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Assessment of Abundance, Biomass and Production of the Lower Trophic Levels in the Eastern Basin of Lake Erie, 1994

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ASSESSMENT OF THE ABUNDANCE, BIOMASS AND PRODUCTION OF THE LOWER TROPHIC LEVELS IN THE EASTERN BASIN OF LAKE ERIE, 1994.

by

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ABSTRACT

The Lake Erie Biomonitoring (LEB) program conducted in 1994, focused on the eastern basin of the lake, resampling the same sites as in 1993. Nutrient conditions were similar in the two years. Responses differed between the stratified offshore and unstratified nearshore.

At the offshore station, seasonal phytoplankton biomass was 56% higher in 1994 than in 1993 and apparently resulted from a reduction in grazing pressure by *Dreissena*. *Dreissena* biomass and their potential clearance rates at the offshore station were much lower in the spring of 1994 than in the spring of 1993 (2.5 vs. 14.9 $m^3 \cdot m^{-2} \cdot d^{-1}$), respectively. Despite this increase in phytoplankton biomass, chlorophyll (Chl) and phytoplankton photosynthesis (PP) were not significantly higher in 1994. Dinoflagellates, which have lower Chl:C and lower photosynthesis:Chl ratios than other groups of phytoplankton, accounted for much of the increase in biomass. Rotifer biomass decreased by 50% and zooplankton biomass by 40% between the two years. Calanoids were responsible for much of the decrease in zooplankton biomass. Composition also shifted towards larger bodied cladocerans, such as *Daphnia* and *Bythotrephes*, and away from *Bosmina*. This shift coincided with changes in predation pressure. Age-one smelt abundance was extremely high in 1993 and low in 1994, while the reverse was true of the YOY smelt. Age-one smelt consume mainly cladocerans and the YOY, copepods (REF).

At the nearshore stations, seasonal PP and Chl were well below that expected given the total phosphorus (TP) concentration, indicating that *Dreissena* had an important impact on phytoplankton photosynthesis in this region. Low transparency due to suspended sediments also contributed to the low PP at station E1. Zooplankton biomass was lower in 1994 than in 1993, and species composition and size shifted. *Daphnia* increased and calanoids and *Bosmina* decreased in the nearshore as in the offshore, presumably in response to changes in the smelt population. However, *Bythotrephes* decreased and rotifer biomass increased unlike in the offshore.

RÉSUMÉ

En 1994, le Programme de biosurveillance du lac Érié (BLE) a concentré ses activités sur le bassin est du lac et l'équipe est notamment retournée aux mêmes endroits qu'en 1993 pour procéder à de nouveaux échantillonnages. Il n'y a pas eu de changement d'une année à l'autre pour ce qui est des nutriants. La réponse a différé entre les stations du large, aux eaux stratifiées, et les stations proches de la côte, aux eaux non stratifiées.

Aux stations du large, la biomasse phytoplanctonique saisonnière de 1994 dépassait de 56 % celle de 1993. Cette situation était apparemment attribuable à une réduction de la pression de broutage exercée par *Dreissena*. À ces stations, la biomasse de cette dernière et son taux de clairance potentiel étaient bien inférieurs au printemps de 1993 à ce qu'ils étaient à celui de 1994 (2,5 contre 14,9 $m^3.m^{-2}.d^{-1}$). Mais il demeure que, malgré cette augmentation de la biomasse phytoplanctonique, la teneur en chlorophylle (Chl) et la photosynthèse phytoplanctonique (PP) ne se sont pas accrues de manière significative en 1994. Les dinoflagellés, chez qui les rapports Chl/C et photosynthèse/Chl sont inférieurs à ceux mesurés dans d'autres groupes phytoplanctoniques, étaient à l'origine de la majeure partie de cette hausse de la biomasse. Celle des rotifères et du zooplancton a diminué de 50 % et de 40 %, respectivement, d'une année à l'autre. Les calanoïdes sont en grande partie à l'origine de la diminution de la biomasse du zooplancton. On remarque aussi une transformation de la composition, qui est passée d'organismes tels que *Bosmina* vers les cladocères de plus forte taille comme *Daphnia* et *Byotrephes*. Cette transformation coïncide avec des changements au niveau de la pression de prédation. En effet, il y avait énormément d'éperlans d'un an en 1993, mais peu en 1994, à l'inverse de ce qui était observé avec les éperlans de l'année. Les premiers se nourrissent surtout de cladocères, les seconds de copépodes.

Aux stations proches de la côte, la PP et la teneur en Chl saisonnières étaient bien inférieures aux prévisions fondées sur la teneur en phosphore total (PT); cela signifie que *Dreissena* avait un important impact sur la photosynthèse phytoplanctonique de cette région. La turbidité élevée de l'eau attribuable aux sédiments en suspension a également contribué au faible taux de PP à la station E1. La biomasse zooplanctonique était inférieure en 1994 à ce qu'elle était en 1993 et, en outre, la composition spécifique a changé, favorisant des espèces de plus forte taille. *Daphnia* est devenue plus abondante, au contraire des calanoïdes et de *Bosmina*, dans les stations proches de la côte comme dans les stations du large. On peut penser à l'existence d'un lien entre ces changements et les variations de la population d'éperlans. Toutefois, la biomasse de *Byotrephes* a diminué tandis que celle des rotifères s'est accrue, contrairement à ce qui a été observé au large.

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INTRODUCTION

The biomonitoring program conducted in 1993 (Dahl et al. 1995), revealed that the Lake Erie ecosystem had changed in response to the invasion of the zebra and quagga mussels (*Dreissena polymorpha* and *D. bugensis*). Redirection of pelagic production to the benthic food-chain, was evident as a dramatic increase in benthic biomass in all basins. The biomass of endemic benthic organisms had remained relatively unchanged since 1979, however, dramatic increases in total biomass were observed in 1993 due to the presence of *Dreissena* (Dahl et al. 1995). In 1993, the eastern basin appeared to show the greatest response to the invading *Dreissena*. Phytoplankton biomass and photosynthesis were lower in 1993 compared to pre-mussel years and phytoplankton photosynthesis was below the potential set by phosphorus concentrations, due to the removal of phytoplankton biomass by Dreissena filtering.

Changes were occurring in all basins prior to the arrival of *Dreissena*, in response to phosphorus controls which successfully lowered phosphorus (P) loading to the lake. These controls were the result of legislation introduced in the early 1970s aimed at improving the aesthetic and biological quality of the Great Lakes. Phosphorus loading to Lake Erie declined by 40-50% from the early 1970s to the mid 1980s with the greatest reductions occurring in the eastern and western basins (Burns 1985; Lesht et al. 1991). While P loading controls continued to moderate nutrient concentrations in Lake Erie throughout the 1980s, the invasion of *Dreissena* enhanced the effects of P control driving pelagic productivity especially at the primary level, even lower than expected from P control alone.

Spatial studies conducted in the summer and early fall of 1993 in Lake Erie (Lake Erie Trophic Transfer, LETT), indicated that phosphorus in the western basin was consistent with annual means achieved by 1986 (Charlton 1994). Holland et al. (1995) also reported no significant changes in TP in the western basin in 1993 vs. 1987. In the central basin, the ranges of chlorophyll, Secchi and phosphorus values were similar to those found up to ten years previous (Charlton et al. 1993). In the eastern basin, however, phosphorus concentration was lower in 1993 than in pre-mussel years. It is difficult to separate the effects of changing P loading and *Dreissena* on the whole ecosystem, hence, the need arises for a multi-trophic level approach. Changes in nutrient concentrations will affect the total productivity of the lake ecosystem, however, it is the effects observed at various trophic levels and the interactions between these levels, that provide a clearer picture of the changes occurring in the lake.

The effects of the dreissenids in 1993 in the western basin were limited. The changes detected in phytoplankton biomass and composition and the reduction in photosynthesis were not of sufficient magnitude to reduce zooplankton biomass. However, filtration by *Dreissena* represented an important redirection of pelagic production to the benthos. This multi-level effect was more prominent in the eastern basin. The already low phytoplankton biomass was driven to critical levels by the mussels, whereby, zooplankton were affected due to a reduced food supply. The reduction in total zooplankton biomass was the result of food limitation in conjunction with planktivory on the larger species.

The Lake Erie Biomonitoring program (LEB) was initiated in 1993, to establish the status of water quality and lower trophic level production in the lake. This report provides data from the second year of LEB (1994) and compares data for the two years. The goals in 1994 were to again determine the pelagic production of the lower trophic levels, and to determine the variability that would be observed in a stressed system. We focused on the eastern basin because of the impact by the dreissenids noted in this basin in 1993, relative to the western and west central basins, and the limited resources available in 1994. Lower trophic level estimates of abundance and biomass, as well as species composition for phytoplankton, zooplankton and rotifers are presented, in addition to data on chlorophyll a (Chl), Secchi transparencies, phosphorus, other water chemistry components, and phytoplankton photosynthesis.

METHODS

STATIONS

The Lake Erie Biomonitoring project sampled three stations in the eastern basin in 1994 (Fig. 1). These stations corresponded to sites previously sampled during the LEB project in 1993 (see 1993 LEB Report, Table 1, for station descriptions). Pelagic sampling was performed on alternate weeks beginning the week of May 10 and continued until the week of November 8. Beginning the week of June 20 and continuing through to mid September, zooplankton and rotifers were obtained on a weekly basis from all stations.

SAMPLE COLLECTION

All sampling was conducted on Canadian Coast Guard Vessels (402, Spray, 119), based in Port Dover, Ontario. All stations were sampled on each sampling date during the day with the maximum time elapsed between collection and processing of water samples being 7 h.

Physical Parameters

Seasonal means are means calculated for the sampling season, and weighted for variable intervals between sampling dates. Seasonal means are calculated for the entire sampling period at each station for all physical, chemical and biological parameters.

Light extinction and Secchi (20 cm black and white disc) depth were measured at each station. Weather conditions, including wind direction and speed and cloud cover were also recorded. Profiles of temperature, dissolved O_2, conductivity, and pH were obtained using a Hydrolab H20 Profiling System (Hydrolab Co., Texas) and down-loaded to a portable computer. Temperature profiles were converted to density using a computer program (DENS, J.Moore, Dept. of Fisheries & Oceans, Burlington) and used to determine whether the water column was stratified. The water column was considered thermally-stratified when the density gradient exceeded 0.08 $kg \cdot m^{-3} \cdot m^{-1}$ at a depth greater than 4 m (Reynolds and Wiseman 1982; Reynolds et al. 1984). The depth of the mixed layer (Z_m) and the boundaries of the metalimnion and

hypolimnion were determined using this program.

Extinction of photosynthetically available radiation (PAR) was determined by measuring light at intervals through the water column using a Li-192S underwater quantum sensor (Li-Cor, Nebraska). Vertical spacing of the readings depended on the clarity of the water and the station depth. Generally, 1 m spacing was used for profiles deeper than 8 m, while 0.5 m spacing was used for shallower profiles. The extinction coefficient for PAR (ϵ_{par}) was calculated as the slope of a simple linear regression of the natural logarithm of light intensity vs. depth. The natural logarithm of 100 divided by ϵ_{par} is the euphotic depth (Z_{eu} - 1% surface light penetration).

Incident solar irradiance, needed for the calculation of integral photosynthesis, was measured with a Li-190 quantum sensor (Li-Cor, Nebraska) mounted on the roof of the Canada Centre for Inland Waters (CCIW) in Burlington. Thirty minute integrals (moles·m^{-2}) were logged to a Campbell CR5 microprocessor datalogger. Sensors were calibrated annually by the manufacturer.

Water Samples

During isothermal or weakly stratified conditions, composite water samples were collected by pooling aliquots from 4 to 5 equally spaced depths from 2 m above the bottom to within 1 m of the lake surface. Under thermally stratified conditions, water was collected from 1 m below the surface to 1 m above Z_m.

All water samples were collected using a dual diaphragm pump (Shurflo, California) system with attached 0.5" Tygon tubing. The pumping rate was checked periodically to ensure an equal contribution from each of the chosen depths to the composite sample. The tubing was allowed to flush between each depth prior to collecting water. Sample water was collected into well-rinsed, neoprene-wrapped, 10 L, polycarbonate carboys, and transported on ice back to CCIW for processing. The temperature of the sample water was maintained at ± 2°C of ambient during transportation. The water samples were subsampled back in the laboratory for water quality (total phosphorus, TP; total filtered phosphorus, TFP; soluble reactive phosphorus, SRP; total nitrogen, TN; dissolved inorganic carbon, DIC; dissolved organic carbon, DOC; NO_3-NO_2, ammonium, chlorides, silica measured as SiO_2, and sulphides), chlorophyll a (Chl), phytoplankton photosynthesis and biomass.

At the offshore station, under thermally stratified conditions, high transparency of the water column relative to the Z_m resulted in Z_{eu} extending beyond Z_m on some dates. In this situation an additional composite sample was taken from the euphotic portion of the metalimnion for Chl, phytoplankton and water quality. This euphotic sample was a composite of 3 to 4 depths (depending upon thickness of the layer) from 1 m below the Z_m to 1 m above the euphotic depth.

Zooplankton

Macrozooplankton (all zooplankton types other than rotifers; rotifers were sampled separately) were collected using a 110-μm mesh Wisconsin plankton net, 3 m long with a 0.5 m diameter opening. A Rigotia flow meter (Rigotia and Co. Ltd., Tokyo, Japan) was used to determine net efficiency with readings taken before and after each haul. These readings were compared with meter readings at 100% efficiency (a hoop without a net attached) to determine the efficiency of the net. During isothermal conditions, the net was pulled vertically from 2 m above the lake bottom to the surface at a rate of 0.8 to 1.0 m·s⁻¹. In windy conditions, when the net did not go straight down, the wire angle was used to adjust the required line length, ensuring that the desired depth was achieved. Generally, two hauls were performed per station. Each sample was preserved with 4%, sugared and neutralized formalin.

During stratification at the offshore station, each stratum was sampled independently and the contents preserved separately. Depths of the three strata were determined using the temperature profile from the Hydrolab H20 and DENS. Replicate epilimnetic samples were obtained from between 1 m above the thermocline to the surface using the regular net. A closing net, otherwise identical to the regular net, was used to collect metalimnetic and hypolimnetic samples. The net was cinched at the desired depth using a secondary line, and brought to the surface. Metalimnetic samples were taken from 1 m above the hypolimnion to 1 m below the thermocline and hypolimnetic samples were taken from 2 m above the lake bottom to 1 m below the metalimnion.

Rotifers were collected using the same diaphragm pump apparatus described for the water quality sampling. Two integrated water samples of 50 L each, were collected from 2 m above the lake bottom to the surface when conditions were isothermal. A fully integrated sample was obtained by using the pumping rate to determine the speed at which the hose intake should be raised through the water column. During stratification, separate 20 L samples were collected from the epilimnion and the metalimnion, and a 50 L sample was obtained from the hypolimnion. Sampling depth intervals corresponded with those of the macrozooplankton. After collection, the 20 and 50 L samples were filtered through a 20-μm Nitex screen. Each rotifer sample was then narcotized with carbonated soda and preserved separately using 4% sugared, neutralized formalin.

LABORATORY PROCESSING AND EXPERIMENTS

Phytoplankton Biomass and Nutrients

Three replicate aliquots of 1.5 L were collected on GF/C glass fibre filters (Whatman Co.) and frozen for later Chl analysis. The filters were ground in 90% acetone, and the extracts analyzed spectrophotometrically (Strickland and Parsons 1972). Chl concentrations used in the photosynthesis calculations are uncorrected for phaeopigments.

A volume of lake water equal to that filtered for Chl was filtered through an ashed,

preweighed, GF/C filter for the determination of total seston. Filters were stored in the freezer in foil-lined petri dishes prior to analysis. Each filter was dried over night at 60°C and reweighed to determine total seston weight. The filters were then ashed at 480°C for 4 h, cooled, and reweighed to determine ash weight. Subtraction of ash weight from seston weight gives ash-free dry weight (AFDW).

Unfiltered water samples were collected for total phosphorus analysis. Additional sample water was filtered through a 0.45-µm, cellulose-acetate, membrane filter (Sartorius) for total filtered phosphorus, other nutrients and major ions. All analyses were performed by the National Laboratory for Environmental Testing (NLET) (Environment Canada 1995).

Two, 250-mL phytoplankton samples were taken from each composite epilimnetic and euphotic sample and preserved with 1 mL of Lugol's iodine solution. The phytoplankton were identified and enumerated for the offshore station (E2) using the Utermöhl inverted microscope technique (Utermöhl 1958). A 15-mL aliquot was settled and examined using light/dark illumination. At least 200 units/sample were counted at 300x, 600x, and 1500x magnification by the strip method providing an estimate of total cell numbers within ± 14% (Lund et al. 1958). Cell measurements were taken. Phytoplankton volumes were calculated using approximations to geometric shapes, and converted to biomass assuming a density of one.

Phytoplankton Photosynthesis Experiments

All incubations were done back at CCIW. Photosynthetic rates were determined using ^{14}C-incubator methodology. The method used was consistent with that used in other projects, including LEB 1993 (Dahl et al. 1995), Millard et al. (1995) and (Fee et al. 1989, 1992). Tracer solution was prepared by diluting stock $Na_2{}^{14}CO_3$ (Amersham Co.) with a carrier solution of Na_2CO_3 to an alkalinity typical of the lower Great Lakes. Five-mL aliquots were flame-sealed in glass ampoules. To start an experiment, the contents of one ampoule were dispensed from a clean plastic syringe through an in-line, cellulose-acetate, filter into 1 L of whole lakewater. The inoculated sample was well mixed and aliquots were dispensed into 11 to 13 light and 2 dark Pyrex bottles (Corning). Bottles were incubated for four hours at close to *in situ* temperatures (±2°C) in an incubator identical to that described by Fee et al. (1989). The light source used was a 150 W high pressure sodium vapour lamp (Thorn Lighting, Mississauga). Bottles were exposed to a light gradient by positioning them at varying distances from the light source in a clear 3 mm acrylic template. Light levels for all bottle locations were checked during incubation using a manufacturer calibrated Li-Cor spherical quantum sensor Li193SA. The amount of light received by each incubation bottle was overestimated, because of the large size of the sensor. Therefore, readings from the Li-Cor were corrected using a linear relationship established between the Li-Cor and a Biospherical sensor (Biospherical Instruments Inc., California). The Biospherical sensor was fit inside a cut off incubation bottle giving a true light level at each incubation location, and was used for light measurements in the other studies cited.

A 5-mL standard was removed from each of three randomly chosen bottles at the conclusion of the experiment, and placed in scintillation vials with 200 µL ethanolamine to

determine the total ^{14}C available for uptake. Uptake at the end of the experiment was determined by taking a 5-mL aliquot from each bottle and placing it in a glass scintillation vial with 1 mL of 0.5 N HCl. These vials were bubbled in a special vacuum apparatus (Shearer et al. 1985) for 30 min to remove unincorporated inorganic ^{14}C. Samples were removed from the bubbler, capped, shaken and left overnight with caps loosened, to ensure the removal of all unincorporated tracer, prior to the addition of 10 mL of scintillation fluor (Universol, Beckman Co.). Samples were counted in a Beckman LS5000 TD liquid scintillation counter for 20 min or to a 2 sigma level of accuracy of 2%, whichever was achieved first. Quench corrections were made using the external standard and the $H^{\#}$ technique (Beckman Co.).

ANALYSES

Photosynthesis Calculations

Daily and seasonal estimates of photosynthesis were calculated using the computer programs of Fee (1990). Data on Chl, transparency, solar irradiance, photosynthetic parameters and mixing depth are required as input to the programs. The photosynthetic parameters P^B_m (mg C·mg Chl^{-1}·h^{-1}), the carbon uptake rate at light-saturating irradiance, and α^B (mg C·mg Chl^{-1}·μE^{-1}·m^{-2}) the slope of the light-limiting part of the photosynthesis vs. light intensity curve, were derived using the curve-fitting program PSPARMS (Fee 1990) and the photosynthesis vs. light intensity data measured in the incubator. P^B_m and α^B were normalized per unit of chlorophyll, as denoted by the superscript B. P_{opt} (mg C·m^{-3}·h^{-1}), the photosynthesis rate at optimal irradiance, is the product of P^B_m and Chl.

Seasonal areal photosynthesis (g C·m^{-2}) was calculated using the YPHOTO and YTOTAL programs (Fee 1990). Theoretical cloudless irradiance data can be generated with these programs and was used to determine the theoretical maximum rate of photosynthesis when incident light is not limiting. As a result, rates can be compared among systems without the confounding effects of variable solar input. Studies on Lake Ontario (Millard et al. 1995) showed that annual variability in incident irradiance does not contribute to variability in seasonal (May-Oct.) PP.

Macrozooplankton Net Efficiency Calculations

A Rigotia flow meter (Rigotia and Co. Ltd., Tokyo, Japan) was used to determine efficiency of the zooplankton nets. Efficiency was determined by dividing the revolutions·m^{-1} the flow meter turned when mounted on the inside of the hoop with the net attached, by the revolutions·m^{-1} it turned over the same distance without the net (on an empty hoop at 100% efficiency). Empty hoop calibration hauls were performed at many stations and depths throughout the lake during the sampling period. A mean of 10.51 revolutions·m^{-1} was calculated and used in the determination of all efficiencies.

Macrozooplankton Enumeration and Biomass Determinations

Each sample was rinsed to remove excess formalin then resuspended in 50 or 100 mL of distilled water, depending upon the density of material in the samples. The sample was gently but thoroughly mixed and subsampled with a pipette. A minimum of 400 animals were counted, with at least 100 individuals of the major groups included, or if animals were scarce, 20% of the sample was counted.

Zooplanktors were measured using a digitizing system (Summa Sketch III, Oakville, Ontario) combined with a computer program, ZoopBiom, developed by R. Hopcroft (University of Guelph, Ontario). Cladocera were measured from the top of the helmet to the base of the tail spine, whereas copepods were measured from the anterior tip of the cephalothorax to the end of the caudal rami. *Dreissena* veliger length was measured across the widest section of the shell. As in 1993, we could not routinely distinguish *Bosmina liederi* and *Bosmina freyi*, and thus all *Bosmina* were named *Bosmina* sp.

Counts were tabulated and density and biomass ($\cdot m^{-3}$) were calculated by the computer program, ZoopBiom. This program incorporates length-weight regression equations for each species from Downing and Rigler (1984) and for *Dreissena* (Hillbricht-Ilkowska and Stanczykowska 1969) allowing for calculations of mean size, and volumetric measures of density and biomass.

Rotifer Enumeration and Biomass Determinations

Each sample was rinsed to remove excess formalin and resuspended in 25 mL of water. After thoroughly mixing the sample by gentle bubbling, a subsample was removed by syringe to a Sedgewick-Rafter chamber for enumeration at 100x magnification. A minimum of 400 rotifers were counted. Species were identified according to the taxonomic references of Stemberger (1979) and Kutikova (1970). Biomass was estimated according to the formulae of Ruttner-Kolisko (in Bottrel et al. 1976). The regressions developed for the 1993 samples were again used for biomass estimations of the *Polyarthra* species.

Statistical Analyses

Phytoplankton

Composite, epilimnetic samples were used for identifying and enumerating phytoplankton at the offshore station (E2). Seasonal mean total biomass and biomass of each taxa were determined for the entire sampling season, weighted for variable time intervals between sampling dates. Seasonal means were compared between 1993 and 1994 using a paried-sample t test on monthly mean biomass values to reduce the effect of seasonal variability.

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Zooplankton

Whole water column estimates for mean community size, density and biomass for macrozooplankton and rotifers were calculated from data estimates of individual thermal strata, weighted for strata depth. Seasonal means were calculated from these whole water column estimates weighted for variable time intervals between sampling dates. In order to determine if biomass had changed from 1993 to 1994. We compared seasonal means between the two years using a paired-sample *t* test: data were paired by station.

Observations of rotifers in the preserved samples in 1993, indicated that the preservation method may have caused contraction of some soft-bodied animals, which may have led to biovolume underestimations. In 1993, rotifers were preserved in 10% formalin, whereas in 1994, rotifers were first narcotized in carbonated soda then preserved in 4% formalin. A *t* test was used to detect size differences in 1993 and 1994, for a number of species that were present at all eastern basin stations in both years.

RESULTS

LIGHT AND TEMPERATURE

The seasonal patterns in Z_m, Z_{eu} and ε_{par} at each station are presented in Tables 1a-c. The stations ranged from a shallow, well-mixed nearshore station (E1, 5.9 m) to a deep, thermally-stratified station (E2, 38.0 m). Station E3 (9.2 m) was intermediate between these two stations as it is nearshore and shallow, however, some stratification did occur and seasonal light extinction (ε_{par}) values were similar to the offshore station (E2). The two nearshore stations had light penetration to the bottom throughout most of the sampling period. One date at E1 was the exception when Z_{eu} was only 0.81 m, with very high ε_{par} (5.716 m^{-1}) and low Secchi depth (0.3 m). The low transparency may have been due to resuspension of sediments from storm events, however, the ash content of the seston was only 24.5% relative to >68% on other dates with ε_{par} above 0.400, and SRP was not elevated, suggesting that sediment resuspension was not prevalent. Also, Chl was not at a maximum concentration on this date. At station E2 the average Z_{eu} was 19.9 m, with only two dates where Z_{eu} was shallower than Z_m.

Patterns of seasonal ε_{par} were found to be quite consistent between stations E2 and E3, with similar seasonal means (0.252 and 0.254 m^{-1}, respectively) (Fig. 2). ε_{par} values were generally highest at station E1, with one exceptionally high value mentioned above. Seasonal mean ε_{par} was 32% higher at station E1 than at stations E2 and E3 (Table 1a-c). The overall low extinction values in the eastern basin are consistent with the low algal biomass, indicated by low concentrations of Chl and other suspended solids.

The seasonal patterns in mean Z_m temperatures were similar at each station (Fig. 3). Stratification was related to station depth. For example, stratification was established at the deep station, E2, in mid June and remained until mid October. At station E3, some thermal structure

was observed for short periods only, in mid June, mid to late July, and again in mid August. At station E1, the shallowest station, no stratification was observed.

Stratification at station E2 occurred one week earlier in 1994, and lasted almost one month longer than in 1993. This longer stratified period in 1994, was related to early warming of the surface water in June and calm weather in the fall. Surface temperatures increased from 7 to 18°C from June 1 to 16 in 1994 vs. 8 to 16°C from June 11 to 24 in 1993. In the fall, the winds on sampling dates at E2 averaged 6.5 knots in 1994 vs. 12.0 knots in 1993 and surface water temperatures were two degrees warmer in early October in 1994.

NUTRIENTS

Seasonal patterns of TP varied among the nearshore and offshore stations. At the shallow stations, TP concentrations varied somewhat throughout the sampling season with seasonal means of 10.1 and 8.5 $\mu g \cdot L^{-1}$ at E1 and E3, respectively (Tables 2a&c). Very high values for TP and SRP were observed on September 7 at station E1 and on May 18 at station E3. These values were found to be outliers ($\alpha=0.05$, Dixon's test for outliers) (Sokal and Rohlf 1981), and although removing them lowered the seasonal mean TP to 9.9 and 7.6 $\mu g \cdot L^{-1}$ at stations E1 and E3, respectively, these were not significant reductions ($p=0.24$ and $p=0.21$, respectively). Also, high values on these two dates were consistent with elevated concentrations of TP and SRP at the other stations, and high winds which likely caused resuspension. Resuspension in the spring and fall has been shown to increase sediment loads (Charlton and Lean 1987) as well as TP (Rosa 1987), in the water column. Although these values were high, they were not unreasonable given the physical conditions. Therefore, means calculated with these values included will be used. Phosphorus concentrations at station E2, were comparable to E1 during spring and fall isothermy (mean 9.0 $\mu g \cdot L^{-1}$), but mean values during the stratified period were lower, similar to values at E3, averaging 7.7 $\mu g \cdot L^{-1}$ (Table 2b). TP concentrations at E2 reached a maximum level of 10.6 $\mu g \cdot L^{-1}$ in early May and in mid July (Fig. 4).

Seasonal means for selected water quality and photosynthesis parameters from 1993 and 1994 are compared for each eastern basin station (Table 3). Seasonal mean TP concentrations were higher in 1994 than in 1993 at the nearshore stations, however, these differences were not significant at $\alpha=0.05$. The seasonal patterns were similar in the two years, although in 1994, E1 showed a mid-September peak and E3 showed a mid-May peak. Neither peak was associated with an increase in ϵ_{par}, but were accompanied by an increase in SRP. Similar peaks in TP were not observed in 1993. At station E2 mean TP concentration during unstratified conditions was higher in 1993 (12.9 $\mu g \cdot L^{-1}$) than in 1994 (9.0 $\mu g \cdot L^{-1}$), however, mean TP was similar during the stratified period of each year. In 1993, the breakdown of stratification at E2 was marked by an increase in TP to maximum levels observed for the season. In 1994, the breakdown of stratification on the last sampling date in October was not associated with a peak in TP.

Seasonal mean silica concentration was lowest at station E2 (0.26 $mg \cdot L^{-1}$), and were nearly identical (0.41 and 0.40 $mg \cdot L^{-1}$) at the two nearshore stations (Tables 2a-c, Fig. 5).

Spring silica concentrations were 58% lower than in the spring of 1993, and remained lower than 1993 values until mid July at station E2. Silica concentrations were similar through to the fall in the two years, with peaks in October in 1993 and in November in 1994 both timed with the breakdown of stratification. Seasonal mean concentrations were similar in the two years; 0.28 and 0.26 $mg \cdot L^{-1}$ in 1993 and 1994, respectively (Table 3). At the nearshore stations, the temporal variability in silica was similar at both stations and in both years. At E1 and E3, silica concentrations were low from early May to late July, then increased through to the end of sampling. As at station E2, spring silica concentrations at the nearshore stations were much lower in 1994 than in 1993: 46% lower at E1 and 61% lower at E3. Despite lower spring levels, seasonal mean silica concentrations where higher in 1994 at both nearshore stations (Table 3).

Seasonal mean NO_3-NO_2 concentrations were similar between the nearshore stations: 181 and 170 $\mu g \cdot L^{-1}$ at E1 and E3, respectively (Tables 2a&c), although mean concentrations were lower than in 1993: 232 and 224 $\mu g \cdot L^{-1}$ at E1 and E3, respectively. Concentrations declined by an average of 53% at the nearshore stations in 1994, from early May until early August before increasing again in the fall. At station E2, the seasonal mean NO_3-NO_2 concentration was 223 $\mu g \cdot L^{-1}$, similar to the 1993 mean of 243 $\mu g \cdot L^{-1}$, and was 21% higher than the average of the nearshore seasonal means. At station E2, concentrations were lowest during the stratified period, except for one high value of 693 $\mu g \cdot L^{-1}$ in late July (Table 2b).

The seasonal mean chloride ion (Cl) concentration was similar at all stations with an overall mean of 15.3 $mg \cdot L^{-1}$. This value was similar to the 1993 seasonal mean for the eastern basin stations, of 15.1 $mg \cdot L^{-1}$.

INDICES OF ALGAL BIOMASS

There were differences between nearshore and offshore stations in indices of phytoplankton biomass, Chl, POC and PON (Tables 4a-c). Seasonal mean Chl concentrations were 1.54, 2.24 and 1.27 $\mu g \cdot L^{-1}$ at stations E1, E2 and E3, respectively. Although concentrations fluctuated seasonally at all stations, an overall pattern of lower Chl concentrations in the spring and fall with increases during the summer was observed (Fig. 6). Chl concentrations were significantly different among the stations (p<0.001, Friedman's 2-way ANOVA) (Sokal and Rohlf 1981) with the mean at the offshore station (E2) 37% higher than the mean of the nearshore stations. Peak values at E2 reached 3.4 $\mu g \cdot L^{-1}$ in early August. Maximum concentrations were observed at E1 in late September (2.4 $\mu g \cdot L^{-1}$) and at E3 in late August (2.8 $\mu g \cdot L^{-1}$).

Compared to 1993, seasonal mean Chl in 1994 was higher at all stations, however, this increase was only significant at station E1 (p=0.028) (Table 3). At stations E1 and E3, seasonal Chl patterns differed from 1993 to 1994. At E1 in 1993, peaks in Chl were evident in June and August, whereas values were higher and fluctuated more in 1994. At E3, values tended to increase from July to September in both years but a June peak was only evident in 1993.

At station E2, Chl increased following stratification in both years. Epilimnetic Chl concentrations were slightly higher in 1994 than in 1993 from the onset of stratification until mid

August. TP concentrations were also higher in 1994 during this time. The higher TP likely contributed to higher Chl levels initially, however, Chl declined following a mid August peak, whereas in 1993, Chl continued to increase, peaking at a higher maximum in late August before declining.

Seasonal mean POC concentrations at stations E1, E2 and E3 were 0.199, 0.240 and 0.177 $mg \cdot L^{-1}$, respectively, and seasonal mean PON concentrations were 0.030, 0.036 and 0.025 $mg \cdot L^{-1}$, respectively (Tables 4a-c). As with chlorophyll, the offshore station exhibited higher mean POC and PON concentrations than nearshore stations. Mean POC concentration was significantly higher ($p < 0.05$) in 1994 at station E2, and both POC and PON were significantly higher ($p < 0.05$) in 1994 at station E1 (Table 3).

PHYTOPLANKTON

Biomass and Species Composition

Phytoplankton samples were analyzed only for the offshore station, E2. Seasonal mean phytoplankton biomass was determined from early May to early October, inclusive, to compare to the 1993 data. Mean biomass for this period in 1994, was 0.789 $g \cdot m^{-3}$, significantly (paired-sample t test, $p = 0.006$) higher (56%) than the mean for 1993 (Table 5). Mean biomass for the entire sampling period in 1994, May to November, was 0.715 $g \cdot m^{-3}$, which was no different from the 1983-85 mean of 0.683 $g \cdot m^{-3}$, (approximated from Makarewicz 1993a, Fig. 7a).

The seasonal mean biomass of the diatoms and chlorophytes did not change significantly between 1993 and 1994 (paired-sample t test, $p = 0.217$ and $p = 0.250$), respectively, although the percent contribution to total phytoplankton biomass decreased by 13%. The seasonal mean biomass of the Dinophyceae increased by 86%, however, this difference was due to a large spring peak in 1994, with the difference in seasonal means in the two years not highly significant (paired-sample t test, $p = 0.052$). Dinophyceae did, however, make up 37.5% of the seasonal phytoplankton biomass in 1994 vs. only 9.4% in 1993 (Table 5). The mean biomass of the chrysophytes and cryptophytes increased significantly between 1993 and 1994 (paired-sample t test, $p = .001$) and $p = 0.023$), respectively however, these increases were proportional to the increase in overall biomass, hence their percent contribution to the total biomass did not change (Table 5). No important changes were noted in the biomass of the cyanophytes or euglenoids.

Phytoplankton species richness varied between 1993 and 1994 as the total number of species contributing at least 0.1% of the total biomass decreased from 95 in 1993 to 65 in 1994 (Table 6)[1]. The largest differences occurred with the number of diatom species decreasing from

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[1]The totals for the number of phytoplankton species at the offshore station in each basin were reported incorrectly in the 1993 LEB Report as 84, 80 and 78, in the western, west central and eastern basins, respectively. Correct totals are 108, 102 and 95.

21 to 11 and the number of chlorophyte species decreasing from 35 to 18. The majority of those diatom species that contributed ≥5% of the total biomass in 1993, were again important in 1994. Other species, such as *Melosira binderiana* and *Synedra actinastroides*, increased their maximum contribution to the total biomass from ≤0.5%, to ≥10% and ≥5%, respectively (Table 6). In 1993, two chlorophyte species dominated and comprised ≥10% of the total biomass each (*Sphaerocystis schroeteri* and *Tetraedron minimum*), with only *S. schroeteri* doing so again in 1994.

Seasonal Patterns

Total phytoplankton biomass was variable in 1994 and did not show the overall bimodal pattern that was evident in 1993 (Figs 7a&b). However, many consistencies in the seasonality of biomass of individual groups were noted (Figs 8a-e). In the spring of 1994, the Dinophyceae dominated, comprising an average of 70% of the total phytoplankton biomass. Dinophyceae biomass declined through June and July, as was the case in 1993, and reached a second peak in biomass (47% of total biomass) in August. An increase was also noted in August of 1993, although the biomass attained was only one tenth of the level in 1994 (Fig. 8a). The dominant dinoflagellate species in 1994 were *Gymnodinium uberrimum* and *Peridinium aciculiferum* which comprised up to 57 and 81% of the total spring phytoplankton biomass, respectively. In August to early September, these species contributed 21 to 41% to the total biomass. In 1993, the May and August dinoflagellate peaks were dominated by *P. aciculiferum*, which comprised 30 and 12% of the total phytoplankton biomass at these times, respectively. *Gymnodinium uberrimum* was not as important in 1993 as it was in 1994, contributing a maximum of only 4% to the total phytoplankton biomass throughout the sampling season.

Chrysophyte biomass in 1994, steadily increased from late May to a maximum in mid July (68% of the total biomass), before steadily declining to the end of the sampling season. A similar pattern was noted in 1993, as biomass peaked in late July, then declined (Fig. 8b). The dominant chrysophyte species throughout the season and during the mid July maximum in 1994, were *Dinobryon sertularia* and *Ochromonas* sp., each contributing >20% to the total biomass from late June to mid July. In 1993, *D. sertularia* was not observed, however, *D. sociale* dominated throughout the season, and comprised an average of 20% of the total phytoplankton biomass during the mid summer peak.

Diatom biomass in May of 1994, was dominated by *Melosira binderiana* and *M. islandica*. These species dramatically declined prior to stratification and were not observed in the water column again until fall turnover. *Melosira islandica* was also the dominant spring diatom in 1993, comprising an average of 53% of the total phytoplankton biomass. Total diatom biomass peaked in mid June of 1994 at the onset of weak stratification (Fig. 8c), with *Diatoma elongatum* comprising 48% of the total phytoplankton biomass. *Diatoma elongatum* then declined rapidly, disappearing from the water column when stratification was established. In 1993, *D. elongatum* made an appearance during early stratification, but only accounted for 7% of the total phytoplankton biomass on one date. From stratification until late September in 1994, diatom biomass remained low, with *Synedra actinastroides* and *Cyclotella ocellata* dominating,

and reaching maxima of 8 and 9% of the total phytoplankton biomass, respectively. *Fragilaria crotonensis* was evident in the water column from late August, with biomass increasing to a maximum of 79% of the total phytoplankton biomass in mid October. With the onset of fall turnover, *Melosira binderiana* peaked again, and comprised 55% of the total phytoplankton biomass. In 1993, *Nitzschia acicularis*, *Cyclotella kutzingiana* and *C. ocellata* were the dominant diatoms during the stratified period and contributed 13, 10 and 13% of the total phytoplankton biomass, respectively during the mid summer peak in diatom biomass.

The biomass of the cryptophytes fluctuated throughout the sampling season in 1994, and contributed greater than 38% to the total phytoplankton biomass on some dates. The dominant species were *Rhodomonas minuta* and *R. lens*, similar to 1993. Biomass peaked in the spring and late summer in both years with a second fall peak occurring in 1994 (Fig. 8d).

Chlorophyte biomass remained low throughout most of the season in 1994 and 1993, with maximum biomass and maximum contribution to total phytoplankton biomass occurring in late September (Fig. 8e). In 1994, *Sphaerocystis schroeteri* was the dominant chlorophyte and represented 49% of the total phytoplankton biomass during the fall peak. In 1993, the fall peak was comprised of *Tetraedron minimum* in addition to *S. schroeteri*, each contributing approximately 20% to the total phytoplankton biomass.

Phytoplankton Photosynthesis

P_{opt} and P^B_m

Common statistics for P_{opt} and the determinant variables of areal photosynthesis are presented for each eastern basin station (Table 7). P_{opt} varied seasonally at each station with the highest seasonal mean at station E2 and lowest at station E3.

P_{opt} varied seasonally at all stations between approximately 1 and 10 mg $C \cdot m^{-3} \cdot h^{-1}$ with the exception of peak values in August and September of 13.2, 19.3 and 15.3 at stations E1, E2 and E3, respectively. Peaks in P_{opt} corresponded to maximum Chl values at stations E1 and E2, but to maximum P^B_m at station E3. Inter-stations variability in P_{opt} was thus influenced by both P^B_m and Chl.

When photosynthesis was normalized for Chl, seasonal mean P^B_m was similar at stations E1 and E3, 4.18 and 4.34 mg $C \cdot mg\ Chl^{-1} \cdot h^{-1}$, respectively with the mean at E2 (3.03 mg $C \cdot mg\ Chl^{-1} \cdot h^{-1}$) significantly lower (p<0.05) than at the nearshore stations.

Variability in P_{opt} was caused by fluctuations in P^B_m and Chl although the effects varied among stations and between years. In 1993, seasonal fluctuation in P_{opt} at most stations, was due primarily to variability in Chl (C.V.= 48-85%). Station W1 was the exception, with variability in P^B_m as the key factor (partial correlation coefficient for P^B_m on P_{opt} = 0.81). In 1994, P_{opt} was significantly correlated with both P^B_m and Chl.

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Daily and Seasonal Integral Photosynthesis

Mean daily integral photosynthesis (ΣPP mg $C \cdot m^{-2} \cdot d^{-1}$), calculated using empirical solar irradiance data, showed a nearshore-offshore gradient with mean values increasing by 43% from station E1 to E3, and by a further 44% from E3 to E2 (Tables 8a-c). This gradient was partly the result of Z_{eu} differences among the stations. The deeper Z_{eu} at E3 relative to E1, compensated for the slightly lower mean P_{opt} at E3, and resulted in a higher mean areal rate. Z_{eu} was similar at E3 and E2, however, the higher P_{opt} and Chl at E2 accounted for the increase in mean areal photosynthesis. Although P_{opt} and Chl were both higher offshore relative to nearshore, the disproportionately higher Chl relative to P_{opt}, resulted in a lower P^B_m in the offshore.

Areal-based photosynthesis for a standardized period from May 1-Oct. 31, was greatest at station E2 (85.8 g $C \cdot m^{-2}$) and lowest at station E1 (41.2 g $C \cdot m^{-2}$) (Table 9). Mean areal-based photosynthesis for all eastern basin stations was 62.7 g $C \cdot m^{-2}$. However, for comparison to mean areal photosynthesis calculated for the eastern basin stations in 1993, only values from stations E2 and E3 were averaged. The mean for these two stations was 73.4 g $C \cdot m^{-2}$ in 1994, similar to the 1993 mean of 79.6 g $C \cdot m^{-2}$. The low photosynthesis value at station E1 lowered the combined station average.

Both daily and seasonal photosynthetic rates, showed spatial variation in a nearshore-offshore direction. Cloudless solar irradiance data was used to estimate the potential maximum seasonal photosynthesis. Empirical estimates were found to be within a narrow range of these cloudless estimates (Table 9), indicating that yearly variability in seasonal photosynthesis was not greatly impacted by annual differences in solar irradiance (Millard et al. 1995). Areal-based estimates of seasonal photosynthesis differed among the eastern basin stations due to the variable effects of Chl, P^B_m, light extinction and depth occurring at each station. Depth profiles of photosynthesis at E3 were truncated by station depth, and this in addition to lower Chl, resulted in lower seasonal PP than at E2. Depth profiles were also truncated by depth at E1, and this in conjunction with low transparency relative to E3, resulted in lower seasonal PP.

Observed vs. Predicted Phytoplankton Photosynthesis

PP at each LEB station was predicted using seasonal mean TP and Chl and the equations of Millard et al. (1996) and Millard et al. (Dept. of Fisheries and Oceans, Burlington, unpubl. data) for 1993 and 1994 (Table 10). The published equation by Millard et al. (1996) was used in the 1993 LEB report to compare Lake Erie data. The equation was refit with additional Lake Ontario, Bay of Quinte and Lake Erie data, not including data from stations E1 and E3, thought to be impacted by *Dreissena*. The fit of the curve remained unchanged. The refit equation was, therefore, used to assess the observed vs. predicted PP and the impact of *Dreissena* at the eastern basin stations. The equation

1)   *PP = (395.5 * TP)/(19.08 + TP)*

predicts seasonal PP (based on empirical solar irradiance data) from seasonal TP, and is of the

same form as that presented by Vollenweider (1974) which used annual TP loading to predict annual PP. A second equation was developed to predict seasonal PP (based on empirical solar irradiance data) from seasonal Chl, using data from offshore productivity studies in Lakes Ontario and Erie and the Bay of Quinte (Millard et al., unpubl. data)

2) $PP = (311.7 * Chl)/(4.33 + Chl)$

For both equations, the potential PP was obtained by allowing the production models to extend the profiles beyond station depth, to the potential depth set by transparency. This resulted in a slight increase in PP over that observed when profiles were truncated at the station bottom, at W1, E1 and E3 (Table 10). Seasonal PP predicted using equations 1) and 2) were compared to potential PP where applicable.

At the western basin stations in 1993, observed PP was similar to that predicted by Chl. Seasonal PP was 29 and 13% lower than predicted using TP at W3 and W1, respectively. However, Chl was not lower than the potential set by TP and TN according to the equation of Smith (1982), suggesting that other factors contributed to the lower PP. At the west central basin stations, observed PP was similar to that predicted by Chl and TP (Table 10). At the offshore station in the eastern basin, PP predicted using TP and Chl was similar in the two study years. The observed PP was similar to that predicted by Chl and TP in 1993, but in 1994 PP was lower than that predicted by Chl and TP. These discrepancies were largely due to a change in the phytoplankton community and an accompanying decrease in P^B_m and will be discussed further in a later section. At station E3 in 1993 and 1994, observed PP was as predicted by Chl, but well below that predicted by TP. This indicated that Chl was below the potential set by TP (Table 10). As at station E3, observed PP at station E1 in 1994 was below the potential set by TP. In addition, observed PP was below the potential set by Chl due to the added effect of lower transparency.

Irradiance

Areal photosynthesis is dependent upon light levels within the mixed layer. $\bar{I}$, the mean epilimnetic irradiance ($mE \cdot m^{-1} \cdot min^{-1}$), is influenced by the interplay of ε_{par}, Zm and incident solar irradiance. $\bar{I}$ calculated using cloudless irradiance illustrates the change in light environment within the eastern basin throughout the season due to ε_{par} and Zm alone (Table 8a-c). The deep offshore station had a seasonal mean $\bar{I}$ of 7.93 $mE \cdot m^{-1} \cdot min^{-1}$, with values being highest (mean of 10.27 $mE \cdot m^{-1} \cdot min^{-1}$) during the stratified period compared to 5.41 and 2.72 $mE \cdot m^{-1} \cdot min^{-1}$ in the spring and fall, respectively. Low spring and fall values were associated with deep mixing depths. Mean $\bar{I}$ at stations E1 and E3 was similar (13.67 and 14.90 $mE \cdot m^{-1} \cdot min^{-1}$, respectively), and an average of 44% greater than the mean value at station E2. Although transparency was lower at E1 than at E3, the potential effect of lowering $\bar{I}$ was offset by the shallower mixing depth at E1, resulting in similar seasonal mean $\bar{I}$ at these two stations.

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ZOOPLANKTON

Density

Macrozooplankton

Sampling continued later in the season in 1994 than in 1993. Thus, for direct comparison between the two years, seasonal mean density in 1994 was calculated using data up to the last date sampled in 1993 only. Total macrozooplankton density (not including rotifers) in the eastern basin, declined from 1993 to 1994 (p=0.014, paired Student's T test) (Table 11). However, mean density did not decline for all macrozooplankton groups at each station. The following observations are based on trends only; they are not significant differences. Calanoids were the only group which declined from 1993 to 1994 at all three east basin stations. Cyclopoids declined at the nearshore stations E1 and E3 but increased offshore at station E2. Cladoceran numbers decreased at stations E1 and E2 and remained the same at E3, while veligers increased at station E1 but decreased at stations E2 and E3.

Seasonal patterns of macrozooplankton groups varied among the three stations and differences in the communities were evident from 1993 to 1994 (Figs 9, 10, 11). At station E1 there were relatively fewer cladocerans in 1994 throughout the first half of the season, and although cladoceran density was still low in the fall, it appeared higher than at this time in 1993 (Fig. 9). Cyclopoid patterns were very different in 1993 and 1994. In 1993, cyclopoid density peaked four times, once in late May, mid July, late August and early October. In 1994 peaks were higher but there were only two of them, in early and late July, separated by only one week. It is unlikely that the cyclopoid population crashed in between peaks as our data suggests. The variable densities were more likely due to patchy distribution caused by water movements or entrainment from the Nanticoke nuclear station. There was a high veliger peak in late August in 1994 not seen in 1993.

At station E2, cyclopoid copepods were the first group to dominate the water column in 1994, whereas veligers and small-bodied cladocerans dominated the spring population in 1993 (Fig. 10). Cyclopoids contributed more to the overall density throughout the 1994 sampling season than any other group, whereas the 1993 population was dominated by veligers. Veligers, although present in 1994, were not major contributors and did not peak as they did in 1993. Calanoids were present throughout the summer in both years but not in high numbers. Cladocerans formed a major part of the population from mid August to mid October, more so than they did in 1993.

The early population at station E3 was characterized by small numbers of all four macrozooplankton groups in both 1993 and 1994 (Fig. 11). In both years Cladocera gained importance as the summer began, with an additional peak occurring in late July-early August. However an additional peak occurred in mid September in 1994 which did not occur in 1993. In both years the populations were dominated by the presence of copepods, although this domination existed for a longer period of time in 1993 stretching from late July into mid October

when sampling was terminated versus late July to mid September in 1994. In both years veligers contributed to the population throughout the summer but in 1994 there were no major peaks as exhibited in late August in 1993.

Rotifers

Unlike other zooplanktors, rotifer density did not decline at all three eastern basin stations from 1993 to 1994. There appeared to be an increase in rotifer density at the nearshore stations E1 and E3, and a reduction at the offshore station E2. In both years, rotifers were present in the water column in very high densities relative to macrozooplankton (Table 11). In 1994, rotifer density was lowest at station E2, where densities of other zooplanktors was highest and highest at station E3 where macrozooplankton density was lowest. Both rotifer and macrozooplankton densities at E1 were intermediate between E2 and E3.

Seasonal distribution also varied for rotifers from 1993 to 1994 (Fig. 12). The large week to week variability in cyclopoid density was also evident for rotifers nearshore, at station E1 in 1994. The population in 1993 was much less variable. At station E2 there were two peaks in rotifer density in both years, occurring at similar times in the season. At station E3 there was a dramatic increase in the second half of the sampling season from mid August to mid October in 1994 relative to 1993 (a maximum of over $15 \cdot 10^5$ no$\cdot$m^{-3} vs. a maximum of only $4 \cdot 10^5$ no$\cdot$m^{-3}).

Biomass

Macrozooplankton: 1994 vs. 1993

Total macrozooplankton (including veligers) biomass (mg$\cdot$m^{-3}) like density, was lower in 1994 at all three eastern basin stations than it was in 1993 when compared across comparable dates (1994: E1 16.98, E2 21.96, E3 11.50 versus 1993: E1 24.97, E2 36.12, E3 25.69) (Table 12). A paired-sample t test revealed that this was a significant reduction (p = 0.013). Please note that the seasonal mean values for the entire sampling season, with and without veligers, reported for all six stations in the 1993 report (Table 12, Dahl et al. 1995) mistakenly included estimates of rotifers. Rotifers estimates were correctly not included in the seasonal means reported for May and August dates only from 1984-87 and 1993 (Table 12, Dahl et al. 1995).

In 1993, macrozooplankton biomass at stations E2 and E3 was lower than means calculated by J. Makarewicz for 1984-87, whether similar dates or the entire season were compared (Dahl et al. 1995). Zooplankton biomass at stations E2 and E3 were lower still in 1994. Data has since been analyzed for station E1 for both years. Mean biomass in 1984-87 for the eastern basin was 60.8 ± 60.7 mg$\cdot$m^{-3}, using May and August dates only. Whole season macrozooplankton estimates (not including veligers) were 20.18, 20.38 and 19.53 g$\cdot$m^{-3} in 1993 and 12.33, 18.54 and 9.07 mg$\cdot$m^{-3} in 1994 at stations E1, E2 and E3 (Table 12), respectively.

Rotifers

Six of the twenty rotifer species or forms investigated were significantly smaller in 1994 than in 1993 (p<0.05) (Table 13). One of these species, *Kellicottia longispina*, differed in size by only 7%. This small difference in addition to the hard lorica, suggests that this change in size was unlikely a preservation effect. All other species or forms that showed a significant change in size, were soft-bodied animals. *Collotheca* sp. was 43% smaller in 1993 than in 1994, and two species of *Polyarthra*, *P. major* and *P. remata*, were 30 and 23% smaller, respectively. A third species of *Polyarthra*, however, was significantly larger in 1993. The inconsistencies in size differences for the *Polyarthra* suggest that preservation methods may have accounted for some of the size differences, but the possibility of predation on larger individuals in 1993 may have also been important. Only one form of *Synchaeta* showed a significant size difference. Apparent size reduction may also be the result of inconsistent classification between the two years, since species identification of highly contracted rotifers is extremely difficult (J. LeBlanc, Dept. of Fisheries and Oceans, pers. comm.). Therefore, preservation methods used in 1993 may have lead to the contraction of some rotifer species, however, the effects of contraction on biovolume estimates could not be quantified.

Changes in rotifer biomass from 1993 to 1994 follow much the same trend as their density (Table 12). Rotifer biomass increased at the nearshore stations E1 and E3 and decreased at the offshore station E2, in 1994. Rotifer biomass was lowest at station E2, where macrozooplankton biomass was highest, and highest at station E3, where macrozooplankton biomass was lowest. High numbers of rotifers did not translate to high biomass due to their small body size relative to other zooplankton species. At stations E1 and E2 biomass of rotifers is similar to biomass of other zooplankton groups. Only at station E3 where rotifer density was extremely high did they make up a disproportionately large part of the total zooplankton biomass.

Seasonal Trends

The 1994 whole season mean biomass for macrozooplankton was lower nearshore, E1 (15.2 mg·m^{-3}), E3 (10.96 mg·m^{-3}), than offshore, E2 (19.78 mg·m^{-3}) (Table 12). At all three stations, the macrozooplankton community was characterized by three or four major peak and trough cycles, lasting approximately two weeks nearshore and four weeks offshore (Figs. 13, 14, 15). These distinct patterns were not observed in 1993. It is possible these cycles did not occur, but more likely they were simply not detected due to the loss of resolution as a result of less frequent sampling in 1993. Although the timing of cycles in 1994 was similar from station to station the relative contribution of zooplankton groups to each peak was not. For instance, the first peak occurred in early July and was dominated by cyclopoids at station E1, equal proportions of all four macrozooplankton groups (cladocerans, cyclopoids, calanoids and veligers) at E2, and calanoids at E3. As for density, seasonal patterns of macrozooplankton groups varied among the three stations and differences in communities were evident from 1993 to 1994.

At station E1 macrozooplankton entered the water column more than one month later in 1994 than in 1993 (Fig. 13). Although overall seasonal biomass was less in 1994, biomass

between mid June and early August was much greater. There were more cyclopoids (Fig. 13) and rotifers (Fig. 16) in 1994, similar biomass of calanoids and fewer cladocerans at this time. Both years were characterized by a large biomass peak in late August, however, this peak was attributed to calanoids in 1993 and to veligers in 1994. Non-veliger macrozooplankton biomass was greater than 70 mg·m^{-3} in late August in 1993, but only 29 mg·m^{-3} in 1994. Rotifer biomass also increased in 1994 at this time. After August, macrozooplankton, veliger and rotifer biomass crashed and did not recover by the end of the sampling season. This contrasted starkly with 1993. The macrozooplankton population in 1994 was squeezed into a three month period from late June to early September, while in 1993 the population appeared one month earlier and remained at least a month later. Note, the density plot (Fig. 9b) indicating that macrozooplankton were present at E1 until mid October. Much of this population however, was comprised of small bodied cladocerans and cyclopoids whose high numbers do not translate into high biomass.

From mid June to early August, cladocerans, cyclopoids and calanoids contributed similar proportions to the total biomass at station E2, while veligers contributed less (Fig. 14). This differed from 1993 where veligers contributed the most and cyclopoid biomass was relatively low. Biomass of rotifers increased at station E2 during this time. For the next month cladocerans became more important in 1994 but less so in 1993. Veligers remained the most important contributor of biomass in 1993 until sampling ended, with the exception of a short period of time from late July to early August. Although veliger biomass increased beginning mid September in 1994, maximum biomass was less than that attained in 1993. Macrozooplankton biomass declined in mid October then increased in the water column in November. Rotifers increased in mid October, however, they were not sampled beyond this time hence the patterns of rotifer biomass during fall turnover were not determined.

Rotifers were the major contributors to biomass at station E3 in 1994 (Fig. 16). This was particularly evident from August to early October, when they comprised almost three times the biomass of the four macrozooplankton groups combined (Fig. 15). This contrasted with 1993, where calanoids were the major contributors to biomass. Calanoids were important in early July, late July and mid August in 1994 for approximately two weeks at a time, but never to the extent they were in 1993. They contributed little to the community after their last peak in August in 1994, unlike in 1993, when they continued to be a major part of the total biomass in the fall. Cyclopoids had a higher biomass in mid summer in 1994 than they did in 1993, and contributed little throughout the rest of the sampling season, while in 1993 they increased in importance through September and October. Cladoceran biomass was low in both years, though slightly higher in 1994. Veliger biomass was negligible in 1994 except in September, whereas veligers were present throughout the season in 1993 and peaked in late August.

Common Species

Macrozooplankton

The number of "common" (contributed ≥5% of the total zooplankton biomass of a given sample) species was similar in 1993 and 1994 (Table 14). Sixteen of the 28 species found in the

eastern basin in 1994 fall into this category, compared with 13 of the 26 species found in 1993. However, close examination of these species revealed several important shifts in the structure of the zooplankton community from 1993 to 1994.

At station E1, a greater number of cladoceran species were found in 1994 than in 1993 (12 vs. 9). However, *Bythotrephes cederstroemi* was the only cladoceran species "common" more often in 1994. Biomass of both *B. cederstroemi* and *Bosmina* sp. declined from 1993 to 1994 while that of *Daphnia* sp. and *Leptodora kindti* increased. The number of copepods present in 1994 was similar to 1993. *Leptodiaptomus minutus* were "common" less often in 1994 while *Skistodiaptomus oregonensis* and *Epischura lacustris* were "common" more often. Although *E. lacustris* comprised ≥5% of the total biomass on more occasions in 1994 the seasonal mean biomass declined from 6.89 mg·m^{-3} to 2.14 mg·m^{-3}. *Diacyclops thomasi* were "common" more often in 1994 while *Tropocyclops extensus* were "common" less often (27% of the time in 1993 vs. 0% in 1994).

At station E2, large cladocerans formed a more important part of the community in 1994 than in 1993. *Daphnia retrocurva* and *D. galeata mendotae* never comprised ≥ 5% of the total sample biomass in 1993, but *D. retrocurva* were "common" 50% of the time and *D. galeata mendotae* were "common" 10% of the time in 1994. Additionally, their seasonal mean biomass increased from 0.003 mg·m^{-3} to 3.075 mg·m^{-3} in 1994. The seasonal mean biomass of *Bythotrephes* was similar in 1993 and 1994, however, they remained in the water for a longer period of time in 1994 contributing ≥ 5% of the total sample biomass 45% of time compared with 0% in 1993. *Leptodora kindti* was "common" less often in 1994 and declined in mean biomass. In 1993, these two predatory cladocerans, *Bythotrephes* and *Leptodora kindti* were never "common" at the same time and place (Dahl et al. 1995). Mean biomass of *Bosmina* sp. declined from 4.66 mg·m^{-3} in 1993 to 1.91 mg·m^{-3} in 1994, although they were slightly more "common" in 1994. The copepod community was similar in the two years except that *Epischura lacustris* seasonal biomass decreased by more than 50% although they were "common" for most of the season in 1994.

There was a greater number of cladoceran species present in 1994 than in 1993 (8 versus 3) at station E3. Large cladocerans were "common" more often in 1994. *Daphnia retrocurva* biomass increased from 0 to 0.389 mg·m^{-3} and they were "common" on two occasions in 1994 compared with never in 1993. *Bythotrephes cederstroemi* were equally "common" in both years although mean biomass declined from 0.584 mg·m^{-3} in 1993 to 0.233 mg·m^{-3} in 1994. *Leptodora kindti* were never "common" in either year nor did their low biomass change. Most species of calanoids, contributed ≥5% of the total sample biomass on fewer occasions in 1994 than they did in 1993. Specifically, *Leptodiaptomus minutus*, *Skistodiaptomus oregonensis* and *Epischura lacustris* were less "common" in 1994. Biomass of *Epischura lacustris* decreased from 8.13 mg·m^{-3} to 3.08 mg·m^{-3}. *Eurytemora affinis* were no longer "common" and *Leptodiatomus siciloides* were no longer present.

Rotifers

The number of rotifer species that contributed significantly to total biomass at each station was similar, ranging from 25 to 34 (Table 15). The total number of species increased at stations E1 and E3 and decreased at E2, from 1993 to 1994. Station W3 in the western basin was sampled for rotifers in 1994, and the total number of species decreased to 24 from 29 in 1993.

The dominant species at all eastern basin stations were similar in the two years: *Asplanchna priodonta, Conochilus unicornis, Polyarthra* sp. including *P. major, P. remata,* and *P. vulgaris,* and *Synchaeta* sp., each contributed greater than 10% of the total biomass at some time in the season in both years. *Asplanchna herricki* was also dominant in 1994, however, this species was not observed in the eastern basin in 1993.

Differences in species composition were observed at each station in the two years of study. At station E1, the contribution of *Kellicottia longispina, Keratella crassa* and *K. quadrata* increased from ≥0.5% in 1993 to ≥10% in 1994. *Pleosoma truncatum* and *Trichocerca pusilla* were not observed in 1993, but contributed ≥5% to total rotifer biomass in 1994. Species composition at station E2 was similar in 1994, except for the absence of *Filinia longiseta* and *Trichocerca elongata,* which contributed ≥5% and ≥10% of the total biomass, respectively in 1993. *Keratella crassa* decreased from ≥10% to ≥0.5% in 1994 at station E3, whereas *Cephalodella gibba* and *Collotheca* sp. contributed more to total rotifer biomass than in 1993.

Size Comparisons

Zooplankton community size is often used as an index of planktivory, with a value of 0.80 mm indicating a healthy balance between herbivores, planktivores and piscivores (Mills and Schiavone 1982). The zooplankton community mean size in the eastern basin of Lake Erie was low, reaching 0.80 mm on only one occasion offshore (E2) in mid June (Fig. 17). At station E2 the mean size of zooplankton peaked early in the season in both years but was higher in 1994 than in 1993 (0.93 mm vs. 0.71 mm). After this time the mean size was similar in 1993 and 1994 fluctuating between 0.35 mm and 0.55 mm, although in 1994 there appeared to be a decreasing trend from July through to September, which was not evident in 1993.

Mean community size was lower nearshore than offshore, although the early season community was larger in 1994 than it was in 1993 (Fig. 17). In both years, the mean community size nearshore appeared to be lowest in the spring, with the exception of the first sampling date. In 1993 the mean size increased through the summer while in 1994 it remained similar, but in neither case did the mean size decline as it did in the offshore.

Changes in planktivory were also investigated by comparing the mean lengths of individuals of the same species in the two study years (Table 16). We accepted a 10% difference as a significant change in mean length from 1993 to 1994. In the nearshore (E1 and E3) 6 of the species comparisons showed a significant increase in size. No species were significantly smaller. Offshore, at station E2 four of the eight species compared were larger in 1994.

Daphnia retrocurva were uncommon at station E2 in 1993, but in 1994 they were larger at station E2 than at station E1 in 1993. *Eurytemora affinis*, *Diacyclops thomasi* and *Dreissena* veligers were larger by more than 10%. Two species, *Bosmina* sp. and *Mesocyclops edax* were significantly smaller in 1994.

DISCUSSION

The Lake Erie Biomonitoring program has contributed to the understanding of the important links between phytoplankton and zooplankton in the pelagia, planktivory, and the recently established benthic mussel, *Dreissena*. A complex web of top-down and bottom-up mechanisms structured the pelagic community in 1993, resulting in a reduction in pelagic production and redirection to the benthic food-chain, particularly in the eastern basin. Trophic status of the pelagia in the eastern basin was reduced relative to pre-mussel years. However, if we consider the increased productivity of the benthic community due to the redirection of phosphorus and algal biomass, the overall trophic status may not have declined. This compensatory effect was evident in Saginaw Bay, Lake Huron, as the decline in phytoplankton productivity was almost equalled by the increase in benthic algal productivity, following the invasion of *Dreissena* (Fahnenstiel et al. 1995). In 1994, we again observed the controlling influence of *Dreissena* on phytoplankton biomass and production, especially in the nearshore. The control of food supply from below as well as the top-down pressures of planktivory, have structured the zooplankton community. Although *Dreissena* were present in both study years, important changes were noted at each level of the pelagic food-web and in the resulting trophic interactions.

OFFSHORE

In the spring of 1994, the *Dreissena* population at the offshore station (E2) was dramatically reduced in comparison to the spring of 1993, although the individuals that were present in 1994 were much larger than in the previous year. It is likely that a massive winter die-off of those animals which did not reach 10 mm in length by the fall, occurred (R. Dermott, Dept. of Fisheries and Oceans, Burlington, pers. comm.). The potential for the offshore *Dreissena* population to reduce phytoplankton production, is limited to the spring and fall when mixing provides the mussels with access to the entire water column. In contrast, *Dreissena* in the nearshore have access to the entire water column throughout the season. To assess the impact of *Dreissena* on pelagic production in 1993 and 1994 at the offshore station, potential clearance rates of the dreissenids in May of each year were calculated (Table 17).

The mean density of *Dreissena* (mainly *D. bugensis*) at station E2 in May 1993 was 1.6×10^5 individuals (ind)$\cdot$m^{-2}, with an average wet weight of 2.6 mg$\cdot$ind^{-1}, based on a mean dreissenid biomass of 404.3 g$\cdot$m^{-2} (Dahl et al. 1995). The density of *D. polymorpha* in May 1993, was only 57.5 ind$\cdot$m^{-2} with an average wet weight of 7.7 mg$\cdot$ind^{-1}. In this study, wet shell-free weights were converted to dry weights using a wet to dry weight conversion factor of 0.081 for *D. bugensis* and 0.121 for *D. polymorpha* (R. Dermott, Dept. of Fisheries and Oceans,

Burlington, pers. comm). Mean dry weights were calculated as 0.21 and 0.94 mg·ind^{-1} for *D. bugensis* and *D. polymorpha*, respectively. The formula of MacIsaac et al. (1992) (adapted from the formulae of Kryger and Riisgård 1988), was then applied to calculate the clearance rate as,

3) $CR = 1.64 \times 10^8 \, DW^{0.88}$

where CR = clearance rate in µL·ind^{-1}·d^{-1}
       DW = dry weight in g

This relationship was derived from the regression of clearance rate on dry weights for individuals between 6.3 and 31 mm in shell length (MacIsaac et al. 1992). We have assumed, as MacIsaac et al. (1992) did, that this relationship also holds for individuals down to 0.015 mg (1 mm).

Total clearance rate of the dreissenid population in May 1993 at E2, was estimated at 1.49x10^4 L·m^{-2}·d^{-1} (Table 17). In May of 1994, only *D. bugensis* were present at E2 at a density of 7.85x10^3 ind·m^{-2} and an average wet weight of 10.2 mg·ind^{-1}, based on a mean dreissenid biomass of 80.4 g·m^{-2} (Dahl et al. 1995). Dry weight was 0.83 mg·ind.$^{-1}$ using the wet to dry weight conversion factor of 0.081. The estimated clearance rate, using the above formula, for the May 1994 population was only 2.5x10^3 L·m^{-2}·d^{-1} (Table 17).

The reduction in potential clearance rate of the dreissenid population between May 1993 and May 1994, from close to 15,000 L·d^{-1}·m^{-2} to only 2,500 L·d^{-1}, was due to a decline in the population of the dreissenids. Temperature may have also affected the filtration activity of the mussels in 1994. Reeders and Biij de Vaate (1990) showed that *Dreissena* filtration rate dropped sharply at water temperatures below 5°C, with no difference in rate between 5 - 20°C. The average water column temperature from early May until stratification in 1993 was 6.5°C vs. 4.2°C in 1994, which may have affected the potential filtration rates of the mussels. The spring biomass of *Dreissena* was 80% lower in May 1994 compared to May 1993. In the absence of seasonal biomass estimates for 1994, the lower spring value is assumed to translate into a lower seasonal dreissenid biomass. The 75% reduction in mean veliger density from 1993, indicates that the dreissenid population was unlikely to have reached levels attained in 1993. The low numbers of veligers present throughout the sampling season in 1994 were likely due to inflow from the central basin in addition to the small number released by adults within the eastern basin.

The reduction in the dreissenid population appeared to have a positive affect on the biomass of some phytoplankton groups and resulted in a total phytoplankton biomass that was 56% higher than in 1993. Spring phytoplankton biomass, in particular, was 65% higher in 1994 than in 1993 (1.153 vs. 0.399 g·m^{-3} in 1994 and 1993, respectively) consistent with the drastic reduction in potential clearance rate of the dreissenid population in May 1994. In 1994, diatom biomass did not decline during spring isothermy. Values remained relatively stable (0.199, 0.149 and 0.154 g·m^{-3}, respectively from early May until early June), unlike in 1993 where diatom biomass declined rapidly from 0.354 in early May to 0.027 g·m^{-3} in early June in 1993. *Dreissena* were likely responsible for the decline in diatoms in 1993 as diatoms have been found to comprise an important proportion of the stomach contents of *Dreissena* (Ten Winkels and

Davids 1982).

Dinoflagellates may have also benefitted from a reduction in the *Dreissena* population in 1994. Dinoflagellate biomass peaked during spring isothermy, reaching a maximum biomass of 1.641 $g \cdot m^{-3}$. However, during spring isothermy in 1993, dinoflagellate biomass declined from 0.227 to 0.012 $g \cdot m^{-3}$, possibly due to the filtration activities of *Dreissena*.

Although total phytoplankton biomass increased, seasonal phytoplankton photosynthesis was 18% lower in 1994 compared to 1993. The phytoplankton community at the offshore station in 1994, was dominated by dinoflagellates, mainly *Peridinium* and *Gymnodinium*, with diatoms representing a much smaller proportion of the total biomass than in 1993. Studies have shown that diatoms have a much higher photosynthetic rate per unit biomass as well as a higher chlorophyll to biomass ratio than other algal groups, especially dinoflagellates (Thomas et al. 1978; Chan 1980). Therefore, seasonal PP was lower in 1994 than in 1993 likely due to the shift in the phytoplankton community.

More dramatic reductions in seasonal PP have resulted from reductions in Chl due to filtration by *Dreissena* as was the case in Saginaw Bay (Fahnenstiel et al. 1995). Although increases in photosynthetic parameters occurred following establishment of the zebra mussels, these increases were not sufficient to compensate for the decrease in Chl and PP declined. Although dreissenids can have an impressive impact on phytoplankton production in shallow areas, deep, stratifying systems such as the offshore in the eastern basin show less of a response.

Phytoplankton photosynthesis (PP) at the offshore station in 1994, was compared to estimates based on seasonal mean TP. Similar estimates are summarized for all stations in 1993 and 1994 (Table 18). Using the refit equation of Millard et al. (1996) and TP, PP was predicted at 118 g $C \cdot m^{-2}$ (based on empirical irradiance). Using the second equation which predicts PP based on seasonal Chl (Millard et al., unpubl. data), PP was predicted at 106 g $C \cdot m^{-2}$. These predicted values differed by only 10%, thus on a seasonal basis Chl was close to expected given the TP concentration, suggesting limited filtering effects of *Dreissena*. The observed seasonal PP (86 g $C \cdot m^{-2}$) in 1994, was slightly lower than that predicted by Chl because of the low mean P^B_m stemming from the shift in the phytoplankton community to one dominated by dinoflagellates. In 1993 as well, the observed PP (105 g $C \cdot m^{-2}$) was nearly identical to that predicted by Chl (102 g $C \cdot m^{-2}$), and similar to that predicted by TP, suggesting a limited impact of *Dreissena* filtering on PP in the offshore in both years.

Zooplankton populations were thought to be controlled by limited food supply in addition to planktivory in 1993, therefore, increased food resources in 1994 should have allowed zooplankton to increase over 1993 values. However, the increase in food supply did not result in an increase in zooplankton biomass. The decline in seasonal mean zooplankton biomass in 1994 was most likely due to changes in predation pressure. The zooplankton community structure and size of individuals appeared to have responded to a shift in the smelt population, in particular a decline in the age-1 class and an increase in YOY class (Ministry of Natural Resources 1995). Age-1 smelt were virtually absent in 1994, which released grazing pressure

on large *Daphnia* and *Bythotrephes*. The biomass and density of *Daphnia* increased from 1993. The decline in *Bosmina* biomass in 1994 may have been in response to increased competition with *Daphnia* for food. Additionally, *Bosmina* seem to have suffered from the increased duration of predation by *Bythotrephes* in 1994. Specifically, *Bythotrephes* was present in the water column one month earlier in 1994 than in 1993. Yurista and Schulz (1995) suggested that small *Bythotrephes*, like those found in Lake Erie, would select small cladocerans, such as *Bosmina*, resulting in a community shift to larger individuals.

Bosmina are a favoured food item of *Leptodora* (Banstrator and Lehman 1991). The increased competition with *Bythotrephes* for their preferred prey may explain the decrease in mean biomass of *Leptodora* from 1993 to 1994. The decline in biomass of large calanoids in 1994 was likely due to predation by YOY smelt. Smelt begin feeding on calanoids around July of their first year, when they reach approximately 21 mm in length (Seifert 1972). Calanoids can make up between 60 and 85% of the diet of young smelt (B.F. Bidgood, Ontario Ministry of Natural Resources, Wheatley, unpubl. data).

The shift in the zooplankton community to larger *Daphnia* and *Bythotrephes*, and away from large calanoids and *Bosmina* was consistent with the change in predation pressures by smelt. The significant reduction in zooplankton biomass in 1994 was due to a decline in the biomass of *Bosmina*, calanoids, rotifers and veligers. The reductions in *Bosmina*, calanoids and rotifers were most likely the result of predation, whereas the reduction in veligers was due to the reduction in adult *Dreissena* in 1994.

NEARSHORE

The potential clearance rates of the dreissenids at station E3 in May of each year were determined to assess the impact on pelagic production, in the same manner as for the offshore station (Table 17). Spring values are compared as only May samples were collected in 1994. Potential clearance rates, in conjunction with predicted and observed PP, may suggest the extent of the impact of *Dreissena*.

The *Dreissena* population at E3 in the spring of 1994 was characterized by an increase in *D. bugensis* and a decrease in *D. polymorpha* density, with an overall decrease in biomass, relative to spring 1993. The mean density of *D. bugensis* in 1993, was 1.9×10^4 ind·m^{-2} with an average biomass of 2.0×10^2 g·m^{-2} (Table 17). Potential clearance rate was 6.3×10^3 L·m^{-2}·d^{-1}. The density of *D. polymorpha* was 2.9×10^3 ind·m^{-2} with an average biomass of 1.9×10^2 g·m^{-2} and a calculated clearance rate of 6.9×10^3 L·m^{-2}·d^{-1}. Total potential clearance rate of the dreissenid population in May 1993 was 13.2×10^3 L·m^{-2}·d^{-1}.

In May of 1994, the potential clearance rate of *D. bugensis* was 9.5×10^3 L·m^{-2}·d^{-1} based on a mean density of 8.1×10^4 ind·m^{-2} and an average biomass of 2.7×10^2 g·m^{-2} (Table 17). The potential clearance rate of *D. polymorpha* was only 2.3×10^2 L·m^{-2}·d^{-1} due to a density of only 2.9×10^2 ind·m^{-2} and a mean biomass of 5.5 g·m^{-2}. Total potential clearance rate of the dreissenid population in May 1994 was 9.7×10^3 L·m^{-2}·d^{-1}. The decline in spring dreissenid density in

addition to a 55% decrease in seasonal veliger density suggests that the seasonal dreissenid population was much lower in 1994 than in 1993. Therefore, the filtering impact on the phytoplankton community was likely not only less in the spring, but, throughout the seasonal as well. The potential for *Dreissena* to reduce phytoplankton production is much greater at the nearshore stations where mixing provides the mussels with access to the entire water column throughout the year. Seasonal mean Chl and PP increased somewhat at E3 in 1994 relative to 1993, reflecting a decreased impact of filtration by *Dreissena*. However, comparisons of annual PP to predicted values indicate that *Dreissena* were still having an impact on the phytoplankton community.

At station E3 in 1994, PP was predicted at 121 g $C \cdot m^{-2}$ based on the mean TP concentration. The observed PP (61 g $C \cdot m^{-2}$) was only half that predicted by TP, but similar to the value predicted by Chl (71 g $C \cdot m^{-2}$). This indicated that Chl was probably much lower than that predicted by the TP concentration. A similar situation was noted in 1993. In both years, the observed PP was nearly identical to that predicted by Chl, but an average of 39% lower than that predicted by TP. Chl was also 45% lower, in both years, than that predicted by TP and TN and the equation of Smith (1982) (Table 18). The low standing crop compared to the potential set by TP, resulted in a lowered PP. At E3, seasonal clearance rates for *Dreissena* in 1993 were even higher (25%) than at E2 and resulted in a reduced standing crop at E3.

At station E1, phytoplankton photosynthesis experiments were conducted only in 1994. The results obtained for this station were much more dramatic in comparison to the observed vs. predicted PP for the other stations. The observed seasonal PP was only 41 g $C \cdot m^{-2}$ compared to a value of 136 g $C \cdot m^{-2}$ predicted from TP. Based on Chl, predicted PP was 82 g $C \cdot m^{-2}$. Although the predicted PP based on Chl was higher than observed, it was still below the value predicted by TP. Therefore, Chl was likely lower than the potential set by TP, due to filtration by *Dreissena* but in addition, PP was below the potential set by Chl. The additional effect of lower transparency due to the absorbance of light by non-algal particles and not higher standing crop, resulted in a shallower Z_{eu} and increased competition for the available light. Simulations of increased transparency at E1 were performed by substituting seasonal transparency data from E3 into the E1 data set. Results showed that with other variables kept constant, if E1 were as transparent as E3, seasonal photosynthesis would increase by 25%.

Changes in the zooplankton community at the nearshore stations from 1993 to 1994 may have been due to alterations in their food supply, but were likely also due to changes in planktivory. The decline in age-1 smelt decreased predation pressure on *Daphnia*. This was indicated by the increase in biomass and mean length of *Daphnia* at stations E1 and E3 from 1993 to 1994. We expected that *Bythotrephes* biomass would also increase nearshore as it did offshore in response to the decline in age-1 smelt; instead, their biomass decreased. *Bythotrephes* are extremely vulnerable to predation in shallow water where there is deeper light penetration, due to their large size and large, dark eye spot. Therefore, few predators are required to control the *Bythotrephes* population. In contrast *Leptodora,* are quite transparent and are able to compete with *Bythotrephes* in shallow water due to their ability to elude predation. In the nearshore, *Leptodora* biomass did not decrease as it did in the offshore. The reduction in *Bosmina* biomass

at both nearshore stations was most likely a result of predation by both of these invertebrates rather than just *Bythotrephes* which was the case at station E2.

The decline in calanoids, primarily *Epischura lacustris* at both stations, in addition to *Eurytemora affinis* at E3 may have been due to the increase in the population of age-0 smelt. *Epischura lacustris* biomass was reduced by 68% at E1 and by 62% at E3 in 1994. The mean size of *E. lacustris* increased at both stations in 1994 suggesting that the age-0 smelt were selecting the smaller individuals. The reductions in *E. lacustris* density were of the same magnitude as that at station E2 (60%) suggesting a similar response to predator pressures. *Eurytemora affinis* biomass was lower at both stations in 1994, 87% lower at E3 and absent at station E3.

SEASONAL CLEARANCE RATE ESTIMATES - EASTERN VS. WESTERN BASINS

In the eastern basin in 1993, the total potential clearance rate was determined by using estimates at E3 to represent the nearshore (0-15 m), and estimates at E2 to represent the offshore (>15 m). The densities of *Dreissena polymorpha* and *D. bugensis* at E3 (9 m depth) was assumed to be representative of the densities throughout the 0-15 m range based on substrate type. This assumption was supported by the comparison of mussel density at E3 (5,823 ind·m^{-2} from Dahl et al. 1995) to two 13 m stations located along the NE and SE shores of the eastern basin (3780 and 6458 ind·m^{-2}, Dermott et al. 1996, submitted), in June of 1993. Rocky substrate extends to approximately 10 m, with a transitional zone of gravel to sand from 10-15 m (Thomas et al. 1976, Fig. 2; R. Dermott, Dept. of Fisheries and Oceans, Burlington, pers. comm.) and is assumed to support similar densities and proportions of *Dreissena*. The seasonal estimate of clearance rate at E3 was 1.3x10^4 L·m^{-2}·d^{-1} (Table 17). Extrapolating the clearance rate over the area of the basin in the 0-15 m depth range (1.8x10^9 m^2 based on GIS calculations) gives a nearshore estimate of 2.4x10^{13} L·d^{-1}. Substrate at >15 m is primarily mud (Thomas et al. 1976, Fig. 2), and is assumed to support fairly consistent *D. bugensis* densities throughout the offshore region of the basin. Clearance rates at E2 were, then assumed to be representative of those in the offshore region of the eastern basin. Seasonal clearance rate at E2 was estimated at 9.6x10^3 L·m^{-2}·d^{-1} (Table 17). Extrapolating the clearance rate over the area of the basin in the >15 m depth range (4.2x10^9 m^2 based on GIS calculations) gives an offshore estimate of 4.0x10^{13} L·d^{-1}. The sum of the clearance rates from the nearshore and offshore regions was 6.4x10^{13} L·d^{-1}, and represents the basin-wide potential filtration impact of the dreissenid population during spring and fall isothermy. During summer stratification, the impact of dreissenid filtration on the pelagia will be lower due to a limited effect in the offshore because of stratification and reduced access to pelagic material.

The total volume of the eastern basin was estimated at 1.50x10^{14} L using a mean depth of 24.7 m (based on GIS calculations). Based on clearance rate calculations, it is possible that 43% of the water column could be filtered per day during isothermal conditions, but will undoubtedly be lower during stratified conditions. Additionally, refiltration of water directly above *Dreissena* beds may reduce their total filtration impact.

In the western basin, potential seasonal clearance rates at stations W1 and W3 differed 10-fold, due to a large difference in mussel density (Table 17). These stations were not located on reefs (areas of most suitable substrate for *Dreissena polymorpha*), hence, maximum densities in the basin are not represented. Average mussel densities on three reefs in the fall of 1993 were 3.0×10^5 ind·m^{-2} (MNR 1995), 81% higher than maximum fall densities attained at W3. In the western basin, an estimated 15% of the substrate is rocky (Hartman 1973) and therefore, most suitable for colonization by zebra mussels. We assume that clearance rates at W1 and W3 represent the range in dreissenid filtration in the remaining 85% of the basin. Extrapolating the potential clearance rate at W1 (2.5×10^3 L·m-2·d^{-1}) over 85% of the basin area (3.1×10^9 m^{-2}, determined from GIS) gives a potential of 7.7×10^{12} L·d^{-1}. The potential clearance rate (2.6×10^4 L·m^{-2}·d^{-1}) at W3, extrapolated over 85% of the basin area gives an estimate of 7.9×10^{13} L·d^{-1}.

Comparisons of the size frequency of *D. polymorpha* from reef samples (J. Leach, MNR, Wheatley, pers. comm.) and at W3 in the fall of 1993, indicated that the proportion of mussels <5 mm and between 10-15 mm were similar, however, there were 4x more individuals in the 5-10 mm size class at W3 and 10x more individuals in the >15 mm size class from the reef. The relationship between clearance rate and size is exponential, therefore, an increase in the number of large individuals will have a greater effect on total clearance rate than an increase in the smaller size classes, hence the mean clearance rate of the reef population will be greater than that at W3. The mean clearance rate at W3 was 0.81 L·ind·m^{-2}·d^{-1} and is used here as a conservative estimate of the clearance rate on the reefs. The reef population clearance rate based on fall densities using clearance rates at W3, was 2.4×10^5 L·m^{-2}·d^{-1}. We used this estimate to represent the potential clearance rate over 15% of the western basin, giving an estimate of 1.3×10^{14} L cleared per day. Therefore, the range of potential clearance rates of the western basin dreissenid population was determined by summing clearance rates at W1 and at the reefs to give 1.4×10^{14} L·d^{-1} and by summing rates at W3 and at the reefs to give 2.1×10^{14} L·d^{-1}. These calculations indicated that the reef population of *Dreissena* was responsible for 50-90% of the basin-wide filtering impact, although they inhabited only 15% of the total basin area. This resulted in high localized filtering impacts with limited basin-wide effects. The total volume of the western basin was estimated at 2.7×10^{13} L using a mean depth of 7.5 m (based on GIS calculations) suggesting that the entire water column could be filtered between 5.2 and 7.8x per day. This estimate falls within the range of 3.5 to 18.8x suggested by McIsaac et al. (1992).

The nearshore of the eastern basin supports both *Dreissena polymorpha* and *D. bugensis*, on coarse substrate and mud. At our western basin stations in 1993, 99% of the mussels were *D. polymorpha* (Dahl et al. 1995) which are limited to coarse substrate. *D. polymorpha* grow in druses which have a 20-30% lower filtering efficiency than individual mussels (D. Culver, Ohio State, pers. comm.). Therefore, clearance rates may be up to 30% lower than that predicted.

THE PELAGIC-BENTHIC LINK

The establishment of *Dreissena* in the eastern basin of Lake Erie, has altered trophic interactions of the ecosystem. *Dreissena* are efficient and effective consumers of pelagic production, especially in shallow, nearshore areas where they have access to the entire water column. These mussels act as a link between pelagic production and the benthos, actively rerouting nutrients and energy to the sediments. The impact of the dreissenid filtering activities is evident by the reduction in Chl to levels below the potential set by TP, and subsequent reduction in seasonal phytoplankton photosynthesis.

Dahl et al. (1995) concluded that in 1993, pelagic production was redirected to the benthos and resulted in the large biomass of *Dreissena*. This redirection likely occurred in 1994 as well. Zooplankton can have a significant effect on phytoplankton standing crop (Wu and Culver 1992), however, the presence of pelagic grazers did not appear to have as important an effect on phytoplankton in the eastern basin, as the dreissenids. Mazumder (1994) categorizes a system as odd-linked, whereby grazers are controlled by planktivores, if the following criteria are met: 1) large *Daphnia* are absent or less than 5 ind·L, 2) cladoceran mean length is <0.5 mm, or 3) planktivore biomass is >20 kg·ha^{-1}. A system is considered "even-linked", where grazers are not controlled by planktivores, if the criteria for an odd-linked system are not met. In 1993, *Daphnia* were present at very low densities, resulting in an odd-linked system, according to the classification of Mazumder (1994). Using summer TP and the equation for an odd-linked system (Chl=1.38+0.35*TP), mean Chl at the nearshore stations was predicted at 60-79% higher than that observed. In 1994, *Daphnia* were present at the nearshore stations, however, their density and mean size did not meet the criteria for an even-linked system, thus we applied the odd-linked equation to predict Chl as in 1993. The lower than expected Chl in both years suggests that *Dreissena*, rather than *Daphnia*, were acting as a dominant grazer, and the nearshore was functioning as an even-linked system. Recalculating predicted Chl based on TP using the even-linked equation of Mazumder (1994), more accurately estimates Chl at the nearshore stations in 1993 (Table 18). In even-linked systems Chl is regulated by grazers, hence Chl does not show a strong positive response to increasing TP. The lower slope of the Chl-TP relationship should result in a significantly lower Chl:TP ratio in even-linked systems (Mazumder 1994). Comparison of all stations in 1993 and 1994 show that the ratios at E1 and E3 actually were much lower, suggesting a greater *Dreissena* effect than at the other stations (Table 18). The higher yet similar ratios at stations other than E1 and E3 indicate less of an impact by *Dreissena*, but for varying physical and biological reasons. To summarize, the impact of *Dreissena*, offshore in the eastern basin was limited by thermal stratification. In the west central basin, low mussel densities and thermal stratification limited the *Dreissena*'s impact. In the western basin, high algal standing crop, nutrients and warmer water, likely resulted in rapid turnover of phytoplankton that were able to compensate for grazing losses.

Our findings at the nearshore stations indicate that *Dreissena* are efficient grazers, who's presence resulted in an even-linked system. We assumed this to be the case in the offshore and applied the even-linked equation to predict Chl. However, the observed Chl was higher than that predicted by this equation (Table 18). The equation calculating Chl assumes the grazing effect

occurs throughout the stratified period, which would be the case for most zooplankton, but is not so for *Dreissena*-zooplankton systems. Given that *Dreissena* were the dominant grazers in 1993, their effect was limited to the periods when the water column was available to the benthic consumers. The offshore in 1993 and 1994 likely behaved as an even-linked system during isothermal conditions (maximum grazing impact of dreissenids) and as an odd-linked system during stratification (limited grazing impact of dreissenids and cladocerans).

CONCLUSIONS

This study suggests that *Dreissena* had a tremendous impact on seasonal photosynthesis at nearshore stations in the eastern basin. Seasonal PP was on average 52% lower than that predicted by TP. The low Chl:TP ratio was also evidence of the grazing effect of *Dreissena*. The reductions and alterations in the nearshore zooplankton community may have been due to this reduction in food, but are more likely a result of the change in predation by planktivores. In the offshore, *Dreissena* had access to the entire water column only during spring and fall isothermy, thereby limiting their impact on seasonal PP. Seasonal photosynthesis was close to that predicted by TP (differed by only 27%), and the Chl:TP ratio was higher than that nearshore. These observations reflected less of a grazing effect by *Dreissena* in the offshore. Changes in zooplankton biomass and community composition were evident, but due to the limited impact of *Dreissena*, these changes were most likely due to alterations in predation pressures.

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Table 1a. Physical parameters for LEB 1994, station E1. Mixing depths (Z_m), sampling depths, and euphotic depths (Z_{eu} = 1% light penetration) and Secchi are all in meters.

Date	Z_m[1]	Sample Depth	Z_{eu}	ε_{par}	Secchi
94-05-10	5.9	0 - 4	5.0	0.235	5.9
94-05-18	5.9	0 - 4	5.9	0.321	4.5
94-06-01	5.9	0 - 4	5.3	0.268	4.0
94-06-16	5.9	0 - 4	5.9	0.386	2.8
94-06-21	5.9	0 - 4			3.5
94-06-28	5.9	0 - 4	5.9	0.465	2.5
94-07-05	5.9	0 - 4			4.0
94-07-13	5.9	0 - 4	0.8	5.716[2]	0.3
94-07-19	5.9	0 - 4	5.5	0.412	4.8
94-07-27	5.9	0 - 4 .	4.6	0.443	2.0
94-08-02	5.9	0 - 4			1.5
94-08-09	5.9	0 - 4	5.9	0.344	4.0
94-08-16	5.9	0 - 4			2.5
94-08-23	5.9	0 - 4	5.9	0.398	5.0
94-08-30	5.9	0 - 4			4.5
94-09-07	5.9	0 - 4	5.9	0.344	4.0
94-09-13	5.9	0 - 4			3.0
94-09-22	5.9	0 - 4	5.9	0.267	3.5
94-10-05	5.9	0 - 4	5.9	0.200	5.9
94-10-18	5.9	0 - 4	5.4	0.353	5.9
94-11-08	5.9	0 - 4	5.6	0.623	2.3
SM[*]	5.9		5.4	0.365	3.8

[1]Zm= mean station depth
[2]outlier, not included in mean
[*]seasonal mean

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Table 1b. Physical parameters for LEB 1994, station E2. Mixing depths (Z_m), sampling depths, and euphotic depths (Z_{eu} = 1% light penetration) and Secchi are all in metres.

Date	Z_m	Sample Depth	Z_{eu}	ε_{par}	Secchi
94-05-10	38.0	0 - 23	27.8	0.166	7.5
94-05-18	38.0	0 - 36	21.1	0.218	8.5
94-06-01	38.0	0 - 36	20.6	0.224	5.5
94-06-16	14.0	0 - 13	20.0	0.230	4.5
94-06-21	4.1	0 - 6			4.8
94-06-28	11.5	0 - 13	26.4	0.174	5.5
94-07-05	12.5	0 - 13			5.5
94-07-13	9.5	0 - 10	21.6	0.213	8.5
94-07-19	15.5	0 - 16	20.7	0.223	7.5
94-07-27	14.5	0 - 16	22.7	0.203	7.0
94-08-02	12.0	0 - 12			4.0
94-08-09	13.5	0 - 14	8.1	0.571	3.8
94-08-16	12.0	0 - 12			
94-08-23	17.5	0 - 18	19.8	0.233	5.5
94-08-30	15.5	0 - 16			5.8
94-09-07	17.5	0 - 17	14.0	0.330	5.5
94-09-13	14.5	0 - 14			5.5
94-09-22	21.5	0 - 22	22.1	0.208	4.5
94-10-05	19.0	0 - 19.5	17.2	0.268	4.8
94-10-18	29.5	0 - 30	21.6	0.214	4.5
94-11-08	38.0	0 - 36	23.1	0.199	5.8
SM[*]	21.1		19.9	0.252	4.8

[*]seasonal mean

Table 1c. Physical parameters for LEB 1994, station E3. Mixing depths (Z_m), sampling depths, and euphotic depths (Z_{eu} = 1% light penetration) and Secchi are all in metres.

Date	Z_m	Sample Depth	Z_{eu}	ε_{par}	Secchi
94-05-10	9.2	0 - 8	9.2	0.169	9.2
94-05-18	9.2	0 - 7	9.2	0.218	9.2
94-06-01	9.2	0 - 7	9.2	0.488	9.2
94-06-16	7.0	0 - 7	9.2	0.222	7.5
94-06-21	3.0	0 - 8			4.0
94-06-28	9.2	0 - 7	9.2	0.177	4.5
94-07-05	9.2	0 - 7			3.5
94-07-13	5.0	0 - 5	9.2	0.208	9.2
94-07-19	7.1	0 - 7.5	9.2	0.248	5.5
94-07-27	4.0	0 - 8	9.2	0.176	4.0
94-08-02	6.5	0 - 8			5.0
94-08-09	9.2	0 - 7	9.2	0.332	4.5
94-08-16	5.5	0 - 6			
94-08-23	9.2	0 - 7.5	9.2	0.316	3.0
94-08-30	9.2	0 - 7.5			
94-09-07	9.2	0 - 7.5	9.2	0.189	4.5
94-09-13	9.2	0 - 7			4.3
94-09-22	9.2	0 - 7	9.2	0.212	4.8
94-10-05	9.2	0 - 7	9.2	0.283	7.5
94-10-18	9.2	0 - 7	9.2	0.186	3.8
94-11-08	9.2	0 - 7.5	9.2	0.305	5.8
SM[*]	8.2		9.3	0.254	5.7

[*]seasonal mean

Table 2a. Nutrient and major ion data for station E1, including phosphorus (total phosphorus, TP $\mu g \cdot L^{-1}$; total filtered phosphorus, TP-filt $\mu g \cdot L^{-1}$; soluble reactive phosphorus, SRP $\mu g \cdot L^{-1}$), total nitrogen (TN $\mu g \cdot L^{-1}$), NO_3-NO_2 and NH_3 ($\mu g \cdot L^{-1}$), SiO_2 ($mg \cdot L^{-1}$), dissolved inorganic carbon (DIC $mg \cdot L^{-1}$), dissolved organic carbon (DOC $mg \cdot L^{-1}$) and Cl ($mg \cdot L^{-1}$).

Date	TP	TP-filt	SRP	TN	NO_3-NO_2	NH_3	N:P	SiO_2	DIC	DOC	Cl
94-05-10	8.1	4.3	0.6	474	261	10	58.52	0.18	20.9	2.5	15.5
94-05-18	10.9	9.8	2.5	496	247	21	45.50	0.19	20.0	2.4	15.4
94-06-01	7.7	5.3	0.9	545	190	13	70.78	0.18	20.1	3.5	15.8
94-06-16	12.3	7.7	2.3	385	186	11	31.30	0.15	19.6	2.9	15.3
94-06-28	10.0	6.6	2.2	471	186	13	47.10	0.23	19.8	3.0	14.8
94-07-13	8.0	5.4	0.3	469	173	24	58.63	0.15	19.7	2.8	15.3
94-07-27	9.7	4.7	0.4	470	168	41	48.45	0.22	19.3	3.3	15.4
94-08-09	6.1	4.2	1.4	720	139	137	118.03	0.36	19.0	3.2	15.4
94-08-23	8.2	3.7	2.2	537	149	108	65.49	0.45	19.8	6.1	15.7
94-09-07	23.0	14.3	7.4	522	145	8	22.70	0.65	21.0	3.6	15.6
94-09-22	9.3	3.8	0.6	506	130	39	54.41	0.77	21.2	4.6	15.2
94-10-05	5.6	3.8	0.7	476	255	45	85.00	0.88	21.2	1.9	15.1
94-10-18	7.6	5.2	1.7	404	170	10	53.16	0.39	21.8	2.9	15.7
94-11-08	14.7	6.4	3.2	568	227	27	38.64	0.89	21.9	2.8	15.3
SM[*]	10.1 [**](9.9)	6.2 (5.3)	2.0 (1.5)	502	181	37		0.41	20.4	3.3	15.4

[*]seasonal mean
[**]bracketed values are seasonal means without outlier values observed on Septmeber 7.

Table 2b. Nutrient and major ion data for station E2, including phosphorus (total phosphorus, TP $\mu g \cdot L^{-1}$; total filtered phosphorus, TP-filt $\mu g \cdot L^{-1}$; soluble reactive phosphorus, SRP $\mu g \cdot L^{-1}$), total nitrogen (TN $\mu g \cdot L^{-1}$), NO_3-NO_2 and NH_3 ($\mu g \cdot L^{-1}$), SiO_2 ($mg \cdot L^{-1}$), dissolved inorganic carbon (DIC $mg \cdot L^{-1}$), dissolved organic carbon (DOC $mg \cdot L^{-1}$) and Cl ($mg \cdot L^{-1}$).

Date	TP	TP-filt	SRP	TN	NO_3-NO_2	NH_3	N:P	SiO_2	DIC	DOC	Cl
94-05-10	10.6	3.8	0.6	444	252	7	41.89	0.22	20.2	2.5	14.9
94-05-18	10.3	9.0	2.2	384	236	11	37.28	0.17	19.8	2.7	15.1
94-06-01	7.2	6.6	1.2	539	234	12	74.86	0.16	20.2	3.1	16.0
94-06-16	8.6	8.1	0.5	430	194	33	50.00	0.04	19.8	2.8	15.2
94-06-28		4.0	0.6	603	238	28		0.17	19.9	3.1	15.5
94-07-13	10.6	3.6		529	178	9	49.91	0.19	19.0	4.4	15.3
94-07-27	7.3	4.0	0.6	1067	693	109	146.16	0.14	19.2	3.6	15.4
94-08-09	6.1	4.6	1.5	736	132	116	120.66	0.23	19.0	3.3	15.3
94-08-23	6.6	3.7		403	138	4	61.06	0.19	20.4	5.4	15.1
94-09-07	7.9	3.8	1.0	709	150	199	89.75	0.22	20.6	3.6	14.9
94-09-22	6.2	4.2	0.2	424	145	22	68.39	0.37	21.1	2.4	15.0
94-10-05	8.4	4.8		441	174	68	52.50	0.33	20.5	2.2	14.9
94-10-18	7.7	4.9	2.4	550	188	15	71.43	0.47	21.9	2.8	15.1
94-11-08			2.9	502	221	38		0.74	21.6	2.8	15.0
SM*	8.1	5.0	1.2	552	223	51		0.26	20.2	3.3	15.2

*seasonal mean

Table 2c. Nutrient and major ion data for station E3, including phosphorus (total phosphorus, TP µg·L^{-1}; total filtered phosphorus, TP-filt µg·L^{-1}; soluble reactive phosphorus, SRP µg·L^{-1}), total nitrogen (TN µg·L^{-1}), NO_3-NO_2 and NH_3 (µg·L^{-1}), SiO_2 (mg·L^{-1}), dissolved inorganic carbon (DIC mg·L^{-1}), dissolved organic carbon (DOC mg·L^{-1}) and Cl (mg·L^{-1}).

Date	TP	TP-filt	SRP	TN	NO_3-NO_2	NH_3	N:P	SiO_2	DIC	DOC	Cl
94-05-10	8.9	3.5	0.7	447	262	9	50.22	0.12	20.3	2.5	15.2
94-05-18	21.5	6.8	4.7	480	244	16	22.33	0.23	20.0	2.7	15.1
94-06-01	6.4	5.0	0.8	667	222	16	104.22	0.20	20.5	3.1	16.1
94-06-16	10.3	6.8	0.3	392	189	19	38.06	0.20	19.6	2.7	15.1
94-06-28	6.6	4.7	0.6	390	162	4	59.09	0.21	19.9	3.1	14.9
94-07-13	8.4	5.2	0.6	438	143	24	52.14	0.22	18.8	2.7	15.2
94-07-27	9.5	4.1	0.4	407	142	18	42.84	0.14	19.2	2.9	15.3
94-08-09	7.1	4.0	1.4	519	108	35	73.10	0.34	19.0	3.1	15.3
94-08-23	6.8	5.6	1.0	432	132	15	63.53	0.44	19.7	3.7	15.4
94-09-07	9.8	3.7	0.9	570	150	118	58.16	0.59	21.0	4.3	15.6
94-09-22	5.2	3.7	0.2	345	145	22	66.35	0.53	21.1	2.4	15.0
94-10-05	5.4	3.8	0.9	452	216	20	83.70	0.81	20.9	2.4	15.0
94-10-18	6.4	4.6	1.2	510	202	35	79.69	0.62	21.8	2.8	15.4
94-11-08			3.6	458	128	28		0.69	22.0	3.2	14.9
SM*	8.5 **(7.6)	4.8	1.2 (0.9)	480	170	29		0.40	20.3	3.0	15.3

*seasonal mean
**bracketed values are seasonal means without outlier values observed on May 18.

Table 3. Comparison between 1993 and 1994 for selected water quality and photosynthesis parameters at eastern basin stations. All values shown are seasonal means for the entire sampling season in each year, weighted for variable times between sampling dates. Significant differences between years were determined with a non-parametric Mann-Whitney test due to unequal variances or non-normality, and are indicated at $\alpha=0.05$ (*).

Parameter	E1		E2		E3	
	1993	1994	1993	1994	1993	1994
Chl ($\mu g \cdot L^{-1}$)	1.06	1.54*	2.11	2.24	1.12	1.27
TP ($\mu g \cdot L^{-1}$)	7.80	10.10	8.50	8.10	6.60	8.50
SRP ($\mu g \cdot L^{-1}$)	0.80	2.00*	1.50	1.20	0.90	1.20
SiO_2 ($mg \cdot L^{-1}$)	0.34	0.41	0.28	0.26	0.25	0.40
POC ($mg \cdot L^{-1}$)	0.13	0.20*	0.19	0.24*	0.13	0.18
PON ($mg \cdot L^{-1}$)	0.02	0.03*	0.03	0.04	0.02	0.03
ε_{par} (m^{-1})	0.32	0.37	0.23	0.25	0.25	0.25
P_{opt} ($mg\ C \cdot m^{-3} \cdot h^{-1}$)	na[+]	6.66	6.92	7.14	4.55	5.59
Areal PP ($g\ C \cdot m^{-2}$)	na	41.20	105.30	85.80	53.80	61.20

[+]not available

Table 4a. Indices of phytoplankton biomass for LEB 1994, station E1. Chlorophyll ($\mu g \cdot L^{-1}$) values are uncorrected (Chl_{un}) and corrected (Chl_{cor}) for phaeopigments. Particulate organic carbon (POC), particulate organic nitrogen (PON), ash-free dry weight (AFDW), and ash weight (Ash) are in $mg \cdot L^{-1}$.

Date	Chl_{un}	Chl_{cor}	POC	PON	AFDW	Ash	% Ash
94-05-10	1.22	1.11	0.111	0.020	0.451	0.651	59.08
94-05-18	1.03	0.91	0.109	0.020	0.320	0.403	55.76
94-06-01	1.09	1.03	0.189	0.028	0.468	0.659	58.46
94-06-16	0.64	0.48	0.167	0.020	0.509	0.958	65.29
94-06-28	1.03	0.87	0.176	0.033	0.404	1.519	78.99
94-07-13	1.54	1.50	0.123	0.018	0.593	0.192	24.45
94-07-19	2.15	1.87					
94-07-27	1.94	1.73	0.218	0.042	0.590	1.273	68.34
94-08-09	1.27	0.75	0.198	0.037	0.517	0.056	9.80
94-08-23	1.75	1.45	0.232	0.038	0.555	0.907	62.03
94-09-07	1.62	1.50	0.287	0.040	0.597	0.855	58.88
94-09-22	2.64	2.52	0.445	0.060	1.237	1.335	51.89
94-10-05	1.60	1.47	0.217	0.025	0.448	0.503	52.91
94-10-18	2.39	2.28	0.141	0.023	0.421	0.417	49.80
94-11-08	0.91	0.59	0.250	0.036	0.678	6.696	90.81
SM*	1.54	1.36	0.199	0.030	0.562	1.069	55.24

*seasonal mean

Table 4b. Indices of phytoplankton biomass for LEB 1994, station E2. Chlorophyll ($\mu g \cdot L^{-1}$) values are uncorrected (Chl_{un}) and corrected (Chl_{cor}) for phaeopigments. Particulate organic carbon (POC), particulate organic nitrogen (PON), ash-free dry weight (AFDW), and ash weight (Ash) are in $mg \cdot L^{-1}$.

Date	Chl_{un}	Chl_{cor}	POC	PON	AFDW	Ash	% Ash
94-05-10	3.03	2.57	0.207	0.031	0.551	0.466	45.84
94-05-18	1.80	1.45	0.117	0.019	0.368	0.753	67.16
94-06-01	1.14	0.98	0.164	0.022	0.421	0.171	28.94
94-06-16	2.28	2.05	0.287	0.038	0.855	0.263	23.55
94-06-28	1.22	0.95	0.274	0.065	0.507	0.190	27.27
94-07-13	2.13	1.85	0.312	0.049	0.915	1.649	64.33
94-07-19	2.61	2.11					
94-07-27	2.20	1.85	0.261	0.037	0.585	0.203	25.78
94-08-09	3.40	2.83	0.324	0.056	0.831	0.267	24.32
94-08-23	2.98	2.73	0.338	0.044	0.614	0.207	25.24
94-09-07	2.31	2.00	0.256	0.033	0.609	0.289	32.22
94-09-22	2.35	2.12	0.257	0.035	0.603	0.341	36.16
94-10-05	2.78	2.66	0.297	0.038	0.609	0.712	53.91
94-10-18	2.16	1.65	0.214	0.033	0.581	0.571	49.60
94-11-08	1.71	1.49	0.120	0.021	0.430	0.803	65.14
SM*	2.24	1.92	0.240	0.036	0.615	0.486	39.67

*seasonal mean

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Table 4c. Indices of phytoplankton biomass for LEB 1994, station E3. Chlorophyll ($\mu g \cdot L^{-1}$) values are uncorrected (Chl_{un}) and corrected (Chl_{cor}) for phaeopigments. Particulate organic carbon (POC), particulate organic nitrogen (PON), ash-free dry weight (AFDW), and ash weight (Ash) are in $mg \cdot L^{-1}$.

Date	Chl_{un}	Chl_{cor}	POC	PON	AFDW	Ash	% Ash
94-05-10	0.43	0.38	0.086	0.011	0.260	0.369	58.67
94-05-18	0.62	0.55	0.070	0.012	0.283		
94-06-01	0.49	0.41	0.102	0.011	0.273	0.205	42.90
94-06-16	0.95	0.77	0.143	0.017	0.473	0.151	24.17
94-06-28	0.80	0.57	0.105	0.012	0.409	0.472	53.56
94-07-13	0.75	0.52	0.185	0.031	0.360	0.379	51.26
94-07-19	1.74	1.39					
94-07-27	2.00	1.69	0.257	0.036	0.583	0.417	41.67
94-08-09	1.57	1.40	0.307	0.049	0.768	0.316	29.15
94-08-23	2.82	2.53	0.386	0.051	0.985	0.559	36.21
94-09-07	1.64	1.60	0.230	0.036	0.547	1.166	68.08
94-09-22	1.59	1.47	0.208	0.032	0.601	0.351	36.84
94-10-05	1.18	1.05	0.244	0.029	0.463	0.498	51.84
94-10-18	1.22	0.91	0.135	0.024	0.191	0.229	54.52
94-11-08	0.49	0.40	0.070	0.012	0.283	0.981	77.63
SM*	1.27	1.09	0.177	0.025	0.476	0.435	47.61

*seasonal mean

Table 5. Comparison of the seasonal mean (SM) biomass ($g \cdot m^3$) for each major taxonomic group of phytoplankton at the offshore station in Lake Erie during 1993 and 1994, and the percent contribution of each group to the total phytoplankton biomass. Means for 1994 are presented for the period from May 10 to October 5 to correspond to the sampling period in 1993. Significant increases in the seasonal mean biomass of a taxonomic group in 1994 are denoted as $p<0.05$ (*) and $p<0.01$(**).

Taxonomic Group	1993		1994	
	Mean Biomass	% of Total Biomass	Mean Biomass	% of Total Biomass
Bacillariophyceae	0.105	29.9	0.130	16.5
Chrysophyceae	0.066	18.8	0.136*	18.1
Dinophyceae	0.033	9.4	0.296*	37.5
Chlorophyta	0.076	21.7	0.069	8.7
Cryptophyta	0.062	17.7	0.143*	18.1
Cyanophyta	0.008	2.3	0.012	1.5
Euglenophyta	0.001	0.3	0.003	0.4
Total Mean Biomass	0.351		0.789**	

Table 6. Comparison of all phytoplankton species and genera observed at the offshore station (E2) in the eastern basin of Lake Erie in 1993 and 1994. Species are indicated as contributing < 0.5% (o), ≥ 0.5% (+), ≥ 5% (++), and ≥ 10% (+++) of the total phytoplankton biomass at some time during the sampling season (May - Nov.)

Taxon	1993	1994
Chrysophyta		
Bacillariophyceae		
Achnanthes deflexa	+	
A. minutissima		o
Asterionella formosa	+	o
Coscinodiscus denaris	+	
Cyclotella ocellata	+++	++
C. kutzingiana	+++	++
C. sp.	o	
Cymbella minuta		o
Diatoma elongatum	++	+++
D. elongatum minor	+	
Fragilaria crotonensis	++	+++
F. sp.	o	
Gomphonema gracilis lanceolata		o
Melosira binderiana	o	+++
M. islandica	+++	+++
M. italica	o	
Nitzschia acicularis	+++	
N. amphibia		o
Rhizosolenia sp.	+	
Stephanodiscus astraea	+	
S. hantzschii	+	+
S. niagarae	+	
Surirella ovata	o	
Synedra actnastroides	o	++
S. acus	++	+
Chrysophyceae		
Bitrichia chodati	o	o
Chromulina sp.	+	+
Chrysochromulina parva	+++	++
Chrysolykos sp.	+	o
Chrysophyte statospore	o	

Table 6. Continued

Taxon	1993	1994
Chrysophyceae continued		
Chrysosphaerella rodhei	+++	
Chrysostephanosphaera sp.	+	o
Dinobryon crenulatum	+	
D. divergens	+	o
D. sertularia		+++
D. sertularia protuberans	o	
D. sertularia statospore		+
D. sociale	+++	
Kephyrion sp.	+	+
Mallamonas producta		o
M. sp.	+	o
Ochromonas sp.	+++	+++
Pseudokephyrion sp.	+	
Stelexmonas dichotoma	+	o
Cryptophyta		
Cryptomonas curvata	+	+
C. erosa	o	+
C. ovata	+	+
C. reflexa	+	+
Katablepharis ovalis	++	+
Rhodomonas lens	+++	+++
R. minuta	+++	+++
Pyrrophyta		
Dinophyceae		
Ceratium hirundinella		++
Glenodinium sp.	+	o
Gymnodinium helveticum	+++	
G. sp.	+	+++
G. uberrimum	+	+++
Peridinium aciculiferum	+++	+++
P. sp.		+++
Pyrrophyte cyst	+++	+++
Chlorophyta		
Ankistrodesmus convolutus	o	

Table 6. Continued

Taxon	1993	1994
Chlorophyta continued		
A. falcatus	o	
Carteria sp.	o	
Chlamydomonas dinobryonis	o	
C. sp.	+	+
Chodatella subsalsa	o	
Coelastrum cambricum	+	
C. microporum	+	o
C. reticulatum		o
Cosmarium sp.	o	o
Crucigenia irregularis	o	
C. rectangularis	+	
C. tetrapedia	+	
Dictyosphaerium pulchellum	+	
Dimorphococcus lunatus		o
Elakatothrix gelatinosa	o	o
Franceia ovalis	o	+
Kirchneriella microscopia	o	
K. lunaris	o	o
Lagerheimia quadriseta		o
Micractinium pusillum	+	
Microthamnion sp.		+
Mougeotia sp.	+	+
Nephrocytium limneticum	o	
Oocystis parvum	+	+
Pandorina morum	+	
Pediastrum boryanum	+	+
P. duplex clathratum	+	
P. tetras	o	
Scenedesmus bijuga	+	+
S. ecornis	o	+
S. incrassatulus	+	
S. quadricauda	o	
Sphaerella lacustris	+	

Table 6. Continued

Taxon	1993	1994
Chlorophyta continued		
Sphaerocystis schroeteri	+++	+++
Stelexmonas dichotoma	O	
Tetraedron arthrodesmiforme	O	
T. minimum	+++	+
T. trigonium papilliferum	+	
Euglenophyta		
Lepocinclis sp.	+	+
Cyanophyta		
Anabaena sp.	+	+++
Aphanocapsa elachista		O
A. elachista planctonica		O
Aphanothece clathrata brevis	O	
Chroococcus limneticus	+	
C. turgidus		O
Dactylococcopsis linearis	O	
Lyngbya contorta	O	
Merismopedia tenuissima	O	
M. sp.		+
Microcyctis aeruginosa	O	
Oscillatoria limnetica	+	O
Radiocystis geminata	+	+

Table 7. Common statistics for P_{opt} (mg $C \cdot m^{-3} \cdot h^{-1}$) and the determinant variables for intergral phytoplankton photosynthesis, chlorophyll (Chl $\mu g \cdot L^{-1}$), light extinction (ε_{par} m^{-1}), P^B_m (mg $C \cdot mg$ $Chl^{-1} \cdot h^{-1}$) and α^B (mg $C \cdot mg$ $Chl^{-1} \cdot E^{-1} \cdot m^{-2} \cdot h^{-1}$) . Seasonal means ($\pm 1$ SD) are for May to November for all parameters and are weighted for variable time intervals between sampling dates.

	Station	Seasonal Mean	Minimum	Maximum	n
P_{opt}					
	E1	6.66±3.18	2.04	13.21	15
	E2	7.14±4.07	2.17	19.28	15
	E3	5.59±3.87	1.27	15.34	14
P^B_m					
	E1	4.18±1.25	2.09	6.55	15
	E2	3.03±1.00	1.42	5.67	15
	E3	4.34±2.03	2.11	9.77	14
α^B					
	E1	4.10±1.86	1.95	8.06	15
	E2	3.30±1.24	1.42	5.21	15
	E3	3.69±2.86	2.00	8.23	14
Chl					
	E1	1.54±0.57	0.64	2.64	15
	E2	2.24±0.64	1.14	3.40	15
	E3	1.27±0.68	0.43	2.82	15
ε_{par}					
	E1	*0.37±0.11	0.20	0.62	14
	E2	0.25±0.10	0.17	0.57	15
	E3	0.25±0.09	0.17	0.49	14

*outlier ε_{par} value of 5.72 from July 13 not included in seasonal mean

Table 8a. Seasonal data and seasonal means (SM) for phytoplankton photosynthesis rates (P), parameters (P^B_m, α^B), and mean epilimnetic irradiance ($\bar{I}$) at station E1, 1994. P_{opt} (mg $C \cdot m^{-3} \cdot h^{-1}$) is the photosynthesis rate at optimal irradiance and is the product of P^B_m and chlorophyll. The photosynthetic parameters were derived from the photosynthesis vs. irradiance curve. P^B_m (mg $C \cdot mg\ Chl^{-1} \cdot h^{-1}$) is the maximum and α^B (mgC·mg $Chl^{-1} \cdot E^{-1}\ m^{-2}$) the slope of the light-limited part of the curve. The superscript B indicates that both parameters were normalized on chlorophyll as an index of biomass. Daily integral PP rates (ΣPP=mg $C\ m^{-2} \cdot d^{-1}$) and $\bar{I}$ (mE·m$^{-2} \cdot min^{-1}$) were both calculated with theoretical cloudless (cldlss) and empirical (emp) solar irradiance as denoted by the subscripts.

Date	ΣPP_{emp}	ΣPP_{cldlss}	P_{opt}	P^B_m	α^B	$\bar{I}_{emp}$	$\bar{I}_{cldlss}$
94-05-10	176	191	2.55	2.09	3.27	15.85	21.53
94-05-18	133	164	2.38	2.31	2.83	13.12	18.35
94-06-01	226	263	3.75	3.44	3.32	15.99	21.26
94-06-16	86	102	2.04	3.19	1.95	13.70	16.94
94-06-28	94	172	3.99	3.88	2.33	6.82	14.62
94-07-13	36	41	8.60	5.59	5.54	1.02	1.25
94-07-19	355	391	7.63	3.55	2.69	13.42	15.53
94-07-27	178	335	6.99	3.60	2.72	5.57	14.30
94-08-09	145	314	6.35	5.00	3.16	5.88	16.37
94-08-23	358	395	5.82	3.32	8.06	10.28	13.64
94-09-07	283	362	7.80	4.82	3.52	9.14	13.60
94-09-22	525	669	13.21	5.00	4.18	9.08	13.97
94-10-05	392	538	10.48	6.55	5.79	7.98	13.85
94-10-18	246	354	8.62	3.61	3.84	4.80	8.77
94-11-08	105	129	4.90	5.39	7.60	3.02	4.31
SM	229	307	6.57	4.18	4.10	8.73	13.67

Table 8b. Seasonal data and seasonal means (SM) for phytoplankton photosynthesis rates (P), parameters (P^B_m, α^B), and mean epilimnetic irradiance ($\bar{I}$) at station E2, 1994. P_{opt} (mg $C \cdot m^{-3} \cdot h^{-1}$) is the photosynthesis rate at optimal irradiance and is the product of P^B_m and chlorophyll. The photosynthetic parameters were derived from the photosynthesis vs. irradiance curve. P^B_m (mg $C \cdot mg$ $Chl^{-1} \cdot h^{-1}$) is the maximum and α^B (mgC·mg $Chl^{-1} \cdot E^{-1} \cdot m^{-2}$) the slope of the light-limited part of the curve. The superscript B indicates that both parameters were normalized on chlorophyll as an index of biomass. Daily integral PP rates (ΣPP=mg $C \cdot m^{-2} \cdot d^{-1}$) and $\bar{I}$ (mE·m$^{-2} \cdot$min^{-1}) were both calculated with theoretical cloudless (cldlss) and empirical (emp) solar irradiance as denoted by the subscripts.

Date	ΣPP_{emp}	ΣPP_{cldlss}	P_{opt}	P^B_m	α^B	$\bar{I}_{emp}$	$\bar{I}_{cldlss}$
94-05-10	839	1000	5.83	1.92	2.31	4.65	6.31
94-05-18	470	594	4.00	2.22	3.33	3.53	4.94
94-06-01	285	330	2.17	1.92	3.09	3.74	4.97
94-06-16	410	494	5.36	2.35	1.42	10.09	12.48
94-06-28	286	513	3.76	3.08	2.18	8.32	17.82
94-07-13	694	807	6.87	3.23	2.70	14.31	17.51
94-07-19	626	692	7.07	2.71	3.07	9.77	11.31
94-07-27	277	554	5.99	2.72	2.33	4.85	12.47
94-08-09	250	521	19.28	5.67	4.95	1.76	4.90
94-08-23	806	988	9.90	3.32	2.47	6.20	8.22
94-09-07	526	676	7.80	3.38	3.37	3.54	5.27
94-09-22	706	919	8.51	3.62	4.53	3.90	6.00
94-10-05	529	730	8.02	2.89	5.21	2.73	4.74
94-10-18	482	689	7.28	3.37	5.07	1.80	3.29
94-11-08	138	174	2.42	1.42	1.58	1.50	2.14
SM	472	634	7.14	3.02	3.30	5.13	7.93

Table 8c. Seasonal data and seasonal means (SM) for phytoplankton photosynthesis rates (P), parameters (P^B_m, α^B), and mean epilimnetic irradiance ($\bar{I}$) at station E3, 1994. P_{opt} (mg $C \cdot m^{-3} \cdot h^{-1}$) is the photosynthesis rate at optimal irradiance and is the product of P^B_m and chlorophyll. The photosynthetic parameters were derived from the photosynthesis vs. irradiance curve. P^B_m (mg $C \cdot mg$ $Chl^{-1} \cdot h^{-1}$) is the maximum and α^B (mgC·mg $Chl^{-1} \cdot E^{-1} \cdot m^{-2}$) the slope of the light-limited part of the curve. The superscript B indicates that both parameters were normalized on chlorophyll as an index of biomass. Daily integral PP rates ($\Sigma PP = $mg $C \cdot m^{-2} \cdot d^{-1}$) and $\bar{I}$ (mE·m$^{-2} \cdot$min^{-1}) were both calculated with theoretical cloudless (cldlss) and empirical (emp) solar irradiance as denoted by the subscripts.

Date	ΣPP_{emp}	ΣPP_{cldlss}	P_{opt}	P^B_m	α^B	$\bar{I}_{emp}$	$\bar{I}_{cldlss}$
94-05-10	112	130	1.27	2.94	2.67	14.85	20.17
94-05-18	200	267	3.76	6.06	2.97	12.61	17.67
94-06-01	78	93	1.48	3.02	3.87	7.01	9.33
94-06-16	448	532	3.12	3.28	2.00	17.41	21.53
94-06-28	287	429	3.96	4.95	4.62	9.89	21.19
94-07-19	441	477	4.78	2.76	3.44	17.58	20.34
94-07-27	452	464	5.46	2.74	2.09	11.23	28.86
94-08-09	498	1035	15.34	9.77	8.23	4.29	11.95
94-08-23	478	586	9.89	3.51	2.41	8.67	11.51
94-09-07	603	754	9.31	5.68	4.49	10.11	15.05
94-09-22	388	500	6.81	4.29	3.76	7.93	12.21
94-10-05	122	171	3.04	2.57	2.66	4.96	8.61
94-10-18	220	318	3.42	2.80	3.66	5.47	9.98
94-11-08	56	80	2.99	6.11	3.18	3.81	5.44
SM	328	440	5.59	4.34	3.69	9.42	14.90

Table 9. Seasonal (May-Oct.) volume- (g $C \cdot m^{-3}$) and areal-based (g $C \cdot m^{-2}$) phytoplankton photosynthesis (PP). PP was calculated with both empirical (emp) and theoretical cloudless (cldlss) solar irradiance . Areal PP calculated with empirical irradiance was expressed as a percentage of the cloudless values (% Cld).

Station	Volume PP		Areal PP		% Cld
	emp	cldlss	emp	cldlss	
E1	11.6	14.1	41.2	59.4	69.4
E2	13.0	15.4	85.8	126.3	67.9
E3	10.9	13.2	61.2	86.5	70.8

Table 10. Observed and predicted seasonal areal photosynthesis (PP, g C·m^{-2}) for each LEB station in 1993 and 1994. Observed PP was calculated using the programs of Fee (1990) for the standardized season from May 1 to October 31, and vertical profiles of photosynthesis are truncated by depth at shallow stations. Potential PP values were determined by allowing the model to extend the profile beyond the station depth, to the potential depth set by transparency. Seasonal PP was predicted from a) the seasonal mean TP concentration and the equation of Millard et al. (1996) refit with more current data, and b) the seasonal mean Chl concentration and the equation of Millard et al. (unpubl. data). Percent difference between each predicted value and the potential PP are also given.

Station	Observed PP empirical	Potential PP	Predicted PP based on TP	Difference ± %	Predicted PP based on Chl	Difference ± %
1993						
E2	105	-	122	14	102	3
E3	54	66	102	35	65	2
WC1	122	123	143	14	119	3
WC2	171	173	159	8	149	14
W1	151	165	189	13	160	3
W3	142	141	198	29	158	11
1994						
E1	41	50	137	64	82	39
E2	86	-	118	27	106	19
E3	61	73	122	40	71	3

Table 11. Comparison of zooplankton seasonal mean density ($\#\cdot m^{-3}$) from 1993 and 1994, where w indicates mean biomass for the whole season and c indicates mean biomass for season length comparable to 1993. Seasonal mean density for all zooplankton types except rotifers at E2, in 1994 were based on weekly samples. Rotifer estimates at E2 in 1994 and consequently, associated grand total estimates were based on biweekly samples. * indicates a significant difference (p<0.05, (2), 2df, paired t) between 1993 and 1994c seasonal mean density.

	E1			E2			E3		
	1993	1994 w	1994 c	1993	1994 w	1994 c	1993	1994 w	1994 c
Cladocera	3175	878	968	5130	2652	2778	1541	1607	1553
Cyclopoids	7551	5122	5685	3592	5433	5882	6920	3580	3794
Calanoids	7193	2831	3137	3726	1834	1943	7891	2735	2960
[a]Total	17919	8831	9790	12448	9919	10603	16352	7922	8307
Veligers	2702	2734	3087	12373	3145	3121	6496	2675	2935
[b]Total*	20621	11565	12877	24821	13064	13724	22848	10597	11242
Rotifers	147615	215623	241644	309606	[d]161391	[d]161391	331085	424688	476402
[c]Grand total	168236	227188	254521	334427	[d]176803	[d]176803	353933	435285	487644

[a] Includes Cladocera, Cyclopoids and Calanoids
[b] Includes Cladocera, Cyclopoids, Calanoids, Veligers
[c] Includes all five zooplankton types
[d] Because these seasonal means were based on biweekly samples rather than weekly samples, totals plus rotifers will not equal grand totals

Table 12. Comparison of zooplankton seasonal mean biomass ($ug \cdot L^{-1}$) from 1993 and 1994, where w indicates mean biomass for the whole season and c indicates mean biomass for season length comparable to 1993. Seasonal mean biomass for all zooplankton types except rotifers at E2, in 1994 were based on weekly samples. Rotifer estimates at E2 and consequently, associated grand total estimates were based on biweekly estimates. * indicates a significant difference (p<0.05, (2), 3df, paired t) between 1993 and 1994c seasonal mean biomass.

	E1			E2			E3		
	1993	1994 w	1994 c	1993	1994 w	1994 c	1993	1994 w	1994 c
Cladocera	1.89	0.87	0.96	4.94	5.77	6.76	1.03	1.40	1.37
Cyclopoids	3.35	5.58	6.23	4.59	5.29	5.94	3.64	2.61	2.73
Calanoids *	14.94	4.63	5.14	10.85	5.49	5.84	14.86	4.72	4.97
[a]Total	20.18	11.08	12.33	20.38	16.55	18.54	19.53	8.73	9.07
Veligers	4.79	4.12	4.65	15.74	3.23	3.42	6.16	2.23	2.43
[b]Total *	24.97	15.20	16.98	36.12	19.78	21.96	25.69	10.96	11.5
Rotifers	3.27	4.88	5.88	8.02	[d]4.16	[d]4.07	7.79	8.95	10.04
[c]Grand Total	28.24	20.08	22.86	44.14	[d]28.58	[d]29.60	33.48	19.91	21.54

[a]Includes Cladocera, Cyclopoids and Calanoids,

[b]Includes Cladocera, Cyclopoids, Calanoids and Veligers

[c] Includes all five zooplankton types

[d] Because these seasonal means were based on biweekly samples rather than weekly samples, totals plus rotifers. will not equal grand totals

Table 13. Comparison of mean size (as biovolume $\mu m^3 \cdot m^{-1}$) of some rotifer species collected in the eastern basin of Lake Erie in 1993 and 1994. A probability value of less than 0.05 indicates a significant size difference. Body types are indicated as hard (H) or soft (S) and percent difference in size, are given for those species showing a significant difference between the two years. The species tested were present at all three eastern basin stations in both years.

Species	t-value	Probability	Body Type	1993 Mean Size	1994 Mean Size	% Difference
Ascomorpha ecaudia	0.289	> 0.050		155	145	
A. ovalis	1.497	> 0.050		280	127	
Asplanchna priodonta	0.732	> 0.050		31180	24044	
Collotheca sp.	-3.577	0.023	S	32	56	43
Conochilus unicornis	-2.067	> 0.050		306	422	
Gastropus stylifer	1.107	> 0.050		300	234	
Kellicottia longispina	0.905	> 0.050		98	97	
K. cochlearis	-3.604	0.023	H	38	41	7
K. crassa	-0.005	> 0.050		164	174	
K. earlinae	-1.179	> 0.050		80	93	
K. quadrata	-1.382	> 0.050		541	605	
Polyarthra dolichoptera	3.531	0.024	S	266	174	35*
P. major	-3.793	0.019	S	518	743	30
P. remata	-4.839	0.008	S	90	117	23
P. vulgaris	-0.014	> 0.050		261	262	
Synchaeta -round	-2.259	> 0.050		95	112	
Synchaeta -small	-3.385	0.028	S	39	58	33
Synchaeta -large	-0.637	> 0.050		541	604	
Synchaeta -long	-2.219	> 0.050		73	141	
Tylotrocha monopus	2.751	> 0.050		222	186	

*this species significantly larger in 1993

Table 14. Summary of zooplankton species occurrence at 3 stations in eastern Lake Erie in 1993 and 1994. Numbers indicate the percentage of sampling days on which that species comprised $\geq$ 5% of the total sample biomass. + indicates the species was present but never comprised $\geq$ 5% of the total biomass.

Taxon	E1 1993	E1 1994	E2 1993	E2 1994	E3 1993	E3 1994
CLADOCERA						
Bosmina sp.	45.5	28.6	70.0	75.0	41.7	38.1
Daphnia longiremis		+	+	+		
Daphnia retrocurva	9.1	9.5	+	50.0		9.5
Daphnia galeata mendotae	+	+	+	10.0		+
Diaphanosoma sp.	+	+				
Eubosmina sp.	+	+	+	5.0		+
Polyphemus pediculus		+				
Holopedium gibberum			+			
Sida crystallina		+				
Chydorus sphaericus	+	+				+
Alona sp.	+	+				+
Bythothrephes cederstroemi	+	9.5	+	45.0	8.3	9.5
Leptodora kindti	+	+	20.0	5.0	+	+
COPEPODA						
Calanoida						
Leptodiaptomus ashlandi	+	+	10.0	20.0		+
Leptodiaptomus minutus	27.3	4.7	30.0	30.0	50.0	33.3
Leptodiaptomus sicilis			+	15.0	+	+
Leptodiaptomus siciloides	+		+	+	+	
Skistodiaptomus reighardi		+				
Skistodiaptomus oregonensis	+	14.3	20.0	25.0	33.3	14.3
Epischura lacustris	27.3	42.9	70.0	65.0	75.0	47.6
Epischura lacustris copepidid	27.3	47.6	50.0	40.0	58.3	61.9
Eurytemora affinis	9.1	4.8	30.0	10.0	8.3	+
Limnocalanus macrurus			+			
Senecella calanoides copepidid				+		
Calanoid copepidid	63.6	66.7	40.0	40.0	33.3	33.3
Calanoid nauplii	27.3	28.6	30.0	25.0	8.3	28.6

Table 14. Continued

Taxon	E1		E2		E3	
	1993	1994	1993	1994	1993	1994
Cyclopoida						
Diacyclops thomasi	9.1	38.1	80.0	85.0	33.3	33.3
Cyclops vernalis	+	+	+	+		+
Mesocyclops edax	+	+	10.0	15.0	+	+
Tropocyclops extensus	27.3	+	10.0	+	25.0	4.8
Eucyclops agilus	+	+				
Eucyclops speratus				+		
Cyclopoid copepidid	72.7	95.2	50.0	90.0	41.7	66.7
Cyclopoid nauplii	23.7	14.3	+	10.0	16.7	14.3
Harpactacoida			+	+	+	
DREISSENA VELIGERS	63.6	71.4	100.0	90.0	83.3	76.2

Table 15. List of rotifer species found at each eastern basin station in 1994. Also included are data for the western basin station, W3, which was sampled for only zooplankton in 1994. Species are ranked as present but rare (O), contributing $\geq$0.5% (+), $\geq$5.0% or $\geq$10.0% (+++) of total biomass at some time in the season (May - November).

Species	E1	E2	E3	W3
Ascomorpha ecaudia	+	+	++	
A. ovalis	+	O	+	
Asplanchnia herricki	+++	+++	+++	
A. priodonta	+++	+++	+++	+++
Brachionus angularis	+	O		+
B. budapestinensis				+
B. calyciflorus		O		+
B. caudatus				O
Cephalodella gibba	+		++	
Collotheca sp.	+	+++	+++	+
Conochilus unicornis	+++	+++	+++	+
Euchlanis sp.	O			
Filinia longiseta	++			+
Gastropus stylifer	+	+	++	++
Kellicottia longispina	+++	+	+	+
Keratella cochlearis	+	+	+	+
K. crassa	+++	++	+	O
K. earlinae	+	++	++	++
K. hiemalis		O		
K. quadrata	+++	+	+	+++
Lecane flexilis	+			
Lepadella acuminata	+			
L. patella	O			
L. sp.	++	O	+	
Monostyla lunaris			+	

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Table 15. Continued.

Species	E1	E2	E3	W3
Notholca foliacea				o
N. laurentiae		.	+	
N. squamula	o		o	
Pleosoma hudsoni				++
P. truncatum	++	+	+	++
Polyarthra dolichoptera	+	+++	++	+++
P. euryptera			++	
P. major	+++	+++	+++	++
P. remata	+++	+++	+++	+++
P. vulgaris	+++	+++	+++	+++
Synchaeta sp.		+		
Synchaeta -round	+++	+++	+++	+++
Synchaeta -small	++	++	+	o
Synchaeta -large	+++	+++	+++	+++
Synchaeta -long	+++	+++	+++	+++
Trichocerca sp.	+			
T. cylindrica	+	+++	o	+
T. longiseta			o	
T. multicrinis	+	+	++	+
T. pusilla	++	+		+
T. rousseleti	+	+	+	o
T. similis	+	o		
Trichotria sp.	o			
Tylotrocha monopus	+		+	

Table 16. Seasonal mean length (μm) of the most abundant zooplankton species from stations E1, E2 (epilimnion) and E3 in eastern Lake Erie in 1993 and 1994.

Species	E1		E2		E3	
	1993	1994	1993	1994	1993	1994
Bosmina sp.	262	258	320	268*	268	268
Daphnia retrocurva	769	867*		875		946
Diaptomus minutus	893	909	971	950	926	1034*
Epischura lacustris	1389	1486	1277	1309	1148	1451*
Eurytemora affinis	1110	1118	823	1092*	742	979*
Mesocyclops edax	783	776	754	641*	839	829
Diacyclops thomasi	860	957*	568	820*	672	823*
Tropocyclops extensus	459	479	450	432	445	443
Dreissena veligers	180	164	173	197*	192	181

* indicates a difference ≥ 10%.

Table 17. Potential clearance rates (CR $m^3 \cdot m^{-2} \cdot d^{-1}$) of *Dreissena polymorpha* (*D.p.*) and *D. bugensis* (*D.b.*) at each LEB station: spring (May only) and seasonal (May-Oct.). Densities are mean numbers of individuals (ind.) per m^2 from all sampling dates for seasonal estimates, and are average densities from 3 or 4 grab samples for spring estimates. Mean biomass ($g \cdot m^{-2}$) for the sampling season and for spring was determined in the same manner as for density. Average dry weights (g·ind.) were calculated from average wet weight (biomass/density) and a conversion factor of 0.121 for *D. polymorpha* and 0.081 for *D. bugensis*.

		Spring (May)					Seasonal (May - Oct.)					
	Species	Mean Density	Mean Biomass	Aver. Dry Wt.$(x10^{-5})$	CR	Total CR	Species	Mean Density	Mean Biomass	Aver. Dry Wt. $(x10^{-5})$	CR	Total CR
1993												
E2	*D.p.*	58	0.45	94	0.02	14.89	*D.p.*	31	0.552	215	0.02	9.59
	D.b.	156566	404.30	21	14.87		*D.b.*	91679	264	23	9.57	
E3	*D.p.*	2974	195.40	795	6.93	13.24	*D.p.*	1906	115	730	4.13	12.84
	D.b.	19124	200.30	85	6.31		*D.b.*	69697	246	29	8.71	
WC1	*D.p.*	1940	32.66	204	1.36	7.62	*D.p.*	1546	348	2720	10.63	21.76
	D.b.	17306	205.07	96	6.26		*D.b.*	11442	417	290	11.13	
WC2	*D.p.*	101	0.0072	0.86	0.0006	0.0031	*D.p.*	88	0.263	36	0.01	0.157
	D.b.	244	0.0512	1.7	0.0025		*D.b.*	201	5	208	0.14	
W1	*D.p.*	216	0.0740	4	0.0006	0.0006	*D.p.*	2227	65	352	2.53	2.53
W3	*D.p.*	36221	1009.59	337	39.66	39.66	*D.p.*	31615	624	239	25.57	25.57
1994												
E2	*D.b.*	7845	80	83	2.50	2.50	-	-	-	-	-	-
E3	*D.p.*	291	5.53	230	0.23	9.71	-	-	-	-	-	-
	D.b.	81056	266.73	27	9.48							
WC1	*D.p.*	86	84.96	11930	2.18	18.38	-	-	-	-	-	-
	D.b.	3222	758.16	1910	16.20							
WC2	*D.p.*	129	1.56	145	0.07	0.68	-	-	-	-	-	-
	D.b.	140	28.12	1630	0.61							
W1	*D.p.*	11	0.0024	3	0.0002	0.0002	-	-	-	-	-	-
W3	-	-	-	-	-	-	-	-	-	-	-	-

Table 18. Predictions of seasonal mean chlorophyll ($\mu g \cdot L^{-1}$) from total phosphorus (TP $\mu g \cdot L^{-1}$) using the equations of Smith (1982) and Mazumder (1995). Other column headings are defined as follows: mean summer total phosphorus (TP_{sum} $\mu g \cdot L^{-1}$), seasonal mean total nitrogen (TN $\mu g \cdot L^{-1}$), observed seasonal mean chlorophyll (Chl_{obs}), mean summer chlorophyll (Chl_{sum}), and the observed seasonal Chl to seasonal TP ratio (Chl:TP).

Station	TP	TP_{sum}	TN	Chl_{obs}	Chl_{sum}	Smith	Mazumder even-link[1]	Mazumder odd-link[2]	Chl:TP
1993									
E1	7.8	7.6	474	1.06	0.97	2.23	1.72	4.11	0.14
E2	8.5	4.5	486	2.11	2.28	2.35	1.82	4.36	0.25
E3	6.6	5.7	489	1.12	1.14	2.15	1.57	3.69	0.17
WC1	10.8	9.1	499	2.67	3.08	2.64	2.11	5.16	0.25
WC2	12.8	11.5	514	3.99	4.05	2.89	2.37	5.86	0.31
W1	17.5	14.2	686	4.55	4.63	4.25	3.00		0.26
W2	15.5	13.8	635	3.52	4.21	3.78	2.73		0.23
W3	19.1	23.0	695	4.47	4.46	4.45	3.19		0.23
1994									
E1	10.1	9.1	502	1.54	1.31	2.59	2.02	4.92	0.15
E2	8.1	7.8	552	2.24	2.40	2.60	1.76	4.22	0.28
E3	8.5	8.1	480	1.27	1.28	2.33	1.82	4.36	0.15

[1]Chl= 0.71 + 0.13(TP_{sum})
[2]Chl= 1.38 + 0.35(TP_{sum})
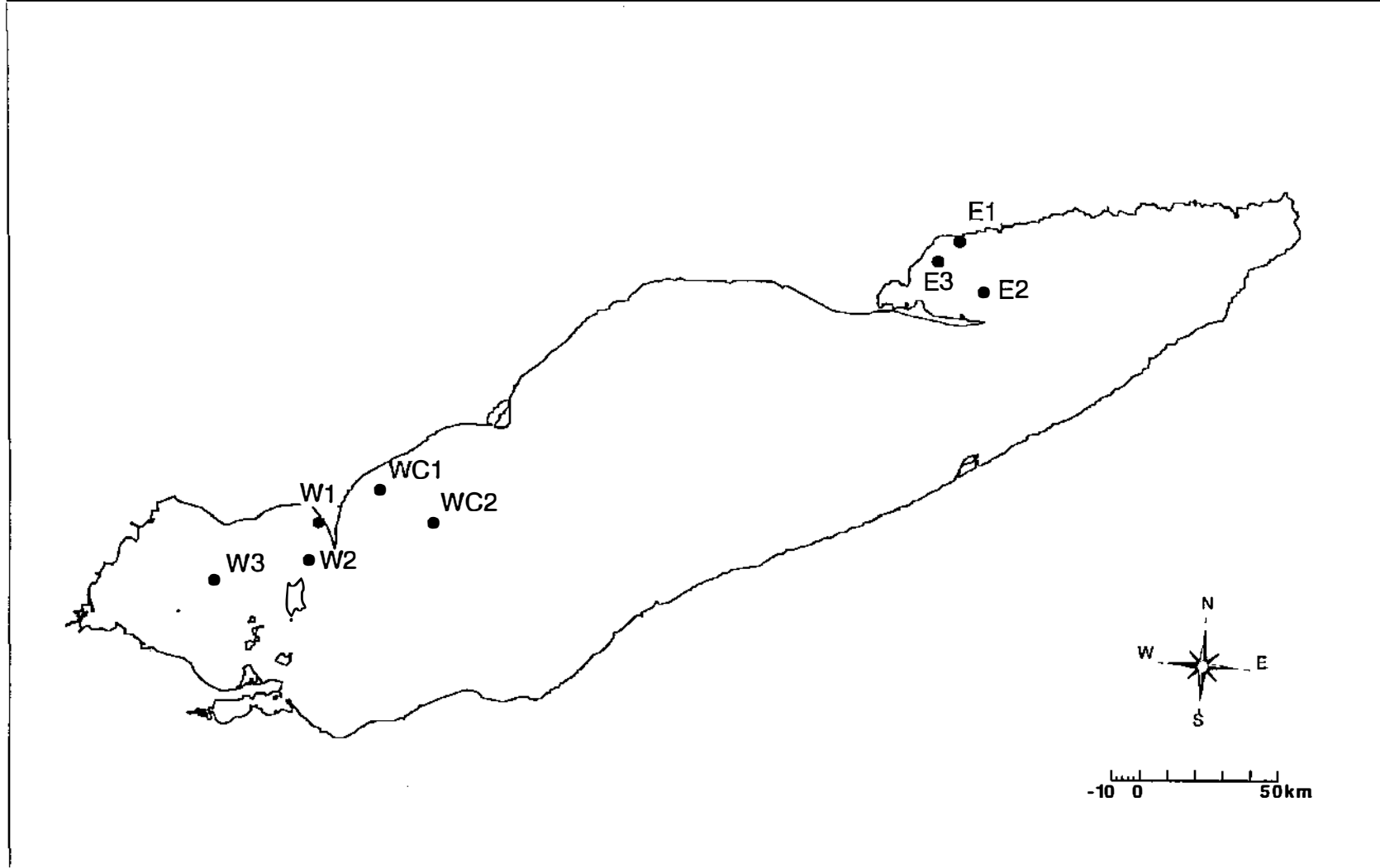
Figure 1. Lake Erie Biomonitoring Program sampling stations: E= eastern WC= west central, W= western.
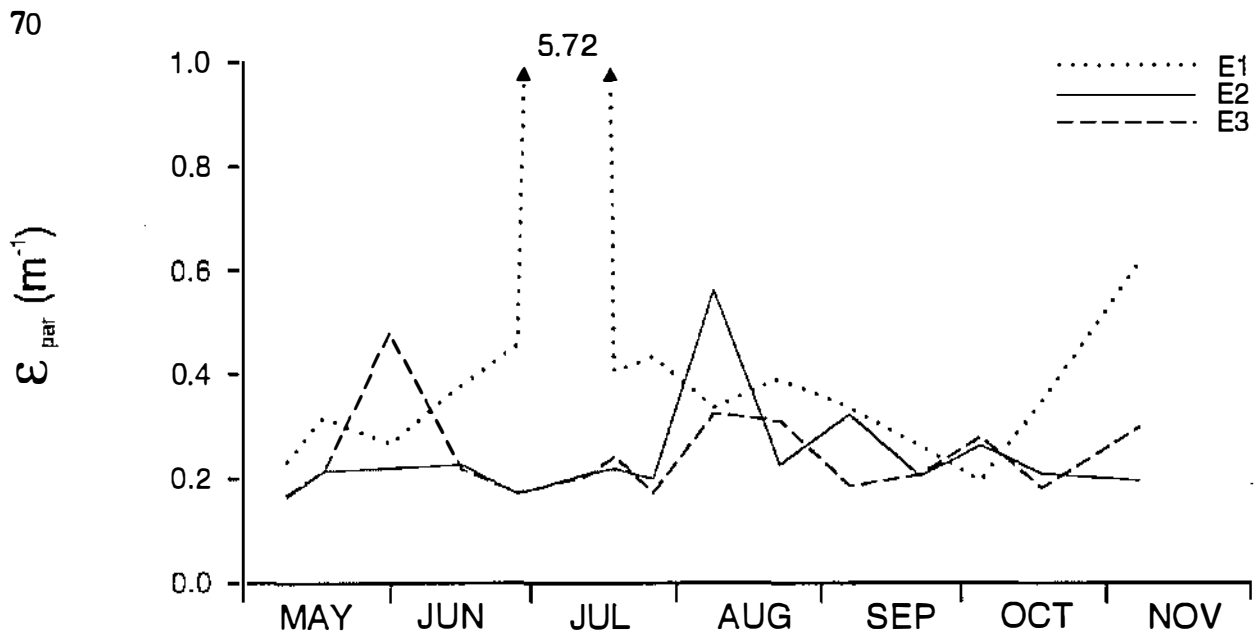
Figure 2. Seasonal (May-Nov.) light extinction (ε_{par}) at nearshore (broken lines) and offshore (solid line) stations in the eastern basin of Lake Erie, 1994.
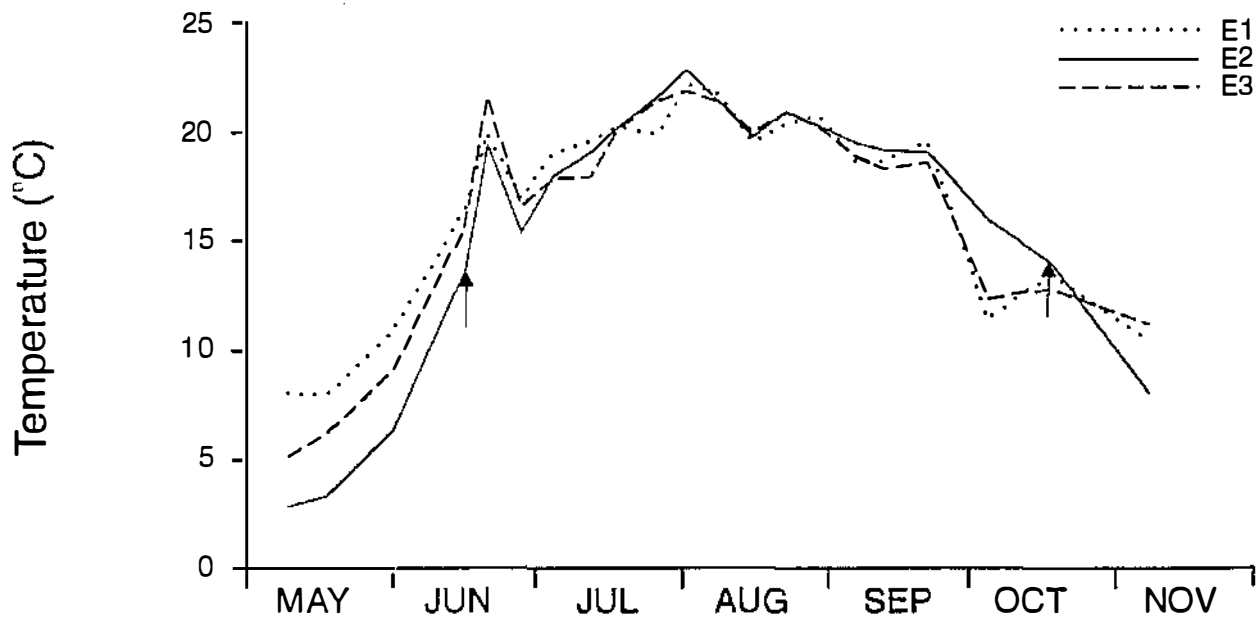
Figure 3. Seasonal (May-Nov.) mean mixing depth temperature at nearshore (broken lines) and offshore (solid line) stations in the eastern basin of Lake Erie, 1994. Onset and breakdown of stratification are indicated for station E2 by the arrows.
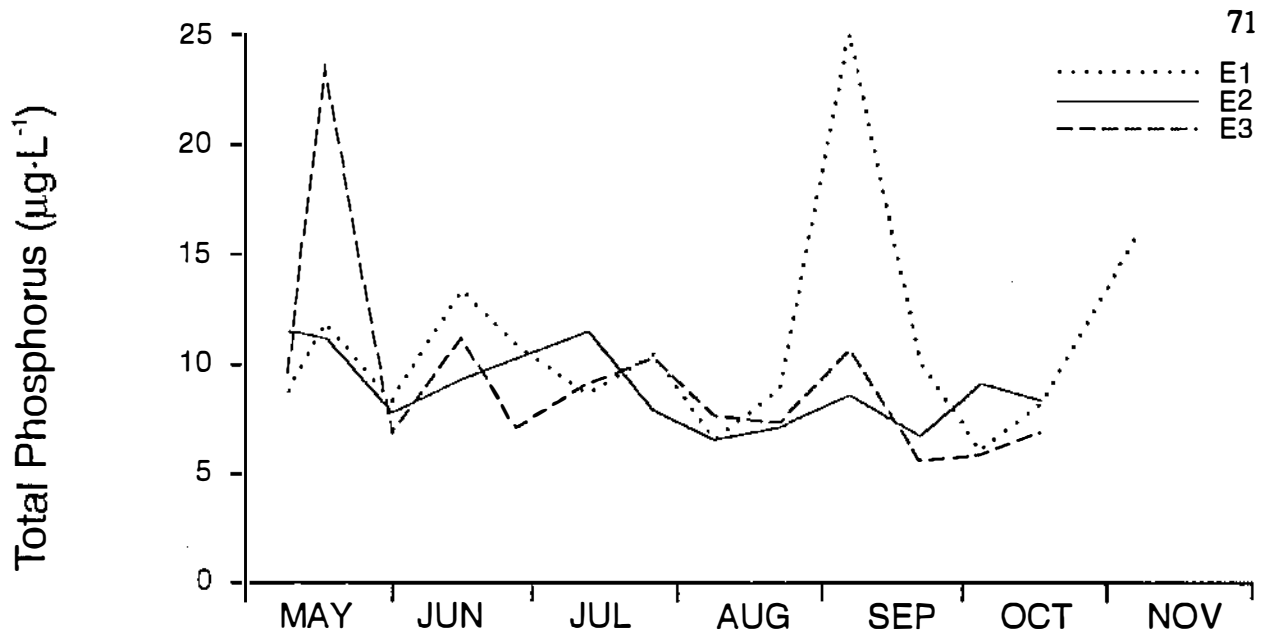
Figure 4. Seasonal (May-Nov.) total phosphorus at nearshore (broken lines) and offshore (solid line) stations in the eastern basin of Lake Erie, 1994. Epilimnetic concentrations when stratified, or whole water column concentrations under unstratified conditions.
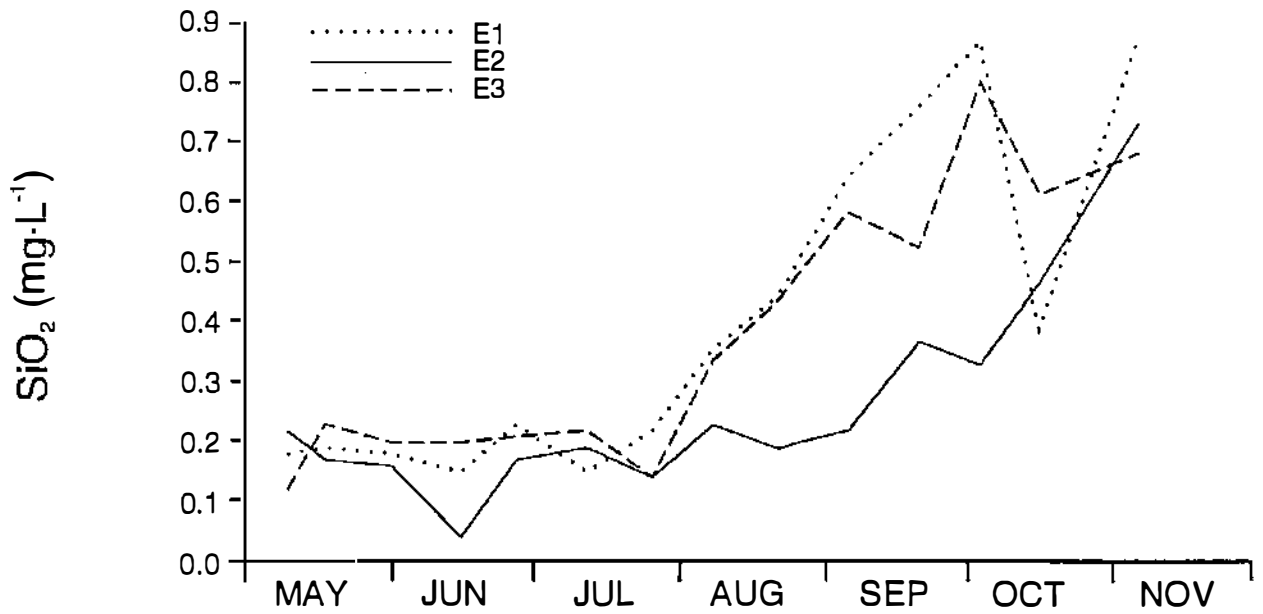
Figure 5. Seasonal (May-Nov.) SiO$_2$ concentrations at nearshore (broken lines) and offshore (solid line) stations in the eastern basin of Lake Erie, 1994. Epilimnetic concentrations when stratified, or whole water column concentrations under unstratified conditions.
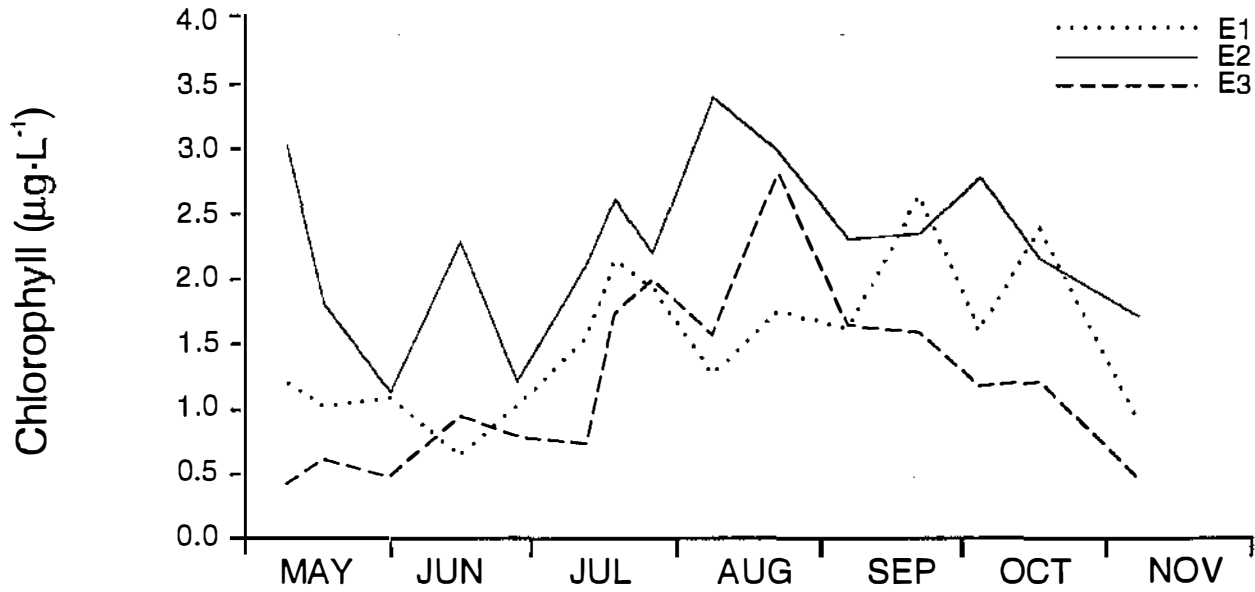
Figure 6. Seasonal (May-Nov.) uncorrected chlorophyll at nearshore (broken lines) and offshore (solid line) stations in the eastern basin of Lake Erie, 1994. Epilimnetic concentrations when stratified, or whole water column concentrations under unstratified conditions.
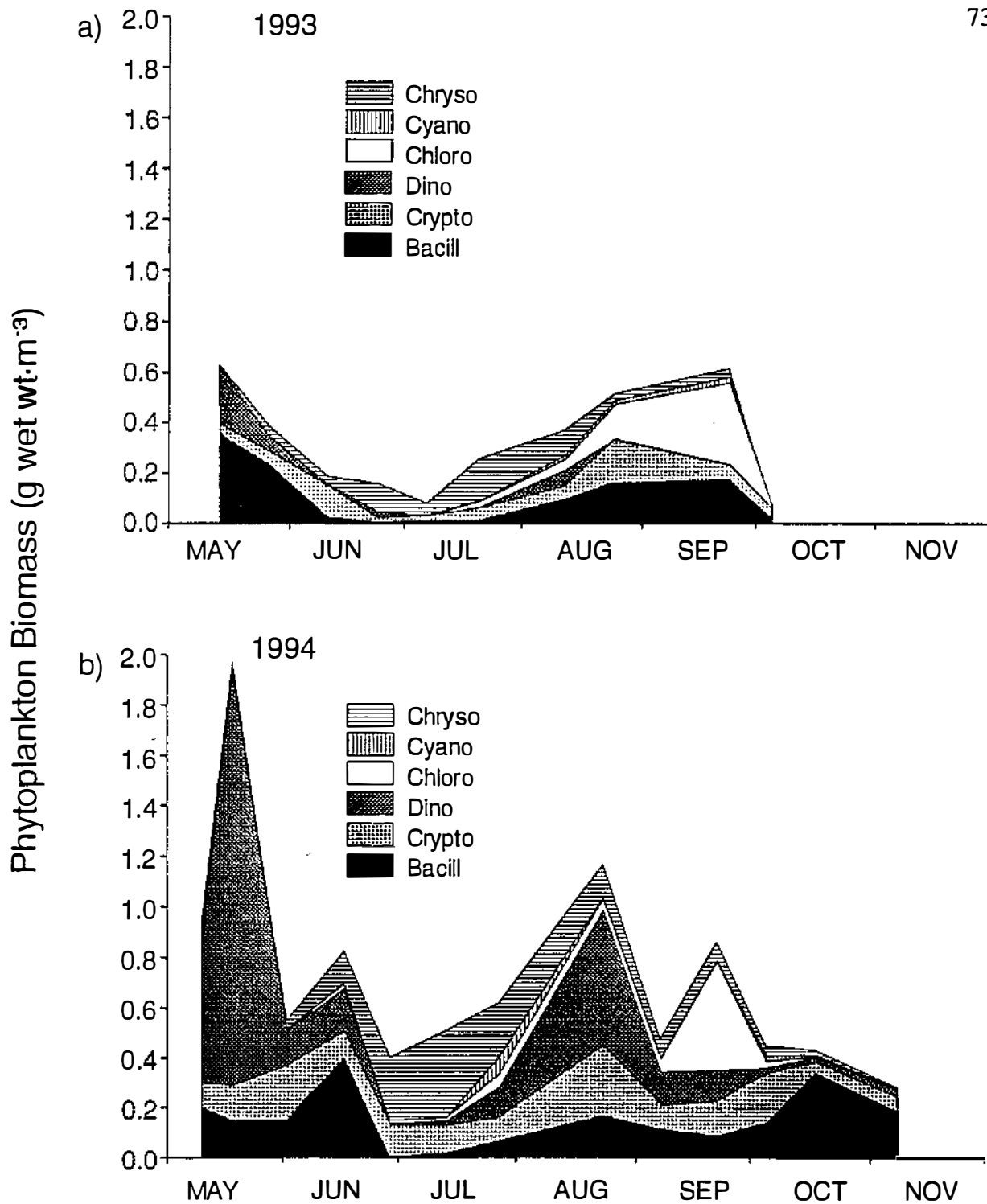
Figure 7. Seasonal trends in phytoplankton biomass and composition at the offshore station (E2) in the eastern basin of Lake Erie in a) 1993 and b) 1994. Values obtained from a composite sample through the epilimnion or whole water column samples under unstratified conditions.

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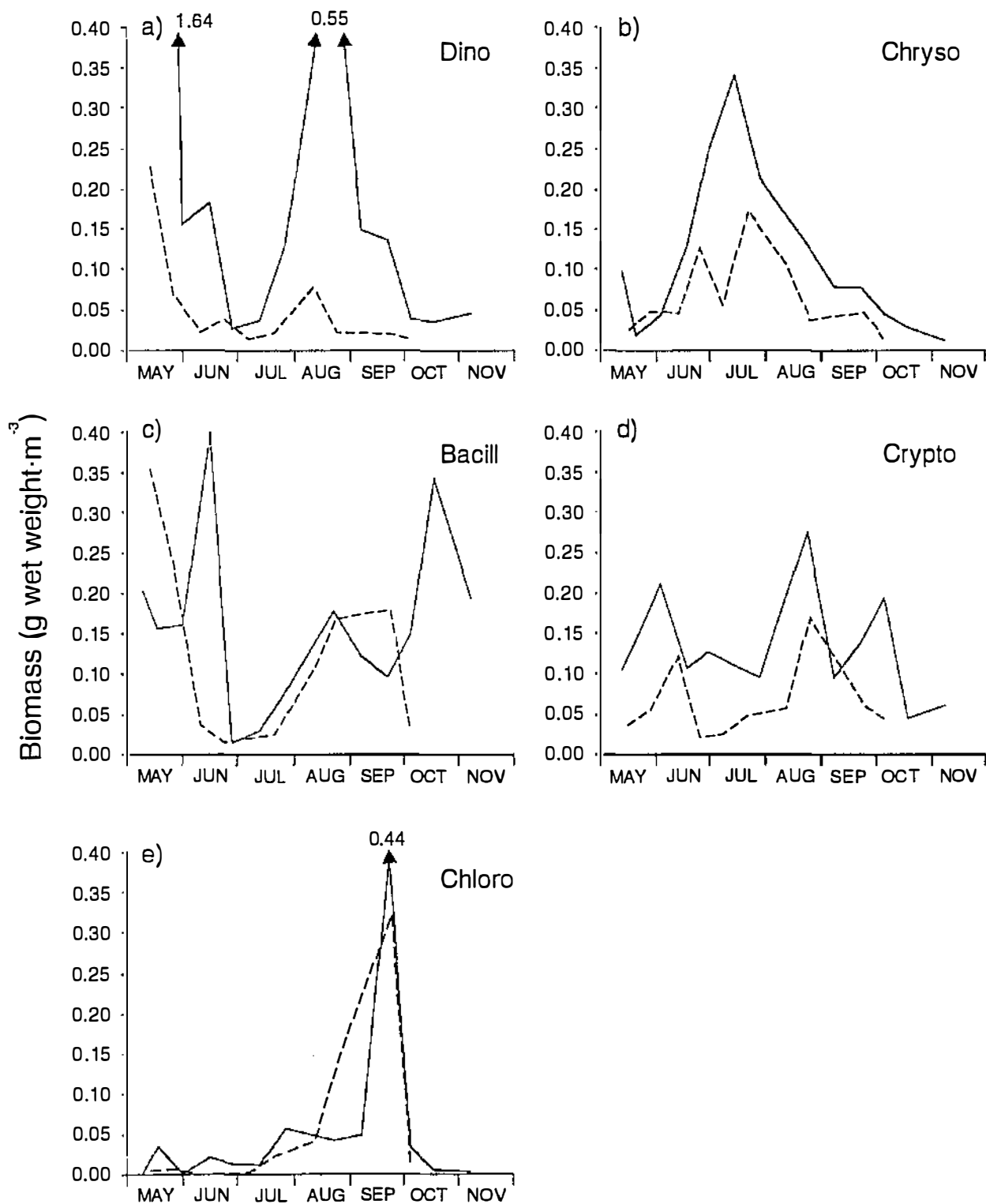
Figure 8. Seasonal trends of the important phytoplankton groups in 1993 (broken line) and 1994 (solid line) at the offshore station (E2) in the eastern basin of Lake Erie.
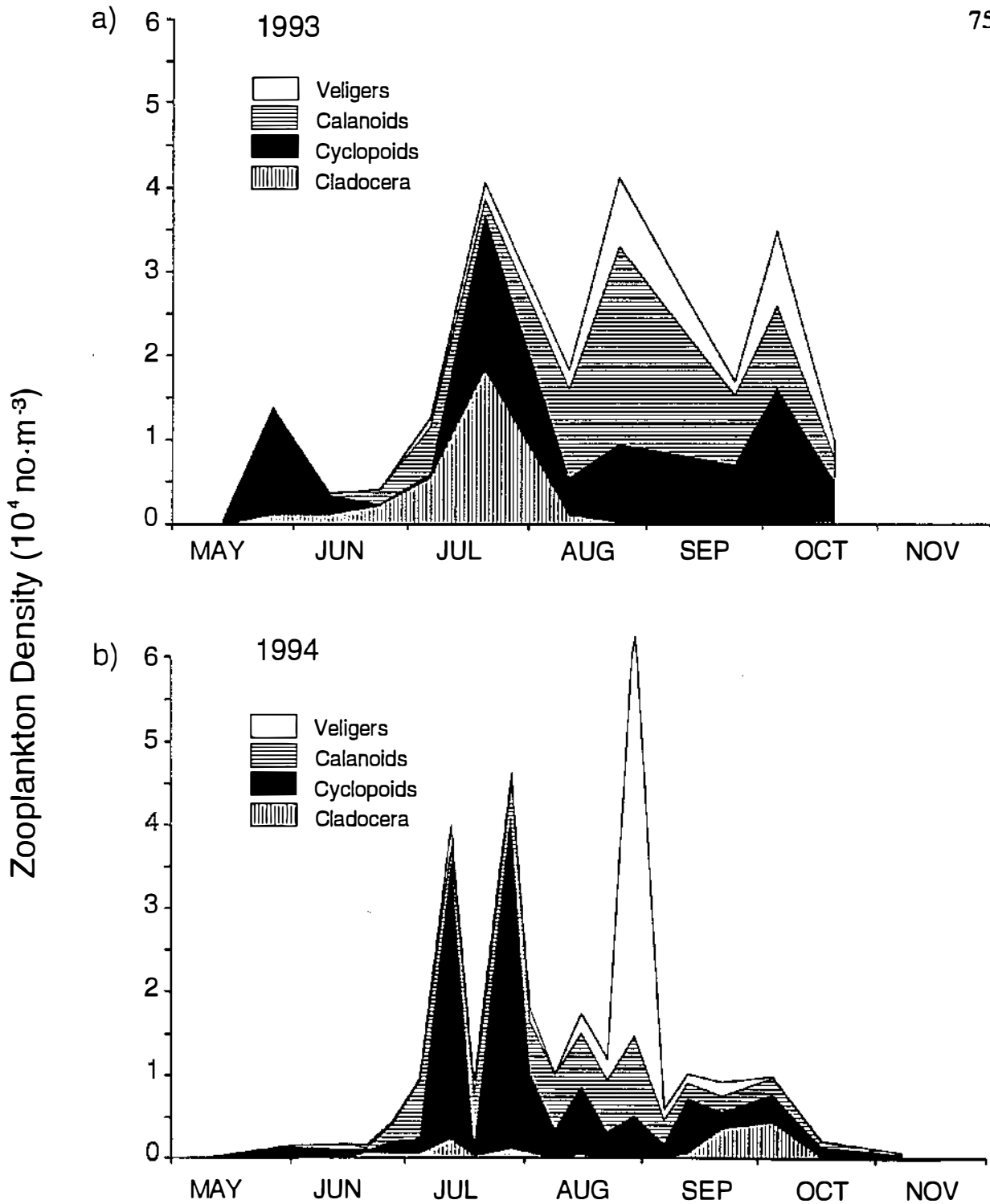
Figure 9. Seasonal trends in macrozooplankton and veliger densities at station E1 (nearshore) in the eastern basin of Lake Erie in a) 1993 and b) 1994. Integrated, whole water column samples, 110 μm mesh.
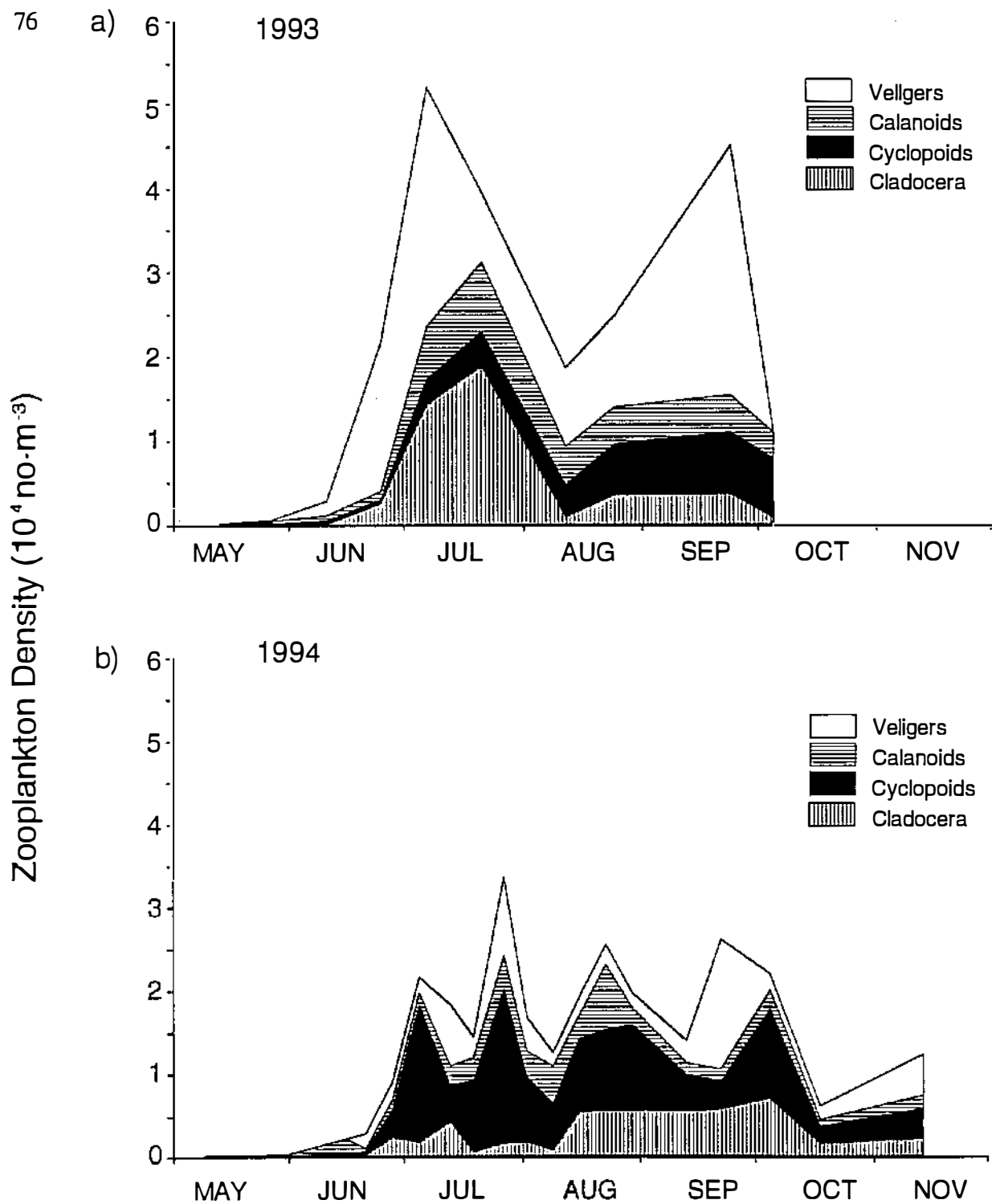
Figure 10. Seasonal trends in macrozooplankton and veliger densities at station E2 (offshore) in the eastern basin of Lake Erie in a) 1993 and b) 1994. In unstratified conditions data are from integrated, whole water column samples. In stratified conditions data are depth-weighted from separate epilimnetic, metalimnetic and hypolimnetic samples. A 110 μm mesh was used.
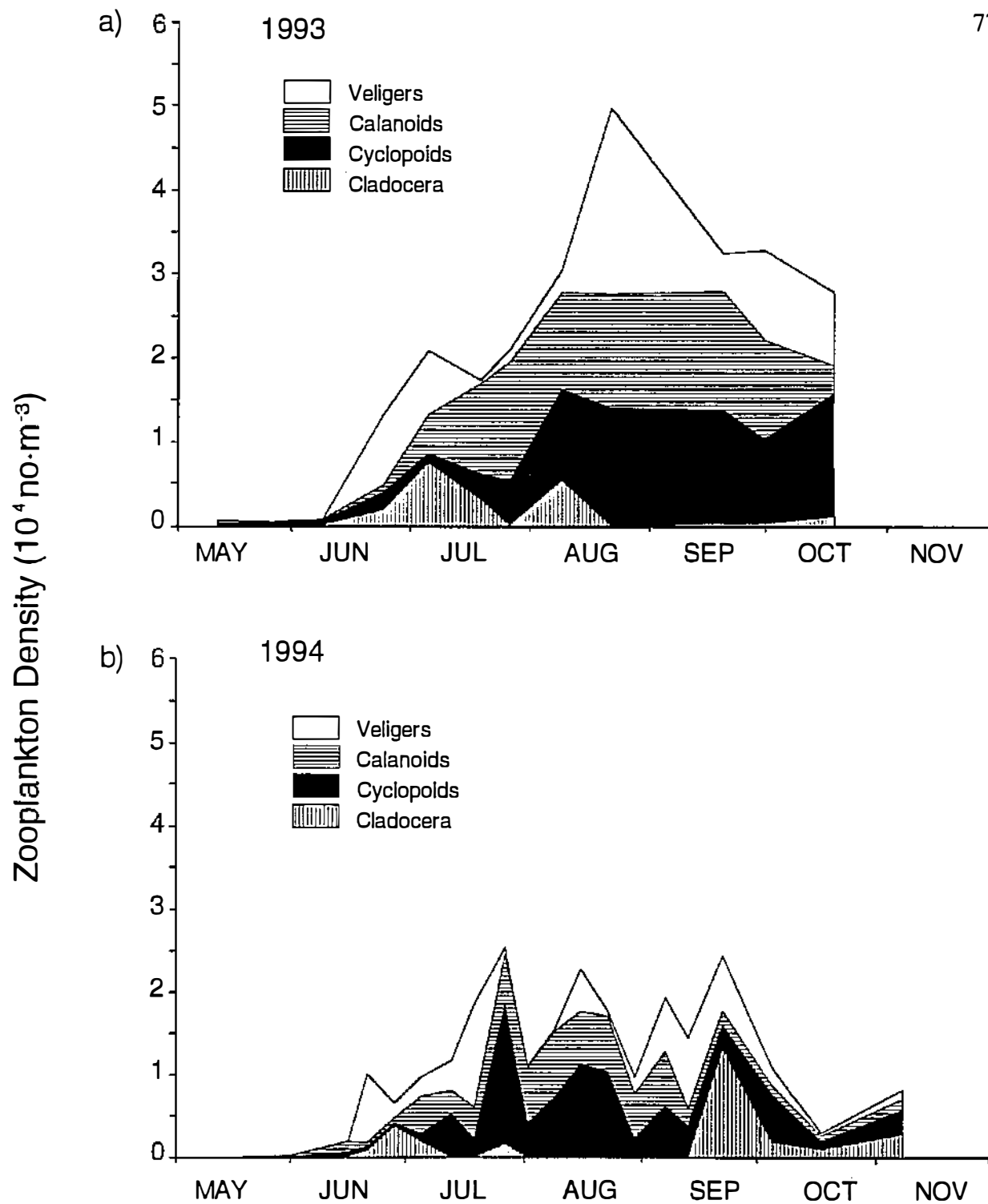
Figure 11. Seasonal trends in macrozooplankton and veliger densities at station E3 (nearshore) in the eastern basin of Lake Erie in a) 1993 and b) 1994. Integrated, whole water column samples, 110 μm mesh.
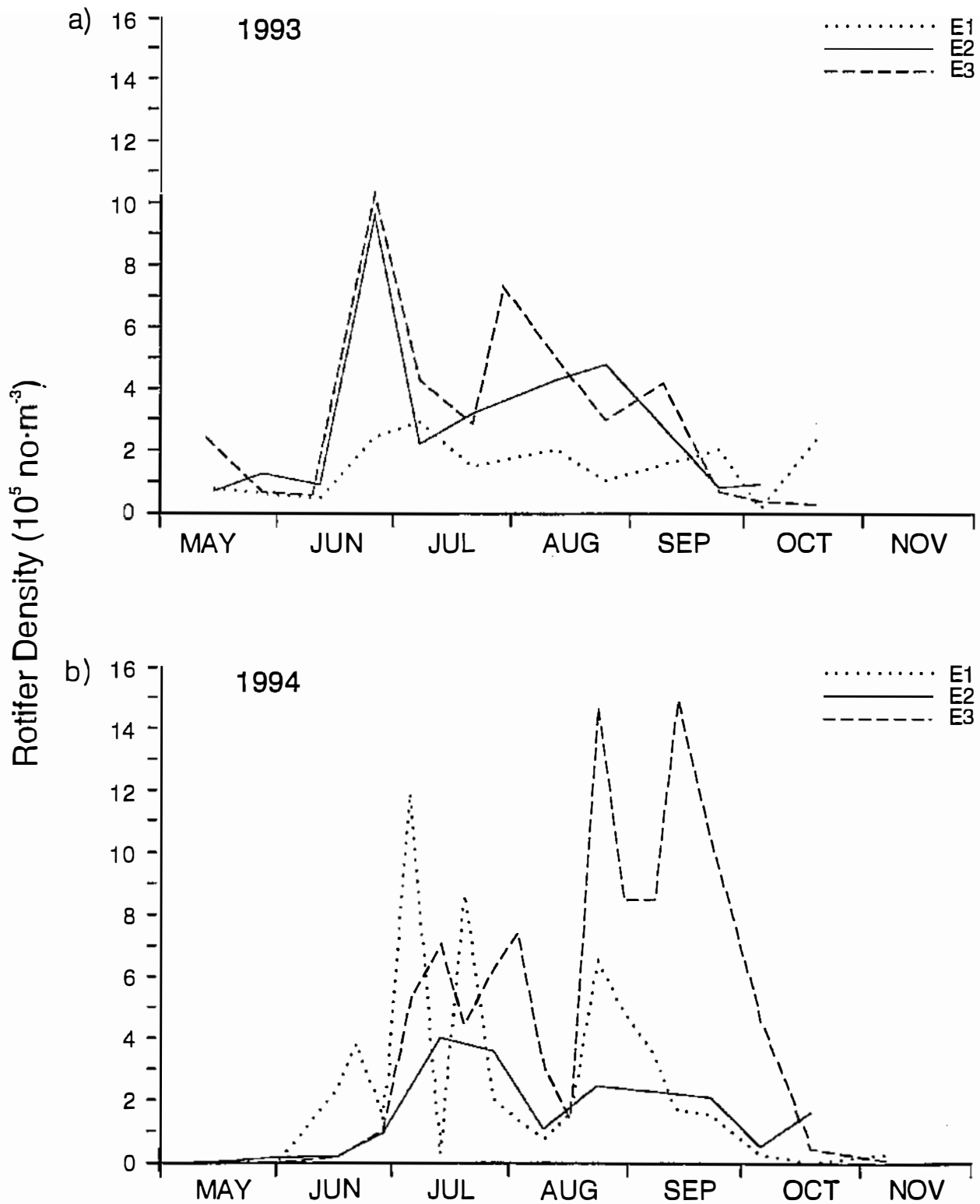
Figure 12. Seasonal trends in rotifer density at nearshore (broken lines) and offshore (solid line) stations in the eastern basin of Lake Erie in a) 1993 and b) 1994. Integrated, whole water column samples, 20μm mesh.
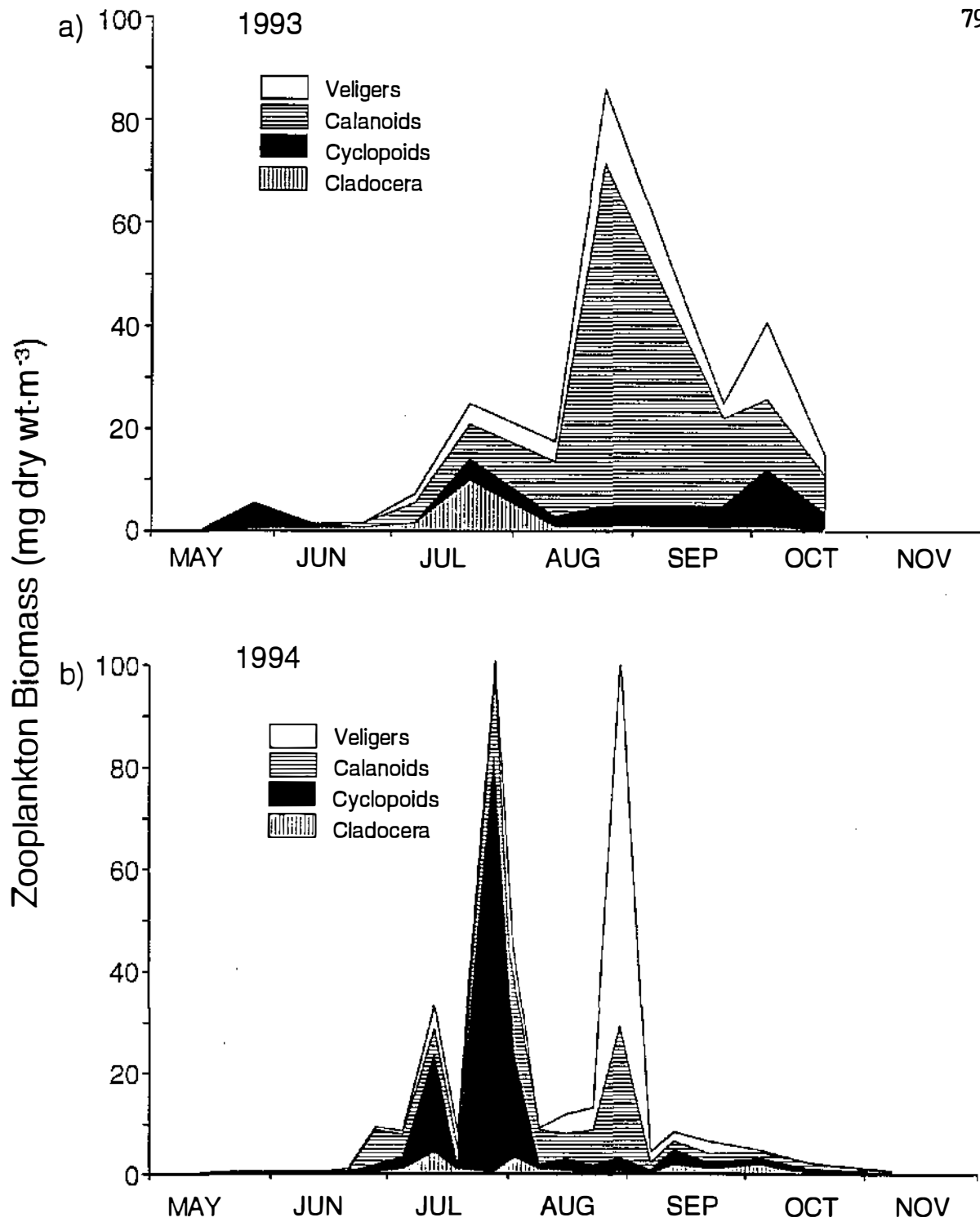
Figure 13. Seasonal trends in macrozooplankton and veliger dry biomass at station E1 (nearshore) in the eastern basin of Lake Erie in a) 1993 and b) 1994. Integrated, whole water column samples, 110 μm mesh.
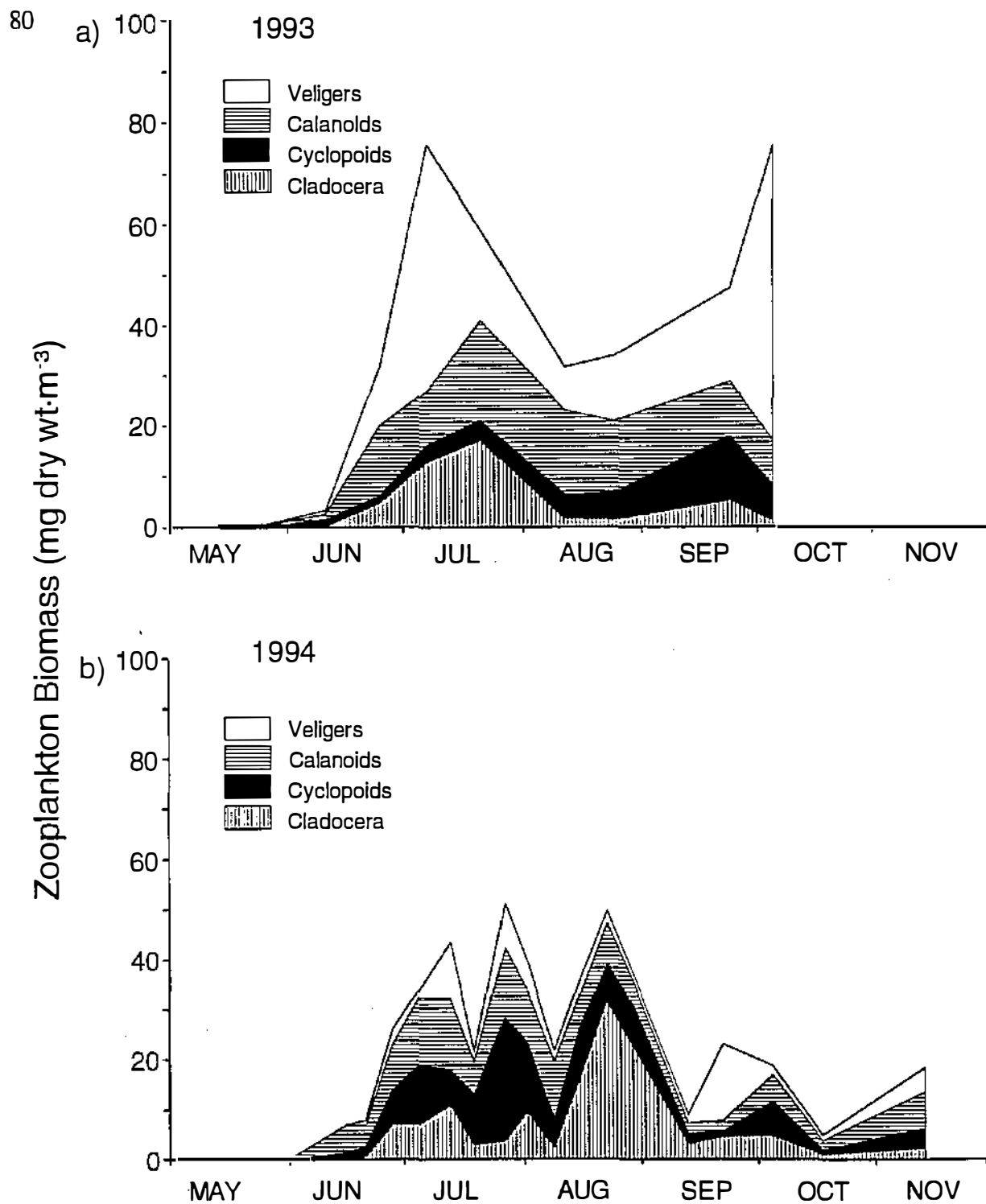
Figure 14. Seasonal trends in macrozooplankton and veliger dry biomass at station E2 (offshore) in the eastern basin of Lake Erie in a) 1993 and b) 1994. In unstratified conditions data are from integrated, whole water column samples. In stratified conditions data are depth-weighted from separate epilimnetic, metalimnetic and hypolimnetic samples. A 110 µm mesh was used.
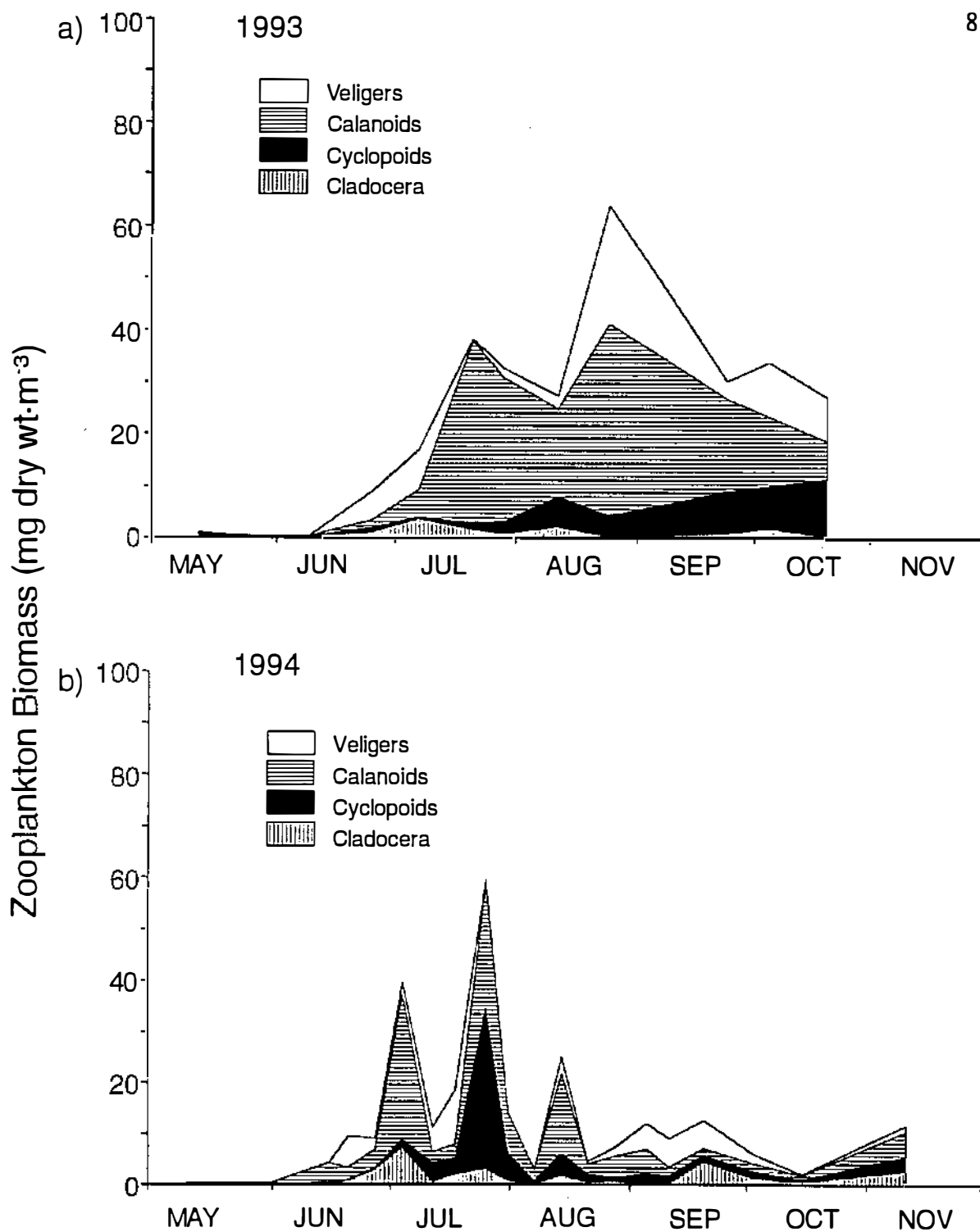
Figure 15. Seasonal trends in macrozooplankton and veliger dry biomass at station E3 (nearshore) in the eastern basin of Lake Erie in a) 1993 and b) 1994. Integrated, whole water column samples, 110 μm mesh.

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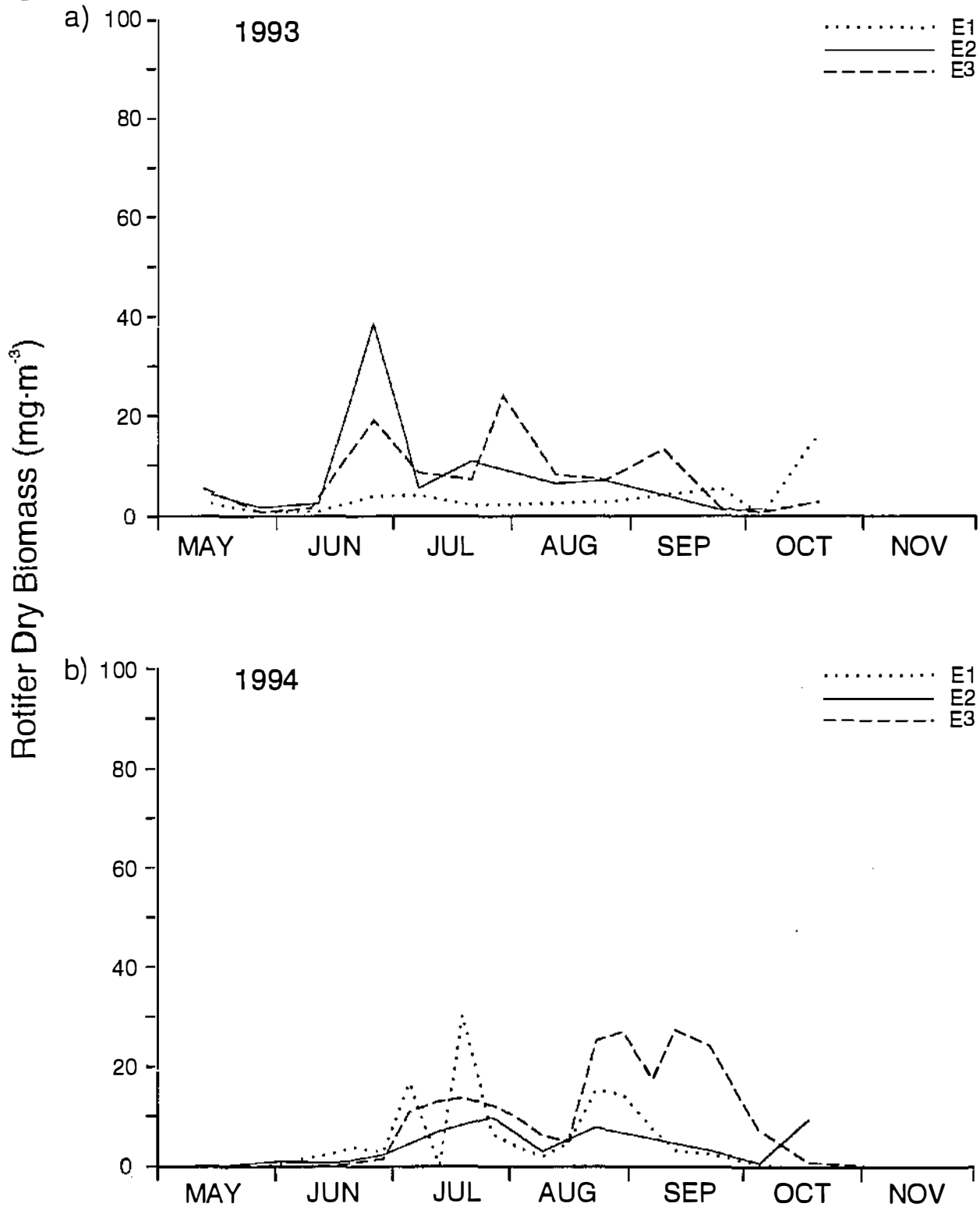
Figure 16. Seasonal trends in rotifer dry biomass of nearshore (broken lines) and offshore (solid line) stations in the eastern basin of Lake Erie in a) 1993 and b) 1994. Integrated, whole water column samples, 20 μm mesh.
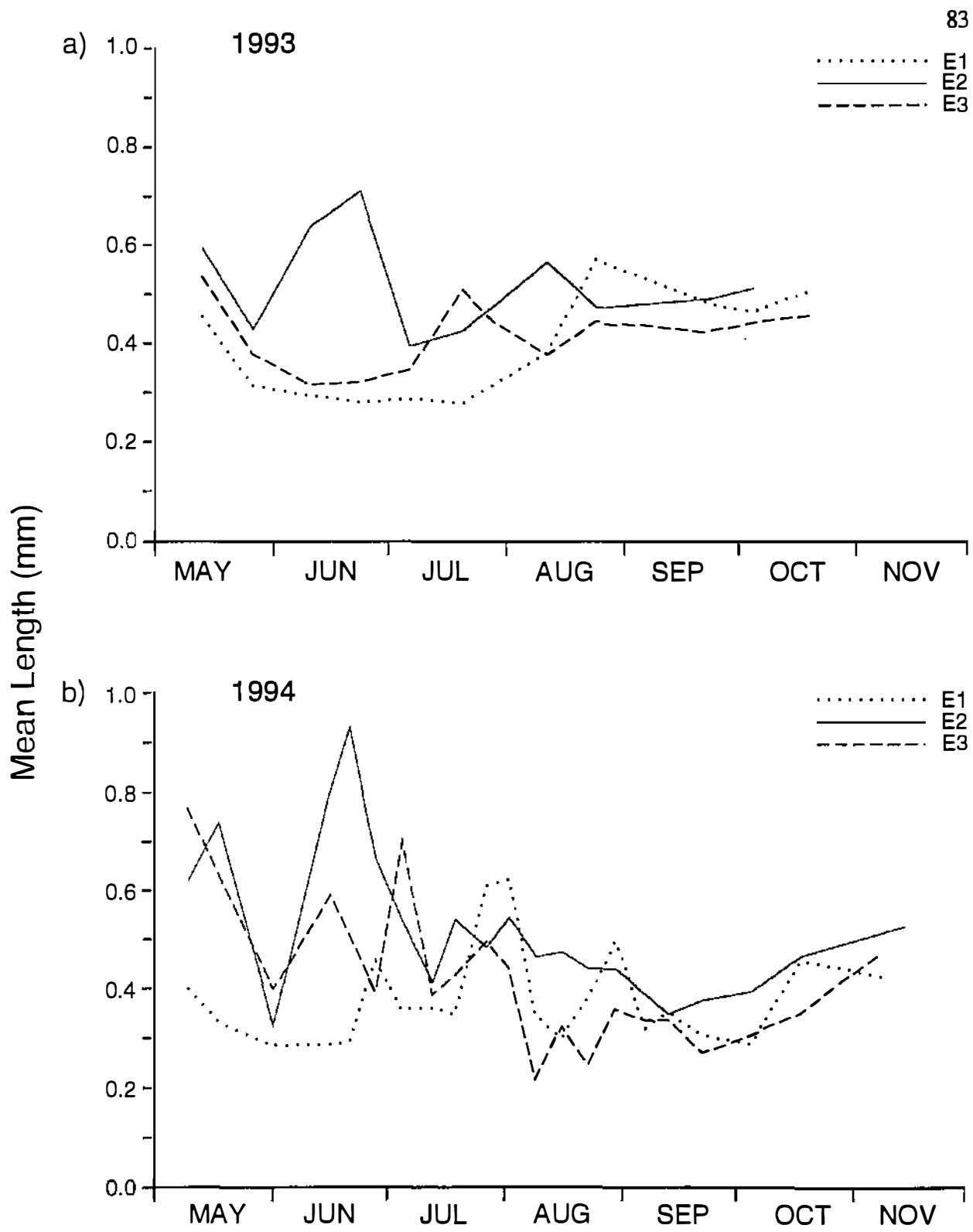
Figure 17. Seasonal trends in macrozooplankton community size (mm) at nearshore (broken lines) and offshore (solid line) stations in the eastern of Lake Erie in a) 1993 and b) 1994. Integrated whole water column samples, 110μm mesh.

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Appendix 1a. Depth-weighted biomass (mg/m³) of each zooplankton species on each sampling date at station E1 in 1993. Seasonal weighted mean (SWM) biomass is given for each species. cop.= copepidid, naup.= nauplii

Species	May-14	May-27	Jun-11	Jun-24	Jul-07	Jul-21	Aug-12	Aug-25	Sep-24	Oct-05	Oct-20	SWM
Bosmina sp.	0.007	0.442	0.672	0.845	1.529	9.113	0.494	0.137	0.102	0.140	0.151	1.434
Daphnia longiremis	-	-	-	-	-	-	-	-	-	-	-	-
D. retrocurva	0.025	-	-	-	0.002	0.309	-	-	-	-	-	0.036
D. galeata mendotae	-	-	-	-	-	0.009	-	-	-	-	0.032	0.003
Diaphanosoma sp.	-	-	-	-	-	0.105	0.063	-	-	-	-	0.019
Eubosmina sp.	-	-	-	-	-	0.090	-	-	-	-	-	0.010
Polyphemus pediculus	-	-	-	-	-	-	-	-	-	-	-	-
Holopedium gibberum	-	-	-	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-	-	-	-	-
Chydorus sphaericus	-	-	-	-	-	-	-	0.009	0.016	0.012	0.016	0.005
Alona sp.	-	-	0.001	-	-	-	-	-	-	-	-	0.000
Bythotrephes cederstroemi	-	-	-	-	-	-	0.328	0.853	0.709	0.903	-	0.317
Leptodora kindti	-	-	-	-	0.127	0.400	0.147	-	-	-	-	0.072
Leptodiaptomus ashlandi	-	-	-	-	-	0.167	0.093	-	0.039	-	-	0.034
L. minutus	0.005	-	-	-	0.013	0.159	2.656	29.068	1.528	0.331	0.038	4.468
L. sicilis	-	-	-	-	-	-	-	-	-	-	-	-
L. siciloides	-	-	-	-	-	-	-	-	0.069	-	-	0.009
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-	-	-	-
S. oregonensis	0.012	-	-	-	-	-	0.267	-	0.224	0.337	0.306	0.101
Epischura lacustris	-	-	-	-	0.042	5.056	0.598	12.294	5.673	-	0.136	3.042
Epischura cop.	-	0.022	0.013	0.075	0.019	0.270	3.845	18.788	6.194	0.532	0.264	3.860
Eurytemora affinis	-	-	-	0.022	0.562	-	-	-	-	-	-	0.050
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-	-	-	-
Calanoid cop.	0.004	0.016	0.047	0.471	2.516	1.030	1.957	5.672	2.687	11.959	6.342	2.980
Calanoid naup.	0.016	0.031	0.034	0.175	0.476	0.055	1.236	0.560	0.610	0.391	0.113	0.395
Diacyclops thomasi	0.360	0.014	-	-	-	0.577	0.255	-	-	0.036	0.115	0.118
Acanthocyclops vernalis	-	-	-	-	-	-	0.018	-	-	-	-	0.002
Mesocyclops edax	-	-	-	-	-	0.160	0.032	-	-	0.055	-	0.026
Tropocyclops extensus	0.006	0.002	0.003	-	0.003	0.096	0.168	2.135	1.347	7.509	2.065	1.204
Eucyclops agilis	0.002	0.016	-	-	-	-	-	-	-	-	-	0.001
E. speratus	-	-	-	-	-	-	-	-	-	-	-	-
Cyclopoid cop.	0.036	3.912	0.564	0.028	0.024	1.971	1.179	1.800	2.781	3.371	1.184	1.686
Cyclopoid naup.	0.012	0.803	0.154	0.010	0.030	1.274	0.263	0.200	0.036	0.143	0.094	0.309
Harpactacoid sp.	-	-	-	-	-	-	-	-	-	-	-	-
Veliger	-	0.104	0.041	0.062	1.860	4.009	3.833	14.440	2.955	14.855	3.952	4.786
Daily Totals	0.485	5.361	1.529	1.688	7.203	24.850	17.432	85.956	24.970	40.574	14.808	

Appendix 1b. Depth-weighted biomass (mg/m³) of each zooplankton species on each sampling date at station E1 in 1994. Seasonal weighted mean (SWM) biomass is given for each species. cop.= copepidid, naup.= nauplii

Species	May-10	May-18	Jun-01	Jun-16	Jun-21	Jun-28	Jul-05	Jul-13	Jul-19	Jul-27	Aug-02	Aug-09	Aug-16
Bosmina sp.	0.005	0.006	0.027	0.029	0.373	0.449	0.265	0.625	0.224	0.515	0.012	0.015	0.196
Daphnia longiremis	-	-	-	-	-	-	-	-	-	-	-	-	-
D. retrocurva	-	-	-	-	-	0.012	0.412	3.030	0.556	0.279	0.505	-	0.006
D. galeata mendotae	-	-	-	-	-	-	0.064	-	-	-	-	-	0.287
Diaphanosoma sp.	-	-	-	-	-	-	-	0.220	-	-	0.063	-	-
Eubosmina sp.	-	-	-	-	-	-	0.073	0.056	0.019	-	-	-	-
Polyphemus pediculus	-	-	-	-	-	-	-	-	0.165	-	-	-	-
Holopedium gibberum	-	-	-	-	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-	-	-	-	0.011	-
Chydorus sphaericus	-	-	-	-	-	-	-	0.009	0.016	0.012	0.016	0.003	0.005
Alona sp.	-	-	-	-	-	-	-	-	0.165	-	-	-	-
Bythotrephes cederstroemi	-	-	-	-	-	-	-	-	-	0.741	-	0.935	0.172
Leptodora kindti	-	-	0.012	-	-	0.096	0.171	0.424	-	0.160	2.303	0.030	0.100
Leptodiaptomus ashlandi	-	-	-	-	-	-	-	0.183	-	0.687	-	-	-
L. minutus	-	0.011	0.015	-	-	0.022	0.023	0.197	0.214	4.213	1.560	1.231	0.339
L. sicilis	-	-	-	-	-	-	-	-	-	-	-	-	-
L. siciloides	-	-	-	-	-	-	-	-	-	-	-	-	-
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-	-	-	-	-
S. oregonensis	-	-	-	-	-	-	-	0.327	-	1.859	0.446	0.725	1.359
Epischura lacustris	-	-	0.019	-	-	5.814	1.446	2.806	0.459	8.632	15.810	1.571	0.872
Epischura cop.	-	-	0.031	0.037	0.043	0.235	0.068	0.137	1.059	2.384	1.309	1.365	1.591
Eurytemora affinis	-	-	-	-	-	0.179	0.675	0.162	0.024	0.514	-	-	-
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-	-	-	-	-
Calanoid cop.	0.001	0.015	0.005	0.082	0.098	0.524	1.279	1.223	0.437	3.647	1.539	1.436	0.249
Calanoid naup.	0.001	0.011	0.038	0.057	0.038	0.176	0.905	0.085	1.046	0.179	0.642	0.603	0.460
Diacyclops thomasi	0.006	0.226	0.021	0.037	-	0.471	1.470	2.764	0.113	34.500	10.562	0.046	0.085
Acanthocyclops vernalis	-	-	-	-	-	-	-	0.081	-	-	-	0.058	-
Mesocyclops edax	-	-	-	-	-	0.022	-	0.032	-	0.375	0.289	0.026	0.080
Tropocyclops extensus	-	0.003	0.001	0.002	-	-	-	-	0.003	-	0.023	0.020	-
Eucyclops agilis	-	-	0.003	0.007	0.004	-	-	-	-	-	-	-	-
E. speratus	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyclopoid cop.	0.037	0.179	0.271	0.271	0.088	0.699	0.959	14.946	0.745	45.609	9.399	0.569	1.816
Cyclopoid naup.	0.001	0.030	0.109	0.084	0.018	0.064	0.102	1.406	0.031	0.280	0.420	0.197	0.326
Harpactacoid sp.	-	-	-	-	-	-	-	-	-	-	-	-	-
Veliger	-	0.007	0.037	0.012	0.500	0.549	0.521	4.458	3.147	0.686	2.516	0.361	3.986
Daily Totals	0.051	0.488	0.589	0.618	1.162	9.312	8.433	33.171	8.423	105.272	47.414	9.202	11.929

Appendix 1b. Continued.

Species	Aug-23	Aug-30	Sep-07	Sep-13	Sep-22	Oct-05	Oct-18	Nov-08	SWM
Bosmina sp.	0.014	0.024	0.048	0.219	1.084	1.856	0.153	0.041	0.333
Daphnia longiremis	-	-	-	-	0.004	0.030	-	-	0.002
D. retrocurva	-	-	-	-	-	0.002	-	-	0.185
D. galeata mendotae	-	-	-	-	0.021	-	0.028	-	0.018
Diaphanosoma sp.	-	-	-	-	-	-	-	-	0.011
Eubosmina sp.	-	-	-	-	-	-	-	-	0.006
Polyphemus pediculus	-	-	-	-	-	-	-	-	0.006
Holopedium gibberum	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	0.003	0.035	-	-	-	-	0.002
Chydorus sphaericus	0.001	-	-	-	-	-	-	-	0.002
Alona sp.	-	-	-	-	-	-	-	-	0.006
Bythotrephes cederstroemi	-	0.509	-	1.521	-	-	-	-	0.155
Leptodora kindti	0.094	0.145	0.040	-	0.032	-	0.100	-	0.144
Leptodiaptomus ashlandi	-	-	-	-	-	-	-	-	0.033
L. minutus	0.317	0.666	0.072	0.060	0.181	0.033	0.011	-	0.357
L. sicilis	-	-	-	-	-	-	-	-	-
L. siciloides	-	-	-	-	-	-	-	-	-
Skistodiaptomus reighardi	-	-	0.007	0.049	-	-	-	-	0.002
S. oregonensis	0.162	15.427	0.015	0.256	0.181	0.023	0.030	-	0.849
Epischura lacustris	1.610	1.957	-	-	-	0.035	-	-	1.546
Epischura cop.	3.784	1.235	0.296	0.299	0.373	0.186	0.311	0.054	0.604
Eurytemora affinis	-	-	-	-	-	-	-	0.009	0.062
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-
Calanoid cop.	0.679	6.116	0.653	0.841	0.843	0.969	0.687	0.221	0.941
Calanoid naup.	0.481	0.335	0.272	0.134	0.106	0.137	0.038	0.011	0.235
Diacyclops thomasi	0.032	-	0.005	0.047	0.016	0.014	-	0.004	1.922
Acanthocyclops vernalis	-	-	0.008	-	-	-	-	-	0.006
Mesocyclops edax	0.095	0.207	0.007	0.007	0.024	0.013	-	0.007	0.046
Tropocyclops extensus	0.012	0.030	0.005	0.032	0.066	0.081	0.054	0.034	0.022
Eucyclops agilis	-	-	-	-	-	-	-	-	0.001
E. speratus	-	-	-	-	-	-	-	-	-
Cyclopoid cop.	1.526	2.263	0.608	2.936	1.025	0.975	0.833	0.256	3.423
Cyclopoid naup.	0.088	0.147	0.081	0.117	0.085	0.140	0.014	0.017	0.158
Harpactacoid sp.	-	-	-	-	-	-	-	-	-
Veliger	4.409	71.994	2.367	1.737	2.500	0.315	0.015	0.105	4.119
Daily Totals	13.304	101.055	4.487	8.290	6.541	4.809	2.274	0.759	

Appendix 2a. Depth-weighted density (no./m^3) of each zooplankton species on each sampling date at station E1 in 1993. Seasonal weighted mean (SWM) density is given for each species. cop.= copepidid, naup.= nauplii

Species	May-14	May-27	Jun-11	Jun-24	Jul-07	Jul-21	Aug-12	Aug-25	Sep-24	Oct-05	Oct-20	SWM
Bosmina sp.	16.56	1202.55	1222.93	2252.23	5503.19	18099.36	998.73	244.59	163.06	295.54	346.50	3119.15
Daphnia longiremis	-	-	-	-	-	-	-	-	-	-		-
D. retrocurva	14.01	-	-	-	2.55	101.91	-	-	-	-	-	12.33
D. galeata mendotae	-	-	-	-	-	10.19	-	-	-	-	20.38	2.12
Diaphanosoma sp.	-	-	-	-	-	40.76	30.57	-	-	-	-	7.98
Eubosmina sp.	-	-	-	-	-	40.76	-	-	-	-	-	4.61
Polyphemus pediculus	-	-	-	-	-	-	-	-	-	-	-	-
Holopedium gibberum	-	-	-	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-	-	-	-	-
Chydorus sphaericus	-	-	-	-	-	-	-	40.76	20.38	76.43	81.53	18.23
Alona sp.	-	-	1.27	-	-	-	-	-	-	-	-	0.11
Bythotrephes cederstroemi	-	-	-	-	-	-	1.27	7.64	5.10	5.10	-	2.25
Leptodora kindti	-	-	-	-	5.10	71.34	61.15	-	-	-	-	15.24
Leptodiaptomus ashlandi	-	-	-	-	-	40.76	20.38	-	10.19	-	-	8.17
L. minutus	1.27	-	-	-	2.55	40.76	621.66	6929.94	366.88	81.53	10.19	1064.82
L. sicilis	-	-	-	-	-	-	-	-	-	-	-	-
L. siciloides	-	-	-	-	-	-	-	-	10.19	-	-	1.31
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-	-	-	-
S. oregonensis	1.27	-	-	-	-	-	40.76	-	30.57	50.96	35.67	14.33
Epischura lacustris	-	-	-	-	2.55	336.31	40.76	1059.87	428.03	-	10.19	241.76
Epischura cop.	-	20.38	10.19	15.29	20.38	101.91	2201.27	7337.58	2608.92	326.12	81.53	1618.56
Eurytemora affinis	-	-	-	2.55	78.98	-	-	-	-	-	-	6.91
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-	-	-	-
Calanoid cop.	3.82	20.38	40.76	519.75	1732.48	713.38	937.58	3342.68	1752.87	7419.11	2119.75	1763.66
Calanoid naup.	90.45	163.06	214.01	1202.55	3750.32	652.23	6766.88	4728.66	3057.33	1793.63	448.41	2473.66
Diacyclops thomasi	92.99	2.55	-	-	-	142.68	71.34	-	-	10.19	30.57	30.30
Acanthocyclops vernalis	-	-	-	-	-	-	10.19	-	-	-	-	1.12
Mesocyclops edax	-	-	-	-	-	50.96	10.19	-	-	20.38	-	8.56
Tropocyclops extensus	5.10	1.27	2.55	-	2.55	81.53	142.68	2527.39	1610.19	9294.27	2568.15	1456.10
Eucyclops agilis	1.27	10.19	-	-	-	-	-	-	-	-	-	0.95
E. speratus	-	-	-	-	-	-	-	-	-	-	-	-
Cyclopoid cop.	25.48	5503.19	754.14	45.86	61.15	2160.51	1263.69	4484.08	4973.25	5299.36	1447.13	2693.70
Cyclopoid naup.	108.28	6889.17	1416.56	91.72	366.88	15816.56	2771.98	2282.80	326.12	1304.46	692.99	3360.11
Harpactacoid sp.	-	-	-	-	-	-	-	-	-	-	-	-
Veliger	-	40.76	20.38	40.76	1059.87	1997.45	2242.04	8071.34	1630.57	8886.62	2160.51	2701.73
Daily Totals	360.51	13853.50	3682.80	4170.70	12588.54	40499.36	18233.12	41057.33	16993.63	34863.70	10053.51	

# Appendix 2b. Depth-weighted density (no./m^3) of each zooplankton species on each sampling date at station E1 in 1994.
cop.= copepidid, naup.= nauplii

Species	May-10	May-18	Jun-01	Jun-16	Jun-21	Jun-28	Jul-05	Jul-13	Jul-19	Jul-27	Aug-02	Aug-09
Bosmina sp.	8.92	6.37	28.03	84.08	759.24	662.42	499.36	1549.05	336.31	774.52	40.76	20.38
Daphnia longiremis	-	-	-	-	-	-	-	-	-	-	-	-
D. retrocurva	-	-	-	-	-	10.19	122.29	611.47	71.34	122.29	163.06	-
D. galeata mendotae	-	-	-	-	-	-	10.19	-	-	-	-	-
Diaphanosoma sp.	-	-	-	-	-	-	-	40.76	-	-	20.38	-
Eubosmina sp.	-	-	-	-	-	-	61.15	40.76	10.19	-	-	-
Polyphemus pediculus	-	-	-	-	-	-	-	-	10.19	-	-	-
Holopedium gibberum	-	-	-	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-	-	-	-	5.10
Chydorus sphaericus	-	-	-	-	-	-	-	40.76	20.38	76.43	81.53	10.19
Alona sp.	-	-	-	-	-	-	-	-	10.19	-	-	-
Bythotrephes cederstroemi	-	-	-	-	-	-	-	-	-	3.82	-	7.64
Leptodora kindti	-	-	1.27	-	-	10.19	15.29	81.53	-	40.76	264.97	10.19
Leptodiaptomus ashlandi	-	-	-	-	-	-	-	30.57	-	122.29	-	-
L. minutus	-	2.55	3.82	-	-	5.10	5.10	40.76	43.31	896.82	346.50	315.92
L. sicilis	-	-	-	-	-	-	-	-	-	-	-	-
L. siciloides	-	-	-	-	-	-	-	-	-	-	-	-
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-	-	-	-
S. oregonensis	-	-	-	-	-	-	-	40.76	-	203.82	61.15	101.91
Epischura lacustris	-	-	1.27	-	-	371.98	86.62	183.44	28.03	570.70	1039.49	122.29
Epischura cop.	-	-	15.29	15.29	12.74	50.96	50.96	40.76	580.89	285.35	856.05	672.61
Eurytemora affinis	-	-	-	-	-	20.38	86.62	20.38	2.55	81.53	-	-
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-	-	-	-
Calanoid cop.	1.27	10.19	3.82	94.27	58.60	326.12	937.58	570.70	305.73	1304.46	468.79	998.73
Calanoid naup.	11.47	137.58	163.06	407.64	224.20	1324.84	5707.01	1141.40	5421.66	2038.22	3342.68	4321.02
Diacyclops thomasi	1.27	42.04	5.10	8.92	-	71.34	259.87	519.75	22.93	6929.94	1997.45	10.19
Acanthocyclops vernalis	-	-	-	-	-	-	-	10.19	-	-	-	25.48
Mesocyclops edax	-	-	-	-	-	5.10	-	10.19	-	122.29	81.53	10.19
Tropocyclops extensus	-	2.55	1.27	1.27	-	-	-	-	2.55	-	20.38	20.38
Eucyclops agilis	-	-	1.27	2.55	1.27	-	-	-	-	-	-	-
E. speratus	-	-	-	-	-	-	-	-	-	-	-	-
Cyclopoid cop.	21.66	154.14	270.06	303.19	91.72	672.61	631.85	16957.96	631.85	28698.09	5014.01	835.67
Cyclopoid naup.	5.10	310.83	1080.26	815.29	163.06	652.23	896.82	15490.45	326.12	3505.73	2649.68	2527.39
Harpactacoid sp.	-	-	-	-	-	-	-	-	-	-	-	-
Veliger	-	2.55	17.83	10.19	366.88	315.92	264.97	2568.15	1712.10	407.64	1385.99	178.34
Daily Totals	49.68	668.79	1592.36	1742.68	1677.71	4499.36	9635.67	39989.81	9536.31	46184.72	17834.39	10193.62

Appendix 2b. Continued.

Species	Aug-16	Aug-23	Aug-30	Sep-07	Sep-13	Sep-22	Oct-05	Oct-18	Nov-08	SWM
Bosmina sp.	326.12	20.38	40.76	96.82	631.85	3587.26	4443.31	280.26	70.06	792.24
Daphnia longiremis	-	-	-	-	--	2.55	10.19	-	-	0.88
D. retrocurva	5.10	-	-	-	-	-	2.55	-	-	42.60
D. galeata mendotae	20.38	-	-	-	-	5.10	-	7.64	-	2.23
Diaphanosoma sp.	-	-	-	-	-	-	-	-	-	2.30
Eubosmina sp.	-	-	-	-	-	-	-	-	-	4.48
Polyphemus pediculus	-	-	-	-	-	-	-	-	-	0.39
Holopedium gibberum	-	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	--	1.27	10.19	-	-	-	-	0.66
Chydorus sphaericus	20.38	2.55	-	-	-	-	-	-	-	9.48
Alona sp.	-	-	-	-	-	-	-	-	-	0.39
Bythotrephes cederstroemi	1.27	-	6.37	-	-	6.37	-	-	-	1.01
Leptodora kindti	25.48	15.29	40.76	2.55	-	10.19	-	5.10	-	20.12
Leptodiaptomus ashlandi	-	-	-	-	-	-	-	-	-	5.88
L. minutus	86.62	81.53	163.06	19.11	12.74	48.41	7.64	2.55	-	81.27
L. sicilis	-	-	-	-	-	-	-	-	-	-
L. siciloides	-	-	-	-	-	-	-	-	-	-
Skistodiaptomus reighardi	-	-	-	1.27	10.19	-	-	-	-	0.47
S. oregonensis	178.34	20.38	2119.75	2.55	35.67	22.93	2.55	5.10	-	114.12
Epischura lacustris	86.62	122.29	163.06	-	-	-	2.55	-	-	104.83
Epischura cop.	1233.12	1528.66	774.52	285.35	234.40	428.03	112.10	188.54	31.85	309.96
Eurytemora affinis	-	-	-	-	-	-	-	-	1.27	8.44
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-	-
Calanoid cop.	132.48	733.76	2282.80	570.70	550.32	591.08	489.17	397.45	118.47	484.92
Calanoid naup.	4647.13	3668.79	4035.67	1997.45	998.73	794.90	1345.22	178.34	49.68	1721.66
Diacyclops thomasi	30.57	5.10	-	1.27	12.74	2.55	5.10	-	1.27	378.59
Acanthocyclops vernalis	-	-	-	5.10	-	-	-	-	-	1.57
Mesocyclops edax	30.57	35.67	81.53	2.55	2.55	7.64	5.10	-	2.55	15.68
Tropocyclops extensus	-	10.19	40.76	5.10	35.67	71.34	89.17	61.15	40.76	24.42
Eucyclops agilis	-	-	-	-	-	-	-	-	-	0.28
E. speratus	-	-	-	-	-	-	-	-	-	-
Cyclopoid cop.	3709.55	1915.92	2771.98	907.01	5177.07	998.73	1467.52	947.77	318.47	2945.32
Cyclopoid naup.	4484.08	1263.69	2242.04	754.14	1365.61	1019.11	1752.87	129.94	113.38	1756.40
Harpactacoid sp.	-	-	-	-	-	-	-	-	-	-
Veliger	2364.33	2608.92	49895.54	1385.99	1121.02	1610.19	173.25	10.19	57.33	2734.83
Daily Totals	17382.17	12033.12	64658.60	6038.22	10205.10	9200.00	9908.28	2214.01	805.10	

Appendix 3a. Depth-weighted biomass (mg/m^3) of each zooplankton species on each sampling date at station E2 in 1993. Seasonal weighted mean (SWM) biomass is given for each species. cop.= copepidid, naup.= nauplii.

Species	May-14	May-27	Jun-11	Jun-24	Jul-07	Jul-21	Aug-12	Aug-25	Sep-24	Oct-05	SWM
Bosmina sp.	-	0.041	0.103	2.465	11.573	16.146	0.994	4.279	3.744	0.645	4.657
Daphnia longiremis	-	-	-	0.002	0.028	-	-	-	0.022	-	0.006
D. retrocurva	-	-	-	0.035	-	-	-	-	-	-	0.003
D. galeata mendotae	-	-	-	0.003	-	-	-	-	-	-	0.000
Diaphanosoma sp.	-	-	-	-	-	-	-	-	-	-	-
Eubosmina sp.	-	-	-	0.053	0.062	-	-	0.075	-	-	0.022
Polyphemus pediculus	-	-	-	-	-	-	-	-	-	-	-
Holopedium gibberum	-	-	-	-	0.145	-	-	-	0.022	-	0.017
Sida crystallina	-	-	-	-	-	-	-	-	-	-	-
Chydorus sphaericus	-	-	-	-	-	-	-	-	-	-	-
Alona sp.	-	-	-	-	-	-	-	-	-	-	-
Bythotrephes cederstroemi	-	-	-	-	-	1.112	0.607	0.752	1.355	0.514	0.538
Leptodora kindti	-	-	-	2.132	0.858	-	-	-	-	-	0.273
Leptodiaptomus ashlandi	-	-	-	0.255	1.162	0.200	0.911	0.665	0.751	0.365	0.488
L. minutus	0.005	0.011	-	0.163	0.968	0.824	2.449	1.730	1.267	0.985	0.984
L. sicilis	-	-	0.044	-	-	-	0.250	0.171	0.261	0.187	0.104
L. siciloides	-	-	-	0.058	0.120	-	0.196	-	0.136	0.172	0.066
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-	-	-
S. oregonensis	-	-	-	0.026	0.039	0.621	0.780	0.797	1.305	1.449	0.539
Epischura lacustris	-	-	0.273	13.130	4.930	11.855	9.521	8.865	3.086	1.120	6.119
Epischura cop.	-	-	0.362	0.013	0.502	1.916	0.855	0.755	0.993	0.111	0.685
Eurytemora affinis	-	0.035	0.200	0.134	0.593	1.749	0.086	0.061	-	-	0.329
Limnocalanus macrurus	-	-	-	-	-	0.044	-	0.011	-	-	0.007
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-	-	-
Calanoid cop.	0.002	0.169	0.204	0.049	0.516	1.557	1.189	0.763	2.809	4.156	1.101
Calanoid naup.	0.001	0.084	0.077	0.005	1.034	1.197	0.283	0.298	0.338	0.072	0.393
Diacyclops thomasi	0.390	0.095	1.200	0.939	1.926	3.635	2.762	2.850	4.154	1.560	2.275
Acanthocyclops vernalis	-	-	-	0.055	0.073	0.017	0.158	-	0.030	0.183	0.045
Mesocyclops edax	0.006	-	0.046	0.228	0.464	0.729	0.382	0.422	1.751	1.504	0.576
Tropocyclops extensus	-	-	0.019	0.010	0.005	0.058	0.068	0.405	4.516	2.883	0.832
Eucyclops agilis	-	-	-	-	-	-	-	-	-	-	-
E. speratus	-	-	-	-	-	-	-	-	-	-	-
Cyclopoid cop.	0.069	0.045	0.086	0.137	0.739	1.814	1.511	2.073	2.153	1.014	1.163
Cyclopoid naup.	0.004	0.015	0.022	0.014	0.236	0.213	0.117	0.186	0.171	0.092	0.124
Harpactacoid sp.	0.002	-	-	0.001	0.003	-	0.015	0.014	-	-	0.004
Veliger	0.048	0.132	0.577	11.930	48.816	18.380	8.642	12.969	18.653	58.454	15.897
Daily Totals	0.527	0.627	3.213	31.839	74.792	62.068	31.777	38.141	47.516	75.466	

Appendix 3b. Depth-weighted biomass (mg/m^3) of each zooplankton species on each sampling date at station E2 in 1994. Seasonal weighted mean (SWM) biomass is given for each species. cop.= copepidid, naup.= nauplii.

Species	May-10	May-18	Jun-01	Jun-16	Jun-21	Jun-28	Jul-05	Jul-13	Jul-19	Jul-27	Aug-02	Aug-09	Aug-16
Bosmina sp.	0.006	-	0.008	0.048	0.032	2.194	2.557	6.631	0.525	2.428	1.557	0.777	6.544
Daphnia longiremis	-	-	-	-	0.040	0.079	-	0.001	-	0.025	0.492	0.092	0.261
D. retrocurva	-	-	-	0.095	0.466	3.214	0.485	2.964	0.076	0.252	4.618	1.250	8.648
D. galeata mendotae	-	-	-	-	0.077	0.474	-	0.132	0.975	0.379	2.544	0.012	-
Diaphanosoma sp.	-	-	-	-	-	-	-	-	-	-	-	-	-
Eubosmina sp.	-	-	-	0.012	0.088	0.747	0.112	0.096	-	0.082	-	-	-
Polyphemus pediculus	-	-	-	-	-	-	-	-	-	-	-	-	-
Holopedium gibberum	-	-	-	-	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-	-	-	-	-	-
Chydorus sphaericus	-	-	-	-	-	-	-	-	-	-	-	-	-
Alona sp.	-	-	-	-	-	-	-	-	-	-	-	-	-
Bythotrephes cederstroemi	-	-	-	-	0.006	0.256	3.823	1.029	1.360	0.498	0.270	0.379	1.244
Leptodora kindti	-	-	-	-	-	-	-	-	-	0.114	-	-	-
Leptodiaptomus ashlandi	0.044	0.036	-	-	-	0.702	0.594	1.525	0.244	1.515	1.332	0.284	0.638
L. minutus	-	0.008	0.009	0.017	-	0.853	0.884	0.645	0.889	0.884	0.626	1.201	0.598
L. sicilis	-	-	-	0.038	-	0.289	-	-	0.261	-	0.465	0.287	0.064
L. siciloides	-	-	-	-	-	-	-	-	0.165	-	0.067	-	-
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-	-	-	-	-
S. oregonensis	-	0.040	-	-	-	-	0.582	0.020	0.121	0.349	0.362	0.194	0.417
Epischura lacustris	-	-	-	1.791	3.700	6.623	11.144	10.972	3.271	8.298	4.986	6.915	2.925
Epischura cop.	-	-	-	3.451	0.230	0.407	0.069	0.570	0.533	0.832	0.206	1.540	1.408
Eurytemora affinis	-	-	-	0.149	0.171	0.104	-	-	-	0.416	-	0.049	0.078
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	0.021	-	-	-	-	-	-	-	-	-
Calanoid cop.	0.021	0.014	0.003	-	0.006	0.090	0.079	0.110	0.460	1.281	1.517	0.729	0.301
Calanoid naup.	0.001	-	0.019	0.105	0.003	0.065	0.090	0.246	0.390	0.336	0.200	0.309	0.156
Diacyclops thomasi	0.351	0.314	0.098	0.851	1.582	5.281	3.890	3.911	5.688	16.839	9.090	3.262	5.023
Acanthocyclops vernalis	-	-	-	-	0.015	-	-	-	0.046	0.063	-	-	0.015
Mesocyclops edax	-	0.016	-	0.009	0.119	0.032	0.008	0.288	0.219	-	1.034	0.106	1.254
Tropocyclops extensus	-	0.002	-	0.003	-	-	-	-	-	0.010	-	0.021	0.023
Eucyclops agilis	-	-	-	-	-	-	-	-	-	-	-	-	-
E. speratus	-	0.011	-	-	-	-	-	-	-	-	-	-	-
Cyclopoid cop	0.036	0.106	0.028	0.214	0.166	1.378	6.851	2.728	3.720	6.467	3.516	2.065	3.470
Cyclopoid naup	0.008	0.003	0.003	0.011	0.006	0.202	1.016	0.243	0.515	1.079	0.250	0.238	0.376
Harpactaoid sp.	0.001	0.002	0.005	0.001	-	-	-	-	0.010	-	-	-	-
Veliger	0.036	0.040	0.002	0.014	1.166	2.868	1.710	11.236	2.192	9.159	5.878	2.069	3.087
Daily Totals	0.504	0.592	0.175	6.830	7.873	25.860	33.896	43.345	21.658	51.305	39.011	21.779	36.530

Appendix 3b. Continued.

Species	Aug-23	Aug-30	Sep-13	Sep-22	Oct-05	Oct-18	Nov-14	SWM
Bosmina sp.	2.524	3.544	2.031	2.466	3.293	1.017	1.983	1.910
Daphnia longiremis	0.175	0.632	0.032	-	0.314	0.045	0.167	0.118
D. retrocurva	27.727	17.287	0.319	0.125	1.051	0.004	0.063	2.912
D. galeata mendotae	-	-	-	-	-	-	-	0.164
Diaphanosoma sp.	-	-	-	-	-	-	-	-
Eubosmina sp.	-	-	0.011	-	-	-	0.200	0.057
Polyphemus pediculus	-	-	-	-	-	-	-	-
Holopedium gibberum	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-
Chydorus sphaericus	-	-	-	-	-	-	-	-
Alona sp.	-	-	-	-	-	-	-	-
Bythotrephes cederstroemi	1.111	0.910	0.841	1.945	0.033	-	1.983	0.742
Leptodora kindti	0.054	0.060	-	-	0.084	-	-	0.015
Leptodiaptomus ashlandi	0.395	0.281	0.012	0.166	-	0.008	-	0.297
L. minutus	0.159	0.545	0.293	0.085	0.718	0.240	2.363	0.552
L. sicilis	0.323	0.644	0.136	0.104	0.557	0.190	1.405	0.274
L. siciloides	0.143	-	-	-	-	-	-	0.014
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-
S. oregonensis	-	0.247	0.350	0.411	2.053	0.597	1.645	0.462
Epischura lacustris	4.756	1.694	0.228	0.252	0.112	0.030	0.200	2.608
Epischura cop.	1.074	0.282	0.283	0.131	0.181	-	0.026	0.493
Eurytemora affinis	-	-	-	-	-	-	0.070	0.042
Limnocalanus macrurus	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	-	-	-	-	0.001
Calanoid cop.	0.880	0.711	0.510	0.914	1.587	0.748	1.487	0.621
Calanoid naup.	0.677	0.073	0.058	0.037	0.009	0.012	0.009	0.111
Diacyclops thomasi	2.803	3.297	0.146	0.068	1.233	0.022	1.255	2.567
Acanthocyclops vernalis	0.106	-	-	-	-	0.026	0.088	0.018
Mesocyclops edax	0.601	1.783	0.710	0.180	2.472	0.087	0.549	0.508
Tropocyclops extensus	0.219	0.029	0.062	0.051	0.357	0.112	0.755	0.110
Eucyclops agilis	-	-	-	-	-	-	-	-
E. speratus	-	-	-	-	-	-	-	0.001
Cyclopoid cop	3.207	2.654	0.901	0.688	2.352	0.623	1.230	1.839
Cyclopoid naup	0.421	0.405	0.242	0.242	0.372	0.050	0.044	0.251
Harpactaoid sp.	-	0.009	-	0.003	-	0.001	-	0.002
Veliger	2.320	1.479	1.817	15.255	1.890	1.093	4.340	3.184
Daily Totals	49.673	36.566	8.982	23.123	18.668	4.904	19.862	

Appendix 4a. Depth-weighted density (no./m³) of each zooplankton species on each sampling date at station E2 in 1993. Seasonal weighted mean (SWM) density is given for each species. cop.= copepidid, naup.= nauplii.

Species	May-14	May-27	Jun-11	Jun-24	Jul-07	Jul-21	Aug-12	Aug-25	Sep-24	Oct-05	SWM
Bosmina sp.	-	30.84	49.32	2486.86	14173.73	18982.09	945.45	3563.03	3698.55	838.66	5139.29
Daphnia longiremis	-	-	-	2.72	15.57	-	-	-	12.42	-	3.47
D. retrocurva	-	-	-	5.45	-	-	-	-	-	-	0.49
D. galeata mendotae	-	-	-	6.21	-	-	-	-	-	-	0.56
Diaphanosoma sp.	-	-	-	-	-	-	-	-	-	-	-
Eubosmina sp.	-	-	6.14	32.25	13.08	-	-	17.94	-	-	7.41
Polyphemus pediculus	-	-	-	-	-	-	-	-	-	-	-
Holopedium gibberum	-	-	-	-	31.14	-	-	-	26.42	-	6.68
Sida crystallina	-	-	-	-	-	-	-	-	-	-	-
Chydorus sphaericus	-	-	-	-	-	-	-	-	-	-	-
Alona sp.	-	-	-	-	-	-	-	-	-	-	-
Bythotrephes cederstroemi	-	-	-	-	-	5.76	4.14	6.18	2.88	4.59	2.73
Leptodora kindti	-	-	-	31.04	83.83	-	-	-	-	-	10.66
Leptodiaptomus ashlandi	-	-	-	32.51	173.47	35.91	170.18	125.90	138.93	88.28	86.32
L. minutus	2.78	2.37	-	26.54	145.16	131.28	472.25	284.94	205.76	176.56	168.74
L. sicilis	-	-	6.14	-	-	-	52.13	9.15	34.84	44.14	14.94
L. siciloides	-	-	-	6.21	17.13	-	22.68	-	26.42	44.14	10.37
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-	-	-
S. oregonensis	-	-	-	5.45	7.79	101.59	97.17	109.05	154.19	176.56	70.70
Epischura lacustris	-	-	61.40	801.20	314.24	839.35	921.74	823.37	288.20	132.42	493.72
Epischura cop.	-	-	153.49	2.72	294.56	919.86	408.96	525.74	567.17	88.28	370.08
Eurytemora affinis	-	4.74	24.56	11.66	61.04	92.85	14.72	27.62	-	-	27.14
Limnocalanus macrurus	-	-	-	-	-	33.86	-	9.15	-	-	5.60
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-	-	-
Calanoid cop.	2.78	97.26	110.52	26.27	383.74	763.82	656.03	466.09	1405.70	1853.89	574.39
Calanoid naup.	5.56	198.53	178.05	15.14	4903.72	5300.52	1682.38	2074.79	1566.27	529.68	1917.96
Diacyclops thomasi	133.32	30.84	399.09	201.52	502.37	1134.83	871.22	807.81	1468.94	662.10	715.86
Acanthocyclops vernalis	-	-	-	20.82	31.15	16.93	52.12	-	12.42	132.42	20.07
Mesocyclops edax	2.78	-	18.42	56.51	73.81	120.55	101.31	80.89	486.57	308.98	134.46
Tropocyclops extensus	-	-	6.14	10.90	4.05	16.93	58.91	406.13	5883.60	3487.07	1042.66
Eucyclops agilis	-	-	-	-	-	-	-	-	-	-	-
E. speratus	-	-	-	-	-	-	-	-	-	-	-
Cyclopoid cop.	83.33	52.19	85.96	138.81	825.93	1835.01	1759.17	2978.68	2501.49	1544.91	1410.18
Cyclopoid naup.	22.22	114.77	49.12	87.52	1558.05	998.14	951.93	1717.45	1572.73	882.80	925.40
Harpactacoid sp.	2.78	-	-	2.72	4.05	-	15.91	18.47	-	-	5.44
Veliger	36.11	78.28	1085.21	17553.46	28476.55	8219.08	9430.86	10853.73	29703.47	53674.45	14441.82
Daily Totals	291.66	609.82	2233.56	21564.51	52094.19	39548.36	18689.25	24906.10	49756.95	64669.93	

Appendix 4b. Depth-weighted density (no./m³) of each zooplankton species on each sampling date at station E2 in 1994. Seasonal weighted mean (SWM) density is given for each species. cop.= copepidid, naup.= nauplii.

Species	May-10	May-18	Jun-01	Jun-16	Jun-21	Jun-28	Jul-05	Jul-13	Jul-19	Jul-27	Aug-02
Bosmina sp.	7.26	-	5.34	41.55	45.00	1565.24	1569.39	3940.61	358.63	1344.48	971.78
Daphnia longiremis	-	-	-	-	12.54	21.40	-		0.73	15.89	130.92
D. retrocurva	-	-	-	20.78	95.06	294.57	73.64	41.72	7.86	123.53	458.45
D. galeata mendotae	-	-	-	-	3.40	21.40	-	36.85	142.00	31.79	195.78
Diaphanosoma sp.	-	-	-	-	-	-	-	-	-	-	-
Eubosmina sp.	-	-	-	3.46	45.30	345.88	58.42	72.24	-	15.89	-
Polyphemus pediculus	-	-	-	-	-	-	-	-	-	-	-
Holopedium gibberum	-	-	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-	-	-	-
Chydorus sphaericus	-	-	-	-	-	-	-	-	-	-	-
Alona sp.	-	-	-	-	-	-	-	-	-	-	-
Bythotrephes cederstroemi	-	-	-	-	0.37	1.86	13.73	3.38	4.80	1.83	1.02
Leptodora kindti	-	-	-	-	-	-	-	-	-	16.27	-
Leptodiaptomus ashlandi	7.26	5.44	-	-	-	102.95	86.69	187.64	39.19	243.44	203.18
L. minutus	-	1.81	1.78	3.46	-	135.67	127.94	58.51	128.54	146.44	107.50
L. sicilis	-	-	-	3.46	-	28.06	-	-	23.48	-	45.72
L. siciloides	-	-	-	-	-	-	-	-	15.72	-	10.62
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-	-	-
S. oregonensis	-	5.44	-	-	-	-	74.95	5.60	19.60	64.70	35.10
Epischura lacustris	-	-	-	276.13	241.65	347.09	589.52	517.38	297.06	785.02	477.83
Epischura cop.	-	-	-	1067.91	44.71	156.45	51.91	330.91	273.55	449.71	139.01
Eurytemora affinis	-	-	-	11.68	15.47	17.36	-	-	-	63.57	-
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	3.46	-	-	-	-	-	-	-
Calanoid cop.	7.26	3.63	1.78	-	1.91	38.76	37.57	36.12	217.05	513.92	415.07
Calanoid naup.	7.26	-	176.13	245.92	9.56	385.58	461.24	1010.63	1757.44	1772.69	1485.52
Diacyclops thomasi	67.14	58.07	24.91	168.68	262.25	988.88	983.05	699.27	1281.13	4334.07	2316.63
Acanthocyclops vernalis	-	-	-	-	2.79	-	-	-	16.04	15.89	-
Mesocyclops edax	-	1.81	-	2.25	14.55	6.66	3.99	47.31	43.49	-	252.12
Tropocyclops extensus	-	1.81	-	1.29	-	-	-	-	-	16.27	-
Eucyclops agilis	-	-	-	-	-	-	-	-	-	-	-
E. speratus	-	1.81	-	-	-	-	-	-	-	-	-
Cyclopoid cop	34.48	68.96	16.01	127.50	99.88	1154.87	7685.82	2280.77	3360.26	6828.94	3332.68
Cyclopoid naup	47.18	16.33	26.69	55.48	38.36	1198.00	7834.78	1483.48	3830.91	7314.69	1984.76
Harpactaoid sp.	1.81	1.81	1.78	0.96	-	-	-	-	11.74	-	-
Veliger	30.85	16.33	3.56	19.00	1772.06	1980.01	1820.95	7530.41	2473.16	9348.03	4076.87
Daily Totals	210.50	183.25	257.98	2052.98	2704.86	8790.71	21473.60	18283.53	14301.64	33447.07	16640.56

Appendix 4b. Continued.

Species	Aug-09	Aug-16	Aug-23	Aug-30	Sep-13	Sep-22	Oct-05	Oct-18	Nov-14	SWM
Bosmina sp.	463.05	3921.71	2437.61	2448.35	5305.37	5581.07	6529.61	1591.47	2036.44	2177.74
Daphnia longiremis	62.74	140.03	96.15	211.89	23.89	-	153.45	13.56	120.98	51.51
D. retrocurva	159.74	1109.14	2941.83	2802.12	66.16	41.94	226.26	1.51	20.16	377.38
D. galeata mendotae	7.93	-	-	-	-	-	-	-	-	15.81
Diaphanosoma sp.	-	-	-	-	-	-	-	-	-	-
Eubosmina sp.	-	-	-	-	3.57	-	-	-	20.16	21.79
Polyphemus pediculus	-	-	-	-	-	-	-	-	-	-
Holopedium gibberum	-	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-	-	-
Chydorus sphaericus	-	-	-	-	-	-	-	-	-	-
Alona sp.	-	-	-	-	-	-	-	-	-	-
Bythotrephes cederstroemi	1.93	5.26	6.43	6.99	5.42	15.78	0.28	-	2036.44	149.44
Leptodora kindti	-	-	14.03	26.25	-	-	28.24	-	-	4.55
Leptodiaptomus ashlandi	51.86	124.84	77.75	55.51	3.57	27.83	-	2.76	-	47.01
L. minutus	266.05	111.75	49.64	144.72	58.48	14.11	193.76	52.50	383.09	101.61
L. sicilis	58.36	12.44	44.81	99.47	24.99	32.54	129.29	56.07	262.12	50.70
L. siciloides	-	-	35.10	-	-	-	-	-	-	2.26
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-	-
S. oregonensis	33.17	71.03	-	44.02	60.76	92.90	460.51	137.37	262.12	88.64
Epischura lacustris	614.22	281.17	453.15	152.30	28.56	41.94	32.32	2.76	20.16	201.81
Epischura cop.	804.04	831.10	599.72	218.88	212.93	134.45	141.19	-	20.16	237.72
Eurytemora affinis	17.28	12.44	-	-	-	-	-	-	20.16	6.68
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-	0.19
Calanoid cop.	358.87	146.85	599.12	619.38	528.01	941.16	1235.37	428.74	625.05	385.44
Calanoid naup.	2248.41	1242.73	5927.23	560.47	412.89	185.41	56.48	71.09	20.16	711.32
Diacyclops thomasi	1030.74	1384.77	814.98	796.07	48.88	23.52	480.40	9.04	443.58	650.48
Acanthocyclops vernalis	-	11.79	49.12	-	-	-	-	9.41	40.33	7.44
Mesocyclops edax	42.55	277.68	143.12	481.27	227.84	61.15	957.26	38.04	201.63	159.56
Tropocyclops extensus	15.87	23.59	304.29	43.74	97.63	78.79	472.05	146.33	987.98	145.76
Eucyclops agilis*	-	-	-	-	-	-	-	-	-	-
E. speratus	-	-	-	-	-	-	-	-	-	0.11
Cyclopoid cop	2300.19	4044.00	3957.14	3583.20	1393.60	948.22	3951.90	960.74	1250.09	2134.78
Cyclopoid naup	2265.88	3147.96	4446.30	5453.96	2687.02	2157.87	4862.97	858.42	564.56	2334.71
Harpactaoid sp.	-	-	-	18.95	-	4.70	-	1.51	-	2.00
Veliger	1673.53	2185.62	2478.60	1804.43	2639.06	15637.83	1948.77	1674.87	5147.01	3163.02
Daily Totals	12476.39	19085.89	25476.14	19571.95	13828.65	26021.22	21860.11	6056.18	14482.39	

Appendix 5a. Depth-weighted biomass (mg/m^3) of each zooplankton species on each sampling date at station E3 in 1993. Seasonal weighted mean (SWM) biomass is given for each species. cop.= copepidid, naup.= nauplii.

Species	May-12	May-27	Jun-09	Jun-24	Jul-07	Jul-21	Jul-29	Aug-12	Aug-25	Sep-24	Oct-05
Bosmina sp.	0.002	0.026	0.039	1.099	3.553	1.554	0.060	2.131	-	0.150	1.516
Daphnia longiremis	-	-	-	-	-	-	-	-	-	-	-
D. retrocurva	-	-	-	-	-	-	-	-	-	-	-
D. galeata mendotae	-	-	-	-	-	-	-	-	-	-	-
Diaphanosoma sp.	-	-	-	-	-	-	-	-	-	-	-
Eubosmina sp.	-	-	-	-	-	-	-	-	-	-	-
Polyphemus pediculus	-	-	-	-	-	-	-	-	-	-	-
Holopedium gibberum	-	-	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-	-	-	-
Chydorus sphaericus	-	-	-	-	-	-	-	-	-	-	-
Alona sp.	-	-	-	-	-	-	-	-	-	-	-
Bythotrephes cederstroemi	-	-	-	-	-	5.171	0.757	1.008	-	0.628	0.185
Leptodora kindti	-	-	-	0.070	0.114	0.109	-	-	-	-	-
Leptodiaptomus ashlandi	-	-	-	-	-	-	-	-	-	-	-
L. minutus	0.013	0.016	-	-	-	6.456	2.911	4.636	10.159	4.445	0.626
L. sicilis	0.015	-	-	-	-	1.378	0.516	-	-	-	-
L. siciloides	-	-	-	-	-	-	-	0.208	-	-	-
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-	-	-
S. oregonensis	-	-	-	-	-	0.847	1.260	2.521	2.996	2.188	3.783
Epischura lacustris	-	0.022	0.019	1.244	0.912	23.460	18.197	5.198	18.534	4.529	0.985
Epischura cop.	-	0.017	0.018	0.149	1.678	1.750	3.138	1.557	3.289	2.822	1.186
Eurytemora affinis	-	-	-	-	1.752	0.086	-	-	-	-	-
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-	-	-
Calanoid cop.	-	-	-	0.037	0.614	0.319	0.569	1.755	1.460	2.267	6.257
Calanoid naup.	0.020	0.026	0.008	0.068	0.317	0.647	1.133	0.808	0.484	1.498	0.547
Diacyclops thomasi	0.837	0.067	0.108	0.226	0.091	0.047	0.266	1.478	-	0.100	1.326
Acanthocyclops vernalis	-	-	-	-	-	-	-	-	-	-	-
Mesocyclops edax	-	-	0.009	-	-	0.089	0.331	0.367	0.095	0.132	-
Tropocyclops extensus	-	0.004	0.003	-	-	0.095	0.029	1.209	1.346	5.841	6.315
Eucyclops agilis	-	-	-	-	-	-	-	-	-	-	-
E. speratus	-	-	-	-	-	-	-	-	-	-	-
Cyclopoid cop.	0.026	0.029	0.073	0.337	0.090	0.346	1.242	2.647	1.986	1.962	0.405
Cyclopoid naup.	0.010	0.026	0.037	0.165	0.108	0.310	0.381	0.444	0.717	0.124	0.060
Harpactacoid sp.	-	0.003	-	0.004	0.193	0.227	0.136	0.384	0.073	-	-
Veliger	-	0.031	0.040	5.559	7.407	0.392	1.673	2.588	22.752	3.448	10.416
Daily Totals	0.923	0.267	0.354	8.958	16.918	43.525	32.635	28.667	63.796	30.134	33.607

Species	Oct-20	SWM
Bosmina sp.	0.208	0.839
Daphnia longiremis	-	-
D. retrocurva	-	-
D. galeata mendotae	-	-
Diaphanosoma sp.	-	-
Eubosmina sp.	-	-
Polyphemus pediculus	-	-
Holopedium gibberum	-	-
Sida crystallina	-	-
Chydorus sphaericus	-	-
Alona sp.	-	-
Bythotrephes cederstroemi	-	0.584
Leptodora kindti	-	0.023
Leptodiaptomus ashlandi	-	-
L. minutus	-	3.004
L. sicilis	0.455	0.151
L. siciloides	-	0.017
Skistodiaptomus reighardi	-	-
S. oregonensis	3.422	1.499
Epischura lacustris	-	6.601
Epischura cop.	0.400	1.534
Eurytemora affinis	-	0.153
Limnocalanus macrurus	-	-
Senecella calanoides cop.	-	-
Calanoid cop.	2.891	1.386
Calanoid naup.	0.121	0.531
Diacyclops thomasi	1.049	0.395
Acanthocyclops vernalis	-	-
Mesocyclops edax	-	0.081
Tropocyclops extensus	7.978	1.915
Eucyclops agilis	-	-
E. speratus	-	-
Cyclopoid cop.	1.668	1.003
Cyclopoid naup.	0.310	0.245
Harpactacoid sp.	-	0.084
Veliger	8.505	6.183
Daily Totals	27.007	

Appendix 5b. Depth-weighted biomass (mg/m^3) of each zooplankton species on each sampling date at station E3 in 1994. Seasonal weighted mean (SWM) biomass is given for each species. cop.= copepidid, naup.= nauplii.

Species	May-10	May-18	Jun-01	Jun-16	Jun-21	Jun-28	Jul-05	Jul-13	Jul-19	Jul-27	Aug-02	Aug-09	Aug-16
Bosmina sp.	0.001	0.017	0.005	0.284	0.616	2.148	0.663	0.025	0.045	0.691	0.045	-	-
Daphnia longiremis	-	-	-	-	-	-	-	-	-	-	-	-	-
D. retrocurva	-	-	-	0.020	0.103	0.797	5.202	0.141	0.029	2.062	0.381	0.024	0.185
D. galeata mendotae	-	-	-	-	-	-	-	-	-	-	-	-	-
Diaphanosoma sp.	-	-	-	-	-	-	-	-	-	-	-	-	-
Eubosmina sp.	-	-	0.003	0.010	-	-	0.049	0.026	-	-	-	-	-
Polyphemus pediculus	-	-	-	-	-	-	-	-	-	-	-	-	-
Holopedium gibberum	-	-	-	-	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-	-	-	-	-	-
Chydorus sphaericus	-	-	-	-	-	0.004	-	-	-	-	-	-	-
Alona sp.	-	-	-	-	-	-	-	-	-	-	-	-	-
Bythotrephes cederstroemi	-	-	-	-	-	-	1.328	0.358	1.753	0.277	0.249	-	1.493
Leptodora kindti	-	-	-	-	-	-	0.046	-	0.145	0.032	0.070	-	0.046
Leptodiaptomus ashlandi	0.008	-	-	-	-	0.037	0.402	0.058	-	1.025	0.344	-	0.358
L. minutus	0.027	0.032	0.012	-	-	0.077	3.415	0.165	0.047	0.841	0.609	0.282	2.291
L. sicilis	-	0.009	-	-	0.043	-	-	-	-	0.686	0.311	0.128	0.355
L. siciloides	-	-	-	-	-	-	-	-	-	-	-	-	-
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-	-	-	-	-
S. oregonensis	-	-	-	-	-	-	-	0.053	-	2.831	0.545	0.507	1.121
Epischura lacustris	-	-	-	0.488	1.844	2.821	23.034	0.891	0.129	13.861	2.359	0.305	6.829
Epischura cop.	-	-	0.013	3.148	0.262	0.107	0.619	0.533	1.753	2.732	1.701	0.158	3.750
Eurytemora affinis	-	-	-	-	0.037	0.446	-	-	-	-	-	-	-
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-	-	-	-	-
Calanoid cop.	-	0.008	0.006	0.018	0.080	0.172	0.439	0.100	0.040	2.166	1.208	0.034	0.545
Calanoid naup.	-	0.003	0.013	0.078	0.023	0.019	0.363	0.379	0.602	0.346	0.748	0.672	0.382
Diacyclops thomasi	0.211	0.170	0.078	0.062	0.097	0.178	1.238	0.666	2.288	20.968	3.524	0.051	0.436
Acanthocyclops vernalis	-	-	0.005	-	-	-	-	-	-	-	-	-	-
Mesocyclops edax	-	-	-	-	-	-	-	-	0.043	1.456	-	-	0.648
Tropocyclops extensus	-	-	-	-	-	-	-	0.011	-	-	0.027	-	0.189
Eucyclops agilis	-	-	-	-	-	-	-	-	-	-	-	-	-
E. speratus	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyclopoid cop.	0.028	0.023	0.063	0.061	0.121	0.115	0.377	2.820	0.775	8.786	1.915	0.033	2.490
Cyclopoid naup.	0.001	0.001	0.011	0.036	0.050	0.018	0.037	0.193	0.089	0.299	0.094	0.607	0.671
Harpactacoid sp.	-	-	-	-	-	-	-	-	-	-	-	-	-
Veliger	0.034	0.003	0.004	0.056	6.217	2.108	2.441	4.792	10.728	0.964	0.057	0.204	3.289
Daily Totals	0.310	0.266	0.213	4.261	9.493	9.047	39.653	11.211	18.466	60.023	14.187	3.005	25.078

Appendix 5b. Continued.

Species	Aug-23	Aug-30	Sep-07	Sep-13	Sep-22	Oct-05	Oct-18	Nov-08	SWM
Bosmina sp.	0.047	0.219	0.018	0.036	4.516	1.116	0.527	2.597	0.743
Daphnia longiremis	-	-	-	-	-	-	-	-	-
D. retrocurva	0.228	0.275	-	0.045	-	0.054	-	0.114	0.389
D. galeata mendotae	-	-	-	-	-	-	-	-	-
Diaphanosoma sp.	-	-	-	-	-	-	-	-	-
Eubosmina sp.	-	-	-	-	-	0.080	-	0.022	0.011
Polyphemus pediculus	-	-	-	-	-	-	-	-	-
Holopedium gibberum	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-	-
Chydorus sphaericus	-	-	-	-	-	-	-	-	0.000
Alona sp.	-	-	-	-	-	-	-	-	-
Bythotrephes cederstroemi	0.129	0.177	0.108	0.096	-	-	-	-	0.233
Leptodora kindti	0.072	0.005	0.015	0.023	0.066	0.007	0.026	-	0.024
Leptodiaptomus ashlandi	-	-	-	-	-	-	-	-	0.086
L. minutus	0.184	0.537	0.323	-	-	0.074	-	0.267	0.371
L. sicilis	-	-	0.147	-	-	-	-	0.404	0.087
L. siciloides	-	-	-	-	-	-	-	-	-
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-
S. oregonensis	-	0.431	0.543	0.137	-	0.169	0.036	2.765	0.412
Epischura lacustris	0.382	0.222	0.230	0.181	-	-	-	-	2.116
Epischura cop.	0.474	2.008	2.109	0.631	0.781	0.716	0.511	0.144	0.979
Eurytemora affinis	-	-	-	-	-	0.015	-	-	0.019
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-
Calanoid cop.	0.195	0.531	0.816	0.499	0.458	0.616	0.124	1.204	0.417
Calanoid naup.	0.715	0.432	0.602	0.159	0.119	0.030	0.048	0.017	0.230
Diacyclops thomasi	-	0.086	-	0.195	0.082	-	0.022	0.322	1.187
Acanthocyclops vernalis	-	-	-	-	-	-	-	0.259	0.015
Mesocyclops edax	0.030	0.050	0.215	0.256	0.041	0.019	-	0.178	0.119
Tropocyclops extensus	0.009	0.134	0.223	0.176	0.215	0.076	0.078	1.093	0.119
Eucyclops agilis	-	-	-	-	-	-	-	-	-
E. speratus	-	-	-	-	-	-	-	-	-
Cyclopoid cop.	0.757	0.305	1.251	0.713	0.754	0.709	0.282	0.980	0.974
Cyclopoid naup.	0.829	0.134	0.373	0.222	0.096	0.488	0.067	0.032	0.191
Harpactacoid sp.	-	-	-	-	-	-	-	-	-
Veliger	0.531	1.748	5.043	5.672	5.515	1.795	0.246	1.170	2.234
Daily Totals	4.582	7.294	12.016	9.041	12.643	5.964	1.967	11.568	

Appendix 6a. Depth-weighted density (mg/m^3) of each zooplankton species on each sampling date at station E3 in 1993. Seasonal weighted mean (SWM) density is given for each species. cop.= copepidid, naup.= nauplii.

Species	May-12	May-27	Jun-09	Jun-24	Jul-07	Jul-21	Jul-29	Aug-12	Aug-25	Sep-24	Oct-05
Bosmina sp.	3.71	11.14	68.24	1852.33	7480.96	3082.58	103.99	5431.65	-	265.28	2228.37
Daphnia longiremis	-	-	-	-	-	-	-	-	-	-	-
D. retrocurva	-	-	-	-	-	-	-	-	-	-	-
D. galeata mendotae	-	-	-	-	-	-	-	-	-	-	-
Diaphanosoma sp.	-	-	-	-	-	-	-	-	-	-	-
Eubosmina sp.	-	-	-	-	-	-	-	-	-	-	-
Polyphemus pediculus	-	-	-	-	-	-	-	-	-	-	-
Holopedium gibberum	-	-	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-	-	-	-
Chydorus sphaericus	-	-	-	-	-	-	-	-	-	-	-
Alona sp.	-	-	-	-	-	-	-	-	-	-	-
Bythotrephes cederstroemi	-	-	-	-	-	31.20	4.33	7.43	-	4.46	1.49
Leptodora kindti	-	-	-	8.12	65.54	37.14	-	-	-	-	-
Leptodiaptomus ashlandi	-	-	-	-	-	-	-	-	-	-	-
L. minutus	3.71	3.71	-	-	-	1337.02	554.62	974.91	2290.27	901.96	212.23
L. sicilis	3.71	-	-	-	-	297.12	103.99	-	-	-	-
L. siciloides	-	-	-	-	-	-	-	46.42	-	-	-
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-	-	-
S. oregonensis	-	-	-	-	-	259.98	381.30	649.94	928.49	636.68	1220.30
Epischura lacustris	-	7.43	6.50	97.49	196.62	2525.49	2114.48	649.94	2166.47	583.62	212.23
Epischura cop.	-	14.86	13.00	162.49	1136.03	1411.30	2738.42	1439.16	2599.77	2599.77	1432.52
Eurytemora affinis	-	-	-	-	633.56	37.14	-	-	-	-	-
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-	-	-
Calanoid cop.	-	-	-	32.50	524.32	222.84	346.64	928.49	866.59	1485.58	4403.69
Calanoid naup.	148.43	111.42	69.51	576.26	2144.62	4622.78	7845.43	6891.91	4744.43	7891.26	4306.93
Diacyclops thomasi	200.55	33.43	77.99	146.24	43.69	37.14	69.33	696.37	-	53.06	636.68
Acanthocyclops vernalis	-	-	-	-	-	-	-	-	-	-	-
Mesocyclops edax	-	-	3.25	-	43.69	37.14	69.33	46.42	-	53.06	-
Tropocyclops extensus	-	3.71	3.25	-	-	74.28	34.66	1392.73	1918.87	8634.94	8356.39
Eucyclops agilis	-	-	-	-	-	-	-	-	-	-	-
E. speratus	-	-	-	-	-	-	-	-	-	-	-
Cyclopoid cop.	33.43	40.85	133.24	536.20	196.62	705.65	2530.44	4874.56	5075.73	4191.46	636.68
Cyclopoid naup.	78.12	111.42	330.20	1389.81	733.69	2210.89	2640.29	3785.69	7016.42	650.83	468.15
Harpactacoid sp.	-	3.71	-	8.12	284.01	334.26	242.64	557.09	123.80	-	-
Veliger	-	37.14	45.50	8449.24	7640.13	334.26	1490.53	2739.04	22005.16	4456.74	10584.76
Daily Totals	471.66	378.82	750.68	13258.80	21123.48	17598.21	21270.42	31111.75	49736.00	32408.70	34700.42

Appendix 6a. Continued.

Species	Oct-20	SWM
Bosmina sp.	371.40	1699.61
Daphnia longiremis	-	-
D. retrocurva	-	-
D. galeata mendotae	-	-
Diaphanosoma sp.	-	-
Eubosmina sp.	-	-
Polyphemus pediculus	-	-
Holopedium gibberum	-	-
Sida crystallina	-	-
Chydorus sphaericus	-	-
Alona sp.	-	-
Bythotrephes cederstroemi	-	3.74
Leptodora kindti	-	8.74
Leptodiaptomus ashlandi	-	-
L. minutus	-	649.31
L. sicilis	92.85	31.90
L. siciloides	-	3.89
Skistodiaptomus reighardi	-	-
S. oregonensis	1021.34	449.48
Epischura lacustris	-	778.45
Epischura cop.	371.40	1327.18
Eurytemora affinis	-	55.66
Limnocalanus macrurus	-	-
Senecella calanoides cop.	-	-
Calanoid cop.	1578.43	897.54
Calanoid naup.	922.92	3711.46
Diacyclops thomasi	557.09	185.19
Acanthocyclops vernalis	-	-
Mesocyclops edax	-	21.87
Tropocyclops extensus	9470.58	2596.47
Eucyclops agilis	-	-
E. speratus	-	-
Cyclopoid cop.	2228.37	2076.37
Cyclopoid naup.	2373.21	2041.49
Harpactacoid sp.	-	127.50
Veliger	8966.54	6515.30
Daily Totals	27954.13	

Appendix 6b. Depth-weighted density (no./m^3) of each zooplankton species on each sampling date at station E3 in 1994. Seasonal weighted mean (SWM) density is given for each species. cop.= copepidid, naup.= nauplii.

Species	May-10	May-18	Jun-01	Jun-16	Jun-21	Jun-28	Jul-05	Jul-13	Jul-19	Jul-27	Aug-02
Bosmina sp.	1.63	20.43	16.51	297.12	853.05	3602.53	1061.13	32.50	34.66	1271.00	86.66
Daphnia longiremis	-	-	-	-	-	-	-	-	-	-	-
D. retrocurva	-	-	-	3.71	32.50	252.55	875.43	16.25	11.56	346.64	43.33
D. galeata mendotae	-	-	-	-	-	-	-	-	-	-	-
Diaphanosoma sp.	-	-	-	-	-	-	-	-	-	-	-
Eubosmina sp.	-	-	2.06	3.71	-	-	26.53	16.25	-	-	-
Polyphemus pediculus	-	-	-	-	-	-	-	-	-	-	-
Holopedium gibberum	-	-	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-	-	-	-
Chydorus sphaericus	-	-	-	-	-	14.86	-	-	-	-	-
Alona sp.	-	-	-	-	-	-	-	-	-	-	-
Bythotrephes cederstroemi	-	-	-	-	-	-	3.71	1.95	7.63	1.30	1.95
Leptodora kindti	-	-	-	-	-	-	26.53	-	6.93	5.85	9.75
Leptodiaptomus ashlandi	1.63	-	-	-	-	7.43	53.06	8.12	-	173.32	64.99
L. minutus	4.88	5.57	2.06	-	-	14.86	530.56	32.50	11.56	115.55	86.66
L. sicilis	-	1.86	-	-	5.42	-	-	-	-	115.55	64.99
L. siciloides	-	-	-	-	-	-	-	-	-	-	-
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-	-	-
S. oregonensis	-	-	-	-	-	-	-	8.12	-	346.64	108.32
Epischura lacustris	-	-	-	48.28	124.57	170.84	1273.36	48.75	11.56	982.13	238.31
Epischura cop.	-	-	6.19	1089.43	113.74	29.71	159.17	251.85	1143.90	1328.77	996.58
Eurytemora affinis	-	-	-	-	5.42	66.85	-	-	-	-	-
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-	-	-
Calanoid cop.	-	1.86	2.06	3.71	32.50	59.42	185.70	32.50	23.11	693.27	498.29
Calanoid naup.	3.25	11.14	61.90	207.98	81.24	200.55	2228.37	2437.28	2634.43	2310.90	4766.24
Diacyclops thomasi	34.12	33.43	18.57	18.57	16.25	37.14	265.28	178.73	577.73	5892.80	1191.56
Acanthocyclops vernalis	-	-	2.06	-	-	-	-	-	-	-	-
Mesocyclops edax	-	-	-	-	-	-	-	-	11.56	231.09	-
Tropocyclops extensus	-	-	-	-	-	-	-	8.12	-	-	21.67
Eucyclops agilis	-	-	-	-	-	-	-	-	-	-	-
E. speratus	-	-	-	-	-	-	-	-	-	-	-
Cyclopoid cop.	19.50	16.71	43.33	59.42	108.32	96.56	371.40	3314.70	785.71	7799.30	1798.17
Cyclopoid naup	8.12	7.43	74.28	233.98	362.88	155.99	344.87	1754.84	831.93	2888.63	996.58
Harpactacoid sp.	-	-	-	-	-	-	-	-	-	-	-
Veliger	30.87	3.71	4.13	59.42	8351.75	1894.12	2414.07	3639.67	12617.53	924.36	86.66
Daily Totals	103.99	102.14	233.15	2025.34	10087.64	6603.41	9819.16	11782.14	18709.77	25427.08	11060.71

Appendix 6b. Continued.

Species	Aug-09	Aug-16	Aug-23	Aug-30	Sep-07	Sep-13	Sep-22	Oct-05	Oct-18	Nov-08	SWM
Bosmina sp.	-	-	95.99	297.12	55.46	44.57	13429.65	1960.97	1089.43	2856.28	1522.08
Daphnia longiremis	-	-	-	-	-	-	-	-	-	-	-
D. retrocurva	15.64	48.51	42.66	39.62	-	14.86	-	29.71	-	69.33	75.49
D. galeata mendotae	-	-	-	-	-	-	-	-	-	-	-
Diaphanosoma sp.	-	-	-	-	-	-	-	-	-	-	-
Eubosmina sp.	-	-	-	-	-	-	-	14.86	-	13.87	3.95
Polyphemus pediculus	-	-	-	-	-	-	-	-	-	-	-
Holopedium gibberum	-	-	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-	-	-	-
Chydorus sphaericus	-	-	-	-	-	-	-	-	-	-	0.57
Alona sp.	-	-	-	-	-	-	-	-	-	-	-
Bythotrephes cederstroemi	-	8.32	1.39	1.39	0.69	0.74	-	-	-	-	1.13
Leptodora kindti	-	7.63	8.32	2.08	2.77	2.97	4.46	0.74	7.43	-	3.88
Leptodiaptomus ashlandi	-	48.51	-	-	-	-	-	-	-	-	13.67
L. minutus	78.19	339.60	53.33	99.04	55.46	-	-	14.86	-	27.73	59.27
L. sicilis	15.64	48.51	-	-	27.73	-	-	-	-	83.19	15.39
L. siciloides	-	-	-	-	-	-	-	-	-	-	-
Skistodiaptomus reighardi	-	-	-	-	-	-	-	-	-	-	-
S. oregonensis	78.19	145.54	-	79.23	110.92	29.71	-	44.57	7.43	485.29	66.75
Epischura lacustris	31.28	679.20	42.66	19.81	27.73	14.86	-	-	-	-	145.87
Epischura cop.	172.02	1552.46	501.29	1802.50	1830.24	653.66	827.68	490.24	430.82	110.92	601.08
Eurytemora affinis	-	-	-	-	-	-	-	14.86	-	-	3.81
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-	-	-
Senecella calanoides cop.	-	-	-	-	-	-	-	-	-	-	-
Calanoid cop.	15.64	339.60	106.66	257.50	360.50	267.41	212.23	341.68	52.00	485.29	181.44
Calanoid naup.	7625.98	3250.47	6100.78	3050.39	4159.63	1129.04	721.57	237.69	245.12	97.06	1647.76
Diacyclops thomasi	15.64	145.54	-	19.81	-	59.42	21.22	-	7.43	124.79	335.10
Acanthocyclops vernalis	-	-	-	-	-	-	-	-	-	124.79	7.36
Mesocyclops edax	-	145.54	10.67	19.81	110.92	118.85	21.22	14.86	-	69.33	31.66
Tropocyclops extensus	-	194.06	10.67	198.08	388.23	252.55	382.01	133.70	111.42	1192.43	154.30
Eucyclops agilis	-	-	-	-	-	-	-	-	-	-	-
E. speratus	-	-	-	-	-	-	-	-	-	-	-
Cyclopoid cop.	78.19	3493.04	1483.60	455.58	2329.39	1143.90	1337.02	1262.74	401.11	1109.23	1175.03
Cyclopoid naup	7130.79	7277.16	8735.21	1303.35	3383.16	2198.66	870.13	4248.76	423.39	318.91	1876.34
Harpactacoid sp.	-	-	-	-	-	-	-	-	-	-	-
Veliger	218.93	5094.01	607.95	2159.04	6489.02	8616.37	6536.55	2124.38	334.26	1026.04	2674.65
Daily Totals	15476.10	22817.72	17801.17	9804.34	19331.86	14547.55	24363.73	10934.62	3109.82	8194.46	