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The seasonality of phytoplankton in the North American Great Lakes, a comparative synthesis

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Abstract

The phytoplankton and productivity of the North American Great Lakes has been studied extensively by Fisheries and Oceans Canada during the past 15 years to monitor the impact of nutrient and contaminant loading on the plankton of the ecosystem. Lakewide cruises were conducted at monthly intervals mainly during the spring to fall period. This provided extensive biomass, species, size, productivity and nutrient concentration data for the Great Lakes. These data were collected using the Utermöhl inverted microscope technique together with standardized taxonomic, productivity and data-handling procedures. These standardized methodologies were applied to all the Great Lakes which resulted in a comprehensive phycological and ecological data base for the first time. These data form the basis for the evaluation of the complex phenomenon of seasonality.

The eutrophic/mesotrophic Lower Great Lakes exhibited well-developed seasonal peaks of high biomass, with inshore-offshore differentiation and spring maxima most pronounced in the inshore region. However, the oligotrophic Upper Great Lakes had low biomass and generally lacked well-developed seasonal patterns. No marked seasonal trends were observed in the ultra-oligotrophic Lake Superior. The seasonality of biomass and various taxonomic groups of phytoplankton showed differentiation between individual lakes and is discussed in detail. The seasonal succession of species provided interesting comparisons between the Lower Great Lakes, which harbour eutrophic and mesotrophic species, and the Upper Great Lakes, which harbour oligotrophic species.

Due to the voluminous nature of our data, a general overview has been given for all the Great Lakes with Lake Ontario treated in detail as a case study. The Lake Ontario case study provides the state-of-the-art status ranging from the lakewide surveys of 1970 to the current research with minute organisms such as ultraplankton and picoplankton.

Introduction

The North American Great Lakes are the largest freshwater body in the world and have been called 'inland seas'. These lakes are amongst the 50 largest and deepest lakes (Table 1) of the world (Herdendorf, 1982). Since considerable industrial and urban development is concentrated along their basins, these lakes play a key role in the economics of both Canada and the United States. Consequently, an international Water Quality Agreement has been signed by both countries and an International Joint Commission established for the protection of the Great Lakes from nutrient and contaminant enrichment.

Phycological records in the Great Lakes date back to the end of the last century. However, this large data base cannot be used with that of current studies for the evaluation of a relationship between long-term changes of phytoplankton assemblages and water quality conditions. This is mainly attributable to the diversity of the procedures used

Table 1. Geographical and morphometric characteristics of the North American Great Lakes.

	Superior	Michigan	Huron	Erie	Ontario
Latitude	47°35′N	44°00′N	45°00′N	43°39′N	43°39′N
Longitude	87°46′W	87°00′W	81°15′W	81°15′W	77°47′W
Geologic origin	glacial scour & tectonic	glacial	glacial	glacial	glacial
Lake area (km²)	82100	57750	59500	25657	19000
Drainage basin (km²)	127700	118100	133900	58800	70000
Elevation (m)	183	177	177	174	75
Mean depth (m)	149	85	59	19	86
Maximum depth (m)	407	282	229	64	245
Volume (km²)	12230	4920	3537	483	1637

for the enumeration and identification of phytoplankton, a shortage of experienced personnel and a lack of standardization in data processing and reporting procedures. Therefore, although extensive phycological work is being currently carried out in the Great Lakes, little effort is being made today to standardize the phycological methodology to ensure good data quality and comparability.

To fill in the gaps and to maintain continuity, the Department of Fisheries and Oceans Canada initiated extensive phycological work in 1969. Since then, it has collected considerable phytoplankton data from all the Great Lakes following the application of the standard inverted microscope technique (Utermöhl, 1958) which is used internationally in fresh and marine waters. Although time-consuming, it is the best procedure and is widely used for quantitative estimation of the total phytoplankton size spectrum covering nannoplankton, picoplankton and netplankton (Munawar & Munawar, 1980; Reid, 1983). We have also rigorously applied data processing procedures which have been standardized in our own laboratory for analyses of all data collected (Munawar & Nauwerck, 1971; Munawar *et al.*, 1974; Munawar & Munawar, 1976). This has resulted in a voluminous lakewide data base which includes many phytoflagellates (Cryptophyceae, Chrysophyceae and Dinophyceae), nannoplankton (<64 μm), ultraplankton (2–20 μm) and picoplankton (<2 μm) size fractions which have not been reported by other investigators. The standardization of techniques and procedures generated consistency and permitted comparability which eventually encouraged the authors to prepare this comparative paper on seasonality of phytoplankton in the North American Great Lakes.

Due to shortage of space, a detailed treatment of all the Great Lakes (Fig. 1) consisting of eight ecosystems is not included. Instead, the paper has been divided into four sections to present a general overview. These areas include the seasonal sequences of biomass, its taxonomic and size composition, species succession and a case study representing a eutrophic-mesotrophic environment (Lake Ontario).

Methods and materials

The lakewide surveys were carried out in various years as part of the Canadian program in the St. Lawrence-Great Lakes system. The sampling pattern is shown in Fig. 1. The mode and period of sampling are given below.

Lake Ontario. Samples were collected from January to December (1970) at 27–30 stations using a Van Dorn bottle at 1 and 5 m and mixed. The 1972 samples were collected at a nearshore station

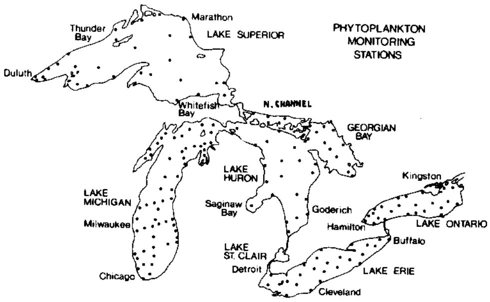

Fig. 1. Distribution of sampling stations in the North American Great Lakes.

(60 m) and an offshore station (180 m) by means of a 10 m integrating sampler (Schroeder, 1969). Samples were collected on two consecutive days during nine cruises extending from April 1972 to March 1973. Microscopic data collected for two consecutive days was averaged for each cruise.

Lake Erie. Samples were collected from April to December (1970) at 25 stations using a Van Dorn bottle at one and five meters and mixed.

Lake Huron. Samples were collected from April to December (1971) at 22 stations by a 20 m integrating sampler.

Lake Superior. Samples were collected from May to October (1973) at 34 stations by a 20 m integrating sampler.

Georgian Bay. Samples were collected from May to October (1974) at 16 stations by a 20 m integrating sampler.

North Channel. Samples were collected from May to October (1974) at 8 stations by a 20 m integrating sampler.

Lake Michigan. Samples were collected at 56 stations in the spring (May) and summer (July and September) of 1982 by a 20 m integrating sampler.

All samples were preserved with modified Lugol's solution. When needed samples were also kept alive prior to preservation to facilitate taxonomic identification of motile forms. The chemical analysis of nutrients was done according to Water Quality Branch, Inland Waters Directorate (1979).

The analyses of the living samples and enumeration of the preserved samples were carried out utilizing an inverted microscope. Depending on the density of the organisms, convenient aliquots (25–100 ml) were sedimented in settling chambers which were then examined with the inverted microscope (Wild model M40). Most of the identifications were made using magnifications of 300, 600, and 1500× with phase contrast illumination. The enumeration procedure followed is described in Munawar & Nauwerck (1971), Munawar *et al.* (1974) and Munawar & Munawar (1978). In all the samples, 200–300 units were usually counted to achieve an acceptable counting efficiency in proportion to the time spent in counting (Lund *et al.*, 1958). The diatoms were cleared by heating in a drop or two of hydrogen peroxide over a Bunsen flame and mounted in Hyrax medium. Identification was then carried out on permanent slides.

Cell volume of each species was computed by using average dimensions and simulating by geometrical shapes most closely resembling the species, such as spheres, cylinders, prolate spheroids, etc. (Vollenweider, 1969). In the case of colonial forms, the average number of cells per colony was determined. These were then multiplied by the volume per cell to give volume per colony. The cell volume was then converted to biomass (as fresh weight) assuming a specific gravity of 1.0 g cm^{-3}.

Based on microscopic measurements, the phytoplankton were classified into different size fractions (<5 μm, 5–10 μm, 10–20 μm, 20–40 μm, 40–64 μm>64 μm) with the help of a computer. The average measure of the longest dimensions has been used as a size criterion (Willen, 1959; Kalff, 1967). At least 30 organisms of each common species were measured to calculate the mean dimensions of a particular species. However, it was not practical to measure that number of organisms for the 'less common' or rare species. Hence, the mean dimensions of such species depended on the limited number of organisms examined, which varied from species to species. Extra care was taken in measuring minute organisms. Such forms were measured at 1500× magnification using oil-immersion objectives. The procedure followed was a standard one adopted by several researchers (Nauwerck, 1963; Pavoni, 1963; Kalff, 1972), and although it was not without errors, it was the only method which could be used to determine the individual contribution of species of various size fractions to the total biomass (Kristiansen, 1971).

Primary production experiments (Vollenweider *et al.*, 1974) and their subsequent fractionations were undertaken to determine the relative photosynthetic rates of different size fractions of algae (Munawar *et al.*, 1978). For this purpose, the samples were subdivided into light bottles and dark bottles. Each bottle was inoculated with approximately 2 μCi of $Na_2{}^{14}CO_3$ and the light bottles were incubated for 4 hours in the same light box (40.1×10^{11} ergs m^{-2} h^{-1}) described by Stadelmann & Moore (1974). Watson *et al.* (1975) reported that the incubator light intensity approximated I_k values in Lake Ontario and the incubator values of photosynthetic-rate (P) were in agreement with light-saturated P_{max} values from moorings *in situ* in Lake Superior. After incubation, the first set of light bottles and a dark bottle were filtered through a 0.45 μm pore size membrane filter to determine total or unfractionated primary productivity. The fractionation experiment was conducted by filtering a second set of light bottles and a dark bottle through a 2 μm membrane filter and collecting the phytoplankton on a 0.45 μm membrane filter to estimate picoplankton (<2 μm) productivity. The third set of light and dark bottles was filtered through a 20 μm Nitex screen and collected on a 2 μm membrane filter to estimate ultraplankton (2–20 μm) productivity. Each set of light bottles had 4 replicates. The filters were analyzed for radioactivity by the liquid scintillation counting procedure (Lind & Campbell, 1969). Chlorophyll *a* fractionation in triplicate was similarly done. Analysis of the pigments was by spectrophotometer after acetone extraction according to Strickland & Parsons (1968).

The fractionation procedure was also not without experimental errors. For example, passage of larger species perpendicularly through the nets was observed at times but was not a serious problem and did not affect the results significantly. Munawar *et al.* (1978) have discussed in detail the size fractionation approach followed by the Great Lakes Fisheries Research Branch in relation to other researchers. In the Great Lakes, the nannoplankton were defined as algae smaller than 64 μm and netplankton as either equal to or larger than 64 μm. The nannoplankton were then further subdivided into various size fractions such as picoplankton and ultraplankton, etc.

Results

Seasonality of biomass in the Lower Great Lakes

Lake Ontario. Figure 2 depict the seasonal fluctuations of phytoplankton which are based on lakewide cruise means of 27–30 stations distributed across the lake. Only one clearly pronounced biomass peak was observed in the middle of the summer with two relatively small maxima occurring during the spring period. During the entire year, higher numbers of maxima (four) were observed at the inshore region whereas the offshore region had a single pulse. Furthermore, the inshore region was not only characterized by a larger number of peaks but also by the development of the maxima earlier than the offshore region. In both the inshore and offshore regions, diatoms contributed the most to the total biomass during the winter and spring period (January to May). The phytoplankton composition began to show more diversity from June onwards when phytoflagellates (Chrysophyceae, Cryptophyceae and Dinophyceae), green algae and blue-green algae contributed significantly throughout the summer and fall periods. The inshore region had relatively more blue-greens than greens, whereas the offshore region had the reverse.

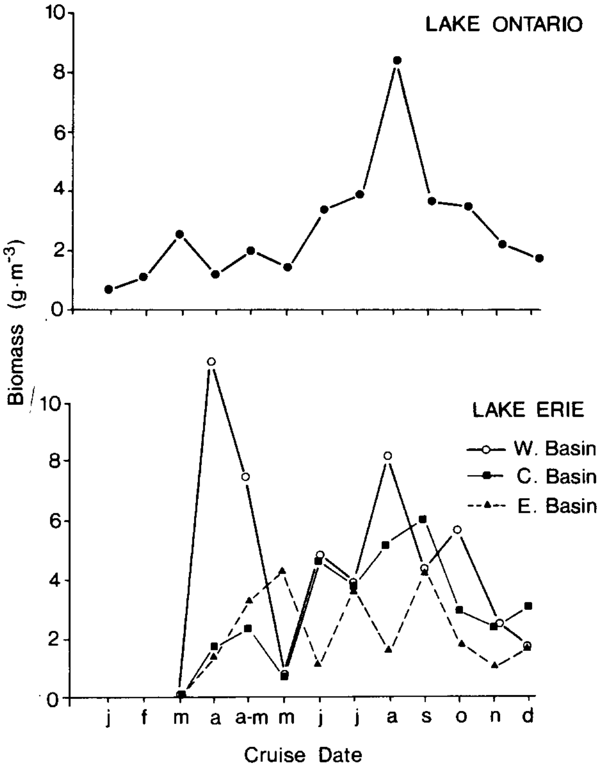

Fig. 2. Seasonal fluctuations of total phytoplankton biomass concentration in the Lower Great Lakes including Lake Ontario (1970) and Lake Erie (1970). Each value is a mean of lakewide and basinwide stations for Lake Ontario and Lake Erie respectively.

Lake Erie. On a lakewide basis, the seasonal fluctuations of phytoplankton biomass indicated relatively high values during the spring (April-May) and maximum densities were recorded during late summer (August-September). Low concentrations were observed in June and during the fall cruises (October-December). Comparative illustrations of the seasonal fluctuations of biomass and its group composition in each of the basins are shown in Figs. 2, 4 and 5, depicting the variability amongst the basins as follows.

Western basin. Two maxima were observed in the western basin, one in early spring (13 g m^{-3}) and a slightly lower one during August (8 g m^{-3}). The spring plankton was essentially composed of diatoms, phytoflagellates and green algae. However, diatom numbers were reduced in summer due to the relative increase of greens and blue-greens. The fall plankton was mainly composed of diatoms but blue-greens were abundant in the early fall (Fig. 2).

Central basin. In contrast to the western basin, no comparable spring peak (April) was recorded in the central basin. However, biomass started to increase from the end of June, remained fairly constant during the early part of the summer and culminated in a maximum in late summer (6 g m^{-3}). Compared to the western basin, the summer pulse in the central basin was 50% smaller in magnitude. The spring phytoplankton consisted of diatoms and phytoflagellates but the latter was more abundant in contrast to the western basin. The summer plankton was also dominated by phytoflagellates and diatoms whereas the greens and blue-greens were limited in their development. During the fall, phytoflagellates decreased but diatoms increased and essentially dominated the plankton (Fig. 2).

Eastern basin. Compared to the western basin, no comparable spring pulse was observed in the eastern basin. However, three maxima of similar order of magnitude (4 g m^{-3}) were observed, one each in late spring (June), summer (July) and late summer (September). The early spring cruise was dominated by diatoms, similar to the western and central basins. In the latter part of the spring (May-June), the diatoms decreased strikingly and were replaced by phytoflagellates (Chrysophyceae, Cryptophyceae and Dinophyceae). From the end of June onwards, and throughout the entire summer, the diatoms were practically absent and were replaced by phytoflagellates, greens and blue-greens. The fall plankton was dominated by diatoms once again (Fig. 2).

Inshore-offshore differentiation. The inshore/offshore differentiation observed in the Lower Great Lakes has a great impact on algal seasonality and species succession (Munawar & Munawar, 1975, 1976; Lorefice & Munawar, 1974). The 'inshore' stations are defined as those of depth less than 18 and 25 m in Lakes Erie and Ontario respectively. The inshore/offshore pattern, determined by pronounced spring peaks, is a characteristic feature of the Lower Great Lakes (Munawar & Nauwerck, 1971; Munawar & Munawar, 1982). For example, in Lake Ontario, a large number of peaks was observed in the inshore region, whereas only one well-developed maximum was recorded for the offshore area. Furthermore, the inshore region was not only characterized by a higher number of peaks than the offshore region but also developed an earlier maximum (Munawar *et al.,* 1974).

Comparing the inshore and offshore regions of Lake Ontario with respect to their phytoplankton composition, certain characteristic features become apparent. For example, diatoms dominated during the winter-spring period in both regions but their abundance in the inshore area was extremely high, producing well-developed maxima. Species composition also differed between these regions. However, in the offshore region, the development of diatoms was restricted and the maximum development was not as striking as the inshore region. Only one pulse was noticed in the offshore area and it was relatively small in size. Furthermore, other inshore-offshore differences were observed in other seasons as well. For example, the inshore region showed two peaks of blue-greens during summer and late fall. Conversely, the offshore region showed only one summer pulse of blue-greens of similar species composition. During the fall period, maximum diversity of phytoplankton composition was seen in both the regions since all the taxonomic groups were well-represented in the community structure. After a period of three months, when the diatoms were either absent or in extremely low numbers, they returned to both regions along with the phytoflagellates, Chlorophyta and Cyanophyta. However, the abundance of diatoms in the offshore region declined (November) compared to the inshore region where they developed earlier in large numbers (September and October).

In Lake Erie, the inshore/offshore differentiation was found to be applicable to the central and eastern basins since western Lake Erie is shallow, mixed and under the influence of rivers such as the Maumee and Detroit. It would be unrealistic therefore, to divide the western basin into inshore and offshore regions. Three biomass peaks were observed in the inshore region of the central basin during the spring and summer period, with a maximum of 12 g m^{-3} in July. The offshore region showed only a single pulse during late summer (September). As far as percent group composition is concerned, certain interesting differences were demonstrated. It appeared that diatoms were the major component in the inshore region for most of the year, whereas phytoflagellates dominated the offshore area during the May-August period, practically replacing the diatoms.

The inshore region of the eastern basin was characterized by a greater number of maxima, which showed significantly greater amounts of biomass (10 g m^{-3}). However, contrary to the characteristic trend of a spring maximum for the inshore region and no pulse for the offshore region (as in the central basin), the offshore region exhibited a well-developed pulse during the spring following the earlier inshore pulse. The pulse, which usually developed in the offshore area during summer (as in the central basin), did not materialize in the eastern basin. Instead, the inshore summer maximum developed in a manner similar to Lake Ontario and central Lake Erie.

Eastern Lake Erie is unique since another pronounced peak developed during the fall, which differs from the normal trends observed in the central basin and Lake Ontario. The species composition presented certain similarities and dissimilarities. For example, in both regions, diatoms dominated during the April-May and October-December periods. The phytoflagellates were abundant in both regions but they were more frequent in the offshore area. The inshore region did not show an abundance of diatoms, characteristic of inshore or shallow environments, but instead had a greater percentage of blue-greens during the summer (more than 50% of total biomass). In general, when the basins were compared by species composition, overall composition of the common species of phytoplankton was not much different between the three basins. Similar species occurred either seasonally or year round but their relative abundance differed from basin to basin.

Seasonality of biomass in the Upper Great Lakes

Lake Superior. The lakewide mean biomass did not show any obvious seasonal trends since no peaks were observed (see Fig. 3). This lack of seasonality is different from the Lower Great Lakes where pronounced pulses were observed during various seasons. Such a lack of seasonality has been suggested as an indicator of the ultra-oligotrophic or pristine nature of the water (Munawar & Munawar, 1978). The biomass was dominated by phytoflagellates (Chrysophyceae, Cryptophyceae and Dinophyceae) followed by Diatomeae. Phytoflagellates and diatoms showed a very smooth pattern with slight seasonal variations.

North Channel. With Lake Superior showing no seasonal trends and with very low biomass, the North Channel connected to Lake Superior continued to have low biomass concentration but showed a single peak in summer (July). However, the biomass concentration during spring and fall was only slightly lower than the summer. Diatomeae dominated throughout all seasons (Fig. 3) followed by Chrysophyceae/Cryptophyceae (spring) and Cryptophyceae/Chrysophyceae (summer and fall).

Georgian Bay. The Georgian Bay ecosystem appears to have a progression over the North Chan-

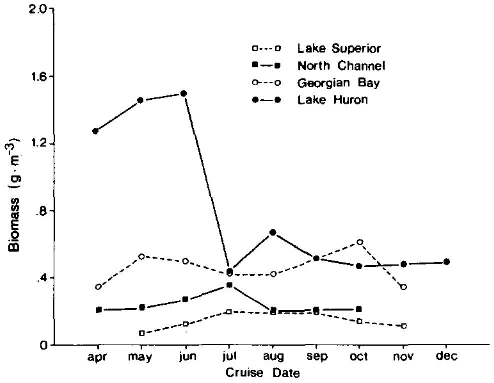

Fig. 3. Seasonal fluctuations of total phytoplankton biomass concentration in the Upper Great Lakes including Lakes Huron (1971), Superior (1973), Georgian Bay (1974) and North Channel (1974). Each value is a lakewide mean of several stations.

nel, exhibiting relatively higher biomass and a bimodal seasonality with a well-developed peak in spring (May) and another one at the end of summer (September). Diatomeae once again dominated in all three seasons, contributing to almost 50% of the biomass. During the spring, Chrysophyceae, Cyanophyta and Chlorophyta were sub-dominant groups; in the summer, Cyanophyta, Chlorophyta and Chrysophyceae were subdominant and during the fall collections, Chrysophyceae, Cyanophyta, Chlorophyta and Cryptophyceae followed the diatom prevalence (Fig. 3).

Lake Huron. Lake Huron showed relatively higher biomass concentrations amongst the Upper Great Lakes which was similar to Lake Michigan (Fig. 3). A pronounced peak occurred during spring (June) and the second pulse which was recorded in the summer (August) was almost half as much as the spring peak. Diatomeae once again was the most prevalent group in all three seasons. During the spring, 86% of the biomass was contributed by diatoms. Cyanophyta/Chlorophyta and Cyanophyta/Cryptophyceae/Chlorophyta followed the diatom abundance during summer and fall seasons respectively.

Lake Michigan. Lake Michigan data, although extensive spatially (more than 50 stations) are restricted seasonally since there was only one cruise in the spring and two cruises in the summer. These observations on Lake Michigan are being made for the first time from our laboratory. The spring cruise (May) showed relatively high biomass concentrations similar to the spring peak observed for Lake Huron. The biomass concentration for the summer (July) was again similar to the summer pulse of Lake Huron observed in August and that observed during September was similar in magnitude to that seen in Georgian Bay (Fig. 3). Diatoms dominated the phytoplankton community during both seasons followed by phytoflagellates such as Cryptophyceae and Chrysophyceae.

Seasonal comparison of the Great Lakes

Total phytoplankton biomass

Figure 4 presents a seasonal comparison of the total phytoplankton biomass during the spring, summer and fall seasons. All the values are means of cruises per season with the excepion of Lake Michigan which had one cruise for spring (May) and the North Channel which also had only one cruise in October. It is apparent that western Lake Erie showed the highest spring biomass followed by eastern Lake Erie and then Lake Ontario. During the summer, similar concentrations to these were exhibited by western Lake Erie, Lake Ontario and central Lake Erie, respectively. Similarly, maxima

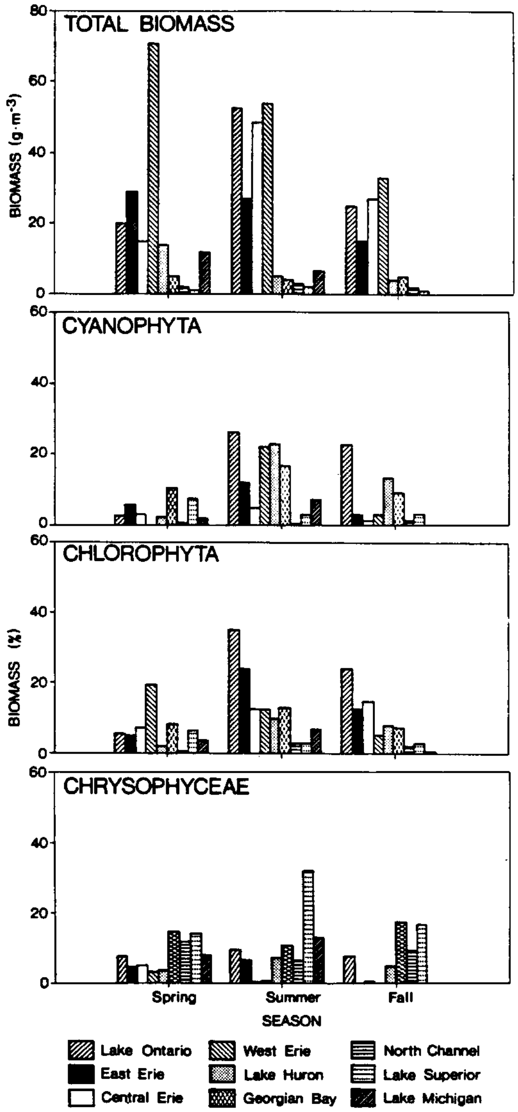

Fig. 4. Comparison of biomass concentrations in the Great Lakes for total biomass, Cyanophyta, Chlorophyta and Chrysophyceae based on lakewide mean biomass concentration.

were shown once again by western Lake Erie, central Lake Erie and Lake Ontario in the fall. It is therefore apparent that the Lower Great Lakes have a more pronounced seasonality of phytoplankton biomass than the Upper Great Lakes. Furthermore, maximum concentrations for the Lower Great Lakes were observed during the summer.

Cyanophyta

Figure 4 also depicts the Cyanophyta biomass given as a percent of the total phytoplankton biomass. The Cyanophyta contributed moderately to the overall biomass during the spring in Georgian Bay, Lake Superior and eastern Lake Erie. These blue-greens appear to grow more profusely during the summer, comprising more than 20% of the total biomass in Lake Ontario, western Lake Erie and Lake Huron. During the fall season, Cyanophyta continued to maintain their summer contribution in Lake Ontario (greater than 20%) followed by Lake Huron and Georgian Bay (greater than 10%).

Chlorophyta

Figure 4 shows the seasonal contribution of Chlorophyta and it is apparent that western Lake Erie has the most green algae, followed by central Lake Erie and Georgian Bay during the spring. Chlorophyta also dominated Lake Ontario and eastern Lake Erie during the summer. Likewise, they continued to be most abundant in Lake Ontario and central and eastern Lake Erie during the fall.

Chrysophyceae

The Chrysophyceae was common during spring occurring in similar proportions in Georgian Bay, Lake Superior and the North Channel. During the summer, they were prevalent in Lake Superior comprising the highest concentration amongst the Great Lakes followed by Lake Michigan and Georgian Bay. Chrysophyceae continued to be common during the fall in Lake Superior and Georgian Bay (Fig. 4).

Diatomeae

The diatoms, the most abundant taxonomic group in the Great Lakes, exhibited an interesting seasonal distribution. They had higher concentrations in all the ecosystems during the spring with the majority (in terms of biomass and species) occurring in Lake Huron followed closely by North Channel and Lake Michigan. During the summer, the diatoms were not as abundant as in the spring. For example, during the summer, their concentration was very low in Lake Ontario and eastern Lake Erie. They dominated the biomass in the North Channel and they continued to be common with similar values occurring in the other Great Lakes. The fall season, like the spring, appear to be suitable for their growth in most of the Great Lakes. Diatoms were very prevalent in western Lake Erie, followed closely by central and eastern Lake Erie and the North Channel (Fig. 5).

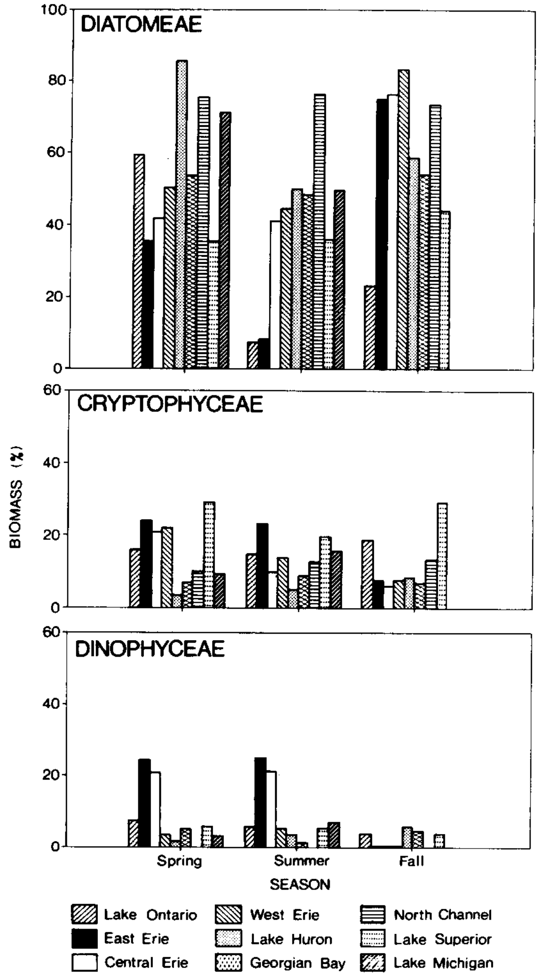

Fig. 5. Comparison of biomass concentrations in the Great Lakes for Diatomeae, Cryptophyceae and Dinophyceae based on lakewide mean concentration.

Cryptophyceae

Figure 5 depicts the seasonal distribution of Cryptophyceae. They were dominant in Lake Superior, followed by the three basins of Lake Erie. During the summer, they appear to be common in eastern Lake Erie, Lake Superior and Lake Michigan. Cryptophyceae continue to be prevalent in the Lake Superior followed by Lake Ontario and the North Channel during the fall season.

Dinophyceae

The seasonal distribution of Dinophyceae across the Great Lakes is shown in Fig. 5 which indicates that the dinoflagellates appear to be prevalent mainly in eastern and central Lake Erie. They contribute almost equally to the spring and summer seasons. The abundance of these phytoflagellates in only two of the basins is intriguing and should be examined in greater detail.

Seasonal succession of species

Lower Great Lakes

The seasonal succession of species is well documented for the Lower Great Lakes and shows distinct seasonal peaks that are predictable in each season (Munawar & Nauwerck, 1971; Munawar & Munawar, 1976, 1982). The Lower Great Lakes harbour species which normally occur in nutrient-rich environments ranging from mesotrophic to eutrophic with some eurytopic species in their distribution. The inshore and offshore developmental pattern of biomass, pointed out earlier, is a typical phenomenon of the Lower Great Lakes and reflects municipal and industrial input of nutrients and contaminants received by these regions.

Due to the large volume of our data base for the Great Lakes, an attempt has been made to concentrate on common species only (contributing greater than 5% to the total biomass). Tables 2a, b, 3a, b and 4 provide lakewide species data for Lake Ontario and other Great Lakes during spring, summer, and fall seasons respectively.

Lake Ontario. Lake Ontario showed a high diversity of species. The spring was dominated by diatoms in both inshore and offshore regions (Tables 2a, b). Comparison of species compositions between inshore and offshore areas of Lake Ontario revealed that pronounced spring maxima appeared in the inshore region only. Although diatoms dominated in both regions, they were more abundant inshore, and the species present were those common to eutrophic habitats.

The March peak in the inshore region was composed mainly of *Stephanodiscus tenuis, S. Hantzschii* var. *pusilla, Asterionella formosa* and *Melosira varians.* During late spring another pulse, dominated by *Melosira Binderana,* was observed with co-dominants *Asterionella gracillima, Stephanodiscus tenuis* and *Melosira varians* during the thermal bar conditions (Munawar & Munawar, 1975). However, in the offshore region, the development of diatoms was restricted and the maximum development was not as striking as the inshore region. Only one relatively small pulse was recorded in the offshore region. This pulse was dominated by *Melosira islandica* subsp. *helvetica.* The characteristic inshore species described earlier were found in low numbers only.

The summer was dominated by Cyanophyta, Chlorophyta and Cryptophyceae in both regions. The highest number of summer species belonged to Chlorophyta (Tables 3a, b), whereas Cyanophyta was represented by a limited number of species such as *Aphanizomenon flos-aquae, Chroococcus dispersus* var. *minor,* and *Oscillatoria limnetica.* Some of the other species recorded in spring continued during the summer season as well. The fall species composition was dominated by diatoms with species similar to those found during spring (Table 4).

Lake Erie. The seasonal characteristic features of the three basins of Lake Erie are summarized from a comparative point of view. In the western basin, diatoms were dominant most of the time, greens and blue-greens were abundant during spring and summer and phytoflagellates were common in the spring. The central basin was also dominated by diatoms but to a lesser extent during spring and summer. Blue-greens were considerably lower in concentration and phytoflagellates were more abundant during spring and found in large numbers during summer. The eastern basin was dominated by diatoms only during the fall and they were absent during the summer. The blue-greens were less abundant, but the green algae were common during the summer. Chrysophyceae were common in this basin and phytoflagellates were most prevalent, en-

Table 2A. Species comparison of the Great Lakes during the spring.

	ONTARIO	WEST ERIE	CENTRAL ERIE	EAST ERIE	HURON	GEORGIAN BAY	NORTH CHANNEL	SUPERIOR	MICHIGAN
CYANOPHYTA									
Anabaena sp.								X	
A. spiroides Klebahn					X				
A. subcylindrica Borge				X					
Aphanocapsa sp.						X		X	
A. pulchra (Kuetz.) Rabenhorst								X	
Chroococcus sp.									X
C. dispersus var. minor G.M. Smith	X		X	X					X
C. minutus (Kuetz.) Naegeli	X								
C. turgidus (Kuetz.) Naegeli						X			
Gomphosphaeria sp.						X			
G. aponina Kuetzing					X				
G. lacustris Chodat						X			
Lyngbya sp.								X	
L. limnetica Lemmermann					X			X	
Oscillatoria sp.								X	
O. Agardhii Gomont					X				
O. limnetica Lemmermann	X							X	
O. prolifica (Grev.) Gomont					X				
O. tenuis Agardh								X	X
CHLOROPHYTA									
Ankistrodesmus falcatus (Corda) Ralfs	X								
A. falcatus var. acicularis (A.Braun) G.S.West					X				
A. falcatus var. mirabilis (West) G.S. West	X								
A. falcatus var. spirilliformis G.S. West								X	
Chlamydomonas sp.					X			X	X
C. globosa Snow	X		X						
Chlorella sp.	X		X		X	X			
C. vulgaris Beyer					X	X			
Coelastrum microporum Naegeli					X	X			
Cosmarium bioculatum De Brebisson									X
C. tenue West & West									X
Gloeocystis sp.						X		X	
G. ampla (Kuetz.) Lagerheim	X								
G. planctonica (West & West) Lemmermann									X
Golenkinia radiata (Chod.) Wille					X				
Gyromitus cordiformis Skuja	X								
Mougeotia sp.									X
Oocystis sp.						X			
O. borgei Snow						X		X	
O. lacustris Chodat						X		X	
O. parva West & West						X			
Pedinomonas minutissima Skuja	X								
Scenedesmus bicaudatus (Hansg.) Chodat						X			
S. bijuga (Turp.) Lagerheim	X				X	X		X	
S. bijuga var. alternans (Reinsch) Hansgirg						X			
Staurastrum paradoxum Meyen		X							
EUGLENOPHYTA									
Euglena variabilis Dangeard									X
CHRYSOPHYCEAE									
Chromulina sp.	X				X	X		X	
Chrysamoeba sp.								X	
Chrysocapsa sp.								X	
Chrysochromulina parva Lackey	X		X		X	X	X	X	X
Dinobryon sp.						X	X		
D. bavaricum Imhof								X	
D. cylindricum Imhof						X	X		
D. divergens Imhof					X	X		X	
D. sertularia Ehrenberg						X		X	
D. sociale Ehrenberg	X							X	X
D. sociale var.stipitatum (Stein) Lemmermann								X	
Mallomonas sp.								X	
Ochromonas sp.				X	X	X	X	X	X
Pseudokephyrion attenuatum Hilliard						X	X		
Tribonema sp.							X		
Uroglena sp.						X			
DIATOMEAE									
Amphiprora ornata Bailey									X
Asterionella formosa Hassall	X				X		X	X	

Table 2B. Species comparison of the Great Lakes during the spring.

	ONTARIO	WEST ERIE	CENTRAL ERIE	EAST ERIE	HURON	GEORGIAN BAY	NORTH CHANNEL	SUPERIOR	MICHIGAN
A. gracillima (Hantz.) Heiberg	X				X	X		X	
Cyclotella sp.								X	
C. bodanica Eulenstein						X	X	X	X
C. comta (Ehr.) Kuetzing					X	X	X	X	
C. glomerata Bachmann					X	X		X	
C. ocellata Pantocsek					X	X	X	X	X
C. stelligera (Cleve) Grunow					X	X		X	
C. striata (Kuetz.) Grunow						X			
Cymbella ventricosa Kuetzing	X								
Diatoma elongatum Agardh							X	X	
D. elongatum var. tenuis Hustedt									X
Fragilaria sp.					X			X	
F. capucina Desmazieres					X			X	X
F. crotonensis Kitton	X	X			X	X	X	X	X
Gyrosigma sp.									X
Melosira sp.					X				
M. Binderana Kuetzing	X	X	X		X				X
M. granulata (Ehr.) Ralfs					X	X		X	
M. islandica O. Muller					X		X		X
M. islandica var. helvetica O. Mueller					X				X
M. italica (Ehr.) Kuetzing									X
M. italica var. subartica O. Mueller					X				X
M. varians Agardh	X								
Nitzschia sp.									X
N. palea (Kuetz.) W. Smith	X								
N. vermicularis (Kuetz.) Hantzsch					X				
Rhizosolenia eriensis H.L. Smith					X	X	X	X	X
R. gracilis H.L. Smith						X			
R. longiseta Zacharias									X
Stephanodiscus sp.					X				
S. astraea (Ehr.) Grunow	X								
S. astraea var. minutula (Kuetz.) Grunow								X	X
S. Hantzschii var. pusilla Grunow	X		X						X
S. niagarae Ehrenberg	X		X	X	X	X			X
S. tenuis Hustedt	X	X	X	X					
Surirella angustata Kuetzing								X	
S. ovalis Brebisson	X								
Synedra sp.					X	X			
S. acus Kuetzing					X	X		X	
S. acus var. angustissima Grunow							X		
S. acus var. radians (Kuetz.) Hustedt					X	X	X	X	X
S. ulna (Nitzsch) Ehrenberg	X				X	X		X	X
S. Utermohli Hustedt	X								
Tabellaria sp.	X								
T. fenestrata (Lyngb.) Kuetzing	X				X	X	X	X	X
T. fenestrata var. intermedia Grunow									X
T. flocculosa (Roth) Kuetzing	X				X			X	X
T. flocculosa var. geniculata Cleve					X				
CRYPTOPHYCEAE									
Chroomonas acuta (Schiller) Utermohl								X	
Cryptaulax rhomboidea Skuja	X								X
Cryptomonas sp.								X	
C. erosa Ehrenberg	X	X	X	X	X	X	X	X	X
C. erosa var. reflexa Marssonii								X	
C. Marssonii Skuja					X	X		X	
C. ovata Ehrenberg	X								
C. phaseolus Skuja								X	X
Katablepharis ovalis Skuja	X						X	X	
Rhodomonas sp.						X		X	
R. lens Pascher & Ruttner								X	
R. minuta Skuja	X	X	X	X	X	X	X	X	X
R. minuta var. nannoplanctica Skuja							X	X	X
DINOPHYCEAE									
Glenodinium sp.	X								
G. pulvisculus (Ehr.) Stein	X								
Gymnodinium sp.	X				X	X		X	X
G. eurytopum Skuja									X
G. helveticum Penard	X	X	X	X		X		X	X
G. helveticum var. achroun Skuja									X
G. uberrimum (Allman) Kofoid & Swezy			X	X	X	X		X	
G. varians Maskell					X	X	X	X	
Peridinium sp.								X	
P. aciculiferum (Lemm.) Lemmermann			X	X	X			X	

Table 3A. Species comparison of the Great Lakes during the summer.

	ONTARIO	WEST ERIE	CENTRAL ERIE	EAST ERIE	HURON	GEORGIAN BAY	NORTH CHANNEL	SUPERIOR	MICHIGAN
CYANOPHYTA									
Anabaena sp.					X	X		X	
A. flos-aquae (Lyngb.) De Brebisson									X
A. planctonica Brunnthaler									X
A. spiroides Klebahn			X		X	X			
A. subcylindrica Borge					X				
Aphanizomenon flos-aquae Ralfs	X	X	X	X					
Aphanocapsa sp.					X			X	
A. pulchra (Kuetz.) Rabenhorst					X			X	
Aphanothece sp					X				
A. clathrata G.S. West					X				
Chroococcus dispersus var. minor G.M. Smith	X			X	X				
C. limneticus Lemmermann					X				
C. turgidus (Kuetz.) Naegeli						X			
Coelastrum sp.					X				
Gomphosphaeria sp.						X			
G. aponina Kuetzing					X				
G. lacustris Chodat						X			
G. Naegeliana (Ung.) Lemmermann					X				
Microcystis sp.					X				
M. firma (Breb. & Len.) Schmidle					X				
Oscillatoria sp.					X			X	X
O. Agardhii Gomont					X				
O. limnetica Lemmermann	X							X	
O. limosa									X
O. tenuis Agardh								X	X
CHLOROPHYTA									
Ankistrodesmus falcatus var. mirabilis (West & West) G.S. West	X								
Carteria cordiformis (Carter) Diesing	X								
Chlamydomonas sp.					X			X	
C. globosa Snow	X								X
Chlorella sp.	X								
C. vulgaris Beyer					X	X			
Coelastrum microporum Naegeli	X				X	X			
C. proboscideum Bohlin	X								
C. sphaericum Naegeli						X			
Cosmarium sp.	X			X					
C. bioculatum De Brebisson									X
C. botrytis Meneghini									X
C. subtumidum Nordst									X
Crucigenia quadrata Morren									X
Dictyosphaerium sp.						X			
Gloeocystis sp.					X	X		X	
G. ampla (Kuetz.) Lagerheim	X								
G. vesiculosa Naegeli						X			
Gyromitus cordiformis Skuja	X								
Lagerheimia ciliata (Lag.) Chodat	X								
Mougeotia sp.	X				X				
Oedogonium sp.	X		X	X					
Oocystis sp.	X				X	X		X	
O. Borgei Snow	X					X		X	
O. lacustris Chodat					X	X		X	
O. parva West & West									X
O. solitaria Wittrock						X			
Pediastrum simplex (Meyen) Lemmermann	X	X		X					
Pedinomonas minutissima Skuja	X								
Phacotus lenticularis (Ehr.) Stein	X								
Scenedesmus bijuga (Turp.) Lagerheim	X				X			X	
Sphaerocystis sp.				X					
S. schroeteri Chodat							X		
Staurastrum sp.	X								
S. paradoxum Meyen	X		X	X					
Tetraedron minimum (A. Braun) Hansgirg					X				
Ulothrix subtilissima Rabenhorst	X								
EUGLENOPHYTA									
Lepocinclis sp.	X								
Phacus sp.	X								
CHRYSOPHYCEAE									
Chromulina sp.	X				X	X			
Chrysamoeba sp.								X	
Chrysocapsa sp.								X	X
Chrysochromulina parva Lackey	X			X	X	X	X	X	X
Dinobryon sp.							X		X
D. bavaricum Imhof							X	X	
D. divergens Imhof							X	X	X
D. sertularia Ehrenberg								X	

Table 3B. Species comparison of the Great Lakes during the summer.

	ONTARIO	WEST ERIE	CENTRAL ERIE	EAST ERIE	HURON	GEORGIAN BAY	NORTH CHANNEL	SUPERIOR	MICHIGAN
D. sociale Ehrenberg	X							X	
D. sociale var. americanum (Brunn.) Bachmann							X		X
D. sociale var. stipitatum (Stein) Lemmermann								X	
Mallomonas sp.					X			X	
Ochromonas sp.					X	X	X	X	X
O. elegans Doflein					X				
Stichogloea Doederleinii (Schmidle) Wille									X
Uroglena sp.						X	X		
U. americana (Calkins) Lemmermann						X	X		X
U. volvox Ehrenberg							X		
DIATOMEAE									
Asterionella formosa Hassall					X		X	X	
A. gracillima (Hantz.) Heiberg	X				X			X	
Coscinodiscus Rothii (Ehr.) Grunow		X						X	
Cyclotella sp.					X	X		X	
C. bodanica Eulenstein					X	X	X	X	X
C. comta (Ehr.) Kuetzing					X	X	X	X	
C. glomerata Bachmann					X	X		X	X
C. kutzingiana Thwaites					X		X		
C. michiganiana Skvortzow					X				
C. ocellata Pantocsek					X	X	X	X	X
C. stelligera (Cleve) Grunow					X	X		X	
C. striata (Kuetz.) Grunow					X	X			
Cymbella sp.					X				
C. ventricosa Agardh					X				
Diatoma elongatum var. tenuis Hustedt									X
Fragilaria capucina Desmazieres			X		X				
F. crotonensis Kitton	X		X	X	X	X	X	X	X
Melosira sp.					X				
M. Binderana Kuetzing					X		X	X	X
M. granulata (Ehr.) Ralfs					X			X	
M. islandica O. Mueller					X				X
M. islandica var. helvetica O. Mueller									X
M. italica (Ehr.) Kuetzing									X
M. varians Agardh	X							X	
Navicula sp.	X								
Nitzschia palea (Kuetz.) G.M. Smith	X				X				
Rhizosolenia eriensis H.L. Smith						X		X	
R. longiseta Zacharias									X
Stephanodiscus sp.								X	X
S. astraea var. minutula (Kuetz.) Grunow					X			X	X
S. niagarae Ehrenberg		X	X						X
S. tenuis Hustedt	X	X			X				
Surirella sp.					X				
S. angustata Kuetzing								X	
Synedra sp.					X				
S. acus Kuetzing					X			X	
S. acus var. delicatissima Grunow									X
S. acus var. radians (Kuetz.) Hustedt					X		X	X	
S. ulna (Nitzsch.) Ehrenberg	X								
Tabellaria sp.					X				
T. fenestrata (Lyngb.) Kuetzing					X	X	X	X	X
T. fenestrata var. intermedia Grunow									X
T. flocculosa (Roth.) Kuetzing	X				X			X	
CRYPTOPHYCEAE									
Chroomonas acuta (Schiller) Utermohl								X	
Cryptomonas sp.					X				
C. erosa Ehrenberg	X	X	X	X	X	X	X	X	X
C. erosa var. reflexa Marssonii								X	
C. Marssonii Skuja					X	X		X	
C. ovata Ehrenberg									X
C. phaseolus Skuja								X	
Katablepharis ovalis Skuja	X				X			X	
Rhodomonas minuta Skuja	X	X	X	X	X	X	X	X	X
R. minuta var. nannoplanctica Skuja							X	X	
DINOPHYCEAE									
Ceratium hirundinella (O. Muell.) Schrank	X	X	X	X	X				X
Glenodinium sp.	X				X				
G. Borgei (Lemm.) Schiller									X
Gymnodinium sp.	X				X			X	X
G. helveticum Penard	X				X	X		X	X
G. uberrimum (Allman) Kofoid & Swezy								X	
G. varians Maskell					X		X	X	
Peridinium sp.								X	
P. aciculiferum (Lemm.) Lemmermann					X				X
P. gatunese Nygaard									X
P. inconspicuum Lemmermann								X	

Table 4. Species comparison of the Great Lakes during fall.

	Ontario	West	Central	East	Huron	Georgian	North	Superior
			Erie			Bay	Channel	
CYANOPHYTA								
Anabaena spiroides Klebahn					X			
A. subcylindrica Borge					X	X		
Aphanocapsa sp.	X							
A. pulchra (Kuetz.) Rabenhorst								X
Aphanothece clathrata var. brevis Bachmann								X
Chroococcus dispersus (Keisel.) Lemmermann					X			
C. dispersus var. minor G.M. Smith	X							
C. limneticus Lemmermann							X	
C. turgidus (Kuetz.) Naegeli						X		
Coelastrum sp.					X			
Gomphosphaeria sp.					X	X		
G. aponina Kuetzing	X				X			
G. lacustris Chodat						X		
G. Naegeliana (Ung.) Lemmermann					X			
Lyngbya sp.								X
L. limnetica Lemmermann								X
Microcystis sp.					X			
M. firma (Breb. & Len.) Schmidle					X			
Oscillatoria sp.					X			X
O. Agardhii Gomont					X			
O. limnetica Lemmermann	X				X			X
O. tenuis Agardh						X		X
CHLOROPHYTA								
Ankistrodesmus falcatus var. mirabilis (West & West) G.S. West	X							
Asterococcus sp.	X							
Carteria cordiformis (Carter) Diesing	X							
Chlamydomonas globosa Snow	X			X				
Chlorella sp.	X					X		X
C. vulgaris Beyer				X	X			
Closterium limneticum Lemmermann	X							
Coelastrum microporum Naegeli	X							
Cosmarium sp.	X							
Gloeocystis sp.					X	X		X
G. ampla (Kuetz.) Lagerheim	X							
Gyromitus cordiformis Skuja	X							
Lagerheimia ciliata (Lag.) Chodat	X					X		
Mougeotia sp.					X			
Oedogonium sp.	X							
Oocystis sp.								X
O. Borgei Snow	X							
O. lacustris Chodat					X			
O. parva West & West						X		
O. solitaria Wittrock						X		
Pediastrum simplex (Meyen) Lemmermann	X		X	X				
Pedinomonas minutissima Skuja	X							
Phacotus lenticularis (Ehr.) Stein	X							
Scenedesmus bijuga (Turp.) Lagerheim	X				X	X		X
S. quadricauda (Turp.) De Brebisson	X							
Staurastrum sp.	X							
S. paradoxum Meyen	X			X				
Tetraedron sp.	X							
T. minimum (A. Braun) Hansgirg					X			
CHRYSOPHYCEAE								
Chromulina sp.					X	X		
C. parvula Conrad						X		
Chrysocapsa sp.								X
Chrysochromulina sp.								X
C. parva Lackey	X				X	X		X
Chrysosphaerella longispina Lauterborn							X	
Dinobryon sp.							X	
D. bavaricum Imhof								X
D. divergens Imhof					X		X	X
D. sertularia Ehrenber								X
Mallomonas sp.					X			X
Ochromonas sp.	X				X	X	X	X
Uroglena sp.						X		
U. americana (Calkins) Lemmermann							X	
DIATOMEAE								
Asterionella formosa Hassall	X				X		X	X
A. gracillima (Hantz.) Heiberg	X				X	X		X
Coscinodiscus Rothii (Ehr.) Grunow		X						
Cyclotella sp.					X	X		X
C. bodanica Eulenstein					X			X
C. comta (Ehr.) Kuetzing					X	X	X	X
C. glomerata Bachmann					X	X		X
C. kuetzingiana Thwaites							X	
C. ocellata Pantocsek					X	X	X	X
C. stelligera (Cleve) Grunow					X	X		X
C. striata (Kuetz.) Grunow					X			
Diatoma sp.					X			
Fragilaria sp.					X	X		X
F. capucina Desmazieres				X		X		
F. crotonensis Kitton		X		X	X	X	X	X
Melosira sp.					X			
M. binderana Kuetzing	X							
M. granulata (Ehr.) Ralfs					X	X		X
M. granulata var. angustissima (O. Muell.) Hustedt								X
M. islandica O. Mueller		X						X
Nitzschia sp.					X			
N. acuta Hantzch								X
N. palea (Kuetz.) G.M. Smith	X							
Stephanodiscus astraea var. minutula (Kuetz.) Grunow								X
S. Hantzschii var. pusilla Grunow	X							
S. niagarae Ehrenberg	X	X	X	X				
S. tenuis Hustedt	X	X						
Synedra acus Kuetzing						X		X
S. acus var. radians (Kuetz.) Hustedt					X		X	X
S. ulna (Nitzsch.) Ehrenberg	X							
S. Utermohli Hustedt	X							
Tabellaria sp.					X			
T. fenestrata (Lyngb.) Kuetzing					X	X	X	X
T. flocculosa (Roth) Kuetzing	X				X			X
CRYPTOPHYCEAE								
Cryptomonas sp.					X			X
C. erosa Ehrenberg	X	X	X	X	X	X	X	X
C. Marssonii Skuja					X	X		X
Katablepharis ovalis Skuja								X
Rhodomonas sp.								X
R. lens Pascher & Ruttner								X
R. minuta Skuja	X		X	X	X	X	X	X
R. minuta var. nannoplanctica Skuja							X	X
DINOPHYCEAE								
Glenodinium sp.	X				X			
Gymnodinium sp.					X			X
G. helveticum Penard	X				X	X		X
G. uberrimum (Allman) Kofoid & Swezy						X		X
G. varians Maskell					X	X		X
Peridinium sp.								X

croaching on diatom growth.

The species found are those which are usually found under mesotrophic and eutrophic conditions. The western basin harboured species such as *Scenedesmus bijuga* var. *alternans, Fragilaria crotonensis, Melosira Binderana, Stephanodiscus tenuis, Cryptomonas erosa, Rhodomonas minuta,* and *Gymnodinium helveticum* during the spring (Tables 2a, b).

During the spring, central Lake Erie contained species such as *Chroococcus dispersus* var. *minor, Chlamydomonas globosa, Chlorella* sp., *Chrysochromulina parva, Melosira Binderana, Stephanodiscus Hantzschii* var. *pusilla, S. Niagarae, S. tenuis, Cryptomonas erosa, Rhodomonas minuta, Gymnodinium helveticum, G. uberrimum* and *Peridinium aciculiferum.*

The spring species composition in the eastern basin was similar to the central basin. However, there were some differences. For example, *Anabaena subcylindrica* and *Mallomonas* sp. were common species in this basin but not in the other two basins. Conversely, species such as *Melosira Binderana,* found in the western and central basins, and *Stephanodiscus Hantzschii* var. *pusilla,* occurring in the central basin, were not among the common species in the eastern basin.

During the summer, a limited number of species was observed in the western basin. The species observed included *Aphanizomenon flos-aquae, Pediastrum simplex, Coscinodiscus rothii, Stephanodiscus niagarae, Tabellaria flocculosa, Cryptomonas erosa, Rhodomonas minuta,* and *Ceratium hirundinella.* The summer species in the central basin included *Anabaena spiroides, Aphanizomenon flos-aquae, Oedogonium* sp., *Staurastrum paradoxum, Fragilaria crotonensis, F. capucina, Stephanodiscus niagarae, Cryptomonas erosa, Rhodomonas minuta,* and *Ceratium hirundinella* (Tables 3a, b). At this time, the eastern basin harboured *Aphani-*

zomenon flos-aquae, Chroococcus dispersus var. *minor, Oedogonium* sp., *Pediastrum simplex, Chrysochromulina parva, Fragilaria crotonensis, Cryptomonas erosa, Rhodomonas minuta* and *Ceratium hirundinella* (Tables 3a, b).

The fall species composition consisted mainly of diatoms in all three basins. *Coscinodiscus rothii, Fragilaria crotonensis, Melosira islandica, Stephanodiscus niagarae* and *S. tenuis* were abundant in the western basin. *Stephanodiscus niagarae* was the most common species in the central basin whereas *Fragilaria capucina, F. crotonensis* and *S. niagarae* were common in the eastern basin. *S. niagarae* was thus abundant in all three basins (Table 4).

Some species occurred all year round. In the western basin, these perennial species were *Stephanodiscus tenuis, Melosira islandica, M. Binderana, Fragilaria crotonensis, Rhodomonas minuta* and *Cryptomonas erosa.* The perennial species of the central basin were *Ochromonas* spp., *Stephanodiscus niagarae, Rhodomonas minuta* and *Cryptomonas erosa.* The perennial species that the eastern basin harboured were *Pediastrum duplex, Fragilaria crotonensis, Rhodomonas minuta* and *Cryptomonas erosa.*

A comparison of common species in the Lower Great Lakes during the three seasons (Tables 2a, b, 3a, b, 4) provides some interesting features. For example, in general, Lake Erie basins had fewer number of species, whereas Lake Ontario showed a higher species diversity of various taxonomic groups. During the spring, certain species were commonly occurring in Lake Ontario and some basins of Lake Erie such as *Chroococcus dispersus* var. *minor, Melosira Binderana, Stephanodiscus Niagarae, S. tenuis, Cryptomonas erosa, Rhodomonas minuta* and *Gymnodinium helveticum.* On the other hand, species such as *Chroococcus minutus, Oscillatoria limnetica, Ankistrodesmus falcatus, A. falcatus* var. *mirabilis, Gloeocystis ampla, Gyromitus cordiformis, Pedinomonas minutissima* and *Scenedesmus bicaudatus* were only found in Lake Ontario. During the summer, *Aphanizomenon flos-aquae, Staurastrum paradoxum, Fragilaria crotonensis, Cryptomonas erosa, Rhodomonas minuta* and *Ceratium hirundinella* were common in Lakes Ontario and Erie. During the fall, a very limited number of species was found in both lakes such as *Pediastrum simplex, Stephanodiscus niagarae, Cryptomonas erosa* and *Rhodomonas minuta.*

Seasonal succession of species

Upper Great Lakes

Lake Superior. As indicated earlier, the lack of seasonality as shown by the seasonal variation of biomass in Lake Superior makes it a unique ecosystem to study, both from the limnological and the phycological point of view. The usual environmental correlates of spring, summer and fall do not apply to Lake Superior due to its unique thermal regime. It has a low summer surface temperature, long periods of extensive vertical mixing during the spring and fall and short intervening periods of stratification (Bennett, 1978; Munawar & Munawar, 1978). However, the species given in Tables 2a, b, 3a, b and 4 have been divided into the traditional seasons and some selected species have been examined for seasonal trends within individual taxa which were commonly found in the samples (Fig. 6). It is apparent that the conventional patterns observed in the Lower Great Lakes and other temperate lakes are not seen in Lake Superior. A few diatoms such as *Cyclotella comta, Asterionella formosa, Tabellaria fenestrata* and *Synedra acus* var. *radians* exhibited maxima during the month of July. Similarly, other species such as *Ochromonas* spp., *Chrysochromulina parva, Uroglena* sp., *Rhodomonas minuta, Cryptomonas erosa, C. Marssonii* and *Gymnodinium* sp. showed higher concentrations during the July to September period (Fig. 6).

Since there are few pronounced seasonal trends of biomass and species in the period covered (May-November), perhaps it is more realistic to study the seasonal succession of species in Lake Superior under stratified and unstratified conditions based on the thermal regime (Munawar & Munawar, 1978). In Lake Superior, unstratified conditions are represented by three cruises (May, June, November) and stratified conditions are represented by another three cruises (July-August, September and October).

Under stratified conditions, the most common species were *Oscillatoria limnetica, Oocystis lacustris, Cyclotella stelligera, C. comta, Asterionella formosa, Tabellaria fenestrata, T. flocculosa, Fragilaria crotonensis, Synedra acus* var. *radians, Ochromonas* spp., *Chrysochromulina parva, Uroglena* sp., *Dinobryon divergens, D. bavaricum, D. sociale, Rhodomonas minuta, Cryptomonas erosa, C. Marssonii, Katablepharis ovalis, Gymnodinium*

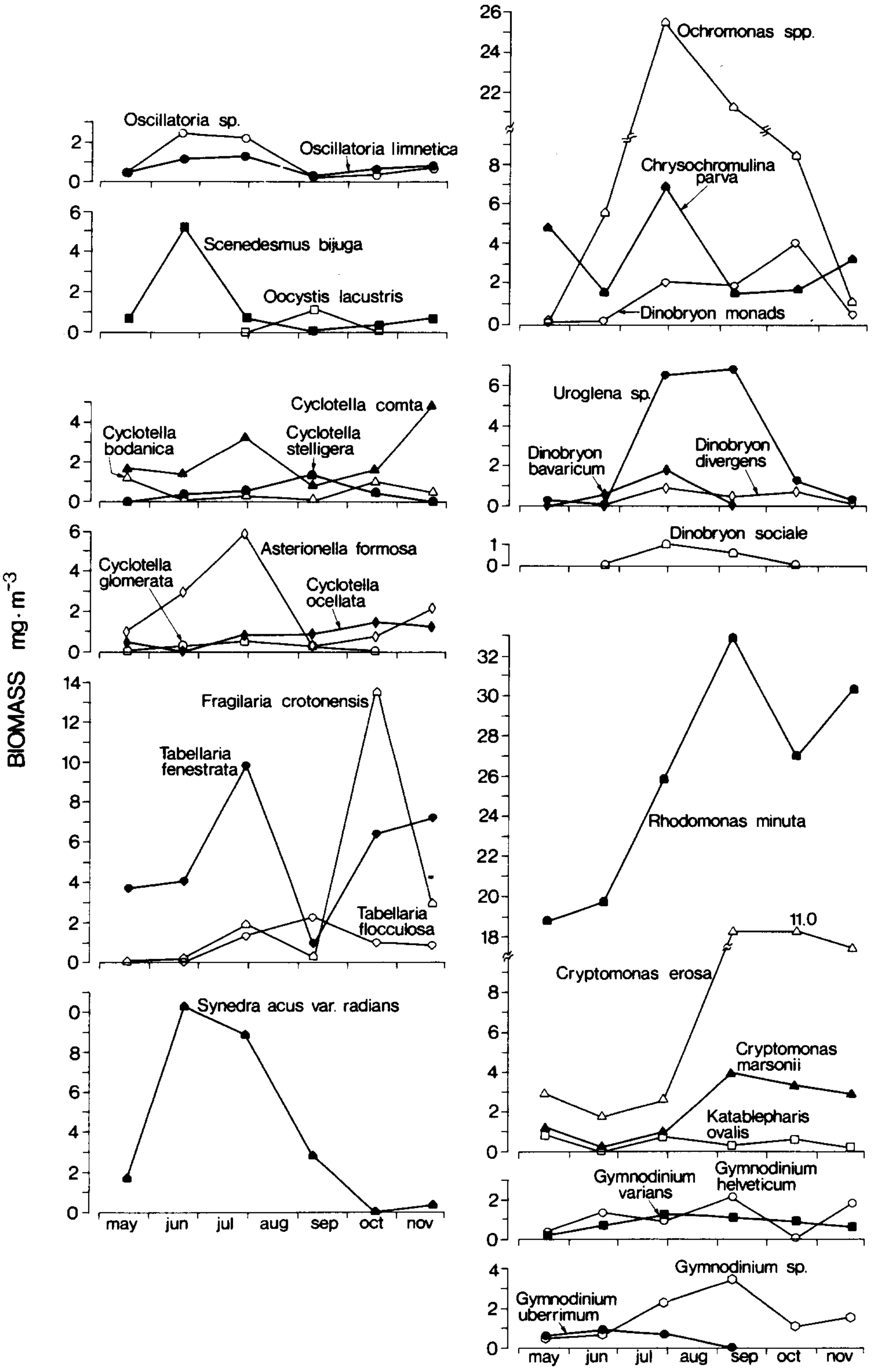

Fig. 6. Seasonal succession of common species in the open Lake Superior (1973) based on mean biomass concentration.

varians, G. helveticum and *G. uberrimum.*

The most common species under unstratified conditions were *Oscillatoria limnetica, Scenedesmus bijuga, Cyclotella bodanica, C. comta, Asterionella formosa, Tabellaria fenestrata, Synedra acus* var. *radians, Ochromonas* sp., *Chrysochromulina parva, Rhodomonas minuta, Cryptomonas erosa, C. Marssonii, Gymnodinium* sp. and *G. helveticum.*

Some species were of prolonged abundance. These included *Cyclotella comta, Asterionella formosa, Synedra acus* var. *radians, Ochromonas* spp., *Uroglena* sp., *Rhodomonas minuta, Cryptomonas erosa, C. Marssonii,* and *Gymnodinium helveticum.*

North Channel. Although the seasonal patterns (May-November) in Lake Superior appear to be relatively small, a single peak was observed in the North Channel during the summer (July). The biomass concentration remained low and was very similar to Lake Superior. During the spring, North Channel was dominated by diatoms, Chrysophyceae and Cryptophyceae such as *Chrysochromulina parva, Dinobryon cylindricum, Ochromonas* sp., *Mallomonas* sp., *Pseudokephyrion attenuatum, Cyclotella comta, C. glomerata, C. stelligera, Diatoma elongatum, Fragilaria crotonensis, Melosira islandica* var. *helvetica, Rhizosolenia eriensis, Synedra acus* var. *angustissima, S. acus* var. *radians, Tabellaria fenestrata, Cryptomonas erosa, Katablepharis ovalis, Rhodomonas minuta, R. minuta* var. *nannoplanctica* and *Gymnodinium varians* (Tables 2a, b).

The dominant species in the summer were similar to the species found in the spring with additional common species such as *Sphaerocystis* sp., *Dinobryon bavaricum, D. divergens, D. sertularia, Uroglena americana, U. volvox, Cyclotella michiganiana* and *Melosira Binderana* (Tables 3a, b). The species composition in the fall cruise was once again similar to the spring and summer (Table 4).

Georgian Bay. As indicated earlier, a transition of seasonal development was observed in the Upper Great Lakes. Lake Superior showed reduced seasonality while Lake Huron exhibited distinct peaks. The pattern for Georgian Bay was between these two extremes, exhibiting two peaks, one in the spring and fall respectively (Fig. 3). The spring composition was mainly made up of diatoms, Chrysophyceae and Cyanophyta with species such as *Gomphosphaeria lacustris, Chlorella* sp., *C. vulgaris, Gloeocystis* sp., *Chrysochromulina parva, Dinobryon cylindricum, D. sertularia, Pseudokephyrion attenuatum, Cyclotella comta, C. glomerata, C. ocellata, C. stelligera, C. striata, Fragilaria crotonensis, Melosira granulata, Rhizosolenia eriensis, R. gracilis, Stephanodiscus Niagarae, Synedra acus, S. ulna, Tabellaria fenestrata, Rhodomonas minuta, Gymnodinium* sp., *G. helveticum,* and *G. uberrimum.*

The species composition in the summer was quite similar to the spring. However some additional species such as *Anabaena spiroides, A. subcylindrica, Chrysamoeba* sp., *Ochromonas elegans, Uroglena americana* and *U. volvox* were also observed (Tables 3a, b). Similarly, the species composition during the fall was very similar to the spring and the summer. Species which occurred during the fall only included *Chrysosphaerella longispina, Fragilaria capucina* and *Melosira granualata* var. *angustissima* (Table 4).

Lake Huron. Among the Upper Great Lakes, Lake Huron showed relatively well-developed patterns of seasonality with a spring maxima (June) and a small peak during the summer (August). No peaks were recorded in the fall. The diatoms were the most common species during all three seasons with Cyanophyta and Chlorophyta as co-dominants. The species composition is detailed in Tables 2a, b, 3a, b and 4. Based on their relative biomass contribution, species such as *Oscillatoria Agardhii, Chlorella vulgaris, Chrysochromulina parva, Ochromonas* spp., *Rhizosolenia eriensis, Melosira granulata, M. italica* var. *subarctica, M. islandica, Asterionella formosa, Fragilaria crotonensis, Synedra acus* var. *radians, Tabellaria flocculosa, Cryptomonas erosa, Rhodomonas minuta* and *Gymnodinium* sp. were important in the spring.

During the summer, *Anabaena subcylindrica, A. spiroides, Oscillatoria Agardhii, Gomphosphaeria aponina, Aphanothece clathrata, Chroococcus limneticus, Chlamydomonas* sp., *Chlorella vulgaris, Gloeocystis* sp., *Oocystis lacustris, Ochromonas* spp., *Chrysochromulina parva, Chromulina* sp., *Cyclotella ocellata, C. glomerata, C. striata, C. stelligera, C. comta, Asterionella formosa, Tabellaria fenestrata, Fragilaria crotonensis, Melosira granu-

lata, M. islandica, Stephanodiscus tenuis, Rhodomonas minuta, Cryptomonas erosa, Katablepharis ovalis, and *Gymnodinium varians* were predominant.

In the fall, species such as *Chroococcus dispersus* var. *minor, Gomphosphaeria aponina, Anabaena subcylindrica, Scenedesmus bijuga, Asterionella formosa, Fragilaria crotonensis, Tabellaria fenestrata, Cyclotella stelligera, Melosira granulata, Cryptomonas erosa,* and *Rhodomonas minuta* were commonly found.

Lake Michigan. Three cruises were conducted in 1982 on Lake Michigan, one during the spring (May) and two during the summer (July and September). Although it is difficult to comment in detail on seasonality because no fall cruise was carried out, it is worthwhile to examine the spring and summer data and compare with the other Great Lakes because of the extensive spatial coverage and the limited studies available for Lake Michigan which use the Utermöhl technique. Further details of studies of phytoplankton investigations in Lake Michigan can be found in Tarapchek & Stoermer (1976) and Claflin (in press). Tables 2a, b and 3a, b show the common species found during the spring and summer cruises that contributed more than 5% of the total phytoplankton biomass. The diatoms dominated in the lake during the spring such as *Melosira Binderana, M. islandica, M. islandica* var. *helvetica, M. italica* var. *subarctica, Stephanodiscus astraea* var. *minutula, S. Hantzschii* and *S. niagarae.* The phytoflagellates included a mixture of Chrysophyceae, Cryptophyceae and Dinophyceae such as *Chrysochromulina parva, Dinobryon sociale, Ochromonas spp., Cryptaulax rhomboida, Cryptomonas erosa, C. phaseolus, Rhodomonas minuta, R. minuta* var. *nannoplanctica, Gymnodinium eurytopum, G. helveticum* and *G. helveticum* var. *achroun.*

Although the spring diatoms continued to be dominant in the summer, Cyanophyta biomass increased significantly compared to the spring. Dominant blue-greens included *Anabaena flos-aquae, A. planctonica, Oscillatoria limosa* and *O. tenuis.* Chrysophyceae contributed more than 5% to the total phytoplankton biomass during July. The phytoflagellates which appeared during the summer were *Dinobryon divergens, Chrysocapsa* sp., *Stichogloea Doederleinii, Uroglena americana, Cryptomonas ovata, Ceratium hirundinella, Glenodinium Borgei, Peridinium aciculiferum* and *P. gatunese.*

Our investigation has provided an extensive lakewide coverage (55 stations) of Lake Michigan. The study has demonstrated the abundance and significance of phytoflagellates and nannoplankton and whose presence within the lakes have been neglected in the past Lake Michigan investigations. This is mainly attributable to the lack of application of the Utermöhl technique (Claflin, in press) for the identification and enumeration of phytoplankton.

Case study

As it is impossible here to deal with all eight ecosystems of the North American Great Lakes, an overview has been presented for all the ecosystems. Also Lake Ontario, which represents a mesotrophic-eutrophic ecosystem has been selected as a case study.

Several papers have been published on the phytoplankton ecology of Lake Ontario (Munawar & Nauwerck, 1971; Stadelmann & Munawar, 1974; Munawar & Munawar, 1975, 1982). The inshore and offshore developmental pattern of phytoplankton is a characteristic feature of Lake Ontario which has been discussed in detail earlier in this paper and elsewhere. An attempt has been made in the following study to explore the seasonality of nutrient and biomass relationships from some 1970 investigations and from an extensive study conducted in 1983 dealing with ultraplankton and picoplankton.

The seasonal fluctuations of physical and chemical variables for the Great Lakes in general have been given by Weiler (1981) and for Lake Ontario by Munawar *et al.* (1974) and Dobson (1984). This study relates major physical and chemical factors to the seasonal fluctuations of phytoplankton biomass and its taxonomic groups (Fig. 7) for the inshore and offshore regions respectively on a lakewide basis. As discussed earlier, four peaks of biomass were observed in this region for the entire year. The winter, spring and summer pulses were well-developed whereas the fall pulse was less pronounced. The winter and spring peaks were mainly composed of diatoms. The winter peak recorded during March developed when the water temperature was about 0.6 °C and consisted mainly of

Stephanodiscus tenuis, S. Hantzschii var. *pusilla, Asterionella formosa, Melosira islandica* var. *helvetica, M. varians* and *Synedra ulna.* Later, this diatom pulse faded out when the water temperature rose to 2 °C. However, another pulse was recorded at the end of April when the temperature was 6 °C. This pulse was dominated by *Melosira Binderana* with *Asterionella gracillima, Stephanodiscus tenuis*

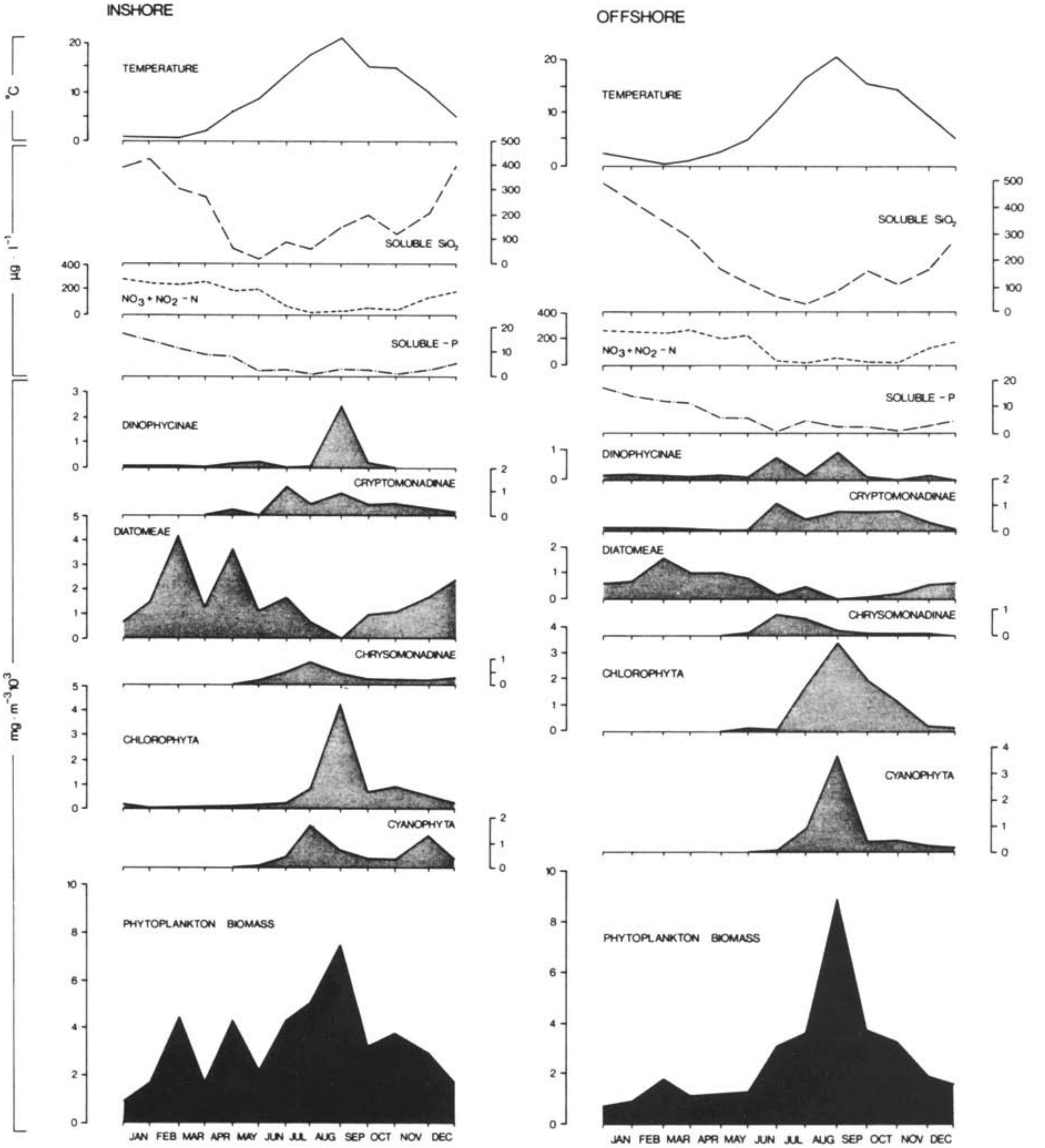

Fig. 7. Seasonal fluctuations of temperature, nutrients, biomass and taxonomic groups in the inshore and offshore region of Lake Ontario, 1970. Each value is a mean of several stations per region.

and *Melosira varians* co-dominating. *Melosira Binderana,* which is often associated with eutrophication (Brunel, 1956; Holland, 1968; Munawar & Munawar, 1975) was the most important species which was responsible for a very striking inshore/offshore gradient. *Melosira Binderana* developed profusely when temperatures ranged between 6 °C and 9 °C. During the cruise (April/May), the thermal bar was largely confined to the inshore region while the rest of the lake was below 4 °C. This area inside the thermal bar contained profuse concentrations of *M. Binderana* (Fig. 8) (Munawar & Nauwerck, 1971; Munawar & Munawar, 1975), high rates of primary production (from 10 to 40 mg C m^{-3} h^{-1}) and greater depletion rates of soluble phosphorus and silicon (expressed as silica). Silica concentration was reduced to extremely low levels (25 μg l^{-1}). The temperature appears to be one of the important factors governing the development of diatoms in the inshore region.

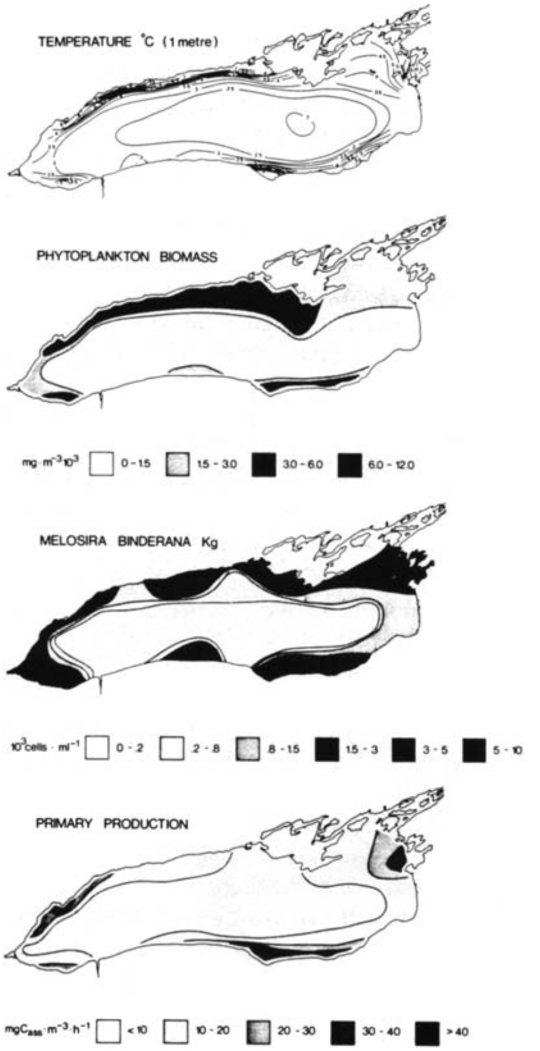

Fig. 8. Distribution of *Melosira Binderana* and other variables in Lake Ontario during the thermal bar conditions (spring), 1970.

During this period of winter and spring, the soluble nutrients were high in concentration (258 μg inorganic N l^{-1} and 432 μg SiO_2 l^{-1}) but showed a decreasing trend at the end of spring resulting in minima (33 μg N l^{-1}, 1.1 μg P l^{-1}, 32 μg SiO_2 l^{-1}) during the summer. During the period of low nutrients in summer, high biomass values were observed when the temperature was high and the population mainly composed of greens, blue-greens and dinoflagellates. Later, in the fall, the nutrients increased while the biomass and temperature declined. Diatoms and blue-greens dominated. The observed seasonal fluctuations of temperature, nutrients and phytoplankton suggest that the abundant growth of algae might have been responsible for the decline or depletion of nutrients (Gächter *et al.,* 1974).

Figure 7 shows the offshore development of phytoplankton on a lakewide basis in relation to temperature and nutrients. The offshore region had a single peak which occurred during summer at high temperature. The diatom concentration was not as great in this region, in contrast to that observed in the inshore region. During winter and spring the diatoms did not materialize into a pulse although the temperature was similar to that of the inshore region (0.7 °C). The nutrient levels were also similar to that of the inshore region and yet the diatoms did not develop as abundantly. This may be due to a different species composition because such typical inshore species as *Stephanodiscus Hantzschii* var. *pusilla* and *Melosira varians* were less abundant in the offshore region. The reduced abundance of such species might be responsible for the reduced concentration of diatoms. On the other hand, *Melosira islandica* subspec. *helvetica* dominated the offshore population. This species is fairly common in the Great Lakes and is known to exhibit low growth rates (Verduin, 1972). This might account for the less abundant concentration of diatoms in the offshore region.

Although the diatoms were not as abundant in the offshore waters during the winter and spring the surface values of silica became much lower by late spring. Nitrogen showed a slow decline until June with the minimum during July (30 $\mu g\ l^{-1}$). Phosphate-phosphorus concentration slowly decreased until April when it declined more noticably. However, the minimum was achieved only in October (1.1 $\mu g\ l^{-1}$). Silica showed a decreasing trend until June when it decreased more and the minimum was recorded in July (45 $\mu g\ l^{-1}$).

Differences in the concentrations of nutrients and phytoplankton in the inshore and offshore regions during the winter-spring period may be explained by taking the depth of the water column into consideration. The entire lake is well-mixed horizontally and vertically during this period (Sweers, 1969). The inshore region is shallow and turbulent when wind-driven currents mix the sediments with the whole water column thus allowing the release of nutrients. The offshore region is deeper (mean depth 97 m) but is also well mixed. Consequently, the diatoms would be mixed to deeper strata and hence high concentrations were not found in the surface waters. Also, since the water column is deeper, the chances of nutrient resupply from the sediments is limited.

At the end of spring and during summer, similar events took place as in the inshore region. The nutrients declined in concentrations and the surface water temperature rose. During this period blue-greens, green algae and dinoflagellates dominated the phytoplankton community.

With the advent of fall overturn, when the temperature dropped and stratification broke down, the nutrients were found to increase and the summer populations of greens and dinoflagellates were replaced by diatoms which appear to prefer lower temperatures. The diatoms increased in abundance as the winter conditions prevailed.

Therefore it appears that phytoplankton seasonality was somewhat complex which may be closely related to a variety of factors such as water temperature, circulation, turbulence, stratification and the resulting nutrient availability.

The relationship between biomass, chlorophyll *a* and primary productivity can now be considered. On a lakewide basis, the seasonal fluctuations of these variables were generally similar during the winter, spring and fall seasons when diatoms dominated the phytoplankton community (Fig. 9). However, during the summer when the production remained constant, a discrepancy was observed between biomass and chlorophyll *a* fluctuations both in the inshore and offshore regions. The biomass showed a pronounced peak during the summer, whereas chlorophyll *a* showed significantly low values during this period when greens and blue-greens dominated the community and diatoms were absent. The discrepancy has been attributed to problems with pigment extraction procedures, nutrient deficiencies and/or the species composition which may be difficult to extract (Vollenweider *et al.,* 1974; Munawar *et al.,* 1982).

The activity coefficients (mg C assimilated per mg of biomass and hour) commonly known as production/biomass quotients (P/B), were calculated (Talling, 1969; Vollenweider *et al.,* 1974; Stadelmann & Munawar, 1974). The hourly activity coefficient showed two peaks in both regions, one each in spring and fall respectively. It ranged from 0.02 to 0.01 mg C $mg^{-1}\ h^{-1}$ in the inshore region where both peaks were equal in magnitude. So, in terms of the relative photosynthetic efficiency of the phytoplankton, it is apparent that spring and fall populations are equally active, whereas the summer population was extremely inefficient and unproductive. In the offshore region, the activity coefficient ranged from 0.002 to 0.02 mg C $mg^{-1}\ h^{-1}$. A higher quotient than that in the fall was recorded in the spring, also higher than that during the spring peak of the inshore region. These results suggest that the offshore population was relatively more efficient (photosynthetically) than the inshore community during the spring, whereas the inshore population seemed to be comparatively more efficient than the offshore assemblage during the fall season. These observations are also supported by Munawar *et al.* (1978). They reported that higher chlorophyll/biomass ratios were observed during the unstratified period (spring and fall) in Lake Ontario (0.31) as opposed to the stratified period (0.14) for the 1970 lakewide study. Furthermore, the seasonal peaks of the activity coefficient are extremely good indicators of the nutrient status and its bioavailability since, as discussed earlier, N, P and Si were abundantly available during the spring and fall seasons (Fig. 7).

Seasonality of phytoplankton size assemblages

Although the size composition of phytoplankton has only recently attracted the attention of limnol-

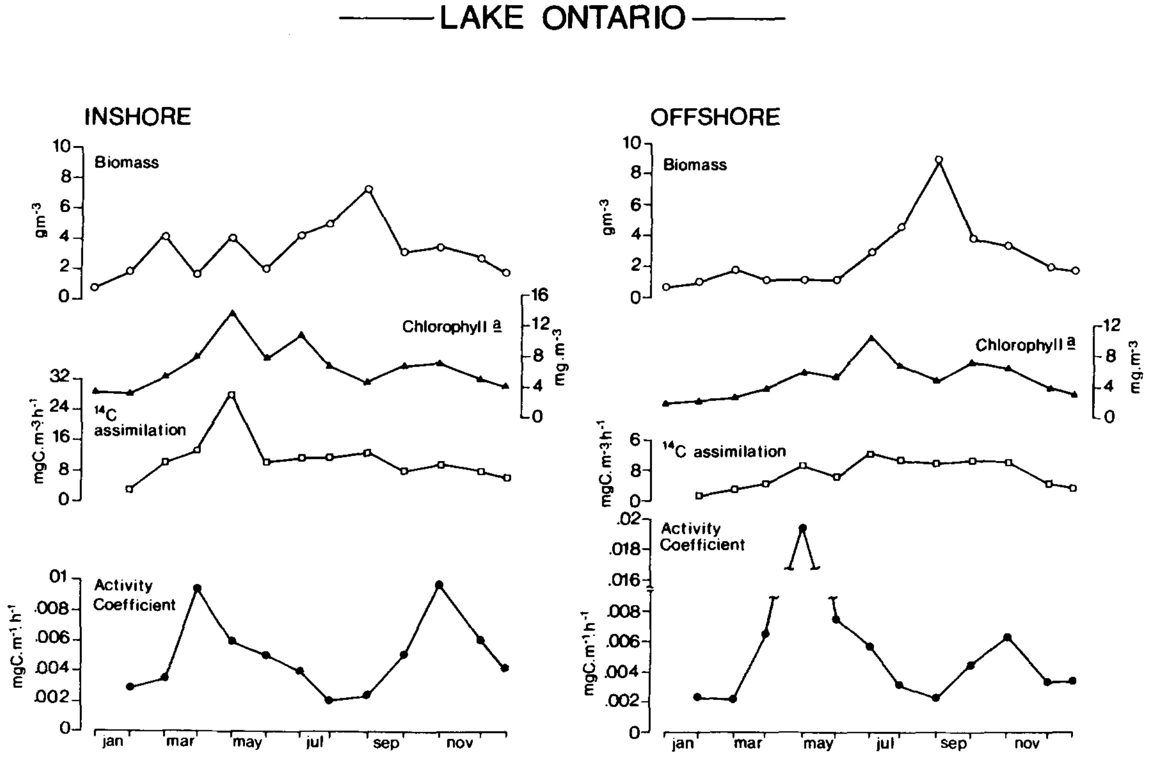

Fig. 9. Seasonality of mean biomass, chlorophyll *a*, primary productivity and Activity Coefficient (P/B) in the inshore/offshore regions of Lake Ontario, 1970.

ogists, toxicologists and fisheries biologists, the size composition of Great Lakes phytoplankton has been studied in our laboratory since 1970 (Munawar *et al.,* 1974, 1978; Munawar & Fahnenstiel, 1982). It perhaps represents the first size spectra data available for Great Lakes phytoplankton in general and Lake Ontario in particular. The algae were grouped according to their largest dimensions, a technique which has been used by several researchers (Pavoni, 1963; Willén, 1959; Kalff, 1972; Munawar *et al.,* 1978). Recently Bailey-Watts (this volume) has analyzed the phytoplankton of Loch Leven based on measurements of the greatest axial linear dimension. In our laboratory, based on microscopic measurements, species larger than 64 μm were considered netplankton whereas those smaller were called nannoplankton. The latter size group (< 64 μm) was further divided into five size fractions (< 5 μm, 5–10 μm, 10–20 μm, 20–40 μm, 40–64 μm).

An example of seasonal variations of phytoplankton size assemblages at a nearshore and an offshore station in Lake Ontario (1972) is given in Fig. 10. It is apparent that the nannoplankton (< 64 μm) dominated the overall phytoplankton community at both stations throughout the study period. A higher percentage of netplankton was found during the spring when the biomass concentration was relatively low. The biomass peak at the nearshore station during late June was dominated by nannoplankton (94%) with the 40–64 μm size fraction containing *Asterionella formosa, Melosira islandica* and *Gymnodinium uberrimum* contributing the most (Table 5). The offshore station recorded biomass minima during the unstratified spring and fall periods with netplankton prevalent during the spring and nannoplankton dominating in the fall (Fig. 10). The 10–20 μm size fraction was also common during the two seasons. The biomass maximum was observed during the stratified (summer) period, once again dominated by nannoplankton (94%). The 40–64 μm size fraction, con-

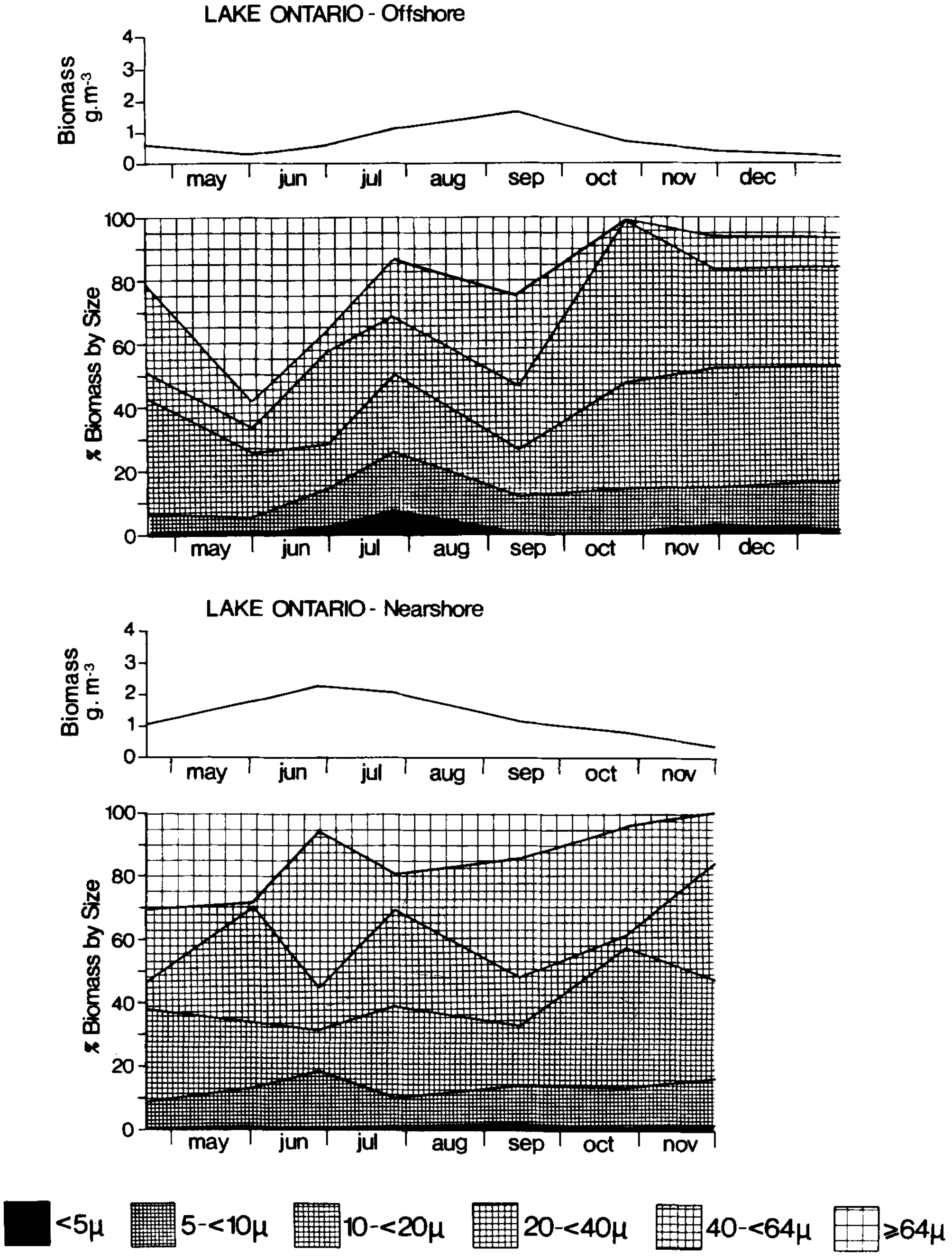

Fig. 10. Seasonality of phytoplankton size assemblages based on microscopic enumeration and measurements at an offshore and a nearshore station of Lake Ontario (1972).

sisting of *Peridinium aciculare* and *Peridinium* sp., were the main components of the summer peak (47%).

The size fractionation technique traditionally used, based on microscopic counts and measurements, has resulted in a detailed seasonal size data base. The base, together with taxonomic data, has succeeded in tracing the changes in species and size

Table 5. Common species of varous size assemblages at a nearshore and offshore station contributing 1% or more to the total phytoplankton biomass, Lake Ontario (1972).

		Spring		Summer		Fall
Nearshore	>64 µm	Oscillatoria sp.	40–64 µm	Asterionella formosa	40–64 µm	Gymnodinium helveticum
		Gomphosphaeria aponina		Tabellaria fenestrata		Tabellaria fenestrata
		Asterionella gracillima		Melosira islandica		
		Diatoma elongatum		Cryptomonas reflexa	10–20 µm	Chlamydomonas sp.
		Melosira Binderana		Gymnodinium helveticum		Cryptaulax rhomboidea
		M. islandica		Peridinium aciculiferum		Cryptomonas erosa
		Nitzschia sp.				Katablepharis ovalis
		Synedra acus	10–20 µm	Phacotus sp.		Rhodomonas minuta
				Gyromitus cordiformis		Glenodinium sp.
				Oocystis Borgei		
				O. lacustris		
				O. parva		
				O. submarina		
				Franceia ovalis		
				Cryptaulax rhomboidea		
				Katablepharis ovalis		
				Cryptomonas erosa		
				C. caudata		
				Rhodomonas minuta		
				Gymnodinium varians		
				G. uberrimum		
				Glenodinium sp.		
Offshore	>64 µm	Asterionella formosa	>64 µm	Oscillatoria sp.	20–40 µm	Cryptomonas erosa
		A. gracillima		Gomphosphaeria aponina		C. gracilis
		Melosira Binderana		Asterionella formosa		C. Marssoni
		M. islandica		A. gracillima		Gymnodinium helveticum
		Nitzschia sigmoidea		Diatoma elongatum		
				Fragilaria crotonensis	10–20 µm	Cryptomonas erosa
	10–20 µm	Chlamydomonas sp.		Melosira islandica		Glenodinium sp.
		Cryptomonas erosa		Oedogonium sp.		Oocystis lacustris
		Glenodinium sp.		Pediastrum sp.		Rhodomonas minuta
		Gymnodinium varians		Sphaerocystis sp.		
		Rhodomonas minuta				
			40–64 µm	Oscillatoria sp.		
				Asterionella gracillima		

composition of phytoplankton which occur due to the impact of nutrients and contaminants. Further research has shown that minute organisms such as ultraplankton/picoplankton are extremely sensitive to contaminants (Munawar *et al.*, 1983) and are an important fisheries food resource via zooplankton grazing (Ross & Munawar, in press). The importance of size spectra has also been recognized in modelling and for the prediction of fish stock and yearly yield (Sprules & Munawar, in press). Therefore, the seasonal monitoring of size spectra could serve as an early warning system towards an efficient management of chemical enrichment of the aquatic food chain.

Picoplankton-ultraplankton seasonality in Lake Ontario

This section of the study explores seasonality of phytoplankton, which has been size fractionated into picoplankton (<2 µm) and ultraplankton (2–20 µm), in terms of chlorophyll *a* and primary productivity. These size fractions were chosen since it has been demonstrated by Munawar & Munawar (1981) that a greater portion of the pigments and primary productivity was contained in these two groups. Moreover, these fractions appear to be sensitive to metal toxicity (Munawar, 1982; Munawar & Munawar, 1982, 1984; Munawar et al. 1984) and comprise a major food source for Lake Ontario zooplankton (Ross & Munawar, 1981). The data base showing the seasonal fluctuations of picoplankton and ultraplankton was collected from April to October 1983 from Station 81 (eastern basin) of Lake Ontario. The data are intensive since they are based on frequent (weekly) collections. The objective was to focus on greater frequency of sampling at one specific site.

The data were organized into two sets. The 'abiotic' set consists of temperature (TEMP, C), total phosphorus (TP, mg l^{-1}), total filterable phosphorus (TFP, mg l^{-1}), soluble reactive phosphorus (SRP, mg l^{-1}), nitrate + nitrite nitrogen (NO_2 + NO_3, mg l^{-1}), and reactive silica (SiO_2, mg l^{-1}). The values used for these variables are epilimnetic means from discrete sampling depths. The total depth of the epilimnion was determined from temperature profiles, with a maximum of 20 m for the year. Under unstratified conditions, 20 m profiles were used, approximating the maximum depth of the epilimnion at the peak of thermal stratification. The second set is comprised of 'biotic' variables, such as particulate organic carbon (POC, mg l^{-1}), ultraplankton production (ULTRAPR, mg C m^{-3} h^{-1}), picoplankton production (PICOPR, mg C m^{-3} h^{-1}), and uncorrected chlorophyll *a* values for phaeo-pigments for both algal fractions, namely ultrachlorophyll (ULTRACHL) and picochlorophyll (PICOCHL mg m^{-3}), respectively. These biotic data were measured using integrated water-column samples from the entire epilimnion.

The overall approach of the study entails the following sequence of data analysis: (1) the use of partial correlation analysis to establish significant 'true' relationships and/or spurious relationships between the variables; (2) the use of canonical correlation analysis to account for variance between the two data sets; and (3) the use of factor analysis to reduce the data sets into a smaller set of unique 'factors', each relating to some particular concept of phytoplankton ecology (Cooley & Lohnes, 1971; Nie *et al.*, 1975; Munawar & Wilson, 1978).

The two data sets were subdivided according to the presence or absence of thermal stratification into unstratified (spring), stratified (summer), and whole-year periods. The unstratified period was comprised of seven observations collected weekly from 11 April-23 May. Because of the relatively small size of this set, it failed to meet the restrictions required for factor analysis, and was therefore excluded from the final presentation.

The nutrient variables are plotted as a function of time in Fig. 11. Figure 12 is an equivalent plot for the biotic variables and temperature. The production of the ultraplankton (ULTRAPR, 2–20 μm) is substantially higher than for the picoplankton (PICOPR, <2 μm) throughout the year. The chlorophyll *a* concentrations of the two size fractions are similar only during the unstratified period in the spring. The production peak in late August is similar to the biomass results of Munawar & Nauwerck (1971). The relationship between temperature and the biotic variables is quite evident from Fig. 12. Irregularities in the temperature regime are closely followed by similar changes in the other variables, particularly ULTRAPR. In addition, the nutrient parameters SiO_2 and NO_2 + NO_3 can be seen to vary with temperature.

For the partial correlation analysis, temperature (TEMP) was chosen as the control variable. The biotic and abiotic parameters were subjected to first-order partial correlations, assessing possible correlations with temperature. During the unstratified

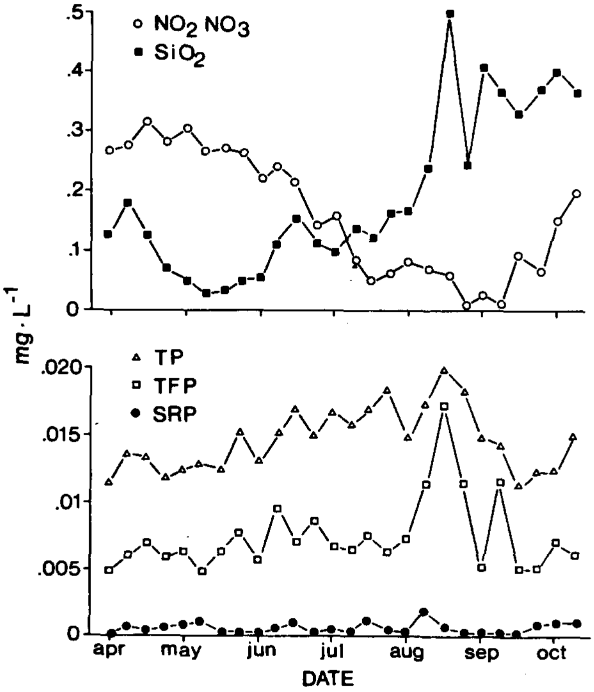

Fig. 11. Seasonality of major nutrients at an offshore station in Lake Ontario, 1983.

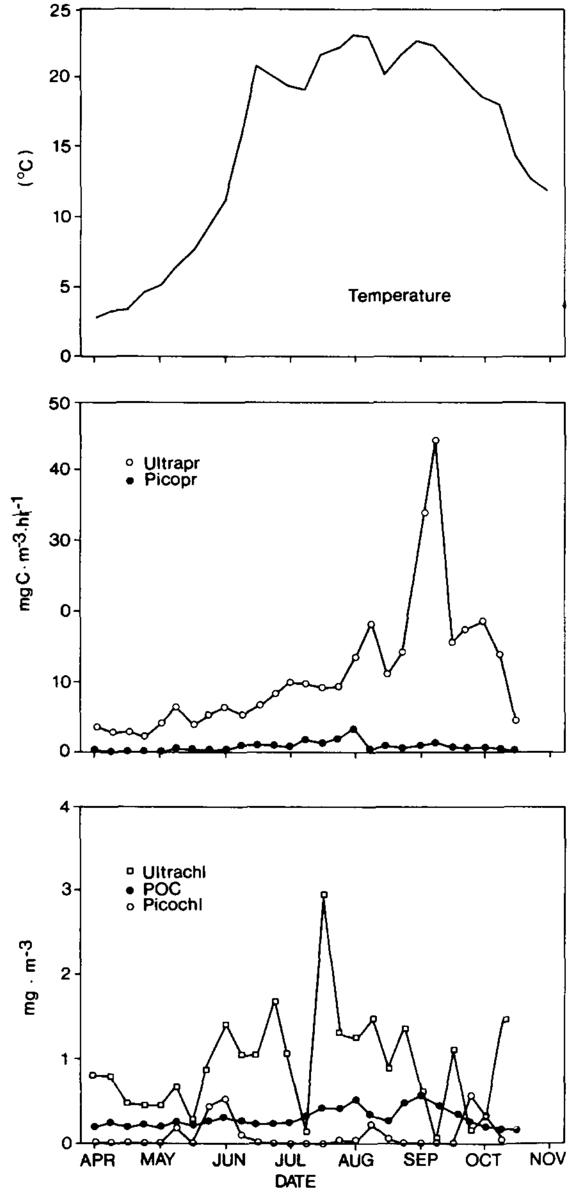

Fig. 12. Seasonal fluctuations of temperature, picoplankton and ultraplankton productivity, and concentration of particulate organic carbon (POC) and chlorophyll *a*, at an offshore station in Lake Ontario, 1983.

period, only two significant partial correlate pairs were calculated: ULTRACHL/TFP ($r = -0.912$), and PICOPR/SRP ($r = -0.927$). During the stratified period, two partial correlate pairs were also found to be significant. They were: ULTRAPR/$NO_2 + NO_3$ ($r = -0.530$), and ULTRAPR/SiO_2 ($r = 0.566$).

The canonical correlation results are presented in Table 6. During the unstratified period, the analysis could not be completed due to technical constraints in the matrix manipulations with this particular data set. In the stratified period, one significant root was found, consisting mainly of the variables PICOPR, POC, $NO_2 + NO_3$, SRP, and TFP. The loadings on these variables suggest that when $NO_2 + NO_3$ and SRP were high and TFP was low, PICOPR (picoplankton production) was high while POC was low. It is logical, then, to assume that picoplankton production was high when nutrients like nitrogen and phosphorus were present in high concentrations and so could not be considered as growth-limiting factors as discussed earlier for the lakewide analyses. That POC is a negative biotic covariate can be explained by the fact that the picoplankton generally have high P/B ratios. In addition, because of their low organic carbon levels and small contribution to the total biomass, the picoplankton might be expected to have such a relationship with POC. For comparison, the whole year's results are included at the bottom of Table 6. The first significant root accounted for 93 percent of the variance. One possible interpretation of the large loading on ULTRAPR and the large negative loading on $NO_2 + NO_3$, is that the nitrate + nitrite levels correspond to consumption by the ultraplankton size fraction.

Due to the presence of negative eigenvalues in the factor analysis computations with the unstratified data, the latter have been disregarded. For the stratified data set, the first factor was heavily loaded on several variables such as: TEMP, TP, TFP, $-NO_2 + NO_3$, POC, $-$PICOCHL, and PICOPR (Table 7). This suggests that when TEMP, TP, TFP, and POC were high, PICOPR was also high, although PICOCHL was low. The second factor heavily loaded $-NO_2 + NO_3$, SiO_2, and ULTRAPR. The relationship of SiO_2 to ULTRAPR is obvious, since the late August peak in ultraplankton production consisted of a small numbers of diatoms. The peak was dominated by Chlorophyta, Cryptophyceae and Dinophyceae when the reactive silica concentrations in the lake were high. The large negative loadings on $NO_2 + NO_3$ in the first two factors indicates the relationship of the nutrient to algal consumption. The third factor is comprised

Table 6. Canonical variates relating to phytoplankton components and environmental factors for Station 81, Lake Ontario.

	Data subset			
	Unstratified	Stratified	Whole year	
Roots significant at 5% level	-	1	1	2
X value	-	55.4	73.9	40.2
Right hand variables				
ULTRACHL	-	0.209	0.195	0.196
PICOCHL	-	0.348	0.045	0.362
ULTRAPR	-	−0.174	0.702	0.442
PICOPR	-	0.510	0.397	0.260
POC	-	−1.200	0.031	−1.137
Left hand variables				
TEMP	-	0.098	0.364	1.070
TP	-	−0.475	0.114	−1.130
SRP	-	0.595	−0.140	0.374
TFP	-	−0.512	−0.243	−0.232
NO_2NO_3	-	0.622	−0.586	0.701
SiO_2	-	0.173	0.182	0.468
Root interpretation:	Right Hand	−POC PICOPR	ULTRAPR	−POC
Variables with |canonical variate| >0.5	Left Hand	NO_2NO_3 −TFP SRP	$-NO_2NO_3$	TEMP −TFP NO_2NO_3

Table 7A. Factor analysis results for stratified period, L. Ontario station 81.

Factor		1	2	3	4	
Sum of squares		3.84	2.46	1.77	1.18	
Percent total S.S.		34.9	22.4	16.1	10.7	
						Communality
Variable:						
Temperature	(TEMP)	0.758	0.333	−0.282	−0.161	0.792
Particulate organic phosphorous	(POC)	0.775	−0.086	−0.440	0.298	0.891
Total phosphorous	(TP)	0.918	−0.209	0.175	−0.014	0.917
Soluble reactive phosphorous	(SRP)	0.328	0.100	0.682	−0.479	0.812
Total filtered phosphorous	(TFP)	0.553	0.149	0.634	0.377	0.872
Nitrate-nitrite	(NO_2NO_3)	−0.572	−0.677	0.280	0.056	0.868
Reactive silica	(SiO_2)	0.067	0.811	0.379	0.206	0.848
Ultraplankton chl-a	(ULTRACHL)	0.325	−0.340	−0.110	0.669	0.681
Picoplankton chl-a	(PICOCHL)	−0.754	0.340	−0.338	0.087	0.781
Ultraplankton production	(ULTRAPR)	−0.044	0.932	−0.258	0.023	0.938
Picoplankton production	(PICOPR)	0.635	−0.271	−0.433	−0.441	
Factor interpretation: Variables with |Factor loading| >0.5		TEMP POC TP TFP $-NO_2NO_3$ −PICOCHL PICOPROD	$-NO_2NO_3$ SiO_2 ULTRAPR	SRP TFP SiO_2	ULTRACHL	

Table 7B. Factor analysis results for whole year for L. Ontario station 81.

Factor		1	2	3	
Sum of squares		4.87	2.12	1.50	
Percent total S.S.		44.3	19.2	13.6	
					Communality
Variable:					
Temperature	(TEMP)	0.917	0.186	−0.095	0.885
Particulate organic phosphorous	(POC)	0.804	−0.210	−0.405	0.855
Total phosphorous	(TP)	0.797	−0.538	0.027	0.925
Soluble reactive phosphorous	(SRP)	0.269	−0.297	0.623	0.548
Total filtered phosphorous	(TFP)	0.575	−0.353	0.531	0.738
Nitrate-nitrite	(NO_2NO_3)	−0.916	−0.307	0.014	0.933
Reactive silica	(SiO_2)	0.552	0.400	0.572	0.791
Ultraplankton chl-a	(ULTRACHL)	0.476	−0.215	−0.342	0.389
Picoplankton chl-a	(PICOCHL)	−0.016	0.864	−0.155	0.770
Ultraplankton production	(ULTRAPR)	0.680	0.673	0.114	0.929
Picoplankton production	(PICOPR)	0.718	−0.187	−0.420	0.727
Factor interpretation: Variables with |Factor loading| >0.5		TEMP POC TP TFP $-NO_2NO_3$ SiO_2 ULTRAPR PICOPROD	−TP PICOCHL ULTRAPR	SRP TFP SiO_2	

of nutrient variables alone.

Throughout the entire year, three factors could be identified. The first factor relates to eight variables. It suggests a relationship between primary production and nutrients. The second factor relates –TP, PICOCHL, and ULTRAPR. The final factor is a nutrient factor, as above.

Although there appears to be some contradiction in the interpretation of canonical correlation analysis, it should be remembered that these two methods are asking different questions. Canonical correlation analysis attempts to explain the maximum amount of variance between two sets of variables, while factor analysis explains the variance for the purpose of data reduction. Note that in spite of some differences in interpretation between these methods, the picoplankton seem to be the most significant size fraction of the two size ranges studied here and plotted in Fig. 12 during the stratified period (in terms of variance, but not in terms of real measurement). The analysis of the whole year shows that ultraplankton production is also an important plankton component.

Discussion

The application of the Utermöhl inverted microscope technique together with standardized taxonomic and data-processing procedures has resulted, for the first time, in an extensive data base in all of the Great Lakes. The eutrophic/mesotrophic Lower Great Lakes system exhibited well-developed high biomass seasonal peaks, with inshore/offshore differentiation and with the spring maxima in the inshore region being the most pronounced. However, the oligotrophic Upper Great Lakes had low biomass and generally lacked well-developed seasonal patterns. No seasonal trends were observed in the oligotrophic Lake Superior.

The seasonal comparison of phytoplankton biomass based on mean biomass concentration indicated that western Lake Erie showed the maximum concentration in all three seasons (spring, summer, fall). Western Lake Erie, central Lake Erie and Lake Ontario showed similar concentrations of biomass during the summer and fall seasons.

The seasonality of various taxonomic groups of phytoplankton show an interesting differentiation between individual lakes. The Cyanophyta were abundant during the summer in Lakes Ontario, Huron, western Lake Erie and Georgian Bay. The Chlorophyta were prevalent in Lake Ontario during all seasons and were also common in eastern Lake Erie and Georgian Bay during summer and fall seasons. The Chrysophyceae were abundant during spring in Georgian Bay, Lake Superior, North Channel and Lake Michigan. During the summer, they showed maximum development in Lake Superior. The Diatomeae (Bacillariophyceae) demonstrated the greatest seasonal fluctuations, with maximum development usually during the spring and fall in most of the lakes with the exception of Lake Superior which did not show any seasonal trends and North Channel where diatoms prevailed even during summer. The Cryptophyceae were most abundant during spring in Lake Superior, eastern and central Lake Erie and Lake Ontario. During the summer, these phytoflagellates were common in eastern Lake Erie, Lake Superior and Lake Michigan whereas they were abundant in Lake Superior, Lake Ontario and the North Channel during the fall. The Dinophyceae contributed significantly to the phytoplankton population of eastern and central Lake Erie only during the spring and summer.

The seasonal succession of species provided interesting comparisons between the Lower Great Lakes harbouring eutrophic to mesotrophic species and the Upper Great Lakes with oligotrophic species. Some species were seasonally unselective and eurytopic in their distribution.

The large data base, generated with standard techniques over a long period, has enabled a comprehensive overview for the first time. Hopefully these data will facilitate a better understanding of algal seasonality – a key factor for the management, protection and conservation of the North American Great Lakes from nutrient and contaminant pollution.

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