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Lake Erie 1993, Western, West Central and Eastern Basins: Change in Trophic Status, and Assessment of the Abundance, Biomass and Production of the Lower Trophic Levels

J. A. Dahl

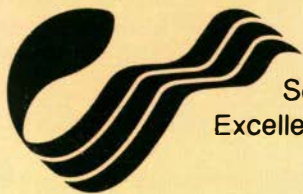D. M. Graham

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Lake Erie 1993, western, west central and eastern basins: Change in trophic status, and assessment of the abundance, biomass and production of the lower trophic levels.

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LAKE ERIE 1993, WESTERN, WEST CENTRAL AND EASTERN BASINS:
CHANGE IN TROPHIC STATUS, AND ASSESSMENT
OF THE ABUNDANCE, BIOMASS AND PRODUCTION
OF THE LOWER TROPHIC LEVELS

by

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ABSTRACT

The western and west central basins were mesotrophic and the eastern basin was oligotrophic, based on many biological and chemical parameters measured in 1993. Gradients were observed for most parameters, with chlorophyll *a*, nitrogen, phosphorus, silica, and light extinction decreasing from west to east. In the western basin, phytoplankton biomass declined by 51% from 1983-85. Phytoplankton photosynthesis (g $C \cdot m^{-2}$), predicted from total phosphorus (TP) using a relationship developed in other offshore productivity studies in Lake Ontario, declined by 35% in 1993, without a corresponding decline in phosphorus (P) loading or TP. Diatoms decreased and there was a shift towards smaller phytoplankton species. These changes were attributed to zebra mussel filtration, but were not of sufficient magnitude to reduce zooplankton biomass. In the west central basin, the reductions in phytoplankton biomass were modest. Photosynthesis (g $C \cdot m^{-2}$) in 1993, was in line with that predicted by TP and the empirical relationship developed in other offshore studies. Limited mussel populations in the west central basin, resulting from low hypolimnetic oxygen concentrations, caused little change in the phytoplankton. There also were no reductions in mean biomass of zooplankton from 1984-87. In the eastern basin, phytoplankton biomass declined by 49% from 1983-85. Photosynthesis (g $C \cdot m^{-2}$) declined by 50% from the value predicted, from TP and the empirical relationship developed for other studies, for 1983-85, without a decline in P-loading. TP was lower in 1993 and was attributed to filtering by *Dreissena* and subsequent redirection of pelagic material to the sediments. Phytoplankton species indicative of eutrophy were reduced and there was an overall shift towards smaller species. Zooplankton biomass was also reduced. Mean zooplankton community size and the loss of *Daphnia* sp. suggest that predation by planktivores as well as a reduced food supply, affected zooplankton biomass in 1993. The *Dreissena* population also affected the benthic community structure as *Diporeia* were virtually eliminated from the eastern basin and *Gammarus* increased in all basins. Benthic biomass was 40% higher on average than in 1979. *Dreissena* dominated benthic production at all stations except offshore in the west-central basin.

RÉSUMÉ

L'analyse des nombreux paramètres chimiques et biologiques mesurés en 1993 nous indique que les bassins ouest et centre-ouest étaient mésotrophes et que le bassin est était oligotrophe. On a examiné les gradients de la plupart des paramètres, et la valeur de ceux de la chlorophylle a, de l'azote, du phosphore, de la silice et de l'extinction de la lumière, baissait d'ouest en est. Dans le bassin ouest, la biomasse phytoplanctonique avait diminué de 51 % par rapport aux valeurs de 1983-1985. La photosynthèse phytoplanctonique (g $C \cdot m^{-2}$), prévue à partir de la quantité de phosphore total au moyen d'une équation tirée d'autres études de productivité des eaux du large dans la lac Ontario, était réduite de 35% en 1993 par rapport à la valeur estimée de 1983-1985, mais sans qu'on ait observé une baisse analogue de la charge en phosphore (P) ou en phosphore total (PT). Les populations de diatomées étaient en recul et on a observé un déplacement en faveur des espèces phytoplanctoniques de plus petite taille. Ces changements ont été attribués à la filtration d'organismes par la moule zébrée, mais cet effet n'était cependant pas suffisamment intense pour réduire la biomasse zooplanctonique. Dans le bassin centre-ouest, la réduction observée de la biomasse phytoplanctonique était modeste. La photosynthèse (g $C \cdot m^{-2}$) mesurée en 1993 concordait avec les valeurs prévues à partir du PT et de la relation empirique tirée des études de productivité des eaux du large. Il est probable qu'une faible partie seulement des changements observés au niveau du phytoplancton pouvait être attribuée à la population limitée de moules dans le bassin centre-ouest, étant donné la faible concentration en oxygène de la couche hypolimnique. En outre, il n'y a pas eu de réduction de la biomasse zooplanctonique moyenne par rapport à 1984-1987. Dans le bassin est, la biomasse phytoplanctonique a diminué de 49% par rapport aux valeurs de 1983-1985. La photosynthèse (g $C \cdot m^{-2}$) était réduite de 50% par rapport à la valeur estimée à partir du PT et de la relation empirique tirée des autres études pour 1983-1985, et ne s'accompagnait pas d'une baisse de la charge en P. En 1993, il y avait moins de PT, ce qui a été attribué à la filtration par *Dreissena* et au transfert subséquent du matériel pélagique dans les sédiments. Le nombre d'espèces phytoplanctoniques indicatives de l'eutrophie s'est abaissé et il s'est produit un déplacement d'ensemble de l'équilibre vers des espèces de plus petite taille. En outre, il y a eu diminution de la masse du zooplancton. Toutefois, la taille moyenne des organismes composant la communauté zooplanctonique et la perte de *Daphnia* sp. paraissent indiquer qu'en plus d'une diminution des ressources alimentaires, la prédation exercée par les planctivores a également exercé un effet sur le zooplancton en 1993. La population de *Dreissena* a aussi pesé sur la structure de la communauté benthique du fait que *Diporeia* a pratiquement été éliminé du bassin est et que *Gammarus* a gagné du terrain dans tous les bassins. En moyenne, la biomasse benthique était 40% supérieure à ce qu'elle était en 1979. *Dreissena* a dominé la production benthique à toutes les stations sauf dans les eaux du large dans le bassin centre-ouest.

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INTRODUCTION

The Lake Erie ecosystem has changed during the last decade in response to a number of factors which have affected all trophic levels. Phosphorus loading controls have lowered phosphorus concentrations, thereby reducing the potential productivity of lower trophic levels. The resurgence of the top predator, walleye, has increased demands on the forage fish base, and may have reduced other commercially important fish stocks such as yellow perch. Also, the prolific and adaptable zebra and quagga mussels (*Dreissena*) has invaded and colonized most of the lake. As a result, changes have occurred in the structure and function of the food web, presenting a potential problem of inadequate energy flow to upper trophic levels.

Control of nuisance algae, particularly *Cladophora*, has been highly successful because of the phosphorus controls that were initiated in the early 1970's. Prior to the implementation of these controls, Lake Erie was plagued by undesirable algal growth that interfered with water supplies, recreation and fish communities (Burns 1985). Extensive algal biomass increased the oxygen demand of both the water column and the sediments due to decomposition of settled organic matter. The result was the periodic decrease in hypolimnetic oxygen concentration to levels that were detrimental to cold-water fish species (Burns 1985). Low oxygen in the bottom water also caused changes in benthic communities, especially in the western basin, as sensitive mayfly nymphs were replaced by more tolerant tubificid worms (Burns 1985). In 1970, legislation was introduced to control the phosphate levels in detergents, and after 1972 a program was implemented to build and upgrade sewage treatment plants to reduce phosphorus loading (Burns 1985). The targets set by the International Joint Commission (I.J.C.) for phosphorus loadings have been achieved since the early 1980s with a commensurate decline in total water column phosphorus concentrations in the offshore of each basin of Lake Erie, to near target levels by the late 1980s (Lesht et al. 1991).

The reduction of algal biomass resulting from phosphorus controls has been enhanced by the establishment of *Dreissena* in the late 1980's. These mussels have a tremendous ability to filter phytoplankton out of the water column (MacIsaac 1992). Work by MacIsaac (1992) suggested the population of zebra mussels in the western basin of Lake Erie in 1990 could filter the entire basin 26 times per day. Thus, there is the potential for a drastic reduction in phytoplankton concentrations. Since their discovery in Lake Erie, the mussels have spread rapidly. *Dreissena polymorpha* has become well established in the western basin, and the genetically distinct *Dreissena, D. bugensis* given the working name of "quagga", has been able to move into and flourish in the deep, cold waters of the central and eastern basins (Dermott and Munawar 1993). The combined effect of continued phosphorus controls and the rapidly expanding mussel population, have resulted in dramatic decreases in chlorophyll concentrations and increases in water clarity.

With the arrival of the zebra mussels in Lake Erie in late 1988, chlorophyll *a* concentrations in the western basin of Lake Erie declined by 43% from 1988 to 1989, Secchi transparencies increased by 85% (Leach 1993), and phytoplankton densities, at four near-shore stations, declined by 90% from 1988 to 1990 (Nicholls and Hopkins 1993). The tremendous filtering capabilities

of the mussels may threaten endemic Lake Erie biota by drastically reducing phytoplankton concentrations that many native zooplanktors and benthic invertebrates, rely on as a food source. This competition between zooplankton and *Dreissena* for phytoplankton may result in changes further up the food chain as growth rate and condition of young planktivores are reduced because of inadequate food supply (see Graham 1993). Similarly, a reduction in *Diporeia hoyi*, an important part of the benthic food chain for whitefish and lake trout, could have an effect on these stocks. The reduction in young fish survival could ultimately effect future fish stocks.

The Council for Great Lakes Research Managers under the direction of the I.J.C., recommended that a cooperative research and monitoring program be developed for Lake Erie, because of concerns for the fate of the Lake Erie fishing industry. The council felt that a cooperative effort between federal and provincial agencies would enhance the scope of the study by encompassing lower trophic levels and the fish community. Federal and provincial agencies intensified their research efforts in 1993 on Lake Erie in response to this recommendation.

The Lake Erie Biomonitoring program (LEB) was initiated in 1993 and continued in 1994, to establish the status of water quality and trophic production in the lake. The LEB program is a seasonal study, closely affiliated with the Lake Erie Trophic Transfer study (LETT) which is a detailed spatial survey of the lake, and involves the cooperation of federal groups and university researchers. Consistent methodology between projects will allow spatial and temporal comparisons between studies, and will also aid in the selection of long-term monitoring sites.

This report documents results from the first year of the LEB program. The results will be integrated with fish data from the Ontario Ministry of Natural Resources (OMNR) to assess the current energetic pathways in the lake and to predict implications for the future of the Lake Erie fishery. We provide lower trophic level estimates of abundance, biomass, and production as well as species composition for benthos, zooplankton, rotifers and phytoplankton. Chlorophyll *a*, Secchi transparencies, phosphorus and other water chemistry components, as well as estimates of phytoplankton photosynthesis and benthic production for each of the three basins will be presented.

METHODS

STATIONS

The Lake Erie Biomonitoring (LEB) project sampled eight stations in 1993: three in the eastern basin (E1, E2, E3), two in the west central basin (WC1, WC2) and three in the western basin (W1, W2, W3) (Fig. 1). Pelagic sampling began in the western and west central basins the week of May 3 and continued on a biweekly basis until the week of October 25. Due to inclement weather, station WC1 was not sampled the week of June 30. Benthic samples were collected from four west end stations (WC1, WC2, W1 and W3). At eastern basin stations pelagic samples were collected biweekly from the week of May 10 until the week of October 18. Due to inclement weather, station E1 was not sampled during the weeks of July 29 and September 9, and station E2 was not sampled during the weeks of July 29, September 9 and

October 5. Benthic samples were obtained from only stations E2 and E3.

Two of the eastern basin stations were chosen that corresponded to sites previously established during the LETT cruises of 1992 (Table 1), while the third, E1, was chosen to correspond to a long term OMNR site set up to monitor effects of the Nanticoke Power Plant. In western Lake Erie, four of the five sites sampled, W1, W2, WC1 and WC2, corresponded to established OMNR sites, while W3 was sampled previously on LETT.

SAMPLE COLLECTION

All sampling was conducted onboard OMNR research vessels, based in Port Dover and Wheatley, Ontario. In the eastern basin, all stations were sampled on the same date under ideal conditions or on consecutive days during bad weather. Western and west central basin stations were usually sampled over two days.

Physical Parameters

At each station, light extinction and Secchi (20 cm black and white disc) depth were measured. 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 (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) as well as the boundaries of the metalimnion and hypolimnion were determined using this program.

The euphotic depth (Z_{eu}), the depth of 1% of incident light penetration, was determined by measuring light extinction at several 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 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 (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} gives the Z_{eu}.

Incident solar irradiance was measured at two locations near the lake with Li-190 quantum sensors (Li-Cor, Nebraska). One sensor was mounted at the Cedar Springs Agroclimatology monitoring station (OMAF, Ridgetown) at the west end of the lake, with solar irradiance recorded as 10 min integrals ($moles \cdot m^{-2}$) on a Li-1000 datalogger. A second sensor was mounted on the roof of the Canada Centre for Inland Waters (CCIW) in Burlington, and logged 30 min integrals to a Campbell CR5 microprocessor datalogger. Sensors were calibrated annually by the manufacturer. Depth integrals of phytoplankton photosynthesis for all stations in the western and

west central basins were calculated using solar data from the Cedar Springs sensor, while the data from the CCIW sensor were used for all stations in the eastern basin. Depth integral were used for calculations of mean epilimnetic irradiance ($\bar{I}$).

Water Samples

Composite water samples were collected 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; particulate organic nitrogen, PON; particulate organic carbon, POC; NO_3-NO_2, ammonium, chlorides, silica measured as SiO_2, sulphides, chlorophyll a (Chl)) and phytoplankton photosynthesis and biomass. During isothermal or weakly stratified conditions, composite 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 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 Shurflo diaphragm pump with attached ½″ 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. Samples were collected in well-rinsed, neoprene-wrapped 10 L polycarbonate jugs. Phytoplankton samples were collected and water was filtered for Chl, onboard in the west end of the lake, usually within 2 h of collection. Water for water quality and photosynthesis experiments was held in the carboys, and processed at the OMNR laboratory at Wheatley. Eastern basin water samples were transported in the carboys, on ice, back to CCIW for processing, usually within 7 h of collection. The temperature of the sample water was maintained at ± 2°C of ambient during transportation.

Under stratified conditions, 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 Z_m to 1 m above Z_{eu}.

Zooplankton

Macrozooplankton were collected using a 110-µm mesh Wisconsin plankton net, 3 m long with a 0.5 m diameter opening. Flow meters (General Oceanic, Miami, Fla.) were mounted on the inside and outside of the net hoop to determine net efficiency. Readings were taken from both meters before and after each haul. 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 washed into a 250 mL jar and preserved with 10% sugared, neutralized formalin. In cases where the meter readings were very different, a third haul was done for a meter reading only.

During stratification, each stratum was sampled independently and the contents preserved separately. Epilimnetic samples were collected from 2 m above the thermocline to the surface. A closing net was used to collect metalimnetic and hypolimnetic samples. The closing net, otherwise identical to the regular net, was cinched at the desired depth using a secondary line, and brought to the surface. Metalimnetic samples were taken from 1 to 2 m below the thermocline to 1 to 2 m above the top of the hypolimnion, and hypolimnetic samples from 1 to 2 m below the metalimnion to 2 m above the lake bottom. Three additional hauls were performed with the closing net to obtain meter readings for calculation of net efficiencies: one haul through the epilimnion, one from the bottom of the metalimnion to the surface and the third from 2 m off the bottom to the surface.

Rotifers were collected using the same diaphragm pump described for the water quality sampling. An integrated water sample of 10 L was collected from 2 m above the lake bottom to the surface when conditions were isothermal. The pumping rate determined the speed at which the hose intake should be raised through the water column. During stratification, separate 10 L samples were collected from each stratum, again by raising the hose intake at a specific rate. Sampling depth intervals corresponded with those of the macrozooplankton. The water was serially filtered through 44-μm and 20-μm Nitex screens after collection. Each sample was preserved separately in 10% sugared, neutralized formalin. This formalin concentration was found to be too strong and resulted in the contraction of the soft bodied rotifers. In subsequent years the rotifers were narcotized in soda water for 2 minutes and preserved in 4% sugared, neutralized formalin.

Benthos

Benthic samples were collected approximately twice monthly between May and October 1993, at stations W1, W3, WC1, WC2, E2 and E3. On each sampling date, 5 mini-PONAR (area $0.0232 \cdot m^{-2}$) grabs were attempted. Each sample was sieved through a 0.25-mm screen, and preserved in 10 % neutral formalin. The temperature of the mud was taken for each initial grab. In addition, a sample of surface mud was obtained for sand content analysis at each station in June and October. In mid August and September, live benthic samples were collected from each basin and used to rear chironomid adults for species determination. Live zebra and quagga mussels were sent to Dr. A. Martel (Museum of Nature, Ottawa) for comparative morphological studies to allow separation of the juvenile mussels.

LABORATORY PROCESSING AND EXPERIMENTS

Chl, Water Quality and Phytoplankton

Four replicate Chl samples were filtered on GF/C glass fibre filters and frozen for later analysis. Volumes filtered were typically 1500 mL for eastern basin samples and 1 L for western and west central basin samples. The filters were ground in 90% acetone, and the extracts analyzed spectrophotometrically (Strickland and Parsons 1972). Chl concentrations used in the

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photosynthesis calculations are uncorrected for phaeopigments.

Unfiltered water samples were collected for total phosphorus analysis. Sample water was filtered through a cellulose acetate 0.45-μm Sartorius membrane filter for total filtered phosphorus, other nutrients and major ions. Particulate organic carbon (POC) and particulate organic nitrogen (PON) samples were collected on ashed GF/C filters. All analyses were performed by the National Laboratory for Environmental Testing (NLET) (Environment Canada 1995).

Two 250-mL 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 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 300 x, 600 x, and 1500 x magnification by the strip method providing an estimate of total cell numbers within $\pm$ 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

Water from the eastern basin stations, E2 and E3, was transported on ice in insulated carboys back to CCIW for ^{14}C uptake experiments. Phytoplankton photosynthesis experiments for stations W1, W3, WC1 and WC2 were conducted at the OMNR station at Wheatley. All experiments were performed within 7 hrs of water collection.

Photosynthetic rates were determined using ^{14}C incubator methodology. This methodology (Millard et al. 1995) is consistent with that used in many other projects on Lakes Erie and Ontario, as well as small lakes (Fee et al. 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. 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 ($\pm 2°C$). The incubator was identical to that described by Fee et al. (1989). The light source used was a 150 W high pressure sodium vapour lamp (Thom 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 to obtain a photosynthesis vs. light curve. Light levels for all bottle locations were checked during incubation using a manufacturer calibrated Li-Cor Li193SA spherical quantum sensor. At times, several stations were incubated simultaneously. As each experiment ended, dummy bottles filled with distilled water were put in place of sample bottles to maintain a consistent light environment for those remaining. 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 further ensure the removal of unincorporated tracer, prior to the addition of 10 mL of scintillation fluor. Five-mL was removed from each of three randomly chosen bottles and placed in scintillation vials with 200 μL ethanolamine to determine the total ^{14}C available for uptake. 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, and mean epilimnetic irradiance on a 24h basis, 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 (mgC·mg Chl^{-1}·E^{-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 (B).

Seasonal areal photosynthesis was estimated using the YPHOTO and YTOTAL programs (Fee 1990). Theoretical cloudless irradiance data can be generated with these programs and used to determine the theoretical maximum rate of photosynthesis. Rates can also be compared among systems without the confounding effects of variable solar input.

Zooplankton Net Efficiency Calculations and Corrections

The following formula was used to calculate net efficiency:

$$\frac{\Delta \text{ outside meter}}{\Delta \text{ inside meter}} \quad X \quad \frac{\text{inside meter calibration coefficient}}{\text{outside meter calibration coefficient}}$$

Where Δ is the number of revolutions the meter turned from the beginning to the end of the vertical haul. Problems with the flow meters resulted in large variability in the data and some unrealistic results. In 1994, we employed the same nets in Lake Erie using a Rigotia (Rigotia and Co. Ltd., Tokyo, Japan) flow meter. The meter was calibrated by dividing the revolutions·m^{-1} obtained when placed on the inside of the hoop with the net attached, by the revolutions·m^{-1} obtained over the same distance without the net (on an empty hoop). Empty hoop calibration hauls were performed at several 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.

Efficiencies in 1994 were approximately 25% higher than those found in 1993 at the same

stations and using the same nets. We compared several lake conditions which might have explained these yearly differences. Increased quantity of suspended solids in the water column, because of windier conditions in 1993, might have accounted for the lower efficiency. A Student's T test revealed no significant difference in the mean ε_{par} between 1993 and 1994 for any of the three eastern basin stations (E1: sl = 0.721, df = 22; E2: sl = 0.481, df = 12; E3: sl = 0.755, df = 23). In addition, correlation analysis showed the predictability of efficiency based upon ε_{par} to be very low. The effects of changing Chl and zooplankton biomass on net efficiency also were examined. However, no significant effects were observed: r^2 values of 0.024 and 0.114, respectively. Since none of the factors examined had an effect on the efficiency of the net, we concluded that 1993 efficiencies were underestimated due to the inconsistency of the meters and assigned the 1994 efficiency values from station E1, E2 and E3 to those stations for 1993.

Stations in the western and west central basins posed more of a problem as these stations were not sampled during LEB 1994. However, two separate comparisons showed efficiencies in the three basins to be very similar. During LEB 1993, net efficiencies at western and west central basin stations were not significantly different (sl = 0.126, df = 69) from the efficiencies at the eastern basin stations. In addition, LETT 1994 data showed no significant difference in efficiency among basins (sl = 0.087, df = 34). Thus, we assigned values from the 1994 eastern basin stations to the 1993 western and west central basin stations. Efficiencies for 1994 metalimnetic and hypolimnetic net hauls were also assigned to 1993 samples.

Zooplankton Enumeration and Biomass Determinations

Each zooplankton 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 known volume 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. Cladocera were measured from the top of the helmet to the base of the tail spine (*Bythotrephes* were measured to the first 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. A recent study reveals strong evidence that the species of *Bosmina* commonly named *Bosmina longirostris* are not *longirostris* at all because of the position of the lateral head pore. They are one of two new species named *Bosmina liederi* and *Bosmina freyi* which can be distinguished with a compound microscope by the number of spines on the proximal pectin of the postabdominal claw (De Milo 1993). We could not routinely distinguish them with our dissecting scope and thus all *Bosmina* were named *Bosmina* sp. Zooplanktors were enumerated and measured using a digitizing system (Summa Sketch III, Oakville, Ontario). Counts were tabulated and densities obtained using a computer program, ZoopBiom, developed by R. Hopcroft (University of Guelph, Ontario). This program incorporates length-weight regression equations for zooplankton (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

Initial examination indicated that some small rotifer species and many rotifer eggs were lost through the 44-µm mesh. Therefore, the 20-µm and 40-µm fractions were combined and counted as one sample. Prior to combining, each sample was rinsed to remove excess formalin and resuspended in 25 mL of water. A 5-mL subsample was taken from each fraction to be archived. The remaining 20 mL from each fraction were then combined.

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).

According to these geometric formulae, *Polyarthra* species should be estimated using the formula for a parallelepiped ($v=abc$, where a=length, b=width and c=height), but a simplified formula is also given, $v=0.28a^3$. Initial examination showed that this was not an applicable simplification for Lake Erie rotifers. Regressions were developed for the Lake Erie *Polyarthra* from measurement of twenty individuals of each of the four *Polyarthra* species. Measurements were taken on two dates at three sites: W3 in the western basin, and a nearshore and offshore station in the eastern basin. For each species, station and date, a non-linear, least-square regression was performed using the formula $v=ka^3$ where $v=$ the volumes determined from the full formula. Within species, there was substantial scatter for each station and date, but there was some separation of the four species, therefore, all data for each species were combined and compared. The 95% confidence intervals about the constant k overlapped for the species *P. remate, P. vulgaris,* and *P. major*. These data were combined and a common equation was used for the three species: $v=0.158a^3$ (95% confidence interval: 0.153-0.163). The equation for *P. dolichoptera* was $v=0.205a^3$ (95% confidence interval: 0.195-0.215).

Benthos Enumeration, Biomass and Production Determination

Three or four of the preserved benthic samples were analyzed from each station on each sample date while the remaining sample was archived. All organisms retained on a 500-µm screen were enumerated. The finer material was subsampled, and a minimum of 1/4 of this material was processed, and the counts converted to number per sample. Invertebrates were identified and their blotted wet weight was measured. The taxonomic groups were placed into distilled water for exactly 60s before weighing to ensure wet weights were consistent. The common taxa were identified to genus or species where possible, but only to family level for the Nematoda, Oligochaeta, Ostracoda and Harpacticoida. Average densities and wet biomass of each taxa were calculated for each station. The most common chironomid species, *Gammarus*, and the zebra and quagga mussels were divided into size classes.

For initial comparison of production among the different basins, the production/biomass (P/B) ratio method was used. For each taxa, the P/B ratio was multiplied by the annual average

wet biomass at each station. P/B ratios were obtained for each taxa from an extensive literature search. Weights reported are wet weights without shells (shell-free).

Annual production of the *Dreissena* species and *Gammarus fasctiatus* was calculated using the size-frequency method of Krueger and Martin (1980). These calculations used the monthly mean densities in the four size classes, the average wet weight per individual (shell-free) for each size class and the geometric weight between the size classes. A cohort generation time of 1 year was used at all sites except E2. Data from near E2 suggested that in deep water, *D. bugensis* grew approximately 6 mm per year. Therefore, the cohort production interval (CPI) used at this site was two years. Where numbers were insufficient to calculate production from the size frequency distribution, the production was calculated using the P/B ratio method.

RESULTS

Seasonal weighted means, weighted for different time intervals between sampling dates, were calculated for the entire sampling period at each station for all physical and chemical parameters. Due to different starting and ending dates at each station, western and west central basin values were averaged over a 13-14 week period versus a 10-13 week period for eastern basin stations. An analysis of means obtained for a standardized period, chosen to be common to all stations, showed a maximum difference of only 12%. A standardized period was not used to determine seasonal means, due to this small discrepancy.

Preliminary analyses were conducted to determine how representative LEB stations were of their respective basins. Data collected during three spatial surveys in 1993 (LETT; June and September, and Charlton, Environment Canada, unpubl. data 1994; August) and the LEB data collected during the same time periods were compared (Table 2). Data for many parameters from LEB stations were within two standard errors of the basin-wide means determined during the spatial cruises.

The region in which the western basin stations in this study are located has been shown by Wallen and Botek (1984) to be less eutrophic than water in the western and southern parts of the basin. This heterogeneity in the basin is due to the influence of river inflows and the subsequent circulation patterns in the basin. In spite of the potential heterogeneity in the basin, most values obtained at each of the western basin stations were comparable to the area-weighted basin-wide means obtained on LETT in 1993. Although station W3 had a higher TP concentration in the spring, and a lower TP concentration in the fall, the mean TP of all stations was within 2 S.E. of the LETT mean for comparable dates. Data from the three western basin stations were combined and the arithmetic mean reported for comparisons to data from the other basins.

Data collected at west central basin stations were comparable to central basin data. Means for WC1 and WC2 were particularly comparable to June and September basin-wide means for TP, Chl and P_{opt}. However, gradients are known to exist (Charlton 1994) from the east to the west boundaries of the central basin. Therefore, west central station data may not be

representative of the central basin, but may approximate central basin values. West central basin data are also important for showing the transition between the central and western basins and the central and eastern basins. Although some variation is evident between WC1 and WC2, both stations stratify and hence behave more like offshore stations. For comparisons to data from the other basins, the arithmetic means of the two west central stations will be used.

In the eastern basin, values obtained at the offshore station (E2) were comparable to the area-weighted mean of the offshore LETT stations, and nearshore stations (E1,E3) were comparable to the area-weighted mean of nearshore LETT stations. In most cases, there was little or no difference between nearshore and offshore LETT means. For this report, eastern basin data will be discussed in terms of nearshore (E1, E3) and offshore (E2) regions. Basin means are the means of all stations and are presented for comparisons to the other basins.

LIGHT AND TEMPERATURE

The seasonal patterns in mixed depth, euphotic depth and light extinction at each station are presented in Tables 3a-h. The stations ranged from shallow, and well-mixed in the western basin to deep and thermally-stratified in the eastern basin. A gradient in transparency exists from the eastern to western basin in the lake (Fig. 2). From east to west, the seasonal mean ε_{par} values at the LEB stations increased from 0.268 (eastern basin) to 0.328 (west central basin) and 0.755 (western basin). Two, nearshore, stations in each of the eastern (E1, E3) and western (W1, W2) basins, although similar in depth and proximity to shore, exhibit very different light environments as indicated by Z_{eu}, ε_{par} and Secchi. At eastern basin nearshore stations the euphotic depth was to the bottom throughout the sampling period, in contrast to the western basin stations. Seasonal weighted mean ε_{par} values were 62% lower at eastern basin stations than at western basin stations (Table 4) and Secchi depths were 59% deeper.

Seasonal trends in maximum and minimum ε_{par} were temporally consistent within each basin. ε_{par} was highest at station E1 with a seasonal mean 27% higher than at station E2 and 20% higher than at E3 (Table 4).

The west central basin had low ε_{par} in mid August, followed by an increase in the fall. Differences in ε_{par} between WC1 and WC2 were most pronounced in mid August and late September (Fig. 2). Seasonal mean values differed by 23%, which was similar to the difference between nearshore (E1) and offshore (E2) sites in the eastern basin (Table 4). In the west central basin, however, the higher mean ε_{par} was observed at the offshore station, WC2, in contrast to the eastern basin stations.

Stations in the western basin showed the greatest fluctuations as well as the highest extinction values particularly at nearshore station W1. Maximum extinction values attained in the western basin were more than 3 times greater than those attained in the other basins (Table 4).

Thermal stratification was observed at the three deepest stations (Fig. 3). Timing of both

onset and breakdown was related to proximity to shore. For example, stratification was established at station WC1 two weeks earlier than at WC2, but continued at WC2 for one month longer. The onset of stratification occurred in late June at E2 and WC2. Thermal structure was evident for a longer period in the eastern basin than in the west central basin. No stratification was evident in the western basin, although on some dates there was a rapid drop in temperature at 1 to 2 m off the bottom.

NUTRIENTS

Seasonal patterns of TP varied between inshore and offshore stations and among basins. Seasonal mean TP concentrations (May to October) increased by 36% from the eastern to west central basin stations and by 32% from the west central to western basin stations (Tables 5a-h). TP concentrations showed low variability throughout the sampling season, at the shallow eastern basin stations, with seasonal means of 7.8 and 6.6 $\mu g \cdot L^{-1}$ at E1 and E3, respectively. At station E2, seasonal mean TP was 8.5 $\mu g \cdot L^{-1}$. Concentrations were elevated during spring and fall isothermy (mean 12.9 $\mu g \cdot L^{-1}$) although the mean during the stratified period (7.2 $\mu g \cdot L^{-1}$) was comparable to that at E1 (Fig. 4). TP concentrations were elevated at the west central basin stations, relative to the eastern basin stations. Seasonal mean TP concentrations were 10.8 and 12.8 $\mu g \cdot L^{-1}$ at stations WC1 and WC2, respectively. Concentrations at both stations were lowest during June, July and early August, and reached maximum levels throughout September and October (Fig. 4). TP concentrations at the western basin stations were comparatively higher throughout the sampling period and tended to increase from May to September. Seasonal means were 17.5, 15.5 and 19.1 $\mu g \cdot L^{-1}$ at stations W1, W2 and W3, respectively.

The seasonality of silica varied widely among basins (Fig. 5). Concentrations in the eastern basin remained low throughout the sampling season showing only slight elevations in the spring and fall. The seasonal mean concentration of the three stations in the eastern basin was 0.31 $mg \cdot L^{-1}$. In the west central basin, silica concentrations were comparable to those in the eastern basin until late July. Concentrations increased to 1.5-2.0 $mg \cdot L^{-1}$ by mid September and remained high until the end of the sampling season. Mean seasonal silica concentration of the two stations in the west central basin was 0.80 $mg \cdot L^{-1}$. At each western basin station, concentrations of silica fluctuated throughout the sampling season showing spring, summer and fall peaks. Maxima were reached at all stations in late August through October with a seasonal mean concentration for the three stations of 0.96 $mg \cdot L^{-1}$.

The seasonal mean NO_3-NO_2 concentrations were similar among the eastern basin stations: 232, 243 and 224 $\mu g \cdot L^{-1}$ at E1, E2 and E3, respectively (Table 5a-h). In the west central basin, seasonal mean NO_3-NO_2 concentrations were higher at the nearshore station than at the offshore station, 250 and 222 $\mu g \cdot L^{-1}$, respectively. Concentrations were higher at western basin stations, than other stations, with means of 362, 324, and 391 $\mu g \cdot L^{-1}$ at stations W1, W2 and W3, respectively. NO_3-NO_2 concentrations were highest in the spring and declined toward the end of the summer at all stations, except WC2. At station WC2, concentrations increased between June and July then declined in September.

At the eastern basin stations the TN:TP ratios were greater than 35 on all but one date at station E2 (Table 5a-h), with values ranging from 23.40 to 141.94. At all western and west central basin stations, TN:TP ratios were within ranges similar to eastern basin stations, however, values dropped below 30 at all these stations in the fall (mid-September to late October). Chl yield is dependent upon with TP and the TN:TP ratio. Chl declines as the TN:TP ratio drops and effects on algal biomass have been demonstrated at ratios <35 (Smith 1982).

The seasonal mean chloride (Cl) concentrations also declined from the eastern (mean of stations= 15.1 mg·L^{-1}) to the western (mean of stations= 11.2 mg·L^{-1}) basin. Mean Cl concentration at west central basin stations was intermediate at 13.6 mg·L^{-1}.

BIOLOGICAL INDICES

East to west gradients were also evident with the indices of phytoplankton biomass, Chl, POC and PON (Tables 6a-h). Chl concentrations at the eastern basin stations were consistently low throughout the sampling period, with peak values reaching 4.41 µg·L^{-1} at station E2 in late August (Fig. 6). Seasonal mean Chl values at stations E1, E2 and E3 were 1.06, 2.11 and 1.13 µg·L^{-1}, respectively (mean of stations= 1.43 µg·L^{-1}).

Seasonal means were 2.67 and 3.99 µg·L^{-1} at stations WC1 and WC2 (mean of stations= 3.33 µg·L^{-1}), representing a 2.3 fold increase in mean Chl concentration from the eastern to west central basins (Table 4). Chl values peaked at west central stations in the fall (Fig. 6).

Chl showed increased variability compared to the other basins, at the western basin stations, with peaks of 7-12 µg·L^{-1} occurring at all stations (Fig. 6). Seasonal mean Chl concentrations were 4.55, 3.52 and 4.47 µg·L^{-1} at W1, W2 and W3, respectively (mean of stations= 4.18 µg·L^{-1}).

Eastern, west central and western basin stations exhibited mean seasonal POC concentrations averaged across stations of 0.149, 0.257 and 0.344 mg·L^{-1}, respectively, and seasonal mean average PON concentrations of 0.025, 0.043 and 0.056 mg·L^{-1}, respectively (Tables 6a-h). Offshore stations in the eastern and west central basins exhibited higher seasonal mean POC and PON concentrations than nearshore stations within each basin, similar to Chl. In the western basin, the opposite was found with nearshore stations showing higher seasonal mean POC and PON concentrations. Although POC and PON concentrations showed an east to west gradient, the ratio of POC to PON for each basin remained fairly constant across the lake, showing a difference of less than 3% between eastern and western basin stations (5.97 to 6.14).

PHYTOPLANKTON

Biomass and Species Composition

Phytoplankton samples were analysed only for the offshore stations in each basin. Seasonal

mean phytoplankton biomass was lowest at the eastern basin station at 0.351 $g \cdot m^{-3}$. A non-parametric Mann-Whitney test showed no difference ($p<0.05$) in the seasonal mean biomass observed at the western and west central basin stations: 0.753 $g \cdot m^{-3}$ and 0.761 $g \cdot m^{-3}$, respectively (Table 7).

Spring and summer mean phytoplankton biomass was determined for comparison to the 1983-87 data of Makarewicz (1993a). Variability in the five year data set was large with the 95% confidence interval for each basin ranging between 22 and 73% of the mean. For the comparison to Makarewicz's data, we selected dates that were closest, however, due to inter-annual variability in timing of phytoplankton peaks, it is difficult to make meaningful or conclusive comparisons. Our value (1.02 $g \cdot m^{-3}$) for the western basin station was found to be outside of the 95% confidence interval (1.46 ≤ 1.88 $g \cdot m^{-3}$) of Makarewicz's data (1993a). The eastern (0.51 $g \cdot m^{-3}$) and west central (0.91 $g \cdot m^{-3}$) basin station spring/summer mean values were not outside of the 95% confidence intervals (0.17 ≤ 0.63 $g \cdot m^{-3}$ and 0.61 ≤ 1.04 $g \cdot m^{-3}$, respectively) for 1983-87. Comparisons were also made to Makarewicz's 1983-1985 April-November mean biomass values. Our mean biomass values were 51, 40 and 49% lower than those reported by Makarewicz (1993a) at the western, west central and eastern basin stations, respectively. Values were again significantly lower in 1993 at the western basin station, and the west central and eastern basin stations were near the lower end of Makarewicz's 95% confidence interval.

Phytoplankton species richness did not vary greatly among offshore stations in each basin (Table 8). The total number of species observed were 84, 80 and 78 at stations W3, WC2 and E2, respectively, with each station showing approximately the same number of chrysophyte, cryptophyte, chlorophyte and cyanophyte species. Notable differences occurred in only two groups, diatoms and dinoflagellates. Station W3 had the greatest number of diatom species and WC2, the greatest number of dinoflagellates.

Species composition varied among the offshore stations from each basin (Table 8). For these comparisons we used only species which represented ≥0.5% of the total biomass (Table 8). Less than a quarter of the diatom, chlorophyte, dinoflagellate and cyanophyte species were common to all three stations. The greatest species similarities occurred with the chrysophytes and cryptophytes; 7 of the 16 species of chrysophytes and 6 of the 8 cryptophyte species were observed at all stations.

At the eastern basin station, three groups made maximum contributions to total biomass during the sampling season: diatoms, chrysophytes, and cryptophytes. Of the diatoms observed, *Cyclotella ocellata, C. kutzingiana, Melosira granulata* and *Nitzschia acicularis* dominated, each contributing ≥10% of the total biomass. The dominant chrysophyte species were, *Chrysochromulina parva, Chrysosphaerlla rodhei, Dinobryon sociale* and *Ochromonas* sp., and the dominant cryptophytes were *Rhodomonas lens* and *R. minuta*. A bimodal pattern in biomass was observed with diatoms as the major contributors during both the spring and fall peaks (Fig. 7a). During the spring peak, dinoflagellates were also important. Chlorophytes and cryptophytes were important in the fall, chlorophytes contributing 52% of the total biomass on one date. The

summer community was dominated by chrysophytes with diatoms making a minor contribution.

In the west central basin, diatoms, chrysophytes and cryptophytes contributed the most to total biomass, similar to the eastern basin (Fig. 7b). However, diatoms contributed the greatest proportion to total biomass on more dates than in the eastern basin. Many diatoms were important, including *Asterionella, Cyclotella, Fragilaria, Melosira* and *Stephanodiscus* species. Spring and fall biomass peaks were dominated by diatoms. Chrysophytes were important from the beginning of June until the middle of August when dinoflagellates and cryptophytes became more abundant. Algal biomass declined in late September and diatom populations increased rapidly in October.

In the western basin, phytoplankton biomass peaked in the spring, summer, and again in fall (Fig. 7c). Diatoms dominated throughout the sampling season, contributing up to 92% of the total phytoplankton biomass on some dates. The diatoms of the western basin were predominantly large, colonial forms of the genera *Fragilaria, Tabellaria*, and *Melosira* as well as centric diatoms of the genera *Stephanodiscus* and *Cyclotella*. The spring community was dominated by smaller centrics giving way to larger forms towards the end of the spring period. In the early summer, the large diatoms declined then peaked in mid-summer with *Melosira* remaining dominant in the plankton through the fall peak. Cryptophytes, largely *Rhodomonas lens* and *R. minuta*, were prevalent in the spring and contributed approximately 50% of the total biomass during the late July peak.

Photosynthesis

Seasonal mean P_{opt} values doubled from the eastern (mean of statiosn= 5.73 mg $C \cdot m^{-3} \cdot h^{-1}$) to west central (mean of stations= 13.26 mg $C \cdot m^{-3} \cdot h^{-1}$) basin and again between the west central and western basins (23.52 mg $C \cdot m^{-3} \cdot h^{-1}$). When uptake was normalized for Chl, however, mean P^B_m was similar at the eastern and west central basin stations, at 3.58 mg $C \cdot mg \ Chl^{-1} \cdot h^{-1}$ and 3.99 mg $C \cdot mg \ Chl^{-1} \cdot h^{-1}$, respectively. The elevated P^B_m at the western basin stations may be due to the positive relationship between P^B_m and increased temperature found in most lakes (Fee et al. 1992; Millard et al. 1995).

Photosynthetic parameters fluctuated seasonally within each basin. In the eastern basin (Tables 9a-b), P_{opt} was higher at station E2 than at station E3 on all but one date in late June. At station E3, P^B_m values were higher than station E2 on all except two dates in July, and no patterns were found with α_B. Daily areal photosynthesis was higher at station E2 than at E3 on all dates, due to the increased euphotic depth. Seasonal mean daily photosynthesis estimates calculated using empirical irradiance data were 58% higher at E2 (736 ± 317 mg $C \cdot m^{-2} \cdot d^{-1}$) than E3 (312 ± 167 mg $C \cdot m^{-2} \cdot d^{-1}$), respectively.

Similar to the eastern basin, inshore-offshore differences in the west central basin were observed (Tables 9c-d). P_{opt} was higher at WC2 than at WC1 throughout most of the season. WC1 had higher values on all but two dates and no consistencies in α_B. Daily photosynthesis was not always higher at WC2 as at the offshore station in the eastern basin. On two dates in

the summer and two in the fall, WC1 had higher photosynthesis. Seasonal mean daily photosynthesis calculated using empirical irradiance data was 33% higher at station WC2 (1086 ± 556 mg $C \cdot m^{-2} \cdot d^{-1}$) than at WC1 (732 ± 420 mg $C \cdot m^{-2} \cdot d^{-1}$), respectively.

Stations W1 and W3 did not differ as greatly as inshore-offshore comparisons in the other basins (Tables 9e-f). P_{opt} was generally higher at station W3 than at W1 until late July, with the reverse occurring during the remainder of the season. P^B_m values were higher at station W3 on all but two dates, with α^B also greater at W3 except for a period during late July to mid August. Daily integral photosynthesis based on empirical irradiance data was higher at W1 during the period from mid July to mid September. Seasonal mean daily photosynthesis was almost identical at the two stations, 844 ± 683 mg $C \cdot m^{-2} \cdot d^{-1}$ at W1 and 871 ± 453 mg $C \cdot m^{-2} \cdot d^{-1}$ at station W3.

In summary, photosynthetic rates differed spatially in a nearshore-offshore direction in the eastern and west central basins, though this was not the case in the western basin. Similar to P_{opt}, seasonal photosynthesis on a volume basis showed a trend of higher values at the offshore stations in the eastern and west central basins.

An east to west gradient in the means of all stations for each basin was also observed (Table 10). Mean areal photosynthesis of the eastern basin stations (79.6 g $C \cdot m^{-2} \cdot yr^{-1}$), was about half that of the other two basins. Seasonal areal photosynthesis for the west central and western basin stations were identical with means of 146.5 g $C \cdot m^{-2} \cdot yr^{-1}$ and 146.6 g $C \cdot m^{-2} \cdot yr^{-1}$, respectively. Western basin stations differed by < 6%, although estimates differed by 30% in the west central basin. Using cloudless solar irradiance data to estimate seasonal photosynthesis gives potential maximum photosynthesis. Empirical values fall within a narrow range of cloudless estimates (Table 10), indicating that yearly variability in seasonal photosynthesis is not greatly impacted by solar irradiance (Millard et al. 1995), but daily values can be (Table 9).

Areal phytoplankton photosynthesis is dependent on the mean epilimnetic irradiance ($\bar{I}$, $mE \cdot m^{-1} \cdot min^{-1}$). $\bar{I}$ is influenced by the interplay of incident solar irradiance, ε_{par}, and Z_m. $\bar{I}$ calculated using cloudless irradiance illustrates the change in light environment within each basin throughout the season due to only ε_{par} and Z_m, not cloudy conditions (Table 9). In the western basin, fluctuations in $\bar{I}$ are due to ε_{par}, whereas Z_m has more of an influence in the other basins.

In the eastern basin, the deep offshore station had a mean $\bar{I}$ of 10.5 $mE \cdot m^{-1} \cdot min^{-1}$ during the stratified period when Z_m averaged 13.7 m, compared to 2.5 $mE \cdot m^{-1} \cdot min^{-1}$ during isothermal conditions when Z_m was 38 m. Lowest spring and fall $\bar{I}$ values were also associated with high ε_{par}. At station E3, $\bar{I}$ averaged 15.3 $mE \cdot m^{-1} \cdot min^{-1}$ with a September/October average of 5.1 $mE \cdot m^{-1} \cdot min^{-1}$. Higher $\bar{I}$ at station E3 was due to a shallower mixing depth (mean= 9.2 m) than at station E2. In the west central basin, $\bar{I}$ values averaged 30% higher at WC1 than at WC2, due to the shallower Z_m and lower ε_{par}.

In the western basin, $\bar{I}$ was similar at W1 and W3, with low $\bar{I}$ caused by high ε_{par} values. During the fall, values declined to averages of < 2.0 $mE \cdot m^{-1} \cdot min^{-1}$ at both stations, indicating that

phytoplankton growth may be light-limited. The shift from nutrient to light limitation of phytoplankton growth occurs below approximately 2.5 to 3.5 $mE \cdot m^{-2} \cdot min^{-1}$ (Hecky and Guildford 1984). The decline in $\bar{I}$ to limiting levels at stations W1 and W3 was not unique to the western basin, as $\bar{I}$ at WC2 also declined in the fall. The potential light limitation of phytoplankton growth did not appear to be any more severe in the western basin than in the west central basin given the similarities in the patterns of $\bar{I}$ and the very high P_{opt} in the western basin. It is difficult to reach conclusions regarding light limitation without measurements of phytoplankton growth or nutrient demand.

ZOOPLANKTON

Density

Zooplankton density was similar in the western and west central basins with non-veliger numbers peaking between 8.9 and 13.0 x $10^4 \cdot m^{-3}$ (Figs. 8 and 9). There were far fewer zooplanktors in the eastern basin with peak non-veliger densities reaching a maximum of 3.1 x $10^4 \cdot m^{-3}$ (Fig. 10). There were more animals nearshore than offshore in all three basins. Generally, the relative proportions of zooplankton types in the western basin were similar to those in the west central basin except that very few *Dreissena* veligers were found at the offshore station, WC2, in the west central basin. Cladocerans were in low abundance relative to other zooplankton taxa in the eastern basin. Rotifers were present in very high densities and are shown separately in Fig. 11. Like other zooplankton, their numbers were higher in the western and west central basins than in the eastern basin. There did not appear to be a strong nearshore/offshore gradient in rotifer density as with the macrozooplankton except perhaps early in the spring when rotifers were more abundant offshore at stations W3 and WC2.

Biomass

Like zooplankton abundance, biomass was similar in the western and west central basins and greatly reduced in the east (Figs. 12, 13 and 14). In the west, nearshore (W1) biomass was similar to that offshore, although because animals offshore were larger, offshore density was less (Table 11,12). The seasonal mean lengths of all eight common species of macrozooplankton were greater in the offshore. In particular, *Daphnia retrocurva* which comprised most of the cladoceran abundance and a large portion of the total biomass from June to August, were more than 100 μm longer on average than those at the nearshore station. Biomass declined at both stations after early August. At this time the *Daphnia* disappeared from the water column and were replaced by smaller-bodied *Eubosmina*, *Bosmina* and rotifers. In the west central basin, biomass followed a similar pattern to abundance, although high numbers of *Dreissena* veligers nearshore do not translate into high biomass values due to their small size. Veliger biomass, like abundance, in the offshore station (WC2) was negligible. Eastern basin biomass was low, similar to abundance where cladocera accounted for very little of the total biomass and large *Daphnia* were absent.

We compared macrozooplankton biomass in 1993 to mean 1984-87 values which were recalculated by J. Makarewicz to include only those stations located closest to ours (Table 12). We calculated 1993 biomass by including only those dates which coincided with dates sampled in 1984-87. The inherent problem in comparing select dates from one year to the next is that the effect of timing contributes to the variation in yearly estimates. Thus, seasonal (May -Oct.) means were also calculated for 1993 data to incorporate all variability within the sampling season giving a more accurate estimate of the mean (Table 12). Additional variability between the two studies was due to different sized mesh used to obtain the zooplankton. Makarewicz used a 62-μm mesh while we used a 110-μm mesh. The larger mesh used in 1993 is expected to retain fewer animals, resulting in lower biomass estimates. A significant reduction from 1984-87 to 1993 would be the result of inconsistent methodology in addition to any true reduction in zooplankton biomass.

Variability associated with yearly zooplankton biomass between 1984-1987 was large. The 95% confidence interval ranges from 72 to 100% of the mean, making it difficult to assess the significance of any reduction in zooplankton biomass. Because we have only one post-zebra mussel data point we can only determine if it falls within or outside of the confidence interval of the pre-zebra mussel data. We would require at least three years of data to test whether the mean pre- and post-zebra mussel zooplankton were significantly different. All 1993 zooplankton biomasses fell within the 95% confidence interval about the 1984-1987 data. Therefore no statistically significant differences were detected between pre- and post-zebra mussel periods. However, biomass in the eastern basin for 1993 was at the low end of the 95% confidence interval. 1984-1987 mean biomass was 60.8 μg·L^{-1} while biomass in 1993 was only 24.4 μg·L^{-1} nearshore and 14.9 μg·L^{-1} offshore. 1993 values were higher when the entire season was considered and higher still when veligers were included. However, in each case the 1993 biomass was lower than the mean 1984-1987 biomass. In the western basin, nearshore biomass was lower than estimates from the pre-zebra mussel time period (although still within the 95% confidence interval). This was not the case in the offshore. In contrast to the western basin, biomass from the west central basin in 1993 appeared lower offshore and higher nearshore, although all numbers still lay within the 95% confidence interval.

For comparing rotifer biomass from 1993 to that of 1984-87 (Makarewicz 1993b), 1984-87 whole basin estimates were used. In the case of rotifers, we had data from three stations in each of the eastern and western basins, which we felt better represented the basin as a whole. That Makarewicz used a 62-μm mesh while we used a 20-μm mesh for 1993 collections, means that in similar situations we would expect more rotifers in our samples. This was not the case in the eastern or the western basins. In the west Makarewicz' mean rotifer biomass for the four year period was 17.9 μg·L^{-1} (±10.77, 95% confidence interval), while our western basin stations ranged from 7.6 only up to 13.4 μg·L^{-1}. Because the 1993 values were lower, even though collected with a much smaller mesh, we reason that rotifer biomass decreased since Makarewicz' study. Results in the eastern basin were similar. The 1984-87 mean is 8.6 μg·L^{-1} (±8.59) compared with a range of 3.8 to 8.0 μg·L^{-1} in 1993. The 1993 biomass in the west central basin is slightly higher than Makarewicz' mean for the entire central basin (12.9 and 14.3 μg·L^{-1} vs 11.6 ±11.87 μg·L^{-1}) indicating that rotifers may not have been reduced as much here as in the

rest of the lake.

Seasonal Changes

Two different zooplankton communities existed in the western basin, one from May through to early August and the other from early August through to late October (Figs. 8 and 12). The early community was dominated by cladocera, most of which were large-bodied *Daphnia retrocurva*. Others such as rotifers, cyclopoids, calanoids and some veligers were present but in relatively low biomass. *Daphnia* persisted until early August and then virtually disappeared from the water column. Cladocerans remaining after this time were small bodied *Bosmina* or *Eubosmina*. As *Daphnia* declined rotifers increased, particularly in the offshore. Calanoids and cyclopoids remained consistently low throughout the season except in September and October when calanoids become important nearshore. Veligers were present in the water column from mid June through to the end of August with low peaks in mid August and mid September.

Rotifers contributed most of the biomass in the west central basin early in the season (Figs. 11 and 13). Cladocera, cyclopoids and calanoids were also present but their biomass was low. Through mid-summer cladocera became more important, particularly nearshore, whereas calanoids were equally important offshore. Cyclopoids emerged in two peaks, late July and late September onshore and almost a month later offshore in mid to late August and October. Veligers had one major biomass peak in mid August nearshore and were never a significant component of the offshore community.

There were very few zooplanktors in the eastern basin until mid June (Figs. 10 and 14). Rotifers dominated the early community and remained important contributors throughout the season. Calanoids and cyclopoids were present throughout the summer comprising about two thirds of the total biomass nearshore after mid July. Veligers were present throughout the summer after mid June and comprised approximately one third of the total offshore biomass.

Common Species

Twenty of the twenty-seven species of macrozooplankton that were present in Lake Erie in 1993, were "common" (≥5% of the total biomass) (Table 13). Examination of the pattern of distribution of the "common" species revealed several important shifts in community structure across the basins. 1) *Dreissena* veligers contributed more than 5% of the total sample biomass on more occasions than any other species in both the western and eastern basins of Lake Erie. Their presence was not as important in the west central basin. 2) "Common" species of cladocera varied in the lake from west to east. In the west, *Daphnia retrocurva* was the most frequently encountered cladoceran, attaining "common" status in approximately 50% of the samples examined. *Bosmina sp* contributed ≥5% of the total biomass in approximately one third of the cases. In the west central basin, *Daphnia* were only "common" offshore while *Bosmina* contributed ≥5% of the total biomass in almost every sample examined. In the east, *Bosmina* species were very common, and *Daphnia* species were not "common", a strong contrast to the western basin. 3) The large predatory cladocerans, *Bythotrephes cederstromei* and *Leptodora*

kindti were never "common" at the same time and place. *Bythotrephes cederstromei* were not observed in the west, however they were "common" 50% of the time in both locations in the west central basin and were only "common" on one occasion in the eastern basin, near shore. In contrast, *Leptodora kindti* were "common" only offshore in the western and eastern basins. 4) Large diaptomids such as *Leptodiaptomus ashlandi*, *L. minutus*, *L. sicilis* and *Skistodiaptomus oregonensis*, were much more "common" in the west central basin than in the other two basins. In fact, diaptomids were rarely found in the western basin. 5) The dominant predatory copepod in the zooplankton community changed from basin to basin. The importance of *Epischura lacustris* and *Diacyclops thomasi* decreased from east to west. *Mesocylops edax* was an important component of the west central basin community. While *Limnocalanus macrurus* and *Cyclops vernalis* were not important components in the zooplankton community, each species reached "common" status once in the season, *Limnocalanus macrurus* in the western basin and *Cyclops vernalis* in the west central basin.

Although the number of rotifer species observed per station were similar among the basins, ranging from 29 to 40, fewer species contributed significantly to total biomass in the eastern basin than in the western and west central basins (Table 14). The species dominant lake-wide were: *Asplanchna priodonta*, *Synchaeta spp.*, *Polyarthra major*, *P. vulgaris* and *Conochilus unicornis*. *Kellicottia longispina*, *Keratella cochlearis* and *K. crassa*. *Trichocerca cylindrica* and *T. multicrinis* were also important in the west central basin, and *Asplanchna herricki*, *Keratella cochlearis*, *K. earlinae*, *Pleosoma spp.*, *Trichocerca rousseleti*, *T. pusilla* and *Filinia longiseta* were important, on occasion, in the western basin.

Differences in species composition were observed among the basins. *Brachionus spp.* were observed only in the western basin, *Asplanchna herricki* only in the western and west central basins, and *Polyarthra euryptera* only in the eastern basin. Other species were more prevalent in some basins than others. *Trichocera rousseleti* and *T. pusilla* were important principally in the western basin. *Gastropus stylifer* and *Polyarthra dolichoptera* were important only in the west central basin. *Kellicottia longispina*, *Keratella crassa*, *Trichocercus cylindrica* and *T. elongata* were more important in the west central and secondarily the eastern basin.

Size Comparisons

The mean length of zooplankton from the whole water column at each station on each date was calculated as an index of planktivory, comparable to that of other data bases on Lakes Erie, Ontario and Oneida. The zooplankton communities in Lake Erie are composed of small animals throughout the season, except in the spring in the offshore of the western basin (Fig. 15). From May until the end of July, mean length in the offshore at W3, ranged between 0.60 and 0.90 mm, while the range was from 0.30 mm to 0.50 mm in the nearshore. At the beginning of August, mean length dropped at both sites and varied between 0.20 and 0.35 mm until October when it increased slightly. In the west central basin, mean length ranged from 0.25 to 0.45 mm and was larger in the nearshore than in the offshore on all but two occasions. In the eastern basin, the opposite pattern occurred. Mean length varied from 0.32 to 0.60 mm, but was larger in the offshore than in the nearshore on all but two occasions.

Differences in planktivory between the nearshore and offshore were further investigated by comparing the mean lengths of individuals of the same species between the two locations. This comparison was restricted to epilimnetic samples in order to be more directly comparable. In the western and eastern basins, individuals of the same species tended to be larger at the offshore site than at the nearshore site (Table 11). The difference in length was greater than 10% for six of the eight species dominant in the western basin and three of the six species dominant in the eastern basin. The reverse was true in the west central basin. Seven of the eight dominant species were larger in the nearshore than in the offshore, four of them by more than 10%. *Tropocyclops extensus* (previously *Tropocyclops mexicanus prasinus*, renamed by Dussart and Fernando 1990), a small copepod, showed no difference in size between sites in either the eastern or west central basin. In only two instances were the directions of the size difference contrary to the trend: *Epischura lacustris* in the west central basin, and *Diacyclops thomasi* in the eastern basin. *Dreissena* veligers were also measured. They showed no difference in size in the western basin and tended to be larger nearshore in the other two basins.

BENTHOS

Total abundance of the benthic fauna was greatest at the two eastern basin stations. This was due to the very high density of recently settled quagga mussels of < 1 mm length (Table 15). Other taxa that were most common in the eastern basin were: Nematoda, the amphipod *Gammarus*, the Trichoptera, mostly *Molanna* and *Oecetis,* and the gastropods, mostly *Amnicola limnosa*. The high densities of benthic fauna in the western basin were due to large numbers of small ostracods and harpacticoids. The leeches *Helobdella stagnalis* and *H. elongata* were most numerous in the western basin. Oligochaetes were abundant at all stations, but the greatest densities occurred at stations WC2 and E2. Both of these stations are situated in water >20 m deep. The Sphaeriidae, mostly *Pisidium* spp. were most numerous at station WC2 in the hypolimnion of the west central basin.

The benthic biomass at all stations, except WC2, was dominated by *Dreissena* spp., which represented over 90% of the total wet shell-free weight of the benthic fauna (Table 16, Fig. 16). Quagga mussels (*D. bugensis* or *D. rostriformis bugensis*) were not present in the western basin, but represented 95% to 99% of the mussels at the two stations situated in water beyond 20 m: WC2 and E2. During 1993, quagga mussels became increasingly more common in the central and eastern basins of Lake Erie. Over the year, the density of *D. bugensis* at station WC2 ranged from 445 ind.·m^{-2} in July to 86 ind.·m^{-2} in August. This variability in density was due to both the species' patchy distribution, recruitment and subsequent mortality or translocation of the settled young. Biomass of the quagga mussels at station WC2 increased steadily from 0.051 g·m^{-2} (wet shell-free) in May, 1993 to 28.123 g·m^{-2} in May 1994, as the settled mussels grew over the year.

Excluding the zebra and quagga mussels, the oligochaetes formed the dominant proportion of the benthic biomass at all stations. Oligochaete biomass was greatest at the two deepest stations, WC2 and E2, and ranged from 1.6 to 12.6 g·m^{-2} (Table 16). The chironomids, mostly

Chironomus thummi group, were the next taxa which contributed a large proportion of the biomass with their greatest biomass (12.3 g wet weight·m^{-2}) at station WC2.

The low proportion of *Dreissena* and relatively high biomass of Chironomidae and Sphaeriidae (1.2 g·m^{-2}, wet shell-free) at station WC2 probably reflects the low mid-summer oxygen conditions in the hypolimnion of the central basin. The *Chironomus* species and several of the *Pisidium* species are adapted to survive in water that experience short periods of low oxygen. *D. bugensis* was able to colonize WC2 during 1993. Only one cohort existed at this site, which grew from an average of 0.0002 g·m^{-2} on May 20, 1993 to 0.2917 g·m^{-2} (wet shell-free) by May 20, 1994.

As with biomass, the benthic production at all stations was dominated by *Dreissena*, except at the station in the hypolimnion of the west central basin (WC2). *Dreissena* represented more than 90% of the calculated annual production at five of the stations (Table 17). Midges of the *Chironomus thummi* group dominated the production at this deeper central basin site, WC2. The other important component of the total benthic production of Lake Erie was the oligochaete worms which had an annual production of between 8 to 54 g·m^{-2}·yr^{-1}. The calculated annual production by the Chironomidae at the hypolimnion station in the central basin was 25 g·m^{-2}·yr^{-1} (wet), and represented 25 % of the total benthic production at that station. At station WC2, wet production by *Chironomus semireductus* group was 17.1 g·m^{-2}·y^{-1} (P/B=1.7), and that by *C. thummi* group was 7.2 g·m^{-2}·y^{-1} (P/B=2.9). The oligochaetes at the inshore stations appeared to have two reproductive periods per year (late spring and late summer). Offshore, in depths beyond 20 m, worm densities increased in June. This is the same month that the *Chironomus* adults emerge in the central basin.

Amphipods were only common at the shallow stations. No specimens of the deep-water amphipod *Diporeia hoyi* were found in any of the samples collected for this study. The amphipod *Gammarus fasciatus* was abundant only at the shallow station in the eastern basin (E3). At that 9 m station, the production by *Gammarus* increased to 20 g·m^{-2}·yr^{-1}. However, this production by the *Gammarus* represented only 0.7 % of the total annual production, because of the high biomass of *Dreissena* spp. at that station.

DISCUSSION

The trophic status of each basin of Lake Erie in 1993 has been classified based on nutrient and Chl concentrations, phytoplankton biomass and phytoplankton photosynthesis estimates (Table 18). The western and west central basins were mesotrophic and the eastern basin was oligotrophic. These findings indicate an improvement in water quality since Bartish (1987) classified the western basin as highly eutrophic and the eastern basin as mesotrophic. The move towards oligotrophy was initiated by phosphorous controls in the early 1970s. However, do the continued phosphorus controls explain the acceleration of the trend toward oligotrophy in Lake Erie seen since 1989? We examine the relative effects of phosphorus control, the filtration activity of the newly invaded zebra and quagga mussels (*Dreissena polymorpha, D. bugensis*)

and planktivory in reducing productivity in each basin of the lake.

WESTERN BASIN

Phosphorus abatement from 1970 to the early 1980s resulted in an estimated decrease in P loading to the western basin of >50% (Burns 1985). During this period there was an accompanying decline in phytoplankton biomass of 71% (Makarewicz 1993a) and an estimated reduction in phytoplankton production of 18.5% (Madenjian 1995). Through the 1980s, P loading remained relatively stable and although TP slowly declined (Lesht et al. 1991; Dolan 1993), no decline in phytoplankton biomass was observed (Makarewicz 1993a). In 1993, mean phytoplankton biomass had declined by 51% relative to the 1983-85 seasonal mean reported by Makarewicz (1993). Mean seasonal areal phytoplankton photosynthesis for the western basin from 1983-85 was estimated at 228 g $C \cdot m^{-2}$ using an equation which predicts seasonal phytoplankton production from TP concentration (Millard et al. 1995). The relationship between sesonal PP and seasonal mean TP, was developed using Bay of Quinte and Lake Ontario data and is used as a tool to estimate lower trophic level production. Least-squares regression was used to fit a function to the data of the same form ($Y=(ax)/(b+x)$) as that used by Vollenweider et al. (1974) to relate annual PP to P loading for all of the Great Lakes. Parameterization of the curve fit by Millard et al. (1995) was very similar to that obtained by Vollenweider et al. (1974). Our 1993 seasonal photosynthesis estimates were 146 g $C \cdot m^{-2}$, representing a reduction of 36% from the mid 1980s. Based on TP concentrations in the western basin in 1993, the predicted mean seasonal photosynthesis would have been 191 g $C \cdot m^{-2}$. There are no confidence intervals on the relationship, however, it is interesting that the observed photosynthesis value was on the lower side of the relationship. Seasonal photosynthesis in 1993, was approximately 23% below that predicted by TP. It is unlikely that a change in P loading was responsible for the reductions in phytoplankton biomass and photosynthesis in 1993. Actual P loadings for 1993 are not currently available, but it is doubtful that loadings declined in 1993 as municipal loads were already near 100% compliance in 1986 (Dolan 1993) and no overall decline was observed between 1989-91 (Neilson et al. 1994).

Nicholls and Hopkins (1993) and Holland (1993) demonstrated this decline in phytoplankton in nearshore areas after 1989 and determined it was not related to further decreases in nutrient loading. They attributed the low phytoplankton numbers to filtering by zebra mussels. Nicholls and Hopkins (1993) showed that phosphorus loading remained fairly consistent in the two years preceding the invasion of zebra mussels and the first two years post-invasion. A model predicting the phytoplankton density based on phosphorus loading in the western basin showed that densities should have been dramatically higher than those measured (Nicholls and Hopkins 1993).

Zebra mussels have been implicated in the decline of Chl and increase in water transparency in the western basin. Leach (1993) reported decreases in chlorophyll in the western basin of 54% and increases in Secchi depth of 54%, from 1988 to 1990. Other long-term data sets for the open water regions of the western basin also indicated reductions in spring/summer (stratified period) Chl of 86%, from 7.19 $\mu g \cdot L^{-1}$ in 1988 to 1.03 $\mu g \cdot L^{-1}$ in 1990 (Neilson et al. 1994). In 1993, the

mean spring/summer Chl concentration at the western basin stations (4.04 $\mu g \cdot L^{-1}$) was substantially higher than the mean reported for 1990, indicating a partial recovery of Chl. However, the 1993 mean Chl was still significantly lower than the 1983-87 mean (± 95% CI) (8.73 $\mu g \cdot L^{-1}$ ± 4.24) (Neilson et al. 1994). It is unreasonable to expect Chl to increase to pre-mussel concentrations considering the resident zebra mussel population. Herbivorous *Daphnia* biomass was greater in 1993 relative to 1984-87 and although Wu and Culver (1991) showed evidence for phytoplankton control by *Daphnia*, MacIsaac et al. (1992) showed that the filtering impact of *Dreissena* may be up to 30 times greater than that of *Daphnia*.

Not only has total phytoplankton biomass declined in the western basin since the invasion of the zebra mussels, but it appears as though species composition has also changed. In 1970, the species of phytoplankton found in western Lake Erie were indicative of eutrophic conditions (Munawar and Munawar 1982). Makarewicz (1993a) found that from 1970 to 1983-87, the phytoplankton community did not change drastically, although the abundance of eutrophic indicator species declined while mesotrophic indicator species increased. In 1993, the western basin appeared to be less eutrophic as eutrophic indicator species, *Fragilaria capucina* and *Stephanodiscus tenuis* were not present.

The decline in biomass in 1993 has been due to reductions in diatom biomass, probably resulting from the filtration activities of zebra mussels. Although diatoms were still the dominant group in the western basin in 1993, biomass was 68% lower than in 1983-87. Studies by Holland (1993) support this finding, as she found a dramatic decline in the density of planktonic diatoms in a shallow embayment in the western basin between a pre-mussel period (1984-1987) and a post-mussel period (1990-1993) despite very little change in total phosphorus (Holland et al. 1994). Nicholls (pers. comm.) also observed low diatom abundances from 1990-1993 at nearshore sites, despite high silica concentrations. The reduction in diatoms may have alleviated competition for nutrients, allowing for the increase in chrysophytes observed in 1993. Chrysophyte mean biomass increased by 60% from 1983-87, but given their small size, represented only 8% of the total spring/summer biomass. This shift toward smaller phytoplanktors signals the shift to a more oligotrophic state (Wetzel 1983).

The reductions in phytoplankton biomass and photosynthesis, and the shift to smaller forms of algae in 1993, were attributed to the filtering activities of zebra mussels. Zooplankton, however, did not seem to be affected by these changes in the phytoplankton. There was no significant reduction in mean zooplankton biomass from 1983-87 (Makarewicz 1993b) to 1993 when selected dates were compared. Station W1 was at the lower end of the confidence interval, and biomass differed between W1 and W3 by 74%. When the entire sampling season (May - Oct.) was considered, biomass at W1 was very similar to the 1984-87 mean and there was little difference between the mean biomass at each station. Thus the initial impression of a large difference between stations W1 and W3 based on comparing limited dates, was misleading.

The mean community size of zooplankton at the western basin stations in 1993, was 0.70 mm from spring until early August, when *Daphnia* made up a large portion of the biomass. This value compares to 0.80 mm suggested by Mills and Schiavone (1982) to indicate a balance

between the herbivores, planktivores and piscivores. The mean community size declined in mid August suggesting a natural predation impact by young fish (Mills et al. 1987). In addition, there was little change in the species composition from the 1980s, prior to zebra mussels, to 1993, however, daphnid biomass increased by 38% between 1984-87 and 1993 The pelagic impacts of zebra mussels appear to have been limited to reducing lower trophic level biomass and production. Apparently, in 1993, these reductions did not reach a critical level whereby the zooplankton community was adversely affected.

Benthic production and community structure in the western basin, has been affected by *Dreissena polymorpha*. Production is now almost exclusively dominated by *Dreissena*, accounting for over 90% of the annual production and wet shell-free biomass in the lake. Using the average benthic biomass as a surrogate for production, average annual wet biomass during 1993 was 351.4 $g \cdot m^{-2}$ (shell-free). Average wet biomass (without Unionidae) during autumn 1979, nine years prior to the invasion by the zebra mussels was 8.8 $g \cdot m^{-2}$ (n=52) (Dermott 1994). Comparable biomass of the benthic fauna, excluding that of the mussels, in the western basin during 1993 was 7.0 $g \cdot m^{-2}$. This value was comparable to the benthic biomass value prior to the invasion of the western basin by *Dreissena polymorpha*. This indicates that the huge amount of biomass in the mussel populations is not a result of the replacement of the biomass of the benthic community by *Dreissena polymorpha*.

The only benthic taxa which are being replaced by *Dreissena polymorpha* in the western basin, are the native clams, both Unionidae and Sphaeriidae. A crude estimate of the previous wet weight of the Unionidae alone in the western basin was 112.0 $g \cdot m^{-2}$ (shell-free) during 1979 (Dermott 1994) in contrast to their absence in 1993. This estimate used a dry:wet weight ratio of 0.149. Throughout the near-shore areas of Lake Erie, *Gammarus* populations have dramatically increased in association with the newly established mussel colonies. These mussel colonies provide interstitial spaces and a probable increased food supply in the form of the mussels' pseudofaeces (Dermott et al. 1993). Biomass of *Gammarus* in the western basin increased from an average of 1.6 $mg \cdot m^{-2}$ at 52 sites sampled during 1979 (Dermott 1994) to 487.4 $mg \cdot m^{-2}$ (wet weight) at the two stations sampled during 1993.

CENTRAL BASIN

Phosphorus loading declined in the central basin by >40% from 1970 to the early 1980s (Burns 1985) and phytoplankton biomass declined by 47% (Makarewicz 1993a). Through the 1980s, P loading and phosphorus concentrations remained relatively stable, although lower than in the western basin (Lesht et al. 1991). Phytoplankton biomass did not change during this time (Makarewicz 1993a). Gradients have been shown to exist for many parameters, including TP and Chl concentrations, within the central basin, with values highest toward the west (Charlton 1994). Because of the location of our west central basin stations, at the western end of the basin, seasonal phytoplankton biomass and photosynthesis in 1993 are likely overestimates of the central basin as a whole. Inferences can be made, however, regarding reductions in the central basin by comparison of the west central data to historical central basin data. In 1993 the mean

phytoplankton biomass in the west central basin was 40% lower than the 1983-85 seasonal mean of the central basin (Makarewicz 1993a). Seasonal areal photosynthesis in 1993 for west central stations (147 g $C \cdot m^{-2}$) was also lower, by 17%, than the 1983-85 estimate for the entire central basin (176 g $C \cdot m^{-2}$) using TP (Millard et al. 1995). The relationship between seasonal PP and TP, is only a tool to estimate lower trophic level production, hence, the significance of a 17% reduction is uncertain. However, given that phytoplankton biomass and photosynthesis were lower in the west end of the basin in 1993 relative to the mid 1980s, we assume that values were even lower throughout the rest of the central basin. P loading to the central basin remained relatively stable throughout the 1980s and into the 1990s (Lesht et al. 1991; Neilson et al. 1994) and as in the western basin, was likely no lower in 1993. *Dreissena* and not reductions in P loading, appear to have had an overall effect on phytoplankton in the central basin, however effects were less in the west end of the basin due to low mussel density. In this area, low summertime oxygen concentrations in the hypolimnion may limit the dreissenid population (Dermott and Munawar 1993). The relationship of Millard et al. (1995) predicts seasonal photosynthesis at the west central basin stations in 1993 to be 152 g $C \cdot m^{-2}$. Although the relationship of Millard et al. (1995) does not have confidence intervals, the similarities between observed (147 g $C \cdot m^{-2}$) and predicted values suggest that, unlike the western basin or the nearshore of the eastern basin, photosynthesis was not below that predicted by TP.

Dreissena were implicated in the decline of Chl and the increase in water transparency in the west central basin between 1988 and 1990, but not to the extent reported for the western basin. Leach (1993) reported decreases in chlorophyll of 27% and increases in Secchi depth of 52%, in the west central basin between 1988 and 1990. In the central basin as a whole, Chl reportedly decreased by 66%, from 1.88 $\mu g \cdot L^{-1}$ in 1988 to 0.64 $\mu g \cdot L^{-1}$ in 1990 (Neilson et al. 1994). Prior to the invasion of *Dreissena*, Chl concentrations remained fairly stable in the central basin, averaging 3.23 $\mu g \cdot L^{-1}$ from 1983-87 (Neilson et al. 1994). Chl in the central basin declined with the advent of *Dreissena*, however, the similarity between the 1993 Chl at the west central basin stations (3.38 $\mu g \cdot L^{-1}$) and that observed in 1983-87 in the central basin suggests that Chl is not affected to the same extent in the west central basin as in the central basin as a whole. West central basin stations are in a region of very low *Dreissena* density (Dermott and Munawar 1993) compared to the whole of the central basin.

Using central basin phytoplankton data as an indicator of species composition in the west central basin, phytoplankton composition has not changed greatly from 1983-87, except for the absence of a few species that were important in 1983-87 and an increase in the importance of *Melosira granulata* in 1993. The eutrophic indicator species, *M. binderana* and *Stephanodiscus niagarae* were present in the west central basin in 1993 along with various *Cyclotella* species which prefer more oligotrophic waters (Munawar and Munawar 1978).

Moderate changes in the phytoplankton in the west central basin have been observed, however, there has been no reduction in mean zooplankton biomass at west central basin stations from the pre-invasion (Makarewicz 1993b) to the post-invasion period. When the stations were examined individually in 1993, it appeared as though zooplankton biomass was lower, by 69%, at the deeper station than at the shallower station. *Dreissena* numbers were much lower at the

deeper station and were likely not responsible for this discrepancy. The effects of timing of sampling may again have lead to the conclusion that the zooplankton biomass at stations WC1 and WC2 were different. Means for the entire season differed by only 29%.

Mean length of zooplanktors commonly consumed by planktivores was smaller at the deeper station than their counterparts at the shallower station and thus it is possible the lower biomass is due to predation by planktivores. In terms of species composition, some changes were observed from 1984-87 to 1993. *Daphnia*, although still present in 1993 had a lower biomass than 1984-87. The number of calanoid species common in 1993 increased and contributed a larger portion to the total biomass.

Dreissena have altered production of the benthic community more so at the shallower station (WC1) where they accounted for >99% of the total production, relative to only 27% at the deeper station (WC2). This is consistent with the low mussel density at the deeper station. Benthic biomass is used to compare pre- and post-mussel periods as pre-mussel benthic production is not available. The average wet benthic biomass in 1979 was 16.3 $g \cdot m^{-2}$ (Dermott 1994) compared with 12.2 $g \cdot m^{-2}$ (without *Dreissena*) in 1993. This shows that there has been little change in biomass of endemic benthic fauna, but that *Dreissena* have added to the biomass increasing the total to 396.9 $g \cdot m^{-2}$ (shell-free).

EASTERN BASIN

Nutrient concentrations and phytoplankton biomass and photosynthesis have historically been lowest in the eastern basin (Bertram 1993; Glooschenko et al. 1974). P loading to the eastern basin declined by >40% from 1970 to the early 1980s (Lesht et al. 1991), resulting in a reduction in phytoplankton biomass of approximately 69% (Makarewicz 1993a). Through the 1980s, P loading and TP concentrations fluctuated moderately (Lesht et al. 1991), but an overall decline was not observed. Likewise, no decline in spring/summer phytoplankton biomass was detected (Makarewicz 1993a). In 1993, mean phytoplankton biomass (0.351 $g \cdot m^{-3}$) declined by 49% relative to the 1983-85 seasonal mean (0.683 ± 0.358) reported by Makarewicz (1993a). We estimated phytoplankton photosynthesis for 1983-85 using TP concentrations (Millard et al. 1995). Photosynthesis was estimated at 155 g $C \cdot m^{-2}$ which was similar to the basin-wide 1970 estimate of 160 g $C \cdot m^{-2}$ (Glooschenko et al. 1974). Our seasonal photosynthesis estimate in 1993, for combined nearshore and offshore eastern basin stations was 80 g $C \cdot m^{-2}$, representing a 50% decline from the mid 1980s. However, when photosynthesis at each station is considered separately, it is the disproportionately low photosynthesis in the nearshore that lowers the mean. Based on TP concentrations in 1993, seasonal photosynthesis at the offshore station was predicted at 122 g $C \cdot m^{-2}$, only 14% higher than the observed. At the nearshore, however, the observed seasonal photosynthesis was 47% lower than predicted. Although the predictive relationship of Millard et al. (1995) is a tool to estimate photosynthesis, the difference between the observed and predicted values at station E3 in 1993, suggests that lower trophic level production was affected to a greater extent than at the other stations.

Unlike in the 1970 to early 1980s period, the reductions in phytoplankton biomass and photosynthesis in 1993 were not accompanied by a decline in P loading to the eastern basin. As in the western basin, actual P loading data for 1993 are not yet available, however, the near 100% compliance of municipal loadings since 1986 (Dolan 1993) and the lack of decline in total loadings between 1989-91 (Neilson et al. 1994) suggest that 1993 loads were no lower. However, the mean TP concentration in 1993 was significantly lower than the 1980-86 mean (11.8 ± 1.7 $\mu g \cdot L^{-1}$, 95% C.I.) (Lesht et al. 1991). The decline in TP concentration in the eastern basin in 1993, may have been the result of filtering activities of *Dreissena* redirecting pelagic material to the sediments as faeces and pseudofaeces (Holland et al. 1994). At the offshore station, TP concentrations declined throughout spring isothermy. Quagga mussels exerted their greatest effect during this time, as they had access to algae in the entire water column. Nearshore, the water column remained well mixed allowing mussels access to the water column for the entire sampling season, keeping TP concentrations low throughout. In contrast, western basin stations which also remained isothermal throughout the sampling season, had higher TP concentrations. Although P loading was also higher, the prevalence of internal loading from sediment resuspension, indicated by elevated SRP (Charlton et al. 1993), contributed to the high TP. In the western basin, the mean SRP concentration was 67% higher than at comparable nearshore eastern basin stations.

Nicholls and Hopkins' (1993) study demonstrated this decline in phytoplankton in nearshore areas in the eastern basin, as in the western basin, and attributed the low phytoplankton numbers to filtering by *Dreissena*. They showed that phosphorus loading remained fairly consistent in the two years preceding the invasion of *Dreissena* and the first two years post-invasion.

Long-term data sets for the open water regions of the eastern basin indicate fairly stable spring/summer chlorophyll concentrations from 1983 until 1988 (Neilson et al. 1994). Mean Chl reportedly decreased by 80% between 1988 and 1990, from 1.56 to 0.31 $\mu g \cdot L^{-1}$ (Neilson et al. 1994). In 1993, the mean Chl concentrations were substantially higher than the means reported for 1990. The spring/summer mean of all eastern basin stations was 1.41 $\mu g \cdot L^{-1}$, being as high in 1993 as the pre-invasion period, without a corresponding increase in phytoplankton biomass. Again this may be due to changes in the phytoplankton community.

In the eastern basin, phytoplankton species composition has changed since 1983-87. Biomass of *Rhodomonas*, a cryptophyte, has remained the same despite reductions in total phytoplankton biomass, thereby representing a larger proportion of the total community. *Dinobryon*, a small chrysophyte, was not reported in 1983-87 but at times in 1993 represented greater than 10% of the total biomass. In 1993, May and August mean diatom biomass was greater than that found by Makarewicz in 1983-87. This gives the impression that overall, diatoms have become more important. However, diatom biomass peaked in May and August and was low for the remainder of the stratified period. Thus diatoms may not be as important in the eastern basin as the initial comparison suggests. Specifically, *Stephanodiscus niagarae*, a dominant phytoplanktor in 1983-87 was only ≥0.5% of the total biomass on one occasion in 1993. Another phytoplanktor, *Ceratium hirundinella* was dominant in 1983-87 but was not observed in 1993. The absence of these two eutrophic indicator species in addition to *Melosira binderana* and the increase in small

algae indicates a shift to a more oligotrophic state in the eastern basin in 1993.

The relative decline in phytoplankton biomass in the eastern basin between 1970 and 1993, was similar to the decline in the western basin. However, because phytoplankton biomass was initially lower in the east, the reductions in 1993 have affected zooplankton to a greater extent than in the west. Zooplankton mean biomass in 1993, was reduced by 68% compared to Makarewicz' mean from 1984-87. Unlike in the western and west central basins, mean zooplankton biomass in the eastern basin, calculated for selected dates, was no different than means for the entire season. The similarity in means suggests that timing of sampling was not as critical in the eastern basin as it was in the western and west central basins. This may be due to the lack of *Daphnia* in the eastern basin. It was the variation in timing of the *Daphnia* blooms in the western and west central basins that contributed to the between year variability in zooplankton biomass.

The reductions in zooplankton biomass in the eastern basin were much greater than those observed in the western basin (26%), perhaps due to a disproportionate reduction in the zooplankton food supply. Although the eastern basin had the largest *Dreissena* population with a mean density 5x greater than in the western basin, there was no difference in annual biomass ($\cdot m^{-2}$) and production ($\cdot m^{-2}$) of the dreissenids. The potential removal of phytoplankton by *Dreissena* is much greater in the eastern basin because of the large population. However, given the lower initial phytoplankton biomass in the eastern basin, a larger proportion of the total algal biomass had to pass through the benthos to achieve the observed production. Any further increases in production of the *Dreissena* were hindered because of food limitations.

Zooplankton species composition has changed between 1984-87 and 1993 in the eastern basin. From 1984-87 large *Daphnia* accounted for a substantial portion (22.3%) of the total biomass. In 1993, *Daphnia* were virtually absent from the eastern basin. Instead, smaller-bodied *Bosmina* were the dominant cladocera in 1993, comprising greater than 5% of the total biomass on several occasions (42% and 70% of the sample dates for the onshore and offshore stations, respectively). In the pre-invasion period, *Bosmina* accounted for less than 1% of the total mean biomass. Larger *Daphnia* are more efficient grazers than *Bosmina* (Wu and Culver 1991) and should dominate when planktivory is low. However, *Daphnia* are a preferred prey for young fish, likely due to the ease of catchability, ie. slow swimming speed, large body size and spheroid shape (Mittlebach 1981) as well as their high caloric value (Confer and Lake 1987) and will be selected over *Bosmina*, when planktivory is high. In 1993 there was a very high number of age 1 smelt in the offshore waters of Long Point Bay (OMNR 1994). The geometric mean caught per trawling hour in September and October was 522.0 in 1993 compared with a mean of 84.1 in 1984-87 (OMNR 1994). Thus it is possible that *Daphnia* were reduced due to predation by age 1 smelt. Further evidence for planktivory was the low zooplankton community size throughout the sampling season (Mills and Schiavone 1982). This small size was largely due to the absence of *Daphnia*, but in addition, species common to the nearshore and offshore stations in 1993 were smaller nearshore, where predation is expected to be more intense.

It appears as though zooplankton were "squeezed" by both bottom-up and top-down

mechanisms. The pelagic impacts of *Dreissena* in the eastern basin in 1993 appeared to have extended beyond the primary trophic level, resulting in a reduction in zooplankton biomass. The change in species composition and reduction in community size suggest that zooplankton biomass was also regulated by a top-down mechanism: increased planktivory.

As in the western basin, benthic production and biomass were dominated by *Dreissena* and the huge amount of energy in the mussel population was in addition to the pre-mussel biomass of the benthic community. In 1979, average wet biomass was 7.7 $g \cdot m^{-2}$, compared to 13.8 $g \cdot m^{-2}$ (without *Dreissena*) in 1993. The total benthic biomass including *Dreissena* in 1993, was 326.9 $g \cdot m^{-2}$. Thus, energy transferred to the mussels had to be removed from the pelagic foodweb. Although the biomass of the benthic community has not declined, community composition has been altered. Historically, the burrowing amphipod, *Diporeia*, was located in the profundal zone (>30 m) in the eastern basin (Barton 1988; Flint and Merckel 1978; Dermott 1994). Here they fed mostly on recently settled diatoms just below the sediment surface (Dermott and Corning 1988; Quigley and Vanderploeg 1991). This species' wet weight for the eastern basin during 1979, was estimated at 1.7 $g \cdot m^{-2}$, however no specimens of *Diporeia* were collected in this study at the 38 m station (E2) between May 1993 and May 1994. Populations of this amphipod have disappeared, possibly due to competition with the large populations of quagga mussels now present at depths beyond 30 m (Dermott and Munawar 1993; Dermott and Kerec 1995). In all the other Great Lakes, *Diporeia* accounts for the majority of the benthic production, and is a key component of the foodweb.

The findings of this study suggest that the relative impacts of *Dreissena* invasion and planktivory varied among the basins in 1993, however it is difficult to prioritize these factors. In the western basin, changes in phytoplankton were attributed to filtration by *Dreissena*, however, these effects did not appear to influence zooplankton at the next trophic level. The presence of large daphnids in the western basin indicated that planktivory was not excessive. In the west central basin, *Dreissena* density was low and their influence on phytoplankton appeared limited, although this impact may not be typical of the central basin as a whole. Changes which occurred in the zooplankton were likely due to planktivory not due to reduced food supply caused by *Dreissena*. The phytoplankton in the eastern basin were impacted by *Dreissena*. This reduction in phytoplankton in addition to increased predation by planktivores resulted in changes to the zooplankton community.

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Table 1. Lake Erie station identification and locations. Station depths (m) are seasonal averages.

LEB Station[*]	Established Station	Depth	Latitude	Longitude
E1[**]		5.9	42°46'46"	80°08'42"
E2	LETT #938	38.0	42°37'35"	80°03'16"
E3	LETT #937	9.2	42°42'49"	80°13'46"
WC1	MNR #1	16.3	42°04'36"	82°20'24"
WC2	MNR #3	21.6	41°59'00"	82°08'24"
W1	MNR #8	9.6	41°59'12"	82°34'30"
W2	MNR #5	11.0	41°53'00"	82°36'48"
W3	LETT #970	10.4	41°49'30"	82°58'30"

[*]E - eastern basin - east of Long Point
 WC - west central basin - east of Point Pelee
 W - west basin - west of Point Pelee
[**]historical provincial site

Table 2. Comparison of values obtained during LETT cruises of June and September 1993, and spatial cruise of August 1993 (Charlton 1994) to values obtained at LEB stations for the same time periods. Parameters compared were TP (μg·L^{-1}), Chl (μg·L^{-1}), P_{opt} (mgC·m^{-3}·h^{-1}), ε_{par}(m^{-1}), and Secchi (m). LETT values are area-weighted means (±2 S.E.) of all stations for the western and central basins. For the eastern basin, separate nearshore[†] and offshore[‡] means (±2 S.E.) have been calculated. August spatial cruise values are arithmetic means (±2 S.E.). Values presented for each LEB station are the actual values if the LEB sampling date fell within the LETT or spatial cruise sampling period, otherwise averages of LEB data from the closest dates on either side of the LETT or spatial cruise sampling dates were used.

| Parameter | Western | | | | Central | | | Eastern | | | | |
	LETT	W1	W2	W3	LETT	WC1	WC2	LETT-IN[†]	E1	E3	LETT-OUT[‡]	E2
June												
TP	13.22±2.36	13.60	12.4	23.7	5.58±0.96	5.60	8.40	6.07±0.66	7.20	6.10	4.90±0.64	5.65
Chl	4.68±1.44	5.39	5.54	2.82	1.74±0.58	0.79	2.12	1.26±0.18	0.77	0.68	0.82±0.20	0.88
P_{opt}	22.38±7.12	25.46		24.9	6.15±3.74	3.39	5.27	4.16±0.88		4.02	1.92±0.50	2.71
ε_{par}	0.55±0.14	0.49	0.33	0.36	0.24±0.08	0.16	0.15	0.26±0.04	0.36	0.20	0.19±0.04	0.17
Secchi	2.33±0.64	2.00	3.00	3.00	7.28±1.42	9.00	10.00	7.45±0.10	3.85	8.70	8.31±0.94	9.15
August[*]												
TP	13.17±1.72	14.90	17.5	15.6	8.40±1.90	12.10	14.10	6.50±0.92	8.40	6.10		7.75
Chl	5.12±0.98	5.88	6.29	5.09	2.66±1.06	2.90	4.65	1.67±0.48	2.16	1.73		3.01
Secchi	3.20±0.66	2.10	3.00	2.70	6.44±1.14	4.60	3.30	6.00±0.00	4.90	7.15		6.05
September[**]												
TP	25.09±3.62	26.90	25.2	17.2	20.08±4.00	17.55	19.05	10.90±3.78	8.90	6.55	7.94±1.14	10.80
Chl	6.67±2.00	6.40	2.60	3.76	4.49±1.52	4.93	6.54	1.70±0.54	0.39	0.66	2.82±0.42	2.86
P_{opt}	55.36±24.22	24.18		19.9				9.19±3.54		5.80	10.20±1.54	8.55
ε_{par}	0.96±0.32	1.75	1.07	1.52				0.32±0.06	0.25	0.31	0.30±0.04	0.26
Secchi	1.14±0.44	0.85	1.70	1.87	2.67±1.30	3.00	2.45	7.01±2.94	6.00	6.10	6.30±1.84	6.20

[*] August values taken from spatial cruise by Charlton (1994). For eastern basin stations, no separate nearshore and offshore means were calculated as data for only one nearshore station was given.

[**] September values for Central Basin taken from spatial cruise by Charlton (1994)

Table 3a. Physical parameters for LEB station E1. Mixing depth (Z_m = bottom on all dates), sampling depth, euphotic depth (Z_{eu} = 1% light penetration) and Secchi are all in metres.

Date	Z_m	Sample Depth	Z_{eu} [*]	ε_{par}	Secchi
93-05-14	5.9	0 - 4	5.9	0.354	5.0
93-05-27	5.9	0 - 4	5.9	0.394	6.0
93-06-11	5.5	0 - 4	5.9	0.374	1.7
93-06-24	6.0	0 - 4	5.9	0.347	6.0
93-07-07	5.6	0 - 4	5.9	0.307	2.0
93-07-21	5.3	0 - 4	5.9	0.305	4.0
93-08-12	6.1	0 - 4	5.9	0.366	6.0
93-08-25	5.8	0 - 4	5.9	0.298	3.8
93-09-24	7.2	0 - 4	5.9	0.250	6.0
93-10-05	7.5	0 - 5	5.9	0.316	5.0
93-10-20	5.4	0 - 4	5.9	0.199	6.0
SWM[**]	5.9		5.9	0.319	4.6

[*]euphotic depth extended to bottom on all dates
[**]SWM - seasonal weighted mean

Table 3b. Physical parameters for LEB station E2. Mixing depth (Z_m), sampling depth, euphotic depth (Z_{eu} = 1% light penetration) and Secchi are all in metres.

Date	Z_m	Sample Depth	Z_{eu}	ε_{par}	Secchi
93-05-14	38.0	0 - 20	11.37	0.405	8.0
93-05-27	38.0	0 - 28	20.38	0.226	6.0
93-06-11	38.0	0 - 25	25.30	0.182	8.8
93-06-24	11.8	0 - 9	28.08	0.164	9.5
93-07-07	10.0	0 - 8	23.62	0.195	10.0
93-07-21	10.0	0 - 8	28.08	0.164	5.5
93-08-12	14.5	0 - 13	19.76	0.233	7.1
93-08-25	14.5	0 - 14	18.72	0.246	5.0
93-09-24	21.3	0 - 18	17.71	0.260	6.2
93-10-05	38.0	0 - 20	9.72	0.474	2.1
SWM[*]	17.9		21.3	0.232	6.7

[*]SWM - seasonal weighted mean

Table 3c. Physical parameters for LEB station E3. Mixing depth (Z_m), sampling depth, euphotic depth (Z_{eu} = 1% light penetration) and Secchi are all in metres.

Date	Z_m	Sample Depth	Z_{eu}	ε_{par}	Secchi
93-05-12	9.2	0 - 7	9.2	0.295	6.5
93-05-27	9.2	0 - 7	9.2	0.165	7.5
93-06-09	9.5	0 - 8			6.5
93-06-24	8.7	0 - 8	9.2	0.198	8.7
93-07-07	9.4	0 - 7	9.2	0.241	6.5
93-07-21	7.8	0 - 7	9.2	0.218	7.5
93-07-29	9.1	0 - 6	9.2	0.115	7.5
93-08-12	9.0	0 - 7	9.2	0.294	7.5
93-08-25	9.2	0 - 7	9.2	0.274	6.8
93-09-09	9.2	0 - 7			6.0
93-09-24	9.0	0 - 7	9.2	0.309	6.1
93-10-05	9.1	0 - 7	8.8	0.522	2.2
93-10-20	9.0	0 - 7	9.2	0.167	5.4
SWM[*]	9.2		9.2	0.254	6.5

[*]SWM - seasonal weighted mean

Table 3d. Physical parameters for LEB station WC1. Mixing depth (Z_m), sampling depth, euphotic depth (Z_{eu} = 1% light penetration) and Secchi are all in metres.

Date	Z_m	Sample Depth	Z_{eu}	ε_{par}	Secchi
93-05-06	16.3	0 - 15	16.3	0.245	8.0
93-05-20	16.3	0 - 15	16.3	0.230	6.5
93-05-31	16.3	0 - 15	16.3	0.232	5.5
93-06-16	11.3	0 - 15	16.3	0.155	9.0
93-07-15	9.5	0 - 8	16.3	0.245	6.4
93-07-27	9.0	0 - 8	16.3	0.252	3.0
93-08-04	7.0	0 - 6	16.3	0.225	6.2
93-08-17	6.8	0 - 4	16.3	0.194	4.6
93-09-01	14.3	0 - 14	9.1	0.509	3.4
93-09-16	13.3	0 - 12			2.3
93-09-29	16.2	0 - 14	14.0	0.330	3.7
93-10-13	16.0	0 - 14	11.5	0.402	4.6
93-10-26	16.3	0 - 14	13.3	0.346	4.0
SWM*	13.9		14.6	0.285	5.5

*SWM -seasonal weighted mean

Table 3e. Physical parameters for LEB station WC2. Mixing depth (Z_m), sampling depth, euphotic depth (Z_{eu} = 1% light penetration) and Secchi are all in metres.

Date	Z_m	Sample Depth	Z_{eu}	ε_{par}	Secchi
93-05-06	17.1	0 - 15	12.5	0.370	4.8
93-05-20	21.6	0 - 20	15.5	0.298	6.2
93-06-02	21.6	0 - 20	17.6	0.261	6.8
93-06-16	21.5	0 - 20	21.6	0.146	10.0
93-06-30	13.0	0 - 11	21.6	0.160	7.0
93-07-15	12.0	0 - 10	21.6	0.191	5.5
93-07-27	13.0	0 - 12	17.4	0.265	5.5
93-08-04	15.0	0 - 13	17.9	0.258	4.2
93-08-17	10.5	0 - 9	10.4	0.442	3.3
93-09-01	10.8	0 - 9	11.0	0.420	2.7
93-09-17	17.5	0 - 17			2.7
93-09-29	21.4	0 - 20	6.0	0.765	2.2
93-10-13	21.5	0 - 20	9.3	0.498	2.6
93-10-26	21.3	0 - 20	8.3	0.553	3.1
SWM[*]	17.0		14.4	0.370	4.7

[*]SWM - seasonal weighted mean

Table 3f. Physical parameters for LEB station W1. Mixing depth (Z_m), sampling depth, euphotic depth (Z_{eu} = 1% light penetration) and Secchi are all in metres.

Date	Z_m	Sample Depth	Z_{eu}	ε_{par}	Secchi
93-05-07	9.6	0 - 8	9.6	0.376	3.3
93-05-19	9.6	0 - 8	9.6	0.141	3.5
93-06-02	9.6	0 - 8	9.6	0.458	1.5
93-06-15	9.5	0 - 8	9.4	0.488	2.0
93-06-29	10.1	0 - 8	5.5	0.837	2.0
93-07-14	9.7	0 - 8	9.6	0.313	3.0
93-07-28	9.6	0 - 8	7.7	0.602	1.9
93-08-05	9.6	0 - 8	3.8	1.215	1.1
93-08-17	9.4	0 - 7	9.6	0.194	2.1
93-09-01	9.8	0 - 8	8.7	0.531	1.5
93-09-15	9.5	0 - 8			0.9
93-09-29	9.6	0 - 8	1.6	2.966	0.2
93-10-13	9.7	0 - 8	3.3	1.416	0.6
93-10-26	9.5	0 - 8	2.6	1.791	0.8
SWM*	9.6		6.9	0.927	1.7

*SWM - seasonal weighted mean

Table 3g. Physical parameters for LEB station W2. Mixing depth (Z_m), sampling depth, euphotic depth (Z_{eu} = 1% light penetration) and Secchi are all in metres.

Date	Z_m	Sample Depth	Z_{eu}	ε_{par}	Secchi
93-05-06	11.0	0 - 10	11.0	0.383	3.5
93-05-20	11.0	0 - 10	11.0	0.244	7.2
93-06-02	11.0	0 - 10	11.0	0.305	3.0
93-06-15	10.8	0 - 9.5	11.0	0.328	3.0
93-06-29	11.3	0 - 9	11.0	0.413	2.2
93-07-14	8.8	0 - 7	11.0	0.392	2.2
93-07-27	11.0	0 - 10	10.8	0.427	2.3
93-08-04	7.8	0 - 6	11.0	0.413	2.3
93-08-17	9.3	0 - 9	8.7	0.527	3.0
93-09-01	11.2	0 - 9	9.3	0.495	2.4
93-09-15	11.0	0 - 9			2.1
93-09-29	10.6	0 - 9	2.8	1.647	0.6
93-10-13	11.2	0 - 9	8.4	0.550	1.7
93-10-26	10.9	0 - 8	8.5	0.539	2.2
SWM[*]	10.9		9.3	0.568	2.7

[*]SWM - seasonal weighted mean

Table 3h. Physical parameters for LEB station W3. Mixing depth (Z_m), sampling depth, euphotic depth (Z_{eu} = 1% light penetration) and Secchi are all in metres.

Date	Z_m	Sample Depth	Z_{eu}	ε_{par}	Secchi
93-05-06	10.4	0 - 10	7.3	0.632	2.0
93-05-19	10.4	0 - 9	8.6	0.537	3.0
93-06-02	10.4	0 - 9	10.4	0.321	3.5
93-06-15	8.0	0 - 9	10.4	0.364	3.0
93-06-29	10.7	0 - 9	7.2	0.636	1.5
93-07-14	9.8	0 - 8	9.9	0.465	2.0
93-07-28	10.4	0 - 8	9.7	0.474	3.1
93-08-05	10.3	0 - 8	7.0	0.657	2.2
93-08-18	8.3	0 - 9	10.4	0.376	2.7
93-09-01	10.4	0 - 8	9.7	0.473	2.8
93-09-15	10.4	0 - 8			2.0
93-09-29	10.5	0 - 9	1.8	2.560	0.8
93-10-14	10.3	0 - 8	6.3	0.727	2.1
93-10-27	10.1	0 - 8	5.8	0.801	1.2
SWM*	10.4		8.0	0.771	2.3

*SWM - seasonal weighted mean

Table 4. Common statistics for P_{opt} (mg $C·m^{-3}·h^{-1}$) and the determinant variables chlorophyll (Chl $µg·L^{-1}$), light extinction (ε_{par} m^{-1}), and P^B_m (mg $C·mg$ $Chl^{-1}·h^{-1}$) for integral phytoplankton photosynthesis.

	Station	Seasonal Weighted Mean	Standard Deviation	Minimum	Maximum	n
P_{opt}						
	E2	6.915	3.74	2.69	14.06	10
	E3	4.546	2.14	1.44	8.49	12
	WC1	11.760	8.35	3.30	29.38	12
	WC2	14.766	10.68	4.09	39.58	13
	W1	20.660	17.28	4.20	72.41	13
	W3	26.374	16.44	11.15	74.02	13
P^B_m						
	E2	3.583	1.14	2.10	5.67	10
	E3	4.227	1.08	1.71	5.91	13
	WC1	4.184	0.78	3.51	5.58	12
	WC2	3.801	1.39	2.10	6.99	13
	W1	4.450	1.96	0.83	9.39	13
	W3	6.384	2.22	2.97	10.64	13
Chl						
	E1	1.055	0.82	0.38	3.30	11
	E2	2.110	1.19	0.48	4.41	10
	E3	1.125	0.55	0.45	2.00	13
	WC1	2.670	2.04	0.94	7.95	13
	WC2	3.986	2.74	1.36	10.40	14
	W1	4.548	2.08	1.28	7.71	14
	W2	3.517	2.29	1.25	9.60	14
	W3	4.468	3.08	1.45	12.53	14
ε_{par}						
	E1	0.319	0.057	0.199	0.394	11
	E2	0.232	0.104	0.164	0.474	10
	E3	0.254	0.109	0.115	0.522	11
	WC1	0.285	0.099	0.155	0.509	12
	WC2	0.370	0.177	0.146	0.765	13
	W1	0.927	0.801	0.141	2.966	13
	W2	0.568	0.353	0.244	1.647	13
	W3	0.771	0.579	0.321	2.560	13

Table 5a. Nutrient and major ion data for station E1; 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 $\mu g \cdot L^{-1}$), SiO_2 ($mg \cdot L^{-1}$), DIC ($mg \cdot L^{-1}$), DOC ($mg \cdot L^{-1}$) and ions ($mg \cdot L^{-1}$).

Date	TP	TP-filt	SRP	TN	NO_3-NO_2	NH_3	N:P	SiO_2	DIC	DOC	Cl	SO_4
93-05-14	9.1	4.9	0.5	439	240	19	48.24	0.42	22.9	5.7	15.5	24.3
93-05-27	6.1	4.6	0.4	447	281	5	73.28	0.28	23.9	2.6	14.9	25.1
93-06-11	8.7	3.9	0.7	438	240	7	50.34	0.17	18.3	4.4	15.0	24.1
93-06-24	5.7	3.4	0.7	476	230	9	83.51	0.22	23.2	3.0	15.0	23.4
93-07-07	8.5	4.6	0.7	524	202	16	61.64	0.15	20.4	3.3	14.6	24.8
93-07-21	6.6	4.2	0.6	442	209	17	66.97	0.17	19.2		14.0	26.1
93-08-12	8.7	4.6	0.8	475	243	17	54.60	0.32	20.5	6.6	15.9	23.9
93-08-25	8.1	4.0	1.3	406	195	29	50.12	0.46	21.3	3.7	16.1	21.8
93-09-24	8.9	5.0	1.2	443	232	27	49.78	0.39	20.3	10.1	15.8	22.9
93-10-05	8.4		0.6	697	263		82.98	0.59	20.6	9.0	15.8	25.7
93-10-20	7.1	3.8	0.8	593	263	13	83.52	0.71	20.8	13.2	15.9	22.4
SWM*	7.8	4.3	0.8	474	232	17		0.34	20.9	5.8	15.3	24.0

*SWM - seasonal weighted means

Table 5b. Nutrient and major ion data for station E2; 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 $\mu g \cdot L^{-1}$), SiO_2 ($mg \cdot L^{-1}$), DIC ($mg \cdot L^{-1}$), DOC ($mg \cdot L^{-1}$) and ions ($mg \cdot L^{-1}$).

Date	TP	TP-filt	SRP	TN	NO_3-NO_2	NH_3	N:P	SiO_2	DIC	DOC	Cl	SO_4
93-05-14	12.9	5.8	5.3	470	291	11	36.43	0.44	21.4	5.1	15.2	23.3
93-05-27	11.1	4.6						0.38			15.0	25.1
93-06-11	6.5	4.4	0.4	524	299	25	80.62	0.50	23.5	2.6	15.4	24.2
93-06-24	4.8		0.7	514	268	18	107.08	0.27	23.5	3.0	15.2	24.1
93-07-07	7.5	4.7	0.5	471	253	11	62.80	0.18	20.6	2.7	14.5	23.8
93-07-21	6.3		0.6	452	215	1	71.75	0.16	19.5	3.6	13.2	25.2
93-08-12	11.5	4.6		472	226	23	41.04	0.27	19.1	7.7	15.4	23.8
93-08-25	4.0	3.7	1.3	517	207	50	129.25	0.10	21.0	3.4	15.9	
93-09-24	10.8	3.6	0.2	466	206	12	43.15	0.26	20.1	2.7	15.7	22.5
93-10-05	20.9		9.7	489	241	33	23.40	0.78	20.5	8.8	15.7	25.0
SWM[*]	8.5	4.4	1.5	486	243	21		0.28	21.0	4.0	15.1	23.9

[*]SWM - seasonal weighted means

Table 5c. Nutrient and major ion data for station E3; 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 $\mu g \cdot L^{-1}$), SiO_2 (mg$\cdot L^{-1}$), DIC (mg$\cdot L^{-1}$), DOC (mg$\cdot L^{-1}$) and ions (mg$\cdot L^{-1}$).

Date	TP	TP-filt	SRP	TN	NO_3-NO_2	NH_3	N:P	SiO_2	DIC	DOC	Cl	SO_4
93-05-12	10.5	5.5	0.7	497	244	33	47.33	0.56	22.9	2.9	15.5	24.2
93-05-27	7.1	5.0	0.6	525	303	16	73.94	0.35	23.6	2.8	14.9	25.8
93-06-09	5.7		0.3	411	264	6	72.11	0.27	23.2	2.6	15.0	23.4
93-06-24	6.1	4.6	0.7	411	230	16	67.34	0.25	23.2	2.5	15.1	23.9
93-07-07	5.8	4.1	0.5	429	197	19	73.97	0.17	20.1	2.8	14.2	23.7
93-07-21	3.1	2.6	0.2	440	217	10	141.94	0.17	19.1	2.6	12.1	25.1
93-07-29	6.7	6.4		724		21	108.06	0.13			11.9	24.2
93-08-12	6.0	3.6	0.8	445	234	8	74.17	0.19	20.3	5.8	15.8	23.8
93-08-25	6.2	3.8	1.3	495	206	13	79.84	0.23	21.5	4.1	16.2	24.9
93-09-09	4.7	3.8						0.34		2.4	16.0	23.0
93-09-24	8.4	3.9	2.1	493	233	21	58.69	0.38	20.8	4.0	15.9	22.1
93-10-05	10.6	9.3	1.8	562	252	159	53.12	0.52	20.2	6.9	15.8	25.2
93-10-20	6.6	4.5	0.8	490	253	9	74.24	0.75	20.7	3.5	15.3	22.5
SWM*	6.6	4.7	0.9	489	237	27		0.31	21.3	3.6	15.0	24.0

*SWM - seasonal weighted means

Table 5d. Nutrient and major ion data for station WC1; 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 $\mu g \cdot L^{-1}$), SiO_2 (mg·L^{-1}), DIC (mg·L^{-1}), DOC (mg·L^{-1}) and ions (mg·L^{-1}).

Date	TP	TP-filt	SRP	TN	NO_3-NO_2	NH_3	N:P	SiO_2	DIC	DOC	Cl	SO_4
93-05-06	8.2	4.2	1.1	534	373	21	65.12	0.32	21.5	2.5	14.3	23.6
93-05-20	9.4	4.9	2.1	586	301	15	62.34	0.31	20.4		13.8	21.8
93-05-31	8.0	4.4	0.2	491	300	12	61.38	0.39	22.5	2.5	13.9	23.5
93-06-16	5.6	4.1	0.5	558	292	41	99.64	0.38	22.1	2.9	14.0	22.4
93-07-15	7.0	5.5	0.6	535	281	12	76.43	0.20	20.2	1.9	10.7	19.6
93-07-27	10.6	5.2	0.5	530	252	35	50.00	0.30	19.4	2.3	9.3	20.0
93-08-04	7.2	5.5	0.7	585	262	82	81.25	1.43	20.5	3.7	13.8	22.3
93-08-17	12.1	6.5	1.3	591	235	43	48.84	0.32	21.0	2.3	14.0	22.9
93-09-01	9.3	6.5	0.2		155	20		0.48	19.6	1.9	14.2	27.4
93-09-16	19.2	7.2	0.8	410	190	46	21.35	2.47	21.9	3.3	15.1	21.6
93-09-29	15.9	9.8	5.4	384	160	45	24.15	1.42	21.0	3.7	14.9	24.1
93-10-13	17.1	13.9	4.8	342	221	14	20.00	1.79	19.7	2.3	12.3	23.5
93-10-26	15.8							1.60			12.0	19.9
SWM*	10.8	6.1	1.3	499	250	32		0.82	21.9	2.6	13.3	22.5

*SWM - seasonal weighted means

Table 5e. Nutrient and major ion data for station WC2; 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 $\mu g \cdot L^{-1}$), SiO_2 ($mg \cdot L^{-1}$), DIC ($mg \cdot L^{-1}$), DOC ($mg \cdot L^{-1}$) and ions ($mg \cdot L^{-1}$).

Date	TP	TP-filt	SRP	TN	NO_3-NO_2	NH_3	N:P	SiO_2	DIC	DOC	Cl	SO_4
93-05-06	11.1	5.7	1.0	420	240	1	37.84	0.09	20.0		14.3	24.4
93-05-20	12.3	4.9	0.4	494	248	31	40.16	0.28	21.8	2.5	13.8	21.1
93-06-02	8.3	4.0	0.2	464	257	12	55.90	0.45	22.7	2.6	13.8	23.7
93-06-16	8.4	4.7	1.0	504	231	27	60.00	0.53	22.6	3.3	14.1	22.7
93-06-30	6.0	4.5	0.6	482	263	18	80.33	0.20	22.5	3.0	14.1	23.3
93-07-15	4.0		0.5	590	276	35	147.50	0.08	20.1	2.5	11.0	21.1
93-07-27	7.4	5.9	0.2	650	255	43	87.84	0.06		2.5	10.4	40.4
93-08-04	4.8	3.8	0.2	500	254	22	104.17	0.13	19.9	2.8	13.8	21.8
93-08-17	14.1	7.0						0.70			13.0	22.1
93-09-01	22.8	7.8	0.4		171	45		0.89	20.5	2.3	14.4	23.0
93-09-17	16.6		0.8	505	184	40	30.42	1.76	21.5	3.3	14.9	21.3
93-09-29	21.5	8.7	4.6	650	140	189	30.23	1.60	20.9	2.5	15.2	24.1
93-10-13	21.1	10.7	1.2	452	149	15	21.42	2.08	21.2	2.4	15.1	24.4
93-10-26	18.6	15.6						1.89			15.0	22.5
SWM*	12.8	6.7	0.9	514	222	41		0.77	21.2	2.7	13.8	23.7

*SWM - seasonal weighted means

Table 5f. Nutrient and major ion data for station W1; 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 $\mu g \cdot L^{-1}$), SiO_2 (mg·L^{-1}), DIC (mg·L^{-1}), DOC (mg·L^{-1}) and ions (mg·L^{-1}).

Date	TP	TP-filt	SRP	TN	NO_3-NO_2	NH_3	N:P	SiO_2	DIC	DOC	Cl	SO_4
93-05-07	7.6	6.4	0.5	750	486	51	98.68	0.14	23.5	3.2	15.1	20.2
93-05-19	9.9	4.0	2.4	764	506	29	77.17	0.45	22.6	2.8	14.1	17.6
93-06-02	10.2	4.8	0.6	843	600	10	82.65	0.85	23.9	2.6	15.0	20.2
93-06-15	13.6	5.3	0.3	825	552	16	60.66	0.09	23.6	3.0	15.0	19.0
93-06-29	14.3	7.0	0.5	677	408	34	47.34	0.62	23.8	2.9	12.7	19.3
93-07-14	13.3	5.7	1.2	600	300	25	45.11	0.98	19.9	2.0	9.9	17.0
93-07-28	13.4	7.0	1.1	621	298	58	46.34	0.41	19.2	2.2	7.1	18.5
93-08-05	19.2	6.8	1.9	711	384	24	37.03	0.84	21.2	2.7	11.8	21.4
93-08-17	14.9	7.0	1.3	733	271	114	49.19	0.82	20.7	2.3	11.6	19.5
93-09-01	18.4	8.2	0.6		154	57		1.87	18.7	3.3	10.4	20.1
93-09-15	26.9	7.2	1.0	568	266	5	21.12	1.35	18.8	2.9	12.1	17.0
93-09-29	35.6	10.0	6.7	656	229	4	18.43	1.33	18.7	4.3	12.5	18.4
93-10-13	22.1			596	319	17	26.97	1.48		2.1	10.9	29.0
93-10-26	21.8							1.49			11.2	17.7
SWM*	17.5	6.5	1.3	686	362	34		0.94	21.2	2.8	12.1	19.7

*SWM - seasonal weighted means

Table 5g. Nutrient and major ion data for station W2; 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}), SiO$_2$ (mg·L^{-1}), DIC (mg·L^{-1}), DOC (mg·L^{-1}) and ions (mg·L^{-1}).

Date	TP	TP-filt	SRP	TN	NO$_3$-NO$_2$	NH$_3$	N:P	SiO$_2$	DIC	DOC	Cl	SO$_4$
93-05-06	10.7	4.0	1.0	791	523	16	73.93	1.02	22.7	14.6	12.6	18.1
93-05-20	8.4	5.9	1.2	761	546	25	90.60	0.51	22.4	5.9	14.7	18.1
93-06-02	13.5	5.7	0.4	757	426	56	56.07	0.64		2.2	10.6	
93-06-15	12.4	5.8	0.4	728	441	13	58.71	0.12	23.0	2.4	12.2	18.8
93-06-29	10.1	8.1	0.9	620	318	19	61.39	0.79	22.4	4.0	10.2	17.8
93-07-14	11.6	5.2	0.9	523	268	18	45.09	0.61	19.8	2.2	9.8	17.8
93-07-27	16.4	10.4	2.5	803	314	128	48.96	0.48	20.9	2.4	12.1	23.6
93-08-04	18.7	7.3	1.0	823	405	30	44.01	0.44	20.5	2.6	11.8	20.9
93-08-17	17.5	8.3	0.2	800	255	161	45.71	0.78	20.5	2.3	12.4	44.8
93-09-01	11.8	5.7	0.6		187	41		1.57	18.6	4.2	9.5	21.4
93-09-15	25.2	18.4	11.5	409	217	31	16.23	1.73	19.0	3.6	9.8	35.8
93-09-29	27.5	20.7	12.6	461	183	22	16.67	1.15	18.3	10.4	9.1	25.5
93-10-13	14.9		6.2	419	255	8	28.12	1.30	19.4	2.0	10.1	18.8
93-10-26	17.1		11.3	563	354	16	32.92	1.58	19.1	3.2	9.1	18.5
SWM*	15.5	8.5	3.5	635	324	42		0.90	20.6	4.2	11.0	23.2

*SWM - seasonal weighted means

Table 5h. Nutrient and major ion data for station W3; 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}), SiO$_2$ (mg·L^{-1}), DIC (mg·L^{-1}), DOC (mg·L^{-1}) and ions (mg·L^{-1}).

Date	TP	TP-filt	SRP	TN	NO$_3$-NO$_2$	NH$_3$	N:P	SiO$_2$	DIC	DOC	Cl	SO$_4$
93-05-06	12.0	3.6	0.6	691	485	14	57.58	1.21	22.7	3.4	9.6	17.7
93-05-19	13.0	4.6	0.8	873	576	11	67.15	1.00	21.8	3.5	12.5	16.6
93-06-02	12.7	6.8	0.9	701	526	18	55.20	0.67	23.5	2.5	13.5	20.1
93-06-15	23.7	6.5	0.4	857	546	7	36.16	0.10	23.6	2.5	14.7	19.0
93-06-29	20.7	8.4	1.0	611	343	29	29.52	1.07	21.5	2.9	10.3	19.4
93-07-14	44.4	30.6	20.0	1028	659	35	23.15	1.12	20.8	2.5	10.1	20.8
93-07-28	13.4	5.8	0.6	611	279	33	45.60	0.81	18.8	2.6	6.5	18.0
93-08-05	16.7	7.5	1.9	837	402	52	50.12	0.26	19.3	2.6	10.5	22.3
93-08-18	15.6	8.4	0.7	682	244	103	43.72	1.20		1.9	9.1	
93-09-01	11.5	5.7	0.4		236	58		1.36	17.7	2.1	10.5	34.9
93-09-15	17.2	11.4	3.1	473	197	5	27.50	1.64		4.2	12.1	29.3
93-09-29	23.0			529	288	32	23.00	1.42	19.2	2.3	7.7	21.8
93-10-14	19.4	7.8	1.6	498	283	2	25.67	1.24	19.8	2.0	9.7	18.7
93-10-27	14.9	13.2						1.16			7.2	30.4
SWM*	19.1	9.5	2.9	695	391	32		1.03	20.4	2.7	10.5	22.6

*SWM - seasonal weighted means

Table 6a. Indices of phytoplankton biomass for station E1; chlorophyll ($\mu g \cdot L^{-1}$) uncorrected (Chl_{un}), and corrected (Chl_{cor}) for phaeopigments, particulate organic carbon (POC $mg \cdot L^{-1}$) and particulate organic nitrogen (PON $mg \cdot L^{-1}$).

Date	Chl_{un}	Chl_{cor}	POC	PON
93-05-14	0.84	0.61	0.073	0.010
93-05-27	0.44	0.25	0.057	0.005
93-06-11	1.16	0.84	0.144	0.021
93-06-24	0.38	0.13	0.071	0.024
93-07-07	0.66	0.36	0.106	0.020
93-07-21	0.66	0.51	0.198	0.047
93-08-12	1.01	0.72	0.080	0.027
93-08-25	3.30	3.29	0.291	0.039
93-09-24	0.39	0.27	0.078	0.012
93-10-05	0.66	0.28	0.100	0.013
93-10-20	1.20	0.98	0.101	0.015
SWM*	1.06	0.85	0.129	0.023

*SWM - seasonal weighted mean

Table 6b. Indices of phytoplankton biomass for station E2; chlorophyll ($\mu g \cdot L^{-1}$) uncorrected (Chl_{un}), and corrected (Chl_{cor}) for phaeopigments, particulate organic carbon (POC $mg \cdot L^{-1}$) and particulate organic nitrogen (PON $mg \cdot L^{-1}$).

Date	Chl_{un}	Chl_{cor}	POC	PON
93-05-14	2.96	2.09	0.037	0.006
93-05-27	1.93	1.21	0.183	0.025
93-06-11	1.28	0.84	0.154	0.021
93-06-24	0.48	0.23	0.077	0.015
93-07-07	0.65	0.26	0.115	0.023
93-07-21	1.21	0.72	0.140	0.027
93-08-12	2.20	1.33	0.153	0.038
93-08-25	4.41	3.86	0.314	0.049
93-09-24	2.86	1.83	0.293	0.043
93-10-05	1.98	1.17	0.250	0.037
SWM*	2.11	1.47	0.186	0.031

*SWM - seasonal weighted mean

Table 6c. Indices of phytoplankton biomass for station E3; chlorophyll ($\mu g \cdot L^{-1}$) uncorrected (Chl_{un}), and corrected (Chl_{cor}) for phaeopigments, particulate organic carbon (POC $mg \cdot L^{-1}$) and particulate organic nitrogen (PON $mg \cdot L^{-1}$).

Date	Chl_{un}	Chl_{cor}	POC	PON
93-05-12	1.35	0.87	0.051	0.007
93-05-27	0.45	0.25	0.083	0.013
93-06-09	0.67	0.29	0.090	0.014
93-06-24	0.68	0.19	0.100	0.017
93-07-07	0.62	0.30	0.153	0.027
93-07-21	0.98	0.76	0.132	0.024
93-07-29	1.95	1.52	0.191	0.035
93-08-12	1.46	1.06	0.165	0.033
93-08-25	2.00	1.63	0.216	0.028
93-09-09	1.61	1.40	0.136	0.020
93-09-24	0.66	0.39	0.113	0.017
93-10-05	0.88	0.42	0.164	0.019
93-10-20	1.77	0.83	0.083	0.011
SWM*	1.12	0.75	0.133	0.021

*SWM - seasonal weighted mean

Table 6d. Indices of phytoplankton biomass for station WC1; chlorophyll ($\mu g \cdot L^{-1}$) uncorrected (Chl_{un}), and corrected (Chl_{cor}) for phaeopigments, particulate organic carbon (POC $mg \cdot L^{-1}$) and particulate organic nitrogen (PON $mg \cdot L^{-1}$).

Date	Chl_{un}	Chl_{cor}	POC	PON
93-05-06	1.21	0.85	0.050	0.007
93-05-20	0.94	0.11	0.150	0.016
93-05-31	1.62	1.00	0.228	0.032
93-06-16	0.79	0.46	0.179	0.024
93-07-15	1.70	1.01	0.165	0.027
93-07-27	3.92	2.63	0.254	0.043
93-08-04	1.67	1.30	0.133	0.031
93-08-17	2.90	1.75	0.383	0.061
93-09-01	5.37	4.68	0.316	0.048
93-09-16	7.95	7.74	0.387	0.073
93-09-29	1.91	0.83	0.224	0.037
93-10-13	2.18	1.75	0.154	0.028
93-10-26	3.52	2.61	0.181	0.032
SWM*	2.67	2.00	0.222	0.036

*SWM - seasonal weighted mean

Table 6e. Indices of phytoplankton biomass for station WC2; chlorophyll (μg·L^{-1}) uncorrected (Chl$_{un}$), and corrected (Chl$_{cor}$) for phaeopigments, particulate organic carbon (POC mg·L^{-1}) and particulate organic nitrogen (PON mg·L^{-1}).

Date	Chl$_{un}$	Chl$_{cor}$	POC	PON
93-05-06	7.76	2.44		
93-05-20	2.68	1.31	0.314	0.036
93-06-02	1.95	1.22	0.253	0.039
93-06-16	2.12	1.31	0.236	0.031
93-06-30	1.36		0.150	0.023
93-07-15	1.85	1.20	0.204	0.035
93-07-27	3.50	2.27	0.274	0.054
93-08-04	3.57	2.97	0.286	0.052
93-08-17	4.65	1.72	0.387	0.075
93-09-01	5.23	4.41	0.192	0.023
93-09-17	8.25	7.67	0.454	0.087
93-09-29	4.82	3.61	0.391	0.064
93-10-13	2.51	1.91	0.340	0.066
93-10-26	10.40	9.21	0.387	0.070
SWM*	3.99	2.83	0.292	0.050

*SWM - seasonal weighted mean

Table 6f. Indices of phytoplankton biomass for station W1; chlorophyll (μg·L^{-1}) uncorrected (Chl$_{un}$), and corrected (Chl$_{cor}$) for phaeopigments, particulate organic carbon (POC mg·L^{-1}) and particulate organic nitrogen (PON mg·L^{-1}).

Date	Chl$_{un}$	Chl$_{cor}$	POC	PON
93-05-07	3.17	2.20	0.111	0.014
93-05-19	1.28	0.58	0.195	0.028
93-06-02	1.75	0.97	0.232	0.033
93-06-15	5.39	4.96	0.444	0.062
93-06-29	1.98	0.75	0.196	0.037
93-07-14	4.53	3.52	0.348	0.065
93-07-27	5.57	3.26	0.214	0.047
93-08-05	7.71	6.09	0.290	0.090
93-08-17	5.88	4.30	0.401	0.070
93-09-01	5.14	3.73	0.241	0.044
93-09-15	6.40	4.92	0.994	0.118
93-09-29	7.61	3.35	1.150	0.154
93-10-13	3.08	2.12	0.410	0.058
93-10-26	3.97	2.18	0.546	0.075
SWM*	4.55	3.08	0.427	0.066

*SWM - seasonal weighted mean

Table 6g. Indices of phytoplankton biomass for station W2; chlorophyll (μg·L^{-1}) uncorrected (Chl$_{un}$), and corrected (Chl$_{cor}$) for phaeopigments, particulate organic carbon (POC mg·L^{-1}) and particulate organic nitrogen (PON mg·L^{-1}).

Date	Chl$_{un}$	Chl$_{cor}$	POC	PON
93-05-06	2.16	1.73	0.071	0.008
93-05-20	1.90	0.27	0.204	0.028
93-06-02	1.25	0.49	0.388	0.063
93-06-15	5.54	4.81	0.456	0.066
93-06-29	1.48	1.12	0.175	0.038
93-07-14	2.23	1.15	0.213	0.041
93-07-27	4.10	2.31	0.274	0.061
93-08-04	9.60	7.14	0.743	0.138
93-08-17	6.29	3.67	0.473	0.078
93-09-01	2.56	1.77	0.241	0.044
93-09-15	2.60	2.07	0.249	0.031
93-09-29	4.50	1.35	0.609	0.076
93-10-13	2.83	2.07	0.182	0.028
93-10-26	2.66	1.89	0.170	0.027
SWM*	3.52	2.22	0.326	0.053

*SWM - seasonal weighted mean

Table 6h. Indices of phytoplankton biomass for station W3; chlorophyll (μg·L^{-1}) uncorrected (Chl$_{un}$), and corrected (Chl$_{cor}$) for phaeopigments, particulate organic carbon (POC mg·L^{-1}) and particulate organic nitrogen (PON mg·L^{-1}).

Date	Chl$_{un}$	Chl$_{cor}$	POC	PON
93-05-06	3.13	2.47	0.096	0.011
93-05-19	3.02	2.19	0.345	0.050
93-06-02	1.45	0.77	0.178	0.025
93-06-15	2.82	2.08	0.356	0.055
93-06-29	2.32	1.67	0.192	0.045
93-07-14	4.13	3.23	0.235	0.046
93-07-28	9.79	8.06	0.315	0.075
93-08-05	5.86	4.73	0.327	0.077
93-08-18	5.09	3.40	0.361	0.063
93-09-01	2.69	1.95	0.156	0.018
93-09-15	3.76	3.37	0.231	0.037
93-09-29	2.65	1.05	0.385	0.049
93-10-14	12.53	11.95	0.387	0.069
93-10-27	4.14	3.40	0.287	0.049
SWM*	4.47	3.53	0.280	0.048

*SWM - seasonal weighted means

Table 7. Seasonal weighted mean (SWM) biomass ($g \cdot m^{-3}$) for each major taxonomic group of phytoplankton at offshore stations in Lake Erie during 1993.

Taxonomic Group	Station		
	W3	WC2	E2
Chlorophyta	0.040	0.042	0.076
Euglenophyta	0.001	0.003	0.001
Cyanophyta	0.007	0.026	0.008
Cryptophyta	0.151	0.157	0.062
Dinophyceae	0.005	0.102	0.033
Chrysophyceae	0.045	0.093	0.066
Bacillariophyceae	0.512	0.330	0.105
Total SWM Biomass	0.761	0.753	0.351

Table 8. Summary of all phytoplankton species and genera observed in each basin of Lake Erie. Species are indicated as contributing less than 0.5% (O), greater than 0.5% (+), greater than 5% (++), and greater than 10% (+++) of the total phytoplankton biomass at some time during the sampling season (May - Oct.)

Taxon	Western	West Central	Eastern
Chrysophyta			
Bacillariophyceae			
Achnanthes deflexa	+	O	+
Asterionella formosa	+	+++	+
Cocconeis pediculus		+	
Coscinodiscus denaris		O	+
C. rothii	+		
Cyclotella ocellata	+++	+++	+++
C. kutzingiana	+		+++
C. meneghiniana	+++	+	
C. sp.		+	O
Cymatopleura solea		+	
Diatoma elongatum	+		++
D. elongatum minor	+		+
Fragilaria construens venter	O		
F. crotonensis	++	+++	++
F. sp.	++	+	O
Melosira binderiana	+++	+++	O
M. granulata	+++	++	
M. islandica	+++	+++	+++
M. italica	O		O
M. varians	+	+++	
Navicula cryptocephala	O		
N. lanceolata	O	O	
Nitzschia acicularis	+	++	+++
N. angustata acuta	O		
N. dissipata	+		
N. filiformis	+		
N. palea	O		
N. sigmoidea	+		
Rhizosolenia sp.	O		+
Stephanodiscus astraea	+++	+++	+
S. hantzschii	+++		+
S. niagarae	++	+++	+
Surirella ovata	+		O

Table 8. Continued

Taxon	Western	West Central	Eastern
Bacillariophyceae continued			
S. turgida	+	+	
Synedra actinastroides	+		O
S. acus	+	O	++
S. ulna	+	++	
Tabellaria fenestrata	++	+	
Chrysophyceae			
Bitrichia chodati		+	O
Chromulina sp.	+	+	+
Chrysochromulina parva	+	++	+++
Chrysolykos sp.		+	+
Chrysophyte statospore	O	+	O
Chrysosphaerella rodhei	++	+++	+++
C. sp.		O	
Chrysostephanosphaera sp.		+	+
Dinobryon crenulatum		+	+
D. divergens	++	+++	+
D. sertularia protuberans	+	O	O
D. sociale	+++	+++	+++
Katablepharis ovalis	O		
Kephyrion sp.	+	+	+
Mallomonas sp.	+	O	+
Ochromonas sp.	+	+++	+++
Pseudokephyrion sp.	O	O	+
Stelexmonas dichotoma	+		+
Cryptophyta			
Cryptomonas curvata	++	+++	+
C. erosa	+	+	O
C. gracilis	+		
C. marssonii	O		
C. ovata	+	+++	+
C. reflexa	+	++	+
Katablepharis ovalis	+	++	++
Rhodomonas lens	+++	++	+++
R. minuta	+++	+++	+++

Table 8. Continued

Taxon	Western	West Central	Eastern
Pyrrophyta			
Dinophyceae			
Ceratium hirundinella	O	+++	
Glenodinium sp.	+	+	+
Gymnodinium helveticum		++	+++
G. sp.	+	+++	+
G. uberrimum		++	+
Peridinium aciculiferum	+	++	+++
P. cinctum		+	
Pyrrophyte cyst		++	+++
Chlorophyta			
Actinastrum hantzschii	O		
Ankistrodesmus convolutus	O	O	O
A. falcatus		O	O
Carteria sp.	+	+	O
Chlamydomonas dinobryonis		O	O
Chlamydomonas sp.	+	+	+
Chodatella subsalsa		O	O
Closterium aciculare		O	
C. actum variabile	O	O	
Coelastrum cambricum		+	+
C. microporum	O		
C. sphaericum	O		
C. microporum		+	+
Cosmarium sp.	O	O	O
Crucigenia irregularis			O
Crucigenia rectangularis	O		+
C. tetrapedia	O	O	+
Dictyosphaerium ehrenberianum		O	
D. pulchellum	+	O	+
Elakatothrix gelatinosa	O	O	O
E. lacustris		O	
Franceia ovalis	O		O
Kirchneriella microscopia	O	+	O
K. lunaris	O	+	O
Lagerheimia quadriseta	+		
Micractinium pusillum	+	+	+

Table 8. Continued

Taxon	Western	West Central	Eastern
Chlorophyta continued			
Mougeotia sp.	++	++	+
Nephrocytium limneticum			O
Oocystis parvum	+	+	+
Pandorina morum	+	O	+
Pediastrum boryanum		+	+
P. duplex clathratum	+	+	+
P. simplex duodenarium	++	++	
P. tetras			O
Scenedesmus arcuatus	O		
S. bijuga	O	+	+
S. denticulatus	O		
S. ecornis			O
S. incrassatulus	O	O	+
S. spinosis	O		
S. quadricauda	O	+	O
Schroedaria judayi	O		
S. setigera	O	O	
Sphaerella lacustris			+
Sphaerocystis schroeteri	++	+++	+++
Stelexmonas dichotoma			O
Tetraedron arthrodesmiforme		O	O
T. caudatum	O	O	
T. minimum		+	+++
T. trigonium papilliferum	O		+
Tetrastum glabrum	O		
Treubaria varia	O	O	
Ulothrix sp.	+++	+	
Euglenophyta			
Lepocinclis sp.	O	+	+
Cyanophyta			
Anabaena planctonica		O	
Anabaena sp.	O	++	+
Aphanizomenon flos-aquae	O	+	
Aphanocapsa elachista planctonica	O	O	
Aphanothece clathrata brevis	O	O	O
Chroococcus dispersus	O		

Table 8. Continued

Taxon	Western	West Central	Eastern
Cyanophyta continued			
C. limneticus	O	O	+
C. turgidus	O	O	
Dactylococcopsis linearis		O	O
Lyngbya contorta			O
Lyngbya Major		+++	
Merismopedia tenuissima	O····	O	O
Merismopedia sp.		+	
Microcyctis aeruginosa	+++		O
Oscillatoria limnetica	O	++	+
Radiocystis geminata	O	O	+

Table 9a. Seasonal data and seasonal weighted means (SWM) for phytoplankton photosynthesis rates (P), parameters (P^B_m, α^B), and mean epilimnetic irradiance ($\bar{I}$) at station E2. P_{opt} (mg C·m^{-3}·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·mg Chl^{-1}·h^{-1}) is the maximum and α^B (mgC·mg Chl^{-1}·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 (ΣP=mg C·m^{-2}·d^{-1}) and $\bar{I}$ (mE·m^{-2}·min^{-1}) were both calculated with theoretical cloudless (cldlss) and empirical (emp) solar irradiance as denoted by the subscripts.

Date	ΣP_{emp}	ΣP_{cldlss}	P_{opt}	P^B_m	α^B	$\bar{I}_{emp}$	$\bar{I}_{cldlss}$
93-05-14	685	964	10.83	3.66	7.45	1.51	2.62
93-05-27	582	680	4.68	2.42	3.57	4.10	4.88
93-06-11	525	573	2.69	2.10	4.51	5.46	6.20
93-06-24	515	541	2.72	5.67	5.05	17.77	18.63
93-07-07	335	435	3.30	5.08	4.38	12.66	17.90
93-07-21	718	820	5.11	4.22	4.35	16.55	19.47
93-08-12	836	903	8.17	3.71	3.98	9.56	10.34
93-08-25	1364	1437	14.06	3.19	3.64	8.57	9.12
93-09-24	818	862	8.55	2.99	5.32	4.49	4.91
93-10-05	219	266	5.65	2.85	4.28	0.94	1.35
SWM	736	815	6.92	3.58	4.48	8.97	10.36

Table 9b. Seasonal data and seasonal weighted means (SWM) for phytoplankton photosynthesis rates (P), parameters (P^B_m, α^B), and mean epilimnetic irradiance ($\bar{I}$) at station E3. P_{opt} (mg C·m^{-3}·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·mg Chl^{-1}·h^{-1}) is the maximum and α^B (mg C·mg Chl^{-1}·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 (ΣP=mg C·m^{-2}·d^{-1}) and $\bar{I}$ (mE·m^{-2}·min^{-1}) were both calculated with theoretical cloudless (cldlss) and empirical (emp) solar irradiance as denoted by the subscripts.

Date	ΣP_{emp}	ΣP_{cldlss}	P_{opt}	P^B_m	α^B	$\bar{I}_{emp}$	$\bar{I}_{cldlss}$
93-05-12	334	516	5.75	4.26	5.19	8.53	13.78
93-05-27	150	171	1.44	3.20	4.05	18.09	21.56
93-06-24	388	411	4.02	5.91	4.97	19.37	20.31
93-07-07	250	309	3.04	4.90	5.35	11.88	16.80
93-07-21	317	362	3.49	3.56	3.86	16.69	19.64
93-07-29	594	706	5.93	3.04	3.54	17.55	24.71
93-08-12	399	432	5.58	3.82	3.58	12.22	13.22
93-08-25	639	673	8.07	4.04	4.18	11.97	12.73
93-09-09	270	443	8.49	5.27	5.46	5.54	10.87
93-09-24	199	210	3.10	4.70	5.92	8.40	9.17
93-10-05	111	139	4.00	4.55	4.58	3.48	5.00
93-10-20	103	237	3.03	1.71	2.20	2.89	10.53
SWM	312	371	4.55	4.23	4.49	12.29	15.41

Table 9c. Seasonal data and seasonal weighted means (SWM) for phytoplankton photosynthesis rates (P), parameters (P^B_m, α^B), and mean epilimnetic irradiance ($\bar{I}$) at station WC1. P_{opt} (mg C·m^{-3}·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·mg Chl^{-1}·h^{-1}) is the maximum and α^B (mg C·mg Chl^{-1}·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 (ΣP=mg C·m^{-2}·d^{-1}) and $\bar{I}$ (mE·m^{-2}·min^{-1}) were both calculated with theoretical cloudless (cldlss) and empirical (emp) solar irradiance as denoted by the subscripts.

Date	ΣP_{emp}	ΣP_{cldlss}	P_{opt}	P^B_m	α^B	$\bar{I}_{emp}$	$\bar{I}_{cldlss}$
93-05-20	312	462	3.30	3.51	5.50	5.18	10.75
93-05-31	204	574	4.45	2.75	3.39	2.37	10.93
93-06-16	563	584	3.39	4.29	5.10	20.08	20.14
93-07-15	576	605	6.09	3.58	3.21	15.35	15.87
93-07-27	1803	1957	18.57	4.74	5.45	14.83	15.81
93-08-04	788	951	9.32	5.58	5.35	14.42	19.49
93-08-17	1184	1514	15.41	5.31	5.15	14.49	20.42
93-09-01	1147	1166	23.06	4.29	5.45	4.60	4.64
93-09-16	784	948	29.38	3.70	5.25	3.43	4.90
93-09-29	495	570	8.16	4.27	6.11	4.10	4.86
93-10-13	413	427	8.91	4.09	5.02	3.37	3.44
93-10-26	641	765	15.93	4.53	5.18	2.79	3.42
SWM	732	854	11.76	4.18	4.90	9.69	11.87

Table 9d. Seasonal data and seasonal weighted means (SWM) for phytoplankton photosynthesis rates (P), parameters (P^B_m, α^B), and mean epilimnetic irradiance ($\bar{I}$) at station WC2. P_{opt} (mg C·m^{-3}·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·mg Chl^{-1}·h^{-1}) is the maximum and α^B (mg C·mg Chl^{-1}·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 (ΣP=mg C·m^{-2}·d^{-1}) and $\bar{I}$ (mE·m^{-2}·min^{-1}) were both calculated with theoretical cloudless (cldlss) and empirical (emp) solar irradiance as denoted by the subscripts.

Date	ΣP_{emp}	ΣP_{cldlss}	P_{opt}	P^B_m	α^B	$\bar{I}_{emp}$	$\bar{I}_{cldlss}$
93-05-20	356	516	6.01	2.24	5.46	2.95	6.40
93-06-02	591	717	4.09	2.10	4.58	4.74	7.50
93-06-16	1138	1174	5.27	2.49	4.40	12.95	13.05
93-06-30	843	1023	6.50	4.78	4.63	12.54	17.64
93-07-15	2008	2100	5.07	2.74	3.09	15.67	16.31
93-07-27	1190	1288	14.00	4.00	4.48	10.57	11.06
93-08-04	2062	2458	11.63	3.26	4.09	7.19	9.86
93-08-17	1038	1357	24.01	5.16	5.41	5.42	7.66
93-09-01	1755	1792	24.28	4.64	4.67	7.30	7.31
93-09-17	774	924	25.70	3.12	5.27	2.12	3.09
93-09-29	400	462	14.49	3.01	4.70	1.33	1.59
93-10-13	715	738	17.55	6.99	10.15	2.05	2.10
93-10-26	966	1153	39.58	3.81	4.07	1.32	1.62
SWM	1086	12.24	14.22	3.80	5.04	6.83	826

Table 9e. Seasonal data and seasonal weighted means (SWM) for phytoplankton photosynthesis rates (P), parameters (P^B_m, α^B), and mean epilimnetic irradiance ($\bar{I}$) at station W1. 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 (mg $C \cdot mg\ Chl^{-1} \cdot E^{-1} \cdot m^{-2}$) 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 ($\sum P = mg\ C \cdot m^{-2} \cdot d^{-1}$) and $\bar{I}$ (mE·m^{-2}·min^{-1}) were both calculated with theoretical cloudless (cldlss) and empirical (emp) solar irradiance as denoted by the subscripts.

Date	$\sum P_{emp}$	$\sum P_{cldlss}$	P_{opt}	P^B_m	α^B	$\bar{I}_{emp}$	$\bar{I}_{cldlss}$
93-05-19	459	557	4.20	3.28	5.9	13.35	22.42
93-06-02	414	510	7.36	4.21	5.71	6.23	9.44
93-06-15	1391	1470	25.46	4.72	4.86	8.55	9.01
93-06-29	384	395	11.62	5.87	6.18	5.11	5.07
93-07-14	1054	2021	24.40	5.39	5.25	5.27	12.92
93-07-28	1829	2296	14.31	2.57	1.08	5.41	6.77
93-08-05	1280	1360	72.41	9.39	7.53	3.07	3.32
93-08-17	2234	2818	26.70	4.54	5.06	11.96	16.86
93-09-01	1018	1036	22.45	4.37	5.01	6.36	6.35
93-09-15	380	486	24.18	3.78	2.41	2.34	3.35
93-09-29	40	46	6.29	0.83	1.03	0.77	0.91
93-10-13	153	159	14.39	4.67	3.97	1.58	1.61
93-10-26	130	157	18.85	4.75	4.49	0.91	1.12
SWM	844	1051	20.66	4.45	4.43	5.83	8.03

Table 9f. Seasonal data and seasonal weighted means (SWM) for phytoplankton photosynthesis rates (P), parameters (P^B_m, α^B), and mean epilimnetic irradiance ($\bar{I}$) at station W3. P_{opt} (mg C·m^{-3}·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·mg Chl^{-1}·h^{-1}) is the maximum and α^B (mg C·mg Chl^{-1}·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 (ΣP=mg C·m^{-2}·d^{-1}) and $\bar{I}$ (mE·m^{-2}·min^{-1}) were both calculated with theoretical cloudless (cldlss) and empirical (emp) solar irradiance as denoted by the subscripts.

Date	ΣP_{emp}	ΣP_{cldlss}	P_{opt}	P^B_m	α^B	$\bar{I}_{emp}$	$\bar{I}_{cldlss}$
93-05-19	582	803	12.23	4.05	7.53	4.34	7.28
93-06-02	843	1048	12.08	8.33	9.03	8.04	12.17
93-06-15	1522	1610	24.98	8.86	6.49	13.07	13.77
93-06-29	827	844	24.67	10.63	6.84	6.34	6.29
93-07-14	693	1426	27.70	6.71	4.51	3.69	9.07
93-07-28	975	1221	29.12	2.97	1.89	6.23	7.80
93-08-05	1375	1463	38.68	6.60	6.16	5.24	5.67
93-08-18	1236	1399	24.31	4.78	3.81	10.05	11.18
93-09-01	887	903	19.74	7.34	6.60	6.73	6.71
93-09-15	321	422	19.95	5.31	4.55	2.49	3.56
93-09-29	66	77	11.15	4.21	3.60	0.81	0.96
93-10-14	1478	1645	74.02	5.91	5.40	2.60	2.92
93-10-26	263	258	17.21	4.16	2.90	1.94	2.33
SWM	871	1035	26.37	6.38	5.39	5.64	7.03

Table 10. Volume- (g C·m^{-3}) and areal-based (g C·m^{-2}) phytoplankton photosynthesis (PP) for the May 1 - Oct. 31 period. Areal PP was calculated with both empirical (emp) and theoretical cloudless solar irradiance (cldlss). Areal PP calculated with empirical irradiance was expressed as a percentage of the cloudless values (% Cld).

| Station | Volume PP | Areal PP | | % Cld |
		emp	cldlss	
E2	16.3	105.3	139.6	75.4
E3	10.0	53.8	70.1	76.7
WC1	22.2	121.5	154.9	78.4
WC2	34.8	171.6	216.6	79.2
W1	47.8	150.9	192.8	78.3
W3	54.4	142.1	185.1	76.8

Table 11. Seasonal mean-length (μm) of the most abundant zooplankton species from nearshore and offshore stations in each of the three basins of Lake Erie.

Species	Western		West Central		Eastern	
	Nearshore	Offshore	Nearshore	Offshore	Nearshore	Offshore
Bosmina longirostris	245	251	304	289	268	320*
Daphnia retrocurva	833	939*	855	709*		
Diaptomus minutus	1015	1033	984	967	926	971
Epischura lacustris	987	1422*	1140	1224	1148	1277*
Eurytemora affinis	901	1009*	1065	947*	742	823*
Mesocyclops edax	689	825*	766	625*		
Diacyclops thomasi	682	750*	755	561*	672	568*
Tropocyclops extensus	464	553*	468	467	445	450
Dreissena veligers	175	177	189	161*	192	173*

* indicates a difference $\geq$ 10%

Table 12. Comparison of zooplankton mean biomass ($\mu g \cdot L^{-1}$) from 1984-87 (± 95% confidence interval) and 1993, May and August data. Seasonal weighted means for the sampling period May 1 to October 31 with and without veliger biomass.

Parameters	Western		West Central		Eastern	
	W1	W3	WC1	WC2	E3	E2
1984-87 mean*	81.3 ± 58.9		73.8 ± 64.6		60.8 ± 60.7	
1993 mean for limited dates (May and Aug)**	25.2	95.8	114.3	36.0	24.4	14.9
1993 mean (May-Oct) no veligers	65.3	70.8	91.5	64.9	27.3	28.4
1993 mean (May-Oct) with veligers	79.9	84.9	104.7	65.6	33.5	44.1

*mean biomass from J. Makarewicz, SUNY, Brockport (pers. comm.)
**only dates sampled by Makarewicz in the 1980's were included in these means, veligers were not included.

Table 13. Summary of zooplankton species occurrence at 6 stations in Lake Erie in 1993, where W refers to the western basin, WC refers to the west central basin and E refers to the eastern. Numbers indicate the proportion of sampling days on which that species comprised ≥ 5% of the total biomass. + indicates the species was present but never comprised ≥ 5% of the total biomass.

Taxon	W1	W3	WC1	WC2	E3	E2
CLADOCERA						
Bosmina sp.	0.357	0.214	0.923	1.000	0.417	0.700
Daphnia longiremis	+	0.143	+	0.154		+
Daphnia retrocurva	0.500	0.429	+	0.308		+
Daphnia galeata mendotae						+
Diaphanosoma sp.	0.143		+	+		
Eubosmina sp.	0.143	0.071	0.231	0.231		
Holopedium gibberum			+			+
Bythothrephes cederstroemi			0.154	0.308	0.083	+
Leptodora kindti	+	0.071	+	+	+	0.200
COPEPODA						
Calanoida						
Leptodiaptomus ashlandi	0.143	0.071	0.077	0.308		0.100
Leptodiaptomus minutus	+	+	0.308	0.077	0.500	0.300
Leptodiaptomus sicilis	0.143	0.071	0.154	0.615	+	+
Leptodiaptomus siciloides	+	+	0.231	+	+	+
Skistodiaptomus oregonensis	+	+	0.077	0.038	0.333	0.200
Epischura lacustris	0.071	+	0.385	0.385	0.750	0.700
Epischura lacustris cop.	0.214	+	+	0.231	0.583	0.500
Eurytemora affinis	0.357	0.214	0.154	0.077	0.083	0.300
Limnocalanus macrurus	0.071	0.071	+			+
Senecella calanoides	+	+				
Calanoid copepidid	0.357	0.429	0.692	0.231	0.333	0.400
Calanoid nauplii	0.071	+	0.077	0.231	0.083	0.300
Cyclopoida						
Diacyclops thomasi	0.429	0.286	0.846	1.000	0.333	0.800
Cyclops vernalis	+	+	0.077	0.077		+
Mesocyclops edax	0.071	+	0.308	0.462	+	0.100
Tropocyclops extensus	+	+	0.077	0.308	0.250	0.100
Eucyclops agilus		+		+		
Eucyclops speratus		+				
Cyclopoid copepidid	0.214	0.357	0.846	0.462	0.417	0.500
Cyclopoid nauplii	0.071	+	+	0.231	0.167	+
Harpactacoida	+	+	+		+	+
DREISSENA VELIGERS	0.643	0.571	0.231	0.231	0.833	1.000

Table 14. List of rotifer species found at each station in Lake Erie in 1993. Species are ranked as present but rare (O), contributing ≥0.5% (+), ≥5.0% or ≥10.0% (+++) of total biomass at some time in the season (May - October).

Species	W1	W2	W3	WC1	WC2	E1	E2	E3
Ascomorpha ecaudia	+	+		+	+	++	+++	+
A. ovalis	O	O	O	+	+	+	+	+
A. saltans			O				+	
Asplanchnia herricki	+++	+++		+++	+++			
A. priodonta	+++	+++	+++	+++	+++	+++	+++	+++
Brachionus angularis	+	+	+					
B. budapestinensis			O					
B. calyciflorus	+	+	+					
B. caudatus			+					
Cephalodella rhomboides					O			
Collotheca sp.	+	+	O	+	+	+	+	+
Conochilus unicornis	+++	+++	+	+++	+++	+++	+++	+++
Filinia longiseta	+	++	+	+	+	++	++	+
Gastropus stylifer	++	+	O	+++	+++	+	+	+
G. hyptopus					O			
Kellicottia longispina	+	+	O	+++	+++	+	++	++
Keratella cochlearis(group)			+		+++		+	
K. cochlearis	+	++	+	+++	+++	+	O	+
K. crassa	+	+	+	+++	+++	+	++	+++
K. earlinae	+++	+	+	+	++	+	+	+
K. hiemalis	O	O	+	+	O		O	O
K. quadrata	+	+++	++	+++	++	+	++	+
K. taurocephala				+				
Monostyla sp.						+		
Notholca acuminata		+	O	O	O			
N. foliacea	+	O	O		+	O	O	O
N. laurentiae	+	+	O	+	++	O	+	+
N. squamula		+		++	O	+		
Pleosoma hudsoni	+	++		+	++	+	+	
P. truncatum	++	+	+	++	+		+	+
Polyarthra dolichoptera	O	+	O	++	+++	+	+	+
P. euryptera				+		+++	+	+
P. major	+++	+++	+++	+++	+++	+++	+++	+++
P. remata	+++	+++	+++	+++	+++	+++	+++	+++
P. vulgaris	+++	+++	+++	+++	+++	+++	+++	+++
Pompholyx sp.					O			

Table 14. Continued.

Species	W1	W2	W3	WC1	WC2	E1	E2	E3
Synchaeta sp.	O		++		+++	+	+++	O
Synchaeta -round	+++	+++	+++	+++	+++	+++	+++	+++
Synchaeta -small	+	++	++	+	+	+	+	++
Synchaeta -large	+++	+++	+++	+++	+++	+++	+++	+++
Synchaeta -long	O	+	++	O	+	+	O	++
Trichocerca sp.			+				+	O
T. bicristata			O					
T. cylindrica				+++	+++	+	+++	
T. elongata			+	++			+++	
T. lata			+			+		
T. longiseta							+	
T. multicrinis	+	+++	++	+++	+++	+	+	+
T. porcellus							+	
T. pusilla	+++	+++	+++	O	O			
T. rousseleti	+++	+	+++	+	+		++	+
T. similis	O		+	+	O			
Trichotria sp.	O		+					
Tylotrocha sp.	O	O		O	O	O	O	O
Wierzejskiella velox					O			

Table 15. Average annual densities for different taxonomic groups at selected Lake Erie stations, 1993. Densities are no. of individuals·m^{-2} and averages are calculated over 7 sampling dates, with the exception of Station W3 (n = 5) and E2 (n = 6).

Species	W1 Density	W1 S.E.	W3 Density	W3 S.E.	WC1 Density	WC1 S.E.	WC2 Density	WC2 S.E.	E2 Density	E2 S.E.	E3 Density	E3 S.E.
Nematoda	1679.5	426.9	3491.4	726.6	804.6	370.1	4373.5	547.9	8189.1	1468.2	10004.1	1291.4
Platyhelminthes/Nemertea	1.5	1.5	160.9	76.2	551.1	416.1	153.9	107.0	411.1	155.1	395.1	64.3
Oligochaeta	5382.2	950.6	8126.4	1167.9	6841.6	2342.9	10894.4	1701.8	20632.2	2529.4	3331.3	465.4
Hirudinae	72.9	52.9	247.1	46.9	6.7	4.7	6.2	6.2	7.2	7.2	11.8	8.1
Amphipoda	24.6	15.6	324.7	172.9	38.5	35.0	4.6	4.6	0.0	0.0	1018.1	314.2
Isopoda	0.0	0.0	0.0	0.0	198.6	195.0	0.0	0.0	0.0	0.0	103.1	103.1
Ostracoda	11103.2	1761.4	3341.9	546.7	3545.8	1635.9	4662.9	898.5	4849.6	631.0	2139.3	678.1
Harpacticoida	23716.6	3897.5	13456.9	2006.7	520.3	193.8	5527.5	496.6	1935.2	675.4	21439.5	6313.5
Ephemeroptera	3.6	2.4	2.9	2.9	0.0	0.0	0.0	0.0	0.0	0.0	9.2	9.2
Trichoptera	12.3	12.3	20.1	8.6	0.0	0.0	0.0	0.0	0.0	0.0	204.2	64.4
Chironomidae	887.7	271.3	609.2	119.3	946.7	432.1	1197.2	170.3	316.5	67.5	3077.8	415.8
Gastropoda	3.6	2.4	304.6	97.4	329.9	177.6	0.0	0.0	8.6	7.0	1983.3	496.8
Sphaeriidae	399.7	122.8	267.2	42.8	28.7	14.4	2486.2	353.8	256.5	81.5	108.3	33.9
Dreissena polymorpha	2226.5	2103.5	31614.9	9006.3	1545.6	891.9	88.3	12.7	31.1	15.0	1905.8	723.2
Dreissena bugensis	0.0	0.0	5.8	3.5	11442.4	4487.4	200.6	47.0	91678.6	25690.7	69697.3	19331.2
Total *Dreissena*	2226.5	2103.5	31620.7	9008.2	12987.9	4673.7	288.9	46.6	91709.8	25704.7	71603.0	19085.8
% Quagga	0.0	--	0.0	--	88.1	--	69.5	--	99.9	--	97.3	--
Total Benthos	45514.2	6739.7	61974.1	9178.0	26800.6	8717.2	29595.1	2755.6	128316.5	29009.1	115427.9	23731.9
% *Dreissena*	4.9	2.0	51.0	5.2	48.5	9.3	1.0	0.2	71.5	6.8	62.0	9.2

Table 16. Annual biomass estimates for different taxonomic groups at selected Lake Erie stations, 1993. Biomass is wet, shell-free weight (g·m^{-2}). Averages were calculated from 7 sampling dates, with the exception of Station W3 (n = 5) and E2 (n = 6).

Species	W1 Biomass	W1 S.E.	W3 Biomass	W3 S.E.	WC1 Biomass	WC1 S.E.	WC2 Biomass	WC2 S.E.	E2 Biomass	E2 S.E.	E3 Biomass	E3 S.E.
Nematoda	0.0643	0.0305	0.0810	0.0179	0.0225	0.0096	0.1290	0.0277	0.1547	0.0203	0.1710	0.0298
Platyhelminthes/Nemertea	0.0014	0.0014	0.1871	0.1044	0.0497	0.0311	0.0755	0.0546	0.0741	0.0293	0.3925	0.0718
Oligochaeta	4.0024	0.9886	4.0678	0.8310	1.6492	0.4264	6.6466	1.1853	12.5926	1.5552	3.9064	0.4398
Hirudinae	0.0936	0.0330	0.7517	0.1535	0.0100	0.0068	0.0218	0.0218	0.0043	0.0043	0.0904	0.0637
Amphipoda	0.0497	0.0246	0.9250	0.5853	0.1118	0.1063	0.0023	0.0023	0.0000	0.0000	3.5732	0.9264
Isopoda	0.0000	0.0000	0.0000	0.0000	0.0662	0.0587	0.0000	0.0000	0.0000	0.0000	0.0297	0.0297
Ostracoda	0.2862	0.0459	0.0759	0.0181	0.1051	0.0533	0.1289	0.0225	0.1426	0.0212	0.0552	0.0162
Harpacticoida	0.2223	0.0310	0.1089	0.0195	0.0054	0.0016	0.0700	0.0134	0.0215	0.0055	0.1771	0.0472
Ephemeroptera	0.0089	0.0062	0.0003	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0009	0.0009
Trichoptera	0.0312	0.0312	0.0385	0.0207	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	1.6693	0.5533
Chironomidae	1.6302	0.7806	0.2989	0.0813	1.4453	0.8269	12.3114	1.5832	0.1139	0.0542	2.6531	0.4789
Gastropoda	0.0143	0.0093	0.6555	0.2729	0.2911	0.1255	0.0000	0.0000	0.0003	0.0002	1.6232	0.1386
Sphaeriidae	0.1882	0.0463	0.1481	0.0571	0.0081	0.0049	1.2063	0.1271	0.0915	0.0479	0.0389	0.0110
Dreissena polymorpha	64.7999	64.4157	624.1002	249.5769	347.6303	161.0735	0.2626	0.2179	0.5524	0.3655	115.3820	52.3700
Dreissena bugensis	0.0000	0.0000	0.0010	0.0008	416.4896	171.3745	5.1472	3.8750	264.0047	81.1573	246.2870	63.8931
Total *Dreissena*	64.7999	65.5991	624.1012	254.0333	764.1199	244.8125	5.4098	3.9949	264.5570	79.3209	361.6690	111.459
% Quagga	0.00	--	0.00	--	54.51	--	95.15	--	99.79	--	68.10	--
Total Benthos	71.3926	66.6687	631.4399	250.5328	767.8842	247.2496	26.0015	5.6297	277.7526	83.4142	376.0500	113.823
% *Dreissena*	90.77	8.24	98.84	6.95	99.51	9.44	20.81	5.87	95.25	0.92	96.18	1.58

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Table 17. Annual production estimates for different taxonomic groups at selected Lake Erie stations, 1993. Production is given in wet, shell-free weight ($g \cdot m^{-2} \cdot yr^{-1}$).

Species	W1	W3	WC1	WC2	E2	E3
Nematoda	0.91	1.14	0.32	1.86	2.19	2.42
Platyhelminthes/Nemertea	0.01	1.34	0.30	0.61	0.40	2.60
Oligochaeta	18.70	18.99	7.93	32.66	53.81	15.61
Hirudinae	0.32	2.25	0.03	0.07	0.01	0.25
Amphipoda	0.10	4.87	0.18	0.01	0.00	20.46
Isopoda	0.00	0.00	0.21	0.00	0.00	0.10
Ostracoda	1.16	0.31	0.47	0.54	0.64	0.27
Harpacticoida	1.12	0.55	0.03	0.37	0.11	0.89
Ephemeroptera	0.02	0.00	0.00	0.00	0.00	0.00
Trichoptera	0.16	0.19	0.00	0.00	0.00	8.42
Chironomidae	7.07	1.11	7.44	24.58	0.39	17.34
Gastropoda	0.02	1.18	0.48	0.00	0.00	5.25
Sphaeriidae	0.51	0.32	0.02	3.04	0.18	0.07
Dreissena polymorpha	448.50	3010.67	746.64	1.33	1.79	492.35
Dreissena bugensis	0.00	0.01	1161.54	32.74	532.55	2484.85
Total *Dreissena*	448.50	3010.68	1908.18	34.07	534.34	2977.20
Total Production	478.60	3042.93	1925.59	97.81	592.07	3050.88
% *Dreissena*	93.71	98.98	99.10	34.83	90.25	97.58

Table 18. Indicators of trophic status in each basin of Lake Erie. Total phosphorus, total nitrogen, and chlorophyll values ($\mu g \cdot L^{-1}$) are the mean of all station seasonal weighted means in each basin. Seasonal areal PP (g $C \cdot m^{-2}$) are calculated for the standardized sampling season (May 1 - Oct. 31) at two stations per basin. Phytoplankton biomass (g·m^{-3}) is for offshore stations only: E2, WC2, W3. Classifications are from Wetzel (1983).

	Basin					
	Western		West Central		Eastern	
Parameter	Oligo.	Meso.	Oligo.	Meso.	Oligo.	Meso.
Total Phosphorus		17.37		11.80	7.63	
Total Nitrogen		617		472		460
Chlorophyll		4.18		3.33	1.43	
Phytoplankton Photosynthesis		147		147	80	
Phytoplankton biomass	0.76		0.75		0.35	

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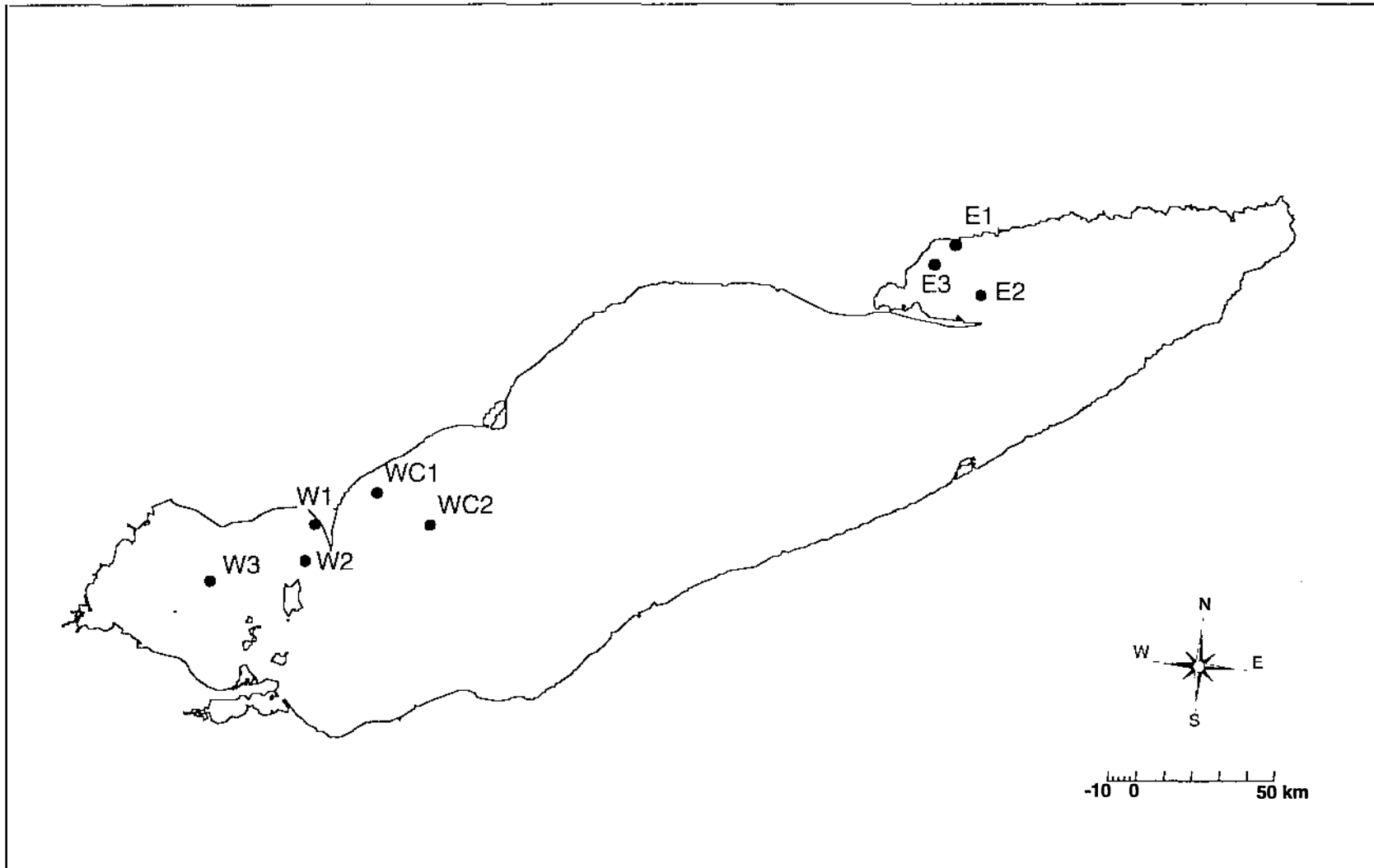
Figure 1. Lake Erie sampling stations in 1993: E= eastern WC= west central, W= western.
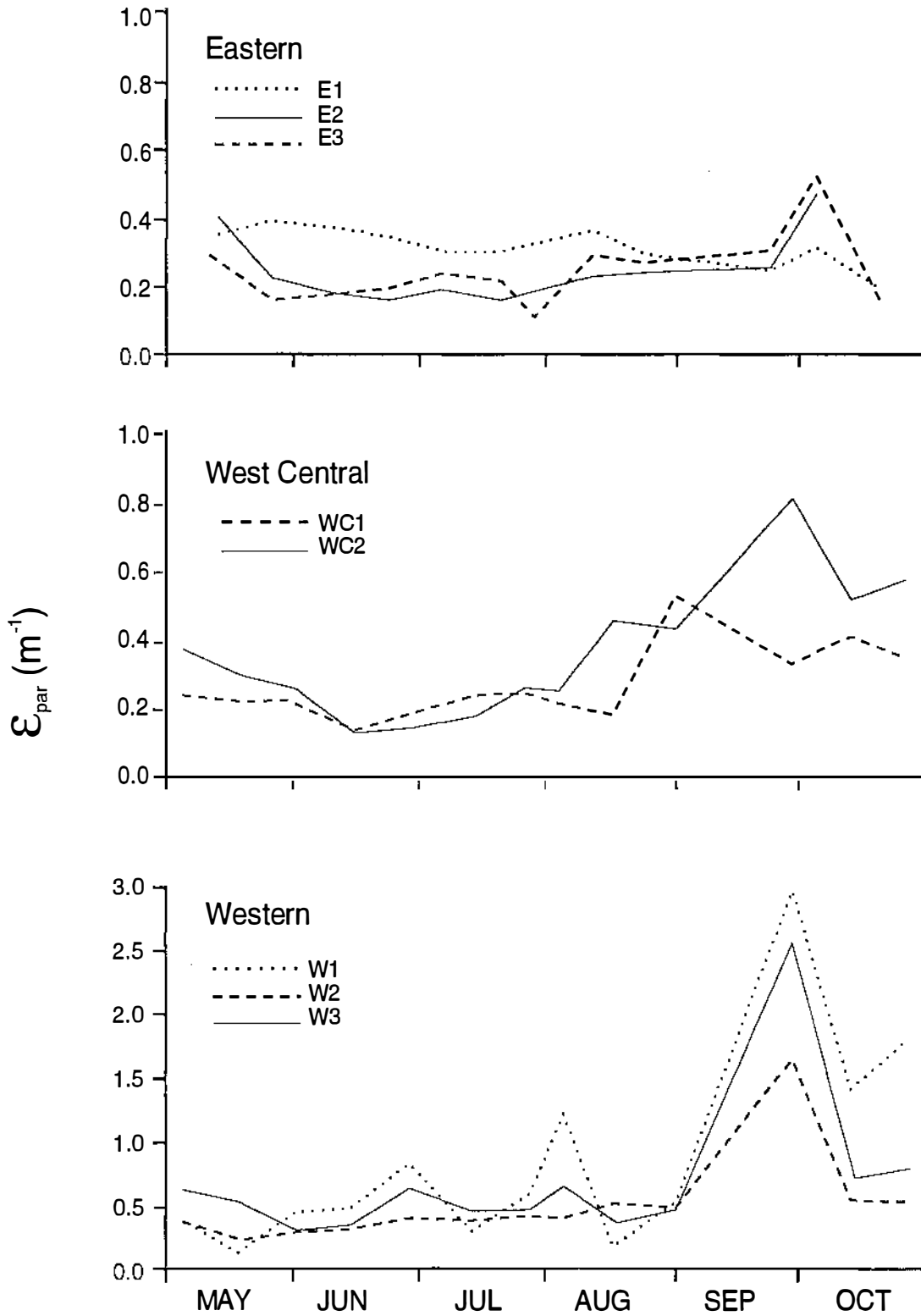
Figure 2. Seasonal (May-Oct.) light extinction (ε_{par} m^{-1}) at nearshore (broken lines) and offshore (solid line) stations in the three basins of Lake Erie, 1993.
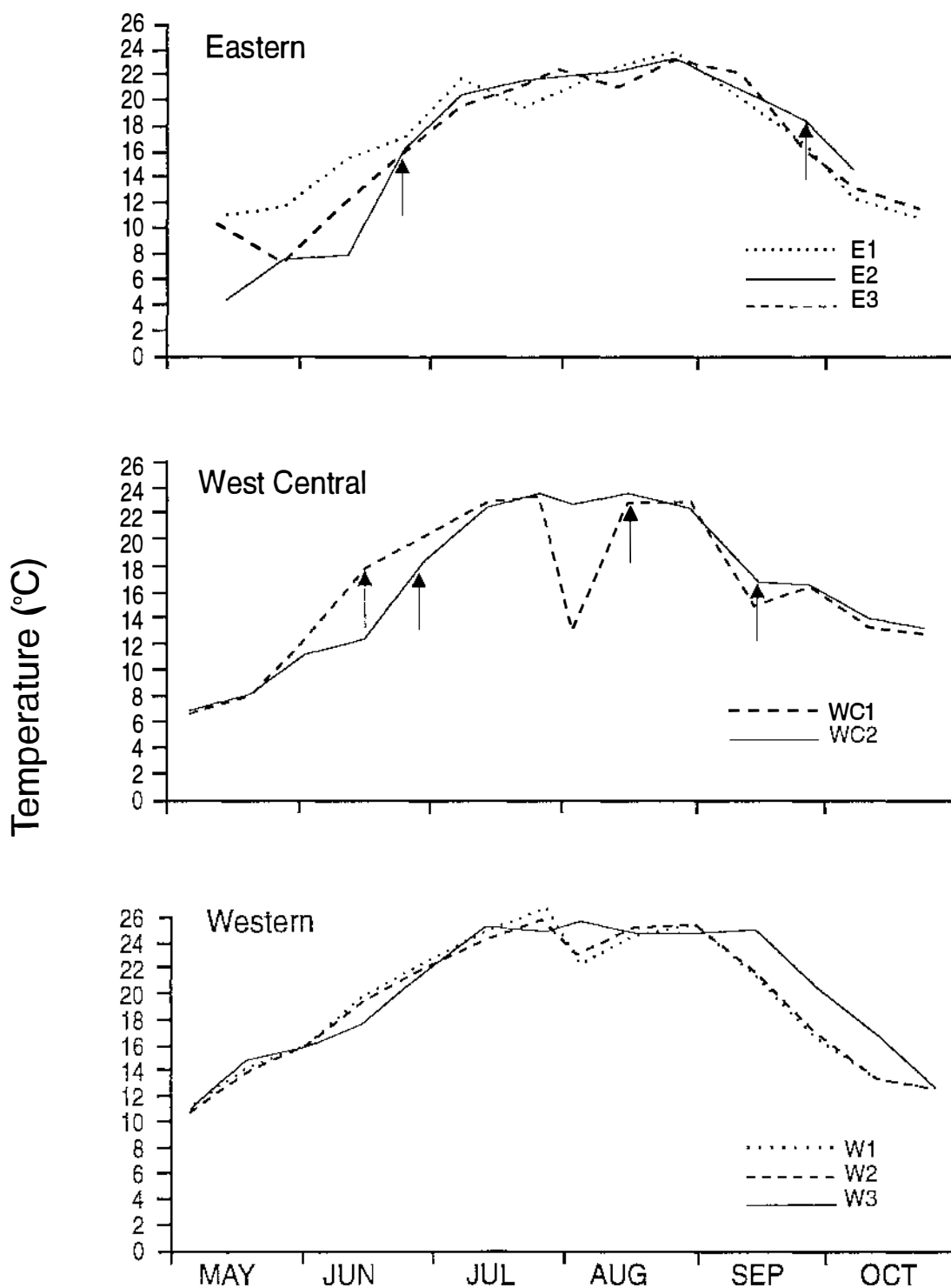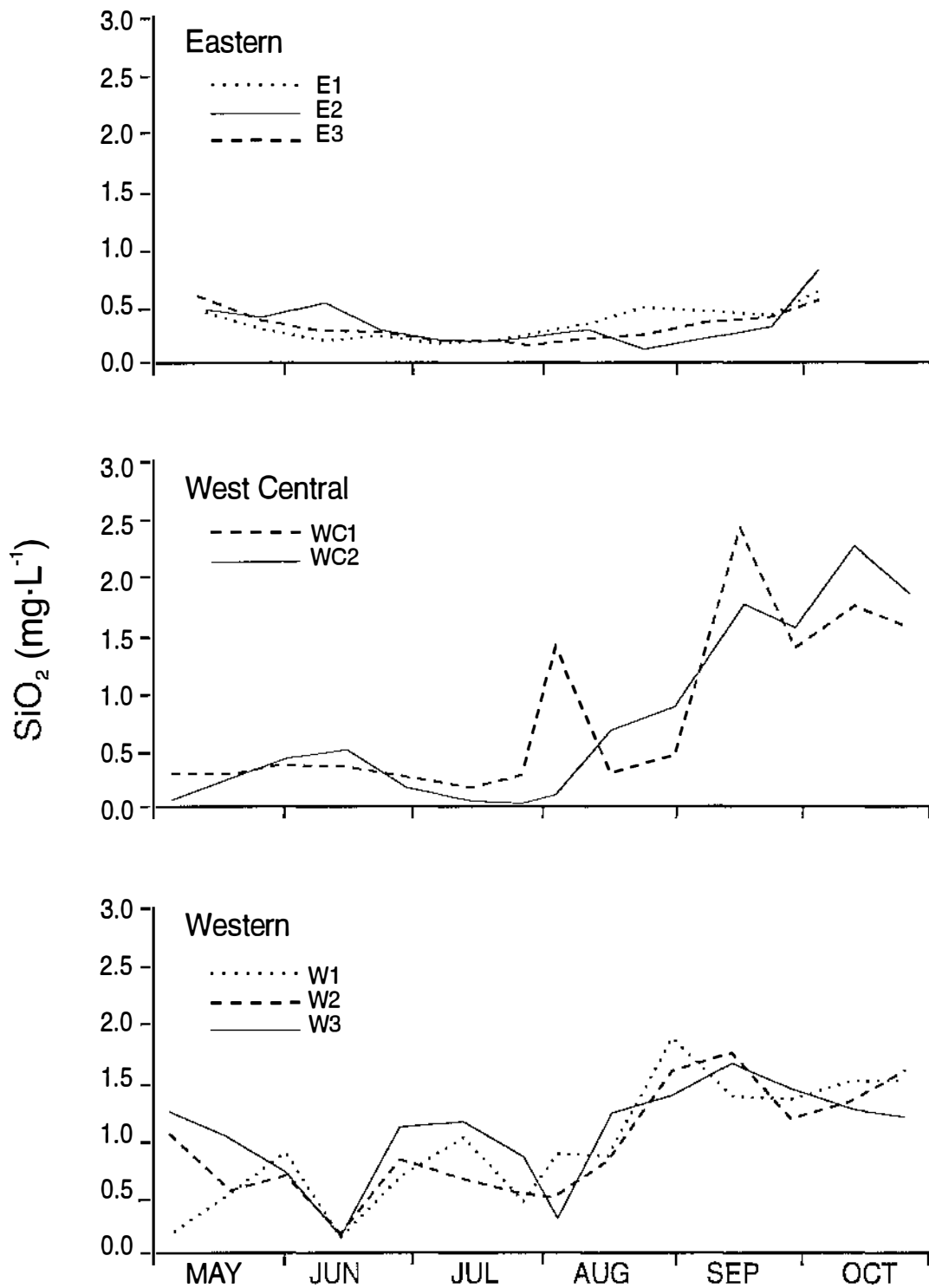
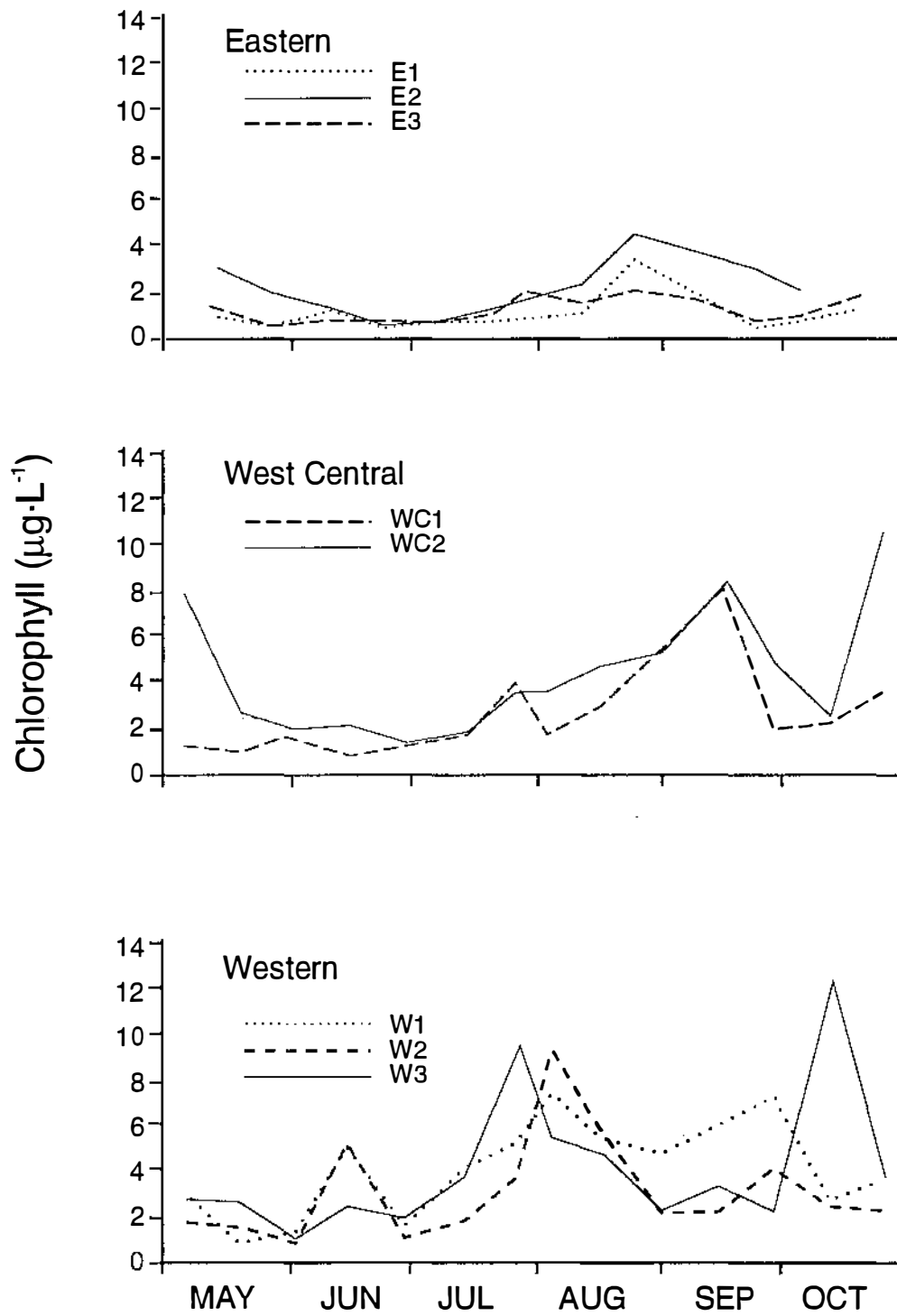Figure 3. Seasonal (May-Oct.) temperature (°C) at nearshore (broken lines) and offshore (solid line) stations in the three basins of Lake Erie, 1993. Onset and breakdown of stratification is indicated for stations E2, WC1, and WC2 by the arrows.
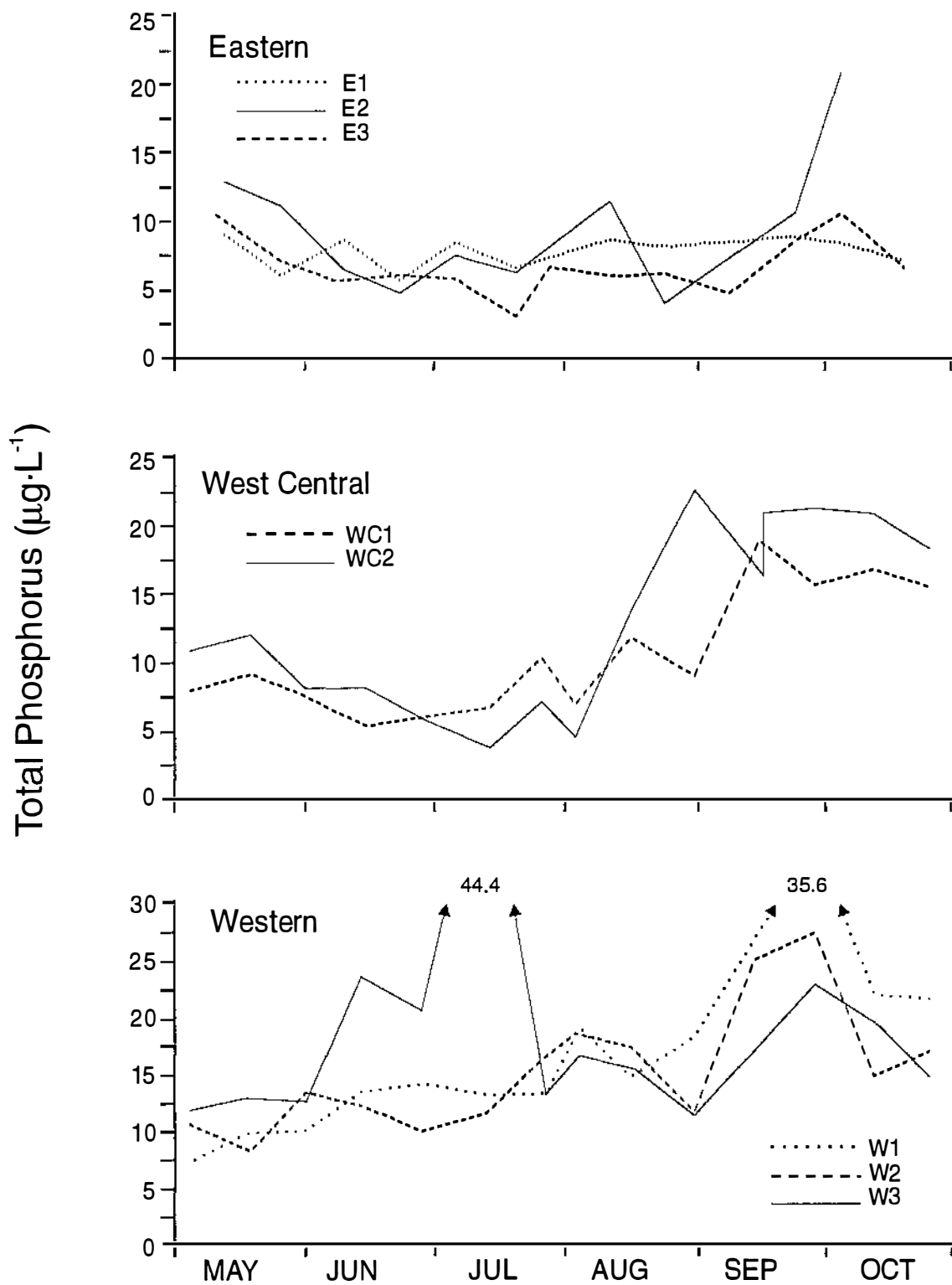
Figure 4. Seasonal (May-Oct.) total phosphorus (μg·L^{-1}) at nearshore (broken lines) and offshore (solid line) stations in the three basins of Lake Erie, 1993.

Figure 5. Seasonal (May-Oct.) SiO_2 concentrations (mg·L^{-1}) at nearshore (broken lines) and offshore (solid line) stations in the three basins of Lake Erie, 1993.

Figure 6. Seasonal (May-Oct.) uncorrected chlorophyll ($\mu g \cdot L^{-1}$) at nearshore (broken lines) and offshore (solid line) stations in the three basins of Lake Erie, 1993.
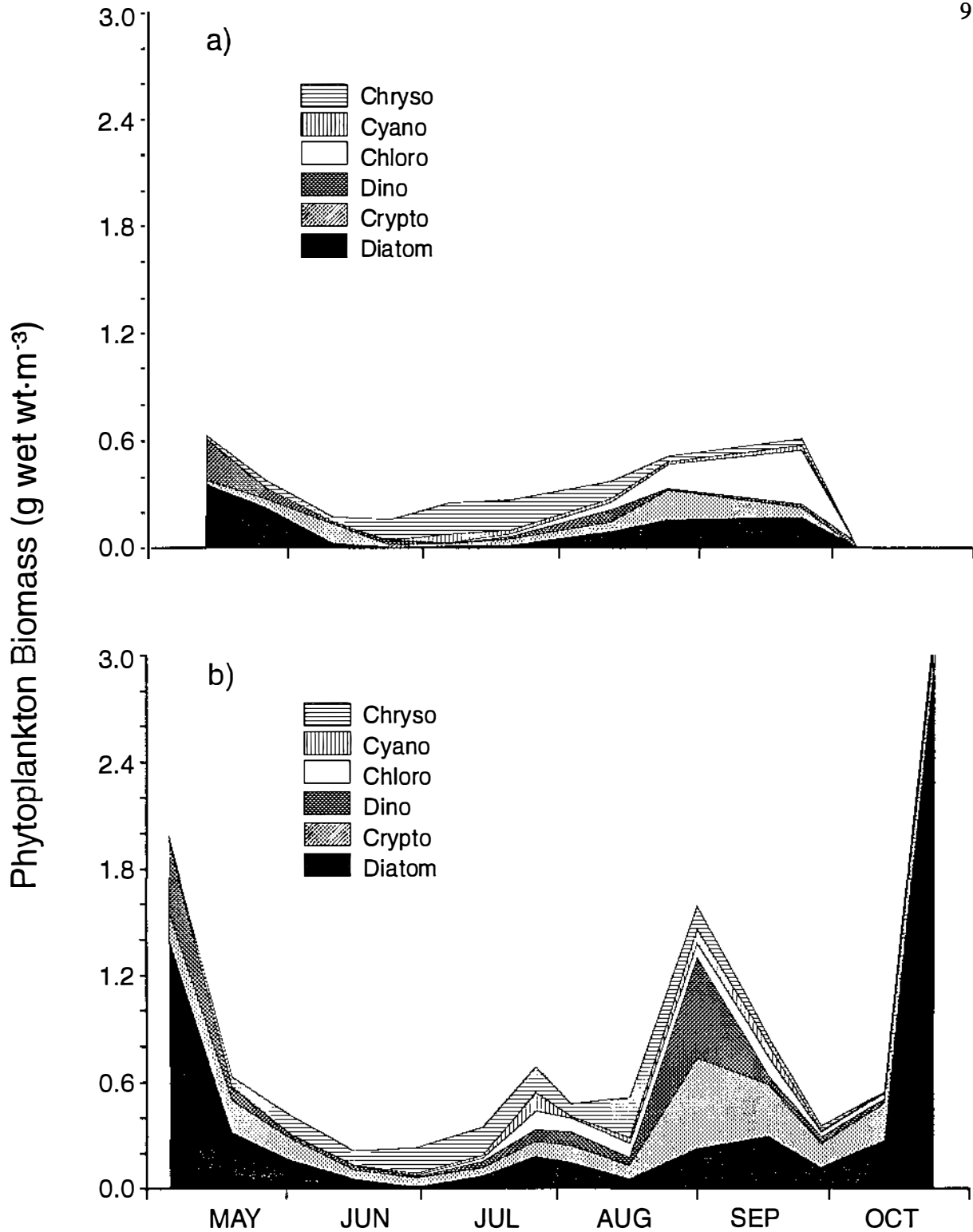
Figure 7. Seasonal trends in phytoplankton biomass and composition at offshore stations in the three basins, a) eastern basin, b) west central basin, and c) western basin of Lake Erie, 1993. Values obtained from integrated samples through the epilimnion or whole water column samples under unstratified conditions.
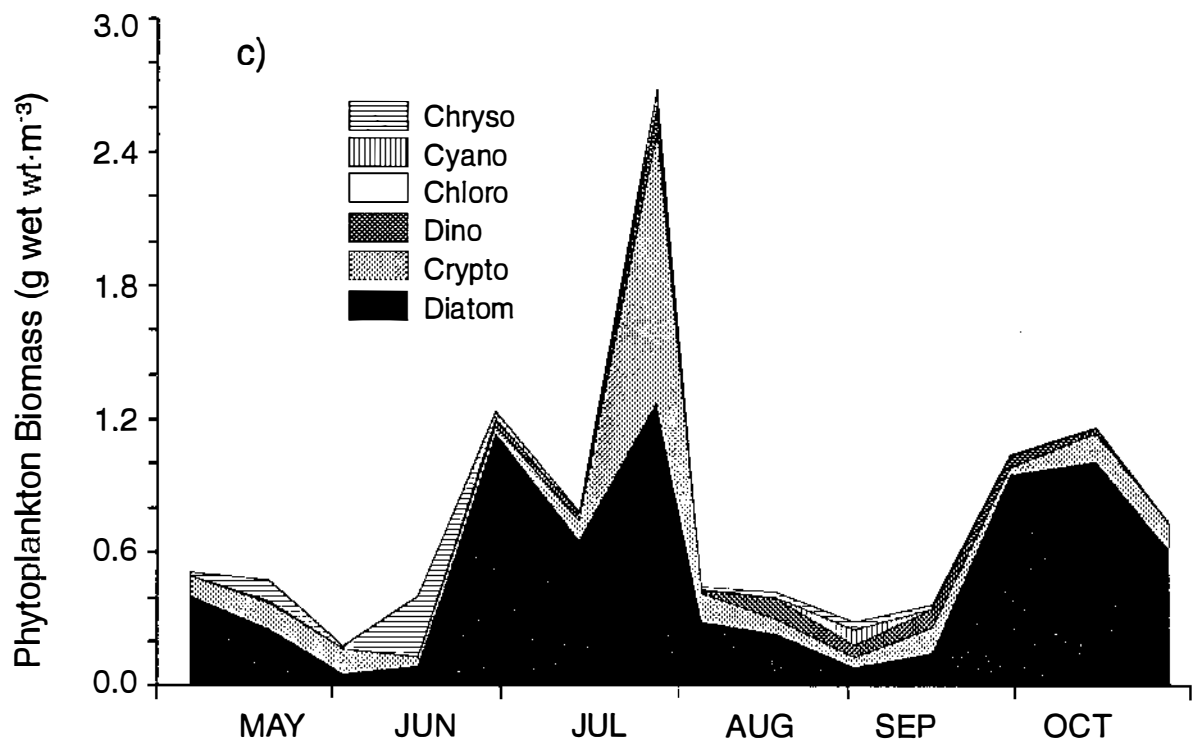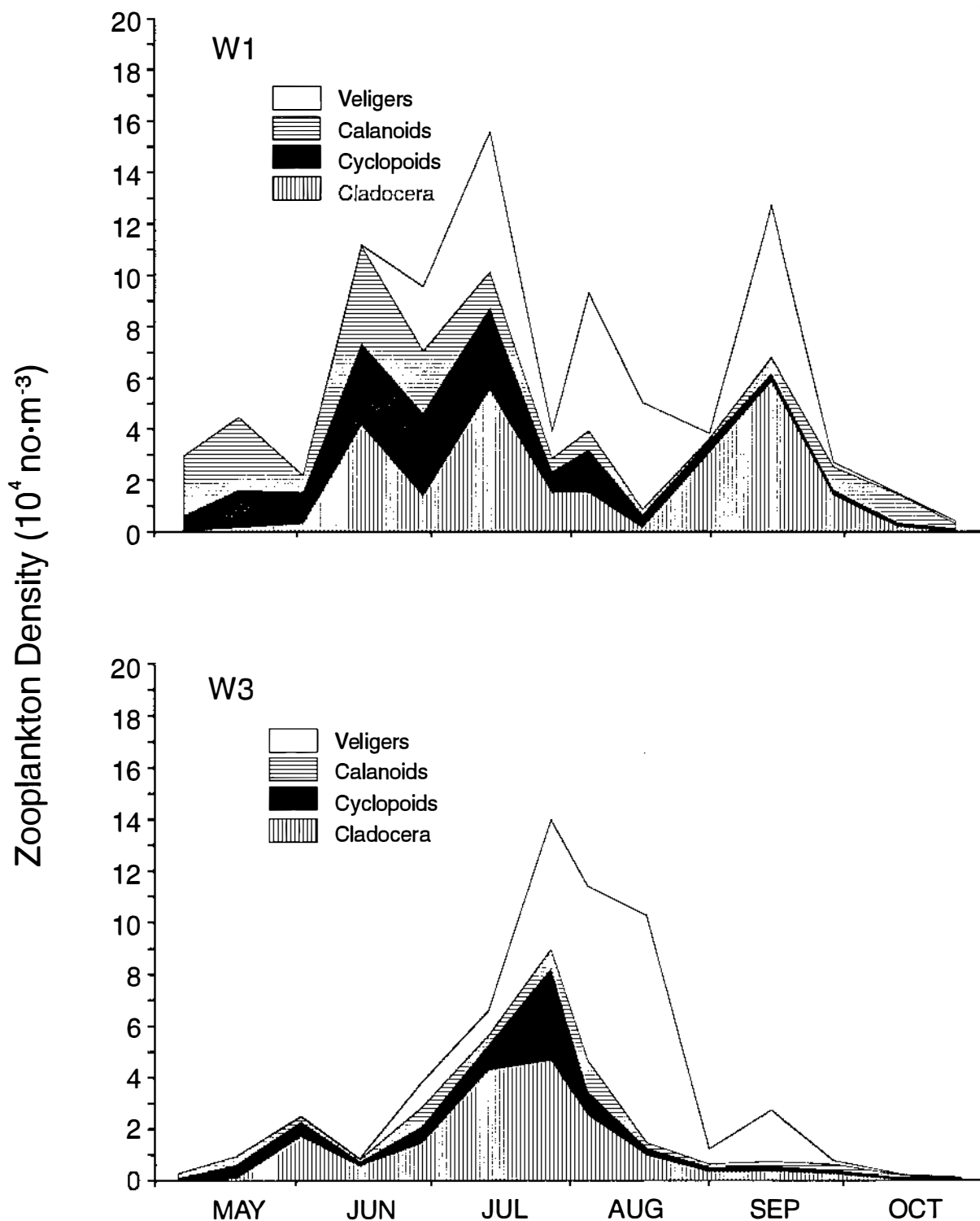
Figure 8. Seasonal trends in macrozooplankton and veliger densities at a nearshore (W1) and offshore (W3) station in the western basin of Lake Erie, 1993. Integrated, whole water column samples, 110–μ mesh.
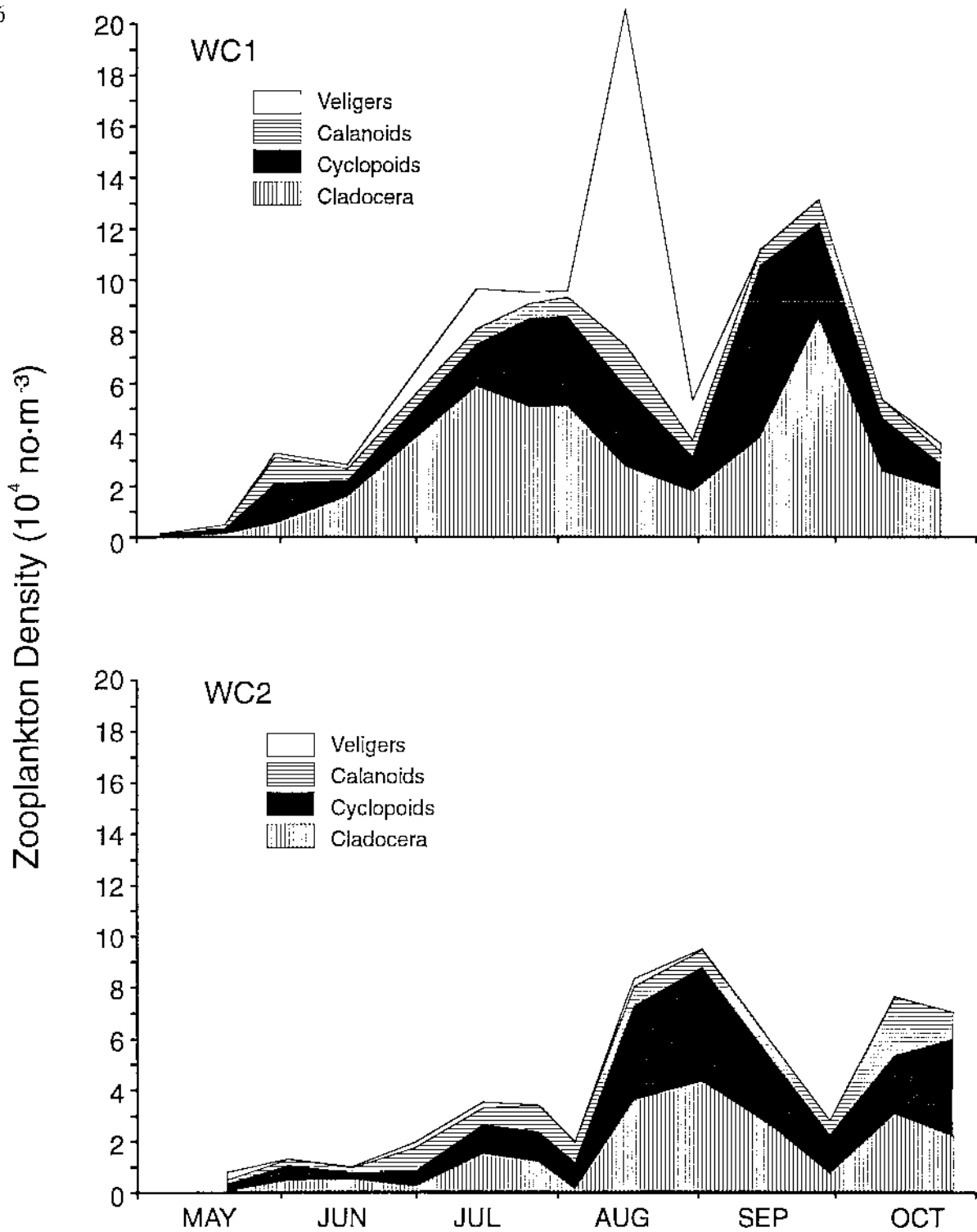
Figure 9. Seasonal trends in macrozooplankton and veliger densities at a nearshore (WC1) and offshore (WC2) station in the west-central basin of Lake Erie, 1993. Integrated, whole water column samples, 110–μ mesh.
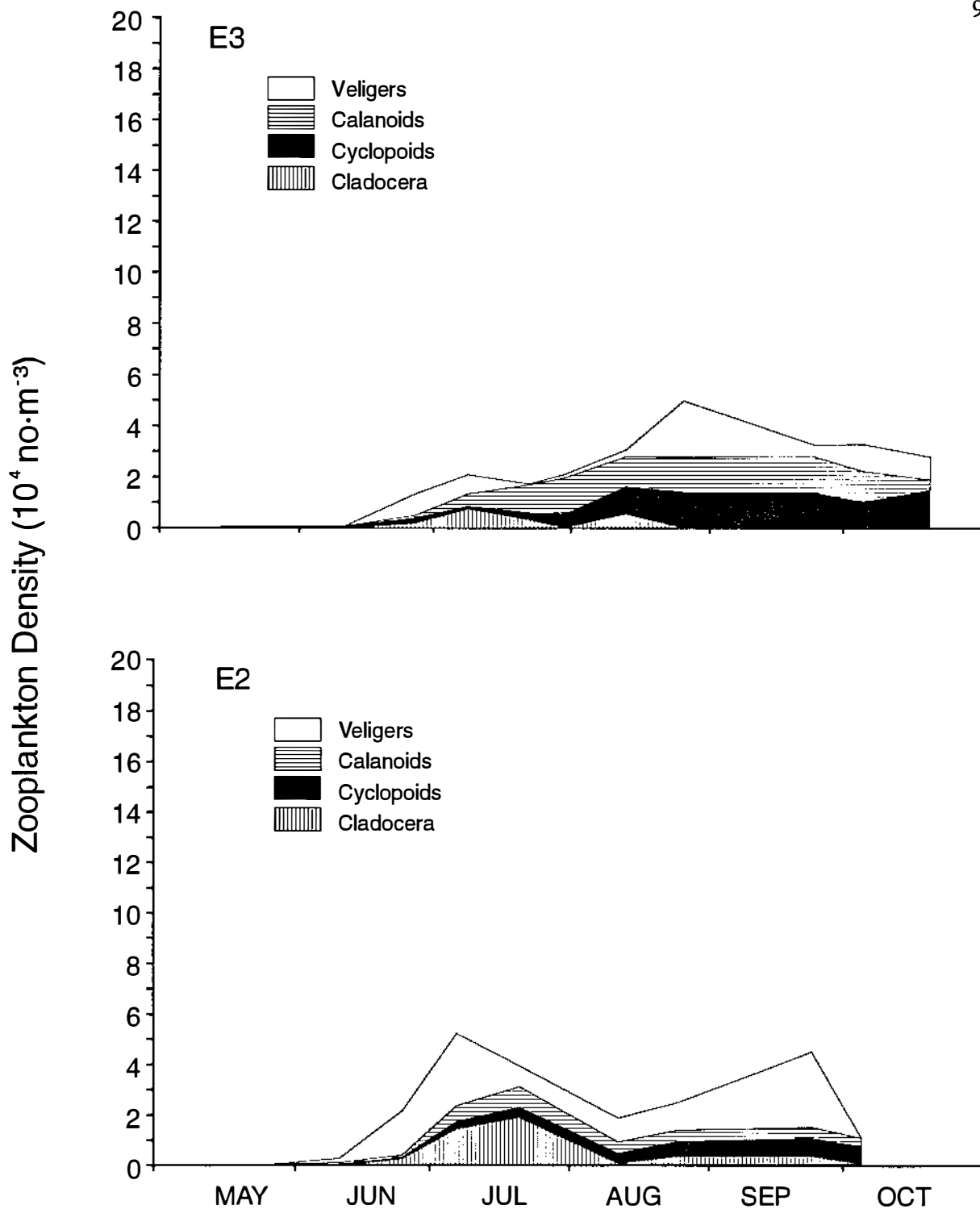
Figure 10. Seasonal trends in macrozooplankton and veliger densities at a nearshore (E3) and offshore (E2) station in the eastern basin of Lake Erie, 1993. Integrated, whole water column samples, 110–μ mesh.
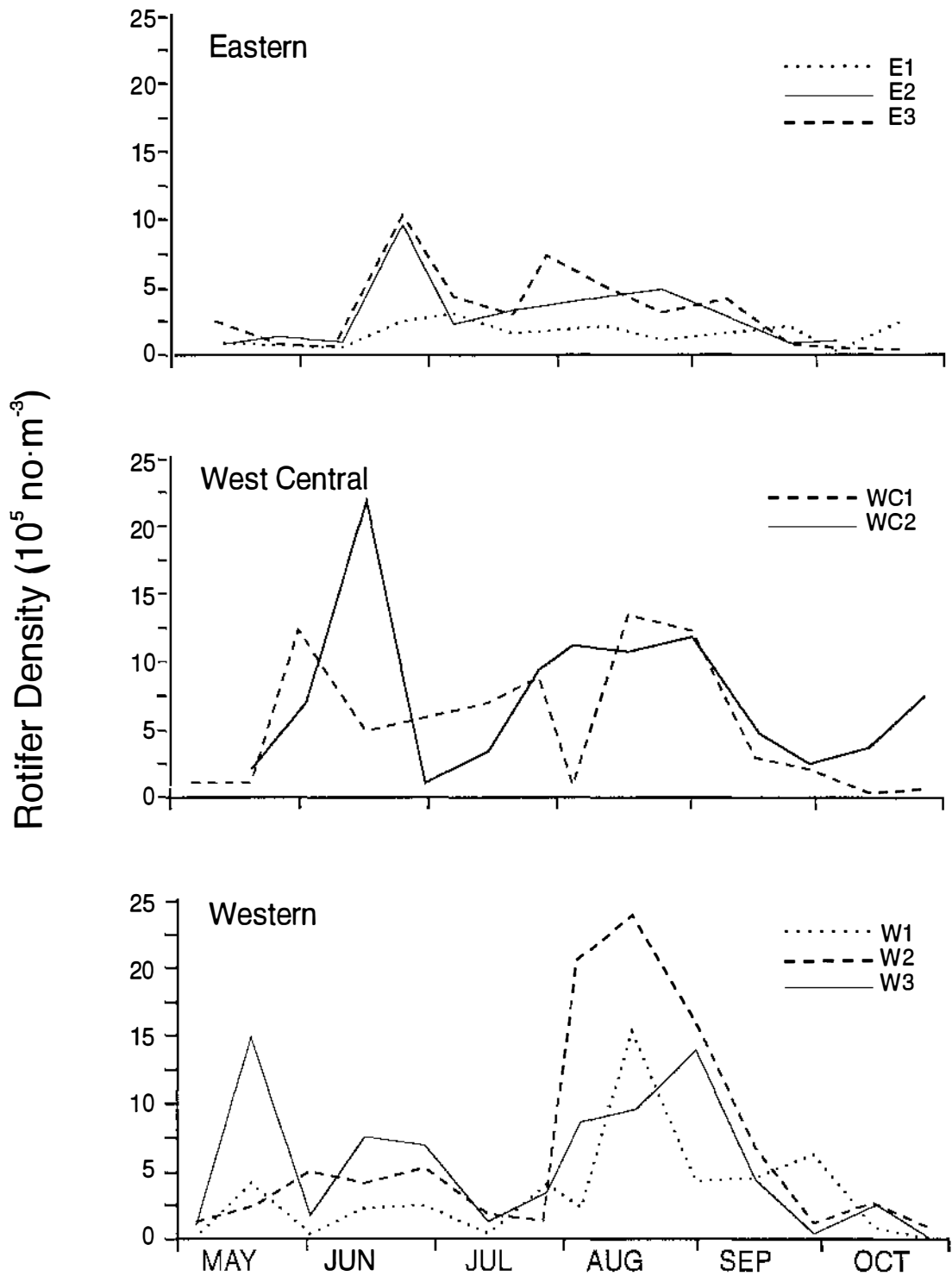
Figure 11. Seasonal trends in rotifer density at nearshore (broken lines) and offshore (solid line) stations in the three basins of Lake Erie, 1993. Integrated, whole water column samples, 20μm mesh.
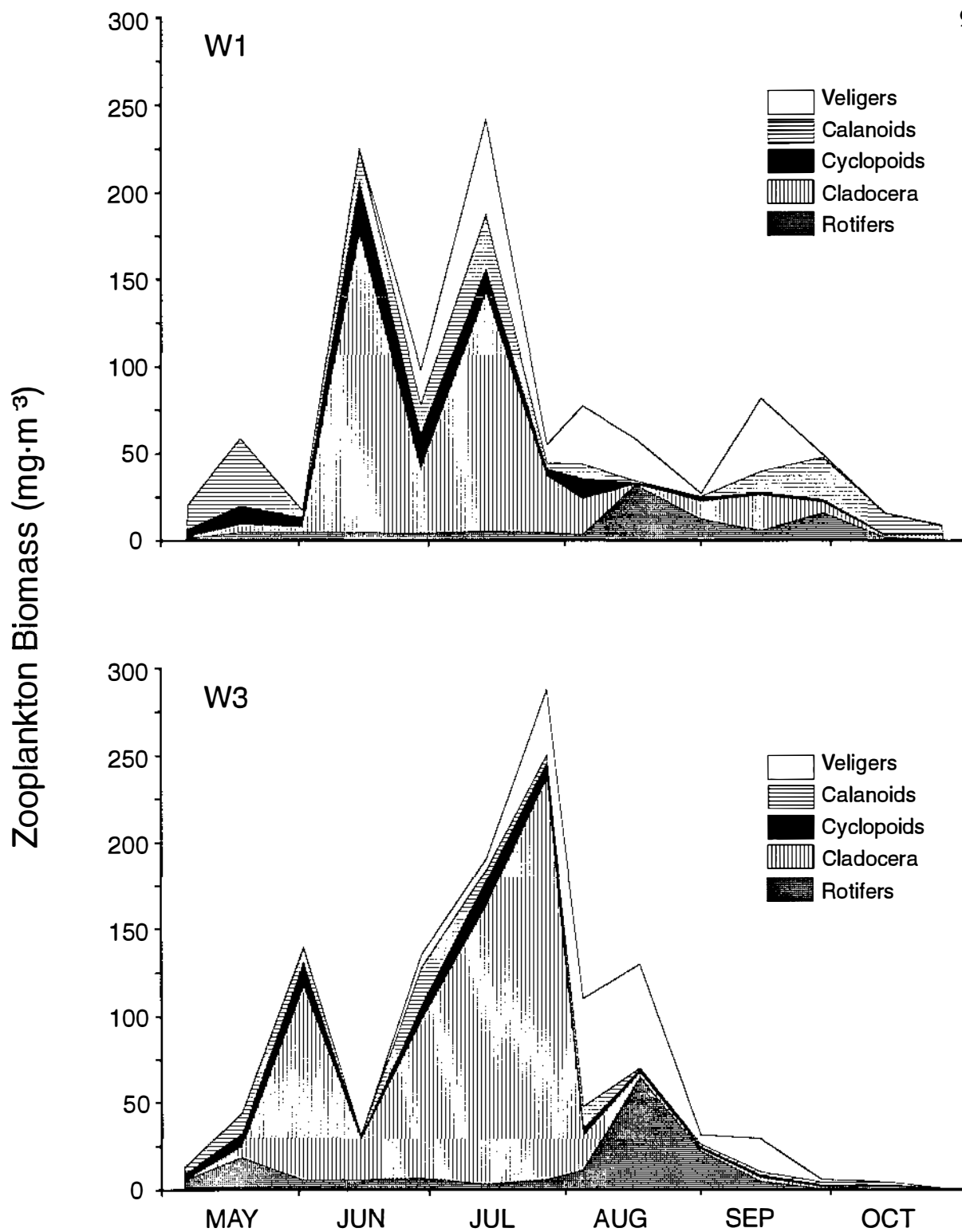
Figure 12. Seasonal trends in zooplankton and veliger biomass at a nearshore (W1) and offshore (W3) station in the western basin of Lake Erie, 1993. Integrated, whole water column samples, 110-μ mesh.
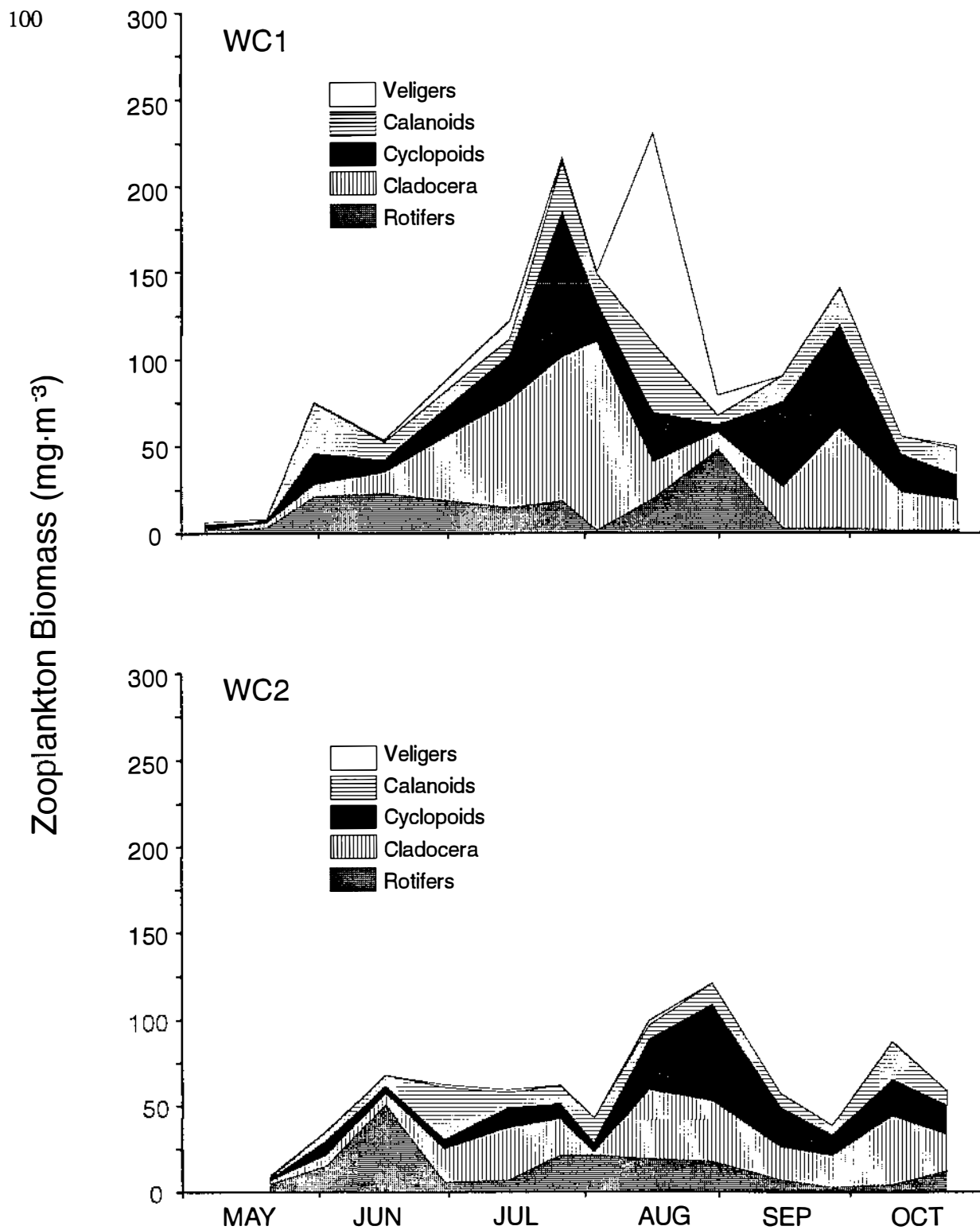
Figure 13. Seasonal trends in zooplankton and veliger biomass at a nearshore (WC1) and offshore (WC2) station in the west-central basin of Lake Erie, 1993. Integrated, whole water column samples, 110–μ mesh.
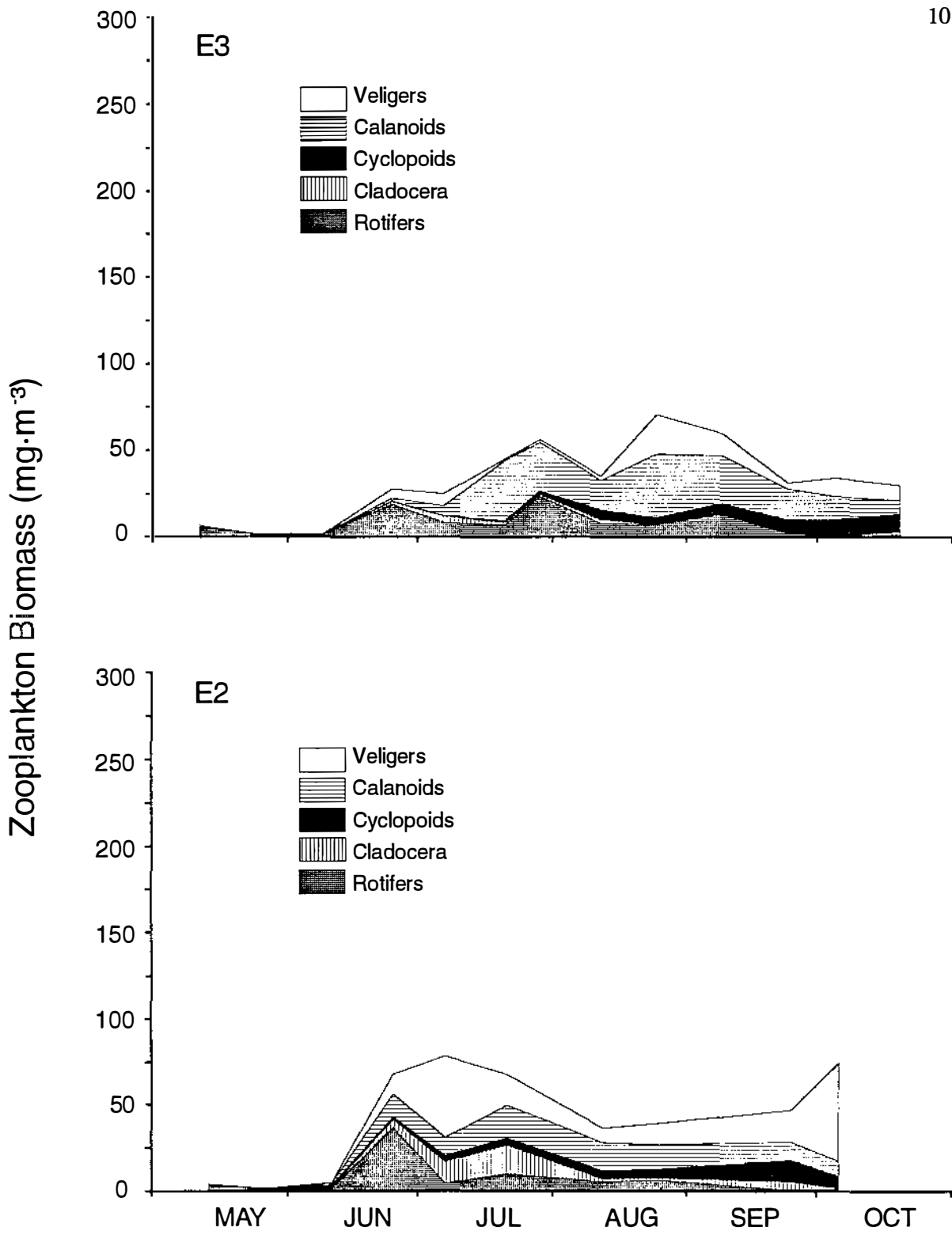
Figure 14. Seasonal trends in zooplankton and veliger biomass at a nearshore (E3) and offshore (E2) station in the eastern basin of Lake Erie, 1993. Integrated, whole water column samples, 110-μ mesh.
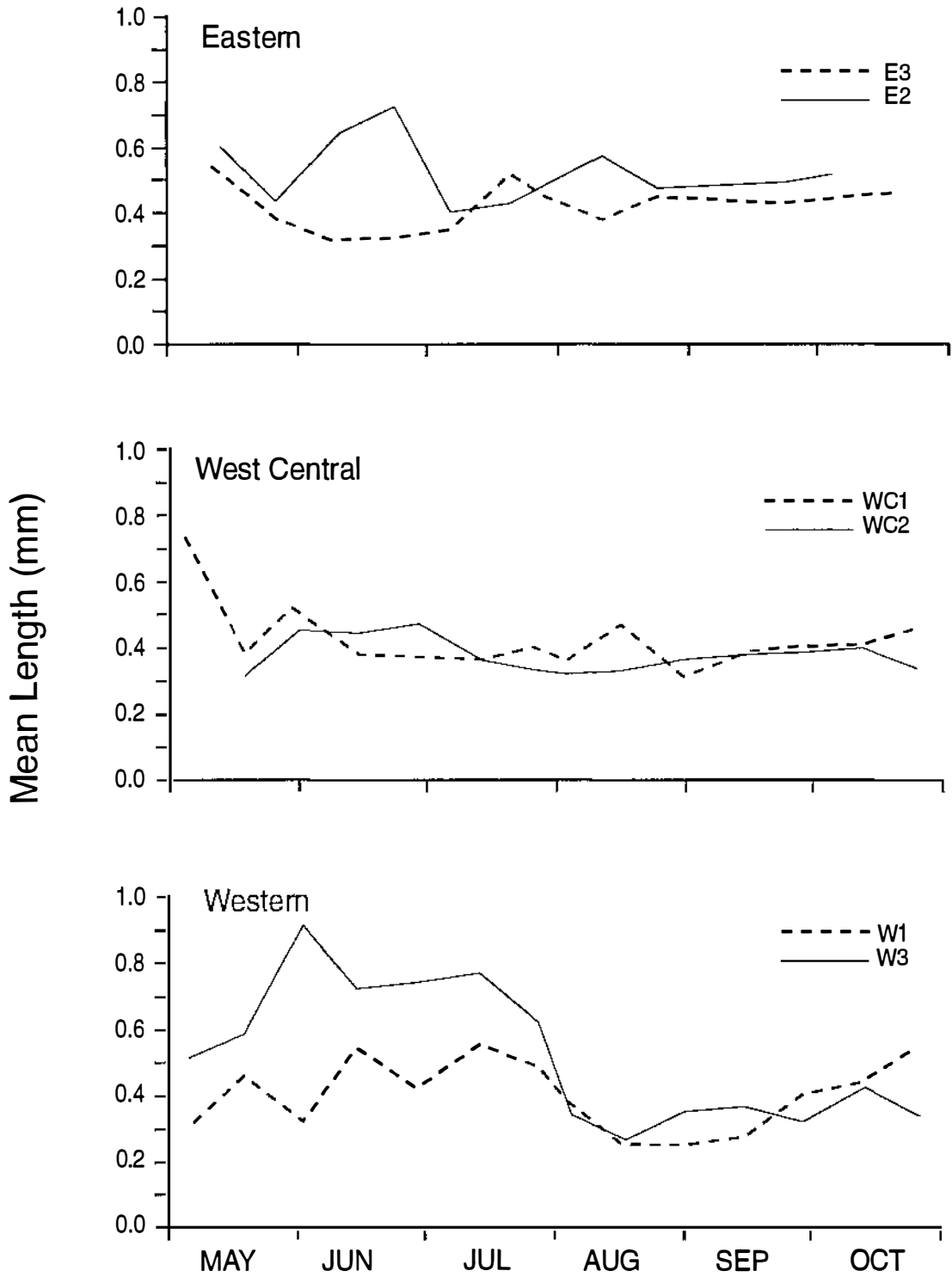
Figure 15. Seasonal (May-Oct.) community size (mm) at nearshore (broken lines) and offshore (solid line) stations in the three basins of Lake Erie, 1993.
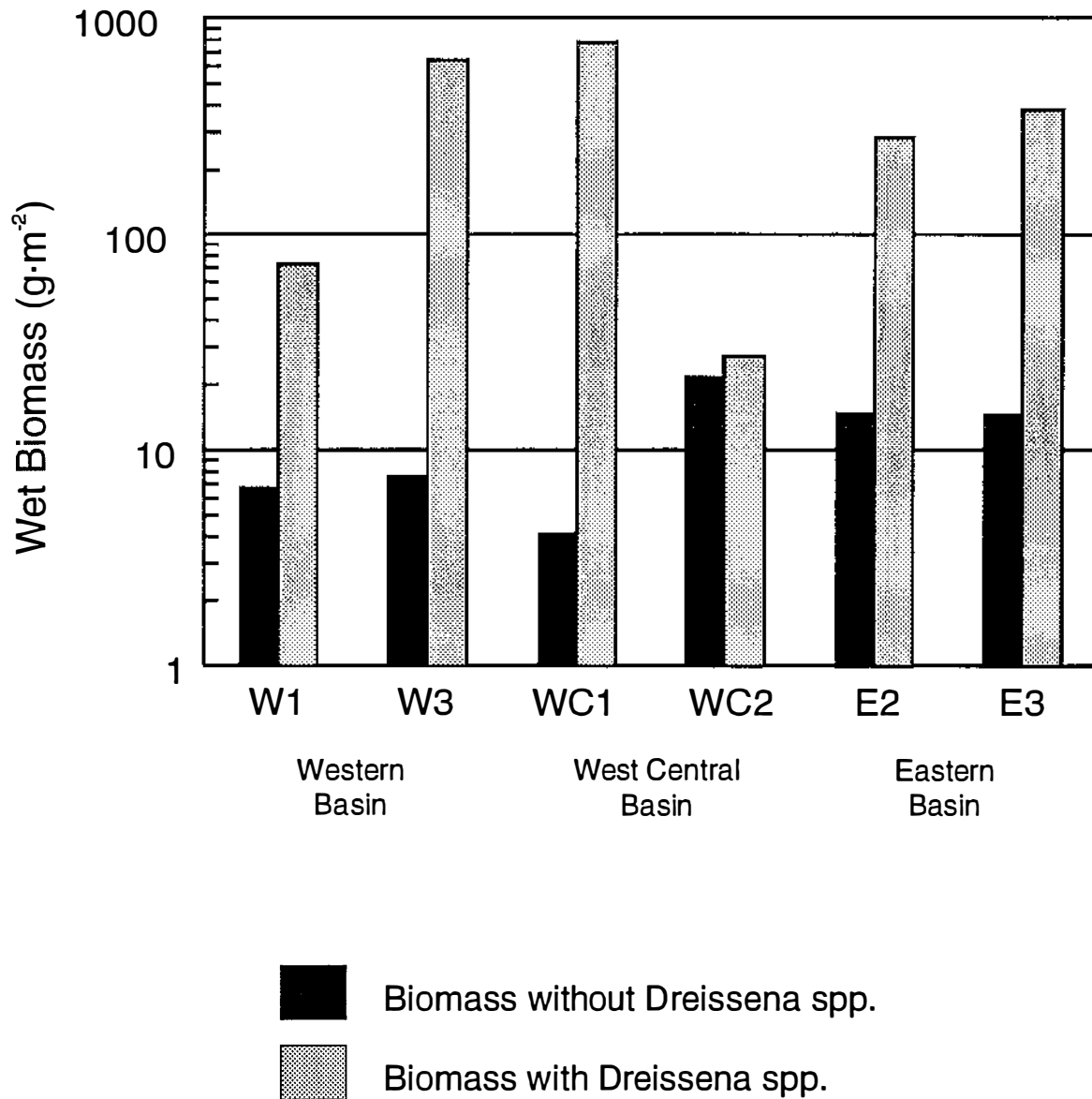
Figure 16. Mean total biomass (wet $g \cdot m^{-2}$ shell-free) of benthic fauna, with and without that of Dreissena, at a nearshore and offshore station in each basin of Lake Erie, 1993.

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Appendix 1. Mean size of the rotifer species observed in Lake Erie at the eight LEB stations in 1993. Values are the averages of the mean May-October species volumes for all stations where the species occurred. Volumes may be underestimated for some species due to contraction of some individuals upon preserving (see page 5).

Species	Average Volume (μm$^3 \cdot 10^3$)	Standard Deviation	n	Coefficient of Variation
Ascomorpha ecaudia	168	58	7	34.6
A. ovalis	243	116	8	47.6
A. saltans	120	6	2	4.8
Asplanchnia herricki	48470	12797	4	26.4
A. priodonta	22978	12903	8	56.1
Brachionus angularis	172	42	3	24.6
B. budapestinensis	84		1	
B. calyciflorus	953	305	3	32.0
B. caudatus	337		1	
Cephalodella rhomboides	10		1	
Collotheca sp.	42	18	8	43.1
Conochilus unicornis	266	98	8	36.6
Filinia longiseta	461	99	8	21.3
Gastropus stylifer	303	102	8	33.7
G. hyptopus	342		1	
Kellicottia longispina	90	9	8	10.0
Keratella cochlearis(group)	42	5	3	12.2
K. cochlearis	36	6	8	15.6
K. crassa	152	18	8	11.9
K. earlinae	76	12	8	16.2
K. hiemalis	251	73	7	29.0
K. quadrata	559	126	8	22.4
K. taurocephala	729		1	
Monostyla sp.	762		1	
Notholca acuminata	352	250	4	70.9
N. foliacea	186	78	7	42.1
N. laurentiae	409	243	8	59.3
N. squamula	318	186	4	58.3
Pleosoma hudsoni	2632	1334	6	50.6
P. truncatum	366	134	7	36.5
Polyarthra dolichoptera	190	84	8	44.0
P. euryptera	960	455	4	47.3
P. major	447	112	8	24.9
P. remata	88	7	8	8.4
P. vulgaris	234	42	8	18.0
Pompholyx sp.	40		1	

Appendix 1. Continued

Species	Average Volume ($\mu m^3 \cdot 10^3$)	Standard Deviation	n	Coefficient of Variation
Synchaeta sp.	248	132	5	53.3
Synchaeta -round	102	11	8	10.5
Synchaeta -small	39	5	8	12.3
Synchaeta -large	561	124	8	22.1
Synchaeta -long	109	44	8	40.5
Trichocerca sp.	186	40	3	21.4
T. bicristata	200		1	
T. cylindrica	1402	138	5	9.8
T. elongata	1158	948	2	81.8
T. lata	402	151	2	37.6
T. longiseta	1754		2	
T. multicrinis	840	79	7	9.4
T. porcellus	423		2	
T. pusilla	109	13	4	12.3
T. rousseleti	84	43	7	51.7
T. similis	204	36	4	17.4
Trichotria sp.	64		2	
Tylotrocha monopus	231	20	8	8.6
Wierzejskiella velox	571		1	

Note: Biomass was assumed to be 10% of wet weight except for *Asplanchna* spp. which was 4% of wet weight. Density was assumed to be 1.

Appendix 2a. Average density (ind.·m⁻²) and biomass (g·m⁻²) estimates, including standard errors, for different taxonomic groups of benthic organism at station E2 in Lake Erie on each sampling date, 1993. Biomass is given in wet, shell-free weight.

Station: E2	May 27, 1993				June 11, 1993				July 7,1993			
Species	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.
Nematoda	14813.2	1958.0	0.2227	0.0678	7399.4	882.1	0.1078	0.0456	8462.6	3036.1	0.1882	0.0660
Platyhelminth/Nemertea	905.2	179.5	0.1351	0.0797	819.0	635.0	0.0704	0.0522	359.2	337.9	0.0489	0.0405
Oligochaeta	20876.4	3023.4	12.2126	1.4090	21637.9	5401.8	9.1839	1.7557	19770.1	7178.9	14.2902	4.7227
Hirudinae	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Amphipoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Isopoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Ostracoda	5287.4	223.0	0.1279	0.0052	4425.3	1265.3	0.1049	0.0325	7643.7	3427.1	0.1911	0.0881
Harpacticoida	4655.2	1039.3	0.0374	0.0080	747.1	402.3	0.0043	0.0025	1551.7	652.7	0.0129	0.0050
Ephemeroptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Trichoptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Chironomidae	186.8	112.2	0.0244	0.0123	172.4	65.8	0.0216	0.0090	373.6	207.2	0.1250	0.0361
Gastropoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Sphaeriidae	589.0	297.0	0.0918	0.0441	129.3	74.7	0.0409	0.0329	100.7	51.7	0.0414	0.0327
D. polymorpha	57.5	28.8	0.4449	0.2226	0.0	0.0	0.0000	0.0000	86.2	65.9	0.5616	0.4486
D. bugensis	156566.1	50961.6	404.2874	85.0036	68908.0	40937.0	96.3425	48.7532	171192.5	75961.5	583.8037	283.5673
Total Benthos	203936.7	47570.7	417.5842	85.5035	104238.5	432465.1	105.8763	51.5802	209540.3	88619.8	599.2630	289.2535
% Dreissena	76.80	7.78	96.9223	0.5925	66.11	12.65	90.9954	2.1284	81.74	9.37	97.5140	6.7699

Appendix 2a. Continued. Note that for September 24, 1993 results, density and biomass standard errors are not shown because only one replicate could be used from this sampling date.

Station: E2	August 12, 1993				September 24, 1993				May 18, 1994			
Species	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomas s S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.
Nematoda	8405.2	1593.8	0.1845	0.0355	5172.4	--	0.1121	--	4881.5	611.2	0.1131	0.0177
Platyhelminth/Nemertea	344.8	86.2	0.1819	0.0307	43.1	--	0.0086	--	0.0	0.0	0.0000	0.0000
Oligochaeta	30862.1	4518.9	17.6233	2.3300	19137.9	--	14.8836	--	11508.6	3143.4	7.3621	1.6618
Hirudinae	0.0	0.0	0.0000	0.0000	43.1	--	0.0259	--	0.0	0.0	0.0000	0.0000
Amphipoda	0.0	0.0	0.0000	0.0000	0.0	--	0.0000	--	0.0	0.0	0.0000	0.0000
Isopoda	0.0	0.0	0.0000	0.0000	0.0	--	0.0000	--	0.0	0.0	0.0000	0.0000
Ostracoda	3939.7	1298.6	0.0966	0.0326	4655.2	--	0.1121	--	3146.6	1115.4	0.2231	0.0843
Harpacticoida	3181.0	1306.3	0.0353	0.0132	344.8	--	0.0129	--	1131.5	224.2	0.0259	0.0047
Ephemeroptera	0.0	0.0	0.0000	0.0000	0.0	--	0.0000	--	0.0	0.0	0.0000	0.0000
Trichoptera	0.0	0.0	0.0000	0.0000	0.0	--	0.0000	--	0.0	0.0	0.0000	0.0000
Chironomidae	206.9	68.7	0.1009	0.0409	603.4	--	0.3707	--	355.6	216.5	0.0409	0.0234
Gastropoda	8.7	8.7	0.0008	0.0008	43.0	--	0.0013	--	0.0	0.0	0.0000	0.0000
Sphaeriidae	353.3	58.3	0.3248	0.2111	301.7	--	0.0375	--	64.7	51.3	0.0123	0.0083
D. polymorpha	43.0	27.3	2.3076	1.7997	0.0	--	0.0000	--	0.0	0.0	0.0000	0.0000
D. bugensis	95215.6	40591.3	272.443	145.0531	50344.9	--	146.7803	--	7844.9	2231.7	80.3711	27.1055
Total Benthos	142560.3	47145.6	293.2987	150.2022	80689.5	--	196.8936	--	28933.2	3699.1	88.1485	28.8174
% Dreissena	66.82	11.22	93.6761	2.1844	62.39	--	74.55	--	27.11	9.67	91.18	3.27

Appendix 2b. Average density (ind.·m^{-2}) and biomass (g·m^{-2}) estimates, including standard errors, for different taxonomic groups of benthic organisms at station E3 in Lake Erie on each sampling date, 1993. Biomass is given in wet, shell-free weight.

Station: E3	May 12, 1993				June 9, 1993				July 7, 1993				August 12, 1993			
Species	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.
Nematoda	9712.6	1101.8	0.0474	0.0132	16196.1	4021.7	0.1498	0.0214	12801.7	466.2	0.2960	0.0152	8146.6	4643.1	0.1886	0.1111
Platyhelminth/Nemertea	316.1	165.7	0.1810	0.1430	194.0	67.0	0.1616	0.0692	445.4	71.8	0.6825	0.1745	237.1	54.2	0.3685	0.1424
Oligochaeta	2988.5	1002.0	4.5359	1.4290	2855.6	528.3	3.4084	0.7413	3347.7	605.7	3.6652	1.4484	1810.3	457.5	3.3319	1.1942
Hirudinae	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Amphipoda	287.4	245.5	2.4095	1.7799	129.3	76.7	1.4946	0.9469	660.9	446.1	4.3118	3.3607	495.7	212.3	1.5453	1.0299
Isopoda	0.0	0.0	0.0000	0.0000	722.0	722.0	0.2080	0.2080	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Ostracoda	761.5	400.0	0.0187	0.0104	1368.5	520.3	0.0334	0.0127	5301.7	1330.2	0.1351	0.0329	4019.4	1567.5	0.0948	0.0395
Harpacticoida	6034.5	867.8	0.0489	0.0080	10937.5	2324.4	0.0657	0.0132	34238.5	3239.4	0.2328	0.0198	42435.3	11135.7	0.3524	0.1009
Ephemeroptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	64.7	41.3	0.0065	0.0041
Trichoptera	86.2	43.1	2.6997	1.4203	75.4	27.1	1.7856	0.9347	0.0	0.0	0.0000	0.0000	495.7	154.9	0.0884	0.0276
Chironomidae	3994.3	1982.5	2.8491	0.5189	1842.7	508.9	2.7220	0.6030	3189.7	24.9	0.4626	0.1303	3836.2	715.7	1.6853	0.3000
Gastropoda	646.7	273.7	1.8440	0.8946	388.0	176.0	1.5097	0.9526	2385.0	1020.0	1.8409	0.3611	4094.7	694.7	2.1158	0.6579
Sphaeriidae	115.0	62.7	0.0616	0.0535	10.7	10.7	0.0048	0.0048	28.7	14.3	0.0129	0.0066	258.7	176.0	0.0634	0.0359
D. polymorpha	2974.1	1489.6	195.3603	97.7042	722.0	386.1	24.9737	14.4408	5502.9	2650.4	383.0239	205.7581	2629.3	1700.9	146.5951	102.0358
D. bugensis	19123.6	10149.3	200.3221	97.3720	5107.7	2260.6	84.3024	31.5326	35244.2	24286.6	585.1957	336.1885	114019.3	13910.3	308.0386	146.5507
Total Benthos	47040.4	15209.9	410.3782	200.8852	40549.5	4943.5	120.8198	45.4673	103146.4	27314.2	979.8594	544.4660	182543.0	19875.8	464.4745	249.9775
% Dreissena	46.98	17.05	96.42	12.00	14.38	6.22	90.45	5.81	39.50	17.01	98.81	4.61	63.90	6.16	97.88	1.20

Appendix 2b. Continued.

Station: E3	September 24, 1993				October 20, 1993				May 18, 1994			
Species	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.
Nematoda	9367.8	2650.6	0.2126	0.0673	6314.7	1684.7	0.1121	0.0297	7489.2	1242.3	0.1907	0.0205
Platyhelminth/Nemertea	689.7	262.2	0.4756	0.2498	377.2	47.8	0.3330	0.1389	506.5	170.9	0.5453	0.1715
Oligochaeta	5689.7	1582.5	3.0517	0.8195	3976.3	1101.2	3.0668	0.4701	2650.9	215.2	6.2845	1.7386
Hirudinae	28.7	14.4	0.1997	0.1121	53.9	27.1	0.4332	0.3164	0.0	0.0	0.0000	0.0000
Amphipoda	1695.4	794.9	2.1264	1.0363	2316.8	1379.0	4.8675	3.0287	1540.9	343.2	8.2575	2.8671
Isopoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Ostracoda	1551.7	24.9	0.0374	0.0038	1357.8	676.6	0.0323	0.0154	614.2	317.9	0.0345	0.0180
Harpacticoida	40071.8	17543.9	0.3233	0.1046	11573.3	5898.6	0.1099	0.0620	4784.5	1170.2	0.1067	0.0261
Ephemeroptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Trichoptera	287.4	141.5	1.2055	0.8212	183.2	66.7	1.7317	0.7306	301.7	102.6	4.1746	2.0501
Chironomidae	4554.6	1575.6	4.2277	1.9553	2252.2	590.6	2.8103	0.4398	1875.0	280.2	3.8147	1.1749
Gastropoda	1207.0	554.3	0.9763	0.4301	2360.0	692.0	1.4334	0.4276	2801.7	931.3	1.6419	0.3643
Sphaeriidae	86.3	66.0	0.0069	0.0051	194.0	166.3	0.0679	0.0531	64.7	41.3	0.0550	0.0378
D. polymorpha	617.9	268.4	25.2137	17.5795	603.4	146.3	26.9820	8.1182	290.9	193.9	5.5252	4.8993
D. bugensis	141896.6	54792.8	165.1805	102.3050	91433.2	17417.6	114.2362	32.2291	81056.0	21694.7	266.7338	88.3254
Total Benthos	207744.5	712705.4	203.2373	125.1417	122995.8	27051.7	156.2162	43.2616	103976.2	22789.7	297.3643	97.1443
% Dreissena	68.60	9.39	93.68	1.70	74.83	4.17	90.40	1.76	78.24	6.01	91.56	2.30

Appendix 2c. Average density (ind.·m^{-2}) and biomass (g·m^{-2}) estimates, including standard errors, for different taxonomic groups of benthic organisms at station WC1 in Lake Erie on each sampling date, 1993. Biomass is given in wet, shell-free weight.

Station: WC1	May 20, 1993				June 16, 1993				July 15, 1993				August 17, 1993			
Species	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.
Nematoda	129.3	43.1	0.0043	0.0000	2834.1	884.1	0.0690	0.0407	1185.3	758.6	0.0259	0.0160	765.1	135.6	0.0431	0.0231
Platyhelminth/Nemertea	0.0	0.0	0.0000	0.0000	474.1	141.9	0.2037	0.0796	226.3	185.7	0.0075	0.0062	3017.2	1461.7	0.1282	0.0585
Oligochaeta	2047.4	1357.8	0.2047	0.1616	14278.0	5181.1	2.3804	1.0491	10075.4	6409.0	2.2608	1.3860	15323.3	3197.0	3.4720	0.3732
Hirudinae	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Amphipoda	0.0	0.0	0.0000	0.0000	247.8	121.1	0.7489	0.4130	0.0	0.0	0.0000	0.0000	21.6	12.4	0.0334	0.0320
Isopoda	21.6	21.6	0.0474	0.0474	1368.5	579.5	0.4159	0.2853	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Ostracoda	64.7	64.7	0.0022	0.0022	5592.7	1904.3	0.1401	0.0483	4525.9	1692.7	0.1153	0.0442	12090.5	5061.2	0.4019	0.1792
Harpacticoida	64.7	21.6	0.0043	0.0000	1400.9	1057.8	0.0140	0.0083	398.7	130.9	0.0043	0.0000	1034.5	473.5	0.0075	0.0032
Ephemeroptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Trichoptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Chironomidae	43.1	43.1	0.1573	0.1573	1637.9	68.2	0.3847	0.2185	2780.2	956.3	4.2155	1.7263	1918.1	254.1	5.0334	1.0534
Gastropoda	21.7	21.7	0.0084	0.0084	592.7	325.7	0.3983	0.1866	291.0	56.7	0.2305	0.1324	1282.3	612.7	0.9866	0.2122
Sphaeriidae	0.0	0.0	0.0000	0.0000	10.7	10.7	0.0052	0.0052	43.0	30.3	0.0094	0.0077	107.7	41.3	0.0362	0.0170
D. polymorpha	1939.6	1853.4	32.6598	30.1447	6637.9	4717.7	1109.6955	497.0318	1314.6	518.0	669.6381	424.1630	754.3	90.5	495.8106	205.6496
D. bugensis	17306.0	16142.3	205.0658	123.2832	7909.4	7554.1	49.0749	45.1543	32446.1	21511.6	578.1185	314.3319	18340.6	6275.2	1218.5147	420.6250
Total Benthos	21638.0	16508.7	238.1543	91.1983	42984.8	12591.4	1163.5305	536.2152	53286.6	29616.8	1254.6258	740.9541	54655.2	4254.7	1724.4678	574.9774
% Dreissena	88.94	36.63	99.82	0.14	33.84	11.13	99.59	0.32	63.36	17.01	99.45	11.75	34.94	11.26	99.41	24.06

Appendix 2c. Continued.

Station: WC1	September 16, 1993				October 10, 1993				May 20, 1994			
Species	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.
Nematoda	161.6	93.7	0.0032	0.0021	459.8	201.1	0.0086	0.0043	97.0	83.2	0.0032	0.0021
Platyhelminth/Nemertea	10.8	10.8	0.0011	0.0011	0.0	0.0	0.0000	0.0000	129.3	115.4	0.0075	0.0062
Oligochaeta	2047.4	1169.4	0.7004	0.3902	2816.1	540.8	1.5086	0.3556	1303.9	1050.7	1.0172	0.8438
Hirudinae	32.3	20.6	0.0442	0.0414	14.4	14.4	0.0259	0.0259	0.0	0.0	0.0000	0.0000
Amphipoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Isopoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Ostracoda	797.4	522.2	0.0205	0.0133	1264.4	165.7	0.0330	0.0038	484.9	427.6	0.0226	0.0183
Harpacticoida	301.7	187.9	0.0022	0.0012	431.0	24.9	0.0043	0.0000	10.8	10.8	0.0011	0.0011
Ephemeroptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Trichoptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Chironomidae	53.9	20.6	0.0733	0.0279	129.3	43.1	0.2443	0.1918	64.7	41.3	0.0086	0.0053
Gastropoda	32.3	20.7	0.1093	0.0634	57.3	28.7	0.2280	0.1253	32.3	10.7	0.0763	0.0733
Sphaeriidae	10.7	10.7	0.0010	0.0010	28.7	14.3	0.0052	0.0034	0.0	0.0	0.0000	0.0000
D. polymorpha	86.2	30.5	40.6501	20.5053	0.0	0.0	0.0000	0.0000	86.2	39.3	84.9577	49.1903
D. bugensis	829.8	530.3	96.9547	71.4005	43.2	43.2	9.5420	9.5420	3221.9	716.1	758.1566	307.5163
Total Benthos	4364.1	1750.5	138.5598	89.7704	5244.2	635.8	11.5999	10.0468	5431.0	2228.4	844.2509	350.1830
% Dreissena	20.99	24.80	99.31	1.66	0.82	0.77	82.26	30.10	60.91	12.59	99.87	0.02

Appendix 2d. Average density (ind.·m⁻²) and biomass (g·m⁻²) estimates, including standard errors, for different taxonomic groups of benthic organisms at station WC2 in Lake Erie on each sampling date, 1993. Biomass is given in wet, shell-free weight.

Station: WC2	May 20, 1993				June 16, 1993				July 15, 1993				August 17, 1993			
Species	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.
Nematoda	3764.4	859.3	0.0805	0.0193	5718.4	1317.4	0.1710	0.0687	5387.9	1187.0	0.2284	0.0782	1738.5	869.3	0.0374	0.0187
Platyhelminth/Nemertea	14.4	14.4	0.0057	0.0057	57.5	57.5	0.0187	0.0187	775.9	172.4	0.3908	0.0687	201.1	112.2	0.1106	0.0623
Oligochaeta	10057.5	655.7	4.1193	0.2471	12658.0	1050.0	6.4799	0.2510	13232.8	623.6	9.1724	1.9037	6321.8	3182.9	3.6710	1.8361
Hirudinae	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	43.1	24.9	0.1523	0.1354	0.0	0.0	0.0000	0.0000
Amphipoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Isopoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Ostracoda	2399.4	354.0	0.0402	0.0094	6092.0	552.2	0.1566	0.0128	5747.1	2342.1	0.1451	0.0586	2342.0	1174.2	0.0603	0.0303
Harpacticoida	5402.3	1194.9	0.0431	0.0108	6997.1	562.2	0.1394	0.0812	6436.8	3415.6	0.0532	0.0291	3290.2	1645.2	0.0560	0.0367
Ephemeroptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Trichoptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Chironomidae	1020.1	250.5	10.2543	1.7040	1106.3	127.7	17.4612	4.7617	1465.5	879.5	11.7399	4.0219	1048.9	575.3	4.4856	2.5215
Gastropoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Sphaeriidae	3477.0	311.0	0.9750	0.0480	3419.7	137.0	1.4401	0.3426	3218.3	438.3	1.7341	0.8254	1163.7	588.3	1.3034	0.9989
D. polymorpha	100.5	51.8	0.0072	0.0042	43.0	24.8	0.0040	0.0021	71.8	51.8	0.0064	0.0032	57.5	38.0	0.0241	0.0174
D. bugensis	244.2	223.1	0.0512	0.0415	129.3	49.8	0.0512	0.0424	445.4	217.5	0.9305	0.3194	86.1	49.8	0.7199	0.7149
Total Benthos	26479.8	1510.3	15.5765	1.3583	36221.3	2266.0	25.9220	4.0659	36824.6	7569.3	24.5532	7.3334	16249.9	1185.4	10.4685	3.2778
% Dreissena	1.30	0.65	0.3751	0.2936	0.48	0.0	0.2130	0.1515	1.40	0.47	3.8161	0.9882	0.88	0.35	7.1077	8.7846

Appendix 2d. Continued.

Station: WC2	September 17, 1993				October 13, 1993				May 20, 1994			
Species	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.
Nematoda	3965.5	597.3	0.0862	0.0124	4166.7	722.3	0.0905	0.0151	5872.8	897.9	0.2091	0.0425
Platyhelminth/Nemertea	28.7	28.7	0.0029	0.0029	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Oligochaeta	17126.4	2592.1	9.4138	0.5832	12931.0	2229.7	10.6839	1.5733	3933.2	705.3	2.9860	0.6973
Hirudinae	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Amphipoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	32.3	20.6	0.0162	0.0103
Isopoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Ostracoda	8146.6	883.7	0.1437	0.0671	5833.3	1768.4	0.2141	0.1087	2079.7	752.4	0.1422	0.0403
Harpacticoida	5718.4	1008.2	0.0474	0.0090	6494.3	1966.7	0.0532	0.0177	4353.4	1281.3	0.0981	0.0296
Ephemeroptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Trichoptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Chironomidae	2040.2	190.1	12.6624	1.9041	1106.3	174.8	14.2572	2.0287	592.7	53.9	15.3190	1.1975
Gastropoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Sphaeriidae	1508.7	431.7	0.7444	0.2570	2083.3	315.0	0.9569	0.3783	2532.3	510.7	1.2899	0.2473
D. polymorpha	86.2	49.8	0.0233	0.0117	129.3	24.8	0.2140	0.0167	129.3	76.8	1.5587	0.7409
D. bugensis	114.9	51.9	1.5213	0.4817	244.2	14.4	4.6326	0.6213	140.1	36.8	28.1239	10.0337
Total Benthos	38735.7	3859.5	24.6453	1.8591	32988.5	6675.9	31.1023	1.5081	19665.9	3732.3	49.7429	12.5035
% Dreissena	0.52	0.30	6.27	2.54	1.13	0.13	15.58	1.50	1.37	0.58	59.67	9.62

Appendix 2e. Average density (ind.·m⁻²) and biomass (g·m⁻²) estimates, including standard errors, for different taxonomic groups of benthic organisms at station W1 in Lake Erie on each sampling date, 1993. Biomass is given in wet, shell-free weight.

Station: W1	May 19, 1993				June 15, 1993				July 14, 1993				August 17, 1993			
Species	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.
Nematoda	1551.7	187.9	0.0216	0.0090	2974.1	472.8	0.0805	0.0128	862.1	273.7	0.0244	0.0052	2356.3	939.2	0.0517	0.0217
Platyhelminth/Nemertea	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Oligochaeta	8304.6	1444.5	4.1207	2.2890	3879.3	1246.5	1.8290	0.6620	3189.7	837.3	1.3434	0.1309	8017.2	3465.8	3.5848	1.9924
Hirudinae	0.0	0.0	0.0000	0.0000	387.9	345.7	0.2069	0.1077	57.5	14.4	0.0474	0.0132	14.4	14.4	0.0445	0.0445
Amphipoda	14.4	14.4	0.1810	0.1810	114.9	57.5	0.0675	0.0338	28.7	28.7	0.0647	0.0647	14.4	14.4	0.0345	0.0345
Isopoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Ostracoda	14712.6	3006.0	0.3247	0.0689	8735.6	5805.5	0.2011	0.1237	15043.1	2527.7	0.4842	0.1614	12413.8	3017.6	0.2917	0.1673
Harpacticoida	33807.5	11612.4	0.3261	0.0921	22557.5	5042.4	0.1523	0.0386	13534.5	2343.5	0.1006	0.0144	32413.8	2417.4	0.2428	0.0087
Ephemeroptera	14.4	14.4	0.0201	0.0201	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Trichoptera	86.2	49.8	0.2184	0.1146	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Chironomidae	2183.9	76.0	3.2399	0.6273	833.3	307.1	0.5761	0.2232	1494.3	225.8	5.6408	0.5982	589.1	125.3	0.6149	0.0870
Gastropoda	0.0	0.0	0.0000	0.0000	14.3	14.3	0.0470	0.0470	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Sphaeriidae	1005.7	162.0	0.4315	0.1161	28.7	14.3	0.0267	0.0212	229.7	165.7	0.1612	0.1147	215.7	89.7	0.2207	0.1815
D. polymorpha	215.5	99.5	0.0740	0.0668	459.8	315.2	2.0952	1.6103	43.0	24.8	0.0660	0.0333	14842.0	14734.3	451.2900	448.8108
D. bugensis	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Total Benthos	61896.5	12618.5	8.9581	2.0957	39985.6	9362.5	5.2824	1.8053	34482.6	2482.3	7.9326	0.6830	70876.5	17419.4	456.3756	451.7180
% *Dreissena*	0.35	0.15	0.83	1.09	1.15	1.04	39.66	17.69	0.12	0.07	0.83	0.38	20.94	14.14	98.89	28.41

Appendix 2e. continued.

Station: W1	September 15, 1993				October 13, 1993				May 18,1994			
Species	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.
Nematoda	273.0	152.1	0.0129	0.0050	689.7	194.4	0.0201	0.0014	3049.6	342.7	0.2392	0.1761
Platyhelminth/Nemertea	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	10.8	10.8	0.0097	0.0097
Oligochaeta	4640.8	1802.2	9.3549	3.8588	2155.2	342.1	4.3348	0.7433	7489.2	1732.3	3.4494	0.4634
Hirudinae	14.4	14.4	0.0618	0.0618	14.4	14.4	0.0675	0.0675	21.6	12.4	0.2274	0.1331
Amphipoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Isopoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Ostracoda	15775.9	1943.6	0.3750	0.0293	7787.4	2481.6	0.1983	0.0624	3254.3	1621.6	0.1282	0.0657
Harpacticoida	36034.5	11624.0	0.2902	0.1142	15890.8	5854.1	0.1724	0.0862	11778.0	955.3	0.2716	0.0222
Ephemeroptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	10.8	10.8	0.0420	0.0420
Trichoptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Chironomidae	316.1	112.2	0.2011	0.0787	129.3	24.9	0.0790	0.0361	668.1	41.3	1.0593	0.1877
Gastropoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	10.7	10.7	0.0533	0.0533
Sphaeriidae	617.7	174.7	0.1522	0.0292	431.0	114.0	0.1461	0.0522	269.3	114.7	0.1788	0.1032
D. polymorpha	0.0	0.0	0.0000	0.0000	14.3	14.3	0.0716	0.0716	10.7	10.7	0.0024	0.0024
D. bugensis	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Total Benthos	57672.3	11407.7	10.4481	3.7143	27112.0	6523.7	5.0899	0.9596	26573.1	2992.2	5.66125	0.7667
% Dreissena	0.0	--	0.0	--	0.05	0.04	1.42	1.13	0.04	0.04	0.04	0.05

Appendix 2f. Average density (ind.·m^{-2}) and biomass (g·m^{-2}) estimates, including standard errors, for different taxonomic groups of benthic organisms at station W3 in Lake Erie on each sampling date, 1993. Biomass is given in wet, shell-free weight.

Station: W3	May 19, 1993				July 14, 1993				August 18, 1993			
Species	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.
Nematoda	5977.0	3220.8	0.1408	0.0784	1537.4	636.6	0.0330	0.0137	2758.6	197.5	0.0603	0.0043
Platyhelminth/Nemertea	143.7	38.0	0.1106	0.0768	273.0	273.0	0.2701	0.2701	0.0	0.0	0.0000	0.0000
Oligochaeta	9827.6	2762.1	4.0690	1.9743	7701.1	4929.4	6.1078	0.2037	7083.3	808.1	5.6624	3.0908
Hirudinae	114.9	14.4	0.5647	0.1549	373.6	309.2	0.3750	0.3041	258.6	108.5	0.6307	0.2906
Amphipoda	100.6	80.0	0.5000	0.4765	301.7	258.6	0.7241	0.5543	28.7	14.4	0.0029	0.0014
Isopoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Ostracoda	2471.3	837.4	0.0330	0.0190	2600.6	771.2	0.0489	0.0283	2586.2	610.1	0.0661	0.0162
Harpacticoida	6364.9	1651.5	0.0330	0.0190	11609.2	1223.5	0.1193	0.0357	16336.2	3138.3	0.1236	0.0200
Ephemeroptera	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Trichoptera	28.7	14.4	0.1049	0.0943	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Chironomidae	560.3	131.7	0.6092	0.1299	273.0	76.0	0.1279	0.0647	589.1	114.9	0.2414	0.0269
Gastropoda	100.7	38.0	0.5711	0.1733	186.7	100.7	0.0353	0.0257	158.0	28.7	0.2052	0.0743
Sphaeriidae	373.7	373.7	0.3466	0.3466	359.3	201.0	0.0888	0.0804	201.0	51.7	0.2034	0.0778
D. polymorpha	36221.3	34548.2	1009.5851	1001.7772	35632.1	35073.0	689.8106	686.1653	1551.8	825.7	2.9159	0.9748
D. bugensis	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Total Benthos	62284.6	38344.9	1016.6680	1005.6193	60847.7	42009.0	697.7407	690.3757	31551.6	4676.2	10.1118	3.1295
% Dreissena	58.15	23.21	99.30	12.60	58.56	23.15	98.86	28.92	4.92	2.37	28.84	7.83

Appendix 2f. continued.

Station: W3	September 15, 1993				October 14, 1993			
Species	Average Density	Density S.E.	Average Biomass	Biomass S.E.	Average Density	Density S.E.	Average Biomass	Biomass S.E.
Nematoda	3534.5	903.1	0.0905	0.0269	3649.4	821.4	0.0805	0.0193
Platyhelminth/Nemertea	0.0	0.0	0.0000	0.0000	387.9	366.6	0.5546	0.5332
Oligochaeta	11408.0	4229.6	2.7486	1.4501	4612.1	1132.5	1.7514	0.7802
Hirudinae	172.4	49.8	1.2443	0.8413	316.1	80.0	0.9440	0.2095
Amphipoda	201.1	180.0	0.1853	0.1832	991.4	991.4	3.2126	3.2126
Isopoda	0.0	0.0	0.0000	0.0000	0.0	0.0	0.0000	0.0000
Ostracoda	5330.5	710.2	0.1351	0.0187	3721.3	1081.7	0.0963	0.0275
Harpacticoida	16192.5	5145.8	0.1236	0.0316	16781.6	3686.7	0.1451	0.0429
Ephemeroptera	0.0	0.0	0.0000	0.0000	14.4	14.4	0.0014	0.0014
Trichoptera	43.1	43.1	0.0675	0.0675	28.7	28.7	0.0201	0.0201
Chironomidae	1020.1	362.6	0.2500	0.0149	603.4	269.2	0.2658	0.1381
Gastropoda	503.0	309.0	1.5707	1.1977	574.7	190.0	0.8953	0.3278
Sphaeriidae	244.3	150.0	0.0362	0.0181	158.0	14.3	0.0655	0.0218
D. polymorpha	27313.2	25830.2	120.6486	120.3940	57356.2	53877.0	1297.5409	1293.1042
D. bugensis	14.4	14.4	0.0042	0.0042	14.4	14.4	0.0008	0.0008
Total Benthos	65977.2	34905.3	127.1045	124.7292	89209.7	50145.7	1305.5743	1298.4057
% Dreissena	41.42	17.85	94.92	28.59	64.31	26.86	99.38	25.87