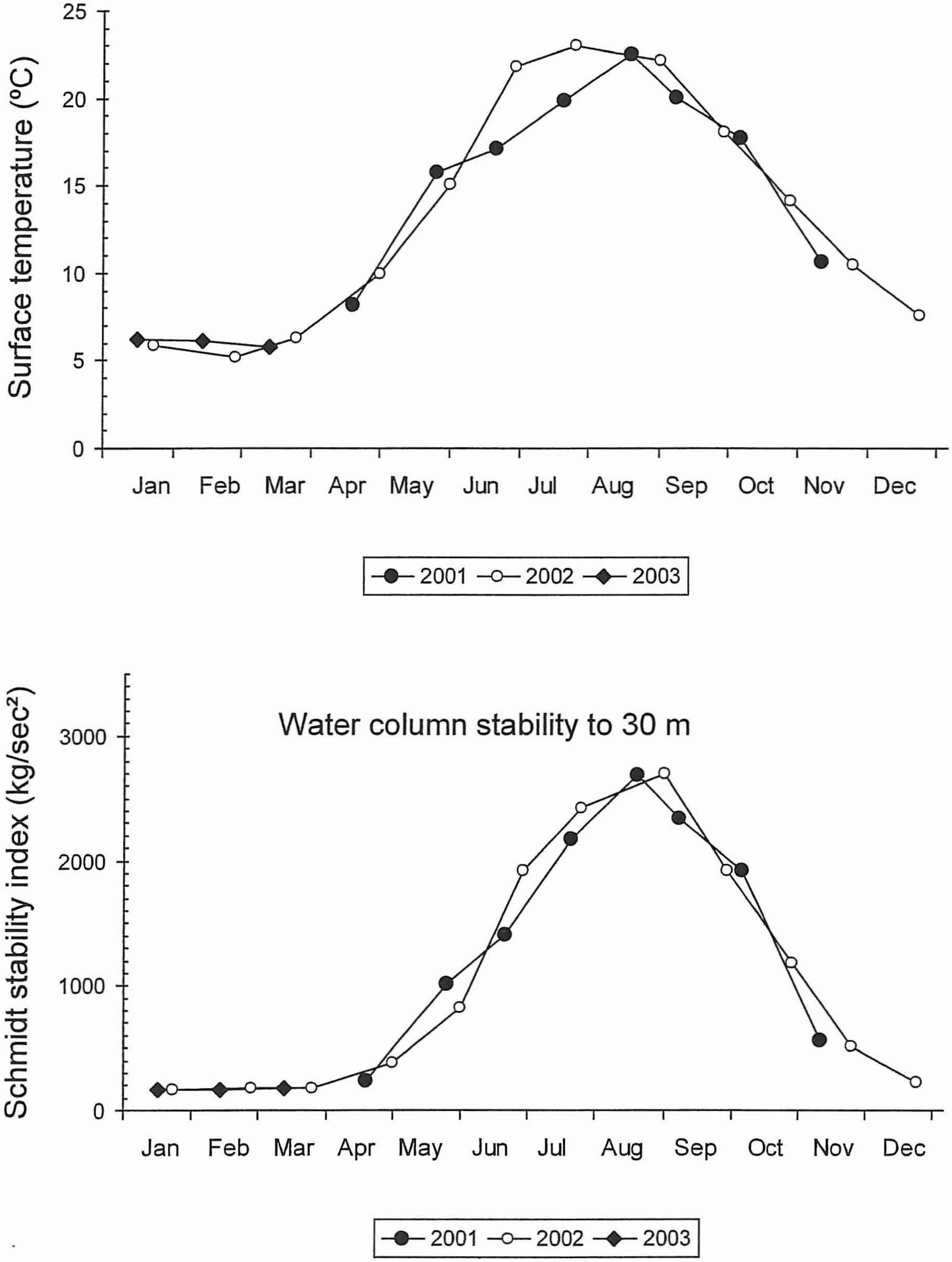


Fig. 3. Seasonal variation in surface temperature and in water column stability.

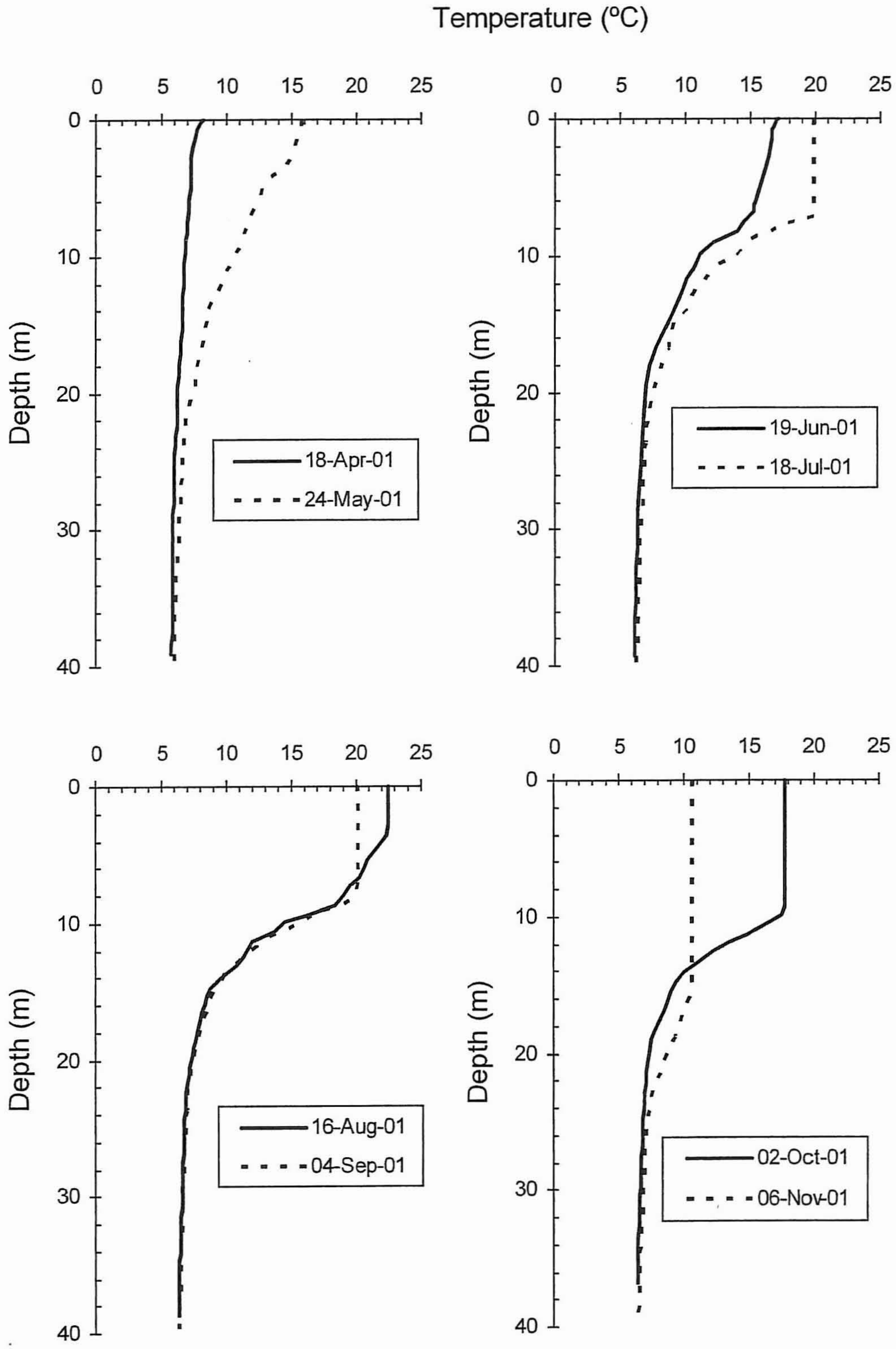


Fig. 4. Temperature profiles obtained during 2001.

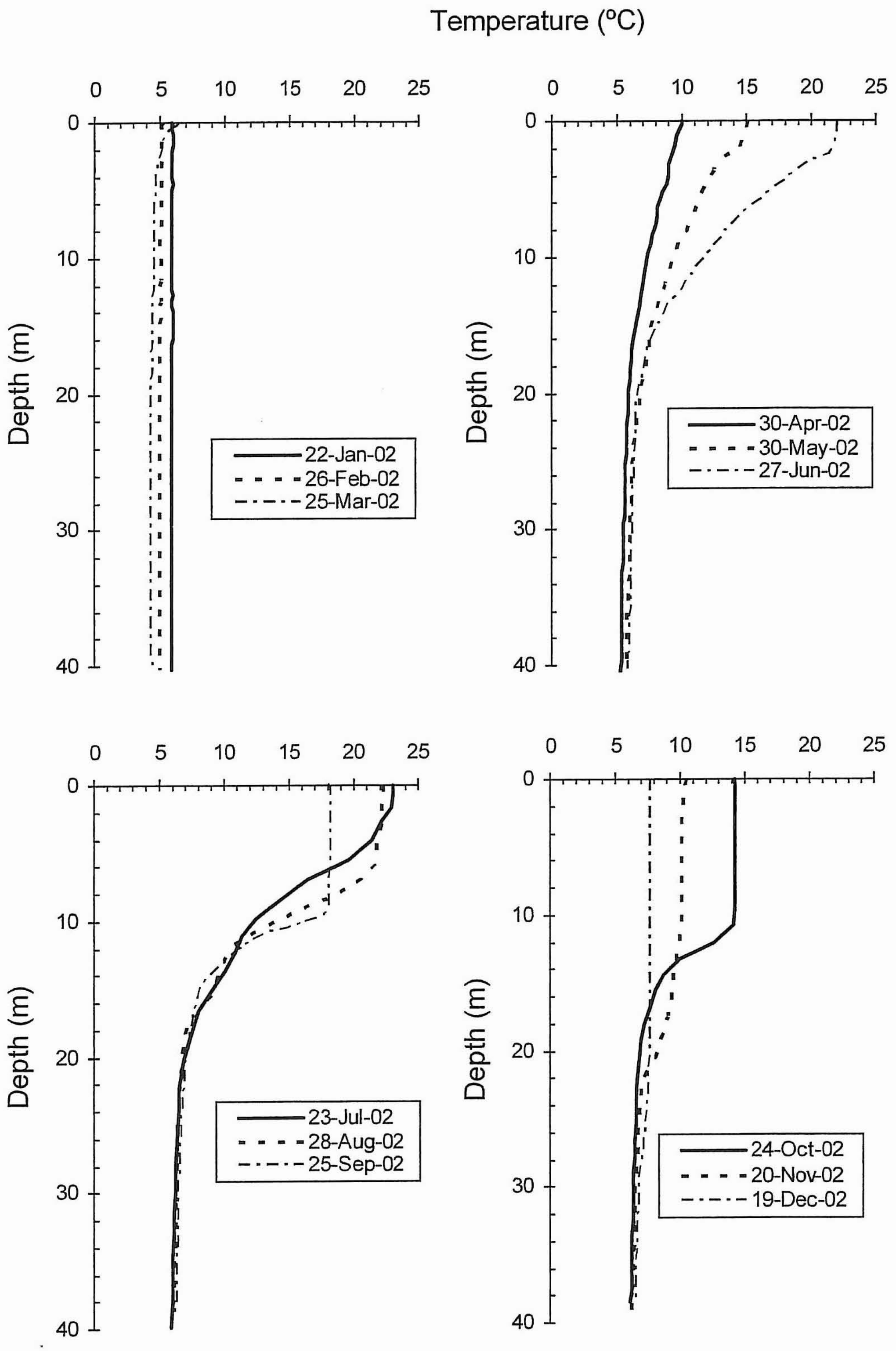


Fig. 5. Temperature profiles obtained during 2002.

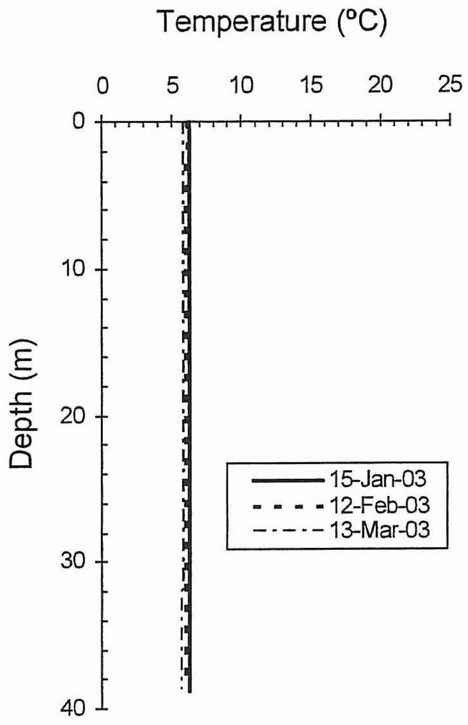
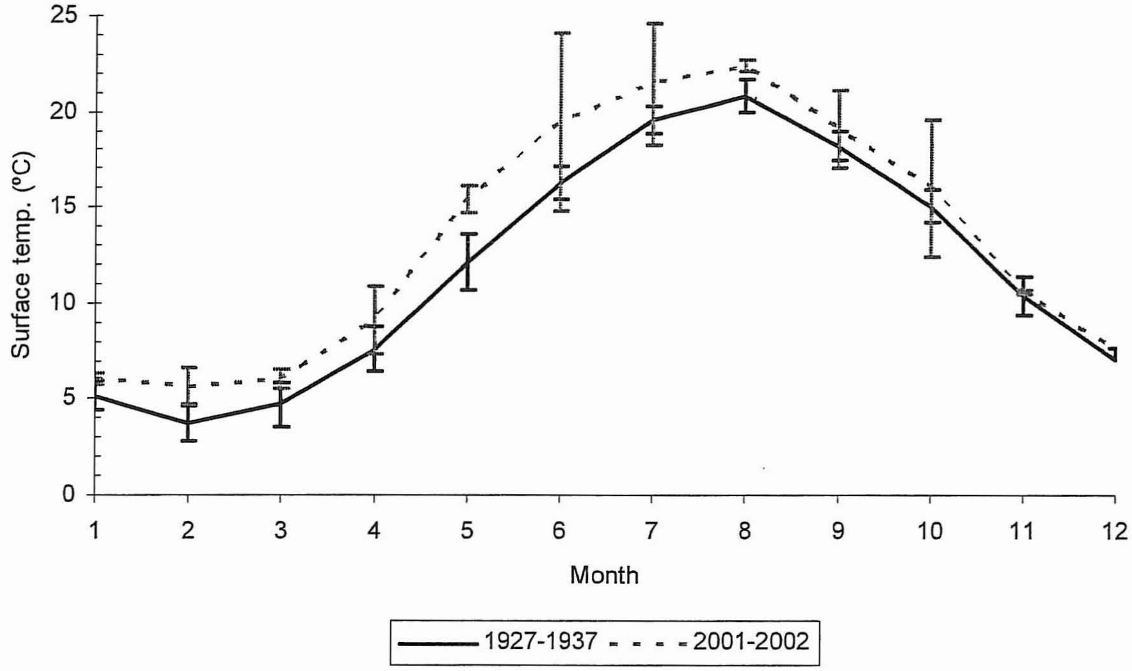


Fig. 6. Temperature profiles obtained during 2003.



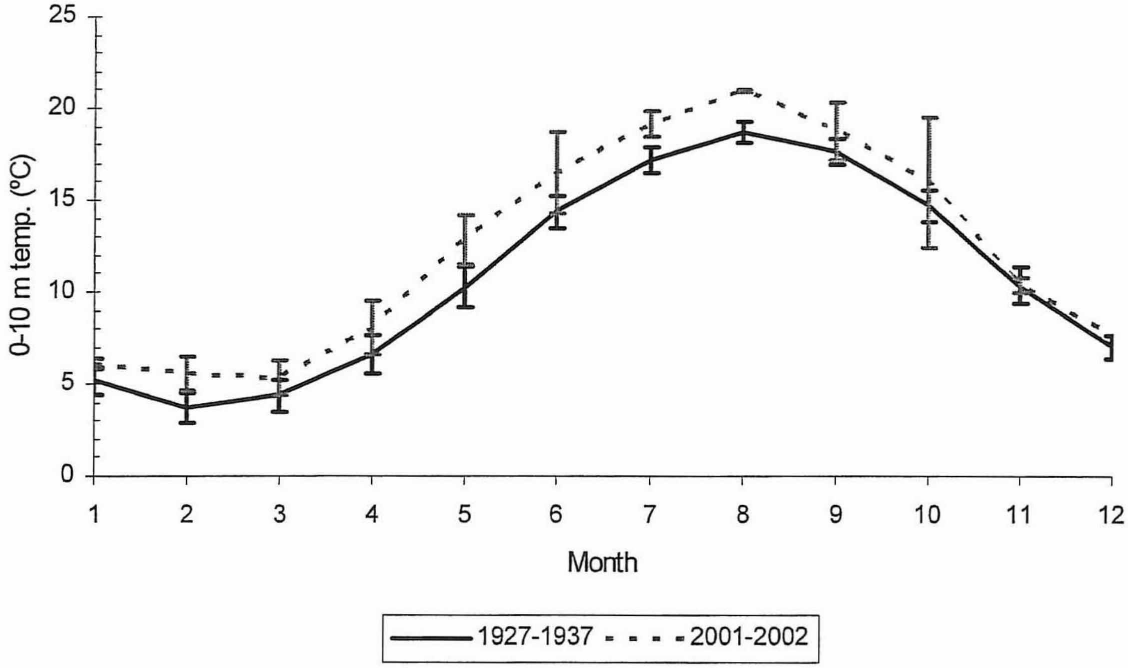


Fig. 7. Differences in mean monthly surface and 0-10 m temperatures in Cultus Lake between the 1920's and 1930's and the present. Vertical bars are ± 2SE.

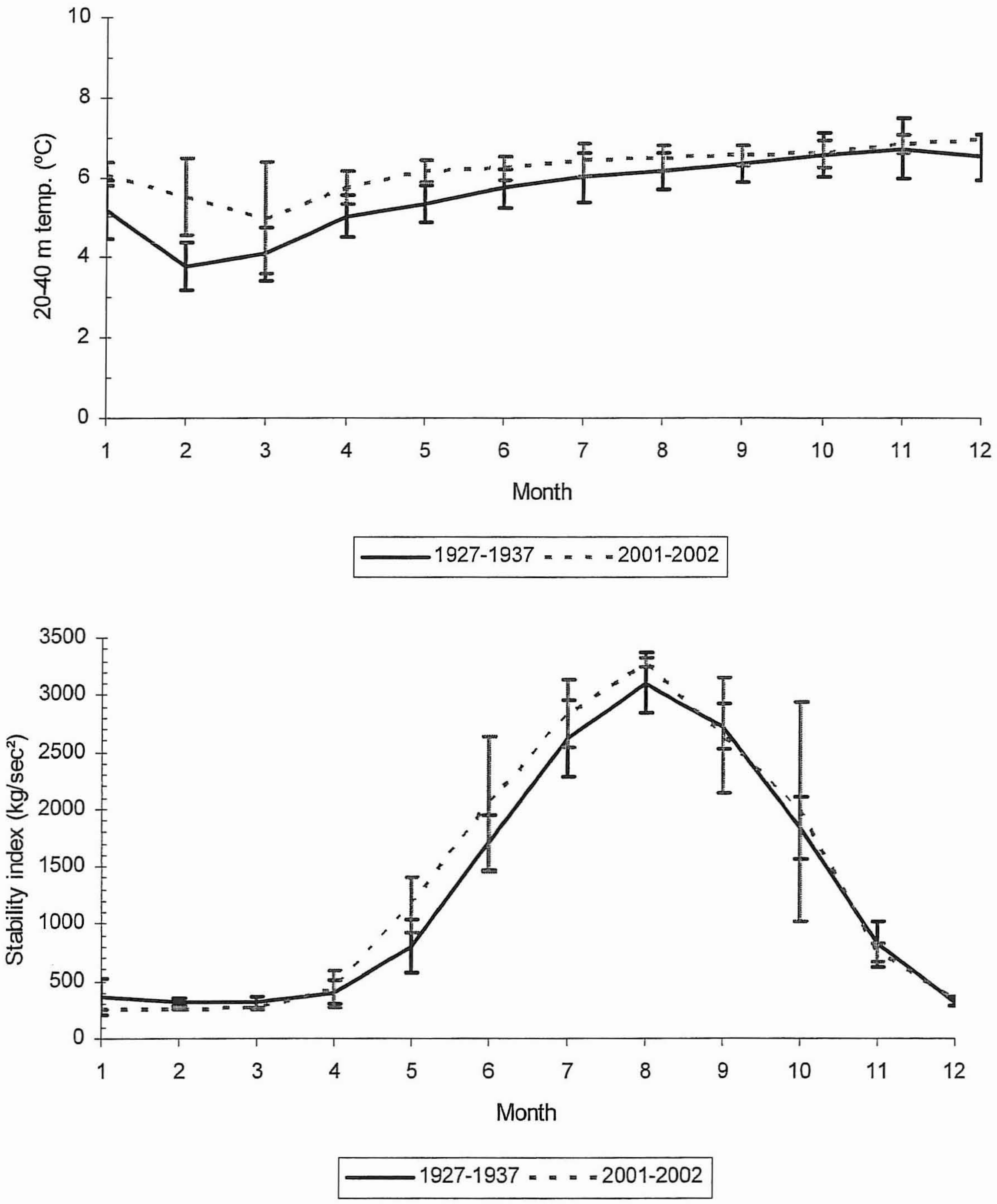


Fig. 8. Differences in mean 20-40 m temperatures and in the Schmidt stability index in Cultus Lake between the 1920's and 1930's and the present. Vertical bars are ± 2SE.

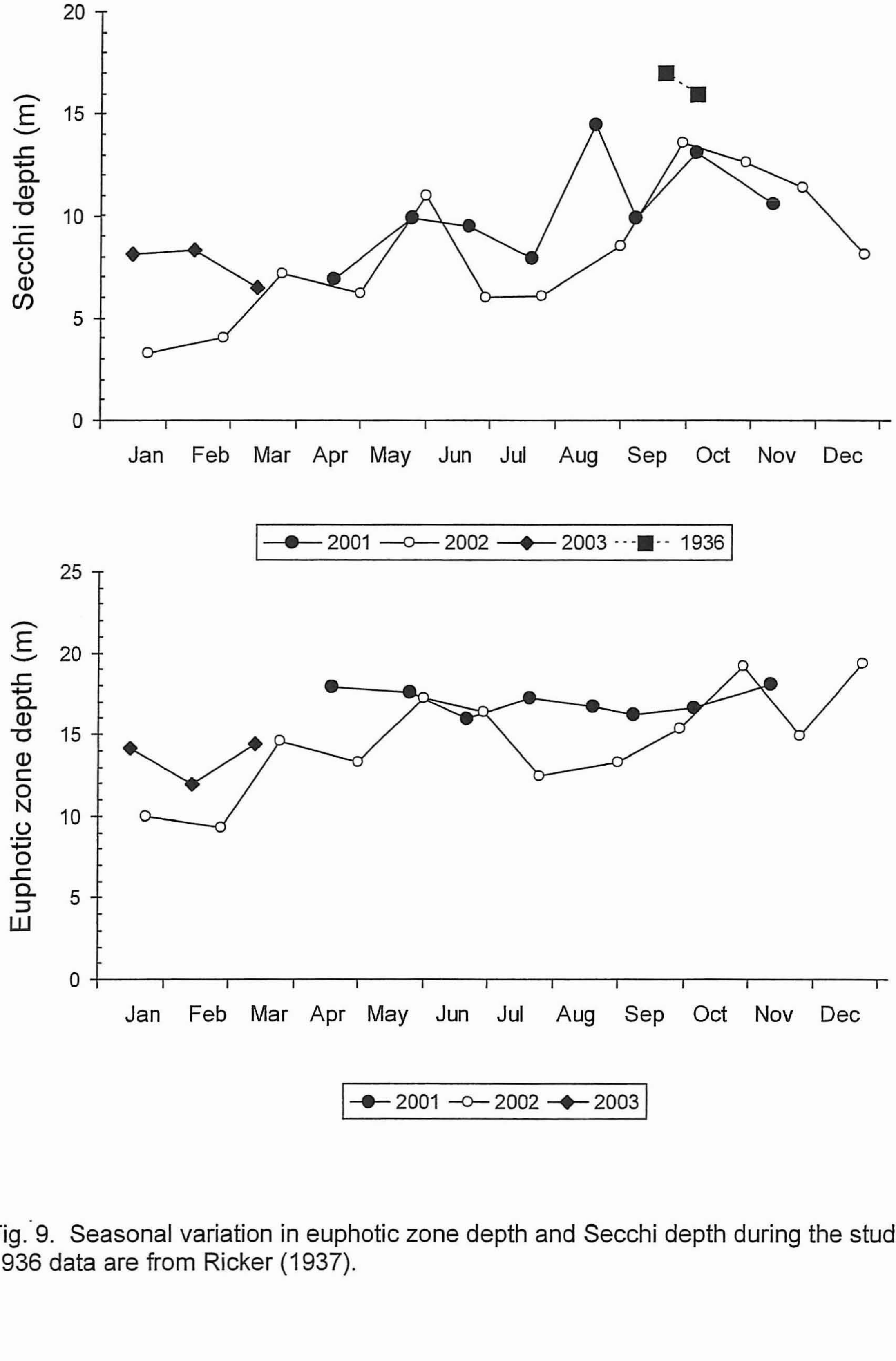
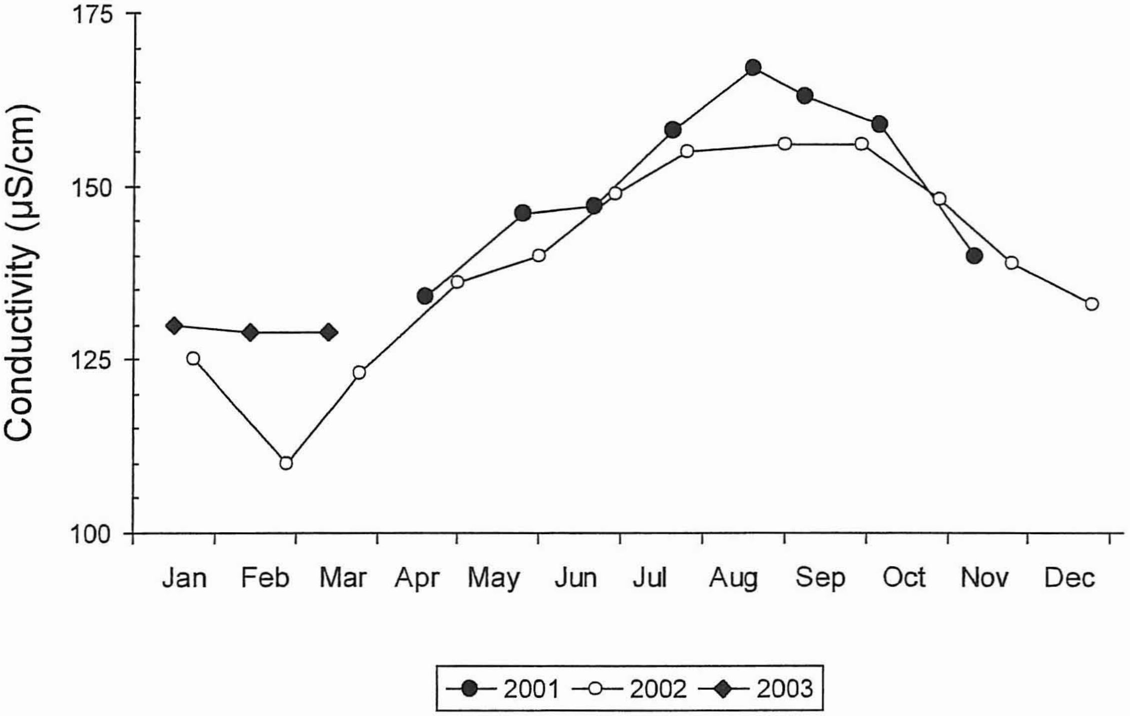


Fig. 9. Seasonal variation in euphotic zone depth and Secchi depth during the study. 1936 data are from Ricker (1937).



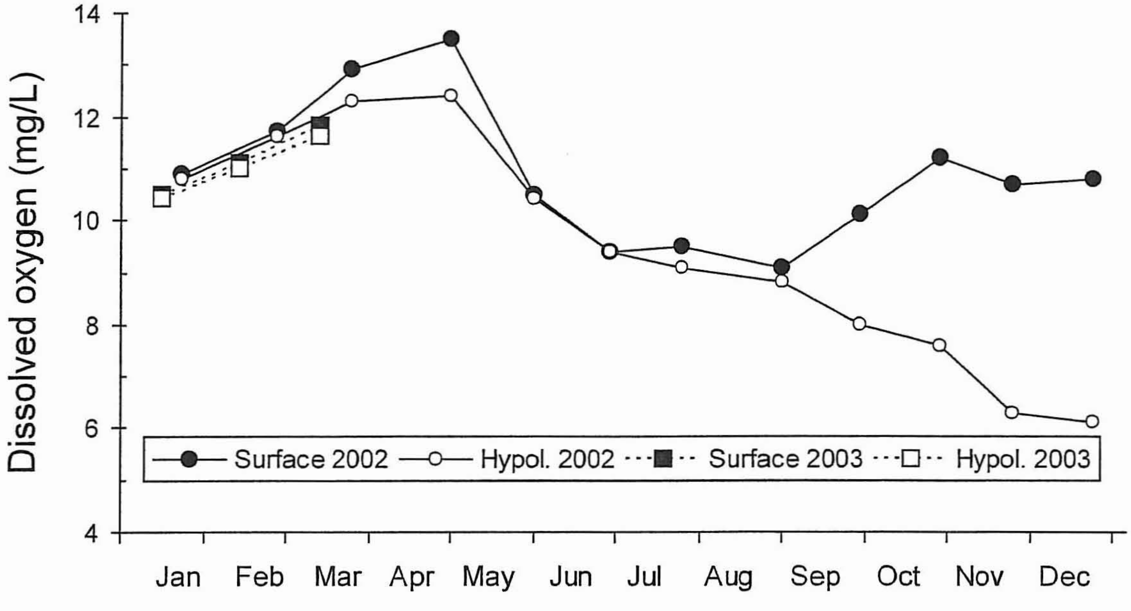


Fig. 10. Seasonal variation in mean epilimnetic conductivity and in both surface and hypolimnetic DO concentrations.

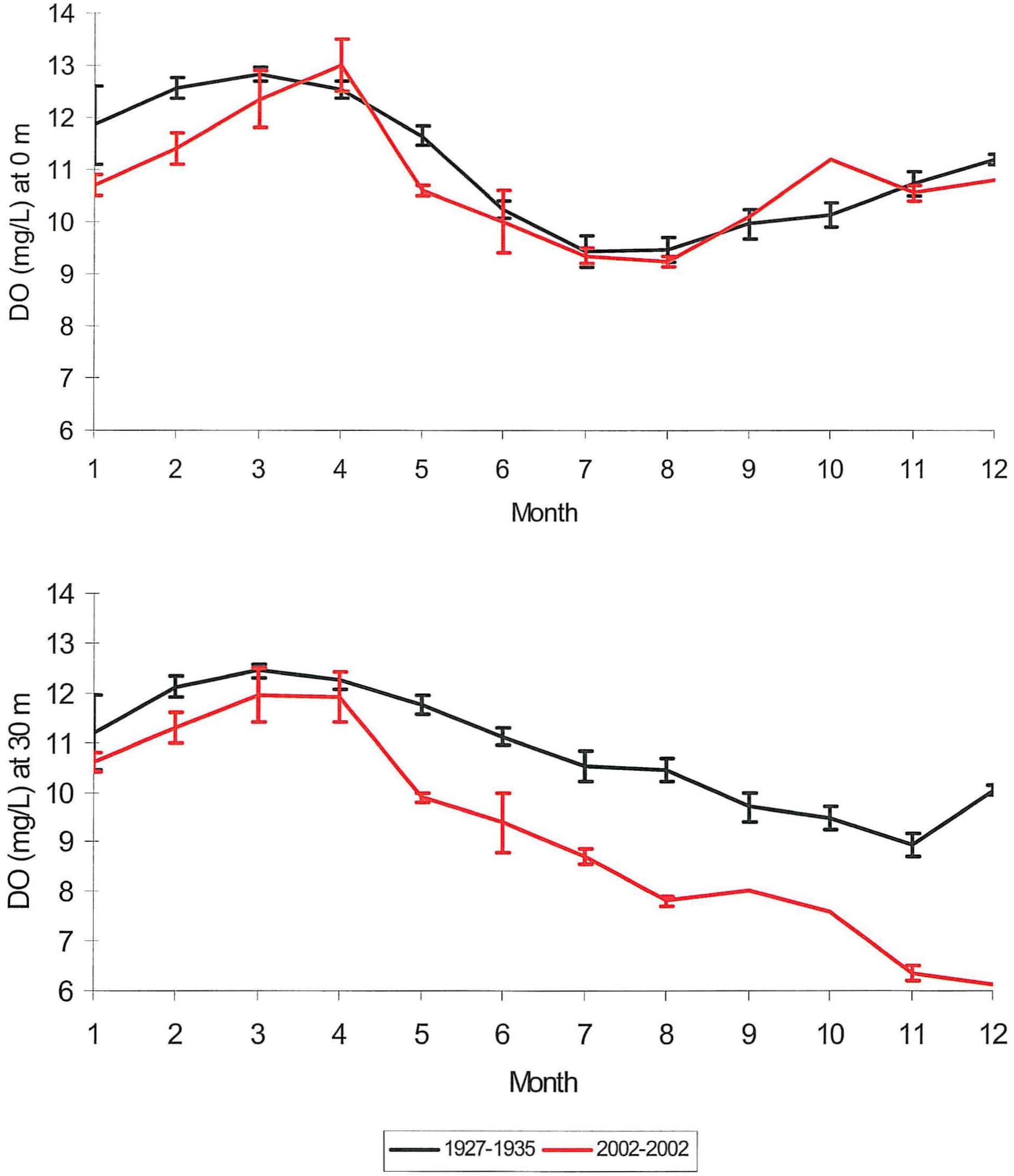


Fig. 11. Average monthly DO concentrations from the 1920's-1930's and from our study. Data are from the surface (top figure) and from 30 m. Bars are ± 2SE.

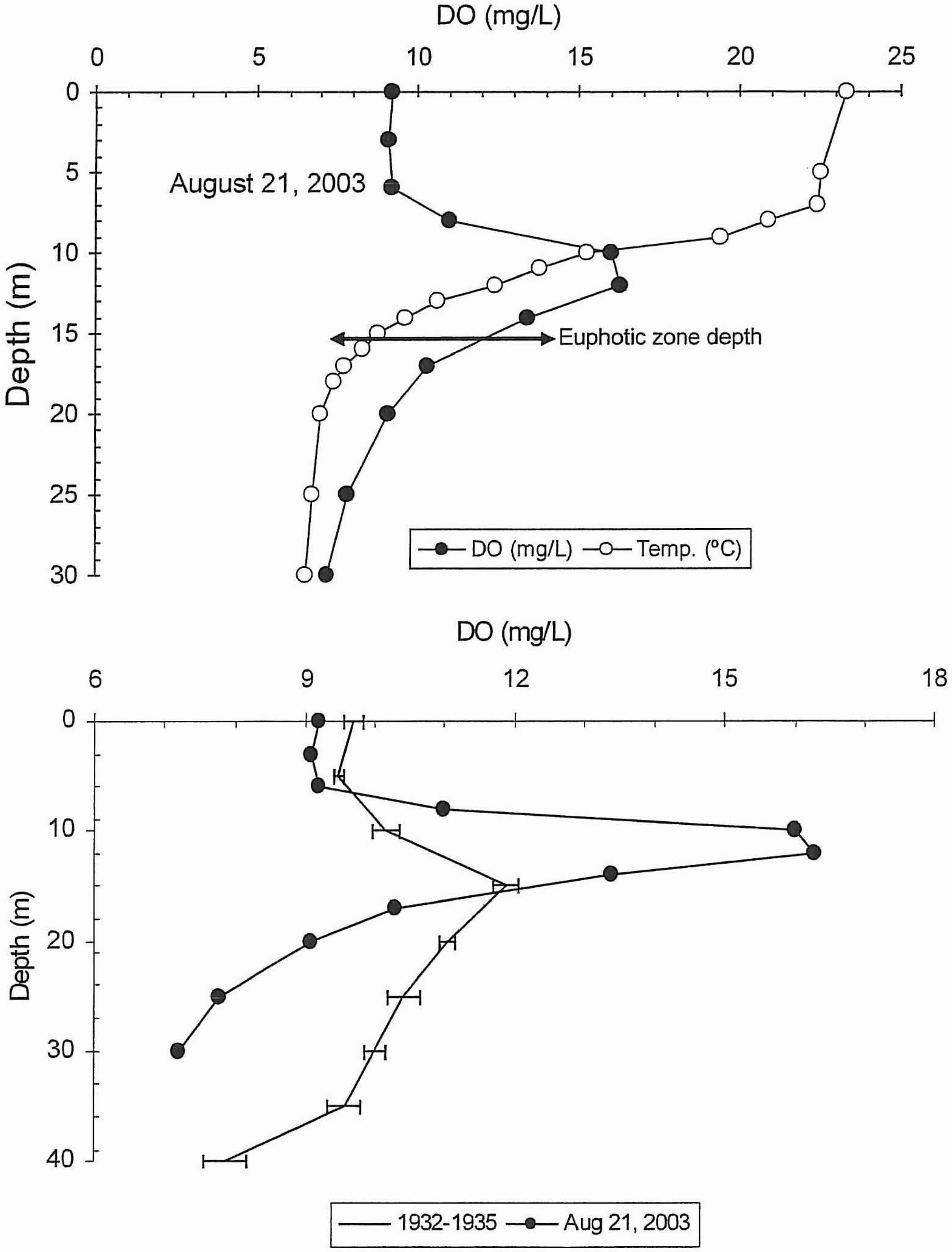


Fig. 12. Vertical DO profiles from August 2003 overlaid with temperature and euphotic zone data (upper figure). The lower figure contains August DO profiles from the 1930's and from 2003 (bars are ± 2SE).

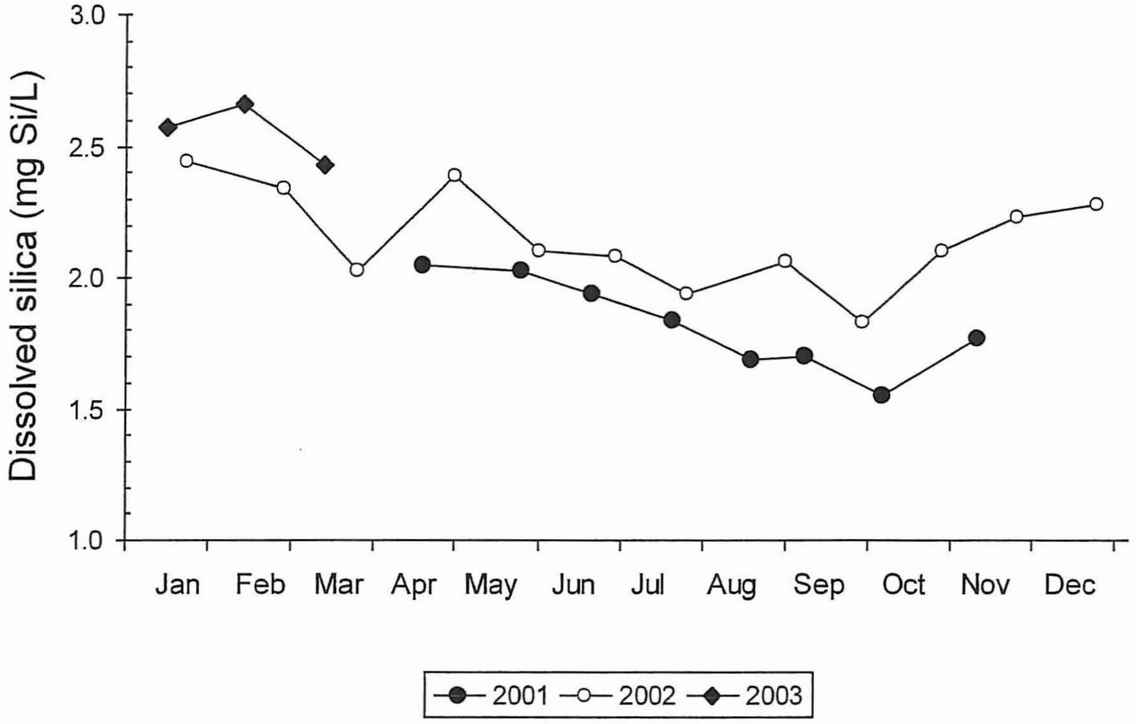


Fig. 13. Seasonal variation in trophogenic zone concentrations of soluble reactive silicon.

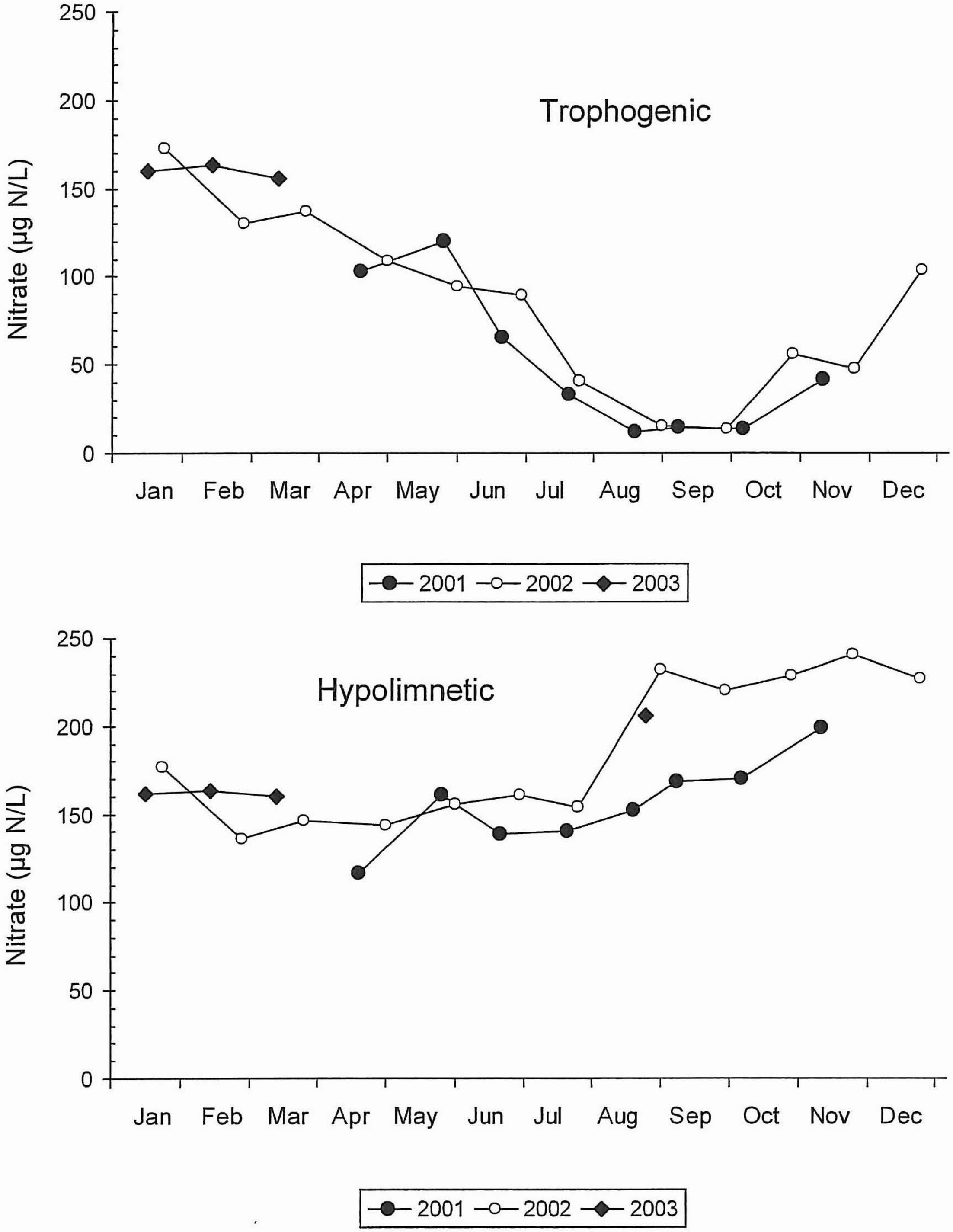


Fig. 14. Seasonal variation in average trophogenic and hypolimnetic nitrate concentrations.

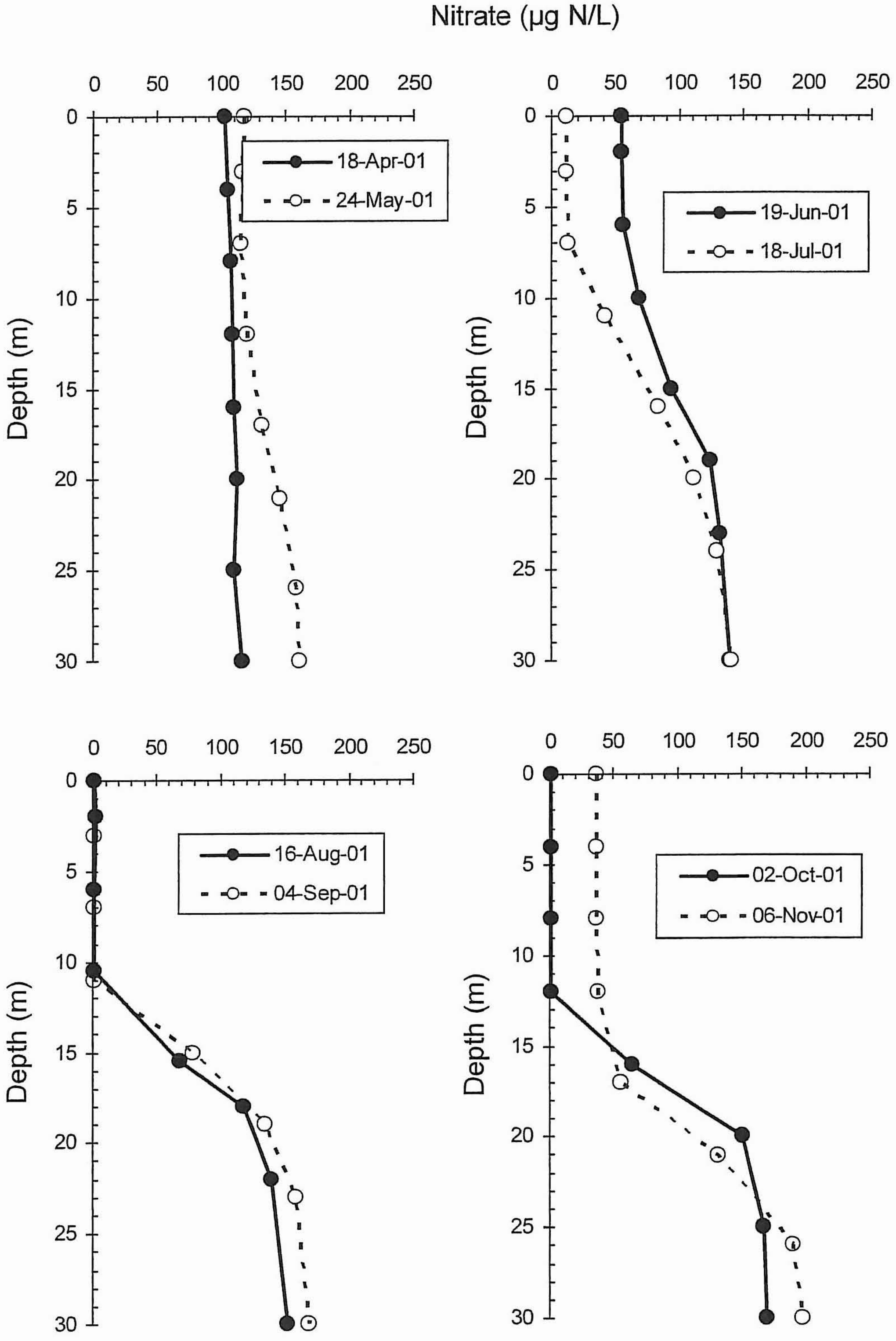


Fig. 15. Nitrate profiles obtained during 2001.

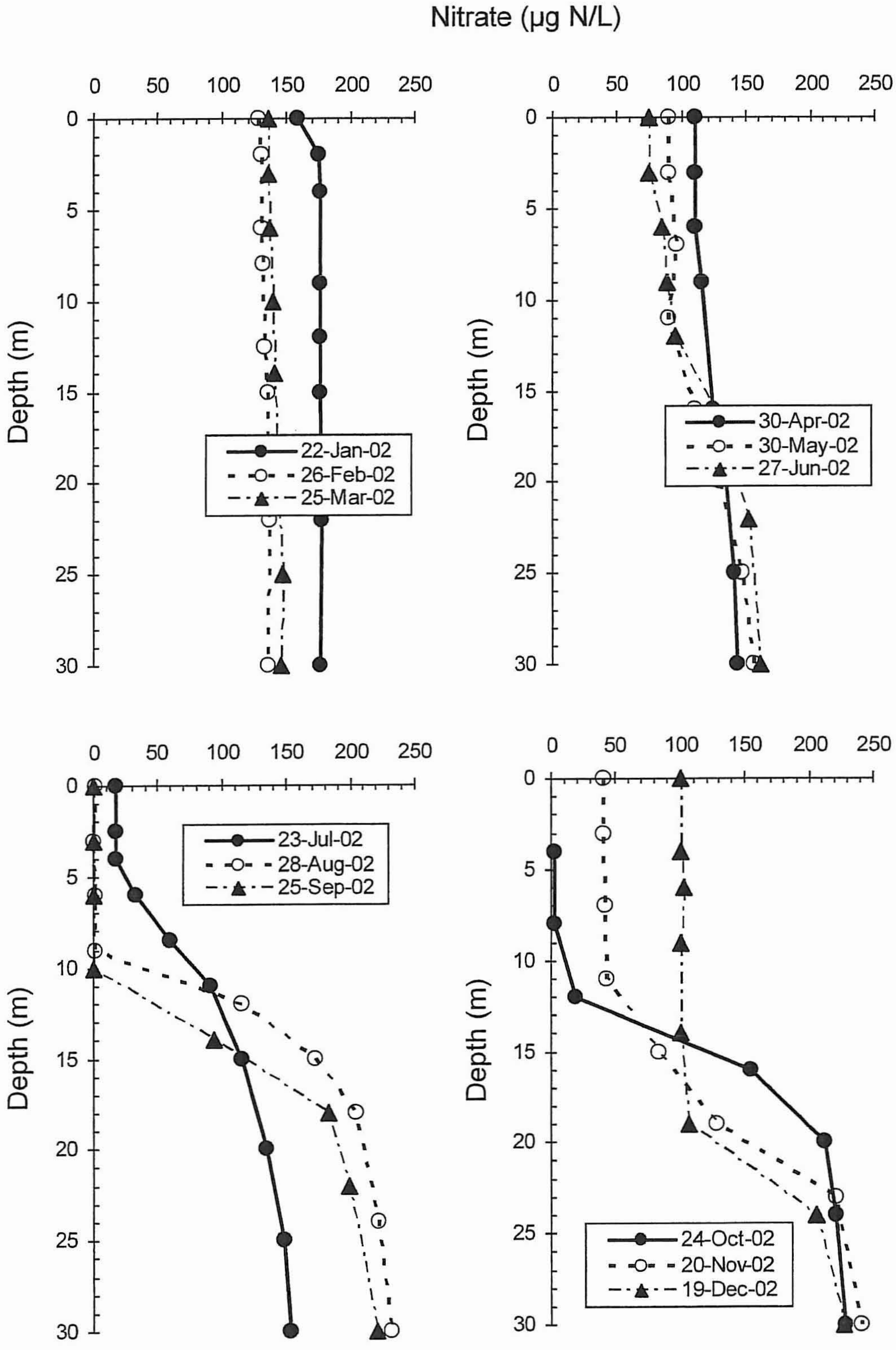


Fig. 16. Nitrate profiles obtained during 2002.

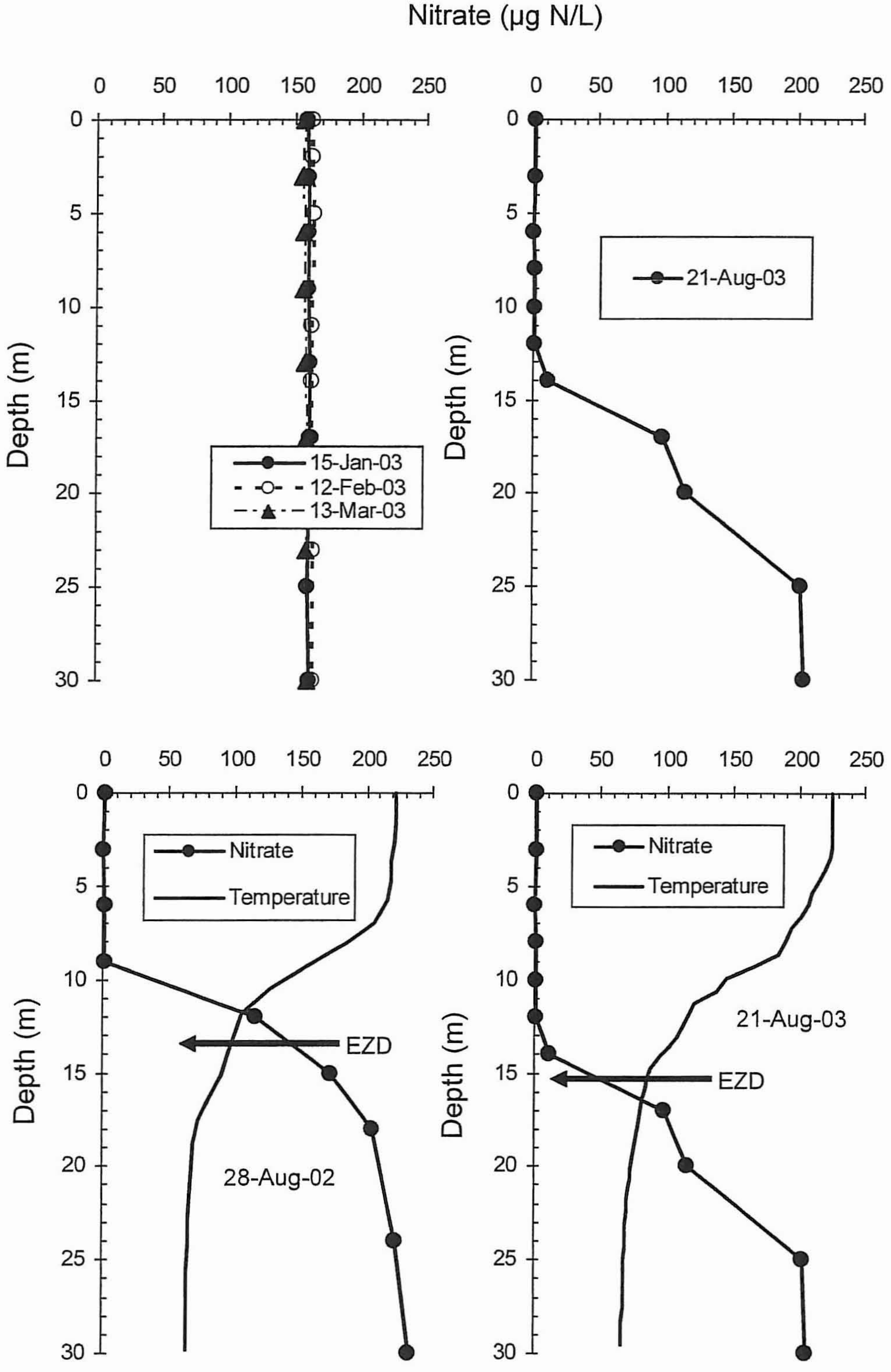


Fig. 17. Upper two plots are nitrate profiles obtained during 2003. The lower plots are August profiles of nitrate and temperature from 2002 and 2003. Maximum temperature values on the x-axis are 25°C.

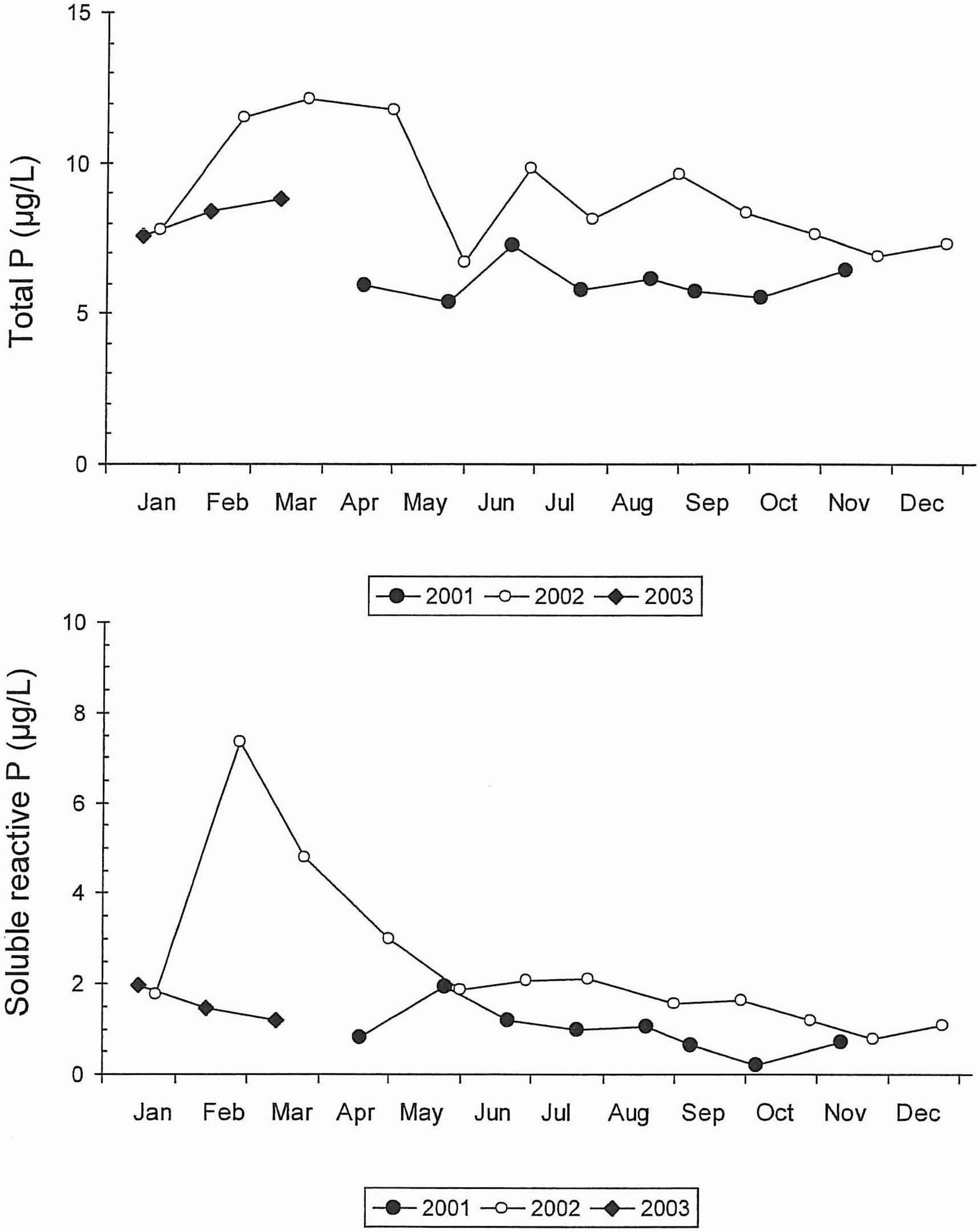


Fig. 18. Variation in euphotic zone concentrations of soluble reactive and total phosphorus.

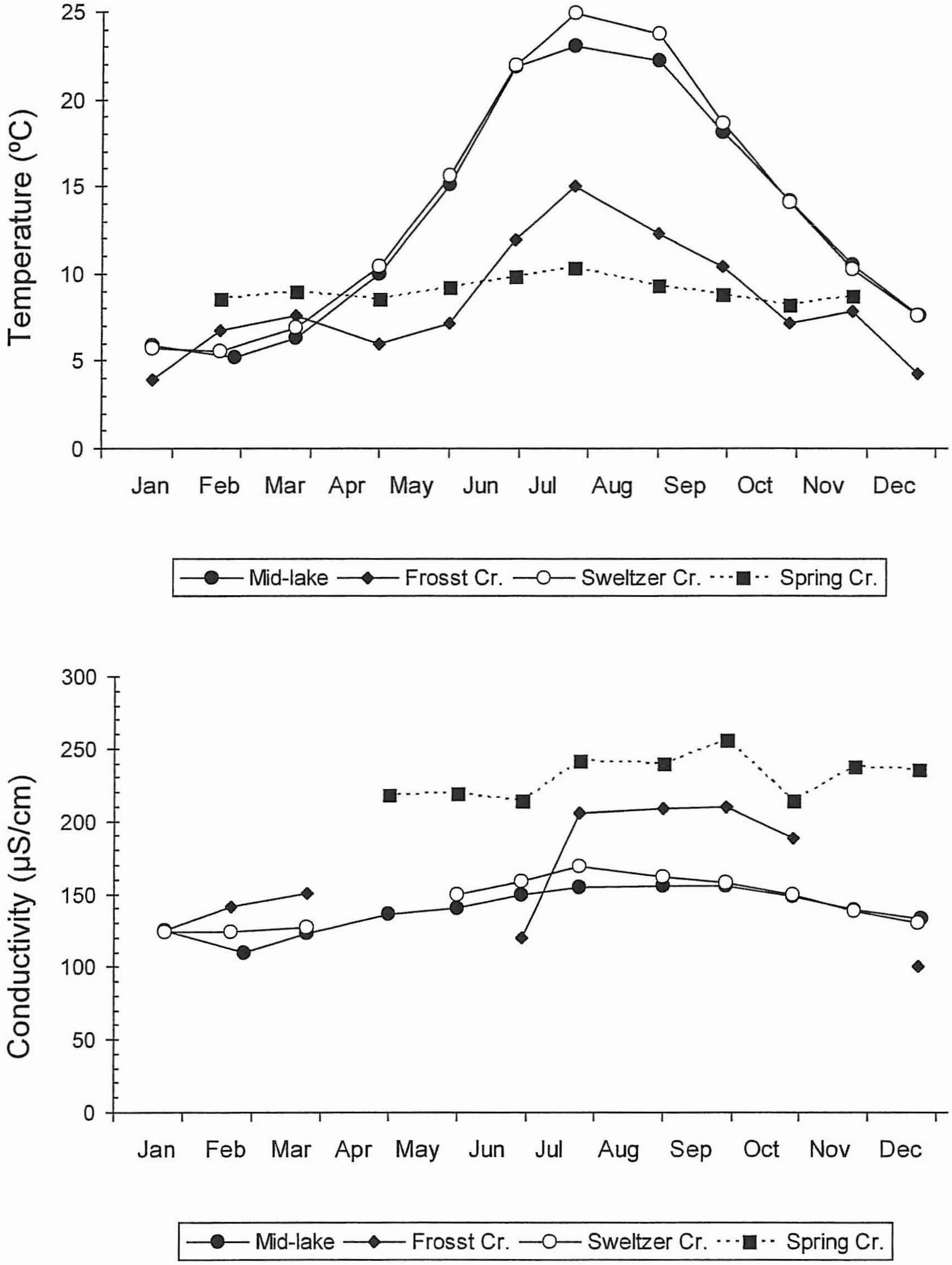


Fig. 19. Monthly variation in temperature and conductivity in Cultus Lake and several of its streams.

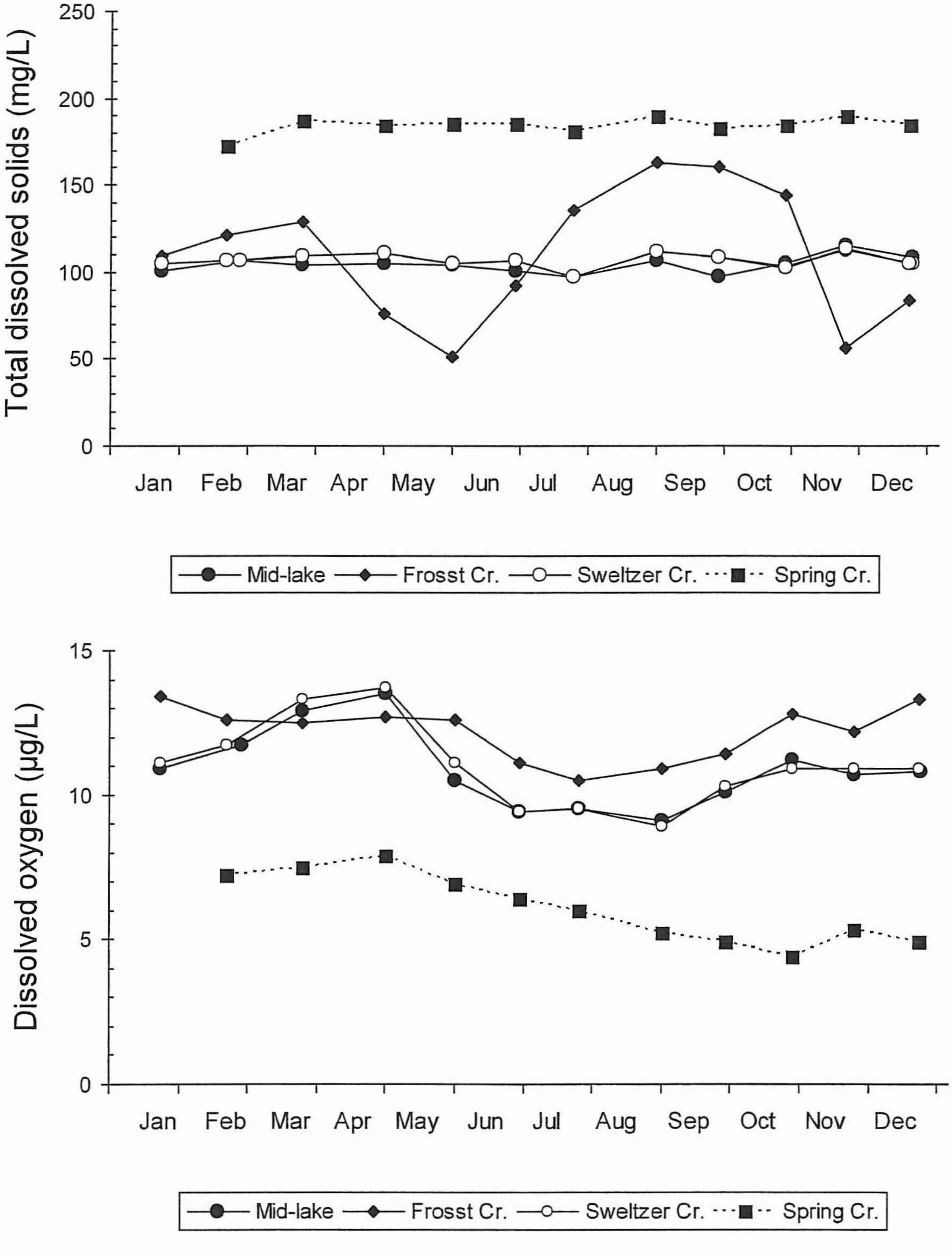


Fig. 20. Monthly variation in concentrations of total dissolved solids and dissolved oxygen in Cultus Lake and several of its streams.

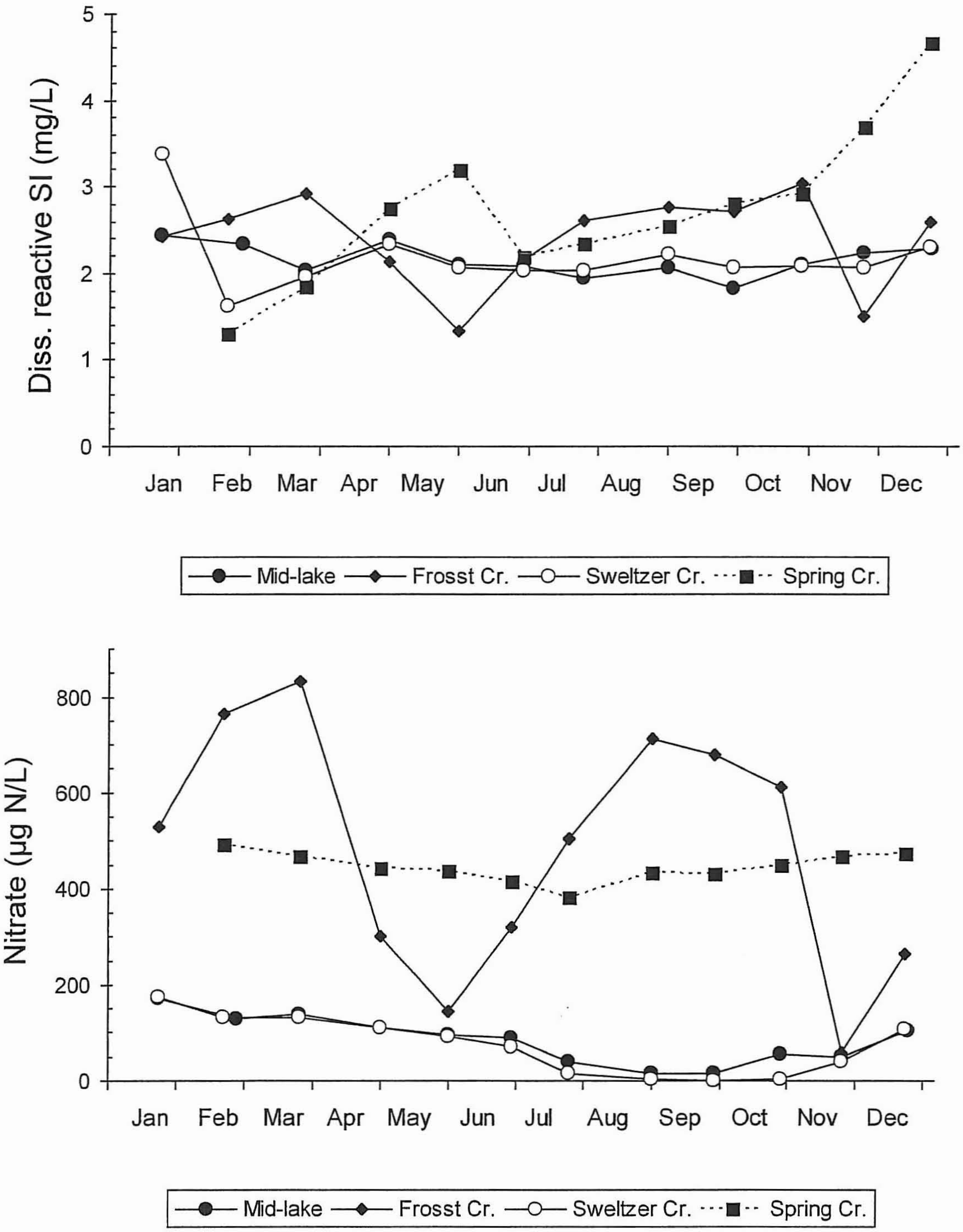


Fig. 21. Monthly variation in concentrations of dissolved reactive silicon and nitrate in Cultus Lake and several of its streams.

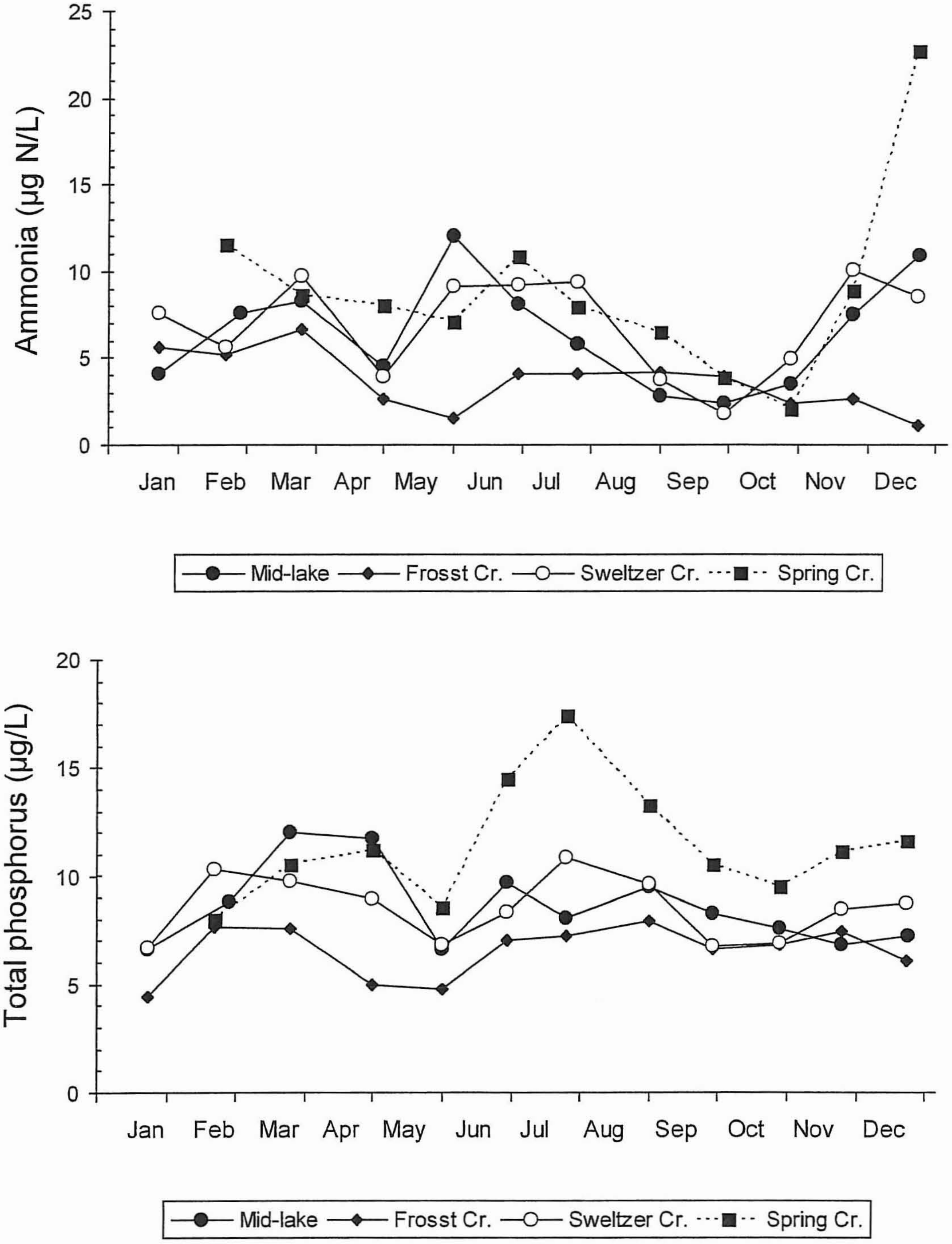


Fig. 22. Monthly variation in ammonia and total phosphorus concentrations in Cultus Lake and several of its streams.

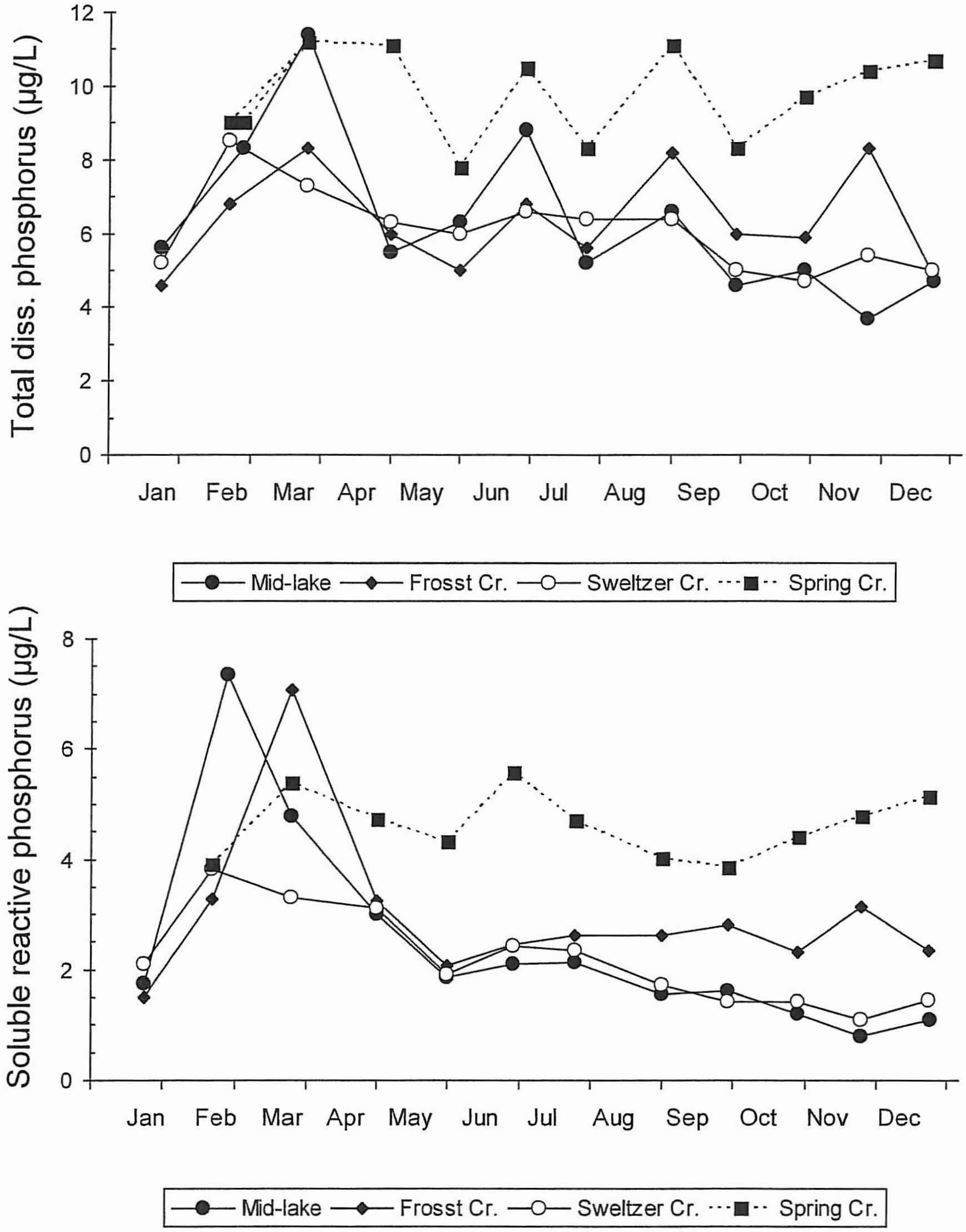


Fig. 23. Monthly variation in concentrations of total dissolved phosphorus and soluble reactive phosphorus in Cultus Lake and several of its streams.

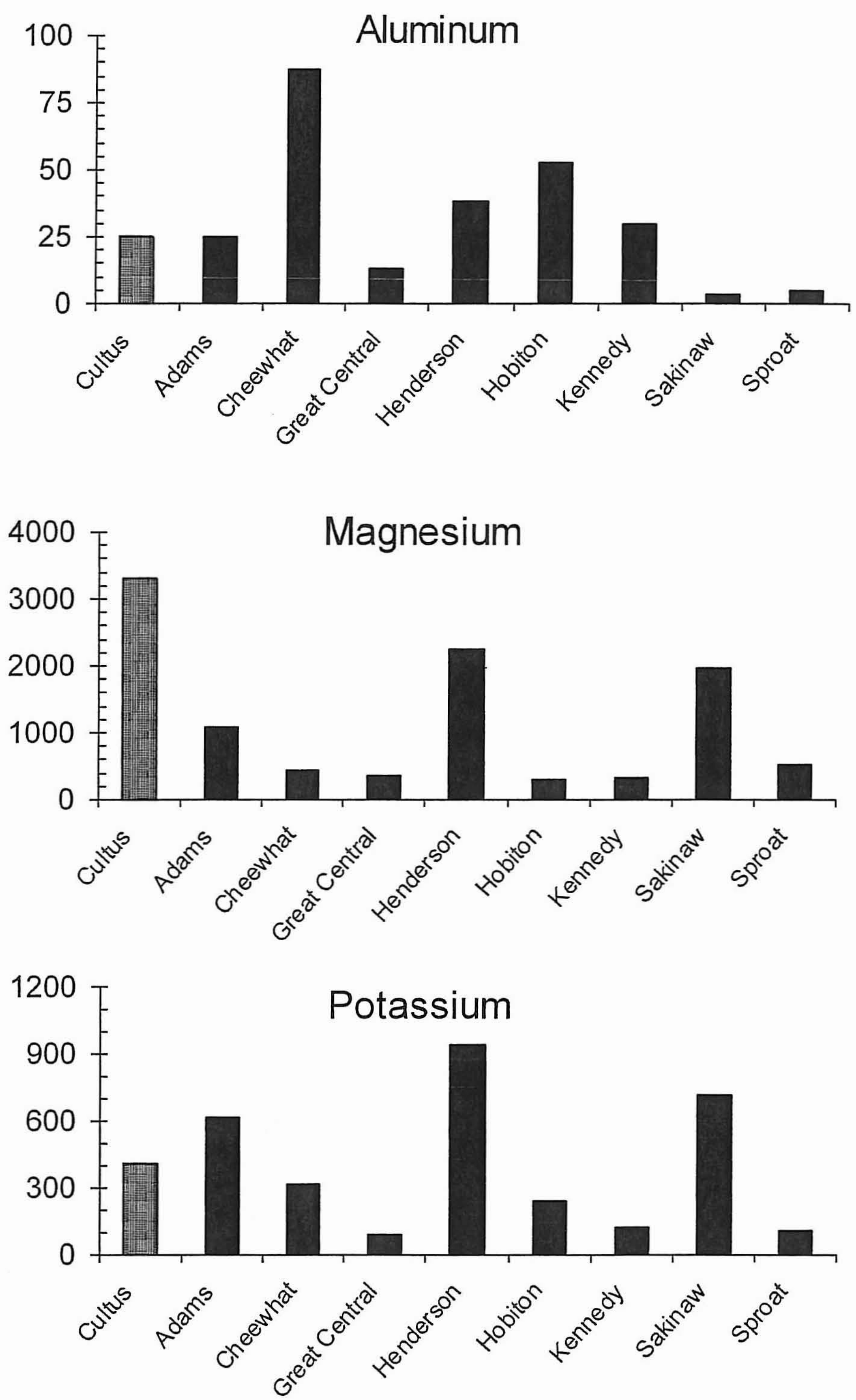


Fig. 24. Variation in metal concentrations in Cultus Lake and a number of other B.C. sockeye lakes.

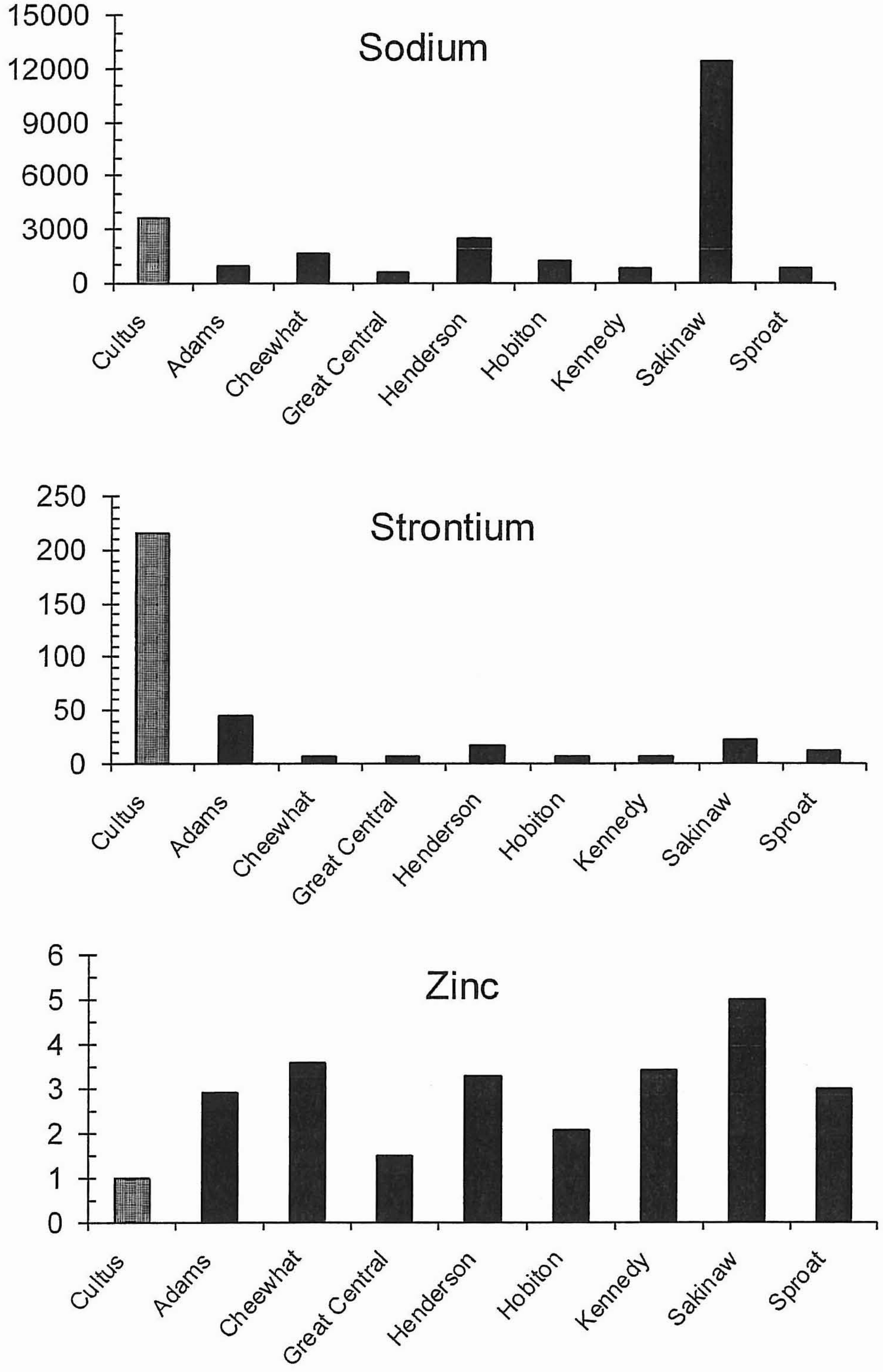


Fig. 25. Variation in metal concentrations in Cultus Lake and a number of other B.C. sockeye lakes.

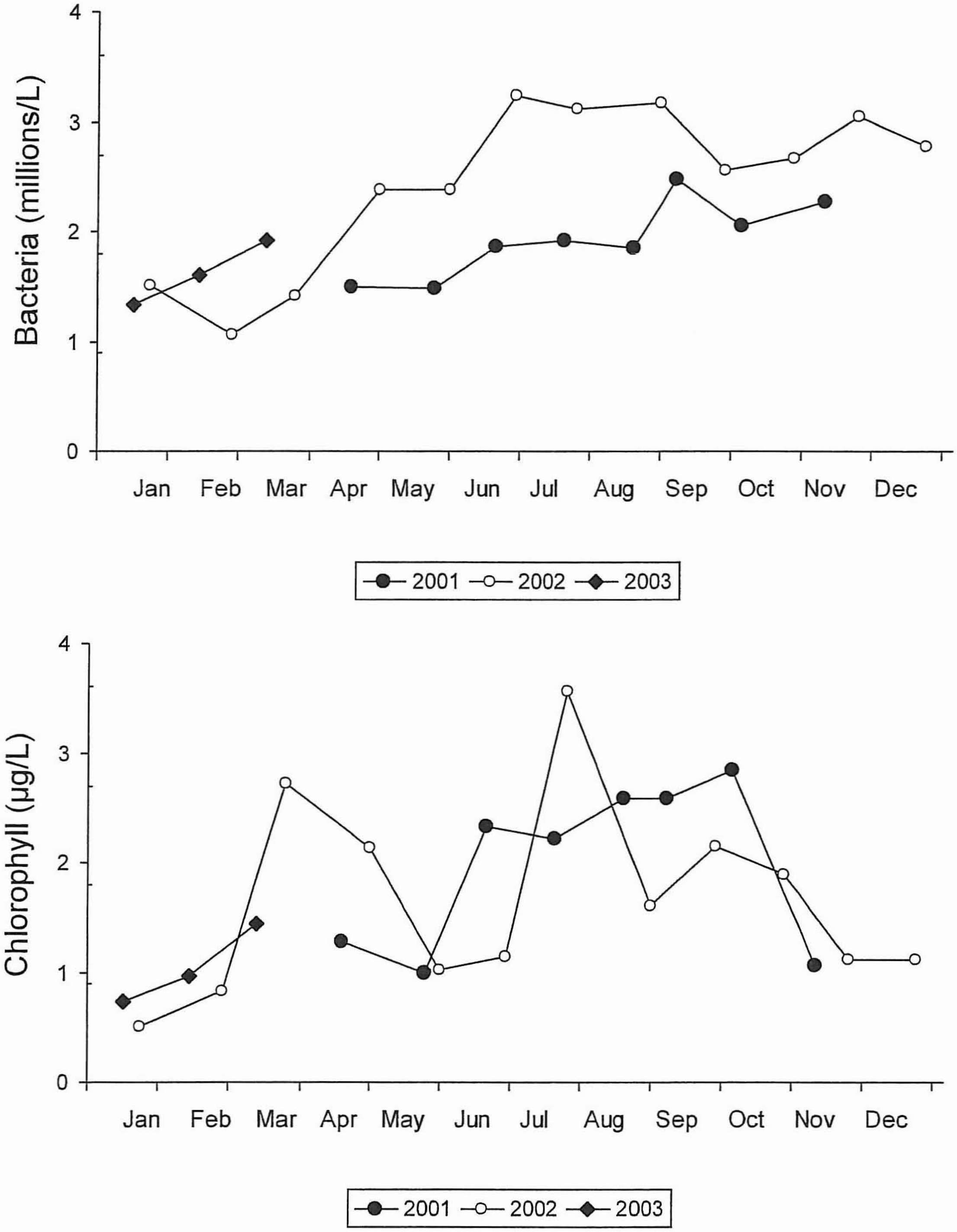


Fig. 26. Monthly variation in bacteria numbers and chlorophyll concentrations in Cultus Lake.

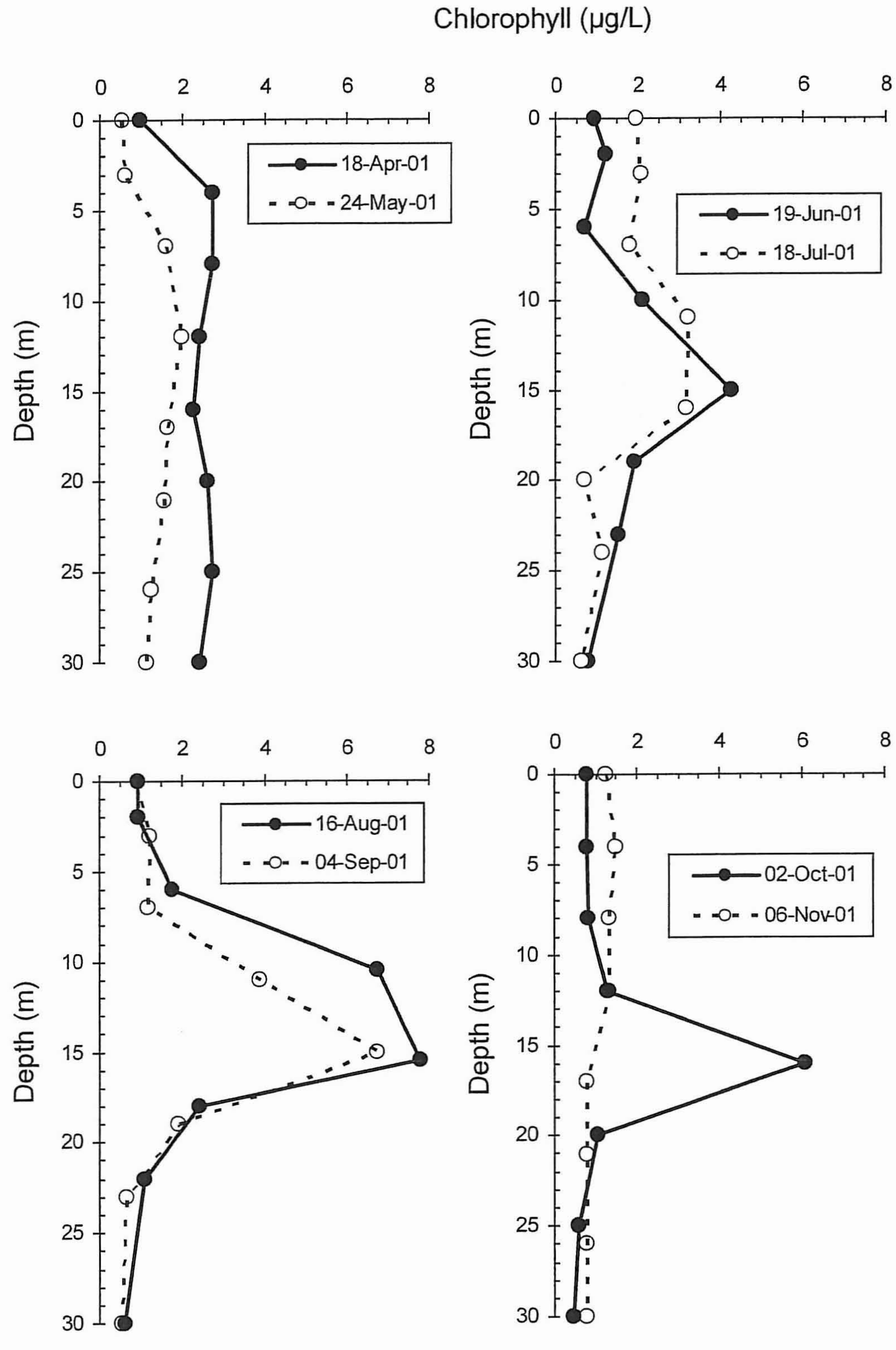


Fig. 27. Chlorophyll profiles obtained during 2001.

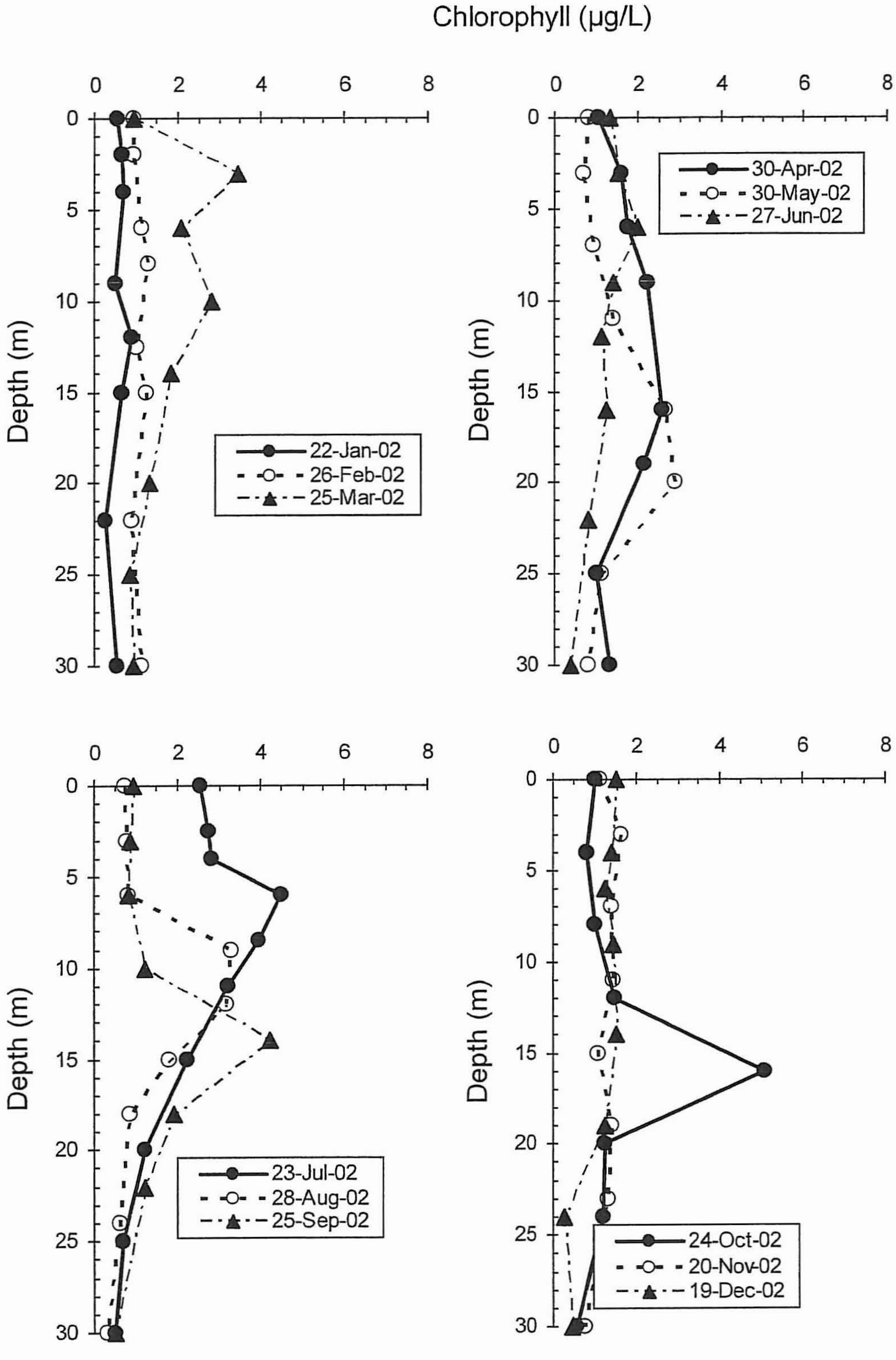


Fig. 28. Chlorophyll profiles obtained during 2002.

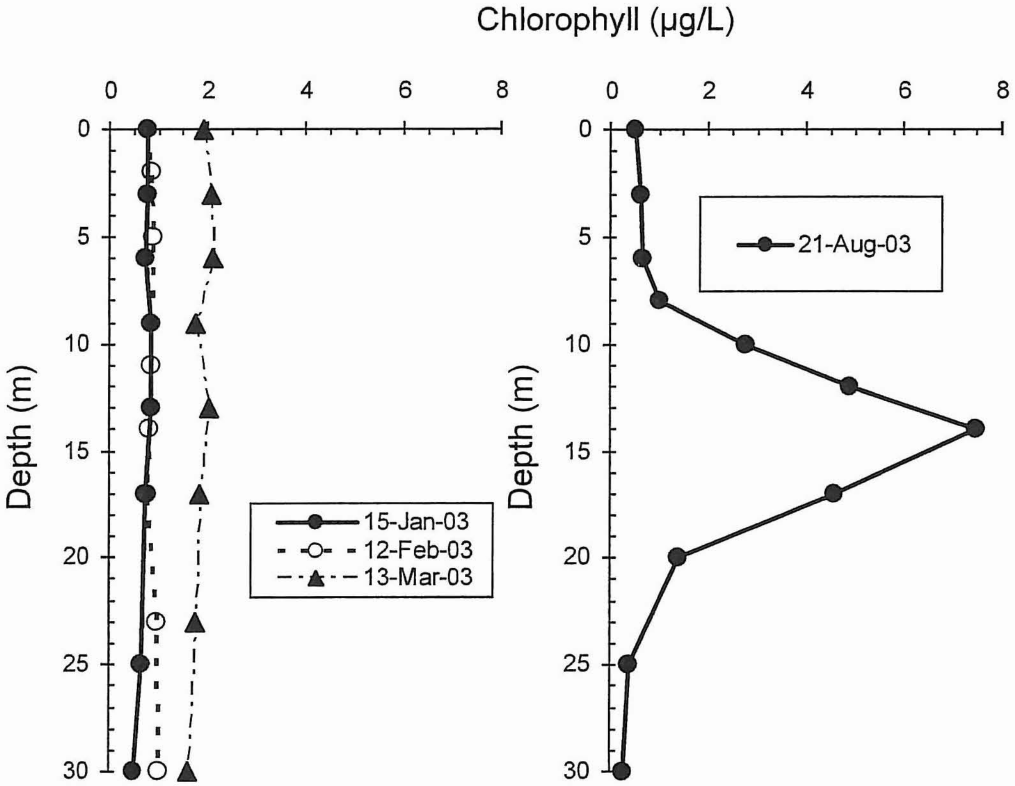


Fig. 29. Chlorophyll profiles obtained during 2003.

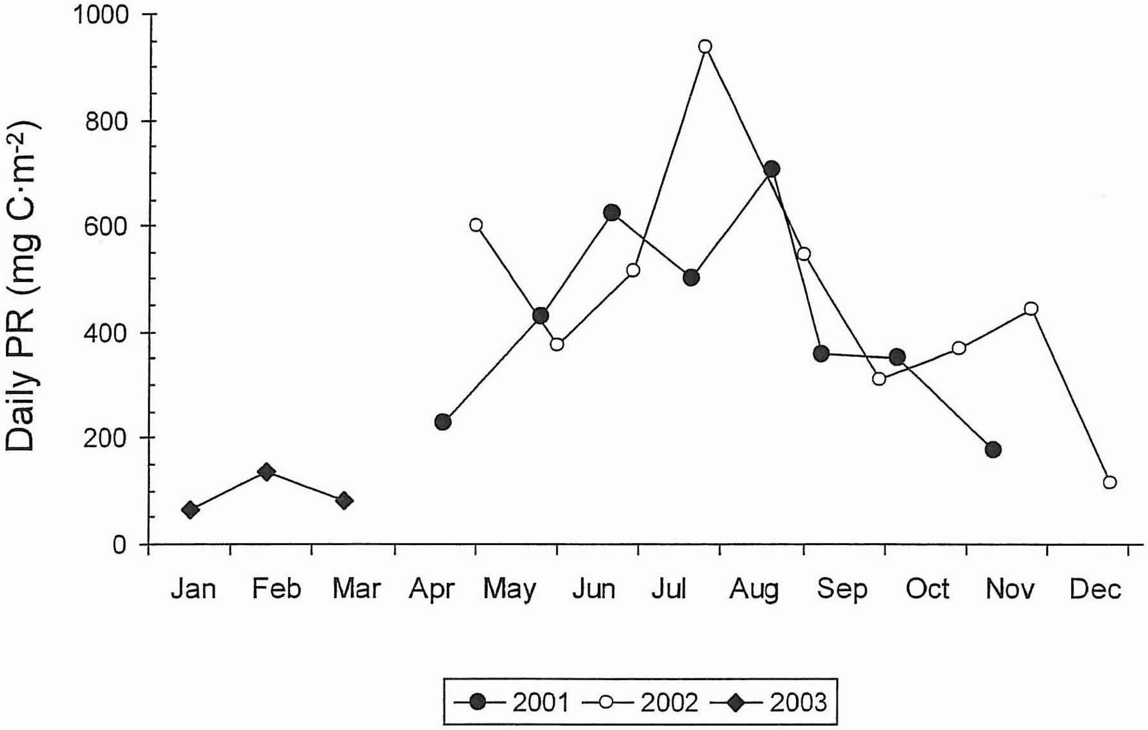


Fig. 30. Variation in daily PR (mg C·m^{-2}·d^{-1}) during the study.

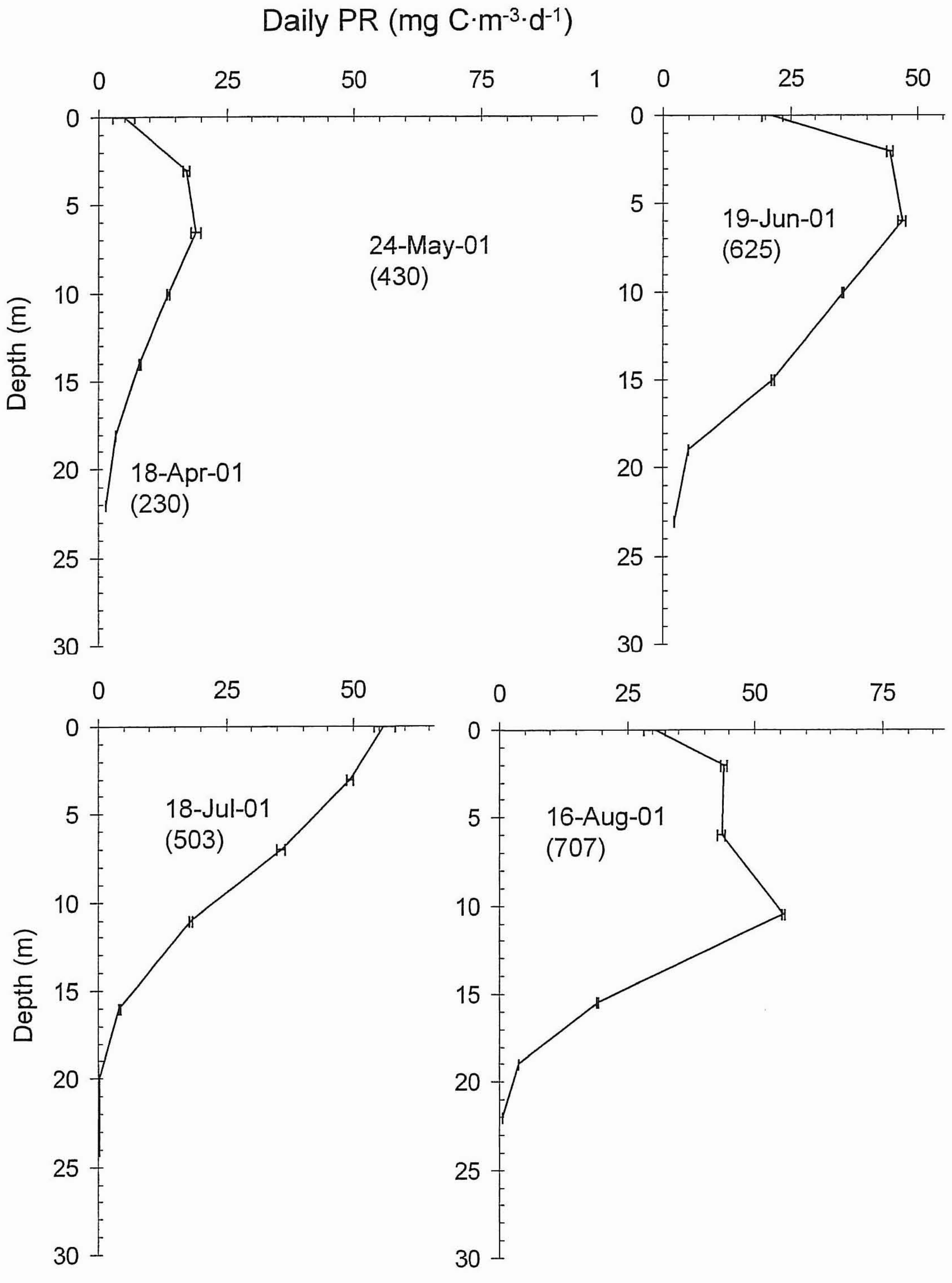


Fig. 31. Vertical profiles of daily PR obtained in 2001. Numbers in brackets are integrated daily values (mg C·m^{-2}·d^{-1}).

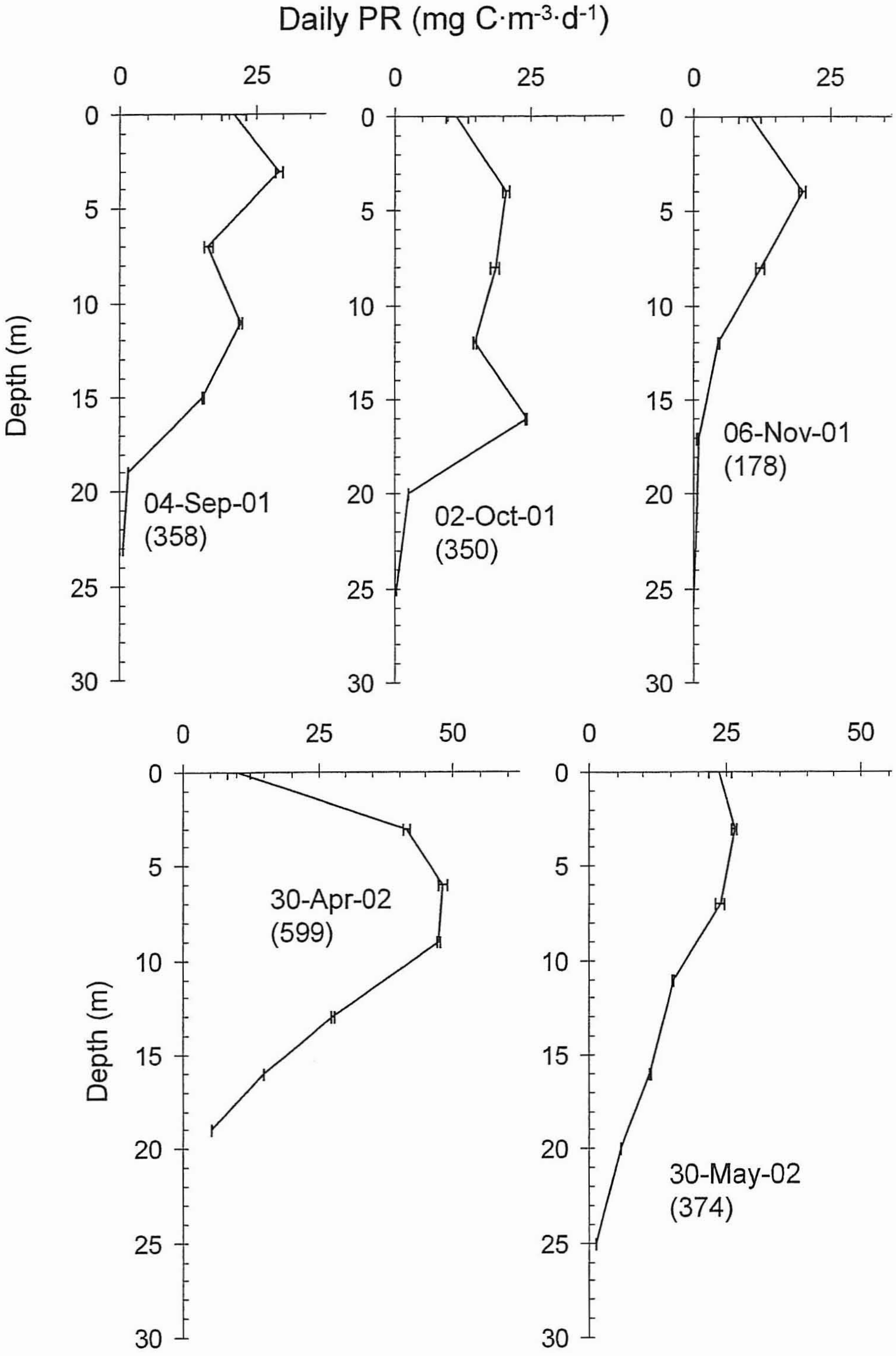


Fig. 32. Vertical profiles of daily PR obtained in 2001 and 2002. Numbers in brackets are integrated daily values (mg C·m^{-2}·d^{-1}).

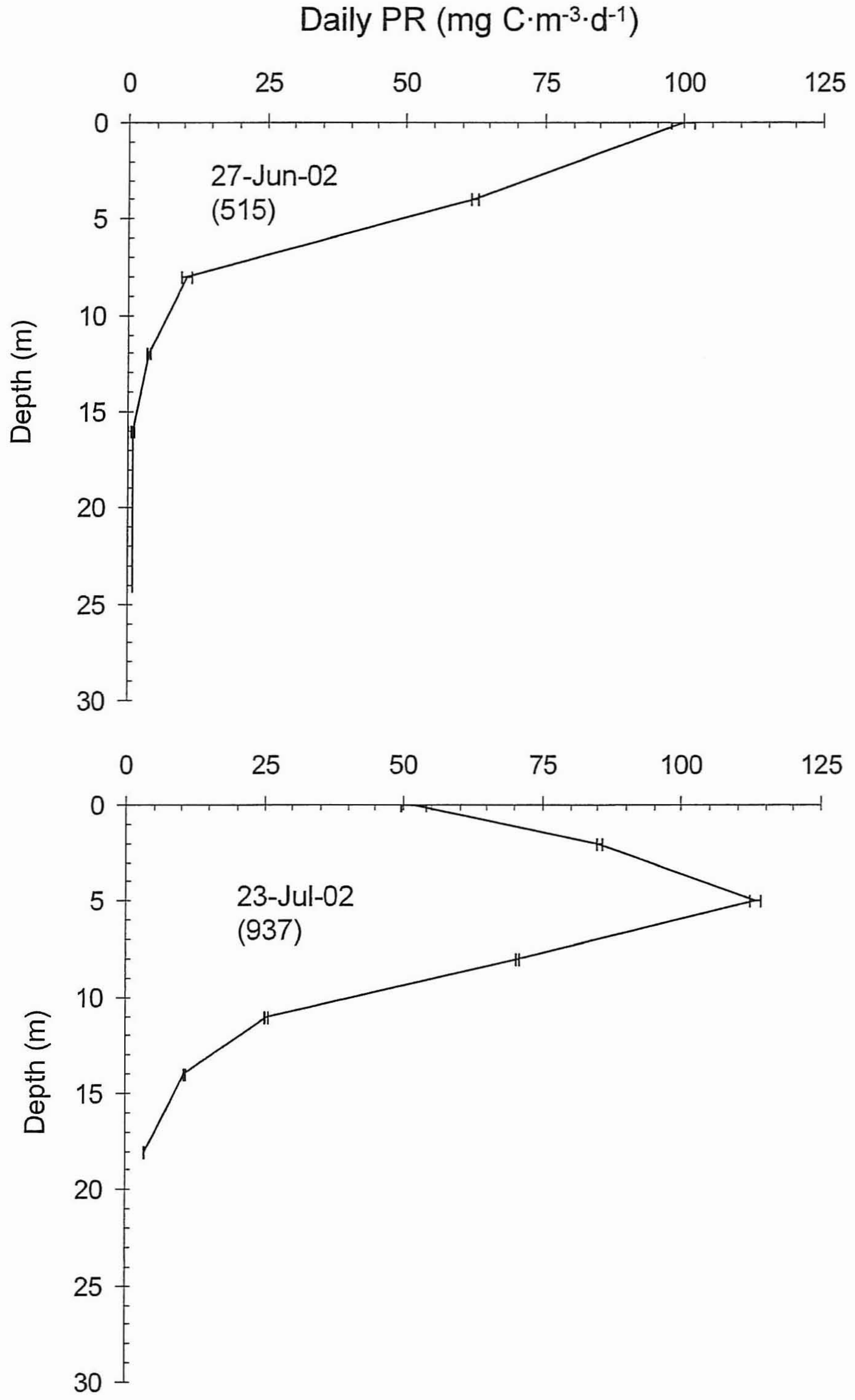


Fig. 33. Vertical profiles of daily PR obtained in 2002. Numbers in brackets are integrated daily values (mg C$\cdot$m$^{-2}\cdot$d^{-1}).

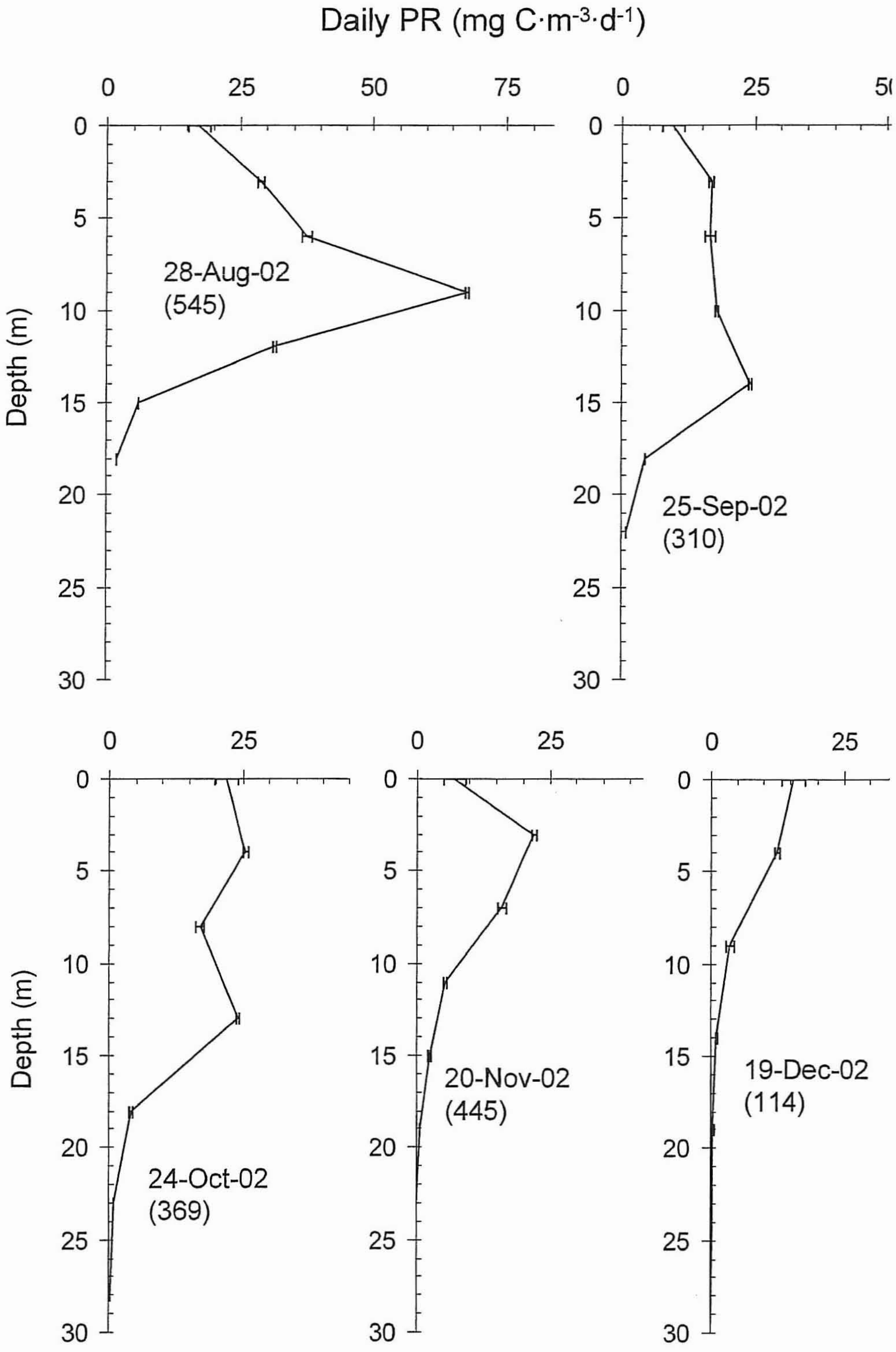


Fig. 34. Vertical profiles of daily PR obtained in 2002. Numbers in brackets are integrated daily values (mg C·m^{-2}·d^{-1}).

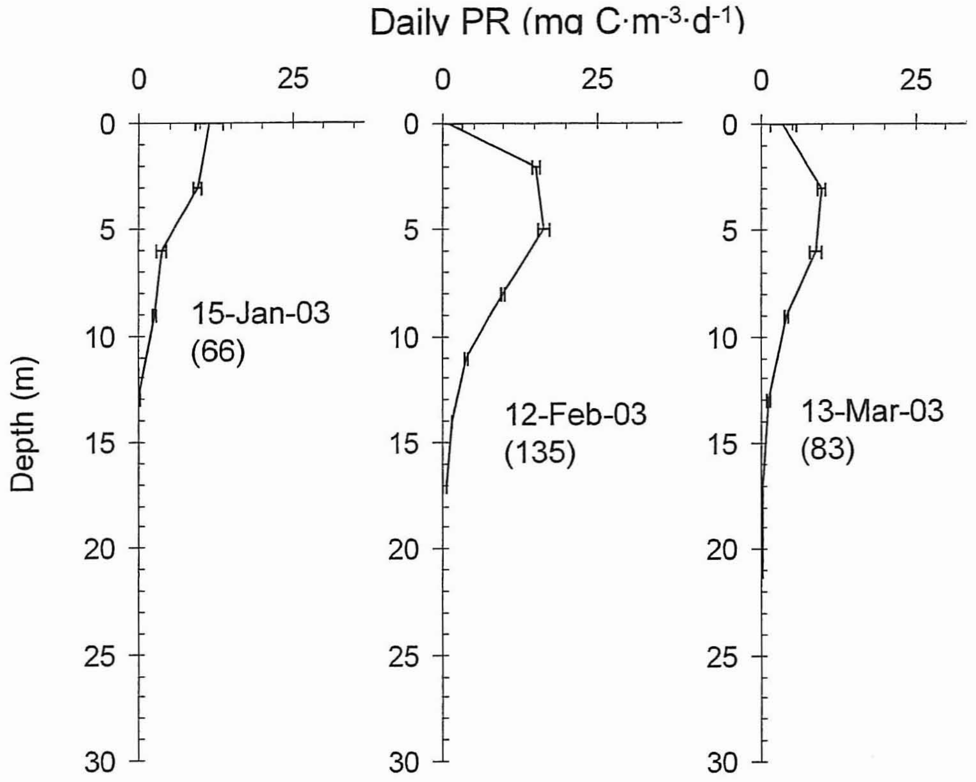


Fig. 35. Vertical profiles of daily PR obtained in 2003. Numbers in brackets are integrated daily values (mg C·m^{-2}·d^{-1}).

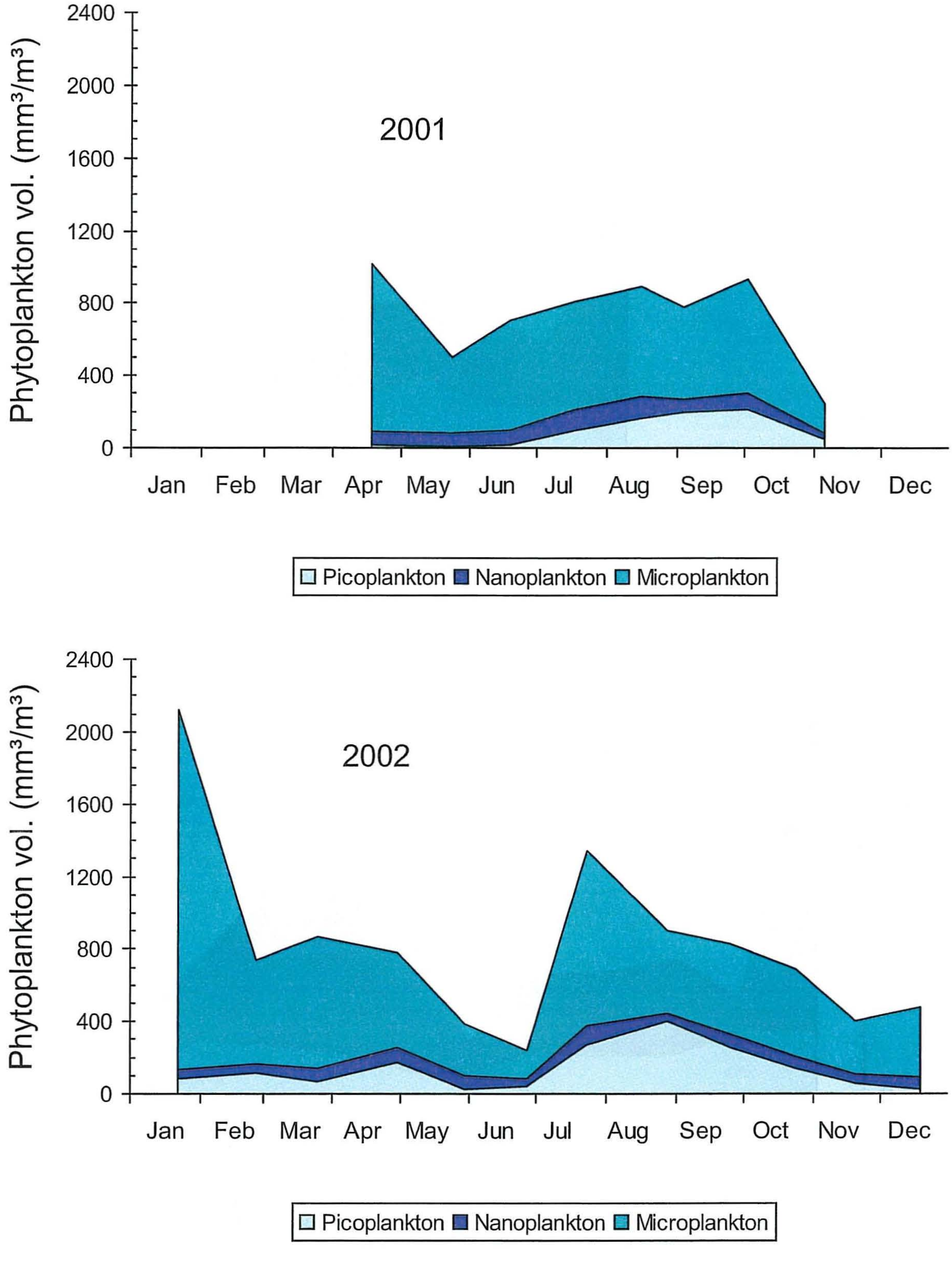


Fig. 36. Seasonal variation in volumes of the picoplankton, nanoplankton, and microplankton size categories.

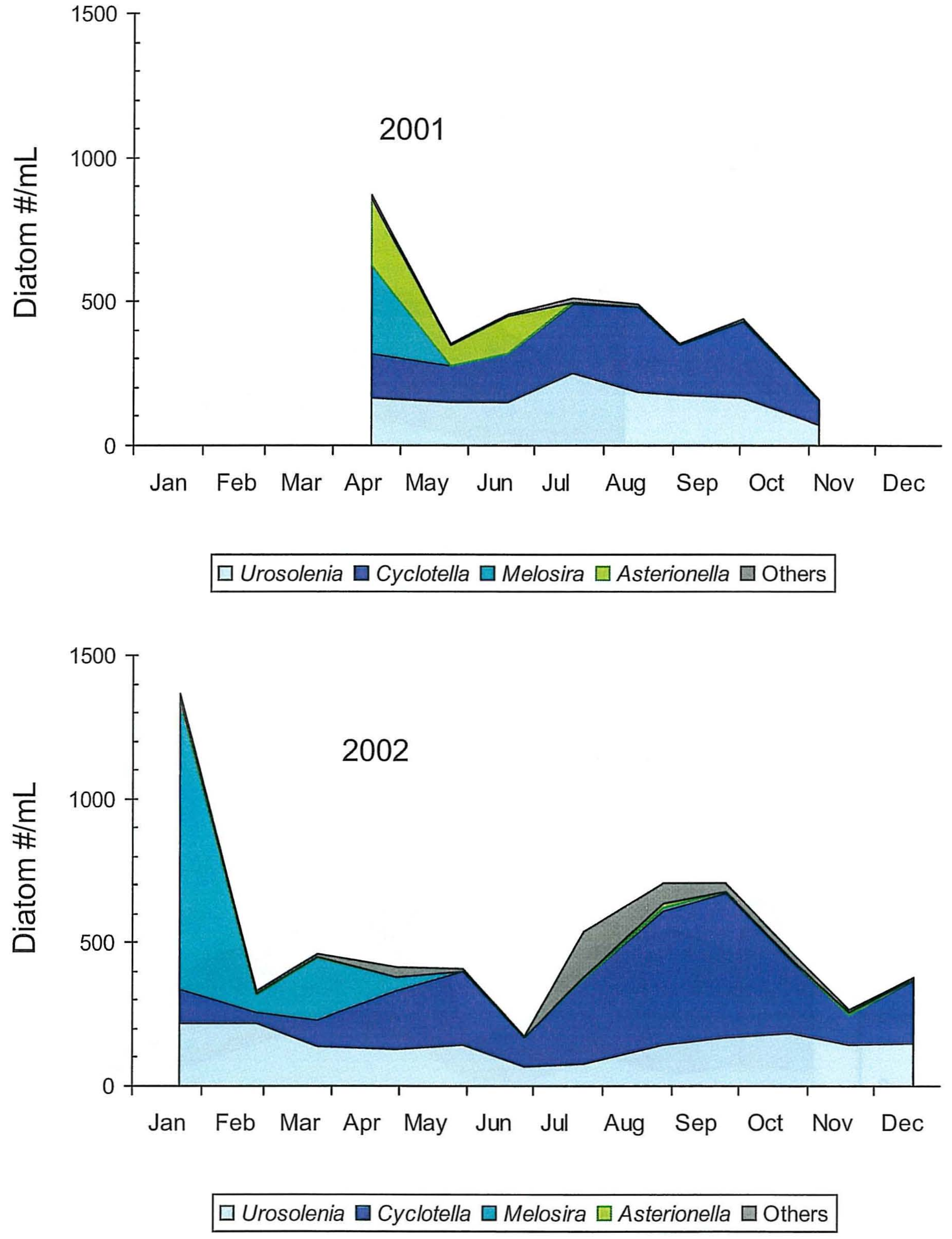


Fig. 37. Seasonal variation in numbers of the major diatom genera.

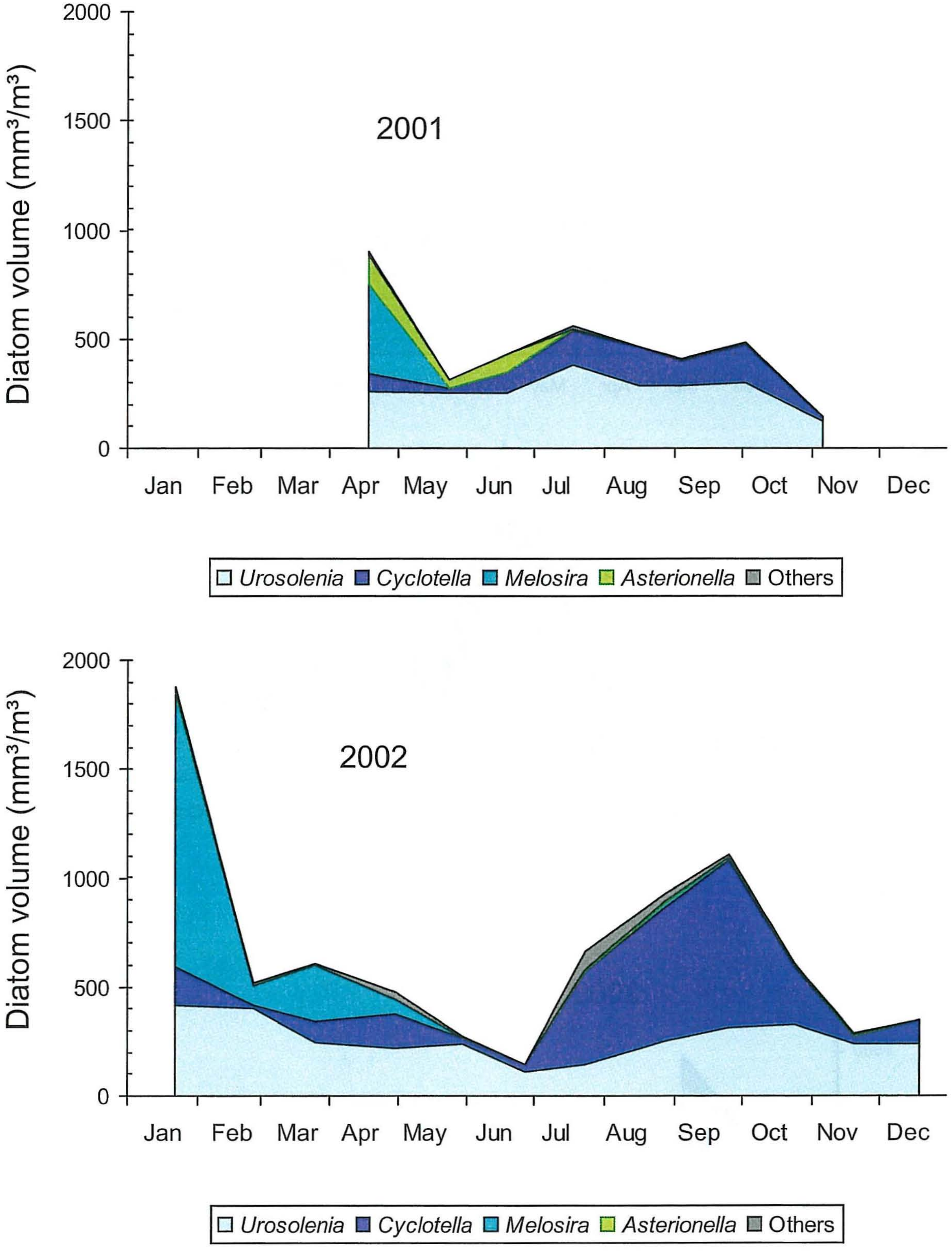


Fig. 38. Seasonal variation in volumes of the major diatom genera.

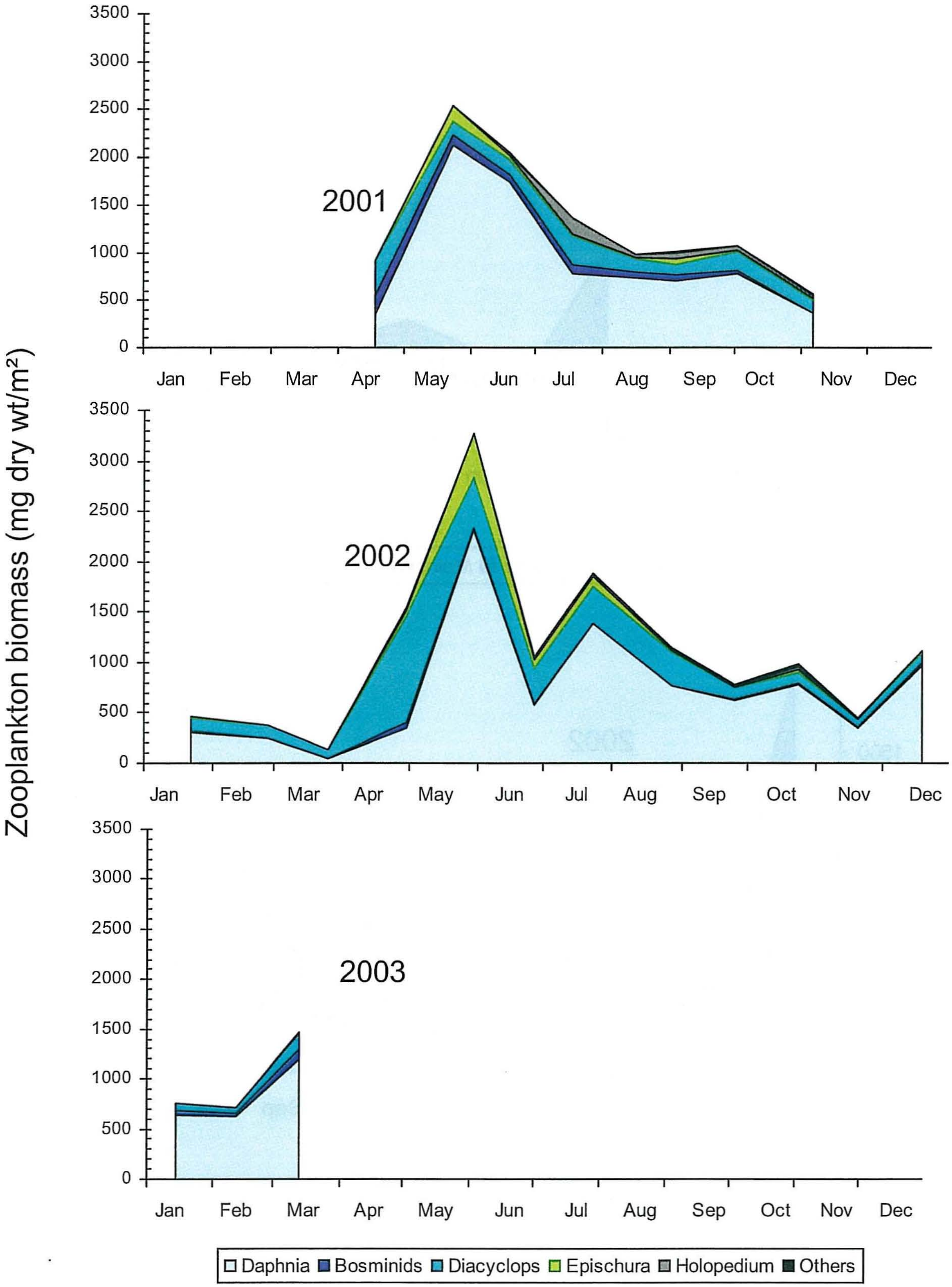


Fig. 39. Seasonal variation in biomass (mg dry wt.m²) of the major zooplankton genera.

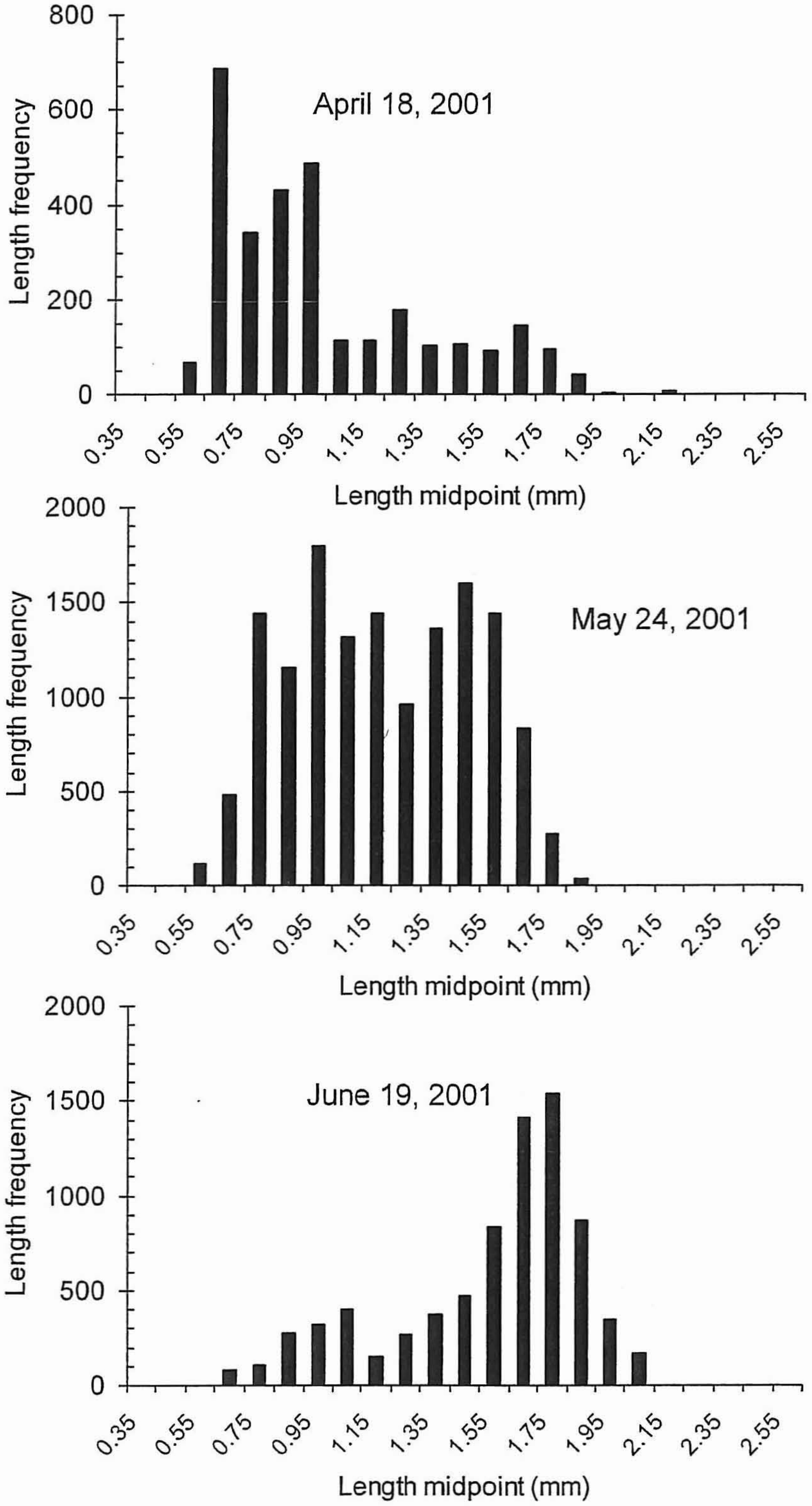


Fig. 40. Length-frequency histograms of *Daphnia* length (mm) from 2001.

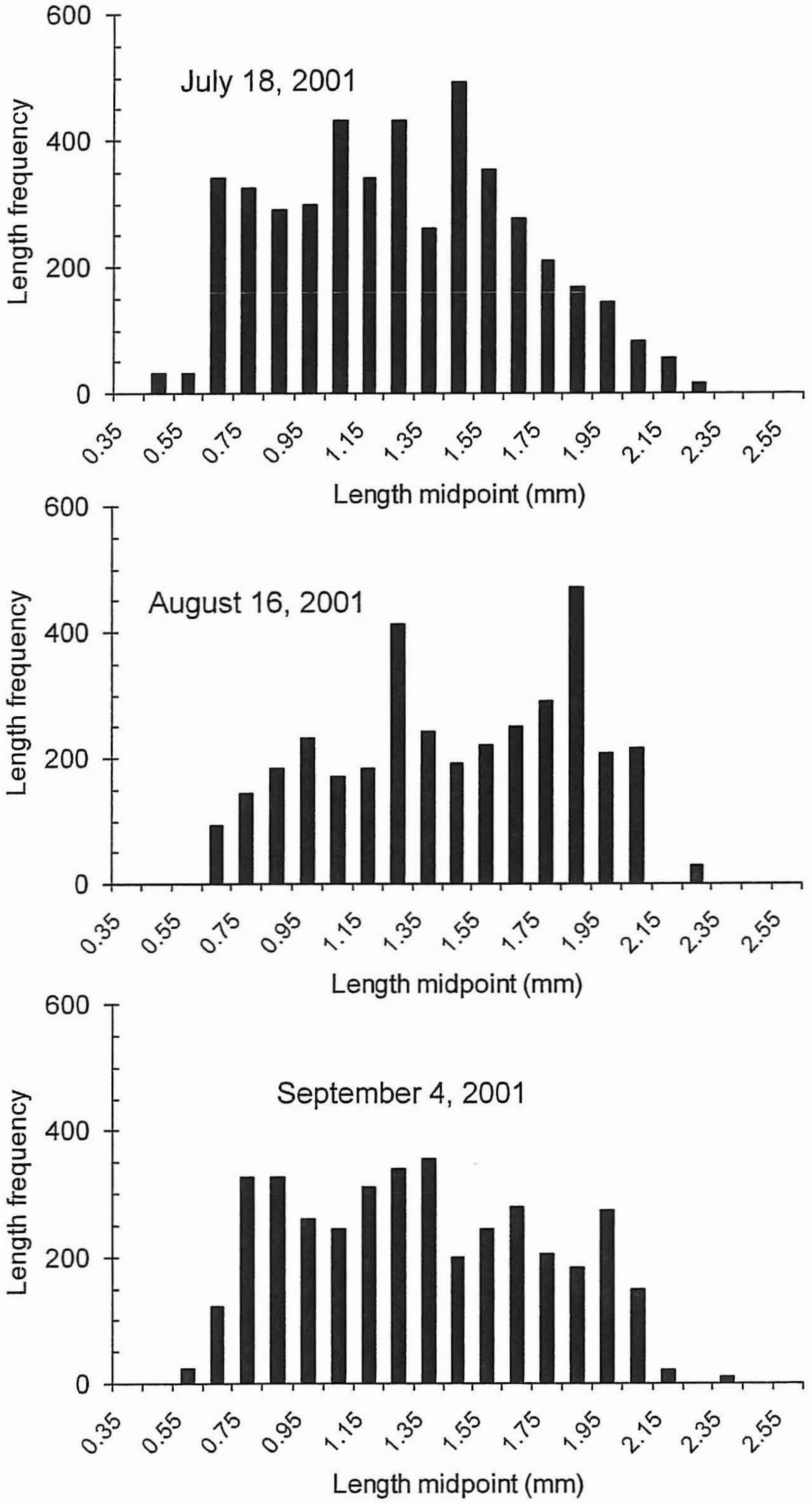


Fig. 41. Length-frequency histograms of *Daphnia* length (mm) from 2001.

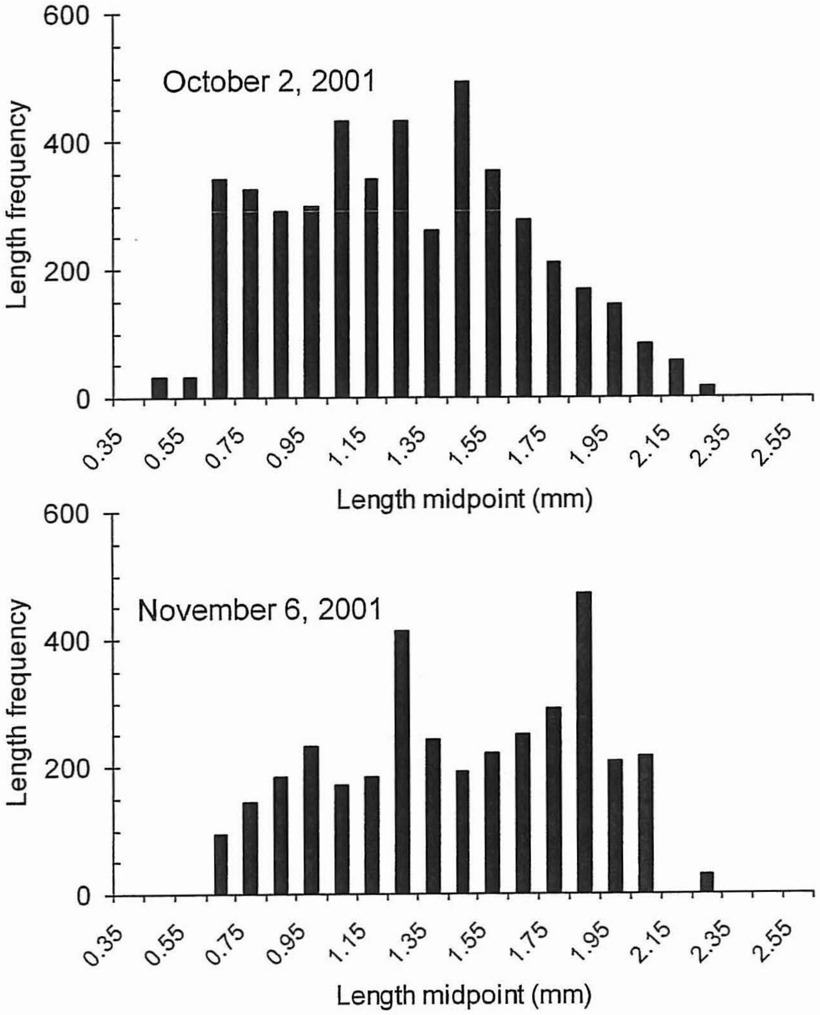


Fig. 42. Length-frequency histograms of *Daphnia* length (mm) from 2001.

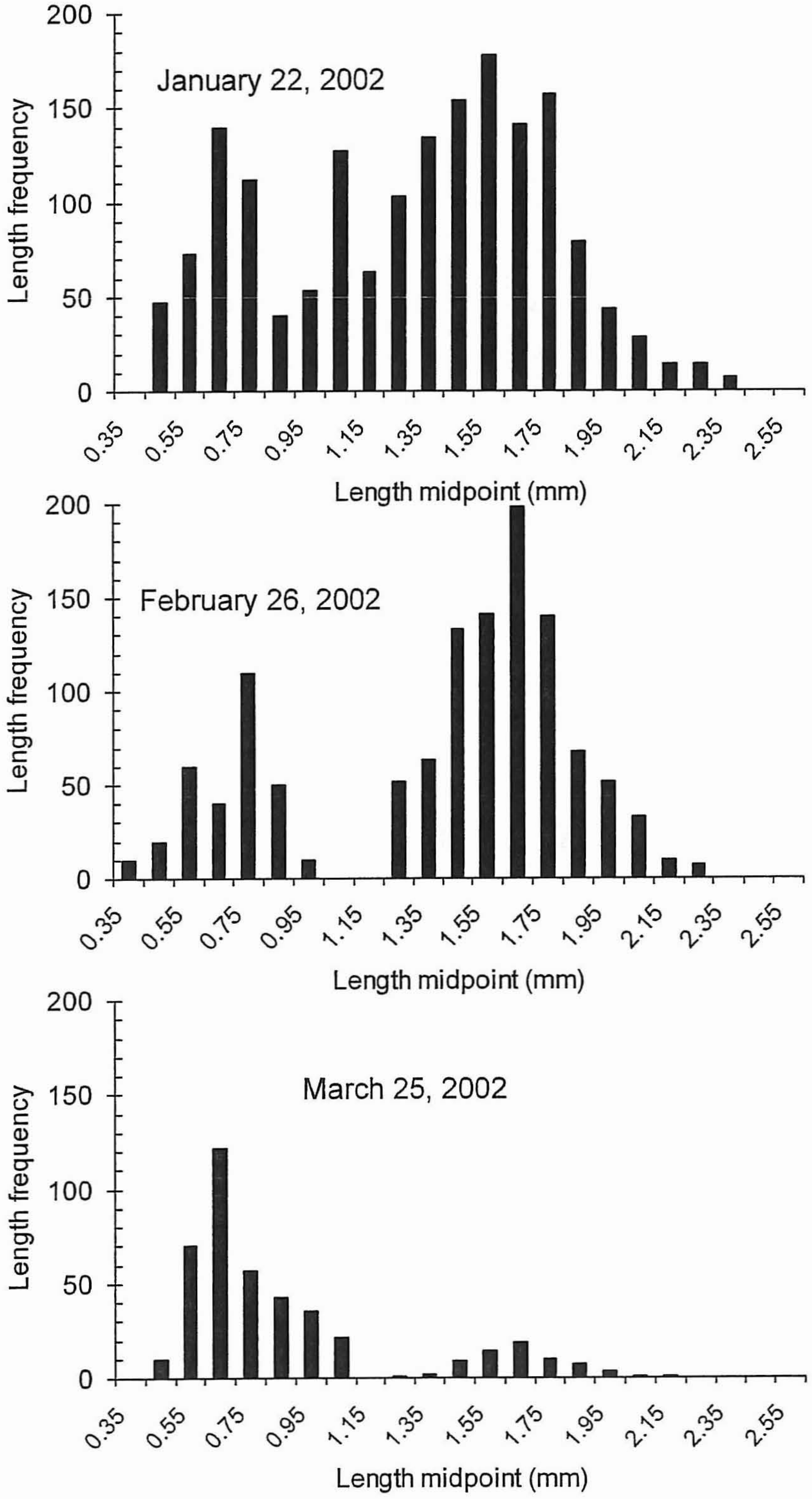


Fig. 43. Length-frequency histograms of *Daphnia* length (mm) from 2002.

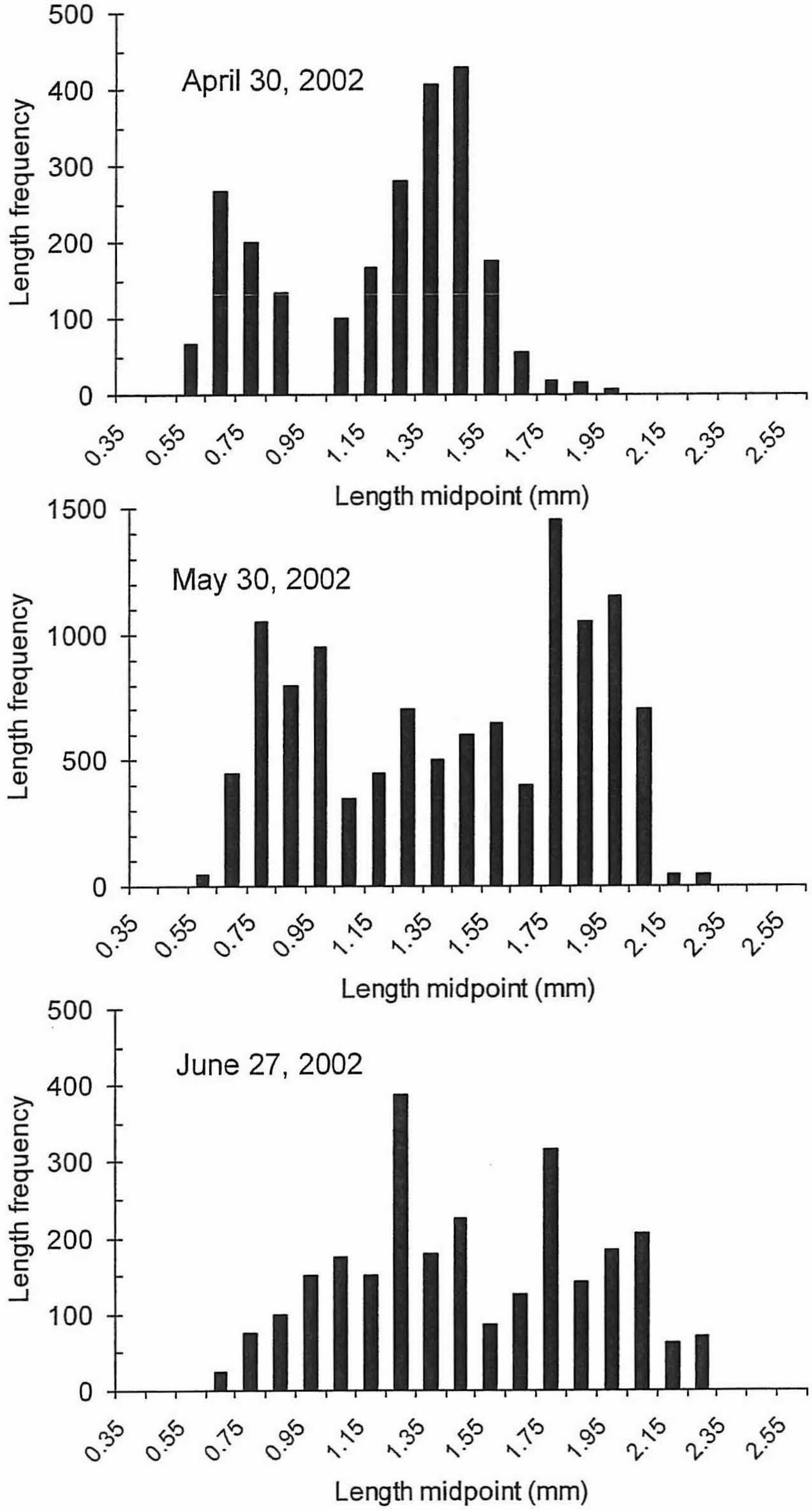


Fig. 44. Length-frequency histograms of *Daphnia* length (mm) from 2002.

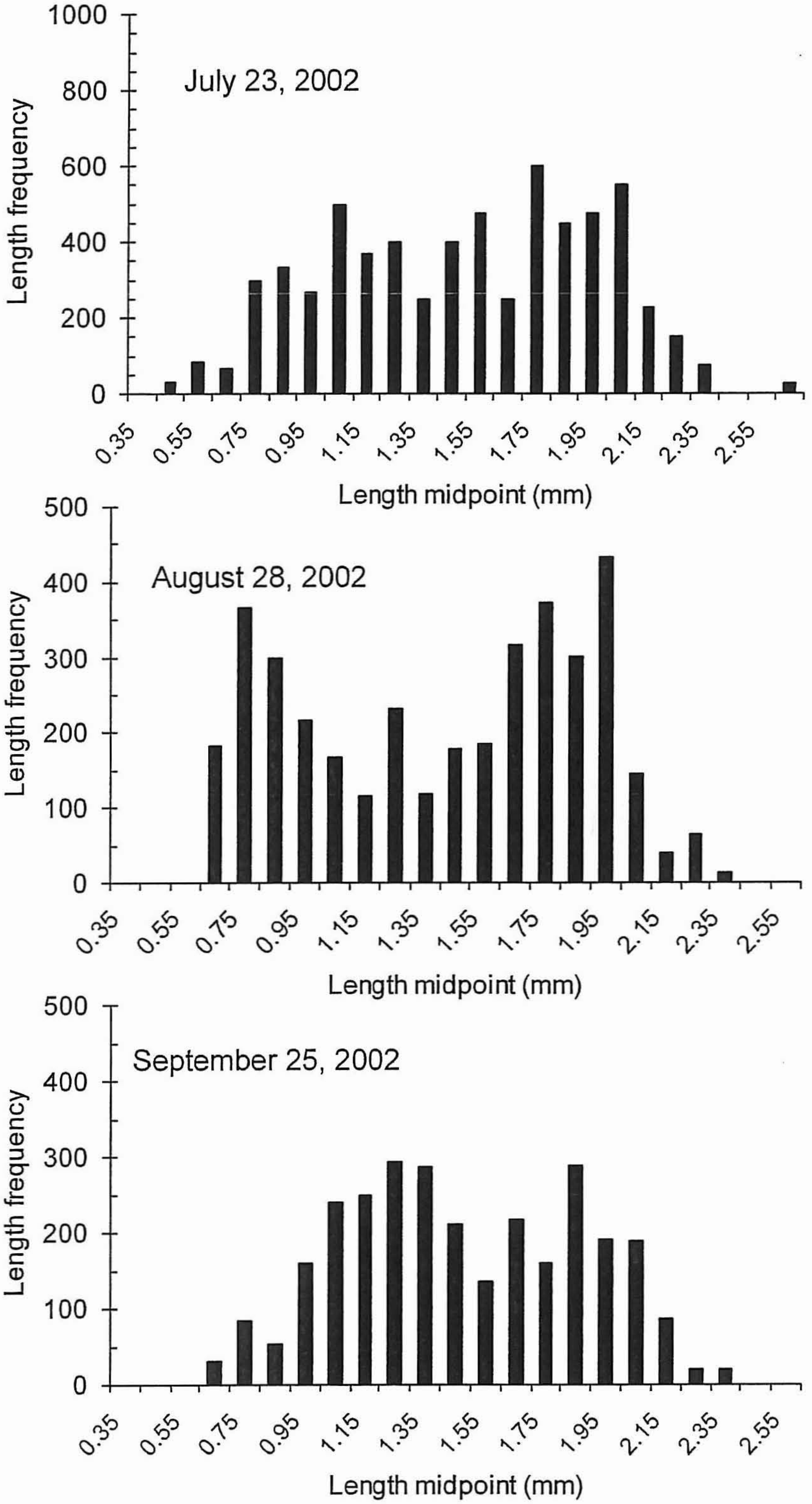


Fig. 45. Length-frequency histograms of *Daphnia* length (mm) from 2002.

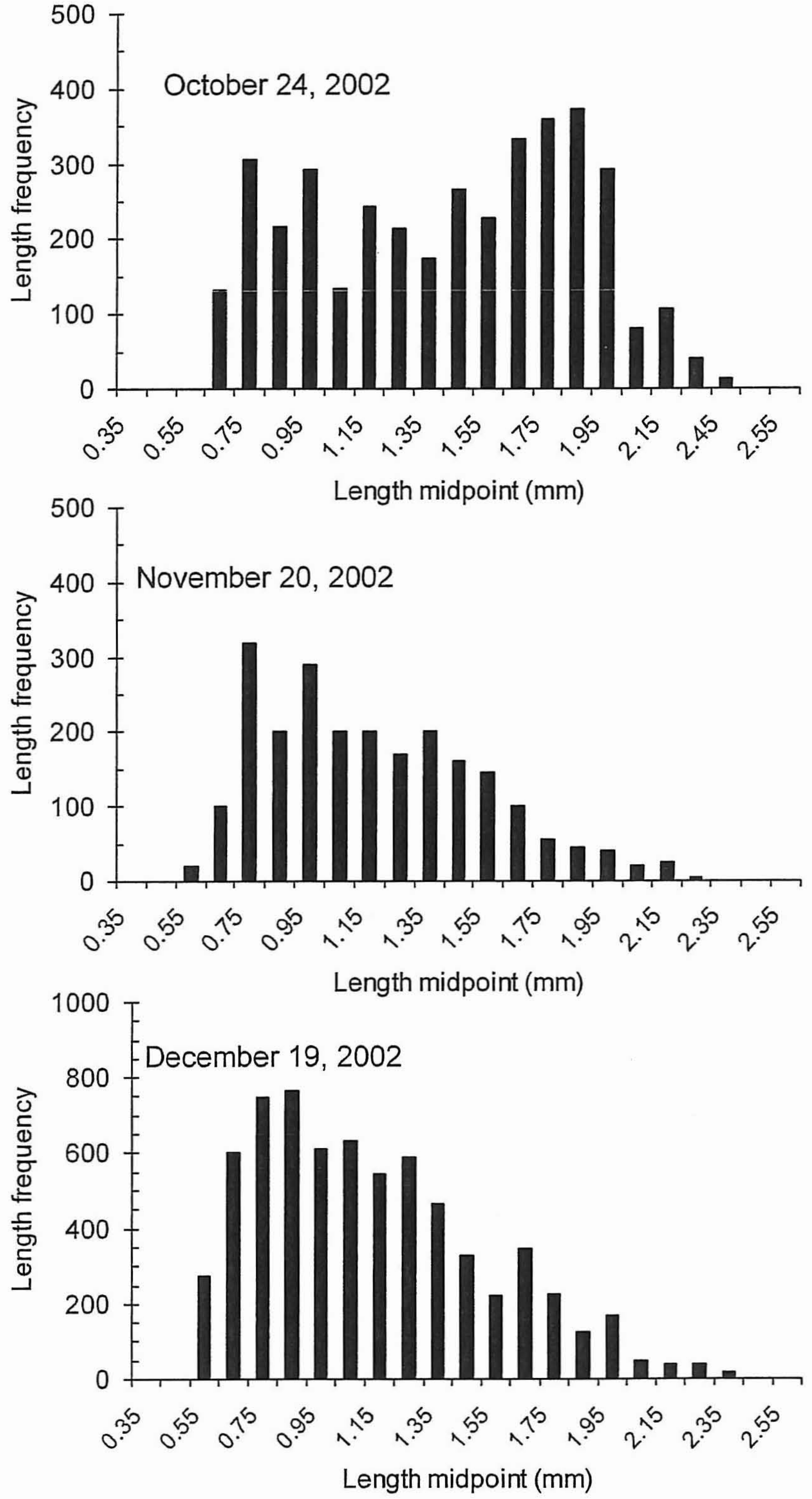


Fig. 46. Length-frequency histograms of *Daphnia* length (mm) from 2002.

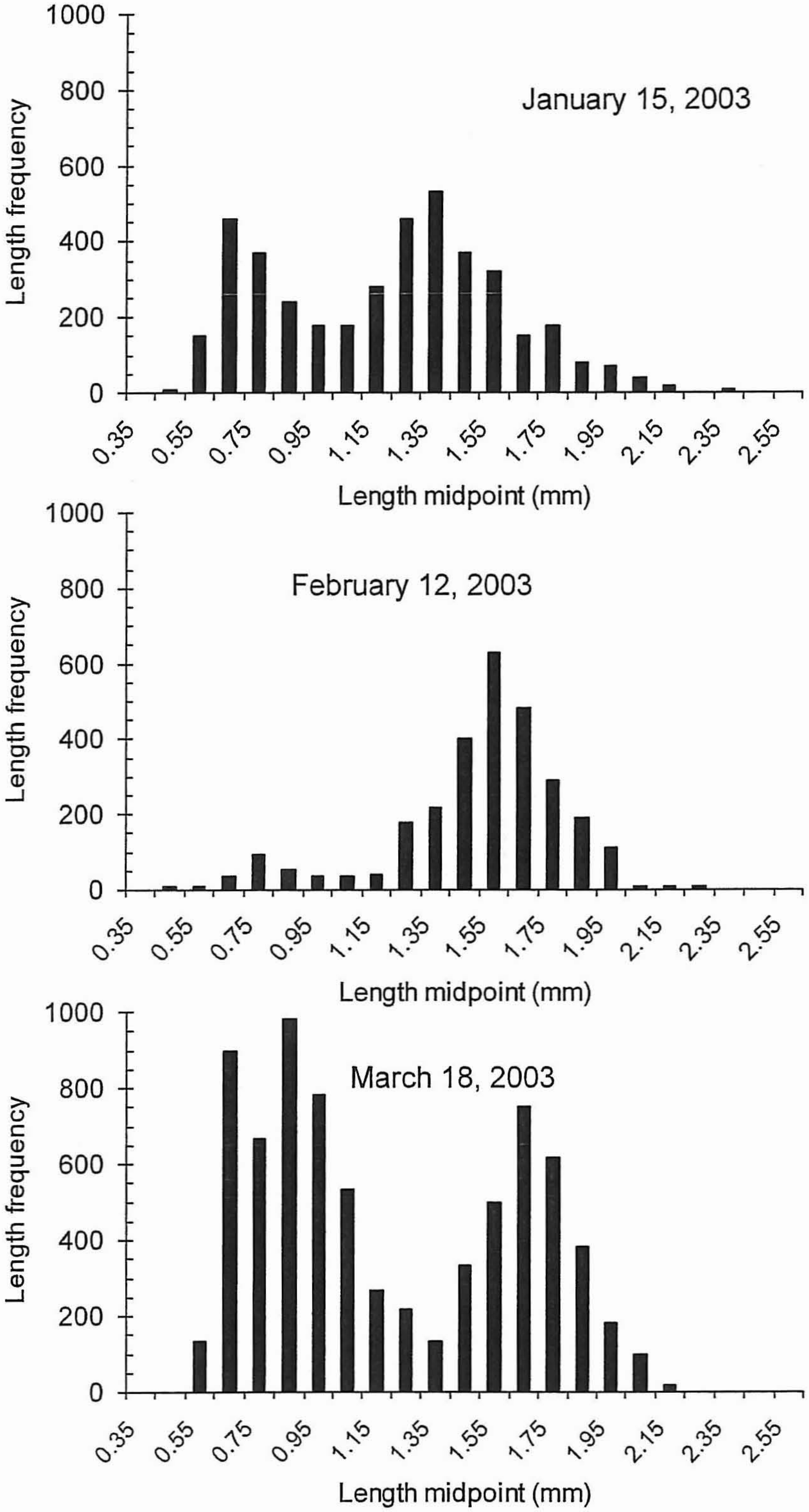


Fig. 47. Length-frequency histograms of *Daphnia* length (mm) from 2003.

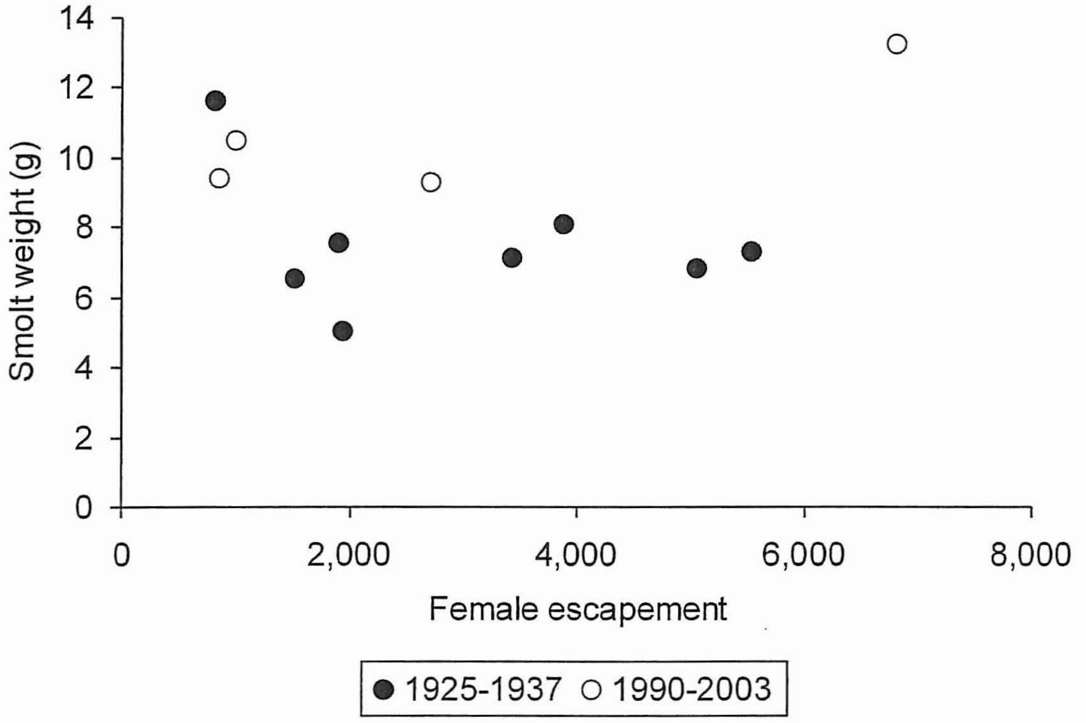


Fig. 48. Smolt weights in recent years and in the 1920's and 1930's from brood years with a similar range in escapements.