Trophic Status and Rearing Capacity of Francois and Fraser Lakes

K.S. Shortreed, J.M.B. Hume and K.F. Morton

Department of Fisheries and Oceans
Science Branch, Pacific Region
Cultus Lake Salmon Research Laboratory
4222 Columbia Valley Highway
Cultus Lake, British Columbia V2R 5B6

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TROPHIC STATUS AND REARING CAPACITY OF FRANCOIS AND FRASER LAKES

by

K. S. Shortreed, J. M. B. Hume, and K. F. Morton

Department of Fisheries and Oceans
Cultus Lake Salmon Research Laboratory
4222 Columbia Valley Highway
Cultus Lake, B. C. V2R 5B6

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ABSTRACT

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This 2-year study was the first on these lakes which systematically examined lake physics, chemistry, all trophic levels important to juvenile sockeye, and juvenile sockeye numbers, diet, and mortality. These data enabled us to document the trophic status of the lakes, the current state of their plankton and juvenile sockeye populations, and to estimate the lakes' rearing capacities for juvenile sockeye. Based on spring overturn total phosphorus concentrations, Francois Lake is in the upper range of oligotrophy and Fraser Lake is mesotrophic but approaching eutrophy. Seasonal average photosynthetic rates (PR) in Francois Lake were 163 mg $C \cdot m^{-2} \cdot d^{-1}$, very similar to those observed in Shuswap Lake (171) and much higher than those seen in Chilko (79) or Quesnel (102) lakes. PR in Fraser Lake (332 mg $C \cdot m^{-2} \cdot d^{-1}$) was higher than seen in any other Fraser system sockeye nursery lake. Juvenile sockeye data indicate that both lakes are excellent rearing areas and are currently under-utilized by juvenile sockeye. We found Fraser Lake to be below its rearing capacity at spawner densities of 40 effective females/ha, densities which considerably exceed rearing capacity in Quesnel or Shuswap lakes. Given sufficient spawning ground capacity, we estimate that an escapement of 1.3 million would maximize smolt production from Francois Lake. However, this is about 26 times greater than current estimates of spawning capacity. We estimate the optimum escapement to Fraser Lake to be 0.5 million, only slightly more than the estimated spawning ground capacity of 0.43 million. Estimated smolt output from the lakes at rearing capacity is 72 million for Francois Lake and 27 million for Fraser Lake. Rebuilding Fraser Lake sockeye stocks can be accomplished solely by management (i.e. increased escapements), but for Francois Lake's rearing capacity to be fully utilized, fry recruitment must be increased far beyond what the current spawning grounds can produce.

RÉSUMÉ

Shortreed, K.S., J.M.B. Hume, and K.F. Morton. 1996. Trophic status and rearing capacity of Francois and Fraser lakes. Can. Tech. Rep. Fish. Aquat. Sci.2151: 58 p.

Cette étude d'une durée de 2 ans est la première oú l'on examine de façon systématique la physique et la chimie de ces lacs, de même que tous les niveaux trophiques importants pour les juvéniles du saumon rouge qui y vivent ainsi que le nombre de ces juvéniles, leur régime alimentaire et leur taux de mortalité. Les données recueillies nous ont pennis d'établir l'état trophique de ces lacs, de déterminer les populations planctoniques et de saumons rouges juvéniles ainsi que d'estimer leur potentiel pour le grossissement de ces juvéniles. Nous avons constaté, à partir de la concentration prinranière de phosphore total au moment du turnover, que le lac François est très oligotrophe et que le lac Fraser est mésotrophe, mais s'aproche du stade eutrophe. La moyenne du rendement photosynthétique saisonnier (RP) est de 163 mg $C \cdot m^{-2} \cdot d^{-1}$ dans le lac François, résultat qui s'apparente beaucoup à celui du lac Shuswap (171) et qui dépasse nettement celui du lac Chilko (79) ou celui du lac Quesnel (102). Le RP du lac Fraser (332 mg $C \cdot m^{-2} \cdot d^{-1}$) est supérieur à celui de n'importe quel autre lac d'alevinage du saumon rouge qui fasse partie du réseau hydrographique du Fraser. Les données relatives aux saumons rouges juvéniles montrent que

les deux lacs sont d'excellents milieux de grossissement et qu'ils sont actuellement sous-utilisés par ces juvéniles. Avec une densité de 40 femelles en mesure de se reproduire par hectare, le lac Fraser n'est pas utilisé à son potentiel de grossissement. Pourtant, cette densité de femelles dépasse largement le potentiel des lacs Quesnel et Shuswap. Nous estimons que, s'il y avair assez de frayères, il faudrait une échappée de 1,3 million de saumons rouges pour que le lac François produise le maximum possible de smolts. Toutefois, ce nombre est 26 fois supérieur à l'estimation de la capacité des frayères. Nous calculons que l'échappée optimale pour le lac Fraser est de 0,5 million de saumons; cette valeur est à peine supérieure à l'estimation de la capacité de ses frayères, soit 0,43 million de saumons. On estime qu'à leur utilisation maximale pour le grossissement, le lac François peut produire 72 millions de smolts, le lac Fraser 27 millions. Il est possible de reconstituer le stock de saumons rouges du Fraser strictement par des techniques d'aménagement (augmenter les échappées), mais pour exploiter le lac François à son potentiel, il faut accroître le recrutement des alevins bien au delà des possibilités actuelles des frayères.

INTRODUCTION

The Fraser River's drainage basin contains a large number of lakes which are nursery areas for juvenile sockeye salmon (*Oncorhynchus nerka*). Total adult sockeye returns to the Fraser River exceed 15 million in some years and sustain valuable commercial and recreational fisheries. Escapements to some Fraser sockeye lakes have been increasing for a number of cycles and some escapements currently exceed optimum levels (Hume et al. 1996). However, production of the whole system has not yet attained the estimated historic production of 100 million fish in dominant years (Ricker 1987). A number of Fraser system lakes which have an apparent potential to be major sockeye producers continue to support relatively small sockeye stocks. To date, enhancement efforts on these stocks have been restricted primarily to catch management (i.e. reduce catch to increase escapement) and spawning channel construction.

Sockeye stocks originating from the two lakes in this study have not exhibited the increases recorded for other Fraser system sockeye stocks (e.g. Chilko, Quesnel, and Shuswap sockeye). Escapements are regarded as below optimum (Anon. 1995) in all cycle years, with subsequent fry recruitment too low to permit substantial increases in smolt output or adult returns. It has been assumed (based on qualitative assessment of small spawning escapements and large lake areas) that the lakes could support considerable increases in their sockeye populations. Although several years of data were available from hydroacoustic and trawl surveys prior to our study, limnological data were limited (Goodlad et al. 1974; Stockner and Shortreed 1983) and not suitable for categorizing rearing capacity.

Our two year (1992 and 1993) study was the first detailed investigation of lake physics, chemistry, and all major trophic levels on these Fraser system sockeye nursery lakes. We had several objectives, which were to determine: 1. trophic status and productivity, 2. factors controlling lake productivity, 3. plankton community species composition and biomass, and 4. juvenile sockeye numbers, size and diet. Our final objective was to use these data and a rearing capacity model (Hume et al. 1996) to estimate optimum escapements to and maximum smolt outputs from Francois and Fraser lakes.

DESCRIPTION OF STUDY LAKES

Francois (54°05' N, 125°45' W) and Fraser (54°10' N, 124°45' W) lakes are located in the north-western portion of the Fraser River drainage basin in west-central British Columbia (Fig. 1). Francois Lake is drained by the Stellako River which flows Northeast for 10 km before entering Fraser Lake, which is in turn drained by the Nautley River. The Nautley River flows east for only 0.5 km before entering the Nechako River, which subsequently enters the Fraser River at Prince George. Francois Lake is situated at an elevation of 715 m and has a surface area of 247 km^2, while Fraser Lake is both lower and smaller with an elevation of 670 m and an area of 52 km^2. Francois Lake is 106 km long and averages 3.5 km wide, while Fraser Lake is 20 km long and 3.5 km wide. Mean depths of Francois and Fraser lakes are 87 and 13 m, respectively. Drainage basin areas of Francois and Fraser lakes are 3,908 and 6,391 km^2 and respective water residence times are 36 and 0.8 years. Drainage basins of the lakes are located both in the Cariboo aspen-lodgepole pine and sub-boreal spruce biogeoclimatic zones (Farley 1979). Annual precipitation ranges from 40-75 cm. Both lakes are dimictic. The climate is continental, with cold winters and warm, dry summers. The Nadina River enters the western end of Francois Lake and is its major tributary.

While no towns are located along the shores of Francois Lake, the lake is heavily used for recreation, and there are a considerable number of permanent and seasonal residences, as well as a number of resorts, campsites, and marinas. A substantial amount of logging is carried out in the lake's drainage basin, but little other commercial activity occurs. Fraser Lake receives considerably more anthropogenic input than does Francois Lake. The Endako River, which enters the Stellako River approximately 3 km upstream of Fraser Lake, drains a large (1,856 km^2) area where considerable recreational, industrial, and agricultural activity takes place. Besides logging, sawmills, mining, farming, and ranching, the town of Burns Lake (population of the town and surrounding area is approximately 9,000) is located alongside Burns Lake, which drains into the Endako River. A substantial number of residences are located on the shores of Fraser Lake, as well as the community of Fraser Lake (population of town and surrounding area is approximately 3,500).

METHODS

LIMNOLOGICAL DATA

We sampled the lakes in 1992 and 1993. Data were collected monthly (May-October) on 5 occasions in 1992 and 6 times in 1993. At Francois Lake we sampled 4 locations (stations 1-4) distributed evenly along the lake's longitudinal axis (Fig. 2). At Fraser Lake we sampled 2 locations (stations 1-2) in 1992 and one site only (station 2) in 1993 (Fig. 2). In addition, we sampled the Stellako River 1.5 km upstream from Fraser Lake (this location was downstream of the Endako River confluence) for selected chemical and biological variables. For calculation of seasonal averages we defined the growing season as May 1 to October 31. This represented the period of active growth in the phytoplankton and zooplankton communities. Time-weighted means for each sampling location were calculated by integrating seasonal data and dividing by length of the growing season.

Temperature profiles from the surface to the lake bottom were obtained at each station with an Applied Microsystems conductivity, temperature and depth meter (Model STD-12). Isotherms were plotted by the SAS procedure Gcontour (SAS Institute Inc., 1990) from a grid of interpolated and smoothed unscaled data computed by the SAS procedure G3grid using a bivariate method described by Akima (1978). To quantify convective stability, we calculated a variation of the Schmidt stability index (Johnson and Merritt 1979). To facilitate comparisons between stations and lakes we calculated the index to 30 m only. The index (S) was calculated with the formula:

$$S = g \sum_{0}^{30} (\rho_z - \bar{\rho})(z - z_{\bar{\rho}})\,\Delta z$$

where:
S = modified Schmidt stability index (kg/sec^2)
g = gravitational constant (9.8 m/s^2)
ρ_z = density of water at depth z (g/cm^3)
$\bar{\rho}$ = mean density of the water column (g/cm^3)
z = depth (m)

$z_{\bar{\rho}}$ = depth where mean density occurs (m)
Δz = change in depth (m)

Water density used in calculation of the index was calculated from temperature and an equation of state given by Chen and Millero (1977). S reaches maximum values during summer stratification and is zero when lakes are isothermal.

Li-Cor light meters (Model 185A) equipped with quantum sensors (Model Li-192S) were used to measure photosynthetic photon flux density (PPFD: 400-700 nm) from the surface to the compensation depth (1% of surface intensity) and vertical light extinction coefficients were calculated. Euphotic zone depth (EZD) was assumed to equal the compensation depth. A standard 22-cm white Secchi disk was used to measure water transparency. A continuous chlorophyll profile from the surface to 40 m was obtained with an Electro-Optik *in situ* fluorometer coupled with a Linear Instruments Model 142 chart recorder.

We used an opaque Van Dorn bottle sterilized with 95% ethanol to collect all water samples. Sampling took place between 0800 and 1200 h. On each sampling date and station we partitioned the EZD into 3 layers. Criteria used in establishing boundaries of each layer included compensation depth, thermocline depth and chlorophyll peaks (if present). Several Van Dorn bottle casts were made in each layer and this water was integrated into one sample. Replicate analyses were carried out on each integrated sample. At each station we also collected a hypolimnetic (40 m) sample. In addition to this integrated sampling, we collected water samples from discrete vertical profiles at station 4 on Francois Lake and station 2 on Fraser Lake. Water from discrete samples was collected in 1-L or 2-L polyethylene bottles, while integrated samples were collected in 20-L polyethylene Nalgene Lowboy carboys. Most chemical analyses were carried out according to methods given in Stephens and Brandstaetter (1983). Acid washed, deionized distilled water (DDW) rinsed, screw-capped test tubes were rinsed and then filled with sample water from each integrated sampling depth, capped, stored at 4°C, and later analyzed for total phosphorus using a molybdenum blue method after persulfate digestion. Water samples for the remaining nutrient analyses and chlorophyll determinations were kept cool and dark and filtered within 2-4 h. Water for dissolved nutrient analyses was filtered through 47-mm Whatman GF/F filters which had been previously ashed (460°C for 4 h). Each filter was placed in a 47-mm Swinnex filtering unit (Millipore Corp.), rinsed with DDW, and then rinsed with approximately 50 mL of sample. An acid washed, DDW rinsed borosilicate glass bottle was rinsed and filled with 100 mL of filtered water, capped, stored at 4°C in the dark and later analyzed for nitrate (Stainton et al. 1977). An additional 100 mL of sample was filtered into a clean, rinsed polyethylene bottle, stored at 4°C in the dark, and later analyzed for soluble reactive silicon and total dissolved solids. For determination of particulate phosphorus concentration we filtered 1- or 2-L of water through an ashed 47-mm diameter Whatman GF/F filter. The filter was placed in a clean scintillation vial and later analyzed for particulate phosphorus using the method of Stainton et al. 1977. To determine chlorophyll-a we filtered 250-mL samples under subdued light through 47-mm diameter 0.8-μm Millipore AA filters, 2.0-μm Nuclepore filters and 20-μm Nitex filters. Filters were folded in half, placed in aluminium foil dishes, and frozen. Samples were later analyzed for using a Turner fluorometer (Model 112) after maceration in 90% acetone.

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

method described by Robarts and Sephton (1981). Eight random fields were counted on each filter and the counts converted to numbers/L. Occasional blanks were prepared to check for significant background bacteria counts in the staining solution and rinse water.

Opaque, 125-mL, polyethylene bottles were rinsed with sample, filled, and fixed with 1 mL of Lugol's iodine solution for identification and enumeration of nano- and microphytoplankton. For analysis, each sample was gently mixed and a subsample 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 counted, identified 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. Care was taken to minimize exposure of the sample to light during sampling and laboratory processing. Filters were placed in opaque petri dishes, air-dried and stored in the dark at room temperature until analyzed. During analysis, each filter was placed on a wet 40-μm mesh nylon screen in a filter holder, 1-2 mL of filtered 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. On each filter 30 random fields were counted at 1250X magnification using an oil immersion lens. Phototrophic picoplankton were identified as cyanobacteria or eukaryotic algae, assigned to general categories based on morphological characteristics and fluorescence colour, and classified into size categories. Phytoplankton data are reported as total numbers for picoplankton (0.2-2.0 μm), nanoplankton (2.0-20 μm), and microplankton (>20 μm).

We measured *in situ* photosynthetic rates (PR) at station 4 in Francois Lake and station 2 in Fraser Lake. Water for alkalinity determinations was placed in glass bottles which were filled completely (one bottle from each sampling depth) and sealed. A Cole-Parmer Digi-Sense pH meter (Model 5986-10) and Ross combination electrode were used to determine the pH and total alkalinity (mg/L $CaCO_3$) of these samples according to the standard potentiometric method of APHA (1980). Dissolved inorganic carbon (DIC) concentrations used in the calculation of PR were established indirectly from pH, temperature, total dissolved solids and bicarbonate alkalinity. For determination of PR, three 125-mL clear and two 125-mL opaque bottles were filled with water from each integrated sampling depth. Each bottle was inoculated with approximately 137 kBq of a ^{14}C-bicarbonate stock solution. At each station the activity of the stock solution was determined by inoculating three scintillation vials containing 0.5 mL of Scintigest (Fisher Scientific). Bottles were incubated at the mid-point of their respective depth intervals for 1.5-2 h between 0900 and 1200 h. After incubation, bottles were placed in light-proof boxes and transported to the field laboratory where filtration started <2 h after incubation stopped. We removed 40-mL aliquots from each bottle and filtered each aliquot at a vacuum not exceeding 20-cm Hg through 47-mm diameter Nuclepore filters (0.2- and 2.0-μm pore size) and a 47-mm diameter, 20-μm mesh Nitex filter. When just dry, filters were placed into scintillation vials containing 0.5 mL Scintigest (Fisher Scientific). All vials were kept cool and stored in the dark. Within a few days of the incubations, 10 mL of Scintiverse II (Fisher Scientific) was added to each scintillation vial and the samples were counted in a Packard

Tri-Carb 4530 liquid scintillation counter. Quench series composed of the same scintillation cocktail and filters as 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 datalogger and Li-Cor 190SA quantum sensors. Picoplankton PR was calculated by subtracting the 2.0- from the 0.2-μm fraction and nanoplankton PR by subtracting the 20- from the 2.0-μm fraction. Total PR was determined from the 0.2-μm filter and microplankton PR from the 20-μm filter.

At each station we collected replicate zooplankton samples with a 160-μm mesh size Wisconsin net (mouth area = 0.05 m^2) hauled from 30 m to the surface. At station 4 in Francois Lake and station 2 in Fraser Lake we also used a 50-L Schindler trap to collect zooplankton from 7 depths from the surface to 30 m. The 20-μm mesh on this sampler enabled us to quantitatively sample rotifers and immature zooplankton. Zooplankton collected with the Schindler trap were anesthetized with carbonated water prior to preservation to prevent expulsion of cladoceran eggs. All zooplankton samples were concentrated into 125-mL bottles and preserved in a sucrose-buffered 4% formalin solution (Haney and Hall 1973). Zooplankton were enumerated and measured using a microcomputer image measuring system (MacLellan et al. 1993) using methods adapted from Koenings et al. (1987). Identification was based on Balcer et al. (1984) and biomass estimates were calculated using length-weight regressions (Bird and Prairie 1985; Culver et al. 1985; Stemberger and Gilbert 1987; Yan and Mackie 1987).

We calculated copepod production rates using a weight increment equation for populations with overlapping cohorts (Winberg et al. 1971) and temperature-dependent instar development rates (Corkett and McLaren 1970; McLaren 1978; Hay et al. 1988). Our estimates of copepod production rates may be high relative to other oligotrophic lakes (Herzig et al. 1980). These high values may be partially explained by our calculation methods. Although duration of embryonic development is regulated exclusively by temperature (Herzig 1983), both food supply and temperature influence duration of each instar (Huntley and Boyd 1984; McLaren et al. 1987). Because we did not measure instar development times in our lakes, we used published values determined with unlimited food supply (Corkett and McLaren 1970; McLaren 1978; Hay et al. 1988). If copepod food supply was limiting in Francois and Fraser lakes, our calculations would overestimate production (Bottrell 1976). In addition when we calculated mean water column temperature (weighted by zooplankton distribution), we assumed that diel vertical migration was negligible and that vertical distribution did not vary between sampling times. Therefore these estimates are useful as indices of production for comparisons between lakes and times, but are not absolute estimates of actual production rates.

Gross production (*P*) was calculated with the formula:

$$P = (N_n \Delta W_n) T_n^{-1} + (N_c \Delta W_c) T_c^{-1} + (N_a \Delta W_a) T_a^{-1}$$

where:
P = gross production rate
N = abundance of specific developmental stages of copepods
(n = naupliar stage; c = early instars; a = late instars)
ΔW = the biomass gain over each developmental stage
T = the duration of instar developmental stages

To calculate instantaneous birth rates and production of *Daphnia* we used the eggs-per-female ratio method (Edmondson 1968, 1972; Paloheimo 1974) and a temperature-dependent egg development rate (Gabriel et al. 1987). Temperatures used in calculation of egg development rates were averages of the water column, weighted by zooplankton vertical distribution in the water column. Temperature at the depth of highest zooplankton density was given the most weight. The formula used in production rate calculations was:

$$b = \ln[(C_t N_t^{-1})] D^{-1}$$

where: b = instantaneous birth rate
C_t = egg count
N_t = number of adults
D = mean egg duration

JUVENILE SOCKEYE

Between 1974 and 1982 juvenile sockeye were sampled in 7 years in Fraser Lake and 5 years in Francois Lake (Mueller and Enzenhofer 1991). On most occasions both hydroacoustic population estimates and trawl samples for size, age structure and species composition were collected. More recently, we conducted fall hydroacoustic and trawl surveys on Francois Lake in 1992 and on Fraser Lake in 1989, 1991, 1992, and 1993.

Prior to hydroacoustic surveys, the lakes were divided into a number of sections. Within each section, from 1 to 3 hydroacoustic transects were established. There was a total of 11 transects on Francois Lake and 5 on Fraser Lake (Fig 2). The same transects were used on all surveys. From 1974 to 1982 acoustic data were collected using a Simrad EY-M echosounder with a 70 kHz transducer producing an 11°beam (at -3dB) and recorded for later processing. Data were analyzed in two stages with the duration-in-beam technique (Thorne 1988). First, recorded voltages were integrated with a Biosonics 121 integrator to give the relative uncalibrated density of fish in each transect. Second, targets were counted on an oscilloscope from selected transects in each lake. These counts were then regressed against the integrated data from the same transect. The regression line was then used to calibrate all the integrated transects to provide a density estimate for each transect.

From 1988 until the present, we collected data using a Biosonics Model 105 dual beam echosounding system with a 420 kHz dual beam (6°/15°) transducer. Data were digitally recorded for later processing as described by Burczynski and Johnson (1986). First, target strengths and mean backscattering cross sections were determined for each transect with a Biosonics Model 121 dual-beam processor. Second, recorded data were echo integrated to give relative density of targets. Target strength and equipment scaling factors were then used to scale the echo integration to provide an estimate of fish density in each transect. Results from each transect were used to provide a mean estimate of density (n/ha) for each lake section. The mean density was then multiplied by the surface area of the section to provide a population estimate for the section and then summed to provide a total population estimate for the lake. Mean lake density was calculated by dividing the lake population estimate by the total surface area. Standard errors were calculated for each section density and were then weighted by section area to provide a standard error for the lake population estimate. Two times the standard error (2SE) are reported here.

Samples of juvenile sockeye were collected from each lake section with a 7- by 3-m midwater beam trawl (maximum mesh size = 10.2 cm, fished at 1.0 m/s) as described by Enzenhofer and Hume (1989). Trawls were made at locations and depths suggested by fish targets on the echosounder. Trawl duration (5-45 min) was chosen to give an adequate sample size for later analysis (100-200 fish). All fish were anaesthetized upon capture in 2-phenoxy-alcohol and then preserved in 10% formalin. Fish were kept in formalin for at least one month before lengths and weights were recorded.

To estimate spring fry recruitment to the lakes we used numbers of female spawners and average fecundity (3,125 eggs/female in the Nadina River and 3,220 in the Stellako River) (T. Whitehouse, DFO, New Westminster, B.C., unpublished data). We used an estimated wild egg-to-fry survival of 20% in the Nadina and Stellako rivers (T. Whitehouse, unpublished data). Actual fry numbers were available for the Nadina spawning channel (G. Lofthouse, DFO, Smithers, B.C.) and we added these to the estimated Nadina wild fry recruitment. We assumed that all fry recruitment to Francois Lake was from the Nadina River and channel and that all recruitment to Fraser Lake was from the Stellako River.

Smolt samples from Francois Lake were collected in 1992, 1993, and 1994 (1990-1992 brood years) and from Fraser Lake in 1993 (1991 brood year) (T. Whitehouse, unpublished data). Smolts were collected in the outlet rivers of each lake (Stellako River below Francois Lake and Nautley River below Fraser Lake) using inclined plane traps and fyke nets. Because Francois Lake smolts pass through Fraser Lake and may have been caught in Nautley River traps, they may have biased Fraser Lake smolt size estimates.

We determined juvenile sockeye diet by examining the stomach contents of sockeye caught during our trawl surveys. We examined stomachs collected in 1989, 1992, and 1993 in Fraser Lake and in 1992 in Francois Lake. Stomach contents were identified and enumerated with the computerized video measuring system. A subjective index of stomach fullness (Haram and Jones 1971) was assigned to each stomach and the relative proportion (by volume) of each prey type ingested was estimated with a technique modified from Hellawell and Abel (1971).

ADULT SOCKEYE

Total adult escapements, numbers of effective female spawners (EFS), and total returns have been estimated from 1948 to the present for the 2 study lakes (Cass 1989). Numbers of effective female spawners (EFS) are widely used in stock-recruitment analyses and are used here as estimators of fry recruitment. EFS are female sockeye that have successfully spawned, as determined by examination of carcasses on the spawning grounds. We assume that EFS numbers are positively correlated to numbers of fry entering the lake the following spring. In the years sampled, EFS averaged 52% of total escapement (range: 39 to 60%) in Fraser Lake, and 59% (range: 37 to 78%) in Francois Lake. High prespawning mortality caused the low proportion of EFS in some years. Gilhousen (1990) attributed this mortality to returning adults being exposed to high water temperatures both during migration and on the spawning grounds.

RESULTS

PHYSICS

Although both Francois and Fraser lakes were stratified from June to October, their thermal regimes differed substantially. Francois Lake was cooler (seasonal average surface temperature ranged from 11.8-14.8°C) than Fraser Lake, where average surface temperatures ranged from 15.1-15.7°C (Table 1). Francois Lake had deeper average thermocline depths (range: 11.4-22.7 m) than Fraser Lake (range: 8.6-12.6 m) (Table 1, Fig. 3,4). Seasonal averages of the Schmidt stability index, which quantifies water column stability, ranged from 447-839 kg/sec^2 in Francois Lake and from 840-904 in Fraser Lake, further illustrating the stronger stratification present in Fraser Lake (Table 1). Francois Lake exhibited spatial heterogeneity in both study years, with surface temperatures and water column stability increasing from west to east (Table 1, Fig. 3,4). Both study lakes exhibited some annual variability in their thermal regimes, with both lakes warmer and more strongly stratified in 1993 than in 1992. Seasonal average euphotic zone depths (EZD) ranged from 10.3-11.9 m in Francois Lake and were lower (range: 7.3-8.3 m) in Fraser Lake (Table 1). Neither lake exhibited substantial seasonal changes in EZD.

CHEMISTRY

With the exception of pH and nitrate, measured chemical variables were higher in Fraser than in Francois Lake. Average pH was the same in both lakes, increasing from 7.3 in 1992 to 7.8 in 1993 (Table 2). Seasonal average epilimnetic nitrate ranged from 5.8-19.0 μg N/L in Francois Lake and was lower (range: 2.4-3.0) in Fraser Lake. In 1993 in Francois Lake average nitrate concentrations were less than one-half of 1992 concentrations. In Francois Lake epilimnetic nitrate was depleted on one occasion only (August 1993), but in Fraser Lake it was at or near our analytical detection limit (1 μg N/L) for most of each year, increasing above these low levels only in September and October (Fig. 5). Seasonal average total phosphorus (TP) concentrations ranged from 4.5-7.3 μg/L in Francois Lake and from 10.5-17.2 in Fraser Lake (Table 2). In both lakes and in the Stellako River TP was higher in 1993 than in 1992. Francois Lake exhibited little seasonality in TP concentration but in both Fraser Lake and the Stellako River TP was higher in spring and fall than in summer (Fig. 6).

BACTERIOPLANKTON AND PHYTOPLANKTON

Bacterioplankton numbers exhibited little seasonality in either lake and were similar between stations and years. Seasonal average bacteria numbers in Francois Lake ranged from 1.12-1.44x10^6/mL and in Fraser Lake from 1.37-1.52x10^6/mL (Table 3).

Chlorophyll concentrations in Francois Lake exhibited no seasonality in either study year (Fig. 7). Seasonal averages ranged from 1.65-2.06 μg/L and whole-lake averages were very similar (1.91 and 1.92 μg/L) in both study years (Table 3). Picoplankton constituted about one-half of seasonal average phytoplankton biomass (as chlorophyll), with the remainder being made up of approximately equal proportions of nanoplankton and microplankton. In Fraser Lake mean epilimnetic chlorophyll increased from seasonal minima of approximately 2 μg/L in June to highs of 5.5-6.5 μg/L in July or August, and remained >4 μg/L for the rest of the season (Fig. 7). Seasonal averages ranged from 3.84-4.36 μg/L (Table 3). Picoplankton made up 42% of total chlorophyll in 1992 and 32% in 1993. Nanoplankton made up 24 and 20% of total chlorophyll in 1992 and 1993, respectively, while the contribution of microplankton increased from 35% in 1992 to 47% in 1993. Vertical distribution of chlorophyll differed considerably between lakes. Francois Lake exhibited a pattern commonly seen in oligotrophic lakes which are subject to considerable wind mixing. It seldom had distinct peaks in chlorophyll down the water column but chlorophyll was somewhat higher in the epilimnion and declined slowly below the thermocline (Fig. 8) . Vertical distribution of chlorophyll in Fraser Lake was quite different. In spring, highest chlorophyll concentrations occurred near the bottom of the water column (Fig. 8). In summer, chlorophyll concentrations in the euphotic zone were much higher than in the deeper waters. By fall, chlorophyll concentrations in the deeper waters were again similar to or higher than surface concentrations.

Seasonal averages of mean epilimnetic picoplankton numbers were similar in both lakes, with numbers slightly higher in Fraser Lake in 1992 and slightly higher in Francois Lake in 1993. Numbers ranged from 4.94x10^4 to 7.89x10^4/mL in Francois Lake and from 6.48x10^4 to 8.67x10^4/mL in Fraser Lake (Table 3). Differences in nanoplankton numbers were slightly greater between lakes, with Francois Lake's whole-lake average ranging from 450-580/mL and Fraser Lake's from 780-920/mL. Microplankton exhibited much greater differences between lakes than either pico- or nanoplankton. Whole-lake averages ranged from 300-340/mL in Francois Lake and were 5 to 12-fold higher (1,510-4,180/mL) in Fraser Lake. Picoplankton exhibited considerable seasonality in both lakes, with seasonal minima occurring in spring and fall (Fig. 9). In Francois Lake seasonal maxima occurred in summer in both study years while in Fraser Lake maxima occurred in June of 1992 and in September of 1993. Seasonal maxima in nanoplankton numbers occurred in spring in both lakes (Fig. 10). In Francois Lake numbers then declined slightly for the remainder of the growing season, while in Fraser Lake the decline was more pronounced. Microplankton exhibited little seasonality in Francois Lake while in Fraser Lake a pronounced summer peak occurred (Fig. 11). The peak was caused primarily by a bloom of large cyanobacteria comprised of the genera *Anabaena*, *Anabaenopsis*, and *Aphanizomenon*. This higher microplankton chlorophyll concentration in 1993 despite lower microplankton numbers was caused primarily by increased numbers of the diatom *Asterionella formosa* and decreased numbers of large cyanobacteria.

Seasonal average photosynthetic rates (PR) were higher in Fraser Lake than in Francois Lake and declined in both lakes from 1992 to 1993. In Francois Lake PR dropped from 201 to 124 mg $C \cdot m^{-2} \cdot d^{-1}$ between 1992 and 1993 and in Fraser Lake from 410 to

254 mg $C \cdot m^{-2} \cdot d^{-1}$ (Table 3). The decline in Fraser Lake was caused by a 2-fold drop in picoplankton PR (nano- and microplankton PR was similar in both years). In Fraser Lake both pico- and nanoplankton PR dropped approximately 3-fold while microplankton PR was nearly the same in both years. Although daily PR varied throughout the growing season, distinct trends were not evident (Fig. 12).

ZOOPLANKTON AND SOCKEYE DIET

Dominant macrozooplankton in the study lakes were Bosminids (both *Eubosmina* and *Bosmina*), *Daphnia*, *Diacyclops*, and *Leptodiaptomus*. *Heterocope* was an important contributor to total biomass in Fraser Lake but was not present in Francois Lake. *Epischura* was common in both lakes but its biomass was lower than the dominant genera (Table 4). Common macrozooplankton species were *Daphnia galeata mendotae*, *Diacyclops thomasi*, *Epischura nevadensis*, *Eubosmina longispina*, *Heterocope septentrionalis*, and *Leptodiaptomus ashlandi*. Seasonal average biomass of major genera varied between stations, but whole-lake seasonal average biomass of most major genera varied only slightly between years (Table 4). Macrozooplankton biomass ranged from 1,230-1,420 mg/m in Francois Lake and was approximately 2x higher in Fraser Lake (range: 2,189-2,564 mg/m2, Table 4). Biomass of all macrozooplankton with the exception of Bosminids was higher in Fraser Lake than Francois Lake. *Daphnia* biomass was lowest in spring and the seasonal maxima occurred at various times from August-October (Fig. 13). A distinct seasonal peak in Bosminid biomass occurred in September in Francois Lake, while in Fraser Lake Bosminids exhibited little seasonality (Fig. 13). In Francois Lake *Leptodiaptomus* biomass was higher in 1993 and had a distinct spring peak while in 1992 biomass exhibited little seasonality. In Fraser Lake a distinct summer peak in *Leptodiaptomus* biomass occurred in both years (Fig. 14). *Diacylops* biomass was highest in spring in both lakes, although the peak was much higher in Fraser than in Francois Lake (Fig. 14). *Epischura* biomass was highest in June in Francois Lake, while in Fraser Lake highest biomass occurred in August, 1992 and May, 1993 (Fig. 15). *Heterocope* had a distinct June peak in Fraser Lake but was absent from August-October samples and did not occur in Francois Lake (Fig. 15).

Production rates of major macrozooplankton genera varied only slightly between years and was approximately 3x higher in Fraser Lake than in Francois Lake (Fig. 16). Seasonal average *Daphnia* production in Fraser Lake was 1.21 mg dry $wt \cdot m^{-3} \cdot d^{-1}$ in 1992 and 1.39 in 1993. Production was lowest in spring and a seasonal maxima of 2.20 mg dry $wt \cdot m^{-3} \cdot d^{-1}$ occurred in fall in 1992. In 1993 the seasonal maxima of 2.30 mg dry $wt \cdot m^{-3} \cdot d^{-1}$ occurred in summer. In Francois Lake seasonal mean *Daphnia* production was 0.28 mg dry $wt \cdot m^{-3} \cdot d^{-1}$ in 1992 and 0.31 in 1993. In both years maximum rates were <1.00 mg dry $wt \cdot m^{-3} \cdot d^{-1}$ and occurred in late summer. Copepod seasonal mean production in Fraser Lake was 4.43 mg dry $wt \cdot m^{-3} \cdot d^{-1}$ in 1992 and 2.76 mg dry $wt \cdot m^{-3} \cdot d^{-1}$ in 1993. Rates were lowest in summer and highest (6.10 mg dry $wt \cdot m^{-3} \cdot d^{-1}$ in 1992; 4.80 in 1993) in fall (Fig. 16). Copepod production in Francois Lake was much lower with a seasonal average of 1.20 in 1992 and 1.54 in 1993. Seasonal maxima of >2.00 mg dry $wt \cdot m^{-3} \cdot d^{-1}$ occurred in May and rates were ca. 1.00 mg dry $wt \cdot m^{-3} \cdot d^{-1}$ for the rest of the season.

Kellicottia and *Keratella* were the most numerous rotifers in both lakes (Fig. 17). Other common rotifers were *Conochilus* and *Polyarthra*. Highest rotifer numbers in Francois Lake were an order of magnitude lower than highest numbers in Fraser Lake. In Francois Lake seasonal maxima in numbers of *Kellicottia* and *Keratella* occurred in summer and highest

numbers of *Conochilus* and *Polyarthra* occurred in fall (Fig. 17). Seasonal patterns in Fraser Lake were quite different, with a spring peak of *Keratella* and a fall peak of *Kellicottia* (Fig. 17).

To quantify the transport of Francois Lake zooplankton downstream to Fraser Lake, we used a Schindler trap to sample plankton in the Stellako River. Seasonal averages of zooplankton data collected from the Stellako River and from the closest sampling locations in Francois and Fraser lakes are presented in Table 5. On all occasions and for all species identified, zooplankton biomass in the Stellako River was much lower than upstream in Francois Lake or downstream in Fraser Lake.

Daphnia predominated in all sockeye stomachs examined (Fig. 18). They constituted 90% of sockeye stomach contents in Francois Lake samples and ranged from 80-90% in Fraser Lake samples. In addition to *Daphnia, Leptodora* were present in all stomachs even though they were rarely found in the lake samples. Bosminids and copepods were present in fall samples. Fraser Lake fall stomach samples had an average fullness between 85-90%. Fraser Lake and Francois Lake summer samples averaged 70% full.

ADULT SOCKEYE

In the past 40 years escapements to Francois Lake have ranged from <1,000 to 60,000 (Cass 1989, Fig. 19). Most Francois sockeye spawn in the Nadina River and spawning channel, which was first operational in 1973. Some spawning occurs in the Nithi River but escapements have not exceeded 1,800 and have been less than 50 spawners since 1984. It is probable that some sockeye spawn along the shores of Francois Lake but their numbers are not known. Spawning capacity of the Nadina River and channel have been estimated as 21,000 and 29,000 total spawners, respectively (Rosberg et al. 1986). Since spawning channel construction, escapements to Francois Lake have reached or exceeded spawning capacity only in 1979 and 1991 (Fig.19). Most other years have had less than 30,000 spawners. Francois Lake's spawning ground capacity is extremely low (2 spawners/ha) relative to the surface area of the lake. Since 1955 Fraser Lake escapements have ranged from 22,000-368,000 and in most years are from 50,000-100,000 (Cass 1989, Fig 19). The majority of Fraser Lake sockeye spawn in the Stellako River and small numbers (<1,300) spawn in the Endako River. Estimated spawning ground capacity of Fraser Lake is 434,000 adults (Anon. 1995) or 79 spawners/ha. This is similar to the estimated capacities of Quesnel and Shuswap lakes at 88 and 101 spawners/ha, respectively.

JUVENILE SOCKEYE

Estimated numbers of emergent fry to Francois Lake ranged from 2-22 million (83-893/ha) and to Fraser Lake from 7-129 million (1,352-24,837/ha) (Table 6).

Acoustic estimates of fry density varied from 0.8-6.6 million (32-268 fry/ha) in Francois Lake (Table 6). Combined August and September data showed some increase in fry density at higher EFS or emergent fry numbers but the trend was not significant ($P>0.05$, Fig. 20). Estimated survival rates from emergent fry to summer and fall acoustic estimates varied from 3 to 100% with a mean of 34%. Kokanee are known to occur in both study lakes, so an unknown proportion of the age-0 *O. nerka* caught in our trawls are kokanee. In Fraser Lake fall acoustic estimates of fry numbers varied from 6.6-24.2 million (1,265-12,337/ha) (Table 6, Fig. 20). There was a positive linear relationship between EFS and subsequent fry numbers in

September (r^2 = 0.97, P<0.01, df = 4), but no relationship was apparent in the August surveys. Emergent to August fry survival averaged 55% (range: 16-88%) and emergence to September survival averaged 35% (range 24-49%).

Since 1975 midwater trawls have caught a total of 1,756 fish in Fraser Lake and 475 fish in Francois Lake. Besides *O. nerka*, species caught in both lakes include lake whitefish (*Coregonus clupeaformis*) and prickly sculpin (*Cottus asper*) (Table 7,8). Additional species caught in Fraser Lake are squawfish (*Ptychocheilus oregonensis*), chinook salmon (*O. tshawytscha)* and 2 unidentified cyprinids. Since 1989 non-*O. nerka* have been a very small (<3%) proportion of the catch in Fraser lake but in earlier years ranged from 6-42% of the catch. In Francois Lake non-*O. nerka* averaged 28% of the midwater catch.

We rarely captured older age classes of *O. nerka* in either lake (total of 7 in each lake) (Table 7,8). As our trawl is biased only against *O. nerka* larger than 150 mm (Parkinson et al. 1994; Hume et al. 1996), we feel our data on the relative abundance of age-0 and age-1 *O. nerka* in Francois Lake are accurate, but may underestimate numbers of age-2 *O. nerka*. Larger fish sizes in Fraser Lake suggest that our data may underestimate numbers of age-1 and older *O. nerka.*

Francois Lake has a large population of resident fish which are both important to the recreational fishery and potential predators on sockeye. In 1988 anglers caught an estimated 15,300 rainbow trout (*O. mykiss*), 1,692 lake trout (*Salvelinus namaycush)*, 241 burbot (*Lota lota*), and 201 kokanee (Bustard 1989). These data indicate either low kokanee numbers or an average size too small to be a major component of the sports fishery. Numbers of potentially piscivorous fish appear to be high relative to Babine Lake, since angler catch was similar in the two lakes even though Babine is twice as large as Francois and receives 33% more angling effort (Bustard 1987). However, mean size of sport-caught fish in Francois Lake was smaller (350 mm) than in either Babine (395 mm) or Quesnel (482 mm) lakes and the Francois Lake fish "do not feed on kokanee" (Bustard 1989). Their significance as sockeye predators therefore may be limited.

Despite much higher age-0 fry densities in Fraser Lake, average size of fall fry was larger than in Francois Lake. Fry grew approximately 1 g in the 6-wk interval between the August and September surveys (3.5 to 4.3 g in Fraser Lake and 2.3 to 3.4 g in Francois Lake). Fry size was not related to EFS density in either lake (Fig. 21). We captured very few older age classes of *O. nerka* but 4 age-1 *O. nerka* from Fraser Lake ranged from 33 to 92 g while 3 age-1 *O. nerka* caught in Francois Lake ranged from 2.8 to 34 g.

Smolts from Francois Lake ranged from 9.7-10.1 g in the 3 years sampled (Table 9). In the spring of 1993 Francois Lake smolts weighed 5-6 g more than the previous fall. Fraser Lake smolts averaged 7.4 g in 1993 and weighed 3.3 g more than they did the previous fall.

DISCUSSION

TROPHIC STATUS AND FACTORS LIMITING PRODUCTIVITY

A lake's rearing capacity for juvenile sockeye is directly related to its trophic status (Koenings et al. 1987; Hume et al. 1996). One of our objectives in this study was to categorize the trophic status of Francois and Fraser lakes, a necessary step in estimating rearing capacity. All relevant chemical and biological variables measured indicated that Fraser Lake is more productive and capable of rearing a greater number of sockeye/ha than Francois Lake (Table 2,3, Vollenweider 1976). Francois Lake is in the upper range of oligotrophy and Fraser Lake is mesotrophic but approaching eutrophy. The key role of phosphorus in limiting productivity has been documented for many western Canadian lakes (Stockner and Shortreed 1985; Shortreed and Stockner 1986) and Fraser system lakes (including Francois and Fraser lakes) are no exception. This is illustrated by the high correlation ($r^2 = 0.99$) between PR and TP_{spr} and between phytoplankton biomass (as chlorophyll) and TP_{spr} ($r^2 = 0.99$) (Fig. 22). Since Chilko, Quesnel, and Shuswap lakes are major sockeye producers in the Fraser River system and have reached rearing capacity in some cycle years (Hume et al. 1996), we found it informative to compare variables which indicate trophic status from these lakes with similar data from Francois and Fraser lakes (Table 10, Fig. 22). Variables such as TP_{spr}, bacteria number, chlorophyll, and PR all indicate that Francois Lake is substantially more productive than Chilko or Quesnel lakes but is quite similar to Shuswap Lake in productivity and trophic status. Fraser Lake is substantially more productive than any of these lakes and is more productive than any B.C. sockeye nursery lake for which data are available. PR, the most important biological variable in documenting trophic status, was lowest (79 mg $C \cdot m^{-2} \cdot d^{-1}$) in Chilko Lake, similar in Francois and Shuswap lakes (163 and 171, respectively), and highest (332) in Fraser Lake.

NUTRIENT LOADING AND ANTHROPOGENIC INPUTS

Nutrient chemistry in the two lakes was substantially different and accounts for their differing productivities. As previously stated, phosphorus concentrations were substantially higher in Fraser than in Francois Lake. Of equal importance to water quality was that nitrate concentrations were much higher in Francois than in Fraser Lake. Nitrate declined in Francois Lake during summer, but on only one occasion was nitrate depleted (<1 μg N/L). In Fraser Lake nitrate was depleted for much of each growing season (Fig. 5). Total phosphorus (TP) concentrations near the outlet of the Stellako River were substantially higher than those in Francois Lake and nitrate concentrations were lower (Table 2). These data indicate that of the Stellako River's nutrient load to Fraser Lake, Francois Lake provides most of the nitrogen and the Endako River provides most of the phosphorus. The higher TP in the Endako River is most likely due to the much higher human population in its drainage basin and the greater agricultural and industrial activity. TP concentrations in Fraser Lake were higher than those in the Stellako River, indicating that an important component of the nutrient load to the lake comes from portions of the drainage basin close to the lake (e.g. the town of Fraser Lake and residences around the lake). Further, Fraser Lake is shallow (mean depth = 13 m). Consequently, during the growing season most of the lake's sediments are in the epilimnion (and in the euphotic zone). Therefore, recycling from the sediments is likely to be another important source of phosphorus in Fraser Lake.

In some lakes with low P loading, nitrate depletion can lead to a complex co-limitation of nitrogen and phosphorus (Suttle and Harrison 1988; Suttle et al. 1991; Stockner and Shortreed

1994), while in lakes with higher P loading it can lead to a summer predominance of cyanobacterial microplankton (Stockner and Shortreed 1988). Conditions (stable stratification, high P, low N) in Fraser Lake are suitable for development of summer blooms of these undesirable phytoplankton. Cyanobacterial blooms we observed in Fraser Lake were not of sufficient magnitude to cause anything other than aesthetic problems (Fig. 11). However, if the population of the drainage basin increases, anthropogenic P inputs will rise through increases in sewage output, logging, mining, farming, ranching, and other industries. This will result in increases in the duration and intensity of the cyanobacteria blooms. When of sufficient magnitude, cyanobacteria blooms become noxious and have deleterious effects on water quality (e.g. taste, smell, hypolimnetic oxygen concentrations) (Lathrop 1992), with potentially serious consequences for the lake's plankton and fish communities. However, blooms of this magnitude normally occur only in highly eutrophied lakes. We suggest that nutrient loading to Fraser Lake would have to increase many times before cyanobacteria blooms reached levels which would adversely affect juvenile sockeye.

ZOOPLANKTON

Trophic status of lakes (such as Fraser Lake) with high riverine input and low water residence times is usually more directly controlled by physics, chemistry and biota of incoming waters than lakes with longer residence times (Carmack et al. 1979; Jasper et al. 1983). Fraser Lake is located only a short distance below Francois Lake, which has low sockeye numbers (Cass 1989) and high zooplankton biomass (Goodlad et al. 1974; Stockner and Shortreed 1983; this study). Prior to our investigation, it was known that Fraser Lake's juvenile sockeye grew at high rates even at high fish densities (Goodlad et al. 1974; J. Hume, unpublished data). Further, sockeye diet data suggested that these high densities had little impact on zooplankton community structure. This led us to hypothesize that Fraser Lake receives an influx of zooplankton from Francois Lake, enabling it to support higher densities of juvenile sockeye. To test this we sampled zooplankton in the Stellako River and at nearby sites in both Francois and Fraser lakes. We found that density and biomass of all macrozooplankton species in the Stellako River (0.5 km above Fraser Lake) were considerably lower than upstream in Francois Lake or downstream in Fraser Lake (Table 5). The majority of zooplankton flushed out of Francois Lake are removed before the Stellako River enters Fraser Lake. The abundant zooplankton community in Fraser Lake is produced in that lake and does not originate upstream.

Rotifers are often an abundant component of a lake's zooplankton community. While they are not a direct food resource for juvenile sockeye, they are critical prey items for adult cyclopoid copepods (Gilbert 1988a), which under certain conditions are in turn utilized by sockeye fry (Hume et al. 1996). It is well documented (see Gilbert 1988b, for review) that some rotifer species (*Keratella cochlearis* in particular) are suppressed in the presence of large (>1.2 mm) *Daphnia*. This suppression is thought to result from interference competition rather than direct predation (Burns and Gilbert 1986; Gilbert 1988a,b). In Fraser system lakes the most common mechanism for suppression of *Daphnia* numbers is heavy grazing pressure by sockeye fry. When this suppression occurs, rotifer numbers increase (Morton and Shortreed 1996). This results in increased numbers of copepods, which in turn provide an alternative (but less desirable) food source for sockeye fry. Given the relatively high densities of *Daphnia* in both Francois and Fraser lakes, we hypothesized that rotifer numbers would be suppressed during portions of the growing season when *Daphnia* was abundant. This proved to be the case in both lakes, since sharp declines in *Keratella* numbers occurred while *Daphnia* numbers

were increasing or at seasonal maxima (Fig. 17). However, in comparisons between lakes, zooplankton numbers appeared to be controlled more by trophic status than sockeye grazing pressure. Despite approximately 10-fold higher planktivore densities in Fraser Lake, both *Daphnia* and rotifer numbers were approximately 10x higher than in Francois Lake. At planktivore densities commonly seen in these and other Fraser system lakes, grazing pressure affects zooplankton community composition and productivity but total zooplankton biomass and productivity is most strongly affected by lake productivity.

We have measured copepod and *Daphnia* production rates in Fraser system lakes (Quesnel and Shuswap) which have considerable annual variation in planktivore density (K. Morton, unpublished data). At equivalent planktivore densities, production rates in Francois Lake were considerably higher than in Quesnel Lake and similar to rates in Shuswap Lake. Even at high fish densities, Fraser Lake had higher secondary production rates than those observed in any other Fraser system lake at any fish density. In some years, escapements and fry recruitment exceeded optimum numbers in both Quesnel and Shuswap lakes. In late summer and fall of these years, *Daphnia* production rates were depressed in both lakes and copepod rates were depressed in Quesnel Lake. This depression did not occur in either Francois or Fraser lakes. These secondary production data provide further confirmation that the rearing capacity of Francois and Fraser lakes is under-utilized and that the rearing capacity (normalized to area) of Fraser Lake exceeds that of any other Fraser system lake.

QUALITY OF SOCKEYE REARING ENVIRONMENT (TEMPERATURE, ZOOPLANKTON, DIET)

Growth and mortality of sockeye in lakes is controlled by a number of factors, both biotic and abiotic. One of the most important abiotic variables is temperature. If temperatures are too cold, energy flow through the lake ecosystem is slowed, with adverse effects on sockeye growth. If temperatures are warm, strong stratification is an inevitable result in the deep lakes of the Fraser River system. Zooplankton occupying a warm, stable epilimnion may not be fully available for sockeye grazing, since sockeye fry do not graze effectively in lake strata where temperatures are too high (Goodlad et al. 1974; Lebrasseur et al. 1978; Levy et al. 1991; J. Hume, unpublished data). Mid-summer epilimnetic temperatures in Francois and Fraser lakes exceeded 17°C for short periods only and deeper portions of the epilimnion never exceeded this temperature (Table 1; Fig. 3, 4). While Fraser Lake stratified more strongly than Francois Lake, for the majority of the growing season both lakes had thermal regimes where the entire water column was available for sockeye feeding.

Of major importance to juvenile sockeye is a zooplankton food resource that is readily available and sufficiently abundant to support sockeye growth. Presence of an adequate food supply for juvenile sockeye is dependent on a number of biotic and abiotic factors. First, the lake must be sufficiently productive to produce an adequate food supply, as zooplankton production and biomass is dependent on a lake's photosynthetic rate. This is illustrated by the high correlation ($r^2 = 0.97$) between mean daily PR and macrozooplankton biomass in Fraser system lakes (Fig. 22). If a lake is sufficiently unproductive, zooplankton will be present in such low numbers that sockeye growth rates will be extremely slow even at low planktivore densities. For example, in ultra-oligotrophic Morice Lake in the Skeena River system, fall fry weights averaged only 0.8 g even though densities were <100/ha (J. Hume, unpublished data).

In Fraser system lakes, juvenile sockeye actively select for large cladocerans (Goodlad et al. 1974; Hume et al. 1996; K. Morton, unpublished data). If *Daphnia* are present, sockeye will feed on this cladoceran almost exclusively. Only when intense grazing greatly reduces or eliminates *Daphnia* from the accessible water column will sockeye fry switch to feeding on smaller, more predator resistant macrozooplankton such as *Eubosmina* and *Diacylops*. In Francois Lake planktivore densities were low in the one year (1992) for which we have diet information, but we feel this is representative of all years since EFS numbers have never exceeded 1.4/ha. Since sockeye stomachs were 70% full, *Daphnia* made up 90% of the stomach contents, and a considerable number of large cladocerans were present late in the growing season, it is evident that Francois Lake sockeye had an abundance of food and that the lake was far below rearing capacity (Fig. 18). This low grazing pressure is further corroborated because *Daphnia* comprised from 22-32% of seasonal average macrozooplankton biomass despite being strongly selected for by sockeye fry (Table 4).

We obtained sockeye diet data from Fraser Lake over a range of fry densities (1,590-11,820/ha), and even at the highest density stomachs were 85% full and 85% of stomach contents were made up of *Daphnia* (Fig. 18). We do not have zooplankton data for the year (1989) of very high fry density, but in 1992 and 1993 (when fry numbers ranged from 1,590-1,730/ha) seasonal average *Daphnia* biomass ranged from 33-37% of total macrozooplankton biomass (Table 4). In 1989 neither stomach fullness nor the proportion of *Daphnia* in the stomachs was different from 1992 and 1993, suggesting that rearing capacity had not been reached even at those very high densities (Fig. 18). In an earlier study of Fraser Lake, Goodlad et al. (1974) also found *Daphnia* to be the primary diet item in summer and fall. We did not collect juvenile sockeye in early summer when Goodlad et al. (1974) found that *Heterocope* was the main food source. However, during our study *Heterocope* exhibited seasonal maxima in June and then rapidly declined to negligible levels by August, providing indirect evidence of its importance as an early season food source. Under high grazing pressure zooplankton communities in sockeye nursery lakes commonly exhibit characteristics such as fewer larger cladocerans, more small Bosminids, more rotifers, and a lower cladoceran to copepod ratio (Kyle et al. 1988). None of these indicators were observed in either lake during the study period.

JUVENILE SOCKEYE SIZE AND NUMBERS

In a recent study of Chilko, Quesnel, and Shuswap lakes, Hume et al. (1996) found that escapements of 15-31 EFS/ha produced the maximum number of fall fry or smolts. In an Alaskan lake, Koenings and Burkett (1987) found maximum smolt numbers were obtained at stocking densities of 10,000 fry/ha (approximately 19 EFS/ha). In all these lakes survival of juvenile sockeye decreased at higher escapement densities, resulting in the same or fewer juveniles. While sufficient data are not available to document the existence of density-dependent mortality in Francois Lake, escapements have never exceeded 1.4 EFS/ha, and it is unlikely to occur at these low spawner densities. Fraser Lake has had two escapements >25 EFS/ha where fall fry data are available, but unlike other Fraser system lakes, these high escapements do not appear to have affected survival of juvenile sockeye.

Hume et al. (1996) found that summer size did not vary with spawner density but that fall fry and smolt size declined rapidly as densities increased to 10 EFS/ha. Above this spawner density there was little decline in fall fry size in Quesnel and Shuswap lakes or in smolt

size in Chilko Lake. Francois Lake summer fry, fall fry, and smolts are comparable in size to those observed at similar densities in Quesnel Lake. At the low densities observed to date, Francois Lake smolts weigh approximately 10 g, but we suggest that size would decrease and mortality (both fry-to-smolt and smolt-to-adult) would increase with increasing fry recruitment (Hume et al. 1996; Hyatt and Stockner 1985, Koenings et al. 1993). Fraser Lake produces the largest fall fry in the upper Fraser River watershed. They averaged >4 g over a spawner range of 4 to 40 EFS/ha, and are larger than seen in either Quesnel or Shuswap lakes at similar densities. Mean size of Fraser Lake fall fry at 40 EFS/ha is similar to mean size of Quesnel fall fry at <10 EFS/ha. In Fraser system lakes with varying fry densities we have observed that overwintering growth of juvenile sockeye declined as fry densities increased (Hume et al. 1996). This also appears to have occurred in Francois and Fraser lakes in the one year we have both fall fry and smolt data for both lakes. In the fall of 1992 Fraser Lake fall fry were larger (4.3 g) than Francois Lake fall fry (3.4 g), but by the following spring Francois Lake smolts were larger (9.7 g) than Fraser Lake smolts (7.4 g). Average size of Fraser Lake smolts may have been biased by Francois Lake smolts emigrating at the same time. In 1992 we estimated there were almost 2/3 as many fall fry in Francois Lake as in Fraser Lake, thus, in the following spring, the large Francois Lake smolts may have caused an over-estimation of the size of Fraser Lake smolts. Francois and Fraser smolts weighed 3-6 g more than fall fry, the largest overwintering growth we have observed in any lake. The large size of Francois and Fraser fall fry and smolts and the high overwintering growth rates provide further indication that rearing capacities have not been fully utilized in either lake at any recorded escapement.

If sufficient data are available, juvenile sockeye numbers (either fall fry or smolts) are useful in predicting subsequent adult returns (Hume et al. 1996). Although at present there are insufficient data from Fraser Lake to reliably predict adult returns from fall fry numbers, a positive trend is evident (Fig. 23). With additional data points from intermediate and high density brood years, a useful predictive relationship may be developed.

OPTIMUM ESCAPEMENT AND REARING CAPACITY

All data indicate that Francois and Fraser lakes provide excellent rearing environments for juvenile sockeye. The data (escapements, juvenile sockeye size and diet, macrozooplankton biomass) also indicate that spawning escapements and fry recruitment to both lakes are below optimal. Even during the 1989 brood year, when total escapement to Fraser Lake was 368,000, its rearing capacity was under-utilized. We have developed a rearing capacity model (PR model - Hume et al. 1996) which is a variation of the Alaskan EV model (Koenings and Burkett 1987) and uses PR data to provide estimates of optimum escapements to and maximum smolt output from sockeye nursery lakes. Our model, which assumes no spawning ground limitation, predicts that optimum escapement to Francois Lake is 1.3 million sockeye, or 27x greater than the estimated spawning ground capacity (including the spawning channel) of 50,000. Our estimated optimum escapement to Fraser Lake is 0.5 million, only slightly greater than the estimated spawning ground capacity of 434,000. The model also predicts that smolt numbers to be expected from optimum fry recruitments are 72 million from Francois Lake and 27 million from Fraser Lake.

Rebuilding Fraser Lake sockeye stocks can be accomplished solely by management of returns (i.e. increased escapements), but for Francois Lake's rearing capacity to be fully utilized, fry recruitment must be increased far beyond what the current spawning grounds can produce. If fry recruitment to these lakes can be substantially increased through higher

escapements and/or enhancement, it is clear they will become major contributors to Fraser River sockeye returns.

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Table 1. Variation in seasonal (May-October) averages of salient physical variables.

Lake and year	Station	Surface temp. (°C)	Schmidt stability index (kg/sec^2)	Thermocline depth (m)	Secchi depth (m)	Euphotic zone depth (m)
Francois						
1992	1	11.8	447	18.4	7.5	10.6
	2	12.8	523	17.8	8.0	11.0
	3	14.0	596	18.3	8.3	11.3
	4	14.8	664	19.4	8.1	11.2
	Mean	13.4	557	18.5	8.0	11.0
1993	1	13.3	584	22.7	7.9	10.4
	2	13.7	714	11.4	8.2	10.3
	3	14.7	797	16.4	9.0	10.6
	4	14.6	839	13.0	8.6	11.9
	Mean	14.1	734	15.9	8.4	10.8
Fraser						
1992	1	15.1	840	9.9	4.0	8.3
	2	15.7	849	8.6	4.1	7.3
	Mean	15.4	845	9.3	4.1	7.8
1993	2	15.5	904	12.6	4.7	7.4

Table 2. Variation in mean epilimnetic seasonal (May-October) averages of selected chemical variables.

Lake and year	Stn.	pH	Total alk. (mg $CaCO_3$/L)	T.D.S. (mg/L)	Silicate (mg Si/L)	Nitrate (µg N/L)	Total P (µg/L)	Part. C (µg/L)	Part. N (µg/L)	Part. P (µg/L)
Francois										
1992	1			54	1.16	19.0	5.0	260	29	2.7
	2			50	1.10	15.8	4.5	250	28	2.9
	3			54	1.09	11.4	4.8	275	29	2.7
	4	7.3	35.5	49	1.05	10.4	5.3	256	27	2.5
	Mean	7.3	35.5	52	1.10	14.2	4.9	260	28	2.7
1993	1			52	1.08	7.0	7.3	368	39	3.1
	2			51	1.05	6.2	6.9	298	31	3.1
	3			53	1.06	5.8	6.0	291	28	3.0
	4	7.8	34.4	55	1.06	6.2	6.7	307	30	2.7
	Mean	7.8	34.4	53	1.06	6.3	6.7	316	32	3.0
Fraser										
1992	1			70	1.42	2.4	10.5	562	83	7.0
	2	7.3	44.9	67	1.40	3.8	13.7	626	78	7.1
	Mean	7.3	44.9	69	1.41	3.1	12.1	594	81	7.1
1993	2	7.8	41.8	70	1.57	3.0	17.2	586	87	6.5
Stellako R.										
1992	1			61	1.22	5.5	8.4	352	30	4.0
1993	1					5.7	13.6			4.8

Table 3. Variation in seasonal (May-October) averages of biological variables.

Lake and year	Stn.	Bacteria #x10^6/mL	Phytoplankton (#x10^3/mL)			Chlorophyll (µg/L)				Photosynthetic rate (mg C·m^{-2}·d^{-1})			
			Pico.	Nano.	Micro.	Total	Pico.	Nano.	Micro.	Total	Pico.	Nano.	Micro.
Francois													
1992	1	1.21	53.311	0.44	0.35	1.88	1.04	0.42	0.42				
	2	1.23	75.700	0.46	0.32	2.00	0.99	0.58	0.43				
	3	1.26	53.011	0.47	0.30	2.06	0.98	0.49	0.58				
	4	1.27	49.411	0.42	0.38	1.69	0.92	0.40	0.37	201	63	74	72
	Mean	1.24	57.866	0.45	0.34	1.91	0.98	0.47	0.45	201	63	74	72
1993	1	1.44	63.966	0.47	0.32	1.99	1.03	0.45	0.51				
	2	1.33	78.877	0.55	0.28	2.06	1.07	0.52	0.48				
	3	1.18	72.477	0.73	0.35	1.99	1.07	0.51	0.41				
	4	1.12	62.600	0.56	0.23	1.65	0.79	0.48	0.38	124	32	73	66
	Mean	1.27	69.477	0.58	0.30	1.92	0.99	0.49	0.45	124	32	73	66
Fraser													
1992	1	1.52	86.700	0.89	4.21	4.21	1.79	1.34	1.08				
	2	1.52	68.277	0.95	4.15	3.84	1.60	0.58	1.75	410	74	172	198
	Mean	1.52	77.499	0.92	4.18	4.03	1.70	0.96	1.42	410	74	172	198
1993	2	1.37	64.766	0.78	1.51	4.36	1.41	0.89	2.07	254	27	48	212
Stellako R.													
1992	1	1.31	39.111	0.56	0.42	1.31	0.79	0.32	0.25				
1993	1	1.17	55.555	0.72	0.33	1.50							

Table 4. Variation in seasonal (May-October) average biomass of major zooplankton genera and of macrozooplankton (>250 μm).

Lake and year	Station	Biomass (mg dry weight/m^2)						
		Bosmina	*Daphnia*	*Diacyclops*	*Epischura*	*Heterocope*	*Leptodiaptomus*	Macrozooplankton
Francois								
1992	1	141	332	467	5	0	251	1202
	2	128	114	399	8	0	255	916
	3	95	579	504	11	0	279	1503
	4	193	535	264	13	0	218	1298
	Mean	139	390	409	9	0	251	1230
1993	1	144	330	374	31	0	641	1526
	2	192	337	503	12	0	437	1500
	3	143	255	525	8	0	360	1312
	4	139	313	603	9	0	251	1341
	Mean	155	309	501	15	0	422	1420
Fraser								
1992	1	23	1282	625	31	777	919	3214
	2	25	637	642	10	350	419	1915
	Mean	24	959	633	21	564	669	2564
1993	2	73	732	551	7	307	680	2189

Table 5. Comparison of seasonal (May-October) average biomass of major zooplankton genera and of macrozooplankton (>250 μm). Data are from station 4 on Francois Lake, from the Stellako River 0.5 km upstream from Fraser Lake, and from station 2 on Fraser Lake. Data were collected in 1992 with a Schindler trap from a depth of 0-1 m.

Group	Biomass (mg dry weight/m^3)		
	Francois Lake	Stellako River	Fraser Lake
Bosmina	2.65	0.13	12.71
Daphnia	9.91	0.31	12.68
Diacyclops	1.89	0.11	6.47
Leptodiaptomus	6.19	0.09	11.65
Macrozooplankton	26.12	0.58	48.66

Table 6. Sockeye populations at various life history stages for Francois and Fraser lakes. See text for methods used for these estimates. Brood year is the year of spawning. Consequently, emergent, summer, and fall fry were calculated or observed in the following year. Numbers in brackets are 2 SE.

Brood year	EFS (#x10^3)	Emergent fry (millions)			Summer fry		Fall fry	
		Channel	Wild	Total	Date	#x10^6	Date	#x10^6
Francois Lake								
1973	9.6	9.91	2.21	12.12	Jul. 29	1.86		
1974	2.1	1.00	1.05	2.05			Sep. 17	2.10
1977	9.3	14.21	0.29	14.50	Aug. 23	2.29		
1979	20.4	19.12	2.90	22.06	Aug. 27	0.80		
1991	33.5	16.35	1.83	18.18	Aug. 7	6.63	Sep. 23	6.00
						(1.19)		(1.05)
Fraser Lake								
1973	15.4		9.93	9.93	Jul. 27	4.83		
1974	23.7		15.27	15.27			Sep. 16	6.58
1977	10.9		7.03	7.03	Aug. 26	4.87		
1979	152.6		98.26	98.26	Aug. 31	15.90		
1981	12.0		7.75	7.75	Aug. 22	6.84		
						(0.65)		
1988	200.5		129.15	129.15			Sep. 28	64.15
								(21.79)
1990	56.5		36.40	36.40			Sep. 13	11.26
								(2.56)
1991	54.4		35.03	35.03	Aug. 11	18.81	Sep. 22	9.38
						(9.41)		(2.07)
1992	55.2		35.54	35.54			Oct. 1	8.66
								(1.39)

Table 7. Size of fish in Francois Lake midwater trawl catches.

			Weight (g)				Length (mm)			
Date	Group/Taxa	N	Mean	±95% C.I.	Min	Max	Mean	±95% C.I.	Min	Max
Sep. 18 , 1975	Age-0	1	5.8	.	5.8	5.8	77	.	77	77
	Whitefish	7	.	.	.	.	.	.	.	.
	Unidentified	1	.	.	.	.	.	.	.	.
Sep. 6, 1976	Age-0	12	2.9	0.84	0.8	4.5	61	7.2	41	73
	Whitefish	6	.	.	.	.	.	.	.	.
Sep. 2, 1977	Age-0	1	8.1	.	8.1	8.1	86	.	86	86
	Age-2+	1	.	.	.	.	.	.	.	.
	Unidentified	1	.	.	.	.	.	.	.	.
Aug. 23, 1978	Age-0	27	2.3	0.31	1.5	4.5	58	2.7	50	74
	Age-1	1	34.2	.	34.2	34.2	136	.	136	136
	Age-2+	2	.	.	.	.	300	0.0	300	300
	Whitefish	3	0.7	0.42	0.5	0.8	40	7.2	37	42
	Sculpin	12	0.2	0.47	0.02	2.6	17	8.8	11	61
	Unidentified	1	0.4	.	0.4	0.4	31	.	31	31
Aug. 26, 1980	Age-0	7	2.9	0.50	1.8	3.5	62	4.4	53	68
	Age-1	1	4.2	.	4.2	4.2	71	.	71	71
	Whitefish	57	3.0	0.60	0.0 3	8.0	64	5.8	12	96
	Sculpin	30	0.03	0.01	0.0 1	0.1	11	0.8	10	19
Aug. 8, 1992	Age-0	282	1.8	0.07	0.5	4.1	54	0.7	38	72
	Age-1	2	2.8	3.62	2.5	3.1	61	25.4	59	63
	Whitefish	11	3.5	5.56	0.1	28.3	50	20.4	18	128
	Sculpin	2	0.2	2.10	0.0 3	0.4	22	114.4	13	31
	Unidentified	3	0.5	1.55	0.1	1.2	36	27.9	26	48
Sep. 23, 1992	Age-0	3	4.1	0.72	3.8	4.3	76	2.5	75	77
	Sculpin	1	0.1	.	0.1	0.1	18	.	18	18

Table 8. Size of fish in Fraser Lake midwater trawl catches.

			Weight (g)				Length(mm)			
Date	Group/Taxa	N	Mean	±95% C.I.	Min	Max	Mean	±95% C.I.	Min	Max
Sep. 16, 1975	Age-0	117	4.8	0.27	1.5	8.6	73	1.6	49	89
	Whitefish	10	.	.	.	.	.	.	.	.
	Cyprinids	1		.	.	.	.	.	.	
Sep. 5, 1976	Age-0	224	4.5	0.18	1.3	9.4	72	1.0	49	92
	Whitefish	12	.	.	.	.	.	.	.	.
	Sculpin	2	.	.	.	.	.	.	.	.
	Unidentified	1	.	.	.	.	.	.	.	.
Sep. 1, 1977	Age-0	156	4.3	0.25	1.4	10.3	70	1.3	49	95
	Whitefish	110	10.2	1.35	0.5	33.8	93	5.9	35	150
	Cyprinids	1	1.0	.	1.0	1.0	43	.	43	43
	Sculpin	1	3.7	.	3.7	3.7	65	.	65	65
	Unidentified	2	12.9	146.82	1.4	24.5	94	495.5	55	133
Aug. 26, 1978	Age-0	166	3.7	0.23	0.7	7.6	68	1.5	40	86
	Age-1	2	76.9	190.91	61.9	92.0	174	177.9	160	188
	Whitefish	2	2.0	23.00	0.2	3.8	49	336.7	22	75
	Sculpin	14	0.2	0.08	0.0	0.5	22	4.2	11	33
	Unidentified	3	91.5	187.05	13.1	163.2	163	176.2	100	240
Aug. 30, 1980	Age-0	152	3.0	0.19	0.7	6.5	63	1.4	40	83
	Whitefish	17	8.8	4.16	0.3	35.8	88	14.1	34	148
	Sculpin	6	0.1	0.17	0.0	0.4	17	11.3	9	34
Aug. 22, 1982	Age-0	64	2.4	0.25	0.8	6.1	58	2.0	41	82
	Age-2+	3	.	.	.	.	.	.	.	.
	Whitefish	3	5.9	1.46	5.6	6.3	83	10.8	80	85
	Chinook	1	.	.	.	.	.	.	.	.
Sep. 20, 1989	Age-0	91	4.6	0.32	1.9	8.1	73	1.7	55	87
Sep. 13, 1991	Age-0	190	3.4	0.19	0.7	8.6	66	1.1	40	85
	Age-1	1	91.5	.	91.5	91.5	184	.	184	184
Aug. 10, 1992	Age-0	152	3.3	0.20	0.7	10.8	66	1.2	42	97
	Age-1	1	33.0	.	33.0	33.0	140	.	140	140
	Whitefish	1	7.7	.	7.7	7.7	88	.	88	88
	Sculpin	1	0.1	.	0.1	0.1	20	.	20	20
	Unidentified	1	0.8	.	0.8	0.8	49	.	49	49
Sep. 21, 1992	Age-0	201	4.1	0.24	0.8	9.9	71	1.3	42	94
	Whitefish	3	.	.	.	.	330	.	330	330
	Squawfish	1	.	.	.	.	.	.	.	.
Oct 1, 1993	Age-0	53	5.0	0.55	2.1	10.8	75	2.6	58	94

Table 9. Sockeye smolt data from Francois and Fraser lakes. All smolts reported here ar age-1. Francois Lake smolts were caught in the Stellako River and Fraser Lak smolts were caught in the Nautley River.

		Weight (g)				Length(mm)			
Date	N	Mean	SD	Min	Max	Mean	SD	Min	Max
Francois Lake									
April 22 - May 15, 1992	132	9.8	1.50	4.9	14.1	99	5.3	78	110
April 15- May 23 , 1993	122	9.7	1.90	5.2	14.6	97	6.6	78	112
April 15- May 20 , 1994	200	10.1	2.15	3.7	16.7	99	7.3	79	121
Fraser Lake									
May 1 - 18, 1993	114	7.4	2.61	3.1	13.6	87	10.1	65	107

Table 10. Comparison of data from Fraser and Francois lakes with data from other Fraser system lakes. Data are whole-lake, multi-year, seasonal averages. Data from Chilko, Quesnel, and Shuswap lakes are from Hume et al. (1996), MacLellan et al. (1994), Morton and Shortreed (1996), Nidle and Shortreed (1994;1996), and K. Shortreed (unpublished data).

	Lake				
Variable	Francois	Fraser	Chilko	Quesnel	Shuswap
Mean epil. temperature (°C)	11.9	13.7	8.4	12.4	14.9
Stability index (kg/sec)	646	875	293	753	1392
Thermocline depth (m)	17.2	11.0	19.5	12.2	10.0
Euphotic zone depth (m)	10.9	7.6	17.7	15.1	12.3
Mean epil. nitrate (μg N/L)	10.3	3.1	12.0	69.3	18.4
Mean epil. TP (μg/L)	5.8	14.7	2.3	2.7	5.1
Mean epil. TP_{spr} (μg/L)	6.4	18.8	1.9	2.7	6.3
Mean epil. bacteria (#x10^6/mL)	1.26	1.45	0.85	0.76	0.99
Mean epil. chlorophyll (μg/L)	1.92	4.20	0.68	1.03	1.81
Photosynthetic rate (mg $C \cdot m^{-2} \cdot d^{-1}$)	163	332	79	102	171
Macrozooplankton biomass	1325	2376	715	894	1005
Daphnia biomass (mg/m^2)	350	846	5	247	400
Daphnia prod. (mg dry $wt \cdot m^{-3} \cdot d^{-1}$)	0.29	1.30		0.10	0.28
Copepod prod. (mg dry $wt \cdot m^{-3} \cdot d^{-1}$)	1.37	3.59	0.36	0.51	1.56

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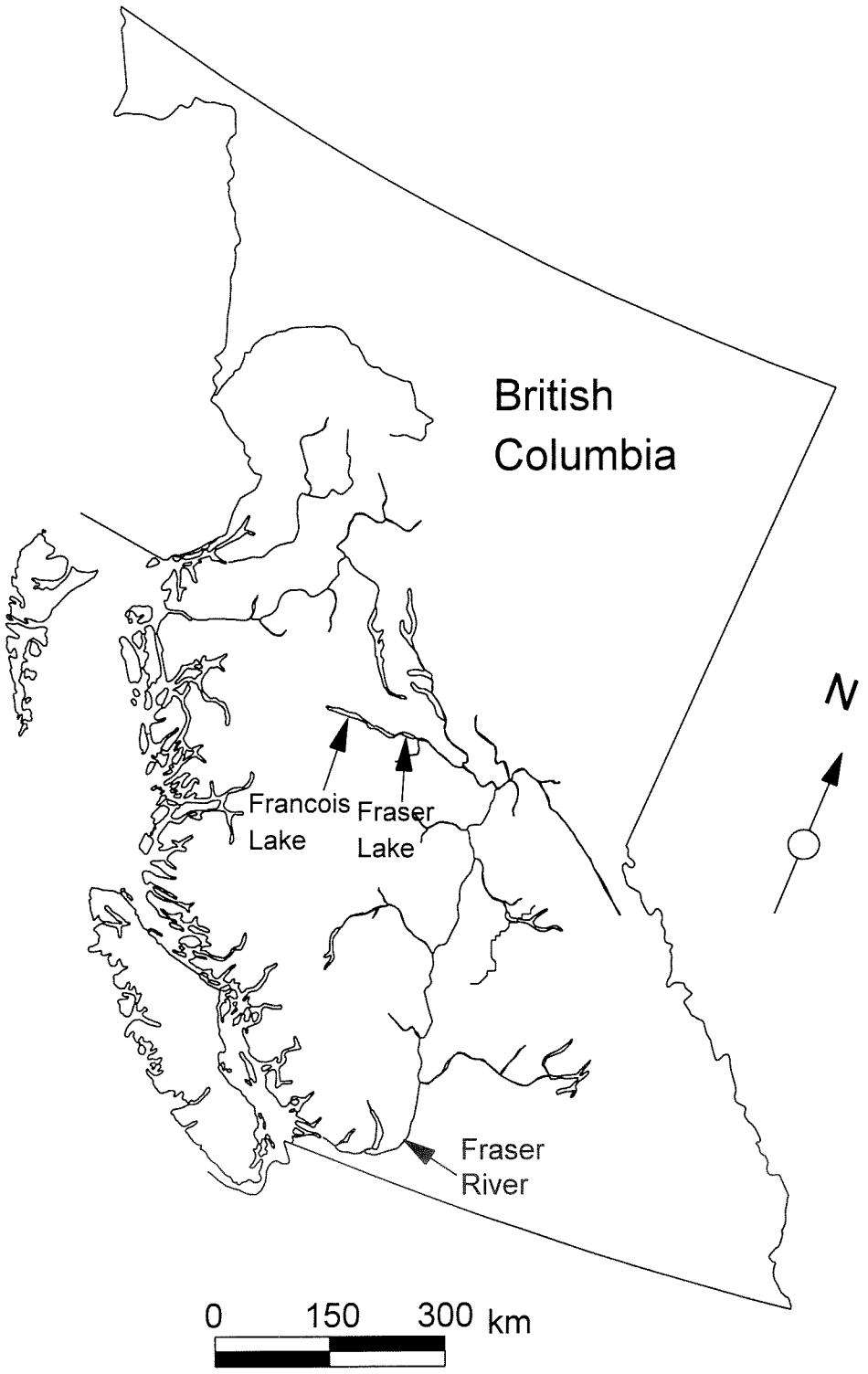
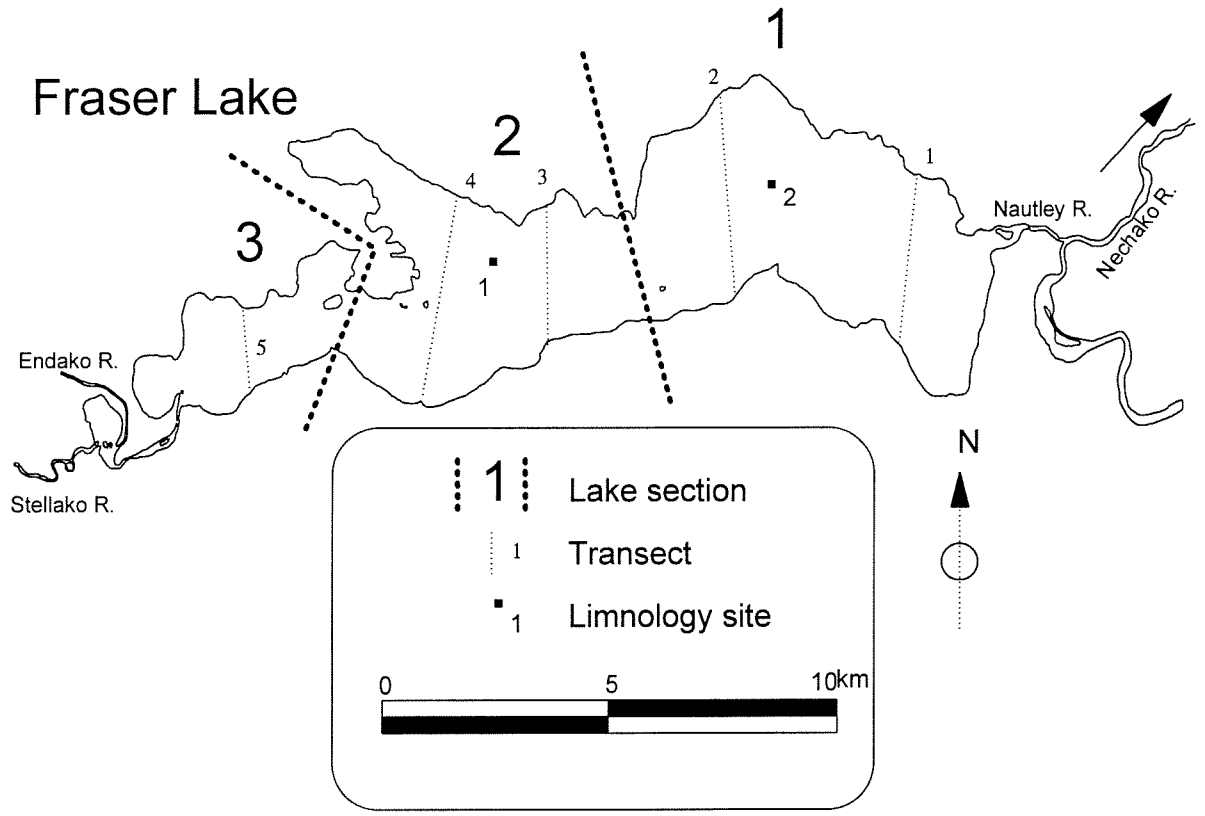


Fig. 1. Map of British Columbia showing location of the study lakes.



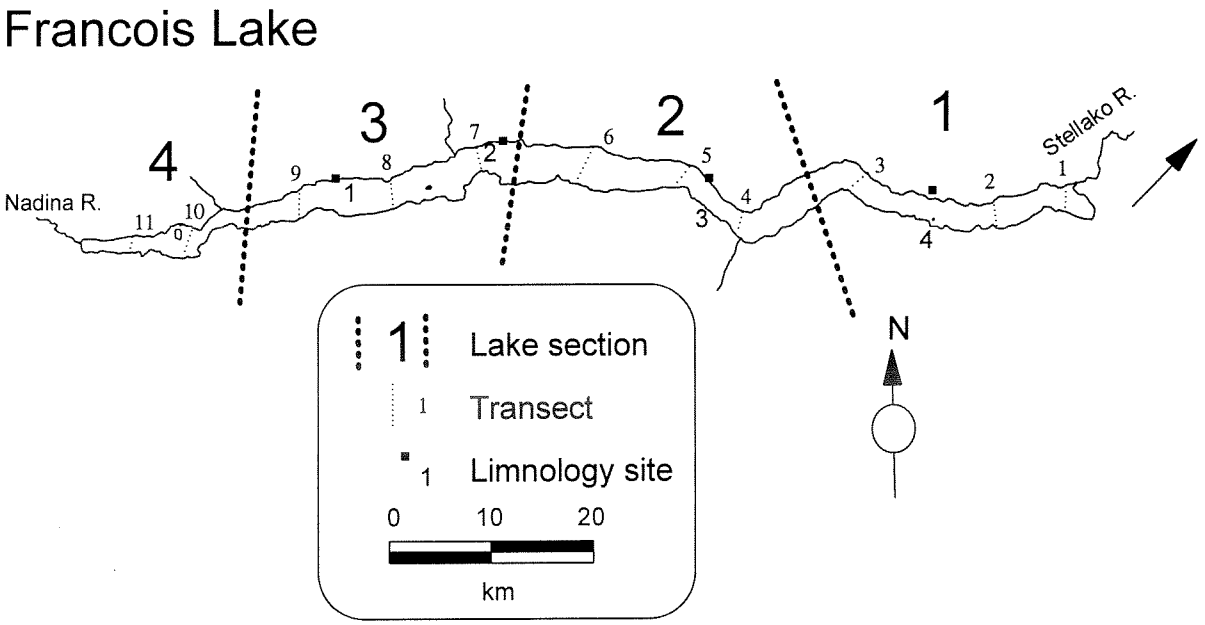


Fig 2. Maps of Francois and Fraser lakes showing sampling locations for limnological, hydroacoustic, and trawl surveys.

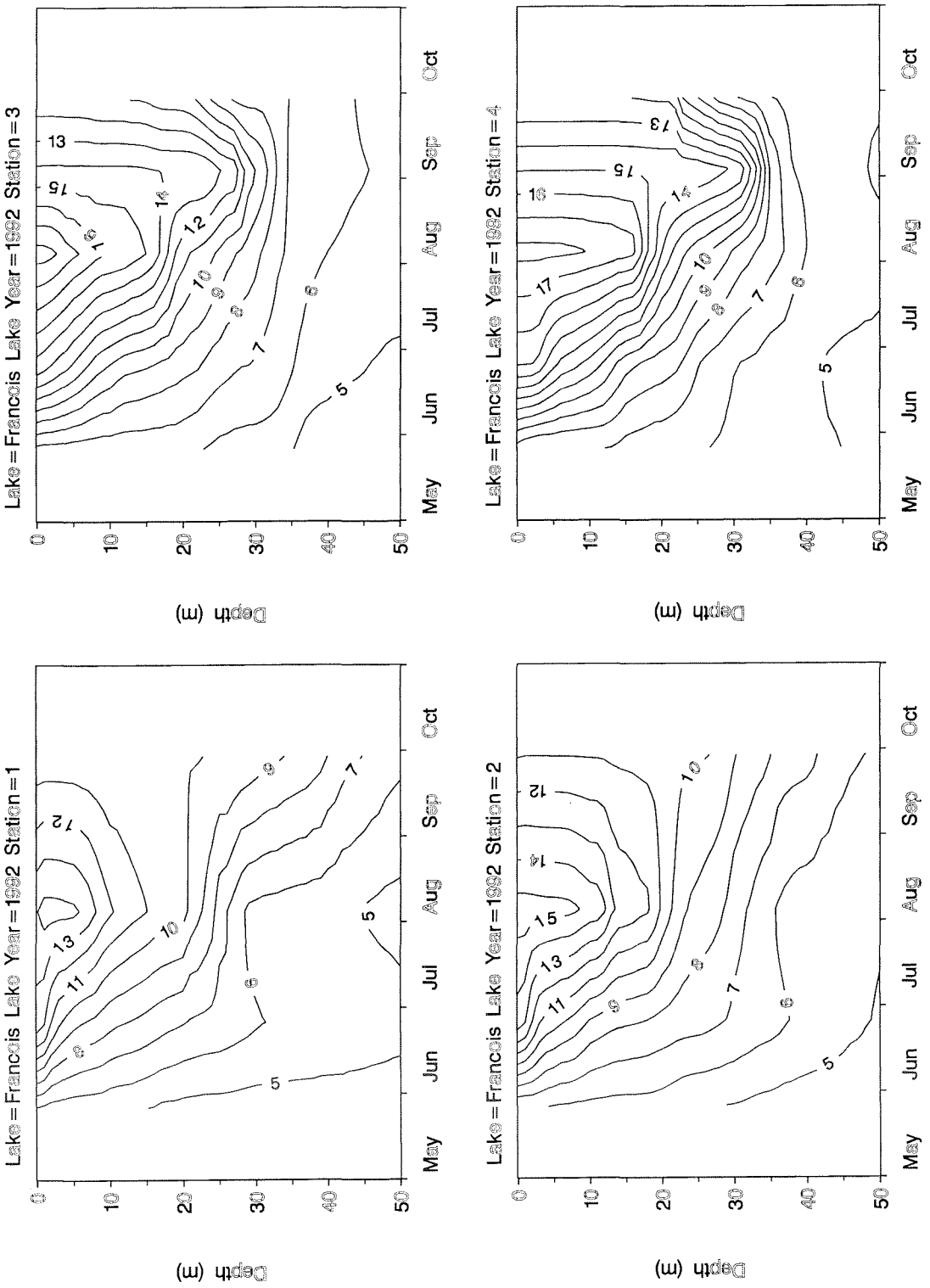


Fig. 3. Variation in seasonal temperature isotherms for Francois Lake in 1992.

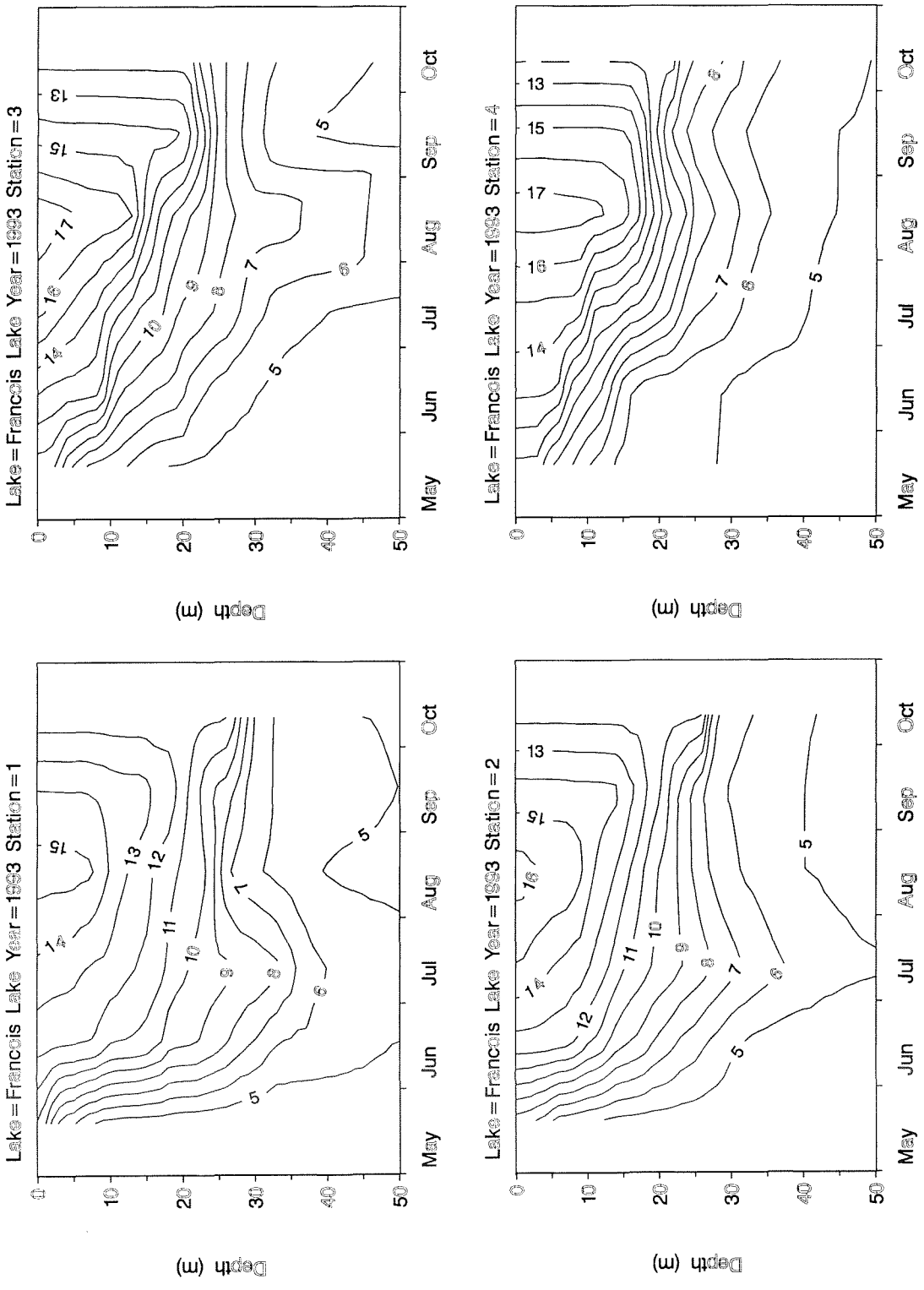


Fig. 3 (Cont.) Variation in seasonal temperature isotherms for Francois Lake in 1993.

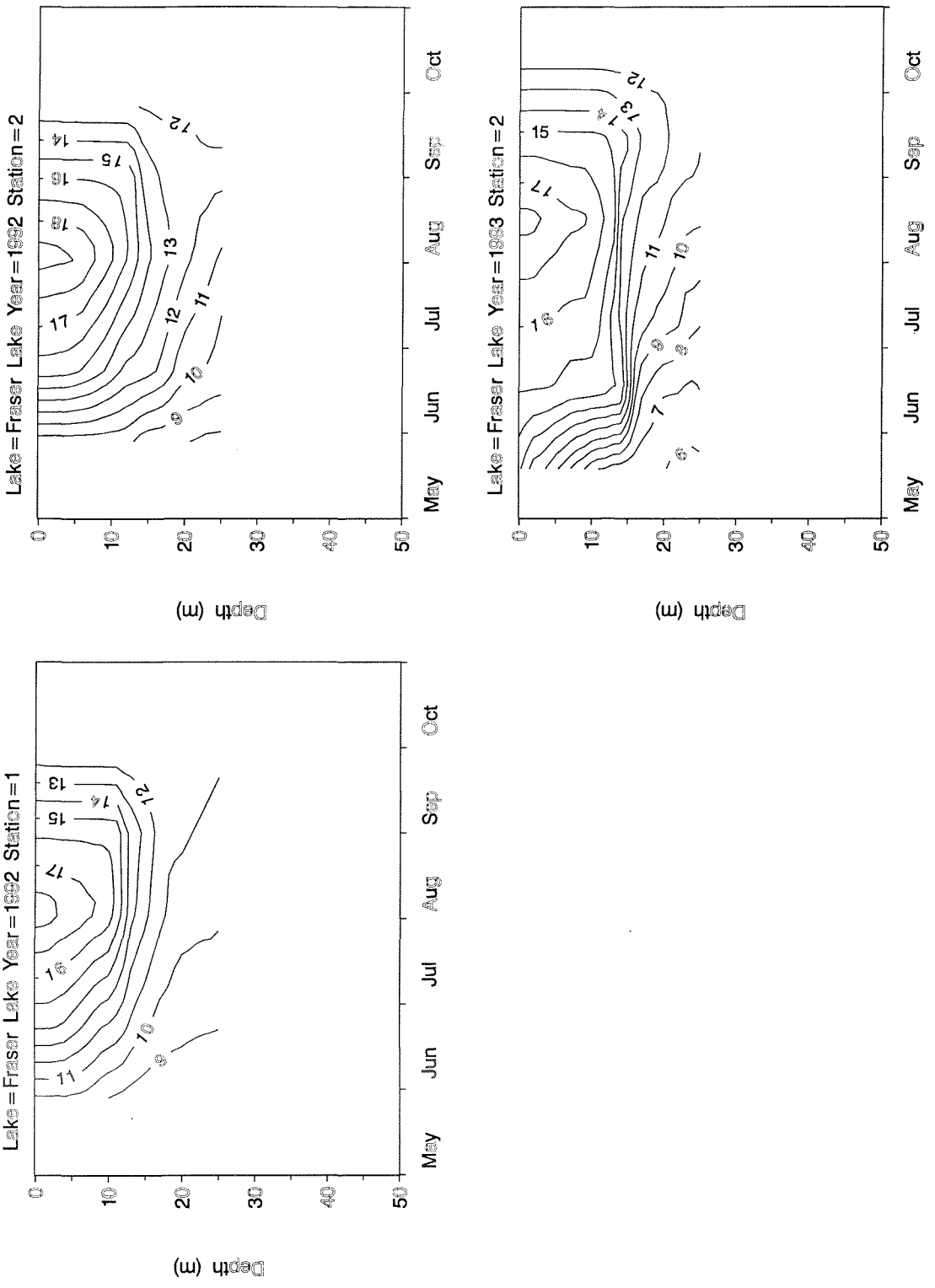


Fig. 4. Variation in seasonal temperature isotherms for Fraser Lake in 1992 and 1993.

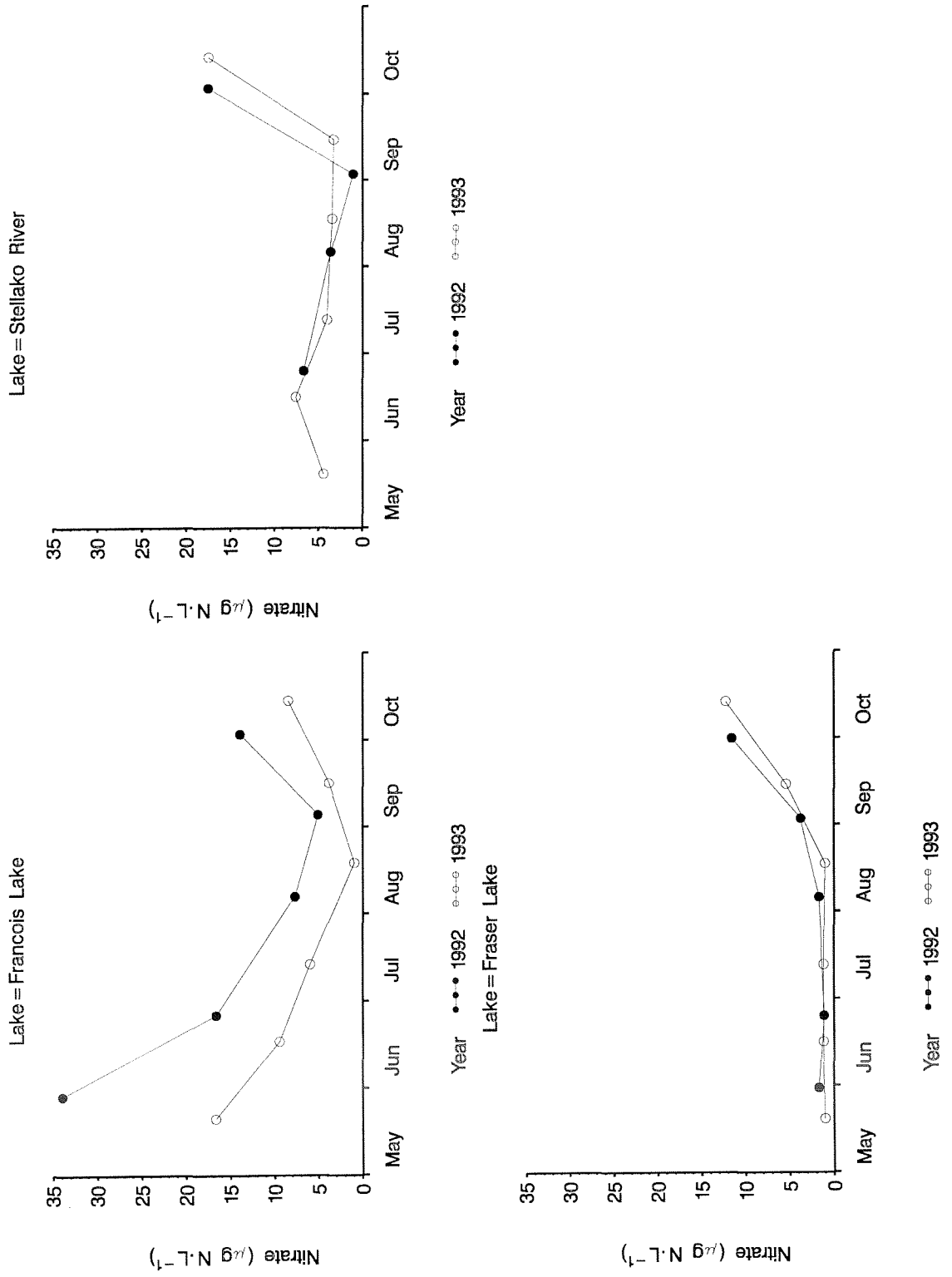
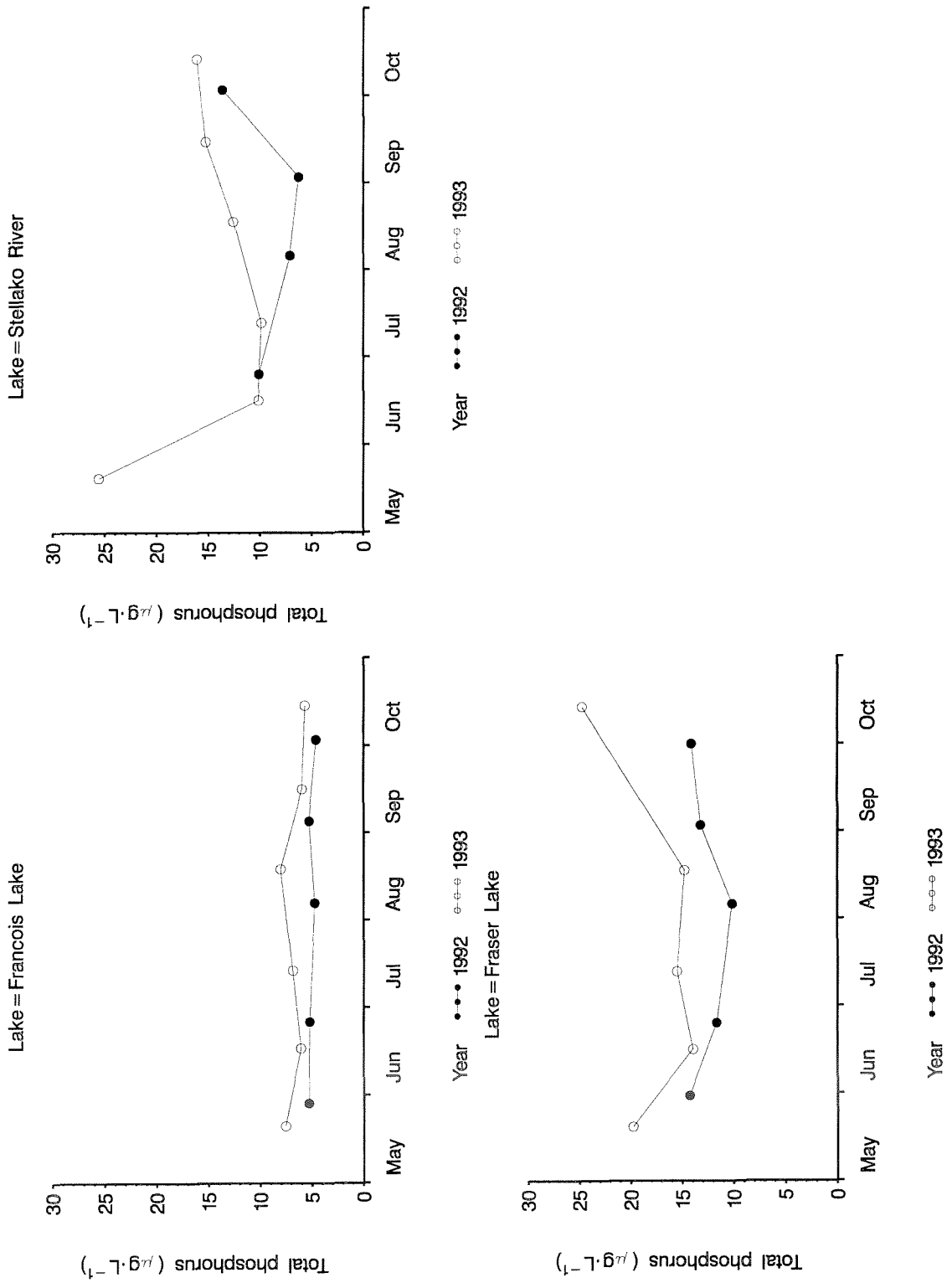


Fig. 5. Variation in mean epilimnetic nitrate concentration in the study lakes and in the Stellako River.



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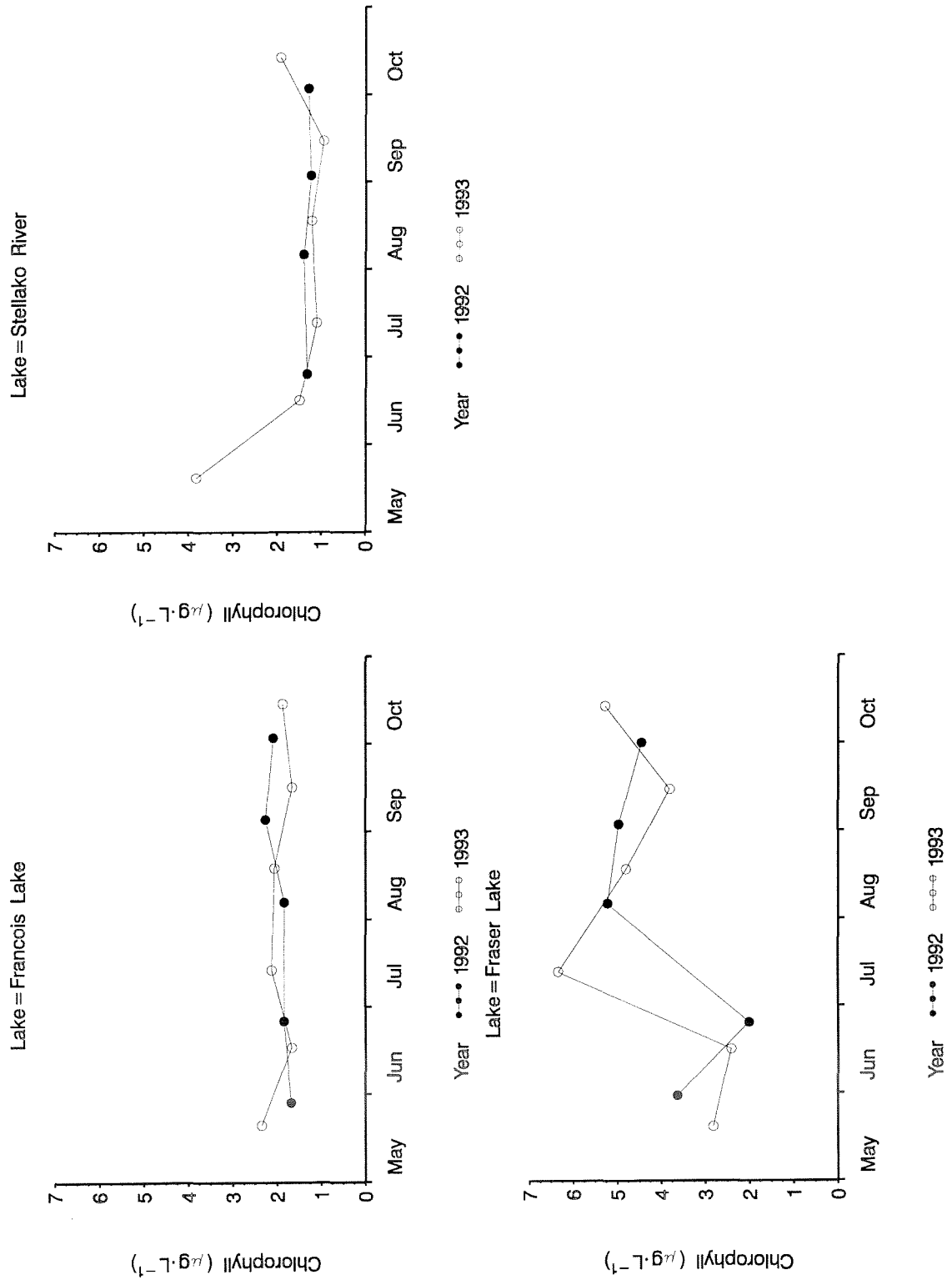
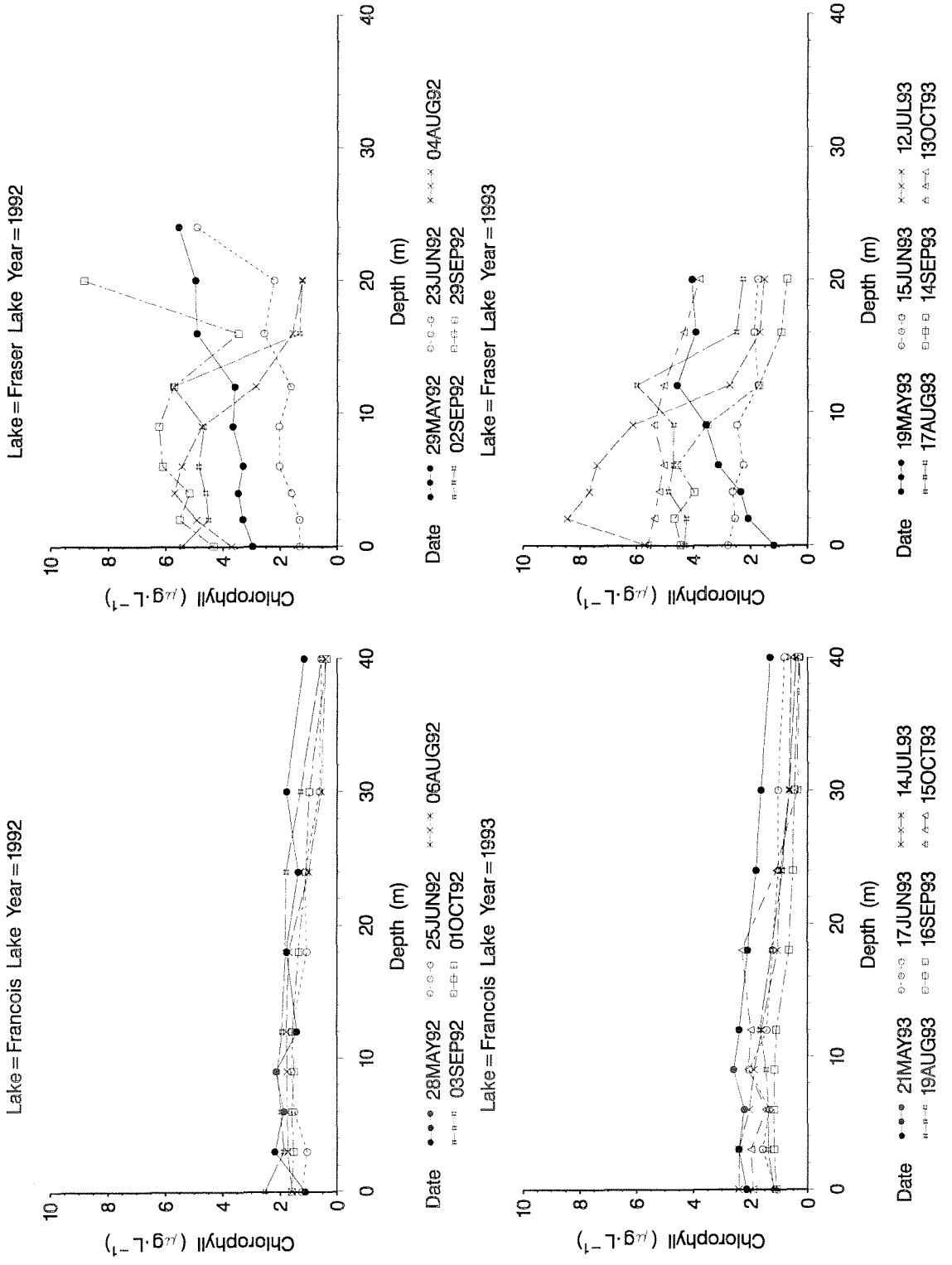


Fig. 7. Variation in mean epilimnetic chlorophyll concentration in the study lakes and in the Stellako River.



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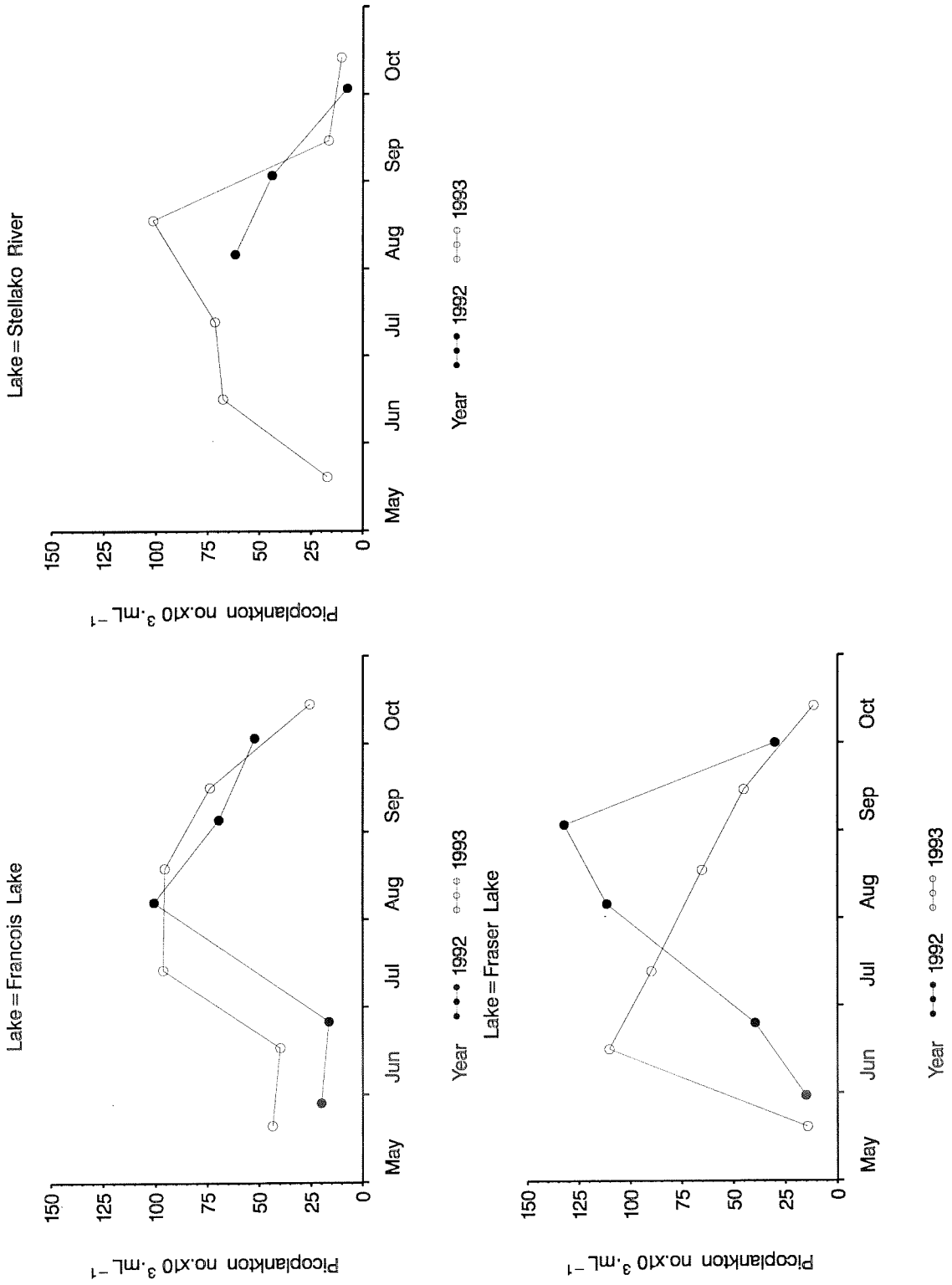

Fig. 9. Seasonal variation in mean epilimnetic picoplankton numbers in the study lakes and in the Stellako River.

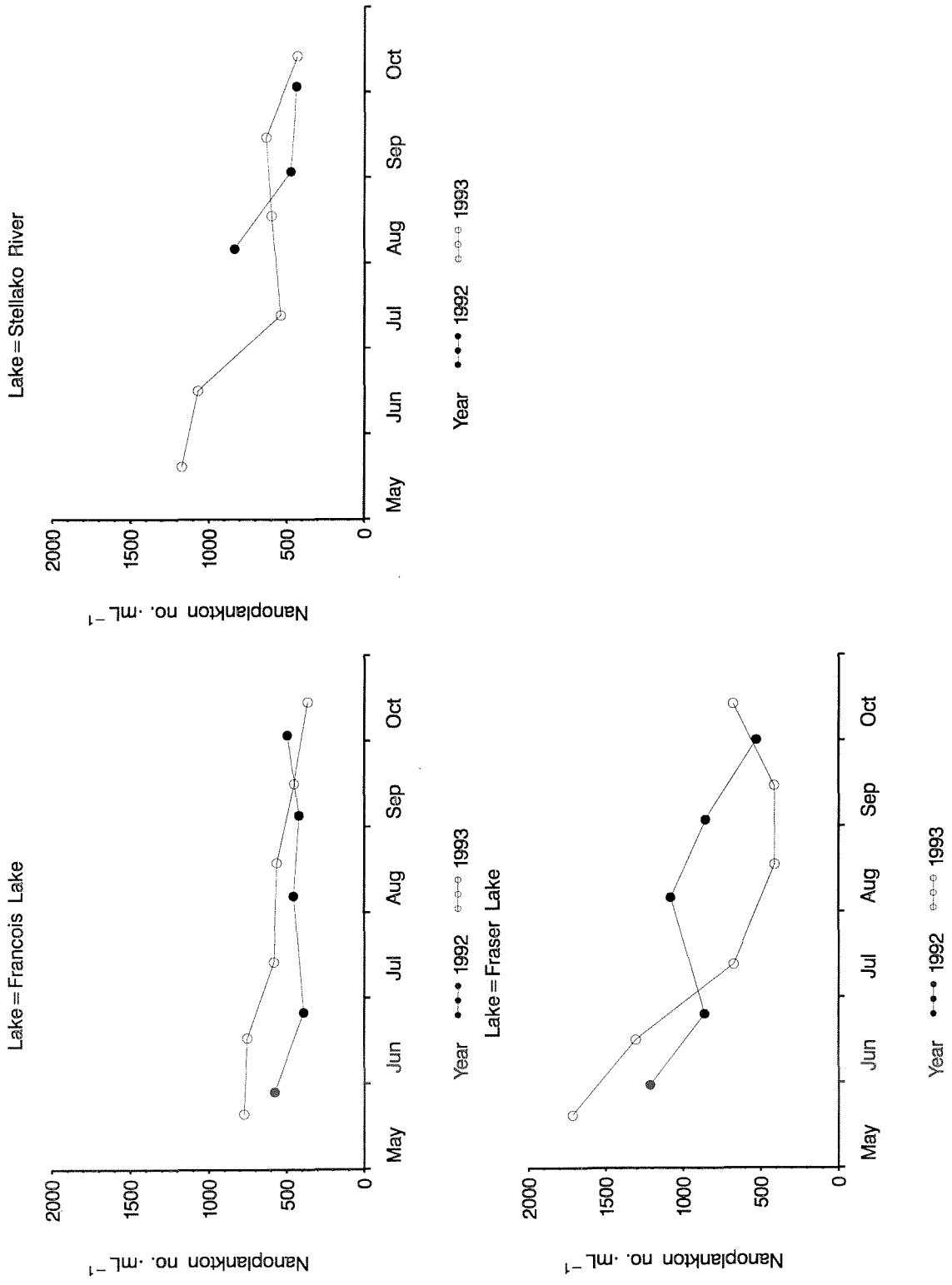

Fig. 10. Seasonal variation in mean epilimnetic nanoplankton numbers in the study lakes and in the Stellako River.

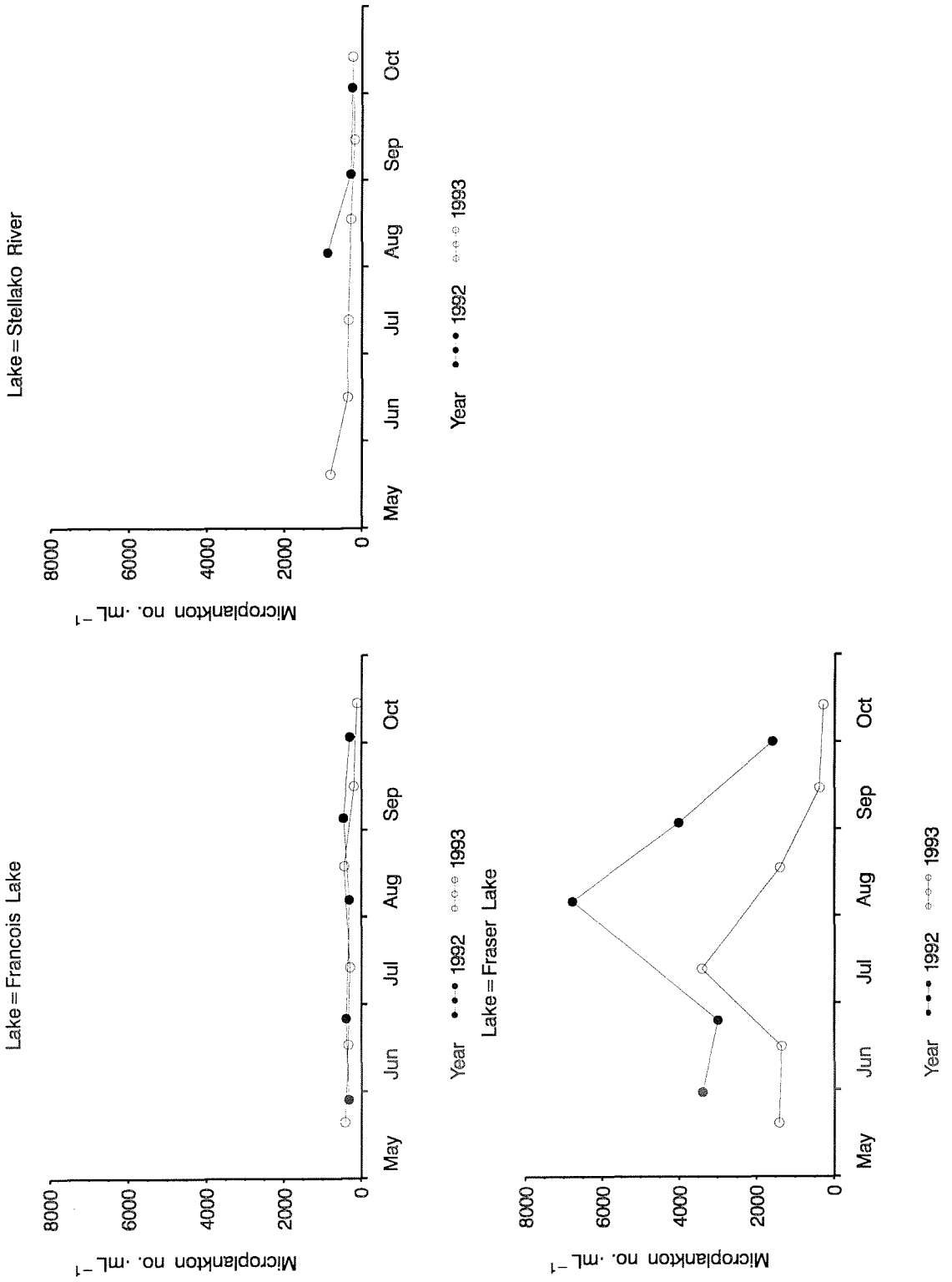

Fig. 11. Seasonal variation in mean epilimnetic microplankton numbers in the study lakes and in the Stellako River.

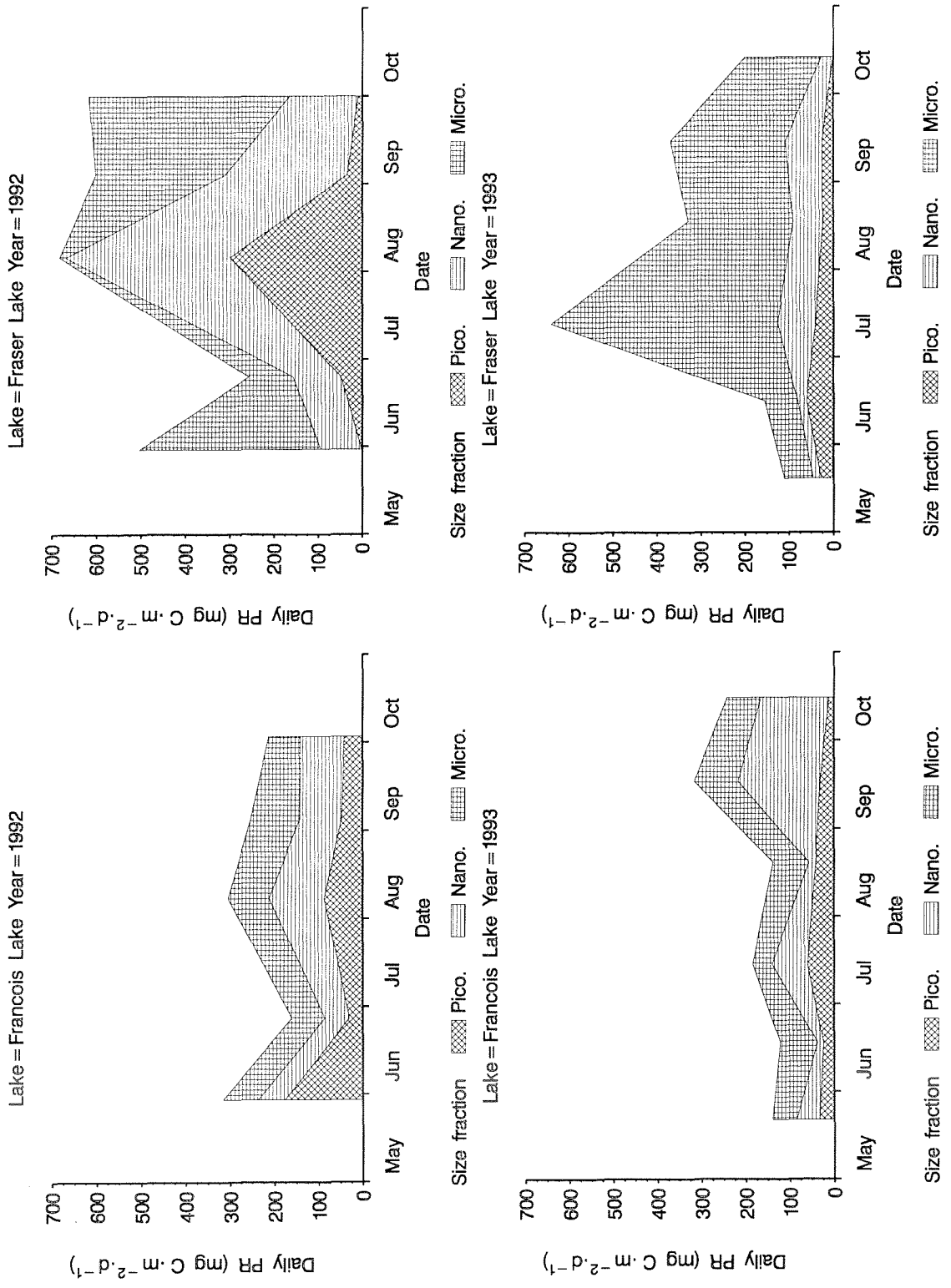

Fig. 12. Seasonal variation in daily PR for the pico-, nano-, and microplankton size fractions in the study lakes. Data are from station 4 in Francois Lake and from station 2 in Fraser Lake.

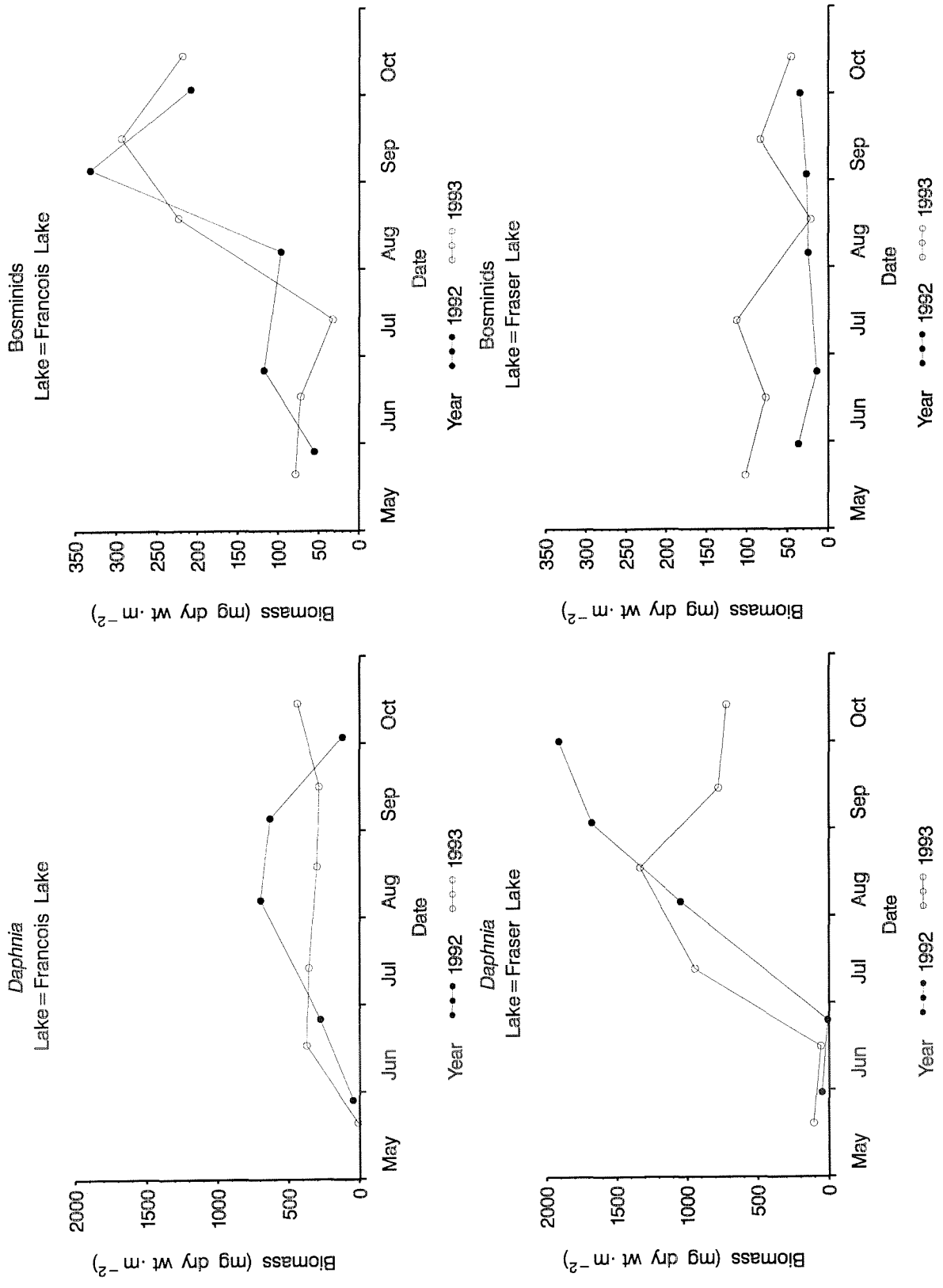

Fig. 13. Seasonal variation in *Daphnia* and Bosminid biomass in the study lakes. Data were collected with 30-m vertical hauls using a Wisconsin net.

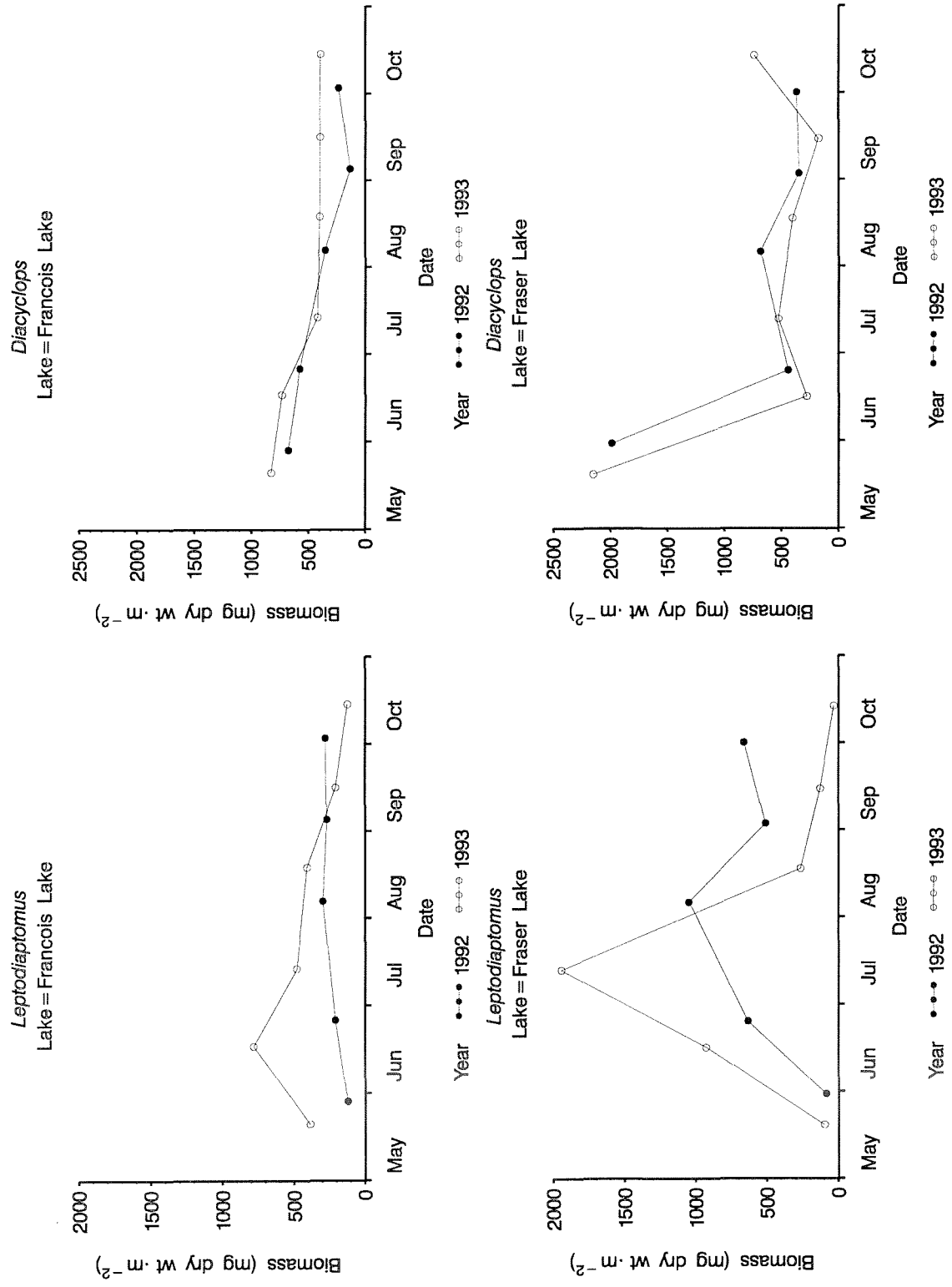

Fig. 14. Seasonal variation in *Leptodiaptomus* and *Diacyclops* biomass in the study lakes. Data were collected with 30-m vertical hauls using a Wisconsin net.

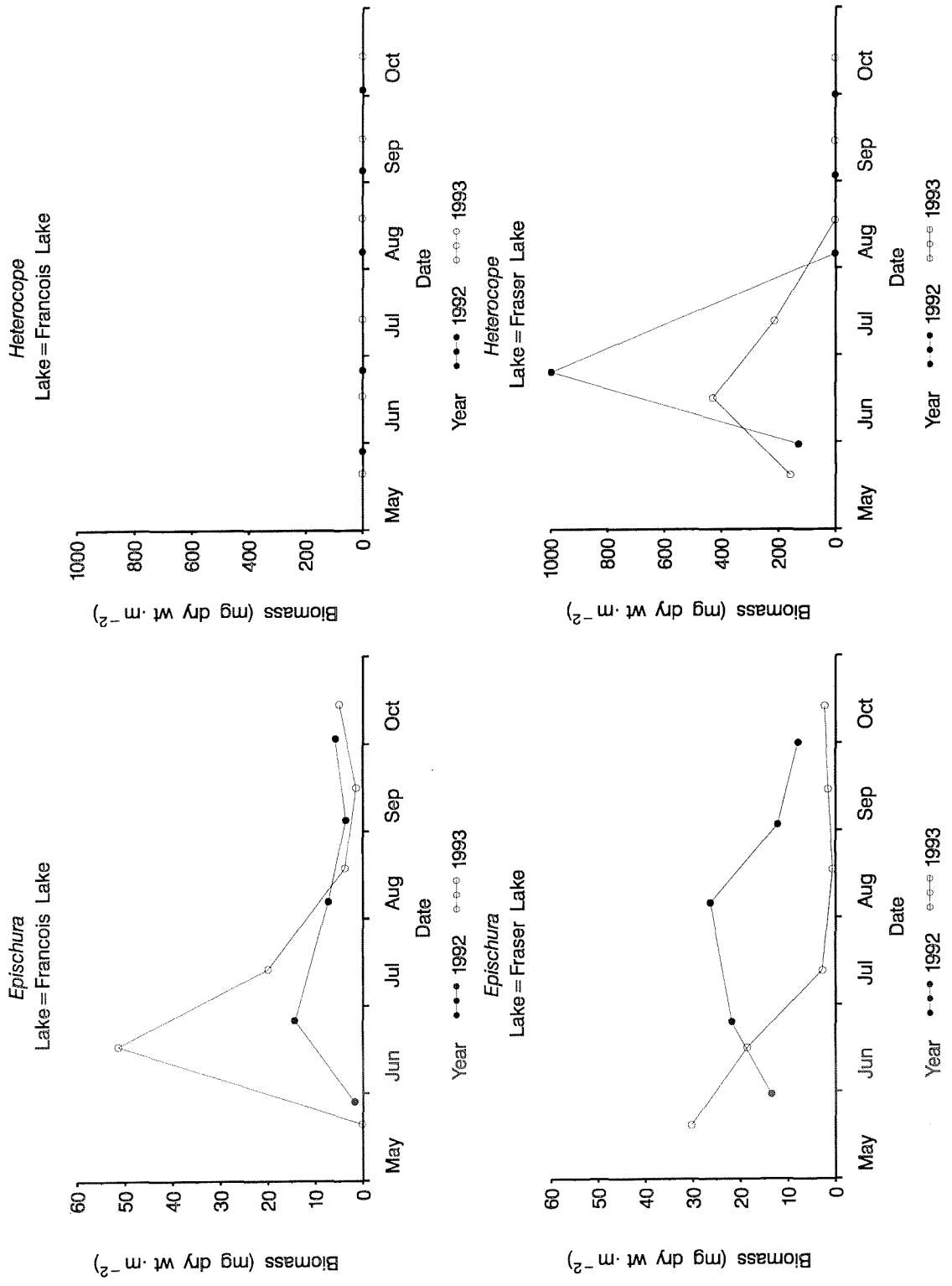

Fig. 15. Seasonal variation in *Epischura* and *Heterocope* biomass in the study lakes. Data were collected with 30-m vertical hauls using a Wisconsin net.

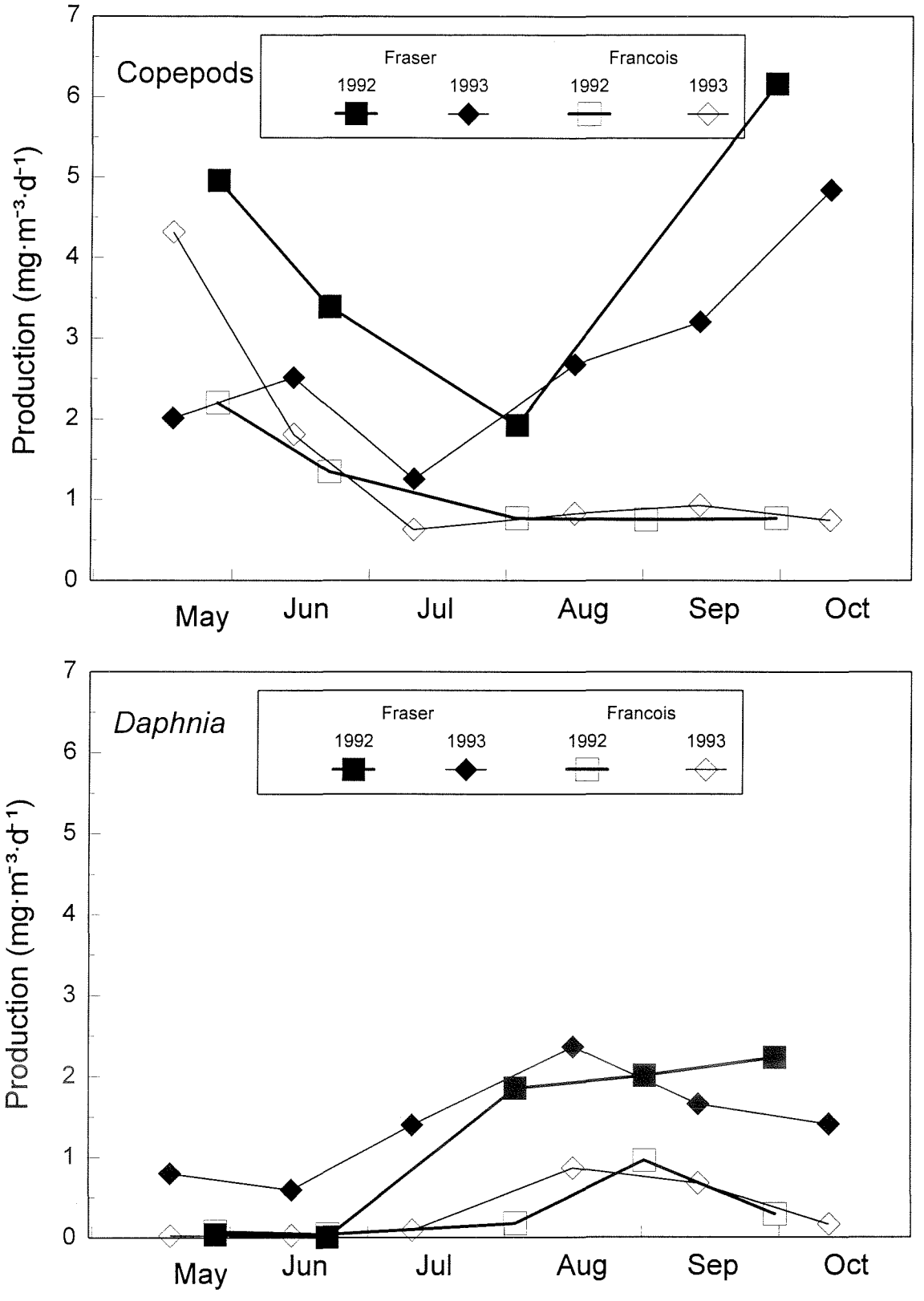

Fig. 16. Variation in production rates of *Daphnia* and of copepods in Fraser and Francois lakes during 1992 and 1993.

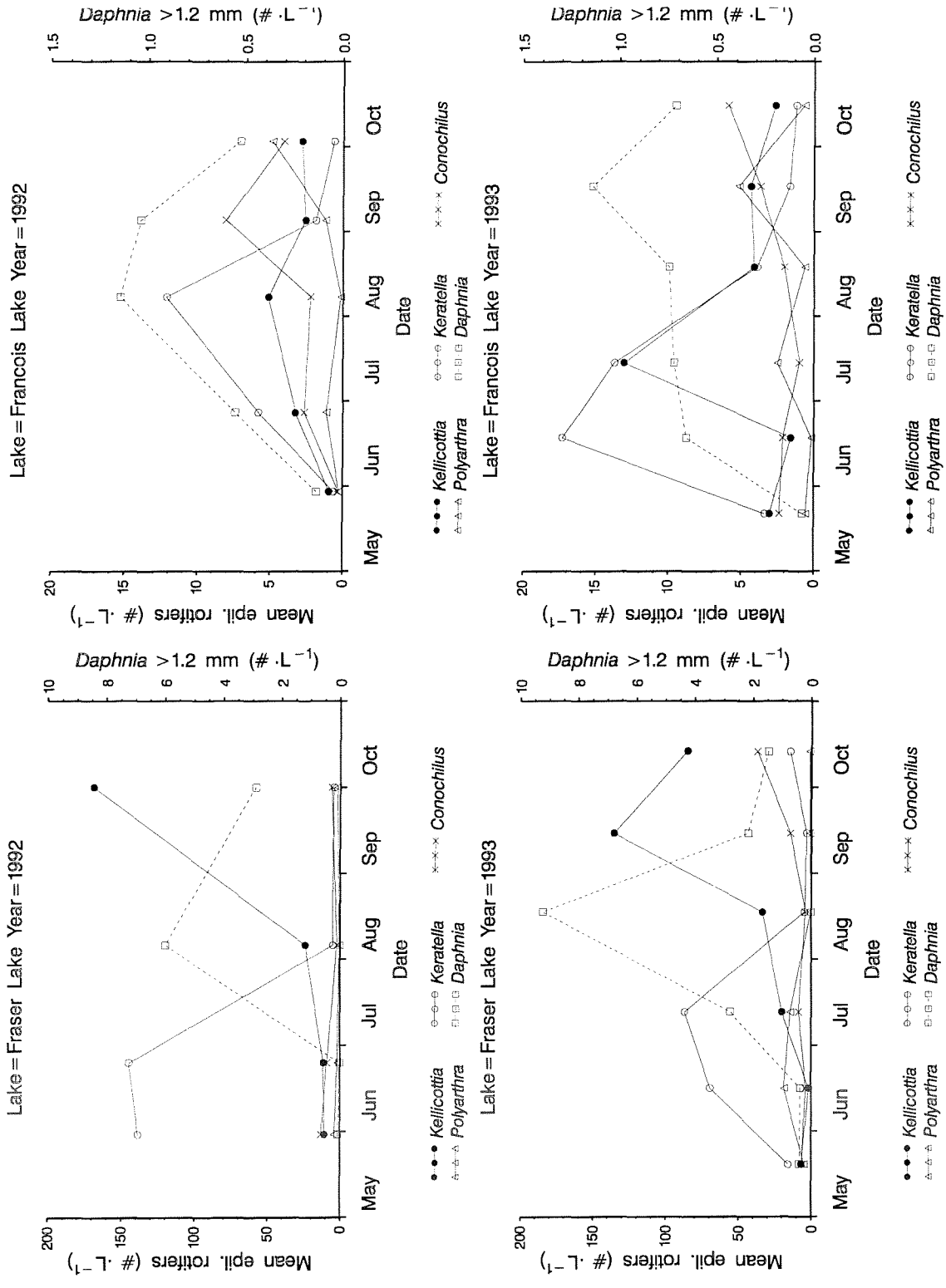

Fig. 17. Seasonal variation in dominant rotifer numbers and in large (>1.2-mm) *Daphnia* numbers in the study lakes. Data were collected with a 50-L Schindler trap equipped with a 20-µm mesh net.

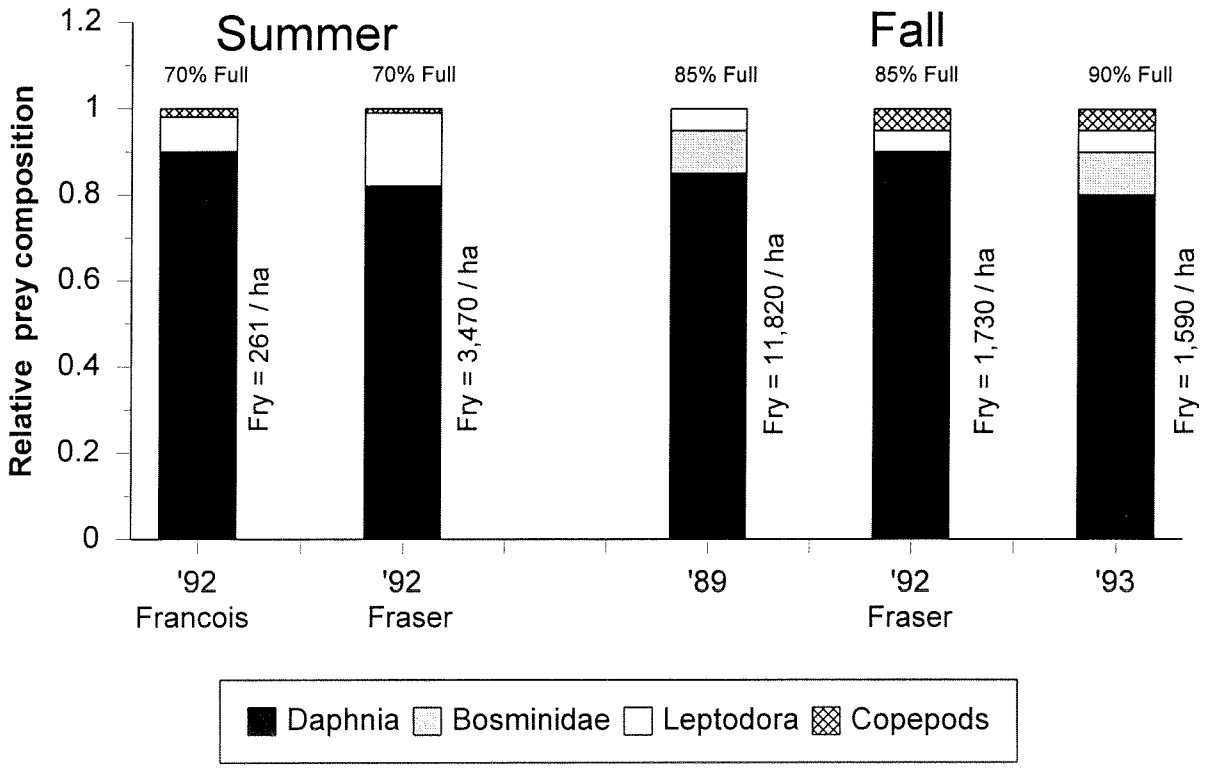

Fig. 18. Variation in stomach fullness (values above bars) and prey composition (bars) at varying fry densities in Francois and Fraser lakes.

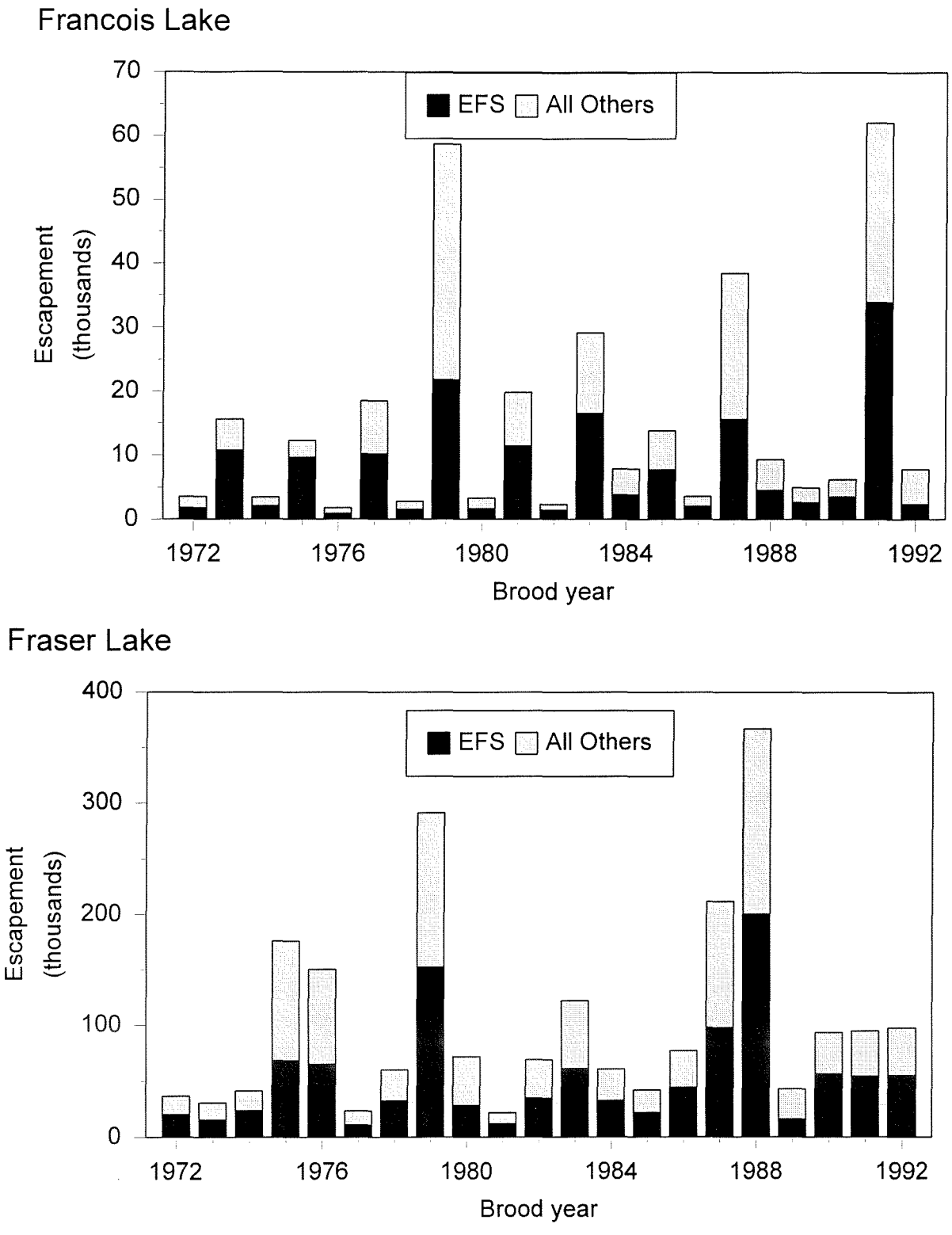

Fig. 19. Escapements to Francois and Fraser lakes showing effective females (EFS) and all other spawners (males, jacks, and other females).

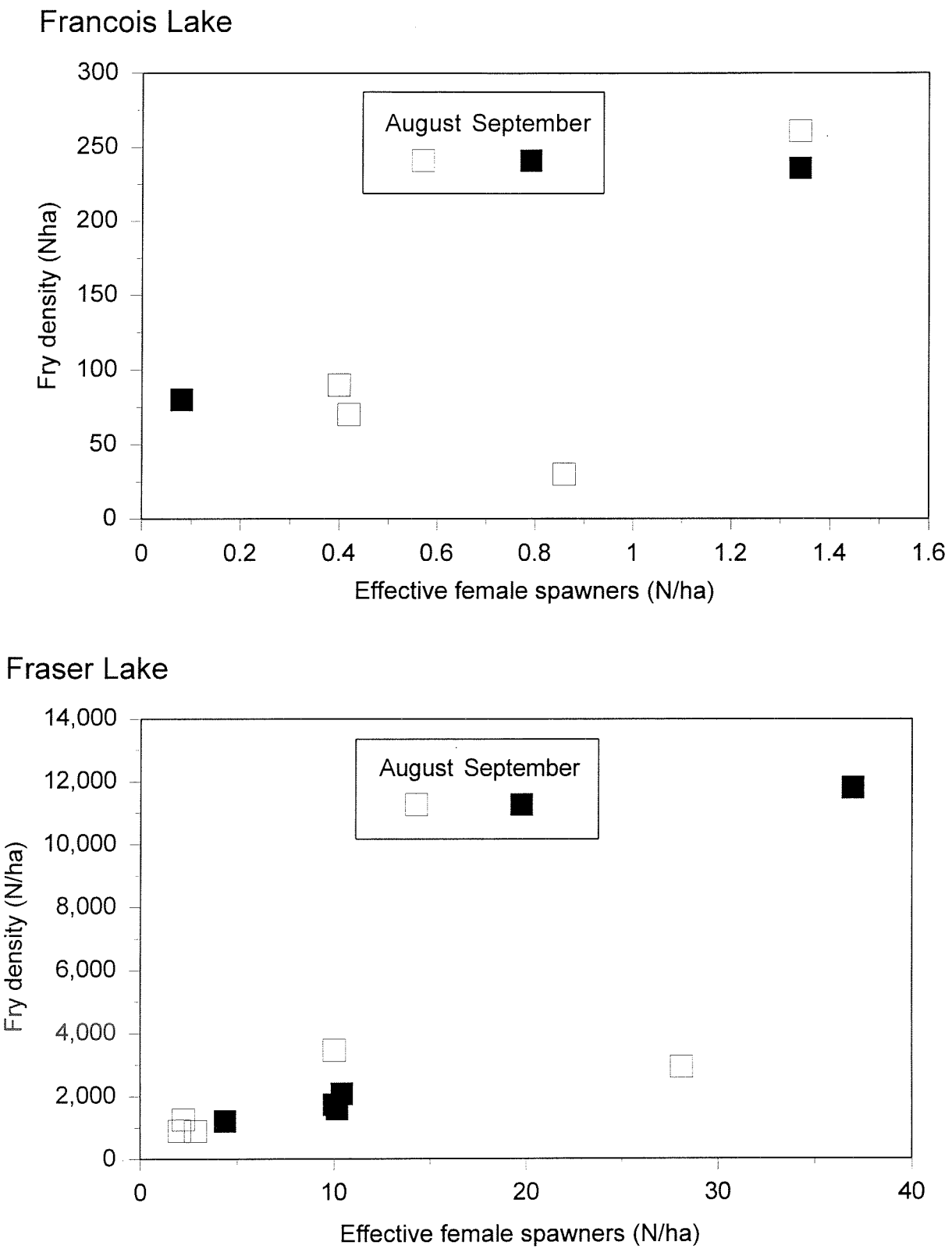

Fig. 20. Changes in the density of summer and fall fry with increasing density of effective female spawners.

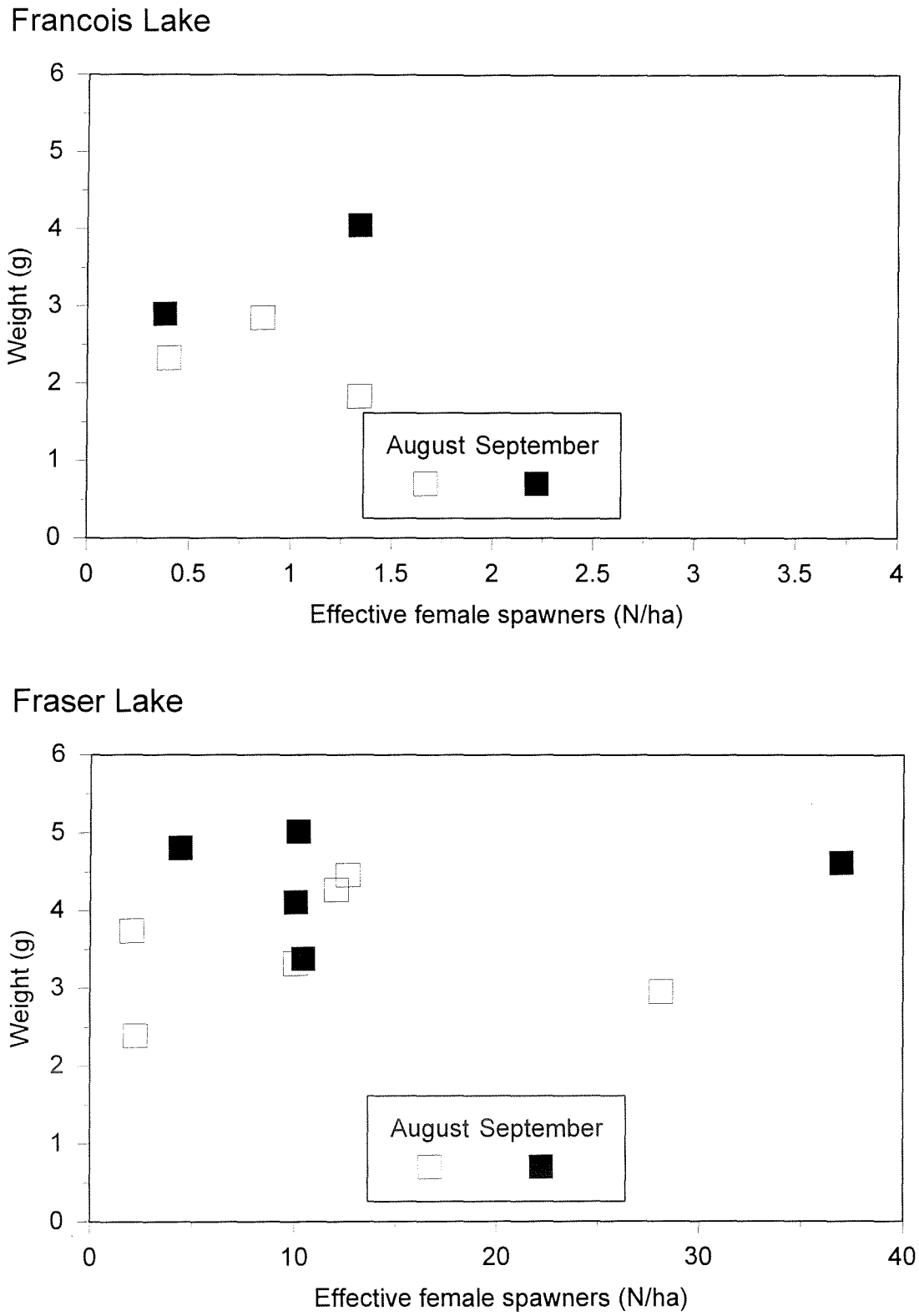

Fig. 21. Changes in the average weight of summer and fall fry with increasing density of effective female spawners.

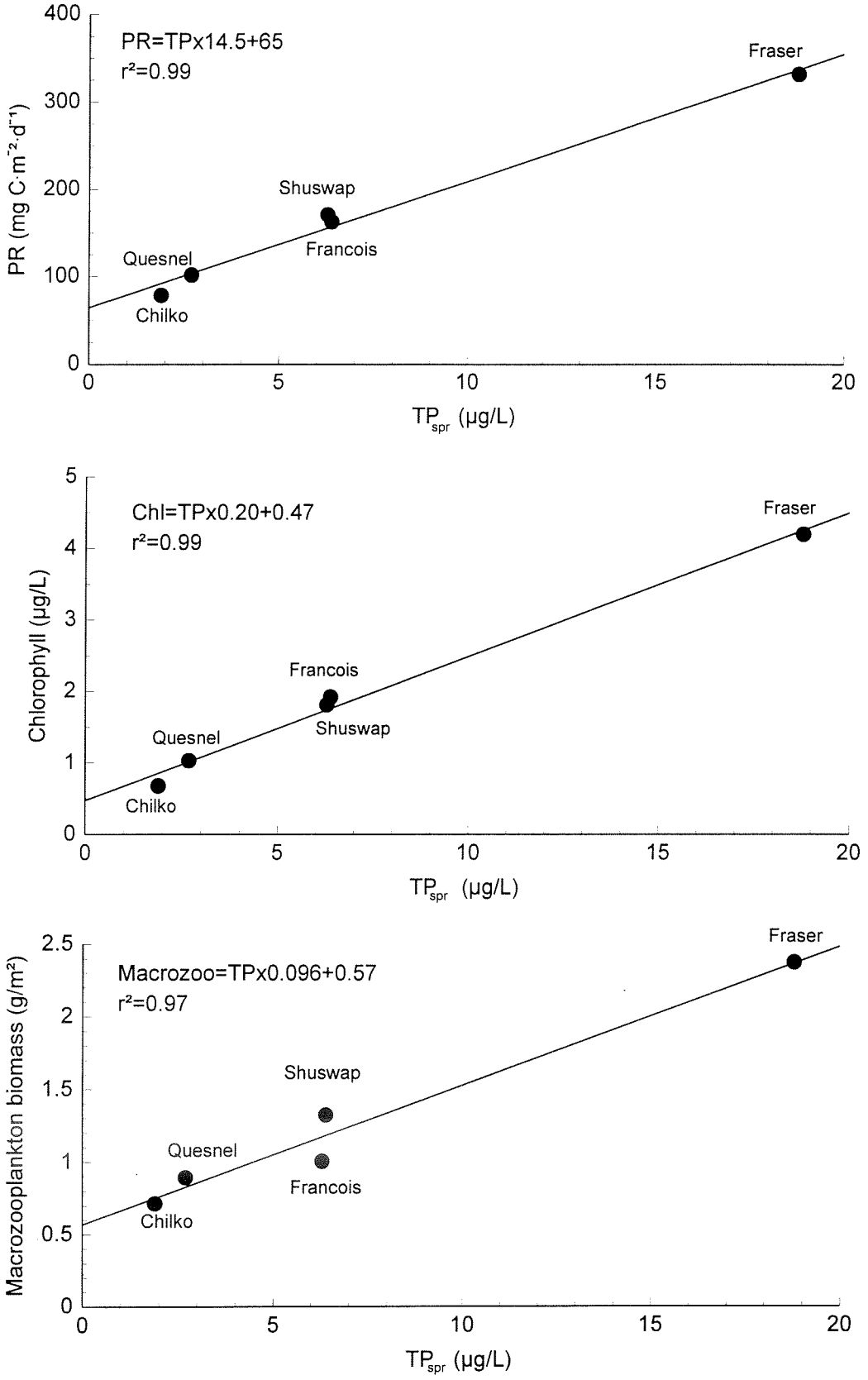

Fig. 22. Correlations between whole-lake, multi-year averages of PR, chlorophyll and macrozooplankton biomass with TP_{spr}.

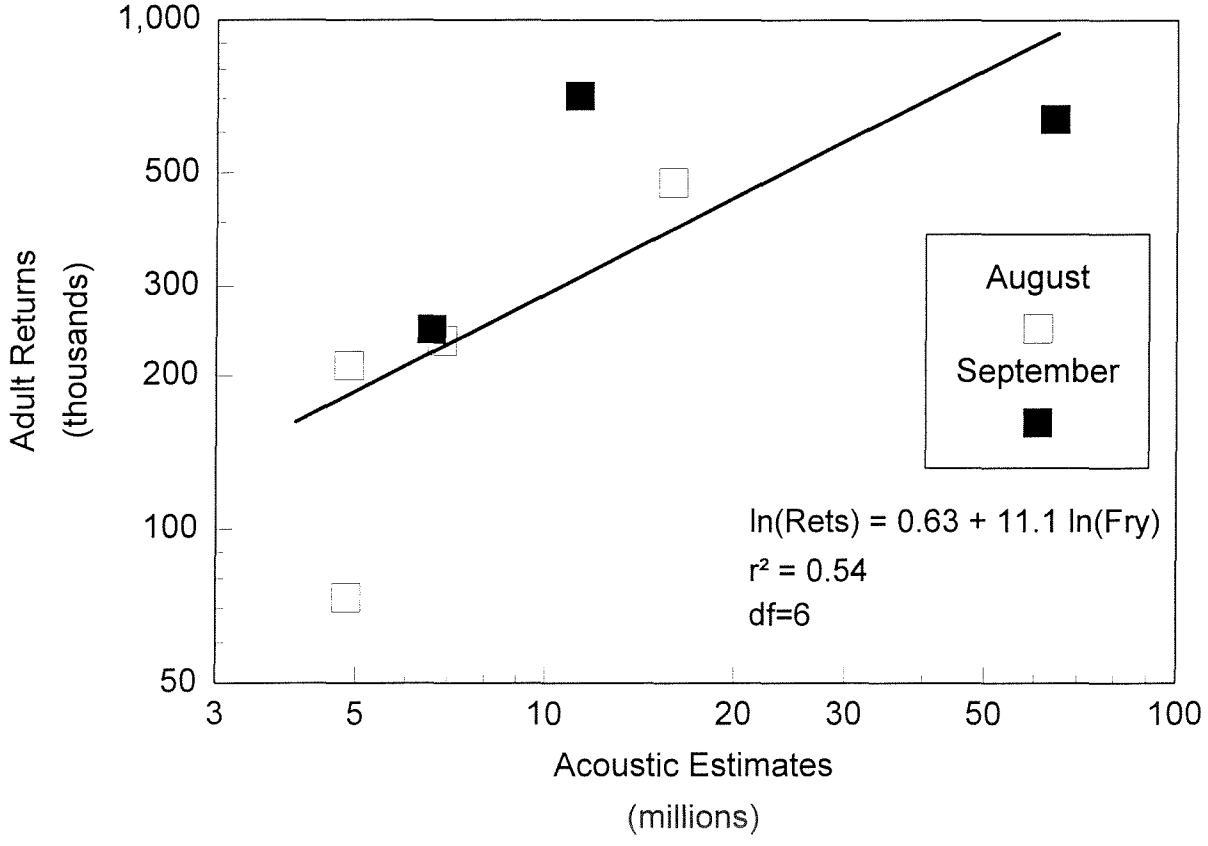

Fig. 23. Relationship between hydroacoustic fry estimates in Fraser Lake and subsequent adult returns to the Stellako River.