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Babine Lake

An Assessment Of The Limnological Status And Productive Capacity Of Babine Lake, 25 Years After The Inception Of The Babine Lake Development Project

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2000

Canadian Technical Report of Fisheries and Aquatic Sciences 2316

Fisheries and Oceans Canada | Pêches et Océans Canada
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Canada

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Cat. No. Fs 97-6/2316E ISSN 0706-6457

Correct citation for this publication:

Shortreed, K.S., and K.F. Morton. 2000. An assessment of the limnological status and productive capacity of Babine Lake, 25 years after the inception of the Babine Lake Development Project. Can. Tech. Rep. Fish. Aquat. Sci. 2316: 52 p.

ABSTRACT

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Construction of spawning channels in the late 1960's during the Babine Lake Development Program (BLDP) has resulted in increased sockeye escapements and fry densities in most years from the early 1970's to the present. In 1994 and 1995 we carried out a limnological study of Babine Lake to determine its current trophic status and rearing capacity for juvenile sockeye salmon (*Oncorhynchus nerka*). We investigated the effect of the increased escapements and fry densities on lake physics, chemistry, lower trophic levels, and sockeye diet by comparing our data with similar data collected before (Johnson 1961, 1964) and shortly after (Stockner and Shortreed 1975; Rankin 1977) the inception of the BLDP. Current spring overturn total phosphorus concentrations (5-9 µg/L), seasonal average chlorophyll concentrations (1.9-2.5 µg/L), and bacteria numbers (<$1.7x10^6$/mL) indicate the lake is in the middle to upper range of oligotrophy. The average C:N:P ratio was 314:31:1, indicating that the lake was P-limited. Total phosphorus loading has increased approximately 38% from estimates prior to enhancement, primarily because of increased sockeye escapements (i.e. nutrients from carcasses). Seasonal daily photosynthetic rates were 125 mg $C \cdot m^{-2} \cdot d^{-1}$ in 1994 and 155 mg $C \cdot m^{-2} \cdot d^{-1}$ in 1995, higher than the 1973 average of 100 mg $C \cdot m^{-2} \cdot d^{-1}$. *Daphnia* were the dominant prey item of juvenile sockeye both before BLDP and during our study. However, in our study grazing pressure on the zooplankton community (inferred from fall fry densities and smolt numbers) was much lower than in most years after BLDP and was similar to years before BLDP. Available evidence indicates that despite consistently higher fry densities as a result of BLDP, Babine Lake remains a quality nursery area for juvenile sockeye and its rearing capacity has not been exceeded. However, evidence from 1973 diets suggests that some of the higher post-BLDP fry recruitments have neared or reached the lake's rearing capacity and that further increases in fry recruitment would not result in additional smolt production.

RESUMÉ

Shortreed, K.S., and K.F. Morton. 2000. An assessment of the limnological status and productive capacity of Babine Lake, 25 years after the inception of the Babine Lake Development Project. Can. Tech. Rep. Fish. Aquat. Sci. 2316: 52 pp.

L'aménagement de chenaux de fraye dans le cadre du projet de mise en valeur du lac Babine, à la fin des années 60, a causé une augmentation des échappées de saumons rouges et des densités d'alevins pour chaque année depuis le début des années 70. En 1994 et 1995, nous avons effectué une étude limnologique dans le lac Babine afin de déterminer son état trophique et sa capacité d'alevinage pour le saumon rouge (*Oncorhynchus nerka*) juvénile. Nous avons examiné l'effet de l'augmentation des échappées et des densités d'alevins sur les caractéristiques physiques et chimiques du lac, les niveaux trophiques inférieurs et le régime alimentaire du saumon rouge en comparant nos données avec des données semblables recueillies avant (Johnson, 1961, 1964) et peu après (Stockner et Shortreed, 1975; Rankin, 1977) le lancement du projet de mise en valeur du lac Babine. Les concentrations totales de phosphore pendant le renversement printanier (5-9 µg/L), les concentrations saisonnières moyennes de chlorophylle (1,9-2,5 µg/L) et le nombre de bactéries (<$1,7x10^6$/mL) indiquent que le lac se situe entre le niveau moyen et le niveau élevé d'oligotrophie. Le rapport moyen C:N:P est de 314:31:1, ce qui montre que le lac est limité en phosphore. La charge totale en phosphore a augmenté d'environ 38 % par rapport aux estimations effectuées avant le projet de mise en valeur, principalement à cause de l'augmentation des échappées de saumons rouges (en raison des nutriants des carcasses). Les rendements photosynthétiques quotidiens pendant la saison étaient de 125 mg $C \cdot m^{-2} \cdot d^{-1}$, en 1994, et de 155 mg $C \cdot m^{-2} \cdot d^{-1}$, en 1995, ce qui est supérieur à la moyenne de 100 mg $C \cdot m^{-2}$ d^{-1} enregistrée en 1973. Avant le projet de mise en valeur et pendant notre étude, la principale proie du saumon rouge était *Daphnia*. Toutefois, pendant notre étude, la pression de broutage exercée sur la communauté zooplanctonique (estimée à partir des densités automnales d'alevins et du nombre de smolts) était beaucoup plus faible que pendant la plupart des années suivant le projet de mise en valeur; elle était plutôt semblable à celle des années précédant le projet. Bien que les densités d'alevins avaient augmenté depuis la mise en place du projet, des éléments probants indiquent que le lac Babine demeure une zone d'alevinage de qualité pour le saumon rouge juvénile et que sa capacité d'alevinage n'a pas été dépassée. Néanmoins, des données recueillies en 1973 sur le régime alimentaire du saumon rouge laissent croire que certaines années, le fort recrutement d'alevins résultant du

projet de mise en valeur a atteint, ou presque, la capacité d'alevinage du lac, et que d'autres augmentations du recrutement n'entraîneraient pas une plus grande production de smolts.

INTRODUCTION

British Columbia's Skeena River system contains 27 sockeye nursery lakes. With a surface area of 461 km^2, Babine Lake makes up over two-thirds of the total sockeye nursery area in the Skeena drainage basin. Research carried out in the 1950's and early 1960's (Brett 1952; Johnson 1958, 1961, 1964) indicated that Babine Lake's sockeye production was limited by spawning ground capacity and that rearing capacity of the Main Arm exceeded spawning ground capacity by a substantial margin. This research led to the creation of the Babine Lake Development Program (BLDP) in the mid-1960's. The BLDP resulted in construction of three spawning channels and flow control structures on two of the Main Arm's largest tributaries (Fulton River and Pinkut Creek). All three spawning channels (two on Fulton River and one on Pinkut Creek) became fully operational by 1971 (West and Mason 1987). With the success of the BLDP, Babine Lake currently accounts for at least 90% of total Skeena sockeye production (McKinnell and Rutherford 1994), which has averaged over four million since 1990 (Wood et al. 1998).

In the early 1970's, a series of limnological investigations was carried out on Babine Lake to determine the impact of increased escapements (Farmer and Spearing 1975; Stockner and Shortreed 1975; Rankin 1977). Since these studies, average fry recruitment to the Main Arm has been three times higher than pre-BLDP fry recruitment, with roughly equivalent increases in smolt output, adult returns, and escapements (Wood et al. 1998). The increased escapements have resulted in increased nutrient loading from carcasses.

In addition to the BLDP, two land-use changes occurred in the Babine drainage basin since the 1960's which had the potential to affect lake trophic status. First, two large copper mines were established on the shore of the northern portion of the Main Arm. Both open pit mines operated for a number of years between the mid-1960's and the mid-1990's. While these mines operated, the town of Granisle, on the western shore of the lake, grew rapidly to a population of about 2,800. Second, since the early 1970's, increased logging, with associated activities such as road building and slash burning, has occurred in the drainage basin.

Objectives of this study were to determine Babine Lake's current trophic status, plankton community structure, and biomass, and to estimate its current rearing capacity for juvenile sockeye. Since annual nutrient loading and sockeye fry densities have been higher in most of the last 25 years than prior to BLDP, an additional objective of this study was to determine if detectable limnological changes had occurred in Babine Lake since previous studies in the early 1970's and the late 1950's and early 1960's.

DESCRIPTION OF STUDY LAKE

Babine Lake is located approximately 600 km north of Vancouver and is on B.C.'s Interior Plateau (Fig. 1). The climate is continental, with warm summers and cold winters. The lake is in the subboreal spruce biogeoclimatic zone and has an annual precipitation of 40-50 cm (Farley 1979). It is at an elevation of 712 m, has a drainage basin area of 6,584 km^2, a surface area of 461 km^2, and is 150 km long. The lake consists of one large, deep (mean depth = 71 m) basin (the Main Arm) and three smaller, shallower basins (Hagan, Morrison, and North arms) which are separated from the Main Arm by shallow sills (Table 1, Fig. 2). Babine Lake is dimictic, with winter ice cover lasting from December to May. In addition to sockeye salmon, Babine Lake and Babine River support a number of fish species important to the commercial and/or recreational fisheries. These include coho salmon (*Onchorynchus kisutch*), rainbow and steelhead trout (*O. mykiss*), cutthroat trout (*O. clarkii*), lake char (*Salvelinus namaycush*), and lake whitefish (*Coregonus clupeaformis*).

About 71% of Babine Lake's drainage basin is forested and unlogged. Subboreal white spruce (*Picea glauca*) is the dominant coniferous species, comprising 80% of the coniferous forest area. The remaining 20% includes Engelmann spruce (*P. engelmanni*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*), with smaller amounts of deciduous species such as trembling aspen (*Populus tremuloides*) and black cottonwood (*P. balsamifera*) occurring near the lake and its tributaries. Clear-cut and selectively logged areas cover 13.5% of the entire drainage basin, while waterways (lakes, rivers, and streams) which drain into Babine Lake total 9%. An additional 6.5% is

comprised of barren lands, wetlands, agriculture land, industrial areas, residential areas, and townsites (Malcolm Gray, Ministry of Environment, Lands and Parks, Victoria, B.C., unpublished data).

Selective logging, primarily of spruce and pine, began in 1925 and clear-cut logging started in the 1950's. By the 1960's there were several openings of >200 ha. Logging activity increased steadily during the 1970's and 1980's but individual clear-cut openings were restricted to an area of 80 ha. In the 1970's, most logging occurred in the drainage basins of Fulton River and Pinkut Creek, where the most important Main Arm spawning areas are located. During the 1980's, logging continued in the upper portion of the Fulton River drainage basin and expanded to the eastern side of the lake near Hagan and Morrison arms. In the 20 years prior to our study, 12.3% or 81,100 ha of Babine's drainage basin was clear-cut logged, while another 7,800 ha or 1.2% was selectively logged. At the time of our study, 22% of the 68 km^2 Fulton River drainage basin and 16% of the 59 km^2 Pinkut Creek drainage basin were clear-cut logged (Malcolm Gray, Ministry of Environment, Lands and Parks, Victoria, B.C., unpublished data).

In 1966, Granby Mining Co. began production in an open pit copper mine located on an island complex in Hagan Arm. A second mine, owned by Noranda Mines Ltd., opened in 1970 on a peninsula separating the Main and Hagan arms (Fig. 2). The Granby mine closed in 1982, as did the Noranda mine in 1992. Final production figures for the two mines were 215 and 305 million kg of copper ore, respectively. Tailing ponds for both mines are located adjacent to the lake. Prior to mine development, the area around Babine Lake was sparsely settled (population <500). During mine operations, the town of Granisle, built primarily to service mine employees, was the major population centre (population about 2,800) in the Babine drainage basin. After the mines closed, the town's population declined to about 400 (Alta Lenard, Granisle Visitor Services, pers. comm.).

Prior to 1970 (pre-BLDP), sockeye salmon production from Babine Lake averaged <80% of total Skeena River production, which ranged from 1 to 3 million (Sprout and Kadowaki 1987). In the 1990's, adult returns of Babine Lake sockeye production have averaged 4 million annually and make up 90% of total Skeena sockeye production. Total sockeye escapement to Babine Lake prior to BLDP averaged 0.5 million (range: 0.1-0.9 million) and since BLDP has averaged 1.4 million (range: 0.5-3.0 million) (Wood et al. 1998). Babine Lake has three distinct sockeye runs (early, middle, and late) (Wood et al. 1998). Early run sockeye are unenhanced and spawn in small tributaries throughout Babine Lake. Middle run sockeye, the largest component of the escapement, are enhanced and spawn primarily in Fulton River, Pinkut Creek, and in the spawning channels at both locations. A relatively small number of middle-run sockeye spawn in the Morrison River and in tributaries flowing into Morrison Lake. Late run sockeye are unenhanced and spawn in the upper and lower Babine River (above and below Nilkitkwa Lake). Fry from middle-run sockeye rear in the Main and Morrison arms and late run fry rear in the North Arm and in Nilkitkwa Lake. There is little movement of fry between arms (McDonald and Hume 1984).

METHODS

In 1994, we sampled four locations (one in the North Arm and three in the Main Arm) once monthly from May to October (n=6 at each station). In 1995, we sampled the same locations twice monthly in spring and fall and once monthly in summer (n=9 at each station). In addition, in 1995, we sampled one location in Morrison Arm eight times from May to October.

We calculated the area of the lake and its various basins by digitizing lake shorelines from 1:50,000 topographic maps using a Kurta electronic digitizer (Model XLC 3648). Lake volume was determined by digitizing depth contours on a bathymetric map of the lake. Temperature and conductivity profiles from the surface to 100 m or the lake bottom (whichever was less) were obtained at each station with an Applied Microsystems conductivity, temperature and depth meter (Model STD-12). Isolines were plotted by the SAS procedure Gcontour (SAS Institute Inc., 1990) from a grid of interpolated and smoothed unscaled data. This was computed by the SAS procedure G3 grid using a bivariate method described by Akima (1978). Li-Cor data loggers (model LI-1000) equipped with quantum sensors (model LI-192S) were used to measure photosynthetic photon flux density (PPFD: 400-700 nm) from the surface to below the compensation depth

(1% of surface intensity) and to calculate vertical light extinction coefficients. We assumed that euphotic zone depth (EZD) was equal to the compensation depth. A standard 22-cm white Secchi disk was used to measure water transparency.

We used an opaque Van Dorn bottle sterilized with 95% ethanol to collect all water samples (water samples were not collected at the Morrison Arm station). Sampling took place between 0800 and 1200 h. At each station, water from 4 to 6 depths within the euphotic zone was collected and equal volumes were mixed in 20-L Nalge Lowboy carboys to provide an integrated sample. From the integrated samples, we carried out replicate analyses of dissolved silicate, total dissolved solids, particulate carbon, particulate nitrogen, nitrate, total phosphorus, particulate phosphorus, chlorophyll, phytoplankton, picoplankton, and bacteria. At each station we also collected a hypolimnetic sample from a depth of 30 m which was analyzed for chlorophyll, nitrate, and total phosphorus. In addition, in 1994, at Station 7 we collected water samples from eight depths down the water column. These samples were collected in 1-L polyethylene bottles and later analyzed for nitrate, total phosphorus, and chlorophyll.

Chemical analyses were carried out according to those methods given in Stephens and Brandstaetter (1983) and Stainton et al. (1977). For total phosphorus determination, clean test tubes were rinsed with sample, filled, capped with teflon-lined screw caps, and stored at 4°C. They were later analyzed using a molybdenum blue method with stannous chloride reduction 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 an ashed 47-mm diameter Micro Filtration Systems (MFS) borosilicate microfiber filter (equivalent to a Whatman GF/F filter). Each filter was placed in a 47-mm Swinnex filtering unit (Millipore Corp.), rinsed with distilled, deionized water (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 silicate and total dissolved solids. 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 chlorophyll analysis we filtered 250 mL of water through a 47-mm diameter, 0.45-µm Millipore HA filter. From integrated samples at Station 7 we also determined chlorophyll concentration of pico- and microplankton by filtering 250 mL of water through 2-µm Nuclepore and 20-µm Nitex filters. Filters were folded in half, placed in aluminum foil dishes, and frozen. They were later analyzed using a Turner fluorometer (Model 112) after maceration in 90% acetone.

Water for alkalinity determinations was placed in glass bottles that were filled completely (one bottle from each sampling depth) and sealed. Within 4 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 (1985). 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) . Eight random fields were counted on each filter and the counts converted to numbers/mL. Occasional blanks were prepared to check for a significant background bacteria count in the staining solution and rinse water.

For nano- and microphytoplankton enumeration and identification opaque 125-mL polyethylene bottles were rinsed with sample, filled, and fixed with 1 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 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. Filters were examined at 1250X magnification under oil immersion, and 30 random fields were counted. Phototrophic picoplankton were placed in four categories based on morphological characteristics, fluorescence color, and size categories (Stockner and Shortreed 1991). Categories were unicellular (USYN) and colonial (CSYN) cyanobacteria containing phycoerythrin (*Synechococcus*), unicellular cyanobacteria (RCYN) containing phycocyanin, and REUK were eukaryotic cells 1-2 μm in diameter with a visible chloroplast.

We measured *in situ* photosynthetic rates (PR) at every sampling date and station with the exception of Station 3 in Morrison Arm. In addition, at Station 7 we measured PR in two additional size fractions using 2- and 20-μm filters. We measured PR at 7 to 8 depths from the surface to below the compensation depth. At each depth two light and one dark 125-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 to 2 hours between 0900 and 1200 h. To determine activity of the stock solution, at each station we inoculated three scintillation vials containing 0.5 mL of Scintigest (Fisher Scientific) with the stock solution. After incubation, bottles were placed in light-proof boxes and transported to the field laboratory where filtration started <2 hours after incubation stopped. When only total PR was being measured, we filtered the entire contents of each bottle through a 25-mL diameter MFS glass fiber filter (equivalent to a Whatman GF/F) at a vacuum not exceeding 20-cm Hg. When fractionated PR was done, we filtered 40-mL aliquots from each bottle through MFS glass fiber, 2.0-μm Nuclepore, and 20-μm Nitex filters. Filters were placed in scintillation vials containing 0.5 mL of 0.5 N HCl and lids were left off the vials for 6 to 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) was added to each scintillation vial and sample activity was determined in a Packard Tri-Carb 4530 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 located near the mouth of Fulton River.

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. In 1995, we collected replicate 30-m vertical samples with a 100-μm Miller sampler (mouth area = 0.01 m^2) in addition to the Wisconsin samples. All samples were placed in 125-mL plastic bottles and preserved in a sucrose-buffered 4% formalin solution (Haney and Hall 1973). Zooplankton (except rotifers) were later counted, identified to genus 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 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).

Seasonal averages of data collected at each station (with the exception of PR) were calculated as time-weighted means from the first sampling date in May to the final date in October. 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 0 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). Whole lake averages and total seasonal PR (PR_{total}) were obtained by weighting each station based on the area of the lake it represented (Stockner and Shortreed 1974). In these calculations, we assumed Station1 was representative of North, Morrison, and Hagan arms. We obtained an estimate of total annual PR in tonnes C/lake (PR_{total}) by multiplying whole-lake average PR by lake area.

To obtain juvenile sockeye for diet analysis, we used a 3 x 7 m closing midwater trawl (Enzenhofer and Hume 1989). Methods used to collect fish are described in Hume and MacLellan (2000). Trawls were from 5 to 45 minutes in duration and were made at locations and depths suggested by fish targets on the echo sounder. To minimize bias caused by different digestion rates of prey, trawls were carried out within 3 hours after the onset of darkness. All captured fish were anaesthetized and then killed with an overdose of 2-phenoxy-alcohol and preserved in 10% formalin. Fish were kept in formalin for at least a month before lengths and weights were recorded. Age composition of *O. nerka* was determined from scales and from length frequency analysis. Stomach contents from up to 20 sockeye/trawl were

analyzed. Samples consisting of the contents of 10 pooled stomachs (two samples/tow) were subsampled with a Folsom plankton splitter and enumerated with a computerized video measuring system (MacLellan et al. 1993). Relative volume of prey types in the stomachs and an index of stomach fullness expressed as a percentage by volume were estimated using a technique modified from Hellawell and Abel (1971).

RESULTS

PHYSICAL

Seasonal average surface temperatures ranged from 13.0°C at Station 9 in 1994 to 15.8°C in Morrison Arm in 1995 (Table 2). Surface temperatures were coolest at Station 9 at the southeastern end of the lake. Thermocline depths increased from the northern to the southern portions of the lake. Average thermocline depths ranged from 6.9 m at Station 1 in 1995 to 14.1 m at Station 9 in the same year. In 1995, thermal stratification developed approximately two weeks earlier, was more pronounced, and persisted longer than in 1994 (Figs. 3-6). Thermocline depths in Morrison Arm in 1995 were deeper than in the North Arm but shallower than in the Main Arm (Fig. 7).

Water clarity in Babine Lake is relatively low because the lake is organically stained. During our study Secchi depths did not exhibit any distinct seasonal patterns and ranged from 2.5 to 7.5 m (Figs. 8-9). Seasonal average Secchi depths were slightly lower in 1995 than in 1994 and ranged from 4.2 m in Morrison Arm in 1995 to 5.6 m at Station 7 in 1994 (Table 2). As with Secchi depth, euphotic zone depths (EZD) did not exhibit seasonal patterns. Recorded EZD ranged from 4 to 9 m. Seasonal averages ranged from 6.0 to 7.7 m and in most cases were slightly lower in 1995 than in 1994 (Table 2).

CHEMICAL

Babine Lake is slightly alkaline, with pH values ranging from 7.0 to 7.8 during our study. In most cases highest values were recorded in spring. Seasonal average pH values ranged from 7.40 to 7.58 and were slightly higher in 1995 than in 1994 (Table 3). Total alkalinity, total dissolved solids (TDS), and dissolved silicate exhibited little seasonal variation and seasonal averages varied only from 36.1 to 36.9 mg $CaCO_3$/L, 58 to 64 mg/L TDS, and 1.39 to 1.53 mg Si/L (Table 3). Both total alkalinity and silicate tended to be slightly lower in 1995 than in 1994.

Spring overturn concentrations of total phosphorus (TP_{spr}) ranged from 5 to 9 µg/L (Fig. 10). Seasonal average epilimnetic TP concentrations ranged from 4.7 to 6.1 µg/L (Table 3). Seasonal average hypolimnetic TP concentrations were slightly lower, ranging from 3.5 to 5.3 µg/L. Highest epilimnetic TP concentrations were generally found in spring, with lowest concentrations occurring in late summer or fall (Fig. 10). Seasonal average nitrate concentrations ranged from 30.1 to 36.8 µg N/L in 1994 and were substantially lower (range: 15.9 to 20.3 µg N/L) in 1995 (Table 3). Spring overturn nitrate concentrations were also much lower in 1995, ranging from 45 to 51 µg N/L (1994 spring concentrations ranged from 65 to 125 µg N/L) (Figs. 11-12). In 1994 epilimnetic nitrate concentrations increased after seasonal minima in August, but in 1995 nitrate concentrations remained at low levels until the end of September. Average hypolimnetic nitrate concentrations were quite similar between stations and years, ranging only from 70.9 to 78.3 µg N/L. In both years of the study highest hypolimnetic nitrate concentrations occurred at Station 1 in the North Arm. Concentrations of particulate C (PC), particulate N (PN), and particulate P (PP) exhibited little seasonal variation, although highest concentrations of PC and PP often occurred in spring. Ranges in seasonal average particulate concentrations were 318 to 414 µg C/L, 32 to 47 µg N/L, and 2.6 to 3.6 µg P/L (Table 4). Molar ratios of the particulate elements were relatively consistent between stations. C/N ranged from 9.3 to 11.2, C/P from 242 to 349, and N/P from 21 to 36. C/P and N/P ratios were higher in 1995 than in 1994, while C/N ratios were slightly lower in 1995.

PHYTOPLANKTON AND BACTERIOPLANKTON

Seasonal average epilimnetic chlorophyll (CHL) concentrations were lowest (1.51 µg/L) at Station 1 in 1994 and were highest (2.77 µg/L) at Station 7 in 1995 (Table 5). In 1995, whole-lake seasonal average CHL was substantially higher (2.53 µg/L) than the 1994 average of 1.87 µg/L. This was partially due to a vernal bloom which we sampled in 1995 but which either did not occur or, more likely, was missed in 1994 because of a lower sampling frequency. However, 1995 CHL concentrations were higher than in 1994 for most of the growing season (Figs. 13-14). Discrete vertical profiles of

chlorophyll concentration were collected at Station 7 in 1994 and no deep chlorophyll maxima were found. Highest concentrations occurred at depths of <5 m. Approximately one-half the chlorophyll occurred in the picoplankton size fraction, about one-third in the nanoplankton, and the remainder in the microplankton (Table 5).

Highest picoplankton numbers occurred in summer or early fall (seasonal maxima were approximately 10^5/mL in 1994 and 1.5 x 10^5/mL in 1995). Seasonal average picoplankton numbers ranged from 3.62 x 10^4/mL at Station 1 in 1994 to 8.74 x 10^4/mL at Station 9 in 1995 (Table 6). Lowest average numbers occurred in the North Arm (Station 1). Whole-lake average numbers were 4.86 x 10^4/mL in 1994 and 7.65 x 10^4/mL in 1995. Average numbers of USYN were similar (approximately 3.2 x 10^4/mL) in both study years but numbers of CSYN increased over three-fold from 1.2 x 10^4/mL to 4.0 x 10^4/mL between 1994 and 1995. RCYN and REUK were both present but each averaged <10% of total picoplankton numbers. Their numbers decreased slightly in 1995.

Nanoplankton exhibited a distinct vernal bloom in the Main Arm of Babine Lake in 1995. In 1994, a vernal bloom was not detected and seasonal maxima occurred in July. As with picoplankton, seasonal average nanoplankton numbers were usually lowest at Station 1 (Table 7). Whole-lake seasonal averages increased from 692/mL in 1994 to 1,077/mL in 1995 (Table 7). Dominant nanoplankton were the flagellates *Chroomonas acuta* and *Chromulina* spp. (Table 7).

Microplankton numbers were highest in fall at all stations except Station 1, where highest numbers occurred in spring. Seasonal average microplankton numbers were highest at Station 9 in both study years and were substantially higher (775/mL) in 1995 than the 1994 average of 292/mL (Table 8). Abundant chlorophycean microplankton were *Ankistrodesmus* sp. and *Elakatothrix* sp., while important diatom genera were *Asterionella formosa, Fragilaria crotonensis, Rhizosolenia* sp., and *Tabellaria fenestrata* (Table 8). Most diatom genera exhibited distinct seasonality, with spring or fall blooms of relatively short duration being most common (Figs. 15-18). Numbers of most microplankton genera were higher in 1995, but the magnitude of the increased numbers was to a large extent due to increases in colonial genera (small cells, large colonies) such as *Aphanocapsa* sp. and *Coelosphaerium* sp.

Photosynthetic rates (PR) were quite variable between sampling dates and distinct seasonal patterns were not apparent (Figs. 19-20). Depth profiles of PR exhibited the shallow (usually <3 m) PR maxima indicative of rapid light attenuation. Seasonal average daily PR ranged from 83 mg C/m^2 at Station 1 in 1994 to 176 mg C/m^2 at Station 9 in 1995 (Table 5). PR was higher in 1995 than in 1994 at all stations, with whole-lake seasonal averages increasing from 125 to 155 mg $C \cdot m^{-2} \cdot d^{-1}$ (Table 5). Relative contribution of the pico-, nano-, and microplankton size fractions to total PR at Station 7 was similar in both study years. Picoplankton PR made up 43 to 46% of the total, nanoplankton PR 38 to 40%, and microplankton PR 15 to 19% (Table 5).

Bacterioplankton numbers did not exhibit distinct seasonal trends. Seasonal average bacteria numbers were slightly higher in the southern portion of the lake and whole-lake average numbers were 1.02 million/mL in 1994 and 0.95 million/mL in 1995 (Table 5).

ZOOPLANKTON

Seasonal average macrozooplankton biomass ranged from 823 to 960 mg dry wt/m^2 in 1994 and from 1,003 to 1,222 mg dry wt/m^2 in 1995 (Table 9). In both years, biomass was lowest in the North Arm (Station 1). At most stations, seasonal maxima in macrozooplankton biomass occurred in spring or early summer. As with other variables, the apparently less pronounced vernal bloom in 1994 may be a result of lower sampling frequency. Copepods formed the majority of plankton biomass. Cyclopidae (primarily *Cyclops scutifer* with lesser numbers of *Diacyclops thomasi*) averaged 334 mg dry wt/m^2 in 1994 and 390 mg dry wt/m^2 in 1995 (Table 9). In both study years, seasonal maxima in Cyclopidae biomass occurred in June (Fig. 21). In 1994, biomass of Diaptomidae (*Leptodiaptomus ashlandi* and *L. pribilofensis*) was similar (396 mg dry wt/m^2) to that of Cyclopidae, but in 1995 Diaptomidae biomass increased to 665 mg dry wt/m^2 (Table 9). Seasonality of Diaptomidae was less clearly defined than that of Cyclopidae, with seasonal maxima occurring from early June to late August (Fig. 22).

Unlike copepod biomass, Bosminidae (primarily *Eubosmina longispina*) biomass was greater in 1994 (49 mg dry wt/m^2) than in 1995 (11 mg dry wt/m^2) (Table 9). Seasonal maxima in Bosminidae biomass occurred in June (Fig. 23). Morrison Arm (Station 3) was sampled only in 1995, and at 200 mg dry wt/m^2 Bosminidae biomass was >10x higher than

at any other station in that year (Table 9). Whole-lake average *Daphnia* biomass was 32 mg dry wt/m^2 in 1994 and 23 mg dry wt/m^2 in 1995. Seasonal maxima in *Daphnia* biomass occurred in summer (usually August) or early fall (Fig. 24).

Average biomass of the large calanoid copepod, *Heterocope septentrionalis*, declined from 73 mg dry wt/m^2 in 1994 to 34 mg dry wt/m^2 in 1995 (Table 9). In the Main Arm, *Heterocope* biomass was reduced to negligible levels by August in both study years, while in the North and Morrison arms it remained relatively abundant through September (Fig. 25). In 1994, average biomass of the calanoid copepod *Epischura* was substantially higher in the North Arm and in the northern part of the Main Arm than in the remainder of the lake. *Epischura* biomass was similar throughout the lake in 1995 (Table 9).

JUVENILE SOCKEYE DIET

Sockeye stomachs collected in summer and fall of 1994 and 1995 were >60% full with the exception of a fall 1994 sample from Morrison Arm, which averaged only 30% full (Fig. 26). Other than the Morrison Arm sample, stomach fullness was similar in both summer and fall samples. *Daphnia* and *Heterocope* were the major prey items at all locations. *Epischura* was rare in North and Morrison Arm stomach samples but was a common prey item in the Main Arm, where it constituted up to 30% of stomach contents.

Since stomach samples were collected only in summer and fall, seasonal changes in sockeye diet are difficult to discern. However, there was a trend toward a more diverse fall diet. Insects (Diptera) and smaller copepod genera such as *Diacyclops* and *Leptodiaptomus* were rare in summer stomach samples and more common in fall samples. In the North Arm, diet in summer was almost exclusively *Heterocope* and was predominantly *Daphnia* in fall. Conversely, *Daphnia* occurrence in the stomach contents declined from summer to fall in Main Arm samples.

Leptodiaptomus and Bosminidae (primarily *Eubosmina longispina*) were the dominant zooplankton prey of juvenile sockeye collected in September, 1993, at Station 7 in the Main Arm. *Diptera* (larval insects) also made up a substantial portion of the diet (50% by volume of stomach content). At the time of sampling, stomachs averaged <30% full (Fig. 27).

DISCUSSION

CURRENT TROPHIC STATUS AND LIMITING NUTRIENTS

The thermal structure of Babine Lake was studied in detail in 1972 and 1973 (Farmer and Spearing 1975) and discussed by Stockner and Shortreed (1974, 1975). They reported that stratification developed by mid-June, maximum epilimnion temperatures were 18°C, and that mixed layer depths increased from north to south (shallowest in the North Arm and deepest south of Topley Landing). In our study, temperature data exhibited similar spatial and seasonal trends to those collected in the earlier studies, with the exception that temperatures in 1994 were cooler than in the earlier studies or in 1995. Babine Lake's thermal structure continues to provide a favorable physical environment for juvenile sockeye and is similar to that found in other large B.C. sockeye nursery lakes such as Francois (Shortreed et al. 1996), Quesnel (Nidle et al. 1994), and Takla (K. Shortreed, unpublished data). Long-term climate change (global warming) is a subject of considerable recent interest and predictions are that it will have deleterious effects on some B.C. sockeye stocks (Henderson et al. 1992). A number of B.C. sockeye nursery lakes such as Great Central (Nidle and Shortreed 1984), Shuswap (Nidle and Shortreed 1996), and Sproat (Shortreed and Stockner 1990) currently have summer epilimnetic temperatures that are unfavorably warm for juvenile sockeye. Global warming will likely exacerbate these conditions and further reduce the lakes' productive capacity. Babine Lake's large size, more northern location, and cooler epilimnion make its sockeye habitat less vulnerable to long-term climate change than those in more southern lakes which already have warm epilimnia.

Spring overturn total phosphorus concentrations in Babine Lake ranged from 5 to 9 µg/L, placing it in the middle to upper range of oligotrophy (Vollenweider 1976). Other limnological variables used as indicators of trophic status also placed it in this trophic range. For example, Forsberg and Ryding (1980) proposed a chlorophyll-based trophic classification where oligotrophic lakes were defined as those with seasonal average chlorophyll concentrations of <3 µg/L. Babine Lake's average chlorophyll concentration ranged from 1.87 to

2.53 µg/L. Bird and Kalff (1984) proposed a trophic classification where oligotrophic lakes had bacteria numbers <1.7 x 10^6/mL. Average bacteria numbers in Babine Lake were approximately 1 x 10^6/mL in both study years.

Babine Lake has a relatively abundant nitrogen supply, with average hypolimnetic nitrate concentrations of 72.8 µg N/L and spring overturn concentrations of 50 to 70 µg N/L (hypolimnetic nitrate concentrations tended to increase seasonally) (Table 3). Epilimnetic nitrate concentrations declined during the growing season in both years at all stations and seasonal minima occurred in August or September. In 1995, seasonal minima were lower (<10 µg/L) and low nitrate concentrations persisted for a longer period than in 1994, but at no time was nitrate depleted (<1 µg/L) (Figs. 11-12). The seasonal average epilimnetic nitrate concentrations of 18 to 34 µg N/L were higher than those in most other Skeena sockeye nursery lakes (Shortreed et al. 1998).

Sestonic ratios of C, N, and P have often been used to estimate the magnitude and type of nutrient limitation (Redfield et al. 1963; Healey and Hendzel 1980; Hecky et al. 1993; Hassett et al. 1997), with the extent of P limitation increasing with increasing C:P and N:P ratios. Marine phytoplankton have been reported to have a C:N:P ratio of 103:16:1 (Redfield et al. 1963), far lower than Babine's average ratio of 314:31:1 (it was 296:28:1 in 1994 and 332:34:1 in 1995) (Table 4). In a suite of lakes in central North America, Elser and Hassett (1994) found an average N:P ratio of 38:1, slightly higher than Babine's ratio of 31:1. With respect to other British Columbia lakes, C:N:P ratios in Babine Lake were higher than the average of 273:25:1 reported for five other Skeena system sockeye nursery lakes (Shortreed et al. 1998). They were similar to a suite of sockeye nursery lakes in the Fraser River system, which had an average C:N:P ratio of 315:26:1 (K. Shortreed, unpublished data). However, Babine Lake's C:N:P ratio was far lower than the ratio of 473:45:1 that Stockner and Shortreed (1985) reported for a range of unfertilized coastal British Columbia lakes. Babine Lake's C:N:P ratio is indicative of a severely P-limited system (Hecky et al. 1993), with the degree of P limitation similar to that in some lakes in the Fraser River system (specifically, its ratios are very similar to those found in Shuswap Lake). However, the degree of P limitation is far less than found in many coastal sockeye lakes in British Columbia.

Babine Lake's seasonal average PR (125 mg $C \cdot m^{-2} \cdot d^{-1}$ and 155 in 1995) was substantially higher than the average of 70 mg $C \cdot m^{-2} \cdot d^{-1}$ reported for coastal British Columbia lakes (Stockner and Shortreed 1985), higher than the overall average of 115 mg $C \cdot m^{-2} \cdot d^{-1}$ reported for other Skeena system lakes (Shortreed et al. 1998), and similar to the overall average of 138 mg $C \cdot m^{-2} \cdot d^{-1}$ reported for Fraser system sockeye nursery lakes (Shortreed et al. 1999). Similarly, Babine Lake's average phytoplankton biomass (as chlorophyll) of 1.87 µg/L in 1994 and 2.53 in 1995 was much higher than the unfertilized coastal lake average of 1.15 µg/L (Stockner and Shortreed 1985) and higher than the average of 1.44 µg/L reported for other Skeena system lakes (Shortreed et al. 1998).

EVIDENCE FOR CHANGES IN TROPHIC STATUS BETWEEN THE 1970'S AND THE 1990'S

Photosynthetic rates (PR) are a direct measure of a lake's productivity. Stockner and Shortreed (1974) reported daily PR rates collected in 1973 on nine occasions (May to October) from each of 10 locations in Babine Lake. These earlier PR data required two modifications to be comparable to our data. First, dissolved inorganic carbon (DIC) was not measured in the earlier study but was assumed to be 10.0 mg/L. Our DIC data averaged 9.5 mg/L, so we assumed 1973 concentrations were the same and adjusted the earlier data downward by a factor of 1.05. This assumption is supported by total alkalinity, total dissolved solids (TDS), and pH data collected in 1976 (Stockner and Shortreed 1978), which were very similar to data collected in our study. The second adjustment to the earlier PR data was necessary because scintillation cocktails then used in determination of C^{14} activity were not alkalized. This resulted in an overestimate of PR values by a factor of 1.49 (Kobayashi 1978), so data were adjusted further downward by this amount. After these modifications, whole-lake seasonal average PR in 1973 was 99.7 mg $C \cdot m^{-2} \cdot d^{-1}$, substantially lower than seasonal averages of 125 mg $C \cdot m^{-2} \cdot d^{-1}$ in 1994 and 155 mg $C \cdot m^{-2} \cdot d^{-1}$ in 1995.

Chlorophyll concentration has often been used as an analog for primary productivity (Forsberg and Ryding 1980; Stockner and Shortreed 1985). This appears appropriate in Babine Lake, because integrated PR (mg $C \cdot m^{-2} \cdot d^{-1}$) was significantly correlated with chlorophyll concentration (µg/L) (r^2=0.41, $p<0.01$, df=88) in both the earlier study (Stockner and Shortreed 1975) and this study (Fig. 28). Although it would have been more appropriate to use volumetric photosynthetic rates in this analysis, these data were not available from the earlier study. If the productivity of Babine Lake has increased since the 1970's, average chlorophyll concentration may have increased as well. Seasonal average

chlorophyll concentrations in the Main Arm were 1.80 µg/L in 1973 (Stockner and Shortreed 1974), 2.00 µg/L in 1994, and 2.57 µg/L in 1995 (these values are averages of data from Stations 4, 7, and 9). Some of the difference between average values in 1994 and 1995 can be explained by differences in sampling frequency. The lake was sampled twice monthly in spring and fall of 1995 and only once monthly in 1994. The data suggest that the lower sampling frequency in 1994 missed the vernal bloom in that year (Figs. 13-14). Since the lake was sampled twice monthly in 1973, the averages for that year (1.80 µg/L) and for 1995 (2.57 µg/L) are more comparable. The 43% increase between 1973 and 1995 does suggest that phytoplankton biomass is higher in the 1990's.

Using the limited available data, Stockner and Shortreed (1974, 1975) developed an annual phosphorus (P) budget for Babine Lake and estimated the annual P load to the lake from precipitation and fluvial inputs to be 19,644 kg. In the past 25 years, no additional data have been collected which would improve this initial estimate. It is well documented that logging and associated activities (road building, slash burning) increases nitrogen and phosphorus loading to streams and lakes (Leonard et al. 1979; Birch et al. 1980; Shepard 1994). Since the early 1970's, 81,100 ha (12.3%) of Babine Lake's drainage basin has been clearcut logged. Following logging, slash burning has been carried out on some openings. Logging has most likely increased fluvial nutrient and sediment loading to Babine Lake in the past 25 years, but the limited available data make it impossible to quantify this increase. Logging-induced increases in nutrient and sediment loads are transitory (usually lasting only until re-vegetation occurs), and we suggest long-term increases in fluvial nutrient inputs have been minimal.

With the success of the BLDP and increased sockeye escapements, nutrient loading to Babine Lake increased (i.e. more nutrients from carcasses). In the 16 years (1950 to 1965) prior to BLDP, escapements to the Main Arm averaged 236,442. In the 10 years (1985 to 1994) prior to our study, average escapements were 975,683 (Wood et al. 1998). To calculate nutrient input from these carcasses we used an average weight/spawner of 2.46 kg, an average P content of 0.46%, and an average N content of 2.48% (Mathisen et al. 1988). Pre-BLDP, P load from carcasses to the Main Arm of Babine Lake averaged 2.7 tonnes P annually. In the 10 years prior to our study it averaged 11.7 tonnes of P annually. Using Stockner and Shortreed's (1975) estimate of 19,644 kg P/year from fluvial inputs and precipitation, prior to BLDP sockeye carcasses contributed an average of 12% of the total P load to the Main Arm of Babine Lake. In the period 1985 to 1994, carcasses contributed an average of 37% of the total annual P load to Babine Lake's Main Arm. The total P load to the Main Arm has increased 40% from an estimated 22.3 tonnes P pre-BLDP to 31.2 tonnes P in recent years. In a phosphorus-limited system, this increase would be likely to result in higher primary and secondary productivity.

Nitrate concentration was measured sporadically in Babine Lake in years prior to our study and in most cases nitrate concentrations in 1994 and 1995 were lower than those in the 1970's (Figs. 11-12). There is no evidence to indicate that nitrogen loading to Babine Lake has declined since the 1970's, and the increased escapements indicate the opposite. The average adult sockeye spawner contains about 61 g of N and 11 g of P, which is a relatively low molar ratio of 12:1 (Mathisen et al. 1988), much lower than the 31:1 ratio found in Babine phytoplankton. Average daily PR in Babine Lake's Main Arm has increased from 107 in 1973 to an average of 152 mg $C \cdot m^{-2} \cdot d^{-1}$ in the 1990's, an increase of 45 mg $C \cdot m^{-2} \cdot d^{-1}$. This is an annual increase of 2,957 tonnes of carbon produced in the Main Arm of Babine Lake. At the average C:N:P ratio of 314:31:1 for Babine phytoplankton, this requires an additional 339 tonnes of N and 24 tonnes of P annually. "New" nutrients from carcasses provide 35% of the additional P requirement while providing only 13% of the additional N. Obviously these calculations are a considerable oversimplification because not all nutrients from carcasses are utilized by phytoplankton. Further, nutrient recycling plays a highly important role in a lake's productivity. Regenerated, rather than "new" nutrients provide a substantial (often major) proportion of required nutrients (Sterner et al. 1995; Hudson et al. 1999). However, the data clearly suggest that increased carbon production in Babine Lake caused by additional N and P from carcasses has placed a greater demand on ambient nitrate, resulting in lower epilimnetic nitrate concentrations in the 1990's.

Babine Lake is organically stained (dystrophic), with the result that there is rapid vertical light attenuation. Seasonal average euphotic zone depths (range: 6.0 to 7.7 m) were from one-half to almost 90% of average thermocline depths, similar to what is found in other dystrophic B.C. sockeye nursery lakes such as Takla and Trembleur (K. Shortreed and K. Morton, unpublished data). Given sufficient nutrients, lakes with these relative depths of euphotic zones and thermoclines are effective nursery areas for juvenile sockeye (Hyatt and Stockner 1985; Stockner and Shortreed 1985). Given the well-documented relationship between phytoplankton biomass and water clarity in B.C. lakes (Hume et al. 1996), higher biomass in Babine Lake could have resulted in shallower euphotic zone depths. Unfortunately, euphotic zone depths were not measured in the earlier study. However, Secchi depths were determined in both studies.

While Secchi depth is an ineffective analog for euphotic zone depth over a range of water types (e.g., clear, glacial, dystrophic), in water of one type (e.g., organically stained Babine Lake), it is often negatively correlated to chlorophyll concentration. When data from our study and the earlier study were combined, there was a significant (r^2=0.36, df=64, $p<0.01$, log-transformed data) negative correlation between Secchi depth and mean epilimnetic chlorophyll. Average Main Arm Secchi depths were 5.6 m in 1973, 5.4 m in 1994, and were 4.8 m in 1995.

Changes in phytoplankton biomass and productivity could have resulted in changes in phytoplankton community structure. In our study, average picoplankton numbers in Babine Lake (46,000 to 76,000/mL) were within the range of 800 to 105,000/mL found in eleven oligotrophic lakes in British Columbia and the Yukon (Stockner and Shortreed 1991). Unfortunately, picoplankton enumeration techniques were not available at the time of the earlier study, so changes in their abundance cannot be determined. However, it is well documented (Fahnenstiel et al. 1991; Stockner and Shortreed 1991) that in oligotrophic lakes, picoplankton numbers increase with increasing nutrient loading. Given the increases in phytoplankton biomass and productivity since the earlier study, we suggest that there is a high probability that picoplankton numbers have increased since the early 1970's. Abundance of colonial *Synechococcus* relative to unicellular *Synechococcus* tends to become greater in more productive lakes (Stockner and Shortreed 1991; Shortreed et al. 1998). It is interesting to note that 1995 was a more productive year than 1994 (lower epilimnetic nitrate, higher chlorophyll, higher PR) and colonial *Synechococcus* increased from 29% to 56% of total *Synechococcus* numbers.

In our study, seasonal average nanoplankton numbers were 692 in 1994 and 1,077/mL in 1995. Nanoplankton numbers are not available from the earlier study, but seasonal plots of major phytoplankton taxa in 1973 are shown in Figures 7 and 8 in Stockner and Shortreed (1974). Qualitative comparisons of our data and data presented in these figures suggest that numbers of smaller phytoplankton are higher now than in 1973. Babine Lake's diatom community structure was examined in detail in 1973 (Stockner and Shortreed 1974; Stockner 1975) and again in our study. Trends in seasonal succession of major diatom genera were similar in both studies (Figs. 15-18). Density of most major genera were also similar in both studies, although numbers of *Melosira italica* tended to be lower in our study while *Cyclotella* spp. numbers tended to be higher than in 1973 (Figs. 15-18)

ZOOPLANKTON

Zooplankton are affected both by "top-down" (planktivore grazing) and "bottom up" (primary productivity) factors (Carpenter et al. 1985; Northcote 1988; Hume et al. 1996). The relative importance of "top-down" and "bottom-up" factors varies between lakes and within a lake; it can vary both seasonally and annually. The changes in phytoplankton biomass, photosynthetic rates, nutrient concentrations, and water clarity we described earlier in this discussion provide evidence that Babine was a less productive lake in the early 1970's (and, by inference, in the 1950's) than it was in the mid-1990's. Thus, "bottom-up" factors suggest that zooplankton production and biomass should be higher now than in the earlier studies. However, "top-down" factors (i.e., grazing pressure) have changed also, and if higher, would reduce biomass of the preferred prey species.

To determine changes in zooplankton community structure and numbers since BLDP, we wished to make comparisons between our data, data collected in the early 1970's (Rankin 1977), and data collected in the 1950's and early 1960's (Johnson 1964). Seven years (1956 to 1958, 1960 to 1963) (Johnson 1964) of pre-BLDP data and 1 year (1973) (Rankin 1977) of 1970's data were available for comparison with our study (post-BLDP). These comparisons were complicated by methodological differences in the three studies. Pre-BLDP zooplankton data were collected with a Clarke-Bumpus (CB) sampler (stratified horizontal tows), 1973 data with a Miller sampler (vertical tows), and our data were collected with a Wisconsin net (vertical tows). Rankin (1977) made quantitative comparisons between Miller and CB data collected simultaneously and adjusted Miller data for differing efficiencies in sampling the four major zooplankton groups (*Daphnia*, Cyclopidae, Diaptomidae, and Bosminidae). In our study, we made similar comparisons between efficiencies of Miller samplers and Wisconsin nets. We then adjusted CB data (Johnson 1965) and CB-equivalent data (Rankin 1977) to Miller-equivalent data using equations from Rankin (1977). Correlations used to make these changes and to normalize these earlier data with our Wisconsin data are listed in Table 11. To focus on periods when sockeye grazing was at its highest and to compensate for a lack of early season data in some years, only data collected between July 1 and September 30 were used in the analysis. We compared pre-BLDP to 1973 data, pre-BLDP to post-BLDP data, and 1973 to post-BLDP data.

From the three periods of interest, estimates of fry recruitment and of smolt numbers are available and provide indices of grazing pressure in Babine Lake. Because methods used for smolt estimates were more consistent than those used for fry estimates, and because of potential underestimates of wild fry recruitment (Wood et al. 1998), we chose to use Main Arm smolt numbers as an index of grazing pressure in the previous year. Smolt numbers were highly variable and ranged from 6.6 million to 41.7 million in pre-BLDP years where both zooplankton and smolt data are available. Smolt numbers were far higher in 1973 (77.9 million) and only slightly higher (24.1 million) during our study than the pre-BLDP average of 19.7 million (Wood et al. 1998) (Table 12).

In lakes with annual variability in planktivore density, *Daphnia* abundance is often negatively correlated with planktivore density (Hume et al. 1996). Using the 7 years of Babine Lake data for which both smolt numbers and zooplankton abundances are available, there was a trend of decreasing *Daphnia* abundance with increasing smolt numbers, although the correlation was not significant (Fig. 29). Average *Daphnia* numbers in 1973 were 1,200/m^2, substantially lower than the pre-BLDP average of 6,900/m^2 (Table 12). Smolt output from the 1973 lake year was 77 million (Wood et al. 1998), while it averaged only 19.7 million pre-BLDP. Smolt output has been as high or higher than 77 million for 12 of the 25 years since the early 1970's (post-BLDP). This suggests that in most post-BLDP years grazing pressure in Babine Lake is high enough to reduce *Daphnia* numbers and affect sockeye diet. In sockeye nursery lakes elsewhere in B.C., sockeye fry densities of >500/ha (measured in fall) had a detectable effect on plankton biomass or community composition (Hume et al. 1996). Average smolt densities in years where zooplankton data are available were 540/ha pre-BLDP, 2,134/ha in 1973, and 660/ha post-BLDP (fall fry densities that produced these smolts would have been substantially higher).

Other studies (Goodlad et al. 1974; Kyle et al. 1988) have indicated that an effect of high grazing pressure is increased relative abundance of less productive, more predator-resistant species such as *Cyclops* and *Leptodiaptomus*. Relative abundance of the small cladoceran *Bosmina* sp. may also increase when grazing pressure is high (Koenings and Kyle 1997). In Babine Lake, relative abundance of copepods and bosminids increased in 1973, commensurate with the highest grazing pressure, further suggesting that in many post-BLDP years "top-down" effects are strongly affecting the lake's plankton community structure (Table 12).

If grazing pressure is sufficient to affect zooplankton community structure, it should be reflected in changes in stomach contents of juvenile sockeye. Juvenile sockeye selectively graze large cladocerans and if available, will feed almost exclusively on *Daphnia* (Narver 1970; Goodlad et al. 1974; Morton and Williams 1990; Hume et al. 1996). The large calanoid copepod *Heterocope* is usually less common than *Daphnia*, but when available it is also preyed on actively (Narver 1970; Goodlad et al. 1974). *Diacyclops*, *Leptodiaptomus*, and small bosminids are heavily utilized only when numbers of preferred food items numbers are very low. Their utilization is indicative of high grazing pressure and/or extreme oligotrophy. Pre-BLDP, *Daphnia* and *Heterocope* were the major components of juvenile sockeye diet in the Main Arm of Babine Lake (Narver 1970; McDonald 1973). From summer to fall, the proportion of *Heterocope* in sockeye stomachs decreased and that of *Daphnia* increased. The high quality of Main Arm sockeye diet in pre-BLDP years indicated an underutilized food resource and was one of the key factors in proceeding with the BLDP (Johnson 1964).

In 1973, 5 years after the completion of Fulton and Pinkut spawning channels, sockeye fry densities were the highest (2,134 smolts/ha) yet recorded for years where zooplankton data are available (Wood et al. 1998). In that year, juvenile sockeye diet in the Main Arm in August consisted primarily of *Daphnia* but shifted to small, predator resistant copepods (*Cyclops* and *Diaptomus*) by fall (Rankin 1977). Rankin attributed this change from pre-BLDP diet to higher grazing pressure on *Daphnia* and *Heterocope* by increased numbers of juvenile sockeye. The shift to less desirable prey species indicates that in 1973 the zooplankton community was heavily exploited.

Sockeye stomach contents collected in our post-BLDP study (>25 years after spawning channel construction) were similar to those collected pre-BLDP, with *Heterocope* and *Daphnia* being major dietary components. As with pre-BLDP studies, the dietary importance of *Heterocope* declined from summer to fall and that of *Daphnia* increased. It is interesting to note that average numbers of *Daphnia* in our study and in the earlier studies were low relative to other large sockeye nursery lakes in B.C.'s interior. For example, in years with similar fall fry densities (ca. 450 to 650/ha), Shuswap Lake has a seasonal average of 30 to 40 x 10^3 *Daphnia*/m^2 and Quesnel Lake has 20 to 30 x 10^3/m^2 (MacLellan et al. 1993; Morton and Shortreed 1996). In comparison, Babine Lake had 3 x 10^3 *Daphnia*/m^2 at these fry densities. Despite these large differences in abundance, *Daphnia* was the major component of sockeye fry diet in all three lakes. This indicates that sockeye feeding in Babine Lake was highly selective (i.e., sockeye did not start feeding on less

desirable, more abundant species until *Daphnia* numbers became extremely low). It also suggests that reproductive rates for Babine *Daphnia* are higher than in the other two lakes, since *Daphnia* is of equivalent importance in stomach contents despite its much lower density. Additional evidence for higher reproductive rates in Babine Lake is that average fecundity of *Daphnia* was significantly higher at 3.3 eggs/female (ANOVA, GT2 test for log-transformed data, $p<0.05$, SAS Institute Inc., 1990) than in either Quesnel (1.7 eggs/female) or Shuswap (2.4 eggs/female) lakes (K. Morton, unpublished data). *Daphnia* clutch size is negatively correlated with density and positively correlated with food quality and body size (Hessen 1989; Gliwicz and Boavida 1996). The predominant *Daphnia* species in Babine Lake was *D. galeata*, while in Quesnel and Shuswap lakes it was *D. thorata*. Seasonal (July to October) average length of *Daphnia* in Babine Lake was 1.22 mm. In years when planktivore densities were similar in all three lakes, average *Daphnia* size (1.28 mm) in Shuswap Lake was not significantly different from that in Babine Lake. With an average size of 1.03 mm, Quesnel Lake *Daphnia* were significantly smaller than *Daphnia* in either of the other two lakes. Although *Daphnia* numbers are low in Babine relative to other lakes where it is also an important diet item, its higher reproductive rate appears to compensate and allows it to maintain a viable population despite sometimes heavy grazing pressure.

PRODUCTIVE CAPACITY

While a lake's rearing capacity has been observed to limit sockeye smolt production in some years in some lakes (Hume et al. 1996), available data indicate that this has not yet occurred in Babine Lake. A sockeye production model (PR model) which utilizes photosynthetic rates and sockeye survivals between life-history stages (Koenings and Kyle 1997) to estimate maximum potential smolt production has been developed for B.C. lakes (Shortreed et al. 1999). PR model predictions are that 92 million smolts are the maximum that Babine Lake's Main Arm could produce and that fry recruitment to the Main Arm to achieve this should be 219 million (Shortreed et al. 1999). Assuming estimated smolt numbers are reliable, this predicted maximum smolt production has been exceeded in 8 of the last 25 post-BLDP years (Wood et al. 1998). PR model predictions are based on a 42% fry-to-smolt survival and the long-term average for Babine Lake is 39% (Wood et al. 1998). In 4 of the 8 years which exceeded model predictions, estimated fry-to-smolt survival was unusually high (61 to 85%). If these survival rates are accurate, then lake conditions must have been exceptionally favorable. Unfortunately, no limnological data are available for any of these years to verify the favorable lake conditions.

In the 30 years since inception of the BLDP, substantial changes have occurred in Babine Lake and its drainage basin. Logging, road building, and mining has taken place, and number of people residing in the drainage basin has increased. However, we conclude that the most important effect on the lake itself has been the increased nutrient loading from carcasses which has occurred as a direct result of the BLDP. This has resulted in increases in phytoplankton biomass and photosynthetic rates. In our study, Babine Lake's zooplankton community was similar to that reported in the 1950's. However, it should be noted that during our study (1994 and 1995) fry densities (inferred from smolt production) and grazing pressure were the lowest recorded since the inception of the BLDP, and were within the range of densities recorded pre-BLDP. The data suggest that most fry recruitments to date have not been excessive, but that increases beyond the maximum recruitments observed to date would likely reach or exceed the lake's rearing capacity, and not result in additional smolt production.

ACKNOWLEDGMENTS

We would like to thank J. Hume, S. MacLellan, K. Masuda, K. Mullen, B. Nidle, J. Rogers, and I. Yesaki for invaluable assistance in collection and analysis of study data. T. Jeffrey and E. MacIsaac provided high quality chemical analyses of collected water samples. Dr. M. Bradford provided valuable advice on analyses used in this study. J. Hume, E. MacIsaac, and P. Rankin provided constructive critical reviews of the penultimate draft of this manuscript.

REFERENCES

Akima, H. 1978. A method of bivariate interpolation and smooth surface fitting for irregularly distributed data points. ACM Transaction on Mathematical Software 4: 148-159.

American Public Health Association, American Water Works Association and Water Pollution Control Federation. 1985. Standard methods for the examination of water and wastewater. 16th edition. Washington, D.C. 1268 p.

Balcer, M.D., N.L. Korda, and S.I. Dodson. 1984. Zooplankton of the Great Lakes. The Univ. of Wisconsin Press. Madison, Wisconsin. 174 p.

Birch, P.B, R.S. Barnes, and D.E. Spyridakis. 1980. Recent sedimentation and its relationship with primary productivity in four western Washington lakes. Limnol. Oceanogr. 25: 240-247.

Bird, D.F., and J. Kalff. 1984. Empirical relationships between bacterial abundance and chlorophyll concentration in fresh and marine waters. Can. J. Fish. Aquat. Sci. 41: 1015-1023.

Bird, D.F., and Y.T. Prairie. 1985. Practical guidelines for the use of zooplankton length-weight regression equations. J. Plankton Res. 7: 955-960.

Brett, J.R. 1952. Skeena River sockeye escapement and distribution. J. Fish. Res. Board Can. 8: 453-468.

Carpenter, S.R., J.F. Kitchell, and J.R Hodgson. 1985. Cascading trophic interactions and lake productivity. Bioscience 35: 634-639.

Costella, A.C., B. Nidle, R. Bocking, and K.S. Shortreed. 1982. Limnological results from the 1980 Lake Enrichment Program. Can. Manuscr.Rep. Fish. Aquat. Sci. 1635: 291 p.

Culver, D.A., M.M. Boucherie, D.J. Bean, and J.W. Fletcher. 1985. Biomass of freshwater crustacean zooplankton from length-weight regressions. Can. J. Fish. Aquat. Sci. 42: 1380-1390.

Elser, J.J., and R.P. Hassett. 1994. A stoichiometric analysis of the zooplankton-phytoplankton interaction in marine and freshwater ecosystems. Nature 370: 211-213.

Enzenhofer, H.J., and J.M.B. Hume. 1989. Simple closing midwater trawl for small boats. N. Am. J. Fish. Manage. 9: 372-377.

Fahnenstiel, G.L., T.R. Patton, H.J. Carrick, and M.J. McCormick. 1991. Diel division cycle and growth rates of *Synechococcus* in Lakes Huron and Superior. Int. Revue ges. Hydrobiol. 76: 657-664.

Farley, A.L. 1979. Atlas of British Columbia. Univ. British Columbia Press, Vancouver, B.C. 136 p.

Farmer, D.M., and L.A.F. Spearing. 1975. Isotherm plots of Babine Lake during the ice-free season. Pacific Marine Science Report 75-9: 266 p.

Forsberg, C., and S. Ryding. 1980. Eutrophication parameters and trophic state indices in 30 Swedish waste-receiving lakes. Arch. Hydrobiol. 89: 189-207.

Gliwicz, Z.M. and M.J. Boavida. 1996. Clutch size and body size at first reproduction in *Daphnia pulicaria* at different levels of food and predation. J. Plankton Res. 18: 863-880.

Goodlad, J.C., T.W. Gjernes, and E.L. Brannon. 1974. Factors affecting sockeye salmon (*Oncorhynchus nerka*) growth in four lakes of the Fraser River system. J. Fish. Res. Board Can. 31: 871-892.

Haney, J.F., and D.J. Hall. 1973. Sugar-coated *Daphnia*: A preservative technique for Cladocera. Limnol. Oceanogr. 18: 331-333.

Hassett, R.P., L.B. Stabler, and J.J. Elser. 1997. Ecological stoichiometry of N and P in pelagic ecosystems: comparison of lakes and oceans with emphasis on the zooplankton-phytoplankton interaction. Limnol. Oceanogr. 42: 648-662.

Healey, F.P., and L.L. Hendzel. 1980. Physiological indicators of nutrient deficiency in lake phytoplankton. Can J. Fish. Aquat. Sci. 37: 442-453.

Hecky, R.E., P. Campbell, and L.L. Hendzel. 1993. The stoichiometry of carbon, nitrogen, and phosphorus in particulate matter of lakes and oceans. Limnol. Oceanogr. 38: 709-724.

Hellawell, J.M., and R. Abel. 1971. A rapid volumetric method for the analysis of the food of fishes. J. Fish. Biol. 3: 29-37.

Henderson, M.A., D.A. Levy, and J.G. Stockner. 1992. Probable consequences of climate change on freshwater production of Adams River sockeye salmon (*Oncorhynchus nerka*). Geojournal 28: 51-59.

Hessen, O. 1989. Factors determining the nutritive status and production of zooplankton in a humic lake. J. Plankton Res. 11: 649-664.

Hudson, J.J, W.D. Taylor, and D.W. Schindler. 1999. Planktonic nutrient regeneration and cycling efficiency in temperate lakes. Nature 400: 659-661.

Hume, J.M.B., and S.G MacLellan. 2000. An assessment of the juvenile sockeye salmon populations of Babine Lake. Can. Tech. Rep. Fish. Aquat. Sci. 2327: 37 p.

Hume, J.M.B., K.S. Shortreed, and K.F. Morton. 1996. Juvenile sockeye rearing capacity of three lakes in the Fraser River system. Can. J. Fish. Aquat. Sci. 53: 719-733.

Hyatt, K.D., and J.G. Stockner. 1985. Responses of sockeye salmon (*Oncorhynchus nerka*) to fertilization of British Columbia coastal lakes. Can. J. Fish. Aquat. Sci. 42: 320-331.

Johnson, W.E. 1958. Density and distribution of young sockeye salmon (*Oncorhynchus nerka*) throughout a multi-basin lake system. J. Fish. Res. Board Can. 15: 961-987.

Johnson, W.E. 1961. Aspects of the ecology of a pelagic, zooplankton-eating fish. Verh. Inter. Verein. Limnol. 14: 727-731.

Johnson, W.E. 1964. Qualitative aspects of the pelagic, entomostracan zooplankton of a multi-basin lake system over a 6-year period. Verh. Inter. Verein. Limnol. 15: 727-734.

Johnson, W.E. 1965. Quantitative studies of the pelagic entomostrachan zooplankton of Babine Lake and Nilkitkwa Lake, 1955-1963: Methods, Stations, and basic data. Fish. Res. Board Can. MS Rep. 821: 224 p.

Kobayashi, Y. 1978. Counting of ^{14}C-bicarbonate solution. *Edited by* Y. Kobayashi and W.G. Harris. *In* Liquid scintillation counting applications notes. New England Nuclear, Boston, Massachusetts. p. 31.

Koenings, J.P., and G.B. Kyle. 1997. Consequences to juvenile sockeye salmon and the zooplankton community resulting from intense predation. Alaska Fish. Res. Bull. 4: 120-135.

Koenings, J.P., J.A. Edmundson, G.B. Kyle, and J.M. Edmundson. 1987. Limnology field and laboratory manual: methods for assessing aquatic production. Alaska Dep. Fish Game, FRED Div. Rep. Ser., Juneau. 71: 212 p.

Kyle, G.B, J.P. Koenings, and B.M. Barrett. 1988. Density dependent trophic level responses to an introduced run of sockeye salmon (*Oncorhynchus nerka*) at Frazer Lake, Kodiak Island, Alaska. Can. J. Fish. Aquat. Sci. 45: 856-867.

Leonard, R.L., L.A. Kaplan, J.F. Elder, R.N. Coats, and C.R. Goldman. 1979. Nutrient transport in surface runoff from a subalpine watershed, Lake Tahoe Basin, California. Ecol. Monogr. 49: 281-310.

MacIsaac, E.A., and J.G. Stockner. 1985. Current trophic state and potential impact of coal mine development on productivity of Middle Quinsam and Long lakes. Can. Tech. Rep. Fish. Aquat. Sci. 1381: 63 p.

MacLellan, S.G., K.F. Morton, and K.S. Shortreed. 1993. Zooplankton community structure, abundance, and biomass in Quesnel Lake, British Columbia: 1985 - 1990. Can. Data Rep. Fish. Aquat. Sci. 918: 151 p.

Mathisen, O.A., P.L. Parker, J.J. Goering, T.C. Kline, P.H. Poe, and R.S. Scalan. 1988. Recycling of marine elements transported into freshwater systems by anadromous salmon. Verh. Internat. Verein. Limnol. 23: 2249-2258.

McDonald, J. 1973. Diel vertical movements and feeding habits of underyearling sockeye salmon (*Oncorhynchus nerka*), at Babine Lake, B.C. Fish. Res. Board Can. Tech. Rep. 378: 55 p.

McDonald, J., and J.M.B. Hume. 1984. Babine Lake sockeye salmon (*Oncorhynchus nerka*) enhancement program: testing some major assumptions. Can. J. Fish. Aquat. Sci. 41: 70-92.

McKinnell, S., and D. Rutherford. 1994. Some sockeye are reported to spawn outside the Babine Lake watershed in the Skeena drainage. PSARC Working Paper S94-11: 43 p.

Morton, K.F., and K.S. Shortreed. 1996. Results from a seven-year limnological study of Shuswap Lake : Part II, Zooplankton. Can. Data Rep. Fish. Aquat. Sci. 1005: 132 p.

Morton, K.F., and I.V. Williams. 1990. Sockeye salmon (*Oncorhynchus nerka*) utilization of Quesnel Lake, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1756: 29 p.

Narver, D.W. 1970. Diel vertical movements and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Board Can. 27: 281-316.

Nidle, B.H., and K.S. Shortreed. 1984. Limnological results from the 1983 British Columbia Lake Enrichment Program. Can. Manuscr. Rep. Fish. Aquat. Sci. 1752: 216 p.

Nidle, B.H., and K.S. Shortreed. 1996. Results from a seven-year limnological study of Shuswap Lake: Part I, Physics, chemistry, bacteria, and phytoplankton. Can. Data Rep. Fish. Aquat. Sci. 993: 116 p.

Nidle, B.H., K.S. Shortreed, and K.V. Masuda. 1994. Limnological data from the 1985-1990 study of Quesnel Lake. Can. Data Rep. Fish. Aquat. Sci. 940: 82 p.

Northcote, T.G. 1988. Fish in the structure and function of freshwater ecosystems: a 'top-down' view. Can. J. Fish. Aquat. Sci. 45: 361-379.

Pennak, R.W. 1978. Freshwater Invertebrates of the United States. 2nd Ed. John Wiley & Sons. New York, NY. 803 p.

Rankin, D.P. 1977. Increased predation by juvenile sockeye salmon relative to changes in macrozooplankton abundance in Babine Lake, British Columbia. M.Sc. thesis, University of British Columbia, Vancouver, B.C. 101 p + ill.

Redfield, A.C., B.H. Ketchum, and F.A. Richards. 1963. The influence of organisms on the composition of sea-water. *In* The sea. *Edited by* M.N. Hill. Vol. 2. John Wiley and Sons, New York, NY. , p. 26-77

Robarts, R.D., and L.M. Sephton. 1981. The enumeration of aquatic bacteria using DAPI. J. Limnol. Soc. Afr. 7: 72-74.

SAS Institute Inc. 1990. SAS/GRAPH Software: Reference, Version 6, Cary N.C. Vol. 2: 664 p.

Shepard, J.P. 1994. Effects of forest management on surface water quality in wetland forests. Wetlands 14: 18-26.

Shortreed, K.S., and J.G. Stockner. 1990. Effect of nutrient additions on lower trophic levels of an oligotrophic lake with a seasonal deep chlorophyll maximum. Can. J. Fish. Aquat. Sci. 47: 262-273.

Shortreed, K.S., J.M.B. Hume, and K.F. Morton. 1996. Trophic status and rearing capacity of Fraser and Francois lakes. Can Tech. Rep. Fish. Aquat. Sci. 2151: 60 p.

Shortreed, K.S., J.M.B. Hume, K.F. Morton. and S.G. MacLellan. 1998. Trophic status and rearing capacity of smaller sockeye nursery lakes in the Skeena river system. Can. Tech. Rep. Fish. Aquat. Sci. 2240: 78 p.

Shortreed, K.S., J.M.B. Hume, and J.G. Stockner. 1999. Using photosynthetic rates to estimate the juvenile sockeye rearing capacity of British Columbia lakes. E.E. Knudsen, C.R. Steward, D.D. MacDonald, J.E. Williams, and D.W. Reiser [eds.]. *In* Sustainable fisheries management: Pacific Salmon. CRC Press, Boca Raton, Florida. pp. 521-525

Sprout, P.E. and R.K. Kadowaki. 1987. Managing the Skeena River sockeye salmon (*Oncorhynchus nerka*) fishery - the process and the problems. *In* Sockeye salmon (*Oncorhynchus nerka*) biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. 96. pp. 385-395

Stainton, M.P., M.J. Capel, and F.A.J. Armstrong. 1977. The chemical analysis of fresh water. Can. Fish. Mar. Serv. Misc. Spec. Publ. No. 25, 2nd edition: 180 p.

Stansby, M.E., and A.S. Hall. 1965. Chemical composition of commercially important fish of the United States. Fish. Ind. Res. 3: 26-46.

Stemberger, R.S., and J.J. Gilbert. 1987. Rotifer threshold food concentrations and the size-efficiency hypothesis. Ecology 68: 181-187.

Stephens, K., and R. Brandstaetter. 1983. A laboratory manual: collected methods for the analysis of water. Can. Tech. Rep. Fish. Aquat. Sci. 1159: 68 p.

Sterner, R.W., T.H. Chrzanowski, J.J. Elser, and N.B. George. 1995. Sources of nitrogen and phosphorus supporting the growth of bacterio- and phytoplankton in an oligotrophic Canadian shield lake. Limnol. Oceanogr. 40: 242-249.

Stockner, J.G. 1975. Phytoplankton heterogeneity and paleolimnology of Babine Lake, British Columbia, Canada. Verh. Internat. Verein. Limnol. 19: 2236-2250.

Stockner, J.G., and K.S. Shortreed. 1974. Phytoplankton succession and primary production in Babine Lake, British Columbia. Fish. Res. Board Can. Tech. Rep. 417: 98 p.

Stockner, J.G., and K.S. Shortreed. 1975. Phytoplankton succession and primary production in Babine Lake, British Columbia. J. Fish. Res. Board Can. 32: 2413-2427.

Stockner, J.G., and K.S. Shortreed. 1978. Limnological surveys of Babine Lake, British Columbia: results of the monitoring program, 1974-1978. Can. Fish. Mar. Serv. Manusrc. Rep. 1494: 35 p.

Stockner, J.G., and K.S. Shortreed. 1985. Whole-lake fertilization experiments in coastal British Columbia lakes: empirical relationships between nutrient inputs and phytoplankton biomass and production. Can. J. Fish. Aquat. Sci. 42: 649-658.

Stockner, J.G., and K.S. Shortreed. 1991. Autotrophic picoplankton: community composition, abundance, and distribution across a gradient of oligotrophic British Columbia and Yukon Territory lakes. Int. Rev. Gesamten Hydrobiol. 76: 581-601.

Strickland, J.D.H. 1960. Measuring the production of marine phytoplankton. Bull. Fish. Res. Board Can. 122: 173 p.

Vollenweider, R.A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Mem. Ist. Ital. Idrobiol. 33: 53-83.

West, C.J. and J.C. Mason. 1987. Evaluation of sockeye salmon (*Oncorhynchus nerka*) production from the Babine Lake Development Project, *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96. pp. 176-190.

Wood, C.C., D.T. Rutherford, D. Bailey, and M. Jakubowski. 1998. Assessment of sockeye salmon production in Babine Lake, British Columbia with forecast for 1998. Can. Tech. Rep. Fish. Aquat. Sci. 2241: 50 p.

Yan, N.D., and G.L. Mackie. 1987. Improved estimation of the dry weight *of Holopedium gibberum* (Crustacea, Cladocera) using clutch size, a body fat index, and lake water total phosphorus concentration. Can. J. Fish. Aquat. Sci. 44: 382-389.

Table 1. Location and physical features of Babine Lake.

Lake basin	Latitude (°N)	Longitude (°W)	Surface area (km^2)	Mean depth (m)
North Arm	55°09'	126°35'	47	23
Main Arm	54°49'	126°07'	365	71
Hagan Arm	54°59'	126°11'	37	27
Morrison Arm	55°07'	126°15'	12	13
Whole lake			461	61
Nilkitkwa Lake	55°23'	126°40'	5	

Table 2. Variation in seasonal (May-October) averages of salient physical variables at Babine Lake. Mean values are whole-lake averages.

Station	Year	Surface temp. (°C)	Thermocline depth (m)	Mean epil. Temp. (°C)	Secchi depth (m)	Euphotic zone depth (m)	Extinction coeff. (/m)
1	1994	15.0	7.3	13.2	5.0	6.5	0.59
4		13.7	9.0	13.0	5.1	7.7	0.51
7		14.3	11.2	14.0	5.6	6.9	0.57
9		13.0	13.7	12.7	5.5	7.4	0.54
Mean		14.0	10.8	13.3	5.4	7.1	0.56
1	1995	14.4	6.9	13.0	4.5	6.0	0.60
4		13.8	11.5	13.3	4.9	6.8	0.54
7		14.8	12.7	14.1	4.5	7.1	0.56
9		13.5	14.1	13.1	4.9	6.8	0.55
3		15.8	9.7	14.8	4.2	6.4	0.63
Mean		14.2	11.7	13.5	4.7	6.7	0.56

Table 3. Variation in average epilimnetic chemical variables at Babine Lake. Data are seasonal (May-October) means. Mean values are whole-lake averages. Data in brackets are hypolimnetic averages.

Station	Year	pH	Total alk. (mg CaCO3/L)	T.D.S. (mg/L)	D.I.C. (mg/L)	Silicate (mg Si/L)	Nitrate (µg N/L)	Total P (µg/L)
1	1994	7.44	36.5	63	9.59	1.45	35.1 (78.3)	5.3 (5.3)
4		7.40	36.6	61	9.75	1.45	32.7 (70.9)	5.4 (4.1)
7		7.46	36.9	58	9.81	1.47	36.8 (72.2)	5.6 (4.3)
9		7.52	36.7	60	9.50	1.53	30.1 (72.7)	5.4 (3.6)
Mean		7.46	36.7	60	9.66	1.48	33.4 (73.3)	5.4 (4.3)
1	1995	7.58	36.1	64	9.24	1.43	18.3 (74.5)	4.7 (4.6)
4		7.53	36.1	63	9.32	1.39	20.3 (71.8)	5.2 (3.6)
7		7.58	36.5	62	9.37	1.39	15.9 (71.8)	6.1 (3.8)
9		7.56	36.5	62	9.38	1.42	18.8 (71.8)	5.8 (3.5)
Mean		7.56	36.4	63	9.33	1.41	17.9 (72.3)	5.6 (3.9)

Table 4. Variation in seasonal averages of epilimnetic concentrations of particulate elements and salient atomic ratios. Mean values are whole-lake averages.

		Particulate mass (µg/L)			Particulate ratio (by atoms)		
Station	Year	C	N	P	C/N	C/P	N/P
1	1994	335	37	3.0	10.6	288	27
4		318	32	3.4	11.6	242	21
7		412	47	3.3	10.2	323	32
9		414	43	3.6	11.2	297	26
Mean		382	41	3.3	10.8	296	28
1	1995	336	42	2.6	9.3	334	36
4		338	39	2.9	10.1	301	30
7		378	46	2.8	9.6	349	36
9		368	45	2.9	9.5	328	34
Mean		360	44	2.8	9.6	332	34

Table 5. Variation in seasonal (May-October) averages of selected biological variables at Babine Lake. Chlorophyll and bacteria data are epilimnetic averages and numbers in brackets are hypolimnetic averages. Photosynthetic rate data are integrated daily rates.

		Chlorophyll (µg/L)				Photosynthetic rate (mg C,m^{-2},d^{-1})				Bacteria
Station	Year	Total	Pico.	Nano.	Micro.	Total	Pico.	Nano.	Micro.	(#x10^6/mL)
1	1994	1.51 (0.64)				83				0.99
4		2.19 (0.53)				150				0.95
7		1.86 (0.42)	0.88	0.59	0.35	123	56	49	18	1.01
9		1.96 (0.36)				144				1.10
Mean		1.87 (0.47)				125				1.02
1	1995	2.35 (0.78)				107				0.90
4		2.63 (0.51)				156				0.93
7		2.77 (0.56)	1.40	0.91	0.46	166	72	63	32	0.94
9		2.30 (0.69)				176				1.02
Mean		2.53 (0.63)				155				0.95

Table 6. Variation in seasonal (May-October) average mean epilimnetic picoplankton numbers. Data are in thousands/mL.

Station	Year	USYN	CSYN	REUK	RCYN	Total
1	1994	20.2	11.7	1.5	2.9	36.2
4		26.7	15.9	1.4	2.8	46.9
7		43.5	14.5	2.0	3.3	63.0
9		28.8	6.6	1.4	4.1	40.8
Mean		31.8	11.9	1.6	3.4	48.6
1	1995	28.3	35.5	1.0	3.8	68.6
4		30.5	40.2	1.2	3.0	74.9
7		34.6	34.9	1.1	2.6	73.2
9		34.0	50.6	0.7	2.1	87.4
Mean		32.5	40.3	1.0	2.8	76.5

Table 7. Variation in seasonal (May-October) average mean epilimnetic numbers of dominant nanoplankton. All data are in numbers/mL.

Station	Year	*Ochromonas* sp.	*Chroomonas acuta*	*Chromulina* spp.	*Cylotella glomerata*	Total nanoplankton
1	1994	48	196	208	97	623
4		57	348	223	123	820
7		48	303	264	86	778
9		47	293	132	47	565
Mean		49	285	208	83	692
1	1995	103	202	358	124	903
4		86	397	291	109	983
7		125	389	331	162	1120
9		86	364	401	206	1203
Mean		103	344	350	158	1077

Table 8. Variation in seasonal (May-October) average mean epilimnetic numbers of total microplankton and major diatoms in the microplankton size fraction. All data are in numbers/mL.

Station	Year	*Asterionella formosa*	*Fragilaria crotonensis*	*Rhizosolenia* sp.	*Tabellaria fenestrata*	*Cyclotella* spp.	Total microplankton
1	1994	12	3	45	5	13	270
4		24	3	34	10	16	270
7		26	7	25	26	13	260
9		42	95	31	49	9	360
Mean		27	30	32	26	12	292
1	1995	6	13	74	5	30	410
4		16	23	58	12	31	450
7		16	34	66	28	48	760
9		28	37	48	38	31	1240
Mean		17	29	61	24	37	775

Table 9. Variation in seasonal average biomass of major zooplankton groups and genera. Bosminidae are primarily *Eubosmina longispina*, Cyclopidae are mainly *Cyclops scutifer* with some *Diacyclops thomasi*, and Diaptomidae are *Leptodiaptomus ashlandi* and *L. pribilofensis*. To maintain comparability between years, data from Station 3 (sampled only in 1995) were not included in the whole-lake means.

		Zooplankton biomass (mg dry wt/m^2)						
Station	Year	Macrozoopl.	Bosminidae	Cyclopidae	Diaptomidae	*Daphnia*	*Heterocope*	*Epischura*
1	1994	823	37	371	290	29	65	18
4		889	43	320	382	5	120	16
7		907	62	296	427	26	84	7
9		960	46	362	444	58	39	7
Mean		902	49	334	396	32	73	11
1	1995	1,003	9	388	480	8	69	11
4		1,222	17	373	727	47	29	13
7		1,208	12	417	684	23	27	17

9	1,177	8	366	744	21	20	11
3	1,209	200	329	565	13	65	17
Mean	1,159	11	390	665	23	34	13

Table 10. Contribution of sockeye carcasses to the phosphorus load to the Main Arm of Babine Lake. In 1973 the annual P load to Babine Lake from precipitation and fluvial inputs was estimated at 19,644 kg P (Stockner and Shortreed 1974). Average P content of each spawner was taken from Mathiesen et al. (1988). Escapement data are from Wood et al. (1998).

		Phosphorus from carcasses		
	Escapement	Total (kg)	mg P/m²/yr	% of total P load
1950-1965 (pre-BLDP)				
Mean	236,642	2,678	7.3	12
Minimum	30,835	349	1.0	2
Maximum	443,398	5,017	13.7	20
1985-1995 (post-BLDP)				
Mean	1,029,555	11,650	31.9	37
Minimum	510,570	5,778	15.8	23
Maximum	1,568,272	17,747	48.6	47

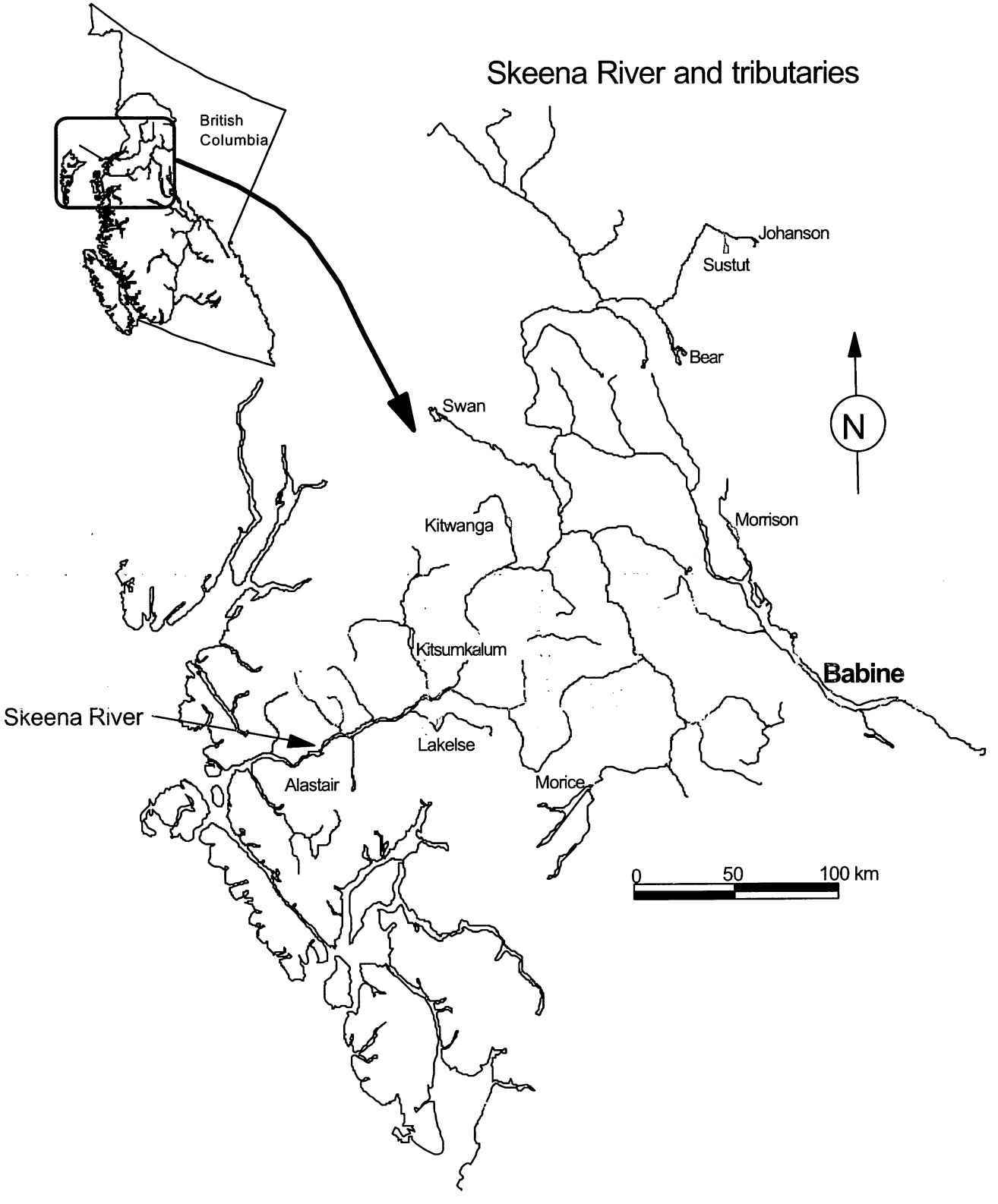
Table 11. Regression equations used to normalize pre-BLDP and 1973 zooplankton numbers with data from our study.

	To convert Miller data (M) to CB data (Rankin 1977)		To convert Miller data to Wisconsin data (W) (this study)	
Zoopl. Group	Equation	r^2 of equation	Equation	r^2 of equation
Cyclopids	CB=0.68M+0.23	0.86	W=0.76M+57	0.88
Diaptomids	CB=0.70M+0.40	0.96	W=0.73M+265	0.83
Daphnia	CB=0.71M+0.03	0.72	W=0.75M-0.43	0.82
Bosminids	CB=0.96M-0.11	0.79	W=0.77M+10.6	0.88

Table 12. Multi-year seasonal averages of Main Arm zooplankton from the 3 study periods. Numbers in brackets are 2 SE. Smolt numbers were not available for the first 3 pre-BLDP years. Smolt numbers are from the year following the lake year (e.g., fry reared in the lake in 1973 and emigrated in the spring of 1974).

	Zooplankton numbers in thousands/m²				Smolt numbers
Era	*Daphnia*	Bosminids	Cyclopids	Diaptomids	(millions)
Pre-BLDP (n=7)	6.9 (2.2)	7.2 (2.5)	168 (25)	147 (35)	19.7 (15.3)
1973 (n=1)	1.2	36.7	193	273	77.9
Post-BLDP (n=2)	3.1 (0.3)	5.6 (6.7)	138 (51)	145 (83)	24.1 (13.6)

LIST OF FIGURES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Bear
Swan
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Morrison
Kitsumkalum
Babine
Skeena River
Lakelse
Alastair
Morice
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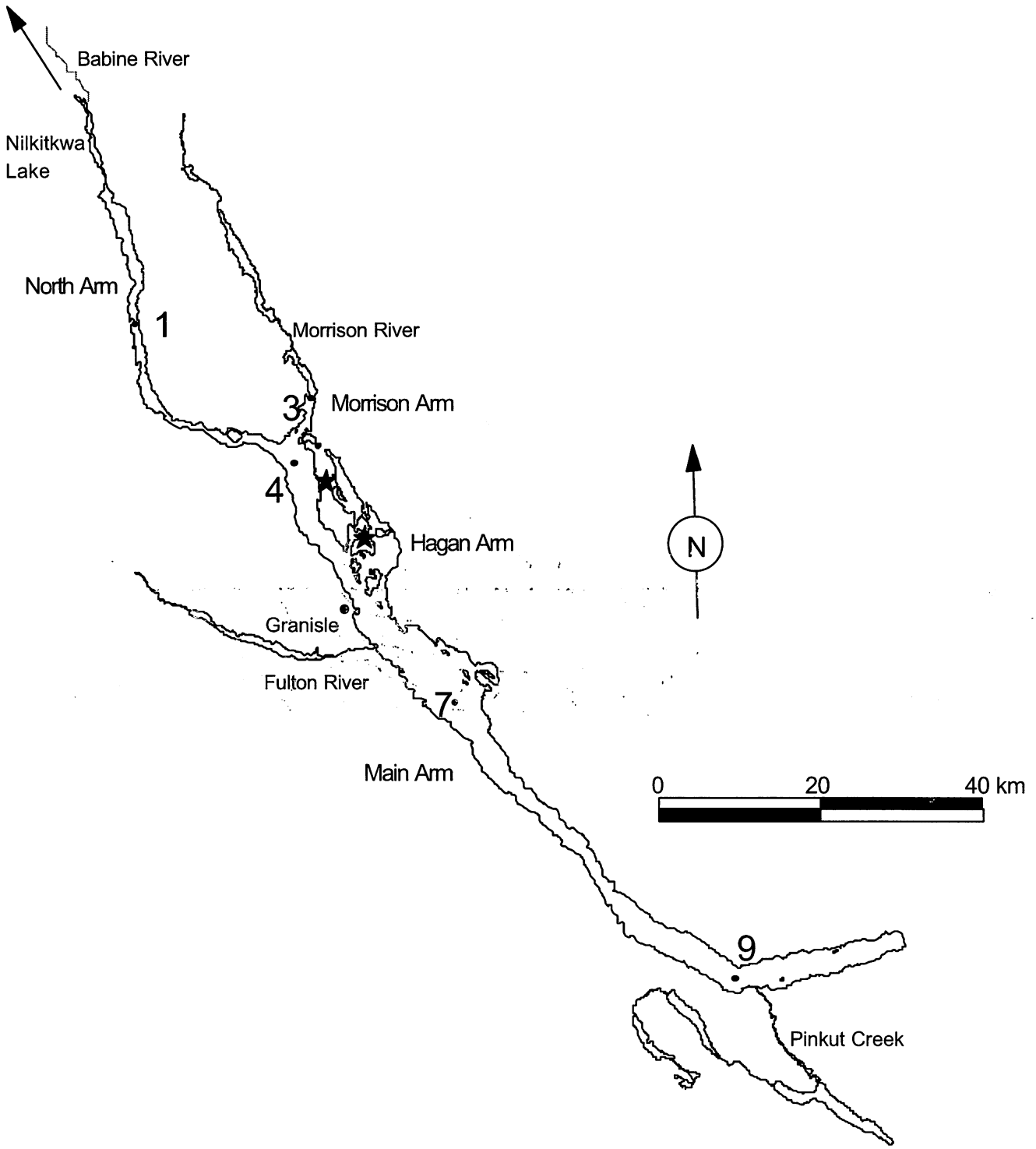
100 km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Granisle
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40 km
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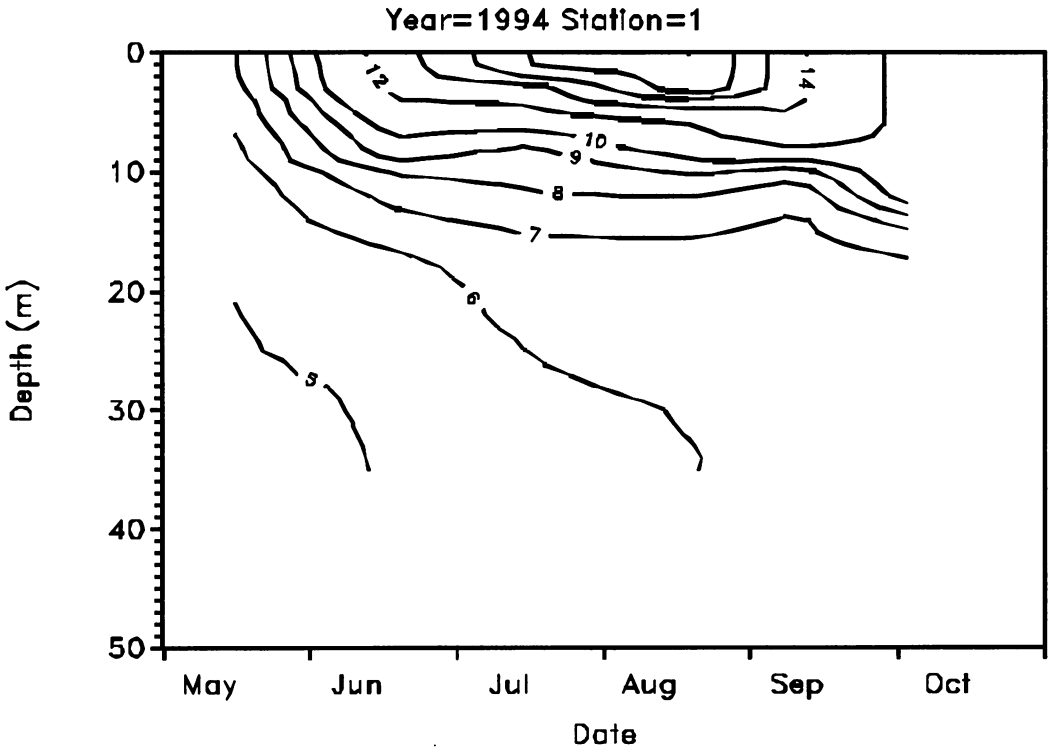
Pinkut Creek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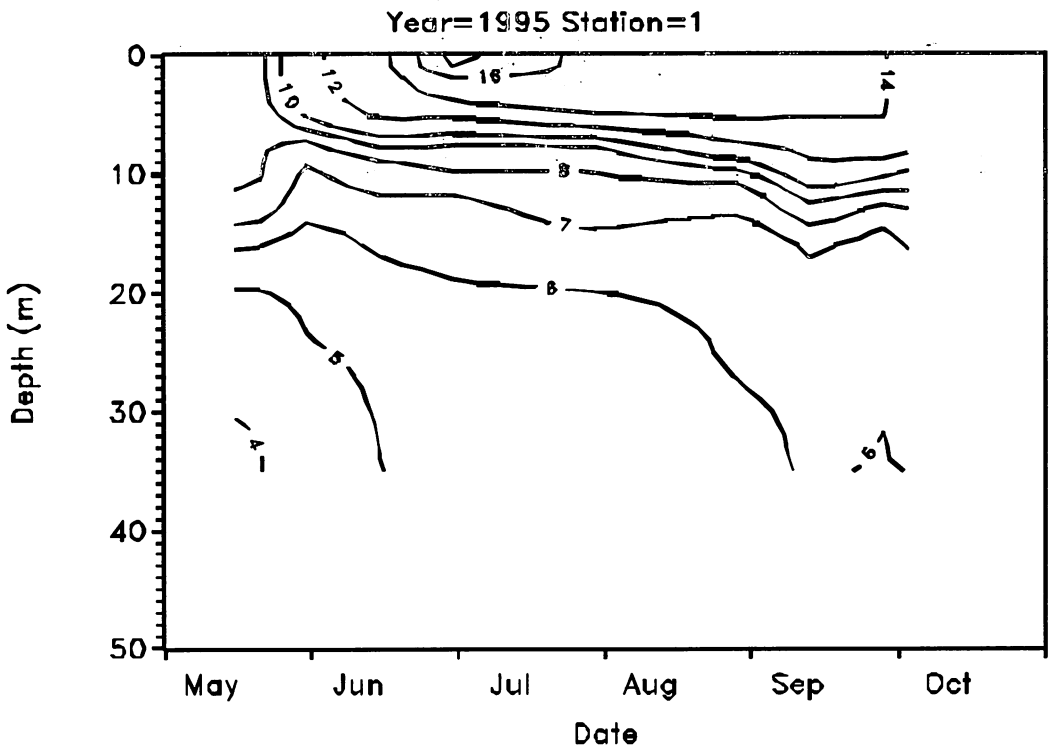
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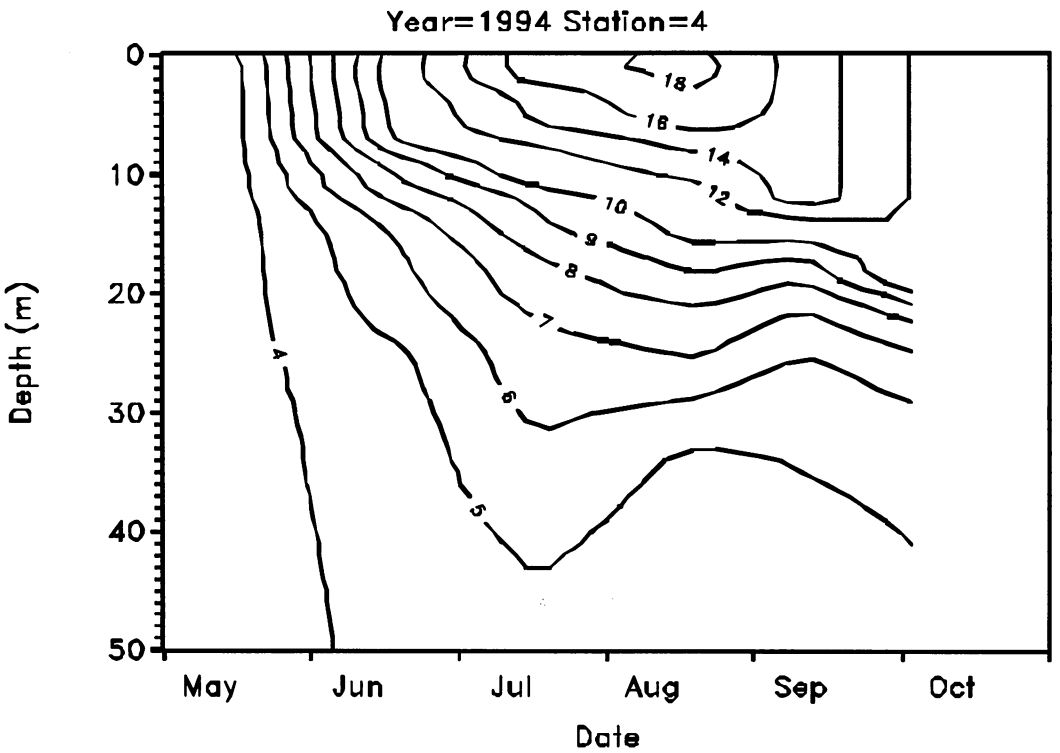
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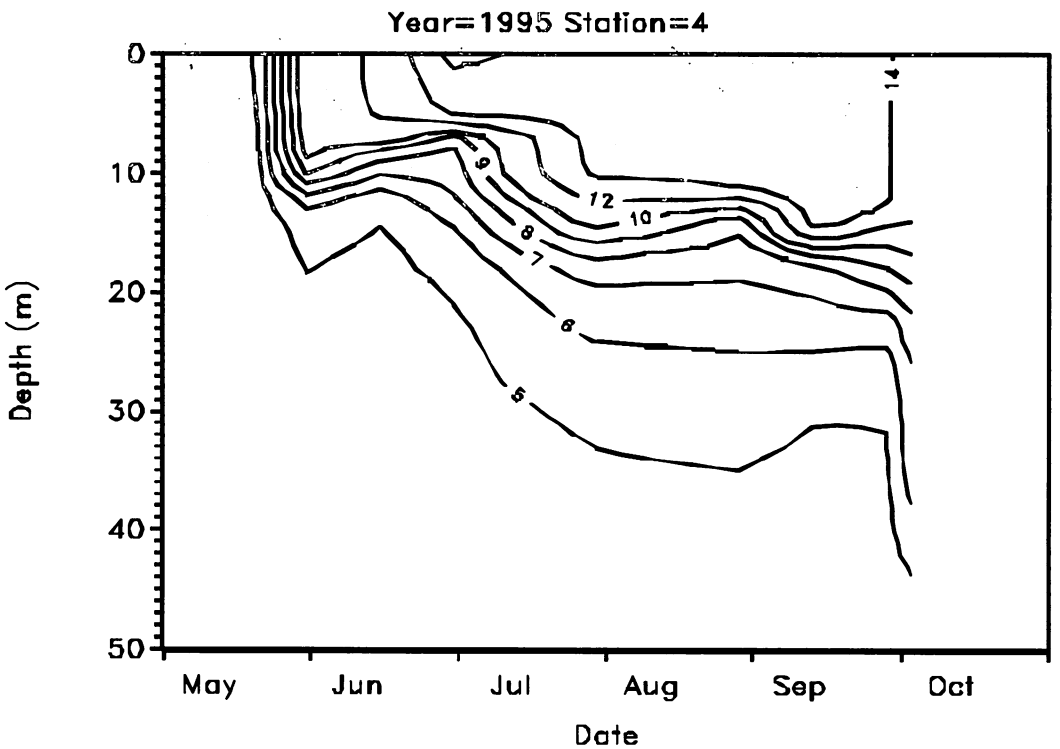
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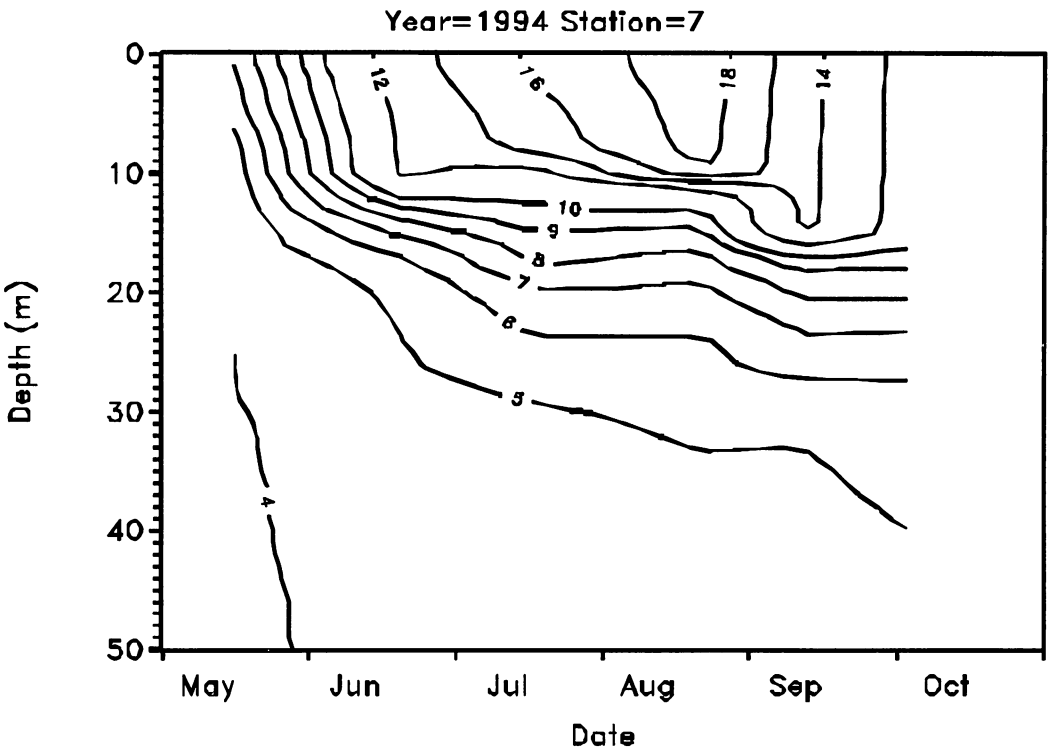
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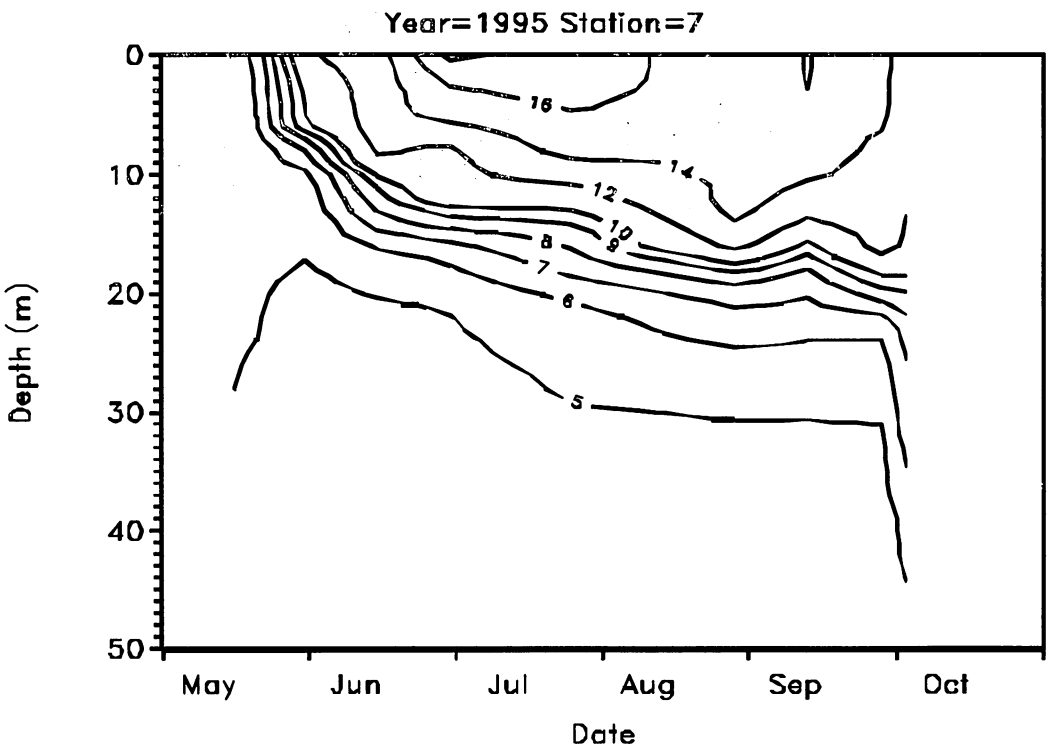
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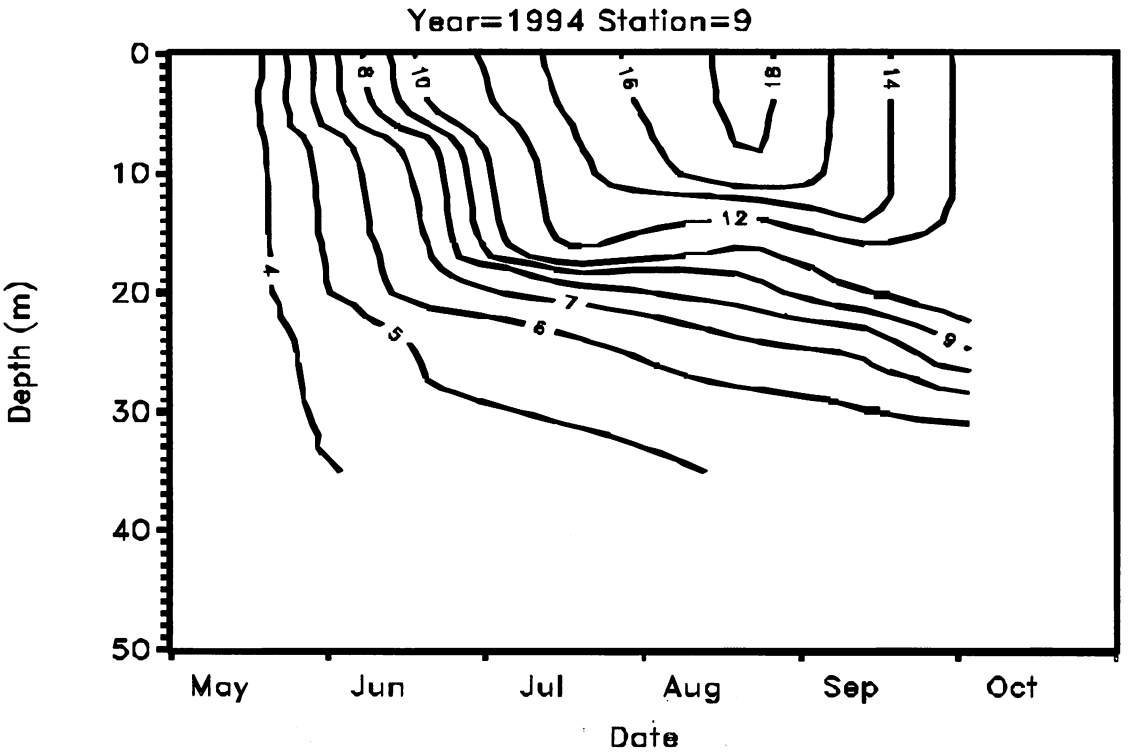
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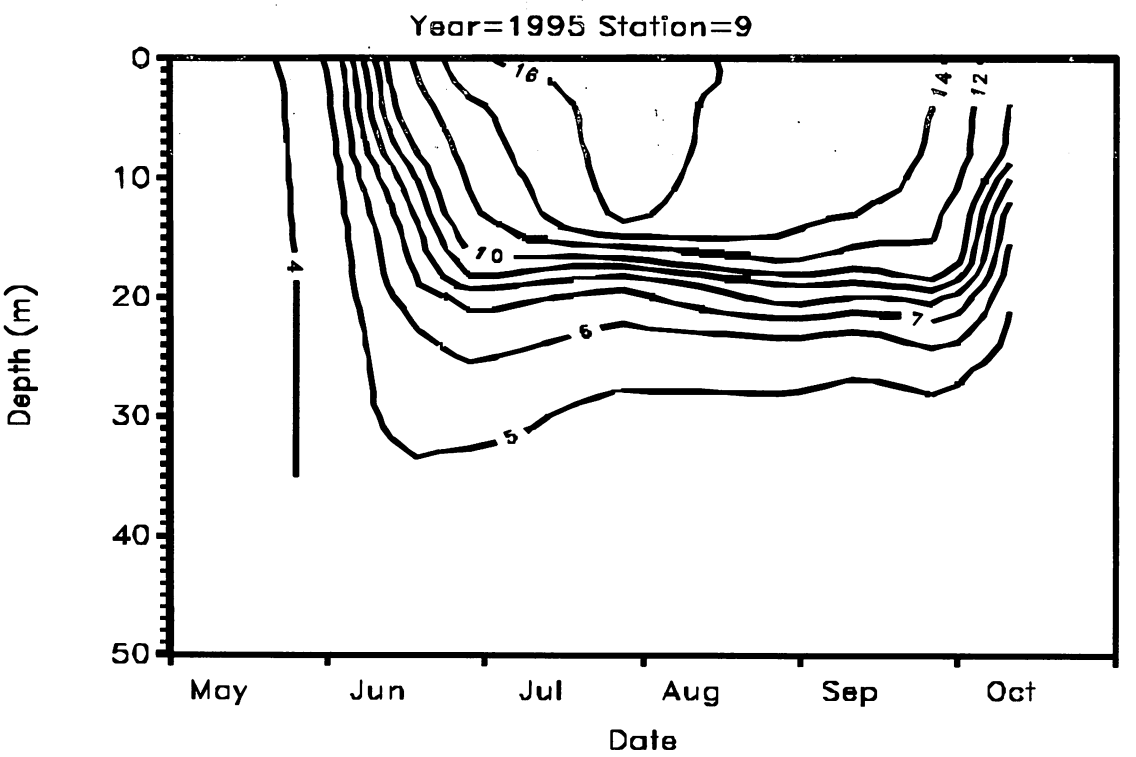
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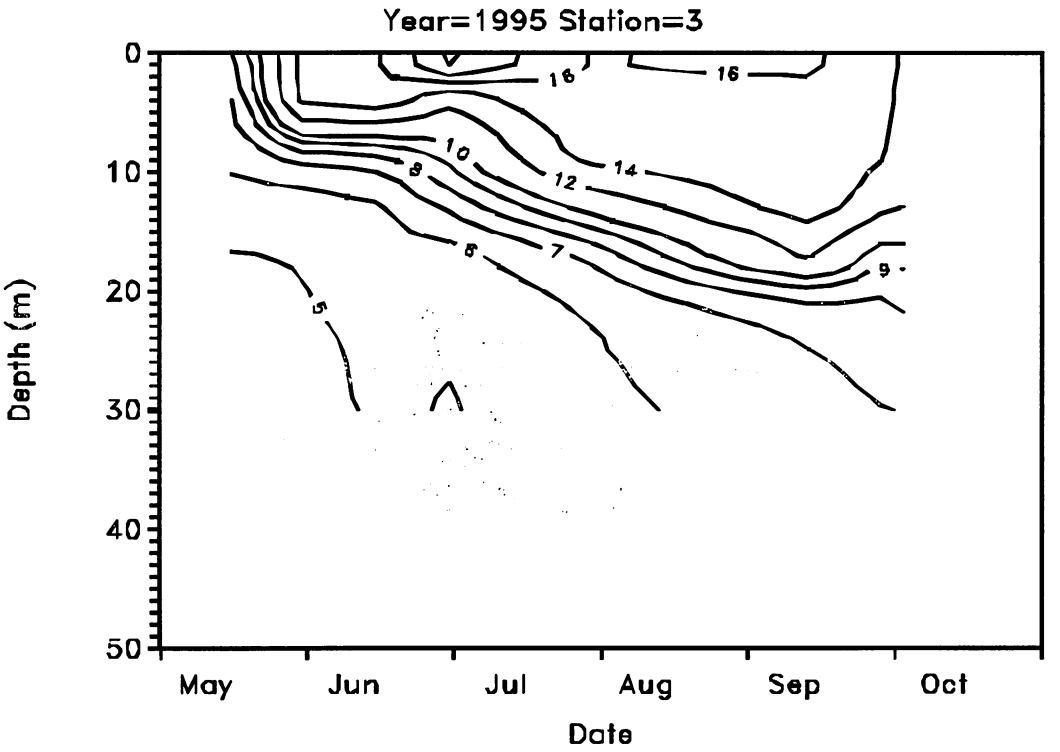
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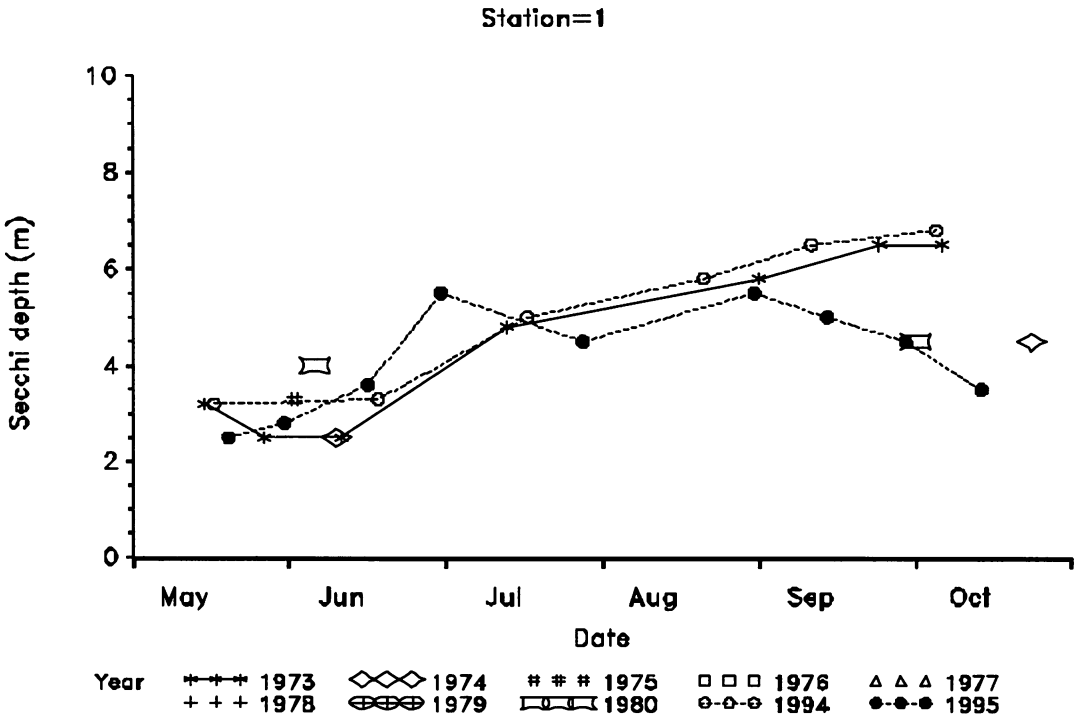
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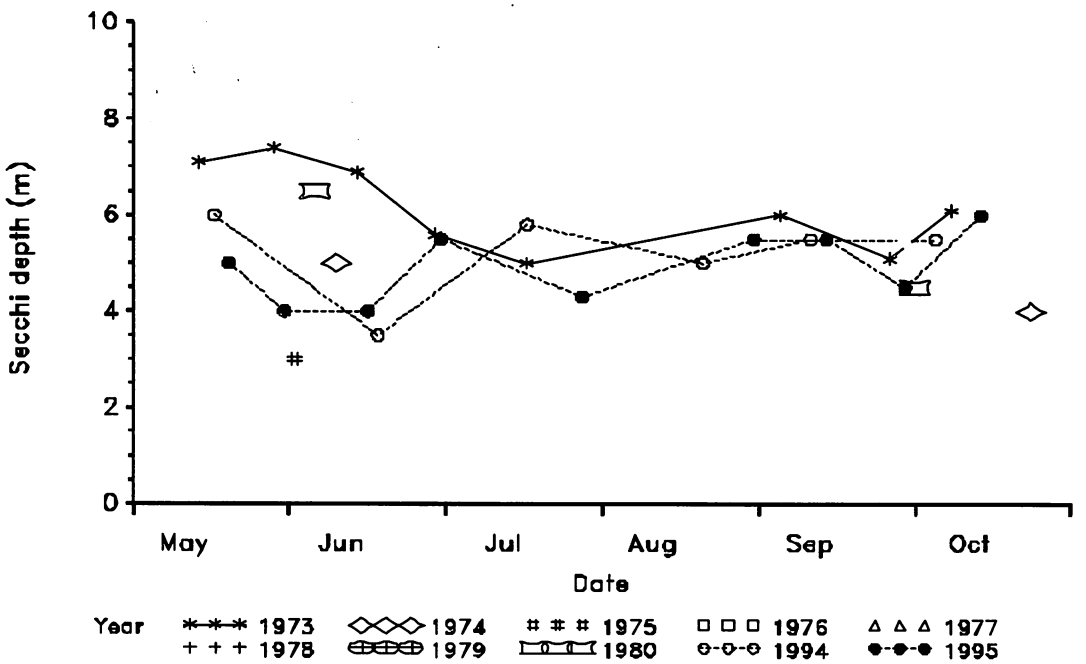
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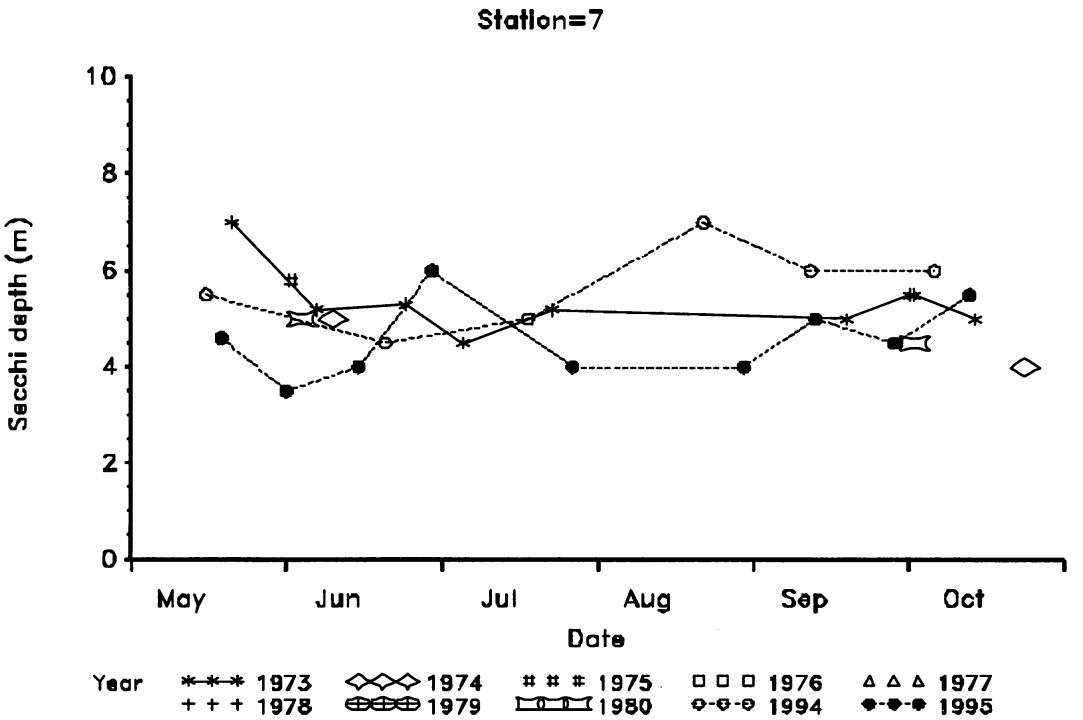
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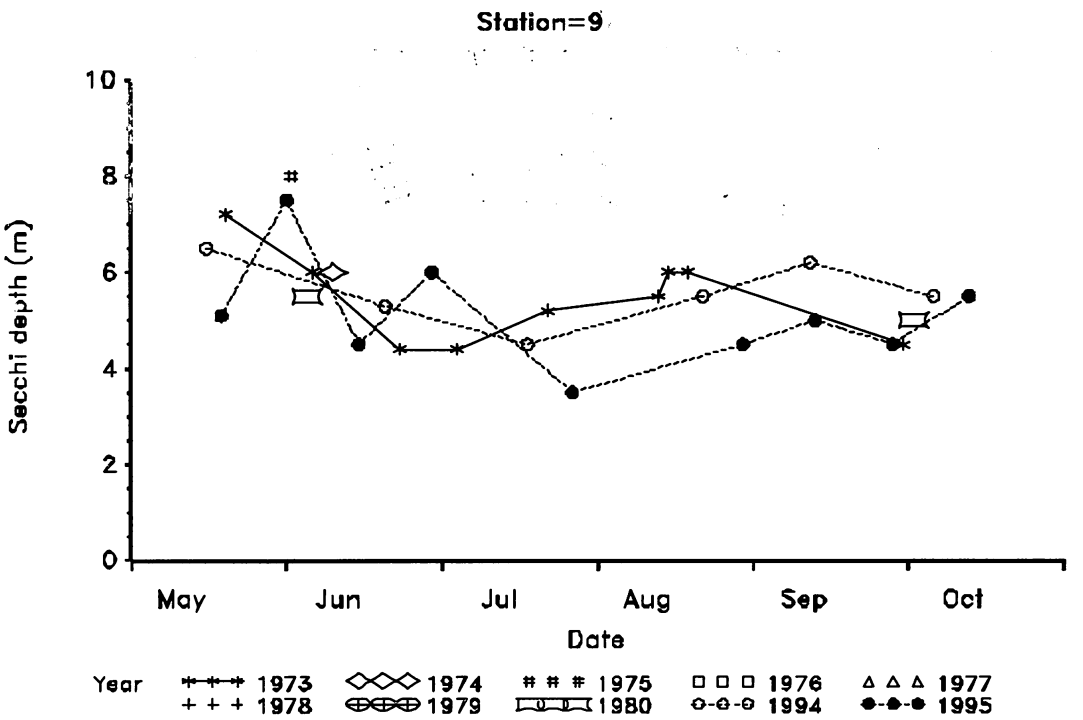
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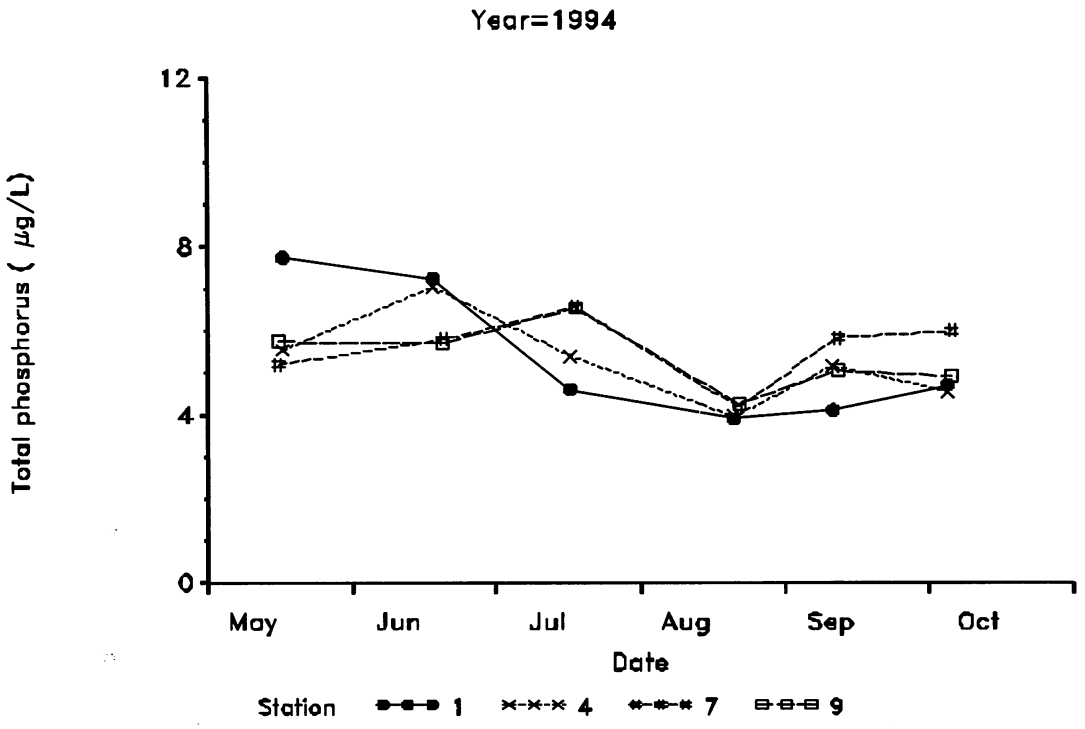
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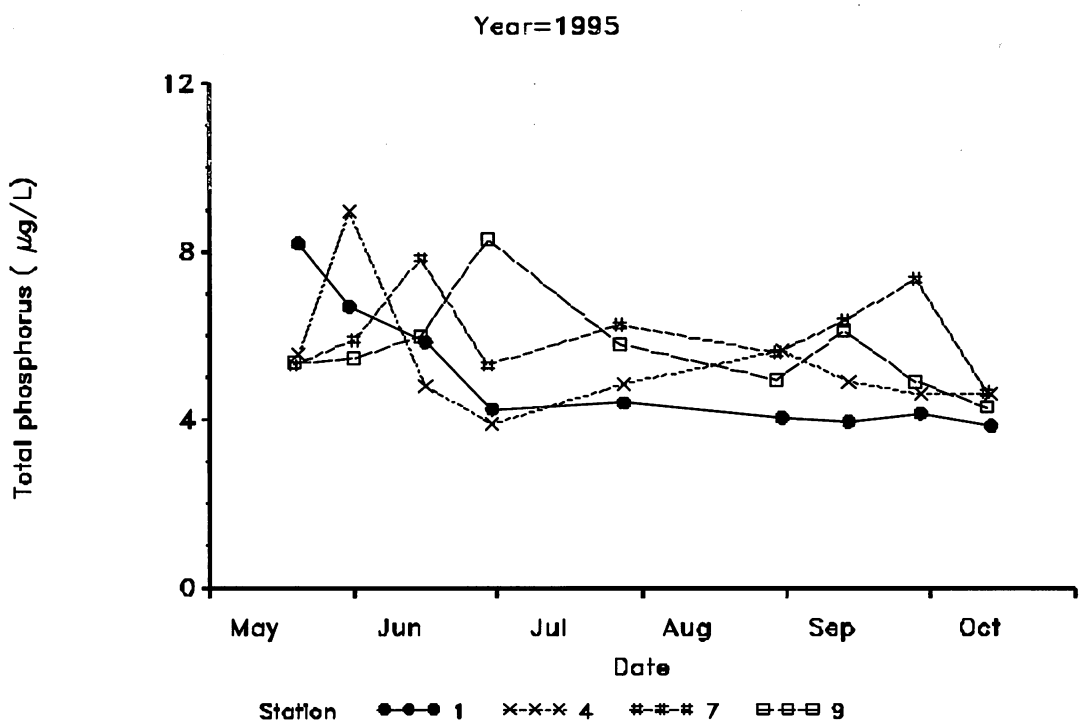
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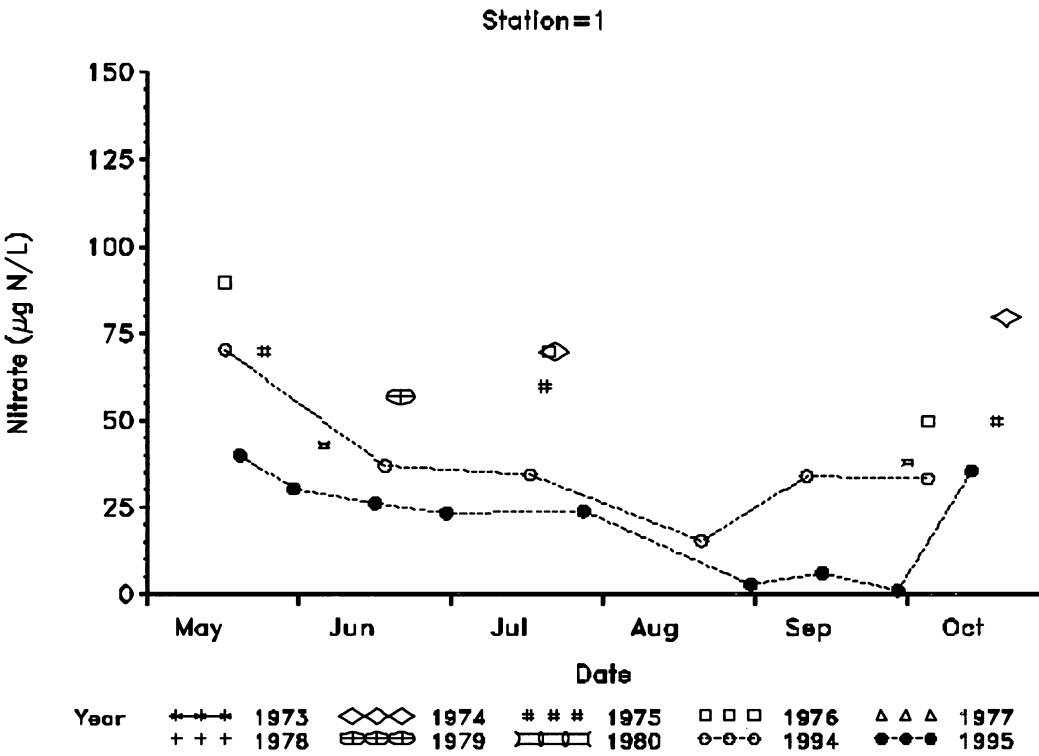
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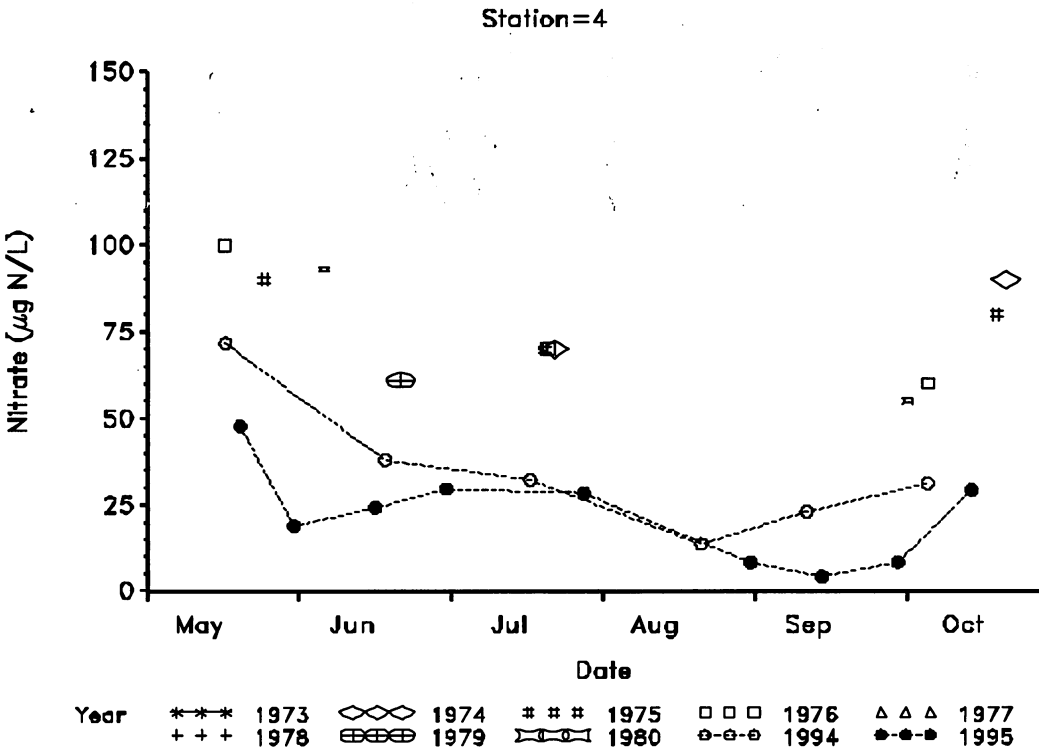
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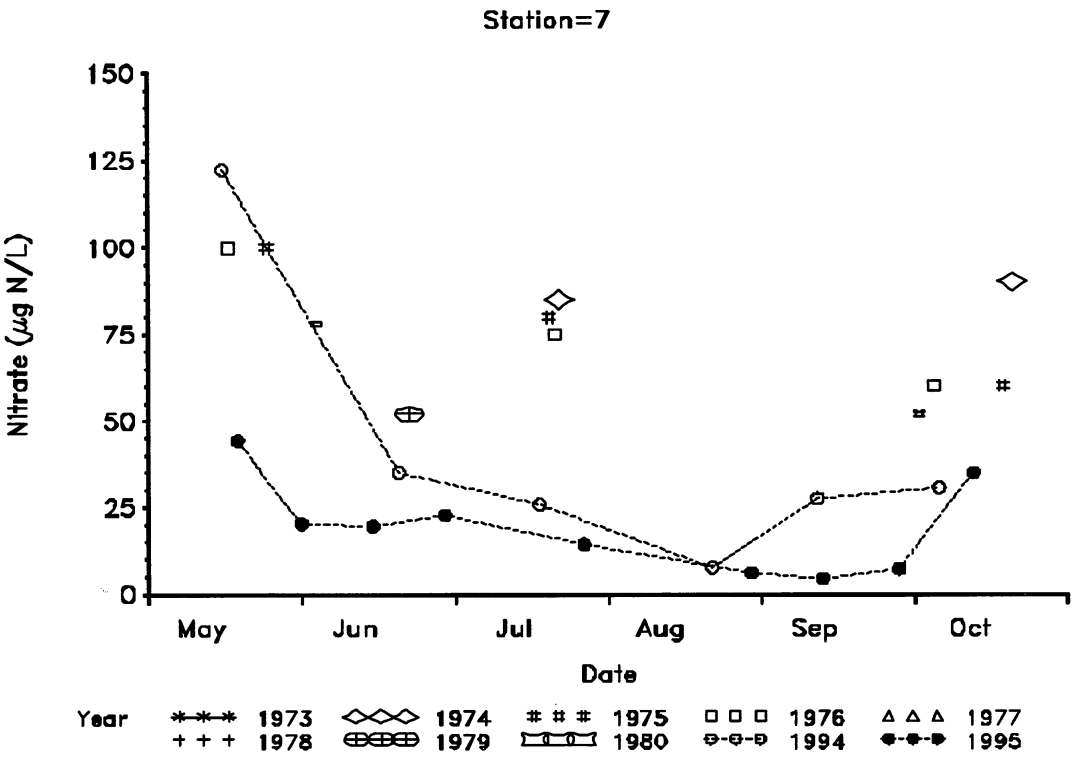
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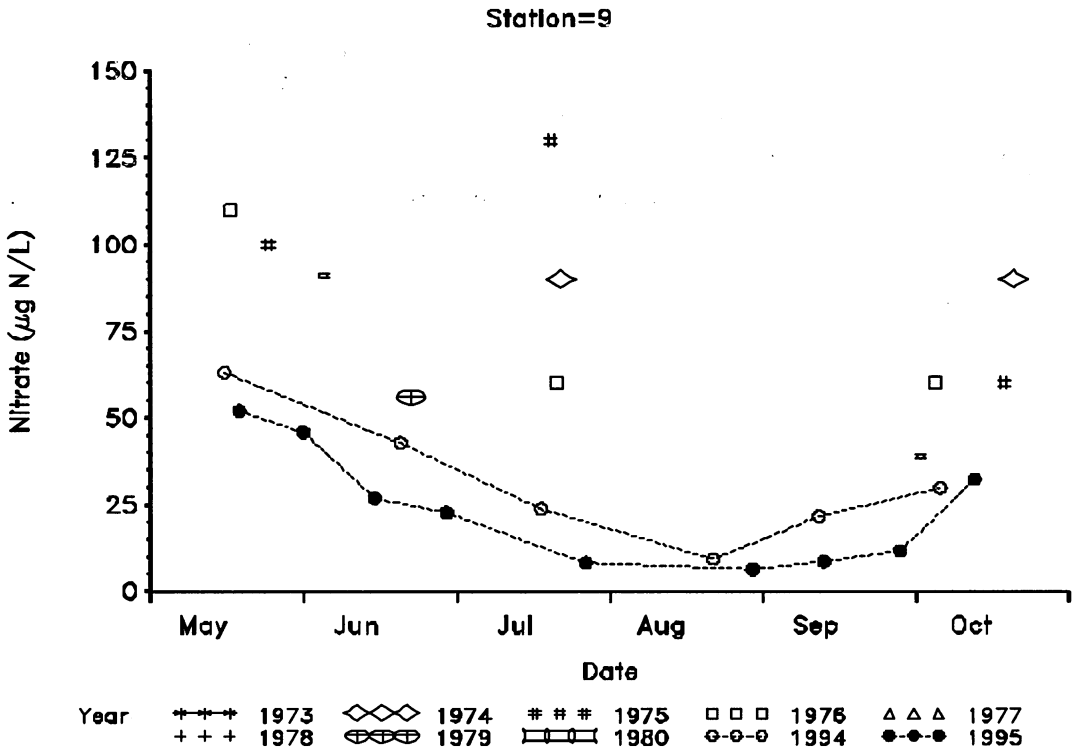
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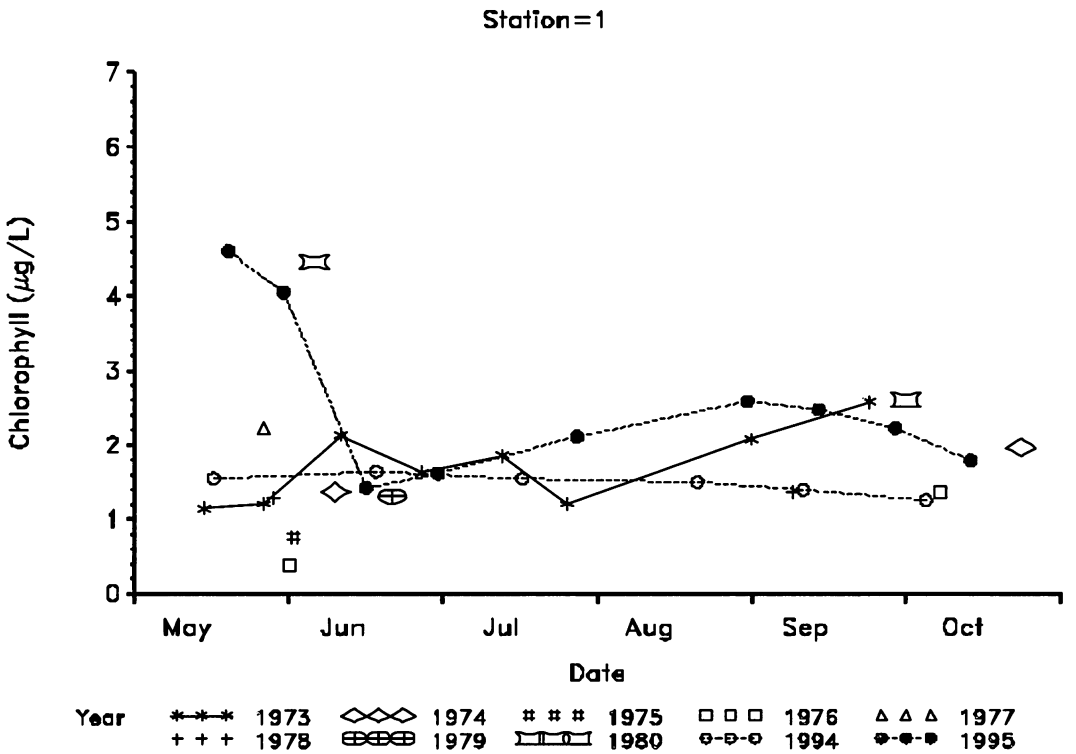
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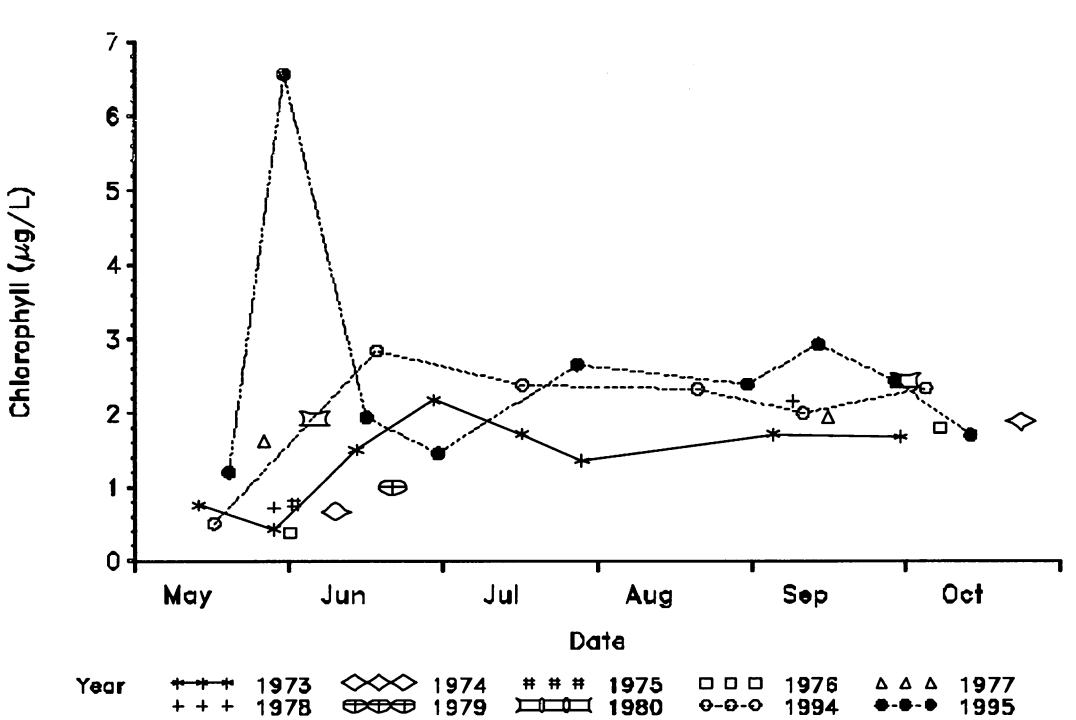
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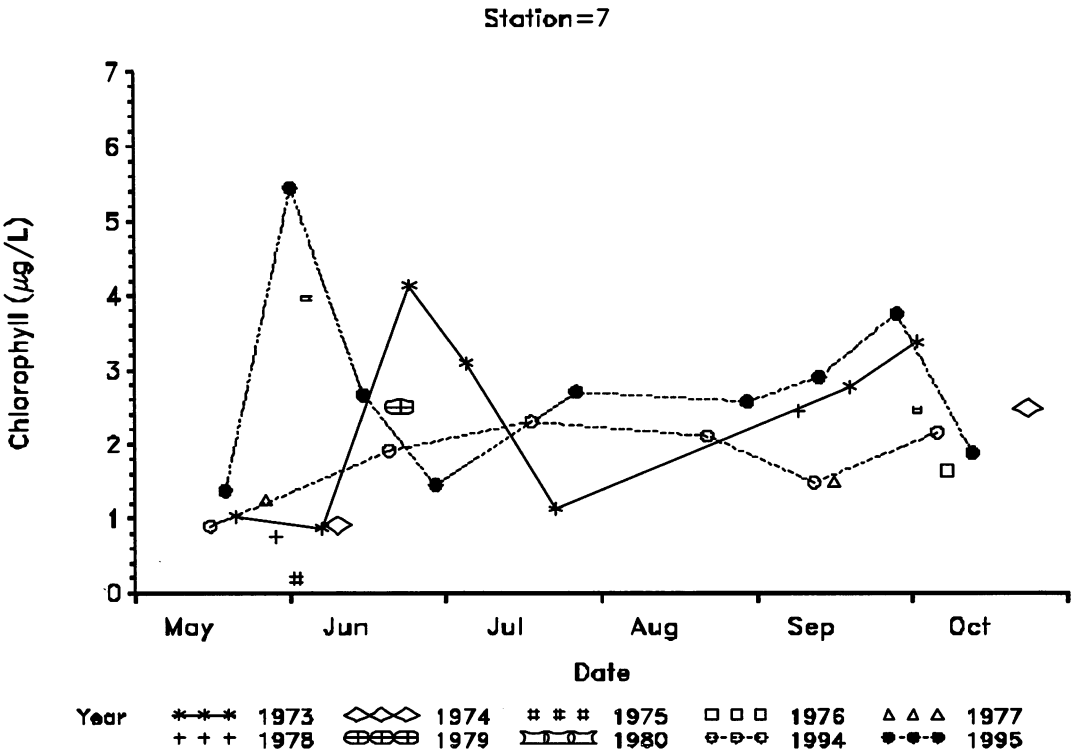
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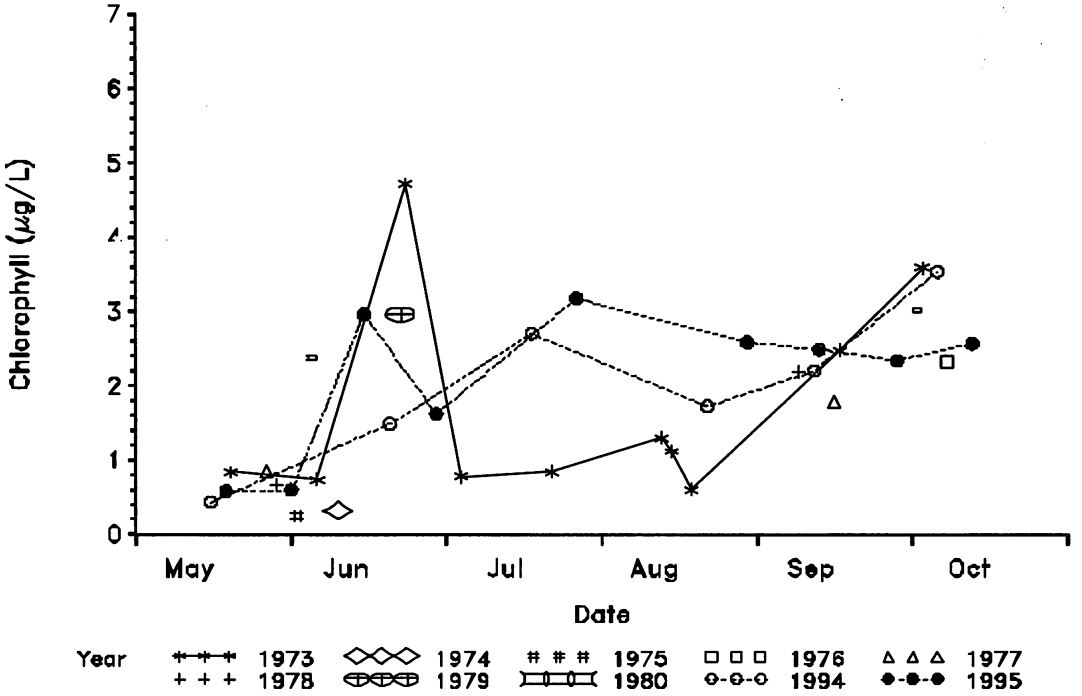
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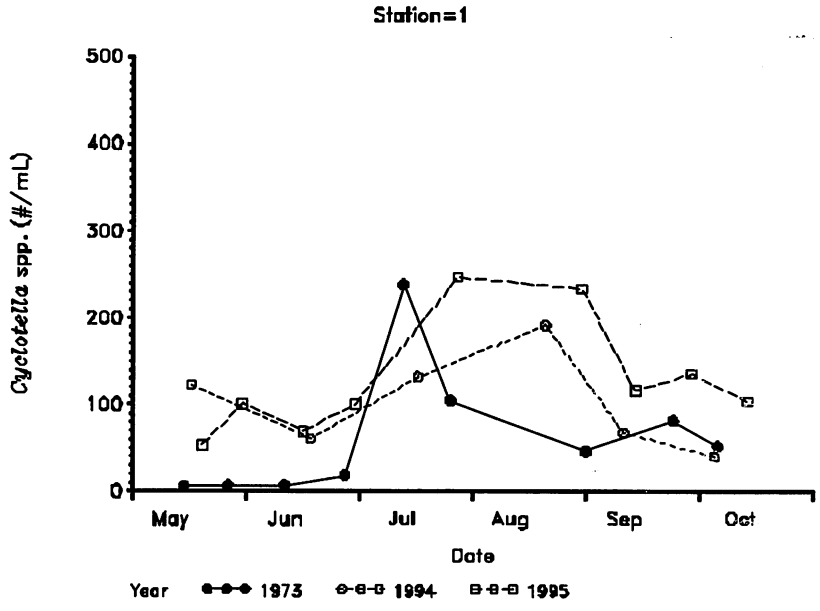
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Date
Year
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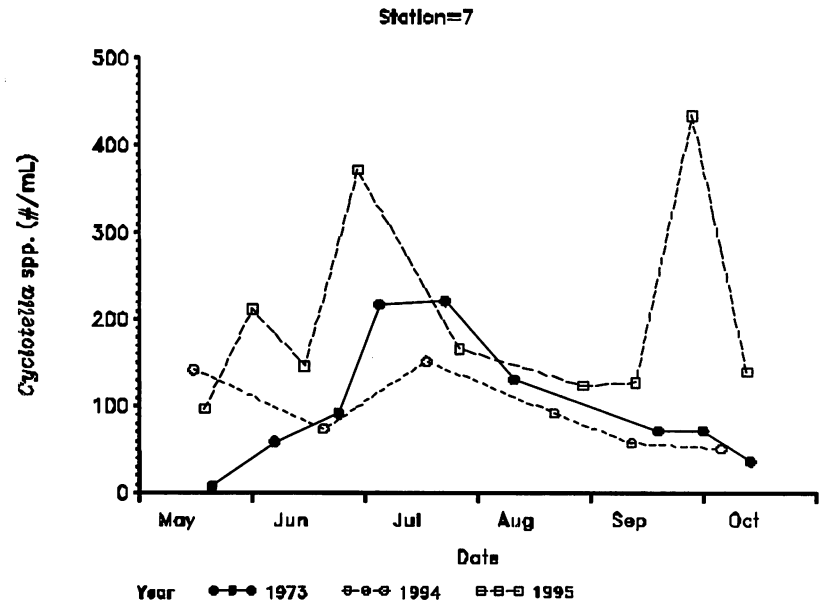
1994
1995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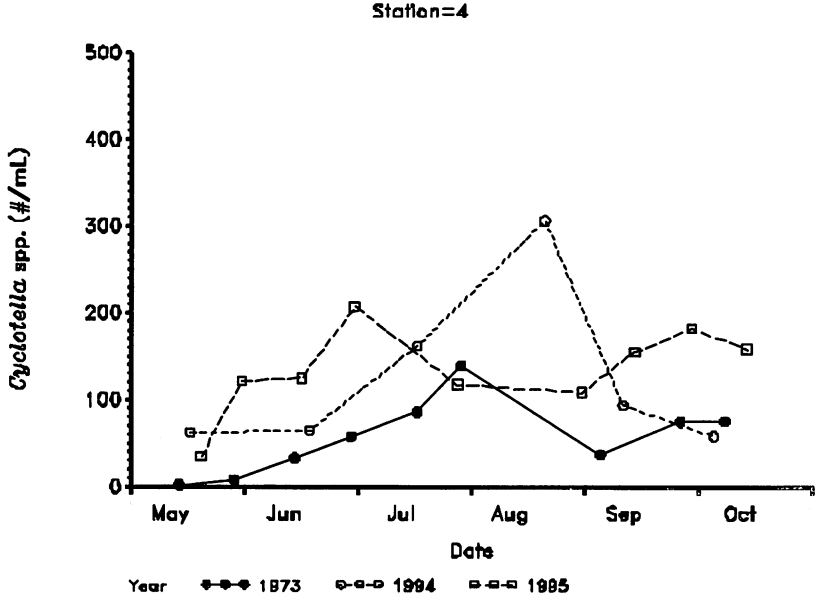
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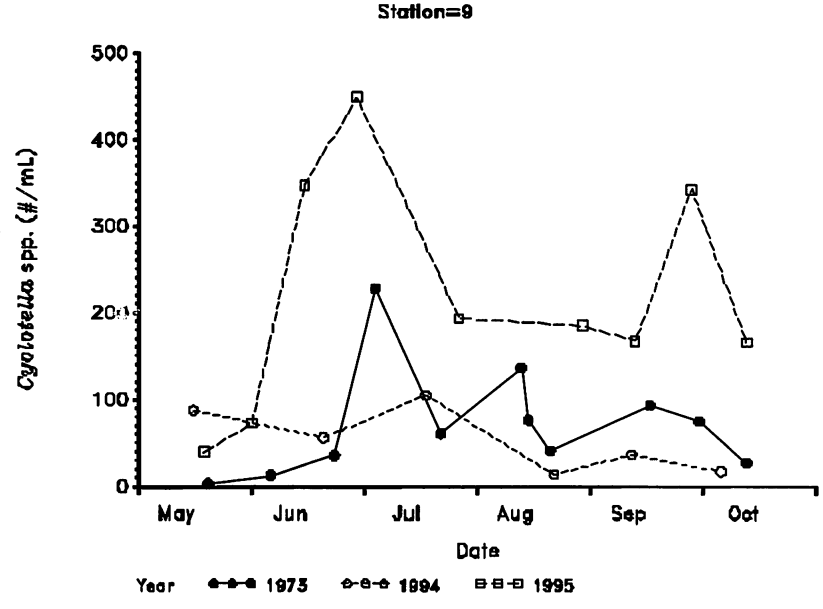
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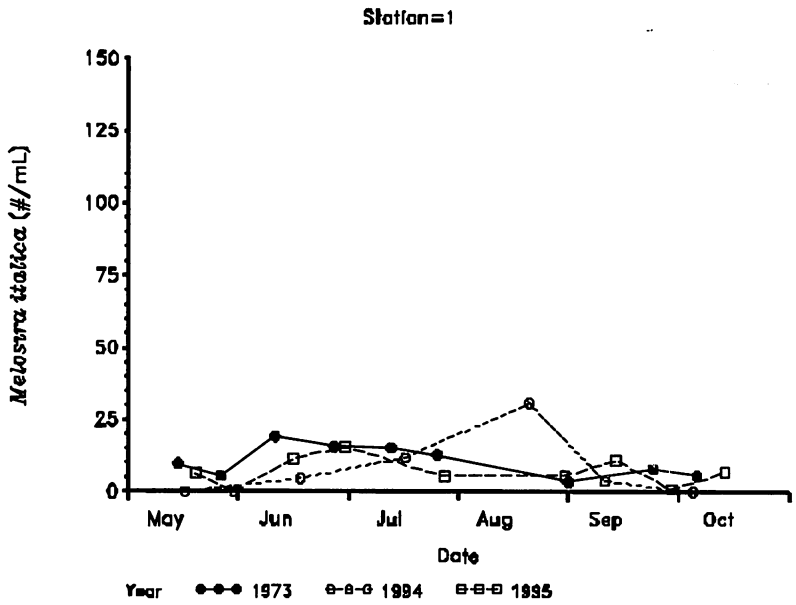
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Date
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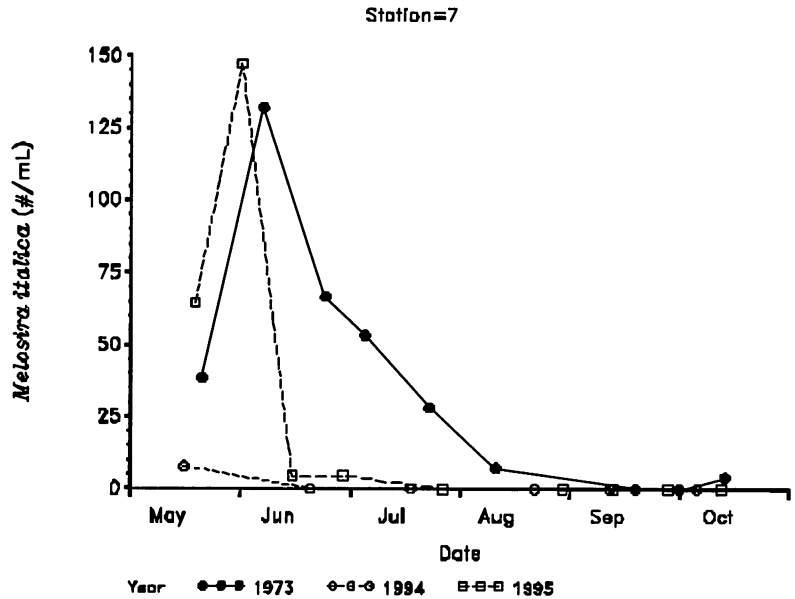
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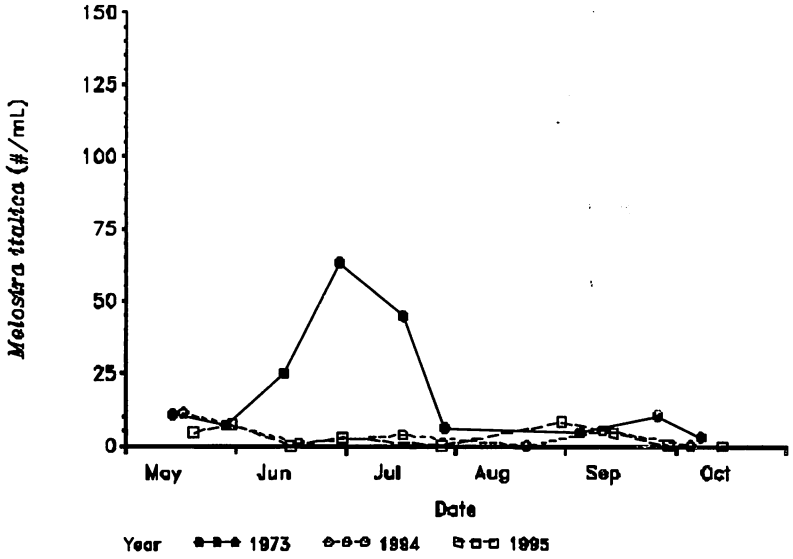
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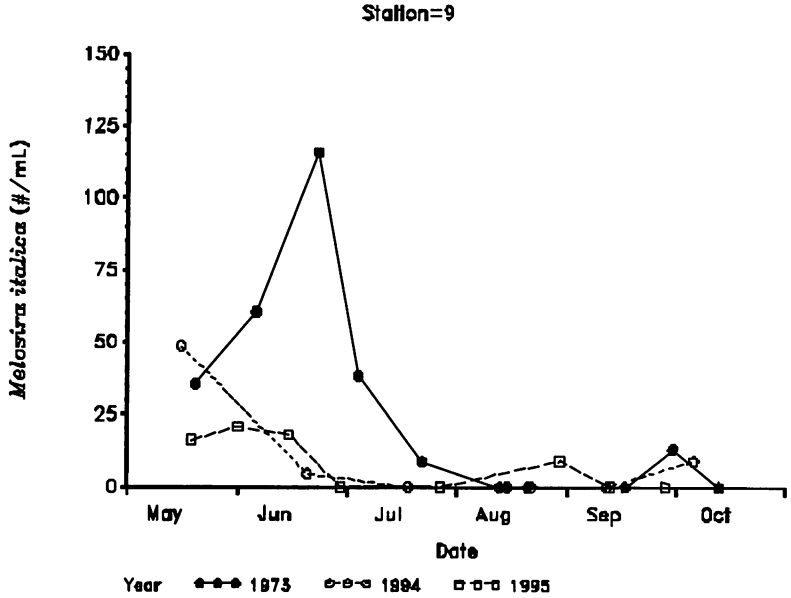
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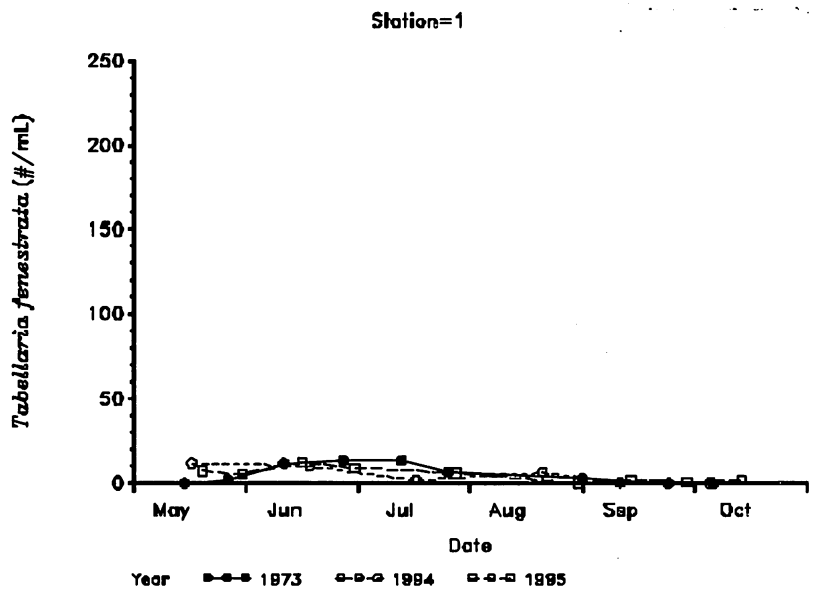
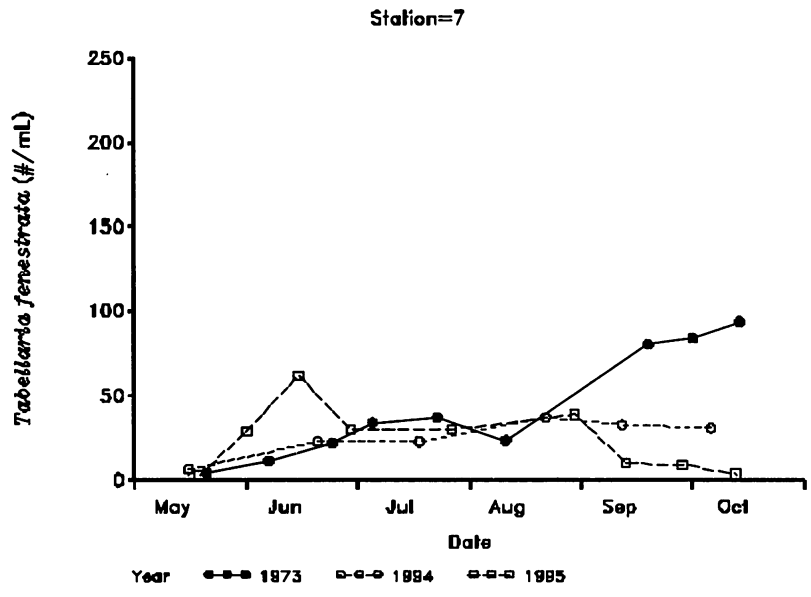
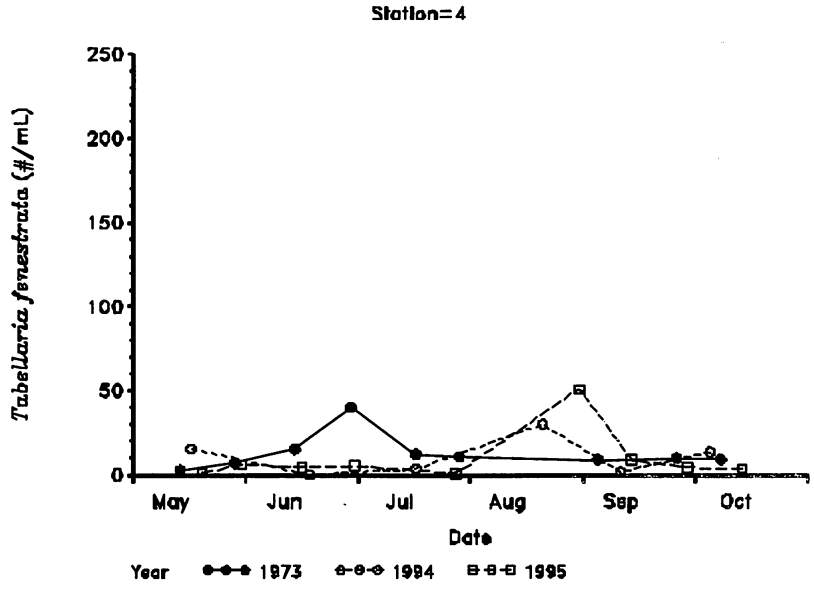
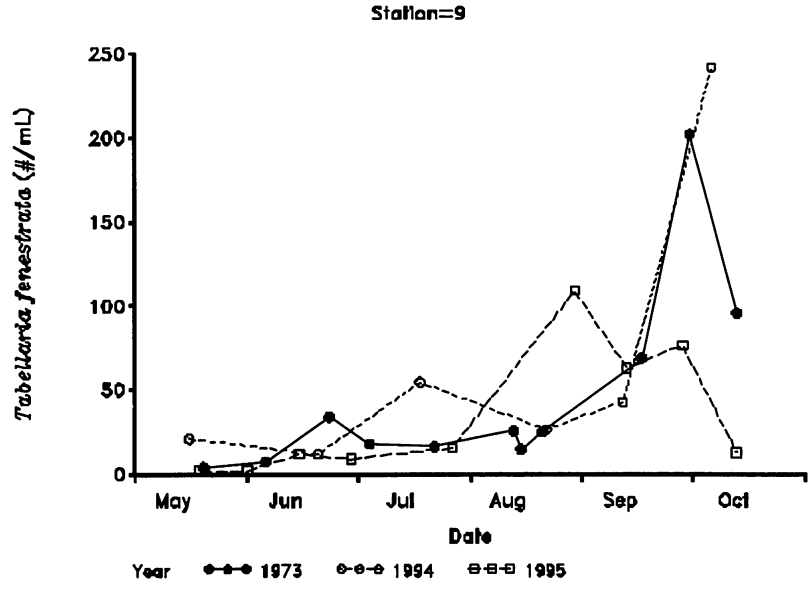
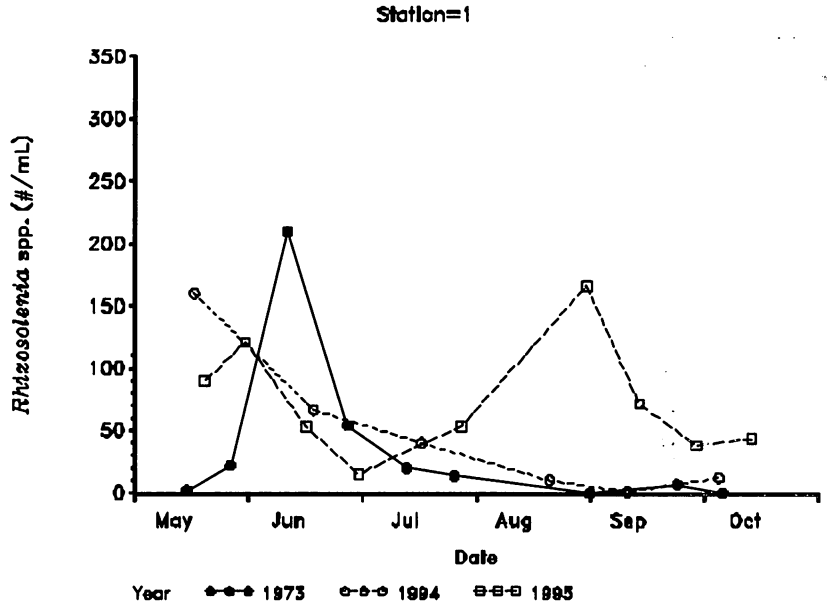
Date
Year 1973 1994 1995

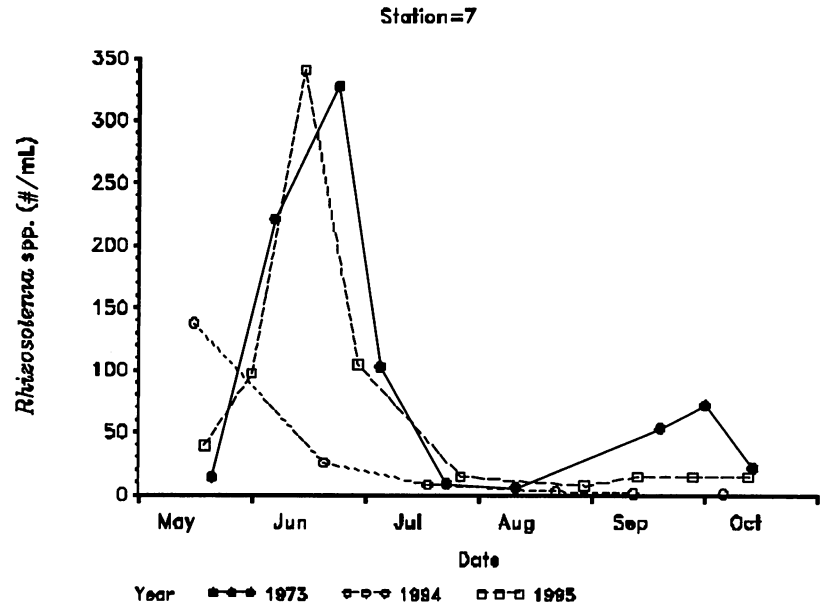

Station=1
Tabellaria fenestrata (#/mL)
250
200
150
100
50
0
May
Jun
Jul
Aug
Sep
Oct
Date
Year
1973
1994
1995

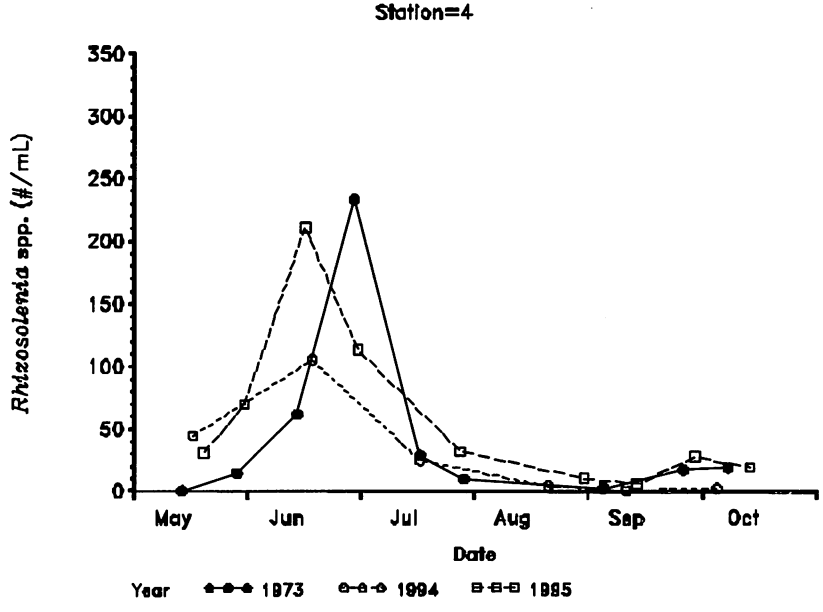

Station=7
Tabellaria fenestrata (#/mL)
250
200
150
100
50
0
May
Jun
Jul
Aug
Sep
Oct
Date
Year
1973
1994
1995

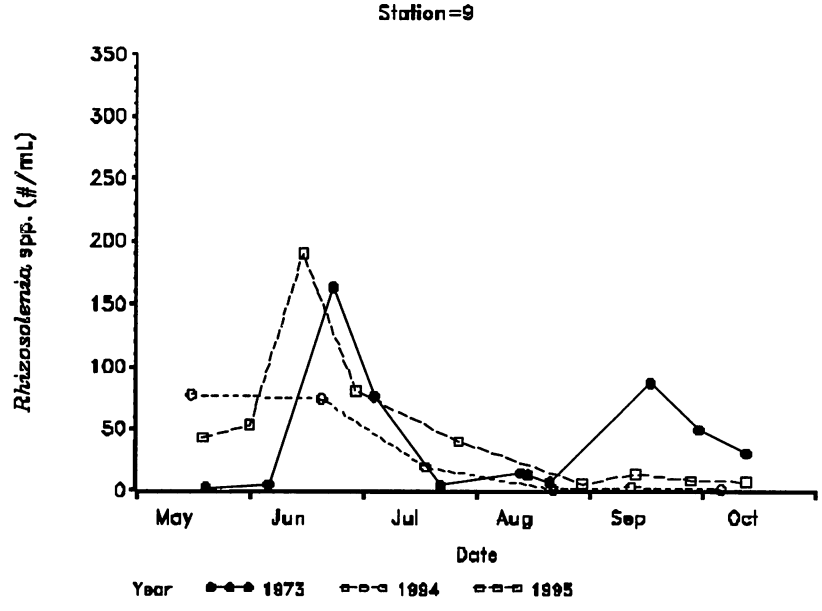

Station=4
Tabellaria fenestrata (#/mL)
250
200
150
100
50
0
May
Jun
Jul
Aug
Sep
Oct
Date
Year
1973
1994
1995

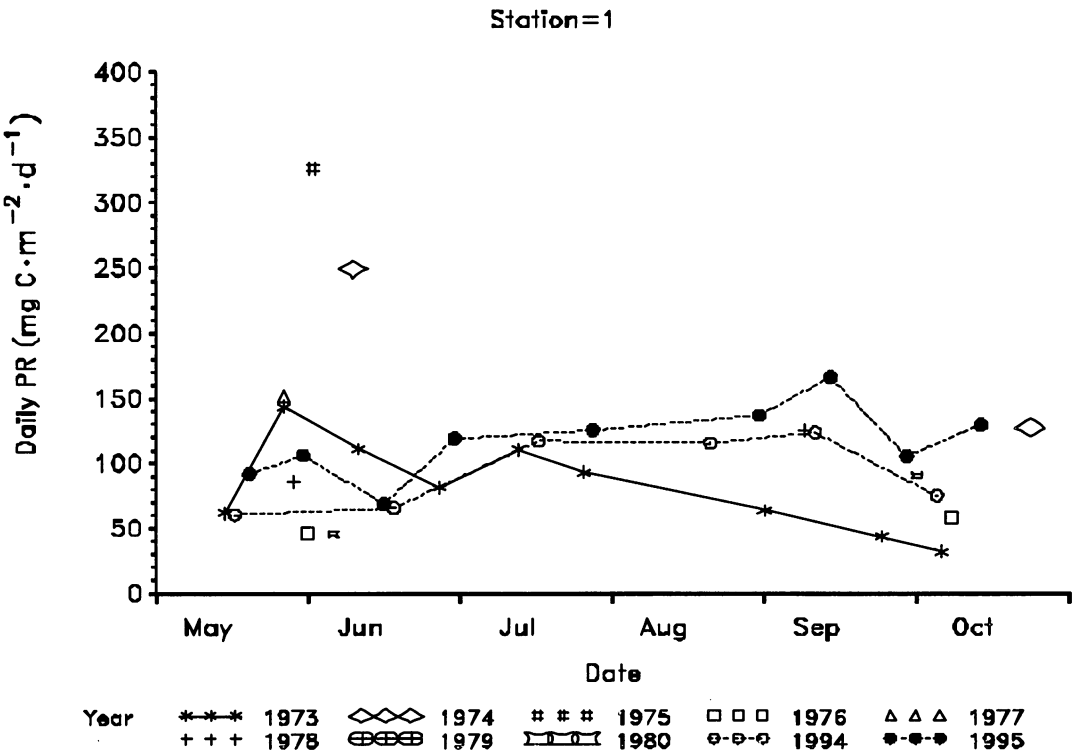

Station=9
Tabellaria fenestrata (#/mL)
250
200
150
100
50
0
May
Jun
Jul
Aug
Sep
Oct
Date
Year
1973
1994
1995

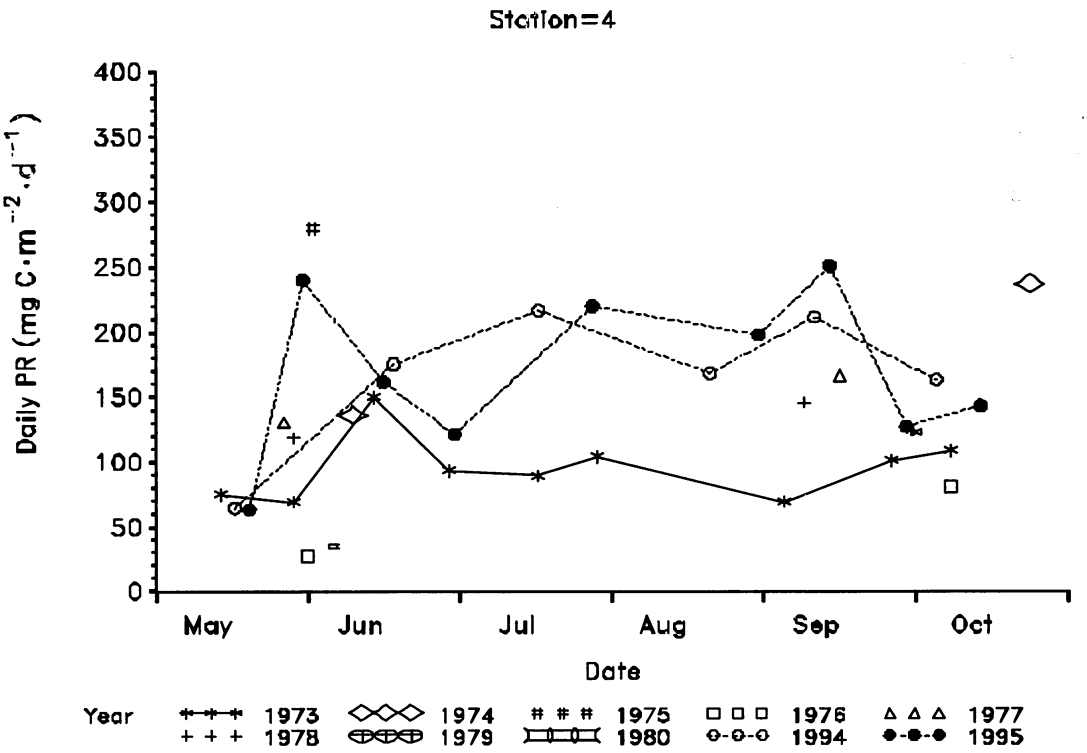

Station=1
Rhizosolenia spp. (#/mL)
350
300
250
200
150
100
50
0
May
Jun
Jul
Aug
Sep
Oct
Date
Year
1993
1994
1995

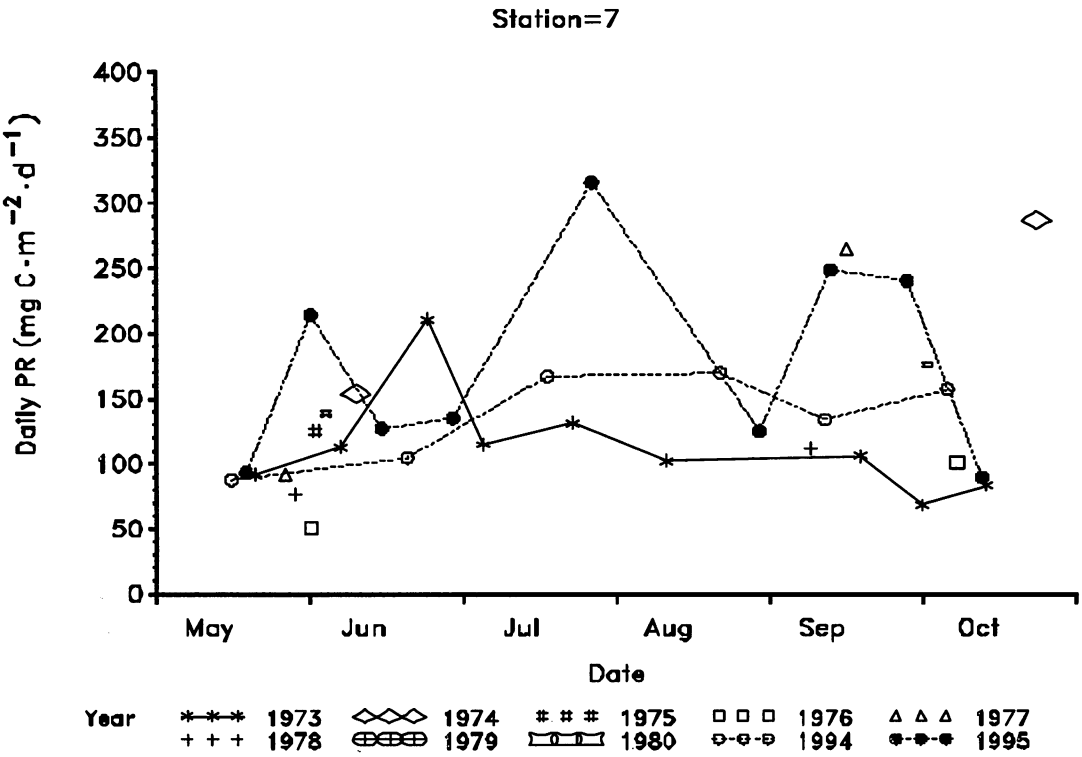

Station=7
Rhizosolenia spp. (#/mL)
350
300
250
200
150
100
50
0
May
Jun
Jul
Aug
Sep
Oct
Date
Year
1993
1994
1995

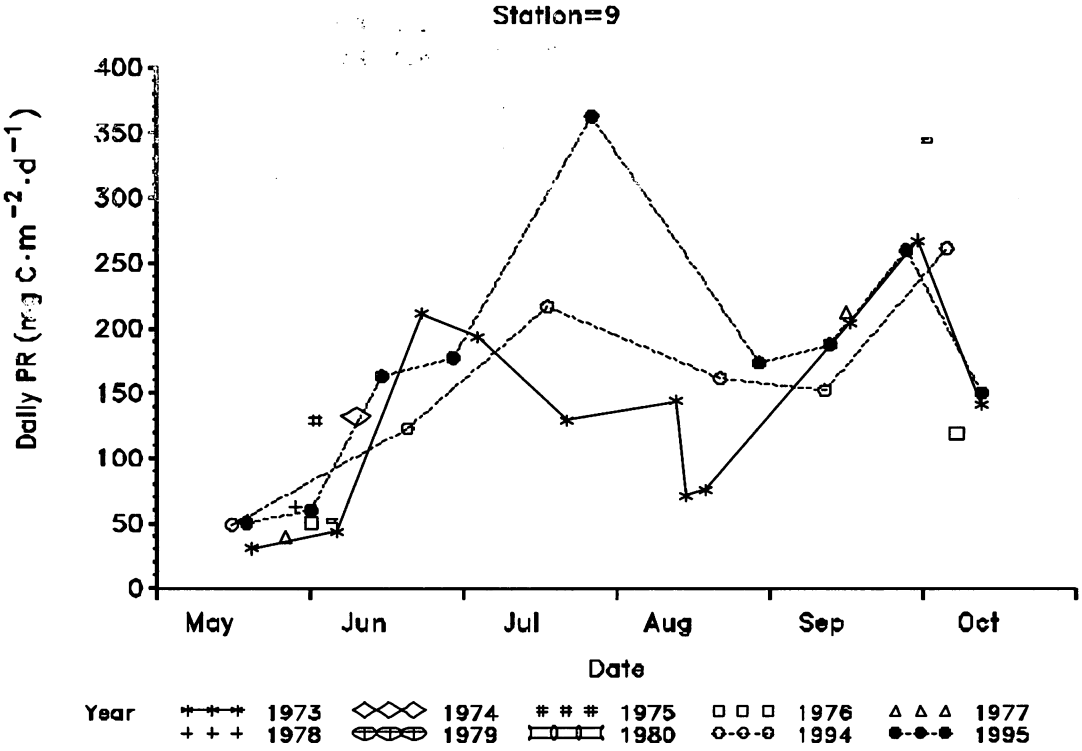

Station=4
Rhizosolenia spp. (#/mL)
350
300
250
200
150
100
50
0
May
Jun
Jul
Aug
Sep
Oct
Date
Year
1993
1994
1995

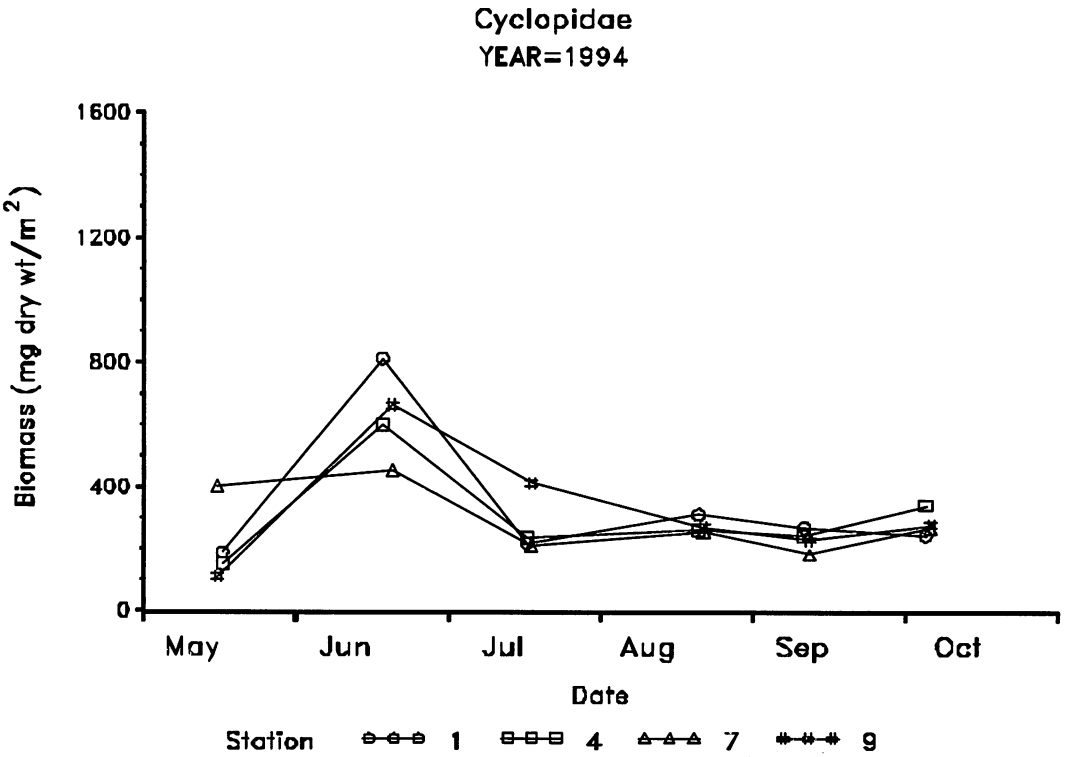

Station=9
Rhizosolenia spp. (#/mL)
350
300
250
200
150
100
50
0
May
Jun
Jul
Aug
Sep
Oct
Date
Year
1993
1994
1995

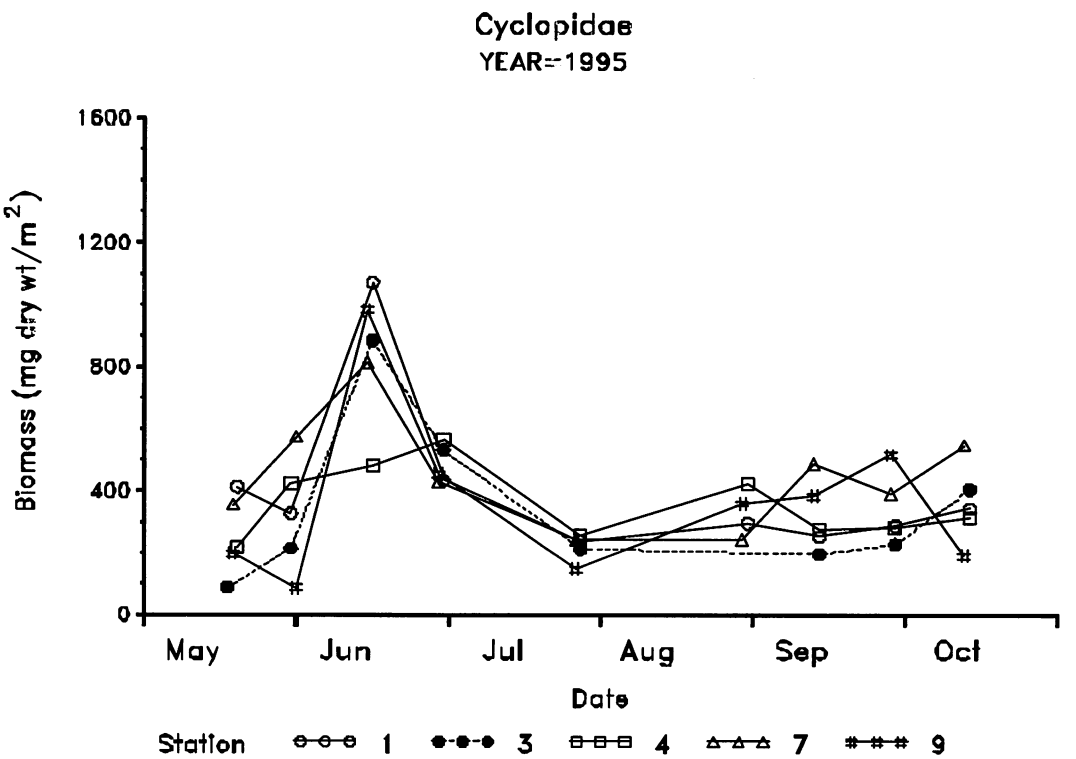

Station=1
Daily PR (mg C·m^{-2}·d^{-1})
400
350
300
250
200
150
100
50
0
May
Jun
Jul
Aug
Sep
Oct
Date
Year
1973
1974
1975
1976
1977
1978
1979
1980
1994
1995

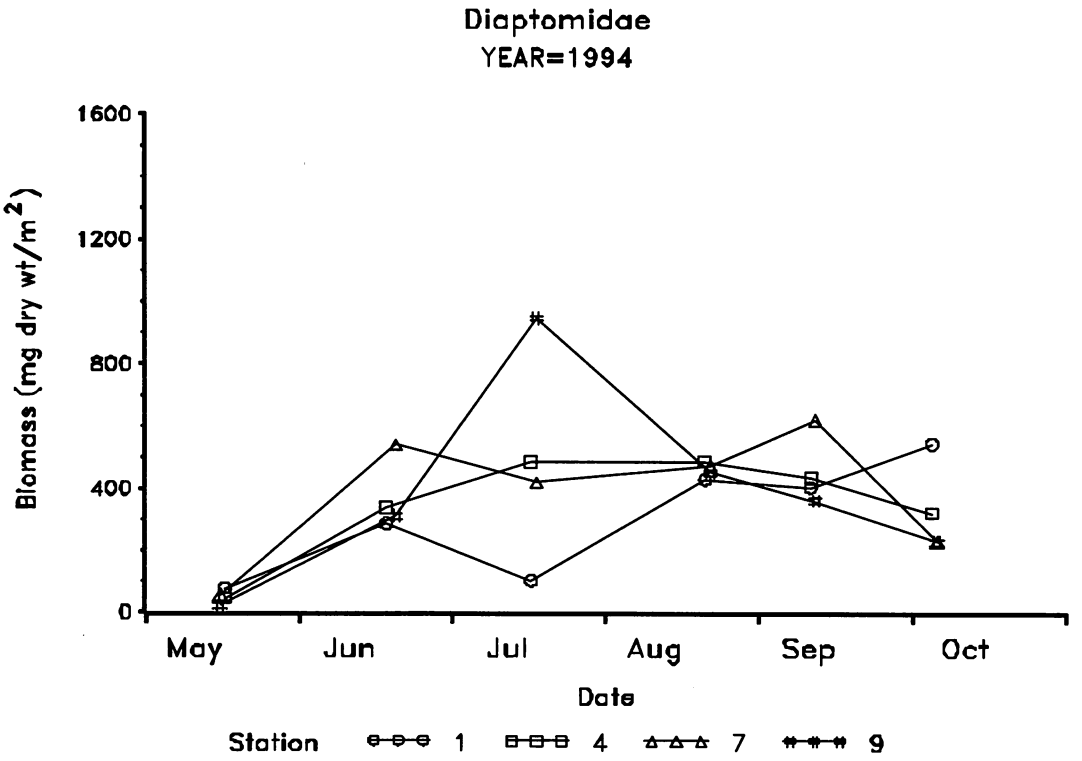

Station=4
Daily PR (mg C·m^{-2}·d^{-1})
400
350
300
250
200
150
100
50
0
May
Jun
Jul
Aug
Sep
Oct
Date
Year
1973
1974
1975
1976
1977
1978
1979
1980
1994
1995

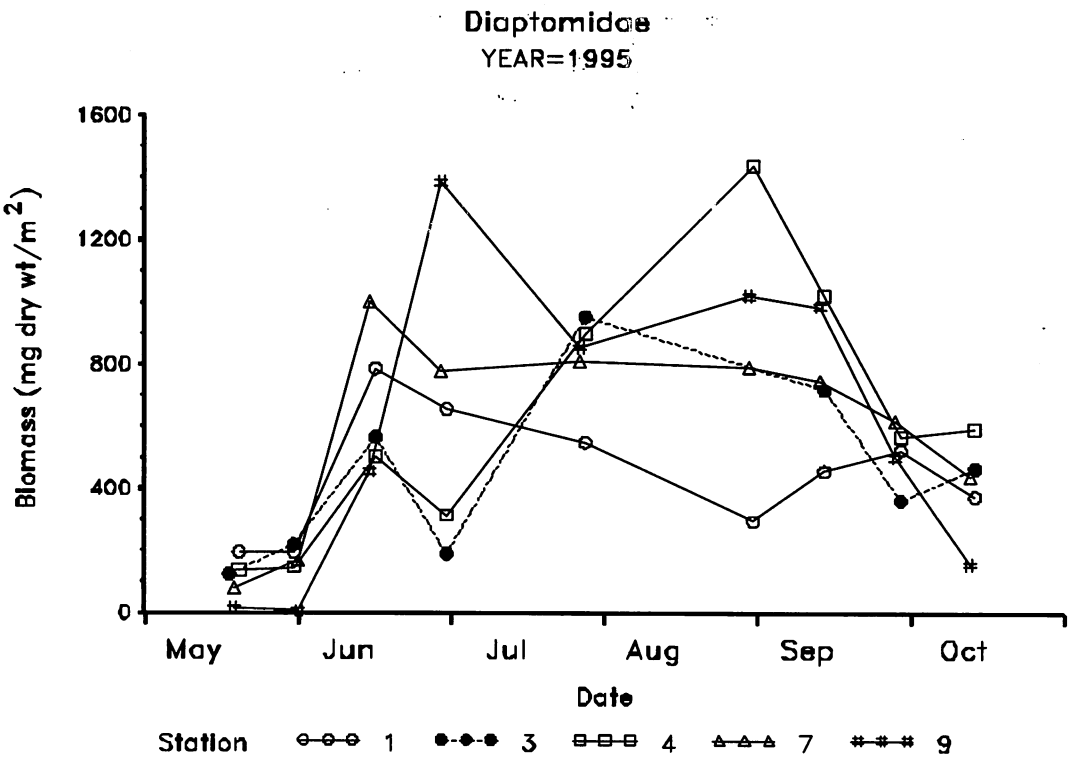

Station=7
Daily PR (mg C·m⁻²·d⁻¹)
400
350
300
250
200
150
100
50
0
May
Jun
Jul
Aug
Sep
Oct
Date
Year
1973
1974
1975
1976
1977
1978
1979
1980
1994
1995

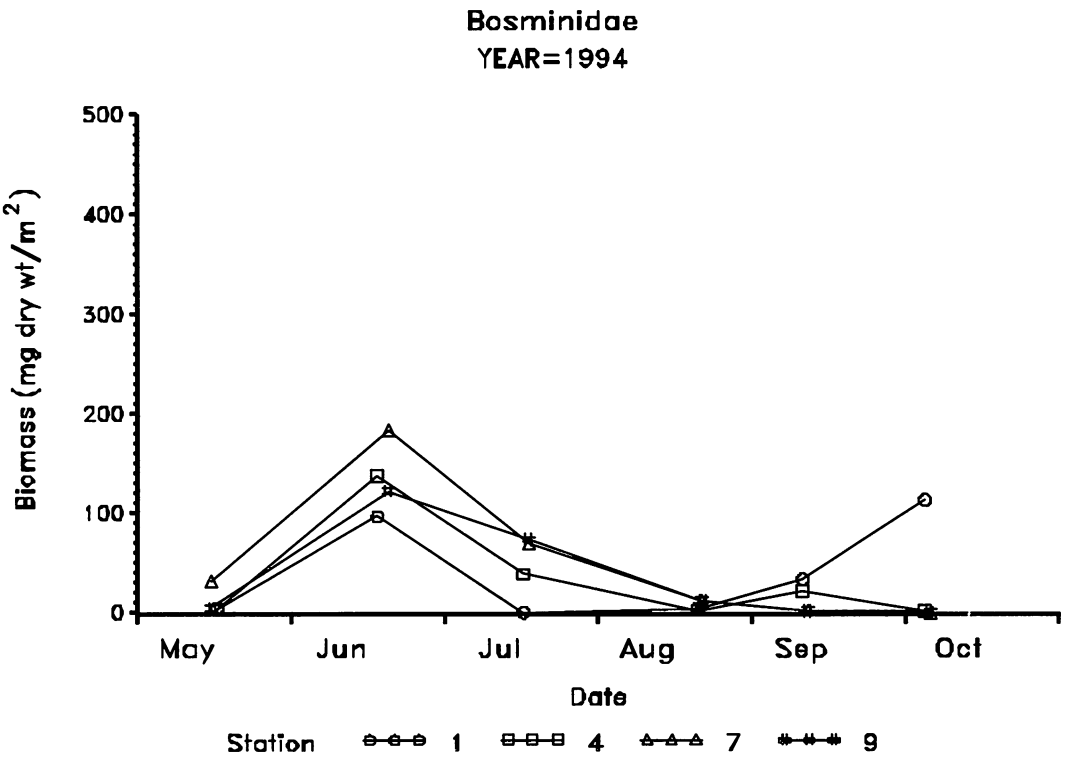

Station=9
Daily PR (mg C·m⁻²·d⁻¹)
400
350
300
250
200
150
100
50
0
May
Jun
Jul
Aug
Sep
Oct
Date
Year
1973
1974
1975
1976
1977
1978
1979
1980
1994
1995

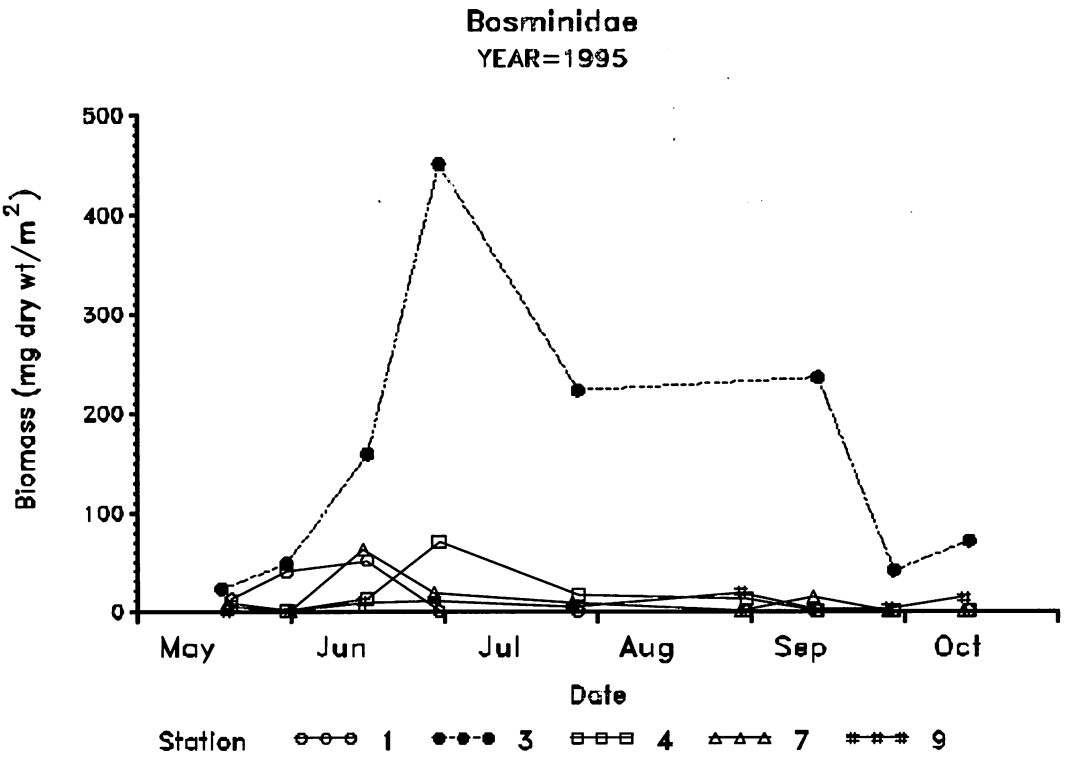

Cyclopidae
YEAR=1994
Biomass (mg dry wt/m 2)
1600
1200
800
400
0
May
Jun
Jul
Aug
Sep
Oct
Date
Station 1 4 7 9


Cyclopidae
YEAR=1995
Biomass (mg dry wt/m 2)
1600
1200
800
400
0
May
Jun
Jul
Aug
Sep
Oct
Date
Station 1 3 4 7 9


Diaptomidae
YEAR=1994
Biomass (mg dry wt/m 2)
1600
1200
800
400
0
May
Jun
Jul
Aug
Sep
Oct
Date
Station
1
4
7
9

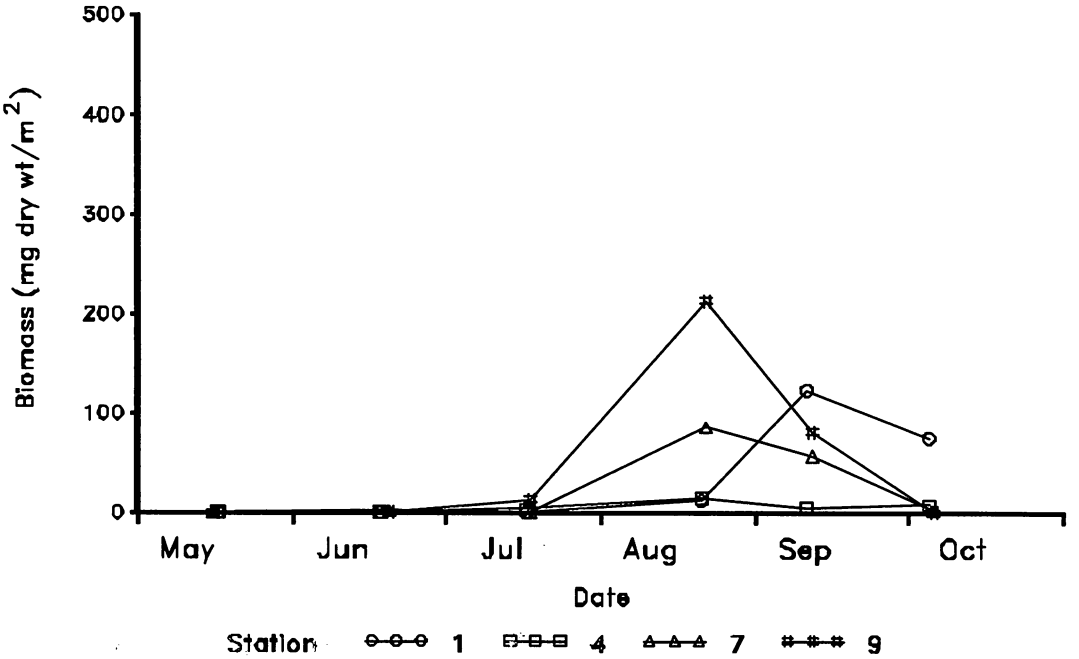

Diaptomidae
YEAR=1995
Biomass (mg dry wt/m 2)
1600
1200
800
400
0
May
Jun
Jul
Aug
Sep
Oct
Date
Station
1
3
4
7
9


Bosminidae
YEAR=1994
Biomass (mg dry wt/m 2)
500
400
300
200
100
0
May
Jun
Jul
Aug
Sep
Oct
Date
Station
1
4
7
9


Bosminidae
YEAR=1995
Biomass (mg dry wt/m 2)
500
400
300
200
100
0
May
Jun
Jul
Aug
Sep
Oct
Date
Station
1
3
4
7
9

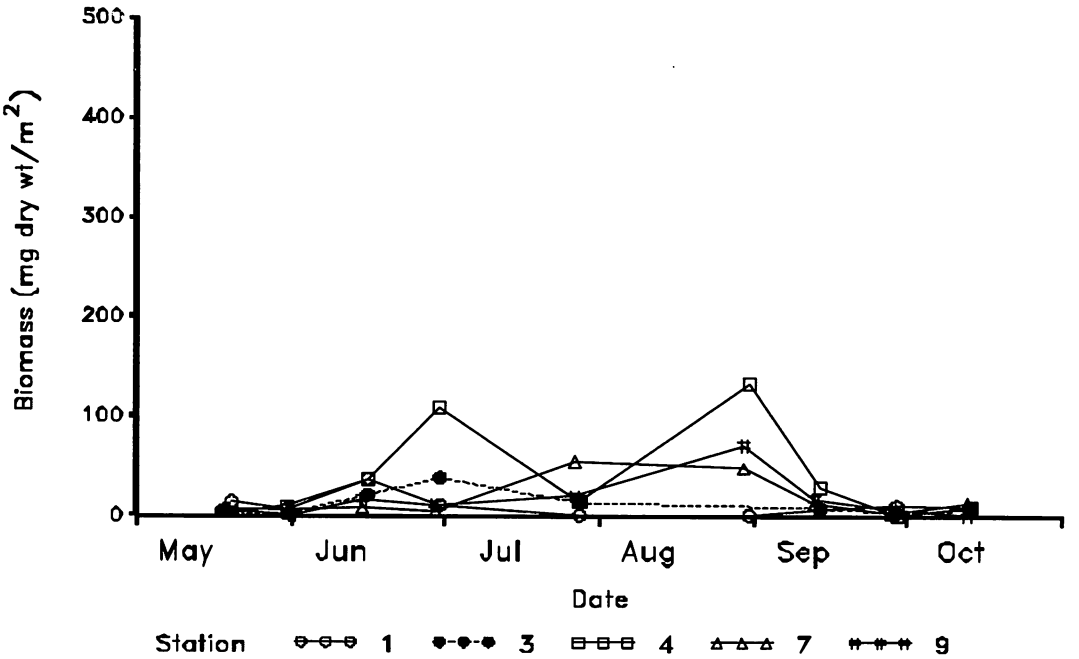
Daphnia

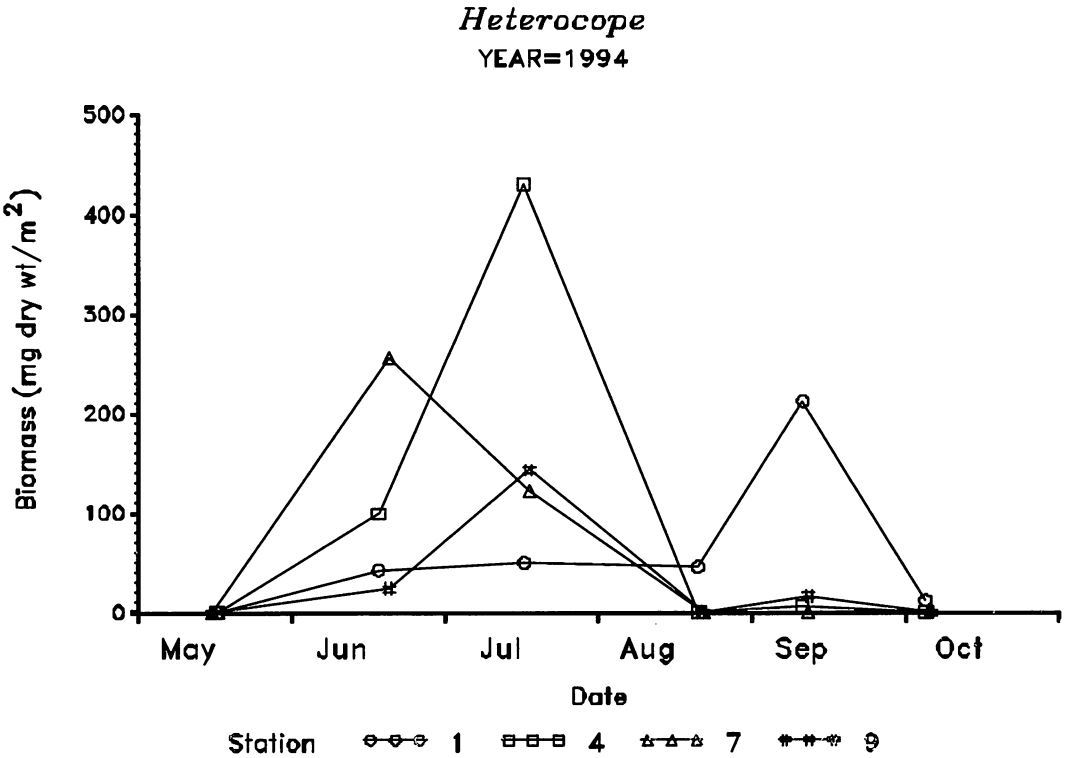
YEAR=1994

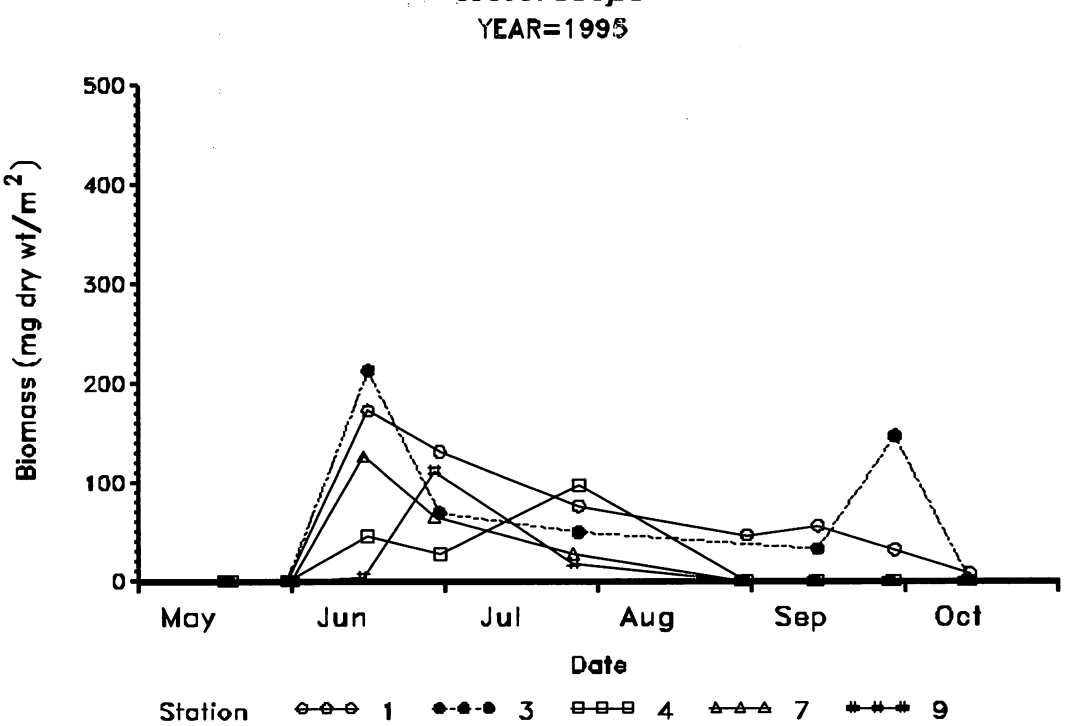


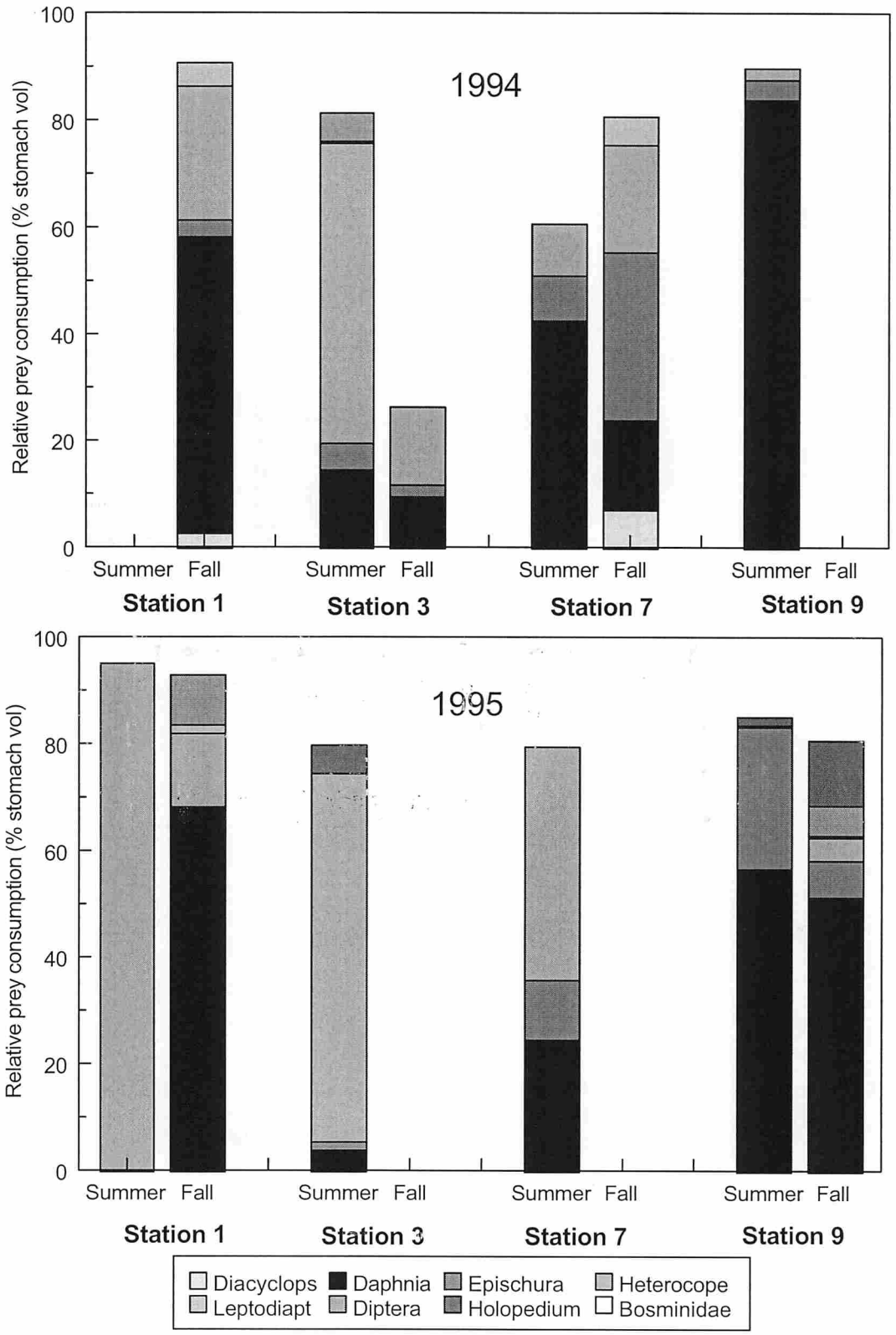
Daphnia

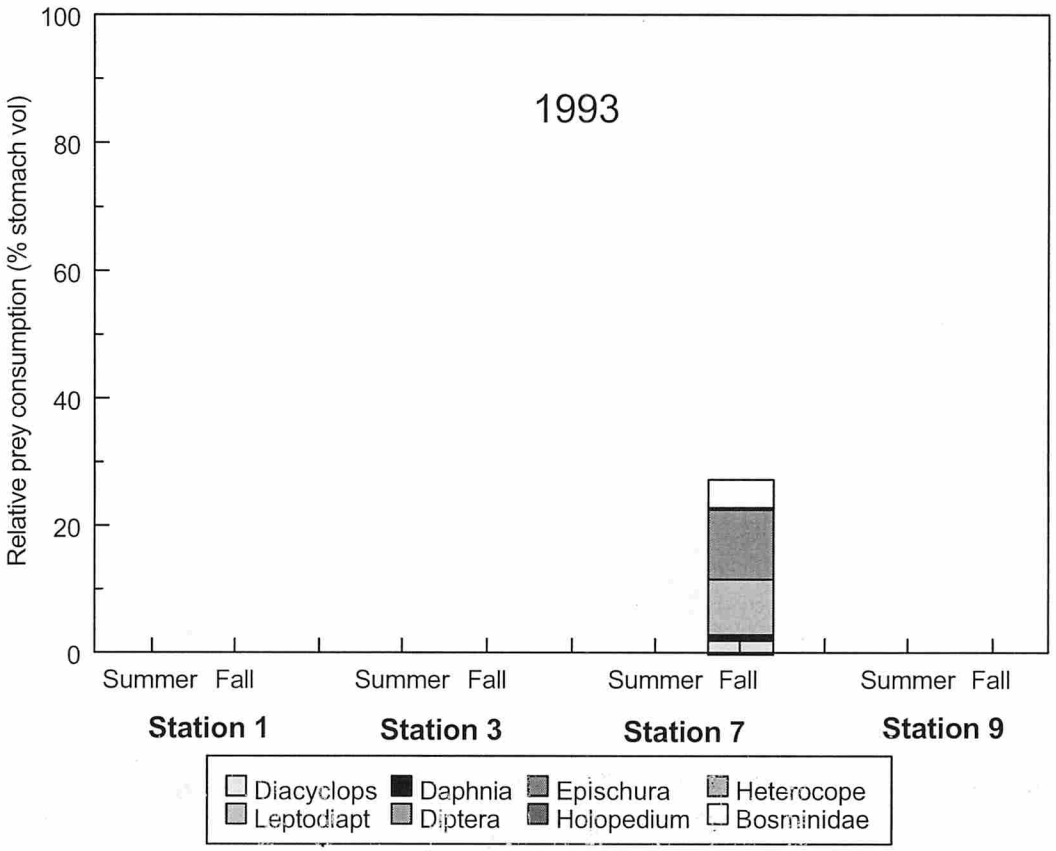
YEAR=1995

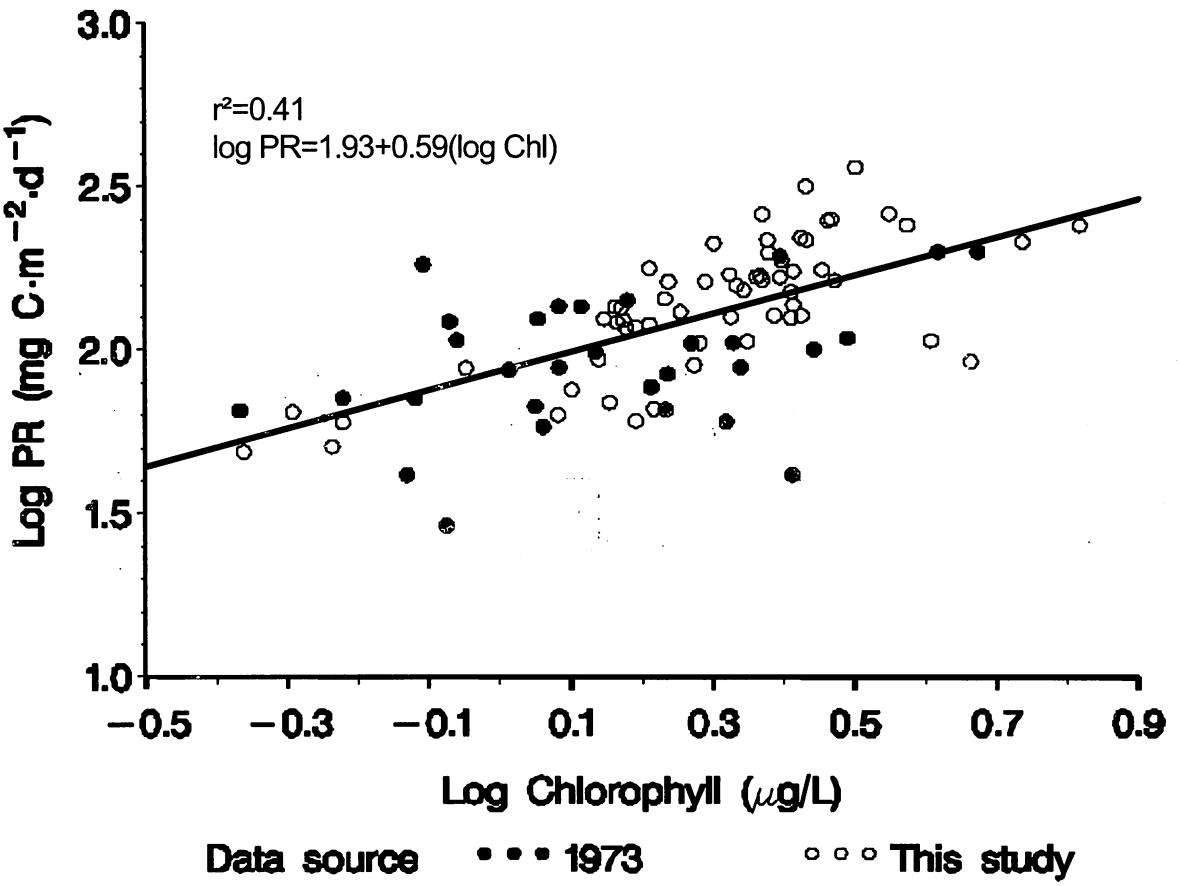


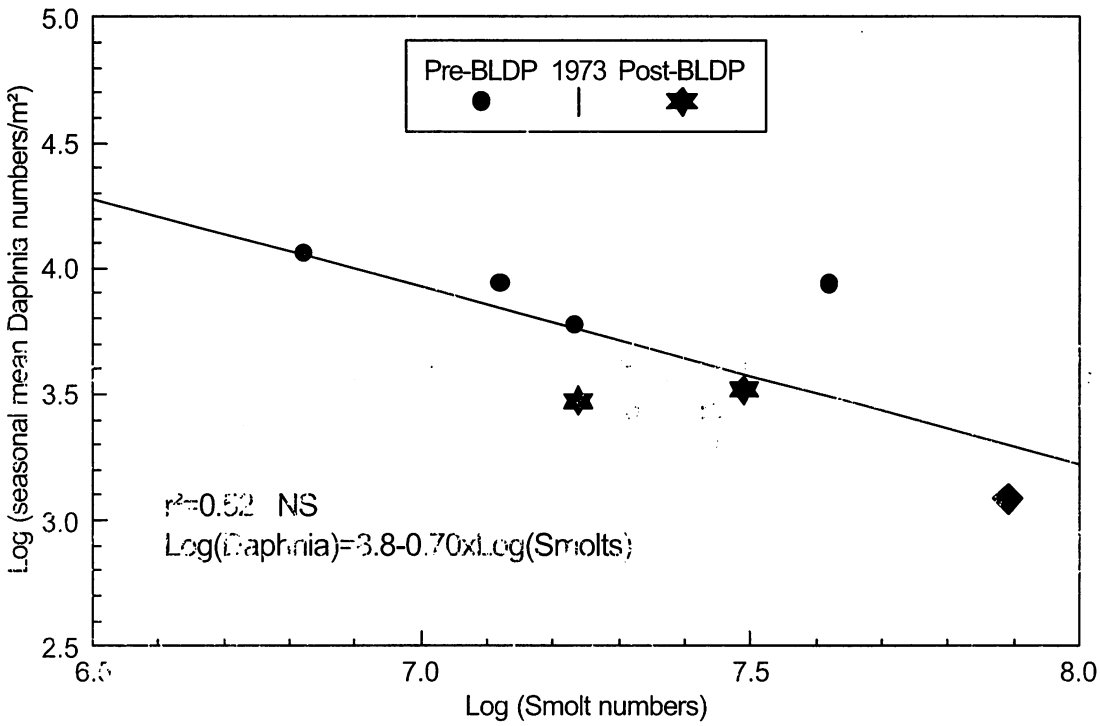

Heterocope
YEAR=1994
Biomass (mg dry wt/m^2)
500
400
300
200
100
0
May
Jun
Jul
Aug
Sep
Oct
Date
Station 1 4 7 9


Heterocope
YEAR=1995
Biomass (mg dry wt/m^2)
500
400
300
200
100
0
May
Jun
Jul
Aug
Sep
Oct
Date
Station 1 3 4 7 9


1994
1995
Relative prey consumption (% stomach vol)
100
80
60
40
20
0
Summer
Fall
Station 1
Station 3
Station 7
Station 9
Diacyclops
Daphnia
Epischura
Heterocope
Leptodiapt
Diptera
Holopedium
Bosminidae


1993
Relative prey consumption (% stomach vol)
100
80
60
40
20
0
Summer Fall
Summer Fall
Summer Fall
Summer Fall
Station 1
Station 3
Station 7
Station 9
Diacyclops
Daphnia
Epischura
Heterocope
Leptodiapt
Diptera
Holopedium
Bosminidae


r²=0.41
log PR=1.93+0.59(log Chl)
Log PR (mg C·m⁻²·d⁻¹)
3.0
2.5
2.0
1.5
1.0
−0.5
−0.3
−0.1
0.1
0.3
0.5
0.7
0.9
Log Chlorophyll (μg/L)
Data source
1973
This study


Pre-BLDP 1973 Post-BLDP
r²=0.52 NS
Log(Daphnia)=3.8-0.70xLog(Smolts)
Log (seasonal mean Daphnia numbers/m²)
Log (Smolt numbers)
5.0
4.5
4.0
3.5
3.0
2.5
6.5
7.0
7.5
8.0