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Phytoplankton Biomass and Species Composition In Lake Erie, 1970 to 1987

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ABSTRACT. *Phytoplankton were collected at offshore sites during 33 cruises in the spring, summer, and autumn from 1983 to 1987. Forty-nine common species and varieties accounted for 83.3% of the total abundance and 83.1% of the biomass. Over the 5-year study period, the phytoplankton biomass (mean ± S.E.) of the western, central and eastern basins averaged 1.88 ± 0.12 g/m*^{3}*, 1.04 ± 0.075 g/m*^{3}*, and 0.63 + 0.071 g/m*^{3}*, respectively. Depending on the basin, a 52 to 89% reduction in mean weighted algal biomass had occurred in the offshore waters of Lake Erie between 1970 and 1983-87. The historically highly productive western basin had a consistent decrease in biomass from 1958 to 1987. In general, occurrences of common species in 1970 and 1983-87 were similar. However, dramatic decreases in the abundances of many nuisance and eutrophic species were evident. A 70 to 98% reduction in biomass of* Stephanodiscus binderanus, S. niagarae, S. tenuis, Aphanizomenon flos-aquae, *and* Rhodomonas minuta *was observed. The decrease in biomass of the nuisance and eutrophic indicator species, the reappearance of mesotrophic species, such as* Asterionella formosa *and* Rhizosolenia eriensis, *common in the 1940s and 1950s, and the decrease in total phytoplankton biomass suggest a major improvement in the offshore waters of Lake Erie.*

INDEX WORDS: *Lake Erie, phytoplankton biomass, abundance, eutrophication.*

INTRODUCTION

Excessive loadings of nutrients, navigation, fish management policies, shoreline alteration, contaminant production and, in general, economic development, ultimately affect lake ecosystems. Ecosystems respond to stress with compensatory changes in community structure and function mediated at the population level (Boesch and Rosenberg 1981). Because phytoplankton have short carbon turnover rates, are sensitive to water quality conditions, and represent an integrative response to perturbation of the lake ecosystem, the determination of phytoplankton abundance and species composition has become established as a method to trace long-term changes in lakes (Munawar and Munawar 1982).

Evidence of appreciable change in the biota and physiochemical conditions in Lake Erie has directed attention to the phytoplankton community (e.g., Makarewicz and Bertram 1991, Dolan 1993, Richards and Baker 1993). Specifically, has there been a reduction or other change in the phytoplankton community concomitant with the decrease in phosphorus loading and in ambient phosphorus concentrations? In this study, the 1983-87 spring and summer phytoplankton data assemblage presented makes it possible to examine the historical, geographic, and seasonal relationships prevailing in Lake Erie and to compare them to previous studies that utilized similar enumeration techniques.

METHODS

Phytoplankton were collected during 33 cruises during the spring, summer, and autumn from 1983 to 1987 (Table 1). An 8-L PVC Niskin bottle mounted on a General Oceanics™ Rossette sampler with a Guildline™ electrobathythermograph (EBT) was used to collect phytoplankton. In deeper waters, phytoplankton samples were obtained by compositing equal aliquots of samples collected at

TABLE 1. Lake Erie phytoplankton sampling dates, 1983 to 1987. Generally, analyses in this report incorporate only the spring and summer sampling dates.

	Stations Sampled
1983	
25/04-26/04	11
09/05-10/05	11
27/06-01/07	11
06/08-08/08	11
22/08-23/08	11
19/10-21/10	11
21/10-24/10	11
1984	
18/04-19/04	11
20/04-21/04	11
01/05-02/05	11
02/07-03/07	11
05/08-06/08	11
07/08-09/08	11
19/08-20/08	11
04/12-05/12	11
05/12-08/12	11
13/01-14/01/85	9
17/02-18/02/85	9
1985	
24/04-26/04	16
27/04-28/04	16
06/08-08/08	17
12/08-14/08	17
21/11-22/11	17
23/11-25/11	17
1986	
16/04-19/04	20
26/04-28/04	20
05/08-08/08	20
14/08-16/08	20
1987	
19/02	5
01/04-04/04	20
18/04-19/04	20
30/07-01/08	19
16/08-19/08	20

depths of 1, 5 , 10, and 20 m. In the shallow western basin, samples were taken from 1 m, mid-depth, and 1 meter above the bottom. One-liter samples were immediately preserved with 10 mL of Lugol's solution, while formaldehyde was added upon arrival in the laboratory. The settling chamber procedure (Utermöhl 1958) was used to identify (except for diatoms) and enumerate phytoplankton at a magnification of 500×. A second identification and enumeration of diatoms at 1,250x was performed after the organic portion was oxidized with 30% H_2O_2 and HNO_3. The cleaned diatom concentrate was air dried on a #1 cover slip and mounted on a slide (75 × 25mm) with HYRAX™ mounting medium. Replicate identifications were made by different analysts on every 10th sample and compared for consistency in species nomenclature and abundances. Precision goals between replicates were based on the Relative Percent Deviation (RPD = ((larger count-smaller count)/average)×100). For example, the precision goal for replicated Bacillariophyta counts was ± 15%. Values outside this goal were rejected and the samples recounted.

The cell volume of each species was computed by applying average dimensions for each species from each sampling station and date to the geometrical shape that most closely resembled the species form, e.g., sphere, cylinder, prolate spheroid, etc. At least 10 specimens of each species were measured from each sample for the cell volume calculation. When fewer than 10 specimens were present, they were measured as they occurred. For most organisms, the measurements were taken from the outside wall to outside wall. The dimensions of the protoplast were measured for loricated forms, while the dimensions of individual cells were measured for filaments and colonial forms. Biovolume ($\mu m^3/L$) was converted to biomass (mg/m^3) assuming a specific gravity of 1.0 for all phytoplankton ($mm^3/L = mg/m^3$) (Willen 1959, Nauwerck 1963).

The phytoplankton data were computerized. Statistical evaluations and other data manipulations were conducted within the INFO (Henco Software, Inc., 100 Fifth Avenue, Waltham, Mass.) data management system. To allow east to west comparisons, data from stations on a north south axis were averaged to give one point. For example, data from Stations 38, 37, and 36 (Fig. 1) were averaged to form one point on an east to west transect reported as Station 37 in Figures 4, 5, and 6.

RESULTS AND DISCUSSION

Annual Abundance of Major Algal Groups

Unless otherwise noted, only the spring and summer data are presented to allow comparisons between years based on seasonal sampling times. From 1983 to 1987, 639 species representing 158 genera from eight divisions comprised the offshore phytoplankton community of Lake Erie (Table 2). Com-

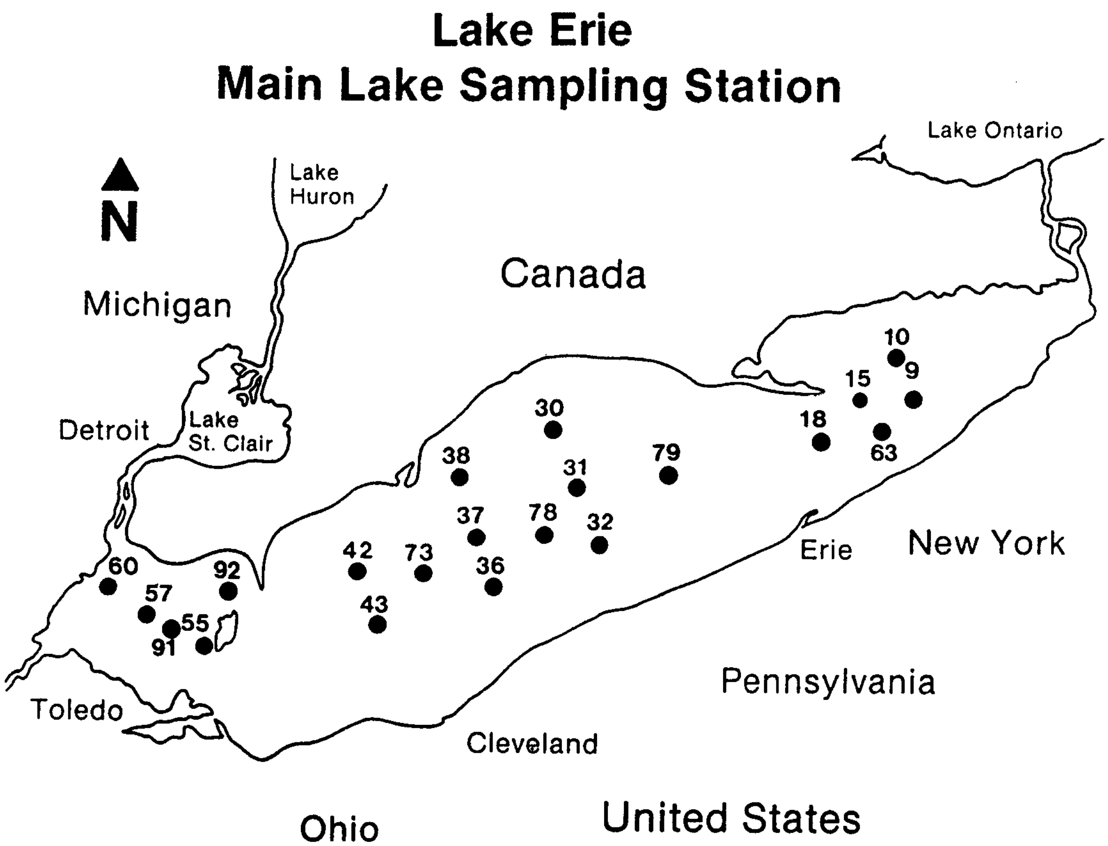

FIG. 1. Lake Erie sampling stations.

mon species by basin for each year are presented in Tables 3 to 5. Averaging all basins, 49 common species and varieties accounted for 83.3% of the total abundance and 83.1% of the total biomass over the five-year period (Table 6). Unidentified organisms represented 16.6% of the total cell numbers but only 4.1% of the total biomass (Table 6).

Highest overall cell abundance was attained by the Cyanophyta and the Cryptophyta (Table 7). The Bacillariophyta contained the largest number (249) of species (Table 2) and the highest relative biomass (range = 39.2% to 56.3% of the total, Table 7). The number of species of Chlorophyta was also high (229), but relative biomass was much lower (range = 10.0 to 18.2%). In contrast, few Pyrrophyta species were present (13), but their relative biomass (range = 11.9 to 19.4%) was greater than the Chlorophyta (Table 7).

Trends in relative biomass of algal divisions from 1983 to 1987 suggest an increase in Cyanophyta and Bacillariophyta and a decrease in Chlorophyta and Cryptophyta (Fig. 2). The biomass of Cyanophyta, however, increased only in the central and western basins, while the Bacillariophyta biomass did not increase and may have decreased slightly in the eastern basin (Fig. 3). The decrease in relative biomass of the Cryptophyta observed for the entire basin was due to a progressive decrease in the cryptophytes in the western basin (Fig. 3). There was no overall pattern of decreasing Chlorophyta biomass by individual basin (Fig. 3).

Geographical Abundance and Distribution of Major Algal Groups

Mean algal biomass (1983 to 1987) decreased in each year from the western to the eastern basin of Lake Erie (Fig. 4b). Although a highly significant ($P < 0.001$, $r^2 = 0.79$) linear line can be fit to the data points (Fig. 4a), there is an obvious step-wise function of decreasing biomass from the western to the central to the eastern basin. Over the 5-year study period, phytoplankton biomass in the western, central, and eastern basins averaged 1.88 g/m^3 (S.E.

TABLE 2. ***Number of species and genera observed in each algal division or grouping, Lake Erie, 1983 to 1987. Spring and summer data only. BAC = Bacillariophyta, CAT = Chloromanophyta, CHL = Chlorophyta, CHR = Chrysophyta, COL = Colorless flagellates, CRY = Cryptophyta, CYA = Cyanophyta, EUG = Euglenophyta, PYR = Pyrrophyta, UNI = Unidentified flagellates.***

	NUMBER OF SPECIES					
	1983	1984	1985	1986	1987	1983–87
BAC	158	124	120	123	130	249
CAT	-	-	1	-	-	-
CHL	103	85	94	134	128	229
CHR	27	27	23	38	38	62
COL	12	10	4	7	6	18
CRY	14	13	16	18	17	23
CYA	14	15	16	21	22	34
EUG	2	-	2	2	1	3
PYR	8	9	6	7	7	13
UNI	3	4	4	6	5	8
TOTAL	341	287	286	356	354	639
	NUMBER OF GENERA					
	1983	1984	1985	1986	1987	1983–87
BAC	27	27	24	26	38	35
CAT	-	-	1	-	-	1
CHL	38	38	36	46	46	68
CHR	11	15	14	16	18	25
COL	5	3	2	2	2	5
CRY	3	3	3	3	3	3
CYA	9	10	8	9	11	14
EUG	2	-	2	2	1	3
PYR	4	4	4	3	3	4
TOTAL	99	100	94	107	112	158

= 0.12), 1.04 g/m^3 (S.E. = 0.075) and 0.63 g/m^3 (S.E. = 0.071), respectively. This geographical pattern resulted mainly from the distribution of the diatoms (Fig. 5). However, the Cyanophyta, Chrysophyta, and Cryptophyta (Figs. 5 and 6) all had a progressively lower biomass from west to east (Figs. 3, 5, and 6). Pyrrophyta biomass was generally higher in the central and eastern basins as compared to the western basin.

Of the 12 common diatom species for the entire lake (Table 6), 11 exhibited a greater biomass in the western basin than in either the central and eastern basins for the 1983-87 period (Tables 3-5). Only the diatom *Stephanodiscus niagarae* Ehr. had a higher abundance in the central basin (Tables 3-5). Nuisance species, such as *Aphanizomenon flos-aquae* and *Oscillatoria limnetica*, possessed a biomass in the western basin that greatly exceeded those in the rest of the lake. One common species exhibited a trend in reverse of that of the diatoms. *Ceratium hirundinella* was more abundant in the eastern basin, where it comprised over 16.4% of the total biomass, than in the central or western basins where it comprised 8.3% and 2.1% of the total biomass, respectively. A difference in species abundance from the various basins of Lake Erie had been documented previously (Munawar and Munawar 1976, Davis 1969).

Historical Changes in Species Composition

WESTERN BASIN: Davis (1969) has reviewed the extensive earlier work on Lake Erie, while Munawar and Munawar (1982), Gladish and Munawar (1980), and Nicholls (1981) discuss the more recent material. Verduin (1964) concluded that before 1950 the

TABLE 3. Summary of common phytoplankton species occurrence in the western basin of Lake Erie during 1983–1987. Summary is based on spring and summer samples only. Summary includes the maximum population density encountered, the average population density and biovolume, and the relative abundance (% of total cells and % of total biovolume). Common species were arbitrarily defined as having an abundance of ≥0.5% of the total cells or ≥ 0.5% of the total biovolume.

TAXON	Maximum Cells/mL	Average Cells/mL	% of Total Cells	Mean Biovolume CU.μM/mL	% of Total Biovolume
BACILLARIOPHYTA					
Actinocyclus normanii f. *subsalsa*	201	16.0	0.13	154,779	8.23
Asterionella formosa	321	42.3	0.34	50,255	2.67
Cyclotella meneghiniana	564	30.2	0.24	10,575	0.56
Diatoma tenus v. *elongatum*	335	27.3	0.22	16,453	0.87
Fragilaria capucina	4,779	357.7	2.88	97,060	5.16
Fragilaria crotonensis	1,673	291.8	2.35	187,135	9.95
Melosira granulate	555	23.5	0.19	10,674	0.57
Melosira islandica	1,564	89.4	0.72	88,840	4.72
Melosira italica subsp. *subarctica*	922	54.1	0.44	14,841	0.79
Rhizosolenia eriensis	671	25.9	0.21	23,610	1.25
Rhizosolenia sp.	507	6.1	0.05	42,387	2.25
Stephanodiscus alpinus	120	16.1	0.13	19,090	1.01
Stephanodiscus binderanus	1,549	69.1	0.56	32,389	1.72
Stephanodiscus hantzschii f. *tenuis*	541	48.7	0.39	10,319	0.55
Stephanodiscus niagarae	32	2.8	0.02	62,234	3.31
Stephanodiscus sp.	776	72.2	0.58	7,358	0.39
Tabellaria flocculosa	626	76.0	0.61	150,351	7.99
Total			10.05		52.00
CHLOROPHYTA					
Cosmarium botrytis	8	0.2	0.00	12,019	0.64
Cosmarium sp.	25	2.2	0.02	71,993	3.83
Green coccoid-ovoid	1,178	118.8	0.96	8,477	0.45
Green coccoid-sphere	1,759	132.5	1.07	21,784	1.16
Monoraphidium contortum	605	99.5	0.80	1,298	0.07
Pediastrum simplex v. *duodenarium*	777	25.7	0.21	15,070	0.80
Total			3.05		6.94
CHRYSOPHYTA					
Chrysophycean coccoids	1,203	141.3	1.14	5,270	0.28
Haptophyceae	2,929	366.8	2.95	9,337	0.50
Total			4.09		0.78
COLORLESS FLAGELLATES					
Colorless flagellates	777	71.1	0.57	2,420	0.13
Stelexmonas dichotoma	990	76.5	0.62	2,354	0.13
Total			1.19		0.25
CRYPTOPHYTA					
Chroomonas norstedtii	515	69.7	0.56	2,114	0.11
Cryptomonas erosa	2905	60.5	0.49	105,477	5.61
Cryptomonas marssonii	90	16.0	0.13	10,599	0.56
Rhodomonas minuta v. *nannoplanktica*	4,712	762.2	6.13	50,287	2.67
Total			7.31		8.95
CYANOPHYTA					
Agmenellum quadruplicatum	4,909	429.0	3.45	284	0.02
Anabaena sp.	4,761	231.7	1.86	14,272	0.76
Anabaena spiroides	6,823	101.7	0.82	12,126	0.64
Amacystis incerta	10,227	119.3	0.96	196	0.01
Anacystis montana v. *minor*	22,253	1,235.9	9.94	8,240	0.44
Anacystis montana v. *montana*	6,954	81.4	0.65	5,716	0.30
Aphanizomenon flos-aquae	9,228	811.0	6.52	51,736	2.75
Coelosphaerium naegelianum	3,436	94.7	0.76	819	0.04
Gomphosphaeria lacustris	8,836	231.0	1.86	2,505	0.13
Merismopedia tenuissima	15,544	387.2	3.11	220	0.01
Microcystis aeruginosa	11,454	431.6	3.47	12,984	0.69
Oscillatoria limnetica	18,588	1,571.9	12.64	11,803	0.63
Oscillatoria minima	3,600	76.6	0.62	596	0.03
Oscillatoria subbrevis	4,140	101.7	0.82	3,588	0.19
Oscillatoria tenuis	5,081	71.0	0.57	3,944	0.21
Total			48.06		6.86
PYRROPHYTA					
Ceratium hirundinella	41	0.9	0.01	37,728	2.01
Peridinium sp.	49	4.9	0.04	22,290	1.18
Total			0.05		3.19
UNIDENTIFIED					
Unidentified flagellate-ovoid	4,303	893.7	7.19	32,752	1.74
Unidentified flagellate-spherical	2,479	411.1	3.31	18,100	0.96
Total			10.49		2.70
Total			84.28		81.68

TABLE 4. Summary of common phytoplankton species occurrence in the central basin of Lake Erie during 1983–1987. Summary is based on spring and summer samples only. Summary includes the maximum population density encountered, the average population density and biovolume, and the relative abundance (% of total cells and % of total biovolume). Common species were arbitrarily defined as having an abundance of ≥ 0.5% of the total cells or ≥ 0.5% of the total biovolume.

TAXON	Maximum Cells/mL	Average Cells/mL	% of Total Cells	Mean Biovolume CU.µM/mL	% of Total Biovolume
BACILLARIOPHYTA					
Actinocyclus normanii f. *subsalsa*	90	1.7	0.04	15,647	1.50
Asterionella formosa	942	51.6	1.09	20,015	1.92
Fragilaria capucina	963	64.1	1.36	17,751	1.70
Fragilaria crotonensis	807	63.5	1.35	47,700	4.57
Stephanodiscus alpinus	198	5.7	0.12	9,033	0.87
Stephanodiscus binderanus	322	10.3	0.22	7,173	0.69
Stephanodiscus niagarae	139	8.4	0.18	210,820	20.20
Surirella ovata	370	2.1	0.05	5,604	0.54
Tabellaria flocculosa	353	38.1	0.81	66,615	6.38
Total			5.20		38.35
CHLOROPHYTA					
Cosmarium sp.	25	0.6	0.01	21,159	2.03
Crucigenia rectangularis	295	3.8	0.08	6,385	0.61
Gloedactinium limneticum	178	1.0	0.02	41,433	3.97
Green coccoid-arcuate	1,031	28.3	0.60	260	0.02
Green coccoid-ovoid	556	42.8	0.91	3,258	0.31
Green coccoid-sphere	1,824	87.5	1.85	11,609	1.11
Monoraphidium contortum	744	58.8	1.25	727	0.07
Oedogonium sp.	237	10.3	0.22	10,708	1.03
Scenedesmus ecornis	2,193	52.9	1.12	8,143	0.78
Sphaerocystis schroeteri	1,227	23.6	0.50	2,598	0.25
Total			6.56		10.18
CHRYSOPHYTA					
Chrysophycean coccoids	1,653	165.1	3.50	3,436	0.33
Haptophyceae	1,309	277.9	5.89	4,896	0.47
Total			9.39		0.80
COLORLESS FLAGELLATES					
Colorless flagellates	2,119	106.1	2.25	3,151	0.30
Stelexmonas dichotoma	998	56.5	1.20	2,393	0.23
Total			3.45		0.53
CRYPTOPHYTA					
Chroomonas acuta	1,121	57.5	1.22	1,369	0.13
Chroomonas norstedtii	278	47.5	1.01	1,504	0.14
Cryptomonas erosa	188	21.0	0.45	37,556	3.60
Rhodomonas minuta v. *nannoplanktica*	2,323	549.8	11.65	41,028	3.93
Total			14.32		7.80
CYANOPHYTA					
Anabaena sp.	843	45.7	0.97	5,930	0.57
Anacystis montana v. *minor*	8,885	513.0	10.87	3,039	0.29
Aphanizomenon flos-aquae	974	68.6	1.46	5,444	0.52
Coelosphaerium naegelianum	5,891	45.7	0.97	668	0.06
Gomphosphaeria aponina	1,186	34.3	0.73	1,742	0.17
Gomphosphaeria lacustris	9,785	220.6	4.68	1,462	0.14
Microcystis aeruginosa	15,749	174.1	3.69	7,774	0.74
Oscillatoria limnetica	2,773	75.9	1.61	886	0.08
Total			24.97		2.58
PYRROPHYTA					
Amphidinium sp.	90	4.0	0.08	10,476	1.00
Ceratium hirundinella	49	3.7	0.08	85,723	8.21
Gymnodinium sp.	74	5.5	1.12	12,013	1.15
Gymnodinium sp. #2	33	2.1	0.04	35,408	3.39
Peridinium aciculiferum	196	5.2	0.11	48,364	4.63
Peridinium sp.	101	8.89	0.19	45,877	4.40
Total			0.62		22.79
UNIDENTIFIED					
Unidentified flagellat#04	2,839	75.4	1.60	7,504	0.72
Unidentified flagellate-ovoid	3,379	704.0	14.92	39,827	3.82
Unidentified flagellate-spherical	1,734	301.2	6.38	10,733	1.03
Total			22.90		5.56
Total			87.42		88.60

TABLE 5. Summary of common phytoplankton species occurrence in the eastern basin of Lake Erie during 1983–1987. Summary is based on spring and summer samples only. Summary includes the maximum population density encountered, the average population density and biovolume, and the relative abundance (% of total cells and % of total biovolume). Common species were arbitrarily defined as having an abundance of ≥ 0.5% of the total cells or ≥ 0.5% of the total biovolume.

TAXON	Maximum Cells/mL	Average Cells/mL	% of Total Cells	Mean Biovolume CU.µM/mL	% of Total Biovolume
BACILLARIOPHYTA					
Asterionella formosa	355	17.8	0.54	6,228	0.98
Cyclotella stelligera	425	27.2	0.83	937	0.15
Fragilaria capucina	135	12.;6	0.38	3,304	0.52
Fragilaria crotonensis	364	30.9	0.94	37,992	6.00
Stephanodiscus alpinus	76	6.2	0.19	11,228	1.77
Stephanodiscus binderanus	176	10.7	0.32	6,087	0.96
Stephanodiscus hantzschii f. *hantzschii*	446	31.1	0.95	2,443	0.39
Stephanodiscus niagarae	30	2.4	0.07	61,568	9.72
Stephanodiscus parvus	503	26.1	0.79	781	0.12
Stephanodiscus sp.	781	56.17	1.72	5,398	0.85
Tabellaria flocculosa	376	14.4	0.44	28,473	4.50
Total			7.17		25.97
CHLOROPHYTA					
Chlamydocapsa planktonica	1,145	35.3	1.07	3,827	0.60
Chlamydocapsa sp.	736	19.1	0.58	971	0.15
Coelastrum microporum	565	18.7	0.57	1,488	0.24
Cosmarium sp.	49	1.3	0.04	38,003	6.00
Golenkinia sp.	8	0.1	0.00	32,432	5.12
Green coccoid-acicular	605	21.6	0.66	327	0.05
Green coccoid-arcuate	1,039	78.3	2.38	619	0.10
Green coccoid-ovoid	311	45.0	1.37	2,405	0.38
Green coccoid-sphere	352	43.4	1.32	34,530	5.45
Monoraphidium contortum	548	47.1	1.43	284	0.04
Oedogonium sp.	57	1.9	0.06	3,231	0.51
Oocystis borgei	153	6.6	0.20	4,948	0.78
Scenedesmus bicaudatus	25	1.0	0.03	4,137	0.65
Scenedesmus ecornis	458	27.3	0.83	1,818	0.29
Staurastrum sp.	8	0.4	0.01	3,512	0.55
Total			10.55		20.93
CHRYSOPHYTA					
Chrysophycean coccoids	524	70.1	2.13	1,771	0.28
Haptophyceae	1,137	197.7	6.00	3,148	0.50
Total			8.13		0.78
COLORLESS FLAGELLATES					
Colorless flagellates	499	65.9	2.00	1,712	0.27
Stelexmonas dichotoma	311	16.7	0.51	581	0.09
Total			2.51		0.36
CRYPTOPHYTA					
Chroomonas acuta	548	29.0	0.88	469	0.07
Chroomonas norstedtii	237	27.4	0.83	633	0.10
Cryptomonas erosa	82	9.9	0.30	20,191	3.19
Rhodomonas minuta v. *nannoplanktica*	1,111	335.6	10.19	21,808	3.44
Total			12.20		6.81
CYANOPHYTA					
Anacystis montana v. *minor*	4,590	411.9	12.51	1,816	0.29
Aphanizomenon flos-aquae	337	27.9	0.85	2,088	0.33
Gomphosphaeria lacustris	965	52.9	1.61	343	0.05
Oscillatoria limnetica	3,812	251.0	7.62	1,475	0.23
Oscillatoria minima	1,358	43.1	1.31	570	0.09
Total			23.89		0.99
PYRROPHYTA					
Ceratium hirundinella	82	3.3	0.10	103,513	16.35
Gymnodinium sp.	31	2.0	0.06	9,596	1.52
Gymnodinium sp. #2	16	1.7	0.05	24,308	3.84
Peridinium aciculiferum	82	3.4	0.10	30,667	4.84
Peridinium sp.	106	5.0	0.15	31,783	5.02
Total			0.47		31.57
UNIDENTIFIED					
Unidentified flagellate #04	524	17.6	0.53	1,910	0.30
Unidentified flagellate-ovoid	2,577	501.9	15.24	13,659	2.16
Unidentified flagellate-spherical	1,235	252.3	7.66	6,453	1.02
Total			23.44		3.48
Total			88.36		90.90

TABLE 6. Summary of common phytoplankton species occurrence in Lake Erie during 1983–1987. Summary is based on spring and summer samples only. Summary includes the maximum population density encountered, the average population density and biovolume, and the relative abundance (% of total cells and % of total biovolume). Common species were arbitrarily defined as having an abundance of ≥ 0.5% of the total cells or ≥ 0.5% of the total biovolume.

TAXON	Maximum Cells/mL	Average Cells/mL	% of Total Cells	Mean Biovolume CU.µM/mL	% of Total Biovolume
BACILLARIOPHYTA					
Actinocyclus normanii f. *subsalsa*	201	5.1	0.08	49,035	4.19
Asterionella formosa	942	41.2	0.64	24,818	2.12
Fragilaria capuncina	4,779	130.1	2.02	35,456	3.03
Fragilaria crotonensis	1,673	116.6	1.81	82,520	7.05
Melosira islandica	1,564	25.4	0.40	25,014	2.14
Rhizosolenia eriensis	671	9.3	0.14	7,516	0.64
Rhizosolenia sp.	507	1.7	0.03	11,654	1.00
Stephanodiscus alpinus	198	8.6	0.13	12,226	1.04
Stephanodiscus binderanus	1,549	26.0	0.40	13,628	1.16
Stephanodiscus niagarae	139	5.5	0.09	136,162	11.64
Stephanodiscus sp.	781	40.5	0.63	3,946	0.34
Tabellaria flocculosa	626	42.6	0.66	79,923	6.83
Total			7.03		41.19
CHLOROPHYTA					
Cosmarium sp.	49	1.2	0.02	38,649	3.30
Gloedactinium limneticum	178	0.5	0.01	20,658	1.77
Golenkinia sp.	25	0.4	0.01	7,840	0.67
Green coccoid-arcuate	1,039	38.7	0.60	440	0.04
Green coccoid-ovoid	1,178	63.6	0.99	4,446	0.38
Green coccoid-sphere	1,824	89.1	1.38	19,710	1.68
Monoraphidium contortum	744	66.9	1.04	775	0.07
Oedogonium sp.	237	6.3	0.10	6,320	0.54
Scenedesmus ecornis	2,193	44.8	0.70	4,847	0.41
Total			4.84		8.86
CHRYSOPHYTA					
Chrysophycean coccoids	1,653	136.5	2.12	3,533	0.30
Haptophyceae	2,929	282.7	4.39	5,666	0.48
Total			6.51		0.79
COLORLESS FLAGELLATES					
Colorless flagellates	2,119	87.4	1.36	2,618	0.22
Stelexmonas dichotoma	998	52.4	0.81	1,957	0.17
Total			2.17		0.39
CRYPTOPHYTA					
Chroomonas acuta	1,121	41.6	0.65	917	0.08
Chroomonas norstedtii	515	48.7	0.76	1,461	0.12
Cryptomonas erosa	295	28.9	0.45	51,545	4.41
Rhodomonas minuta v. *nannoplanktica*	4,712	555.9	8.64	38,970	3.33
Total			10.49		7.94
CYANOPHYTA					
Agmenellum quadruplicatum	4,909	124.9	1.94	77	0.01
Anabaena sp.	4,761	86.6	1.35	7,005	0.60
Anabaena spiroides	6,823	33.8	0.53	4,539	0.39
Anacystis montana v. *minor*	22,253	681.6	10.59	4,135	0.35
Aphanizomenon flos-aquae	9,228	256.6	3.99	16,973	1.45
Coelosphaerium naegelianum	5,891	50.3	0.78	560	0.05
Gomphosphaeria lacustris	9,785	183.9	2.86	1,476	0.13
Merismopedia tenuissima	15,544	103.0	1.60	59	0.01
Microcystis aeruginosa	15,749	201.7	3.13	7,331	0.63
Oscillatoria limnetica	18,588	515.2	8.01	3,930	0.34
Oscillatoria minima	3,600	38.4	0.60	376	0.03
Total			35.37		3.97
PYRROPHYTA					
Amphidinium sp.	90	2.9	0.04	6,020	0.51
Ceratium hirundinella	82	2.9	0.04	77,137	6.59
Gymnodinium sp.	74	4.0	0.06	10,056	0.86
Gymnodinium sp. #2	33	1.5	0.02	23,873	2.04
Peridinium aciculiferum	196	3.5	0.05	32,067	2.74
Peridinium sp.	106	6.9	0.11	36,284	3.10
Total			0.34		15.85
UNIDENTIFIED					
Unidentified flagellate #04	2,839	42.0	0.65	4,223	0.36
Unidentified flagellate-ovoid	4,303	707.0	10.98	31,787	2.72
Unidentified flagellate-spherical	2,479	318.9	4.96	11,687	1.00
Total			16.59		4.08
Total			83.34		83.06

TABLE 7. Time trends in phytoplankton biomass, Lake Erie (1983 to 1987). Only spring and summer data of major divisions are presented. Values are the mean.

BIOMASS (g/m³)

	BAC g/m³ %	CHL g/m³ %	CHR g/m³ %	CRY g/m³ %	CYA g/m³ %	PYR g/m³ %	*Mean Biomass g/m³
1983	.605 (51.0)	.214 (18.2)	.015 (1.3)	.143 (12.1)	.025 (2.1)	.140 (11.9)	1.18
1984	.381 (39.2)	.136 (14.0)	.019 (1.9)	.141 (14.5)	.046 (4.7)	.165 (17.0)	.972
1985	.474 (46.3)	.103 (10.0)	.022 (2.1)	.109 (10.7)	.065 (6.4)	.194 (19.0)	1.02
1986	.814 (46.2)	.284 (16.1)	.048 (2.7)	.148 (8.4)	.054 (3.1)	.343 (19.4)	1.76
1987	.496 (56.3)	.093 (10.5)	.012 (1.3)	.067 (7.6)	.082 (9.3)	.113 (12.8)	.882
Mean	.544	.165	.023	.122	.054	.191	1.16

Abundance (Cells/mL)

	BAC	CHL	CHR	CRY	CYA	PYR	*Mean Abundance
1983	546	796	321	820	1,616	17.6	6,215
1984	686	295	316	802	2,371	22.3	6,461
1985	466	536	560	875	1,386	26.2	5,049
1986	1,270	999	996	780	3,277	36.3	8,165
1987	581	934	349	423	3,303	12.0	5,972
Mean	710	712	508	740	2,391	22.9	6,372

*All Divisions

phytoplankton of western Lake Erie were dominated by *Asterionella formosa* Hass., *Tabellaria fenestrata* Kutz., and *Melosira ambigua* (Grun.) O Mull., whereas in 1960-61 the dominant forms were *Fragilaria capucina* Desm., *Coscinodiscus radiatus* (probably *Actinocyclus normanii f. subsalsa* Hust.), and *Melosira binderana* (= *Stephanodiscus binderanus* Grun).

As with Munawar and Munawar (1976), the 1983-87 collections confirmed Verduin's (1964) observations that those species dominant before 1950 (*A. formosa, T. fenestrata,* and *M. ambigua*) continued to be less important in the western basin during the 1983-87 period. *Actinocyclus normanii f. subsalsa* (= *Coscinodiscus rothii*) and *Stephanodiscus binderanus* were dominant in 1961-62 (Verduin 1964) and in 1970 (Munawar and Munawar 1976). In 1970 the most significant contributions to the species composition were made by *Fragilaria crotonensis* Kitton, *Stephanodiscus tenuis* Hust., and perhaps *Cryptomonas erosa* Ehr. in the spring, *Aphanizomenon flos-aquae* Ralfs and *Actinocyclus normanii f. subsalsa* in the summer, with *Stephanodiscus tenuis, Melosira islandica* O. Mull., *Rhodomonas minuta* Skuja, and *Cryptomonas erosa* occurring in collections all year (Munawar and Munawar 1976).

Those species prevalent before 1950 and during the 1960s did not dominate the phytoplankton of western Lake Erie in 1970 or during 1983-87. The community composition was similar, however, between 1970 and the 1983-87 period. For example, during the 1983-87 spring and summer period, *Fragilaria crotonensis* was the most prevalent diatom in the western basin accounting for 10.0% of the biomass (Table 3). However, dominance varied in the western basin from year to year. *Rhizosolenia eriensis* H.L. Sm. (1983: 14.8% of the biomass), *Melosira islandica* (1984: 12.2%), *Tabellaria flocculosa* Roth (Kutz.)(1986: 11.9%), and *Actinocyclus normanii f. subsalsa* (1985: 12.2% of the biomass) were the dominant diatoms in various years with *Fragilaria crotonensis* (1987: 15.0%) being dominant only in 1987. In addition, *Cryptomonas erosa* and *Rhodomonas minuta* accounted for 8.3% of the total biomass from 1983-87. *Oscillatoria limnetica* Lemm. (12.6%) and *Anacystis montana* Dr. & Daily (10.5%) were the most abundant species (Table 3). Data on the common species demonstrate that

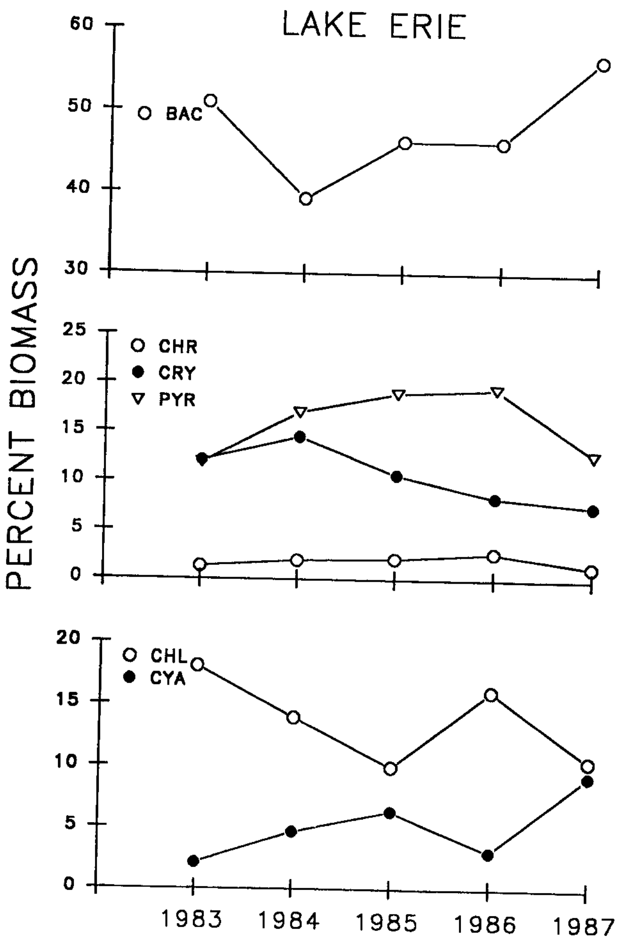

FIG. 2. Yearly trends in relative biomass of selected divisions of phytoplankton, 1983–87. Spring and summer data only. BAC = Bacillariophyta, CHR = Chrysophyta, CRY = Cryptophyta, PYR = Pyrrophyta, CHL = Chlorophyta, CYA = Cyanophyta.

species composition between 1970 and 1983-87 was not very different.

CENTRAL BASIN: In late August of 1960, dominant species were *Fragilaria crotonensis, Tabellaria fenestrata,* and *Melosira granulata* (Ehr.) Ralfs (Hohn 1969). The most significant contributions to the species composition in the central basin in 1970 was *Stephanodiscus niagarae* in the spring, *Fragilaria crotonensis, F. capucina,* and *Ceratium hirundinella* (O.F. Mull.) Schrank in the summer, with *Stephanodiscus niagarae, Ochromonas* spp., *Rhodomonas minuta,* and *Cryptomonas erosa* occurring in collections all year (Munawar and Munawar 1976). For the 1983-87 spring and summer period, *Stephanodiscus niagarae* was the most prevalent species in the central basin, accounting for 20.2% of the biomass (Table 4). However, dominance varied considerably in the central basin from year to year. *Stephanodiscus niagarae* (1983: 44.4% of the biomass), *Asterionella formosa, Rhodomonas minuta,* and *Ceratium hirundinella* (1984: 6.3, 6.8, and 9.2%, respectively), *Stephanodiscus hantzschii* Grun. (1985: 36.1%), *Tabellaria flocculosa* and *Ceratium hirundinella* (1986: 8.6 and 10.0%, respectively), and *Stephanodiscus niagarae* (1987: 29.8%) were the dominant algae in various years.

As with the western basin, composition has not changed greatly between 1970 and the 1983-87 period (Table 4). However, a major change in dominant diatoms had occurred between 1960 and the 1983-87 period. *Melosira granulata,* a dominant diatom in the central basin in 1969 (Hohn 1969), was not common in 1970 and was rare from 1983 to 1986 (abundance generally under 1 cell/mL). However in 1987, the abundance of *Melosira granulata* v. *angustissimia* O. Mull. reached 42 and 64 cells/mL at two stations in April (Stations 38 and 32, respectively). *Tabellaria fenestrata,* a dominant diatom in 1960 (Hohn 1969) and a less common species in 1970 (Munawar and Munawar 1976), was observed only twice in the central basin from 1983 to 1987 at abundances below 10 cells/mL. Similar to the western basin, *Stephanodiscus tenuis,* a dominant species in 1970, had decreased in abundance and was not considered to be a dominant diatom in the 1983-87 study.

EASTERN BASIN: The most significant contributors to the species composition in the eastern basin in 1970 were *Stephanodiscus tenuis* and *Peridinium aciculiferum* Lemm. in the spring, *Ceratium hirundinella* and *Fragilaria crotonensis* in the summer, *Stephanodiscus niagarae* in the fall, and *Pediastrum duplex, Rhodomonas minuta,* and *Cryptomonas erosa* occurring in collections all year (Munawar and Munawar 1976). For the 1983-87 spring and summer period, *Stephanodiscus niagarae* and *Ceratium hirundinella* were the dominant phytoplankters in the eastern basin accounting for 9.7% and 16.4 % of the biomass, respectively (Table 5). However, dominance varied considerably in the eastern basin from year to year. *Stephanodiscus niagarae, Cosmarium* sp., and *Ceratium hirundinella* (1983: 13.9, 12.7 and 17.4%, respectively), *Fragilaria crotonensis, Cosmarium* sp., and *Ceratium hirundinella* (1984: 11.9, 13.8 and 11.6%,

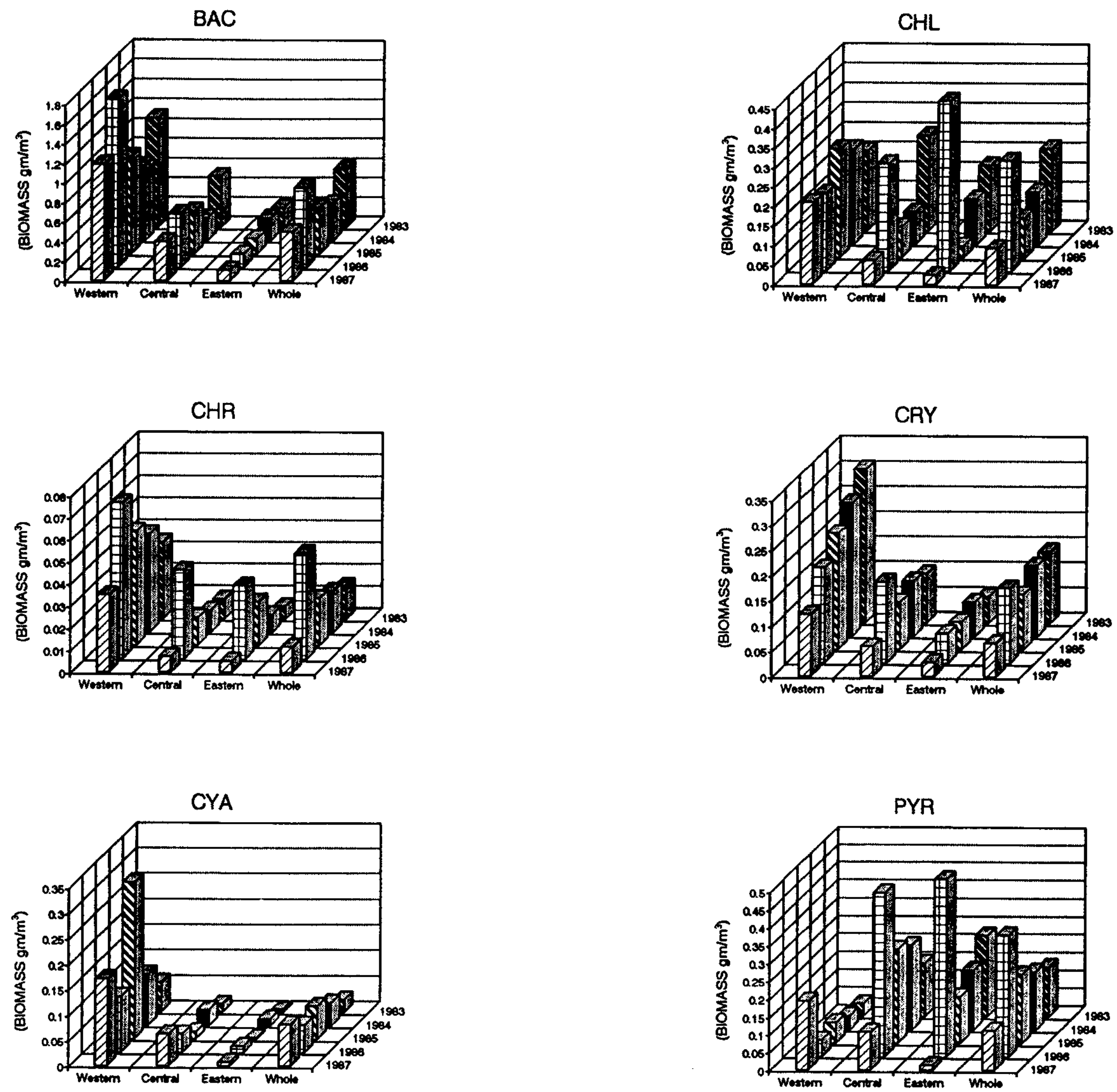

FIG. 3. Yearly trends of selected divisions of phytoplankton by basin, Lake Erie (1983–87). Values are the mean. Spring and summer data only. Whole refers to the average for basins. BAC = Bacillariophyta, CHR = Chrysophyta, CRY = Cryptophyta, PYR = Pyrrophyta, CHL = Chlorophyta, CYA = Cyanophyta.

respectively), *Stephanodiscus niagarae* and *Peridinium* sp. (1985: 27.0 and 14.4%), *Fragilaria crotonensis, Golenkinia* sp., and *Ceratium hirundinella* (1986: 6.9, 14.2 and 25.8%, respectively), and *Stephanodiscus niagarae, Tabellaria flocculosa,* and *Cryptomonas erosa* (1987: 20.8, 21.2 and 7.0%) were the dominant algae in various years. As with the western and central basins, composition had not changed greatly between 1970 and the 1983-87 period with the exception of *Stephanodiscus tenuis*, which had decreased greatly in abundance from 1970 to 1983-87 (Table 5).

Historical Changes in Species Biomass and Abundance of The Western Basin

Munawar and Munawar (1982) concluded that the species of phytoplankton found in Lake Erie in 1970 were indicators of mesotrophic and eutrophic conditions. Evidence of a shift in trophic status since 1970 is provided by a comparison of distribution of dominant species biomass and composition between 1970 and 1983-87 in the western basin (Table 8). In general, occurrences of common species in 1970 and 1983-87 were similar, but dra-

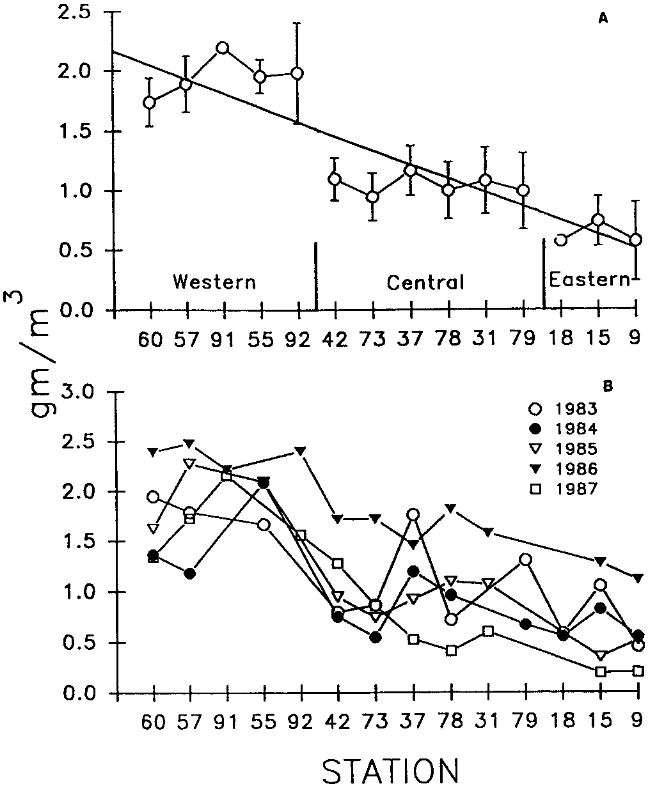

FIG. 4. Geographical trends of algae biomass in Lake Erie, 1983–87. Spring and summer data only. Panel A is the mean biomass for each station for 1983–87 (r^2 = 0.79). Panel B is the annual mean biomass for each station.

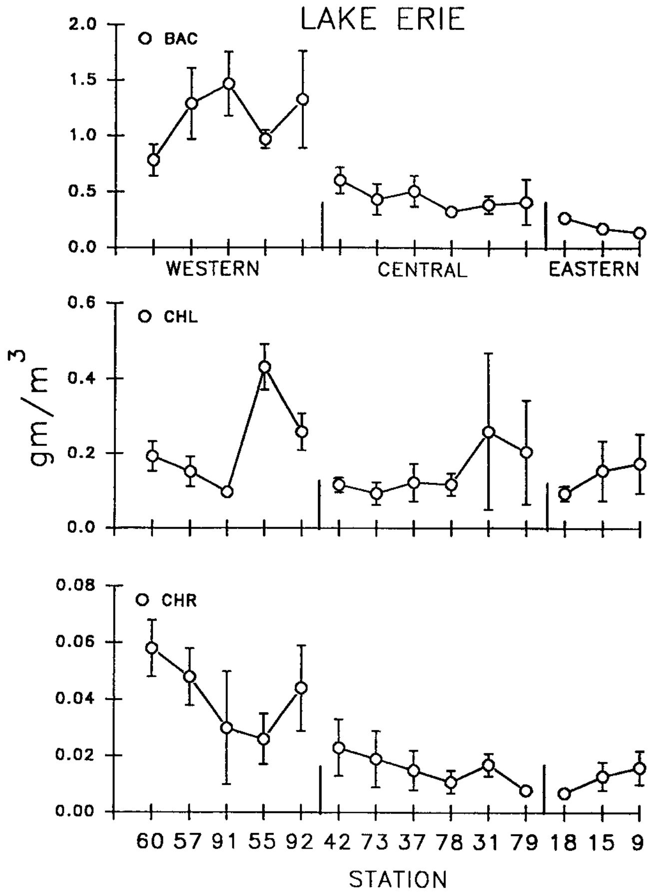

FIG. 5. Geographical distribution of Bacillariophyta (BAC), Chlorophyta (CHL), and Chrysophyta (CHR) biomass in Lake Erie, 1983–87. Spring and summer data only. Values are the mean ±S.E.

matic decreases in abundance of many nuisance and eutrophic species were evident in all three basins (Table 8) while abundance of mesotrophic species had increased.

MESOTROPHIC SPECIES: *Asterionella formosa* has not been prevalent in Lake Erie since prior to 1950. Verduin (1964) stated that before 1950 *Asterionella formosa* was a dominant species in western Lake Erie. Similarly, Davis (1969) reported *Asterionella* as the dominant organism in the spring pulse of the central basin prior to 1949. Numerous workers (Hohn 1969, Nichols *et al.* 1977, Munawar and Munawar 1976, Gladish and Munawar 1980) reported a decline in *A. formosa* after 1950.

However for the 1983-87 period, *A. formosa* was again common in the various basins (44 cells/mL - western basin; 50 cells/mL - central basin; 16 cells/mL - eastern basin). Although average basin abundance of *A. formosa* varied considerably over the 5-year study period (Table 9), abundance in the western basin varied little and appeared to increase. The April, 1984 average abundance was 226 cells/mL (maximum abundance = 942 cells/mL). In 1984 during the three cruises in April and May, *Asterionella formosa* was the dominant spring species on a biomass basis and the second most important diatom on a numerical basis. These densities observed in 1984 are similar to those observed in March of 1938. Maximum density in March of 1938 was 553 cells/mL with a March mean of 97 cells/mL (Hohn 1969). Although abundance was variable from year to year, it is obvious that a species once common in the lake has returned to levels comparable to 1930s and '40s.

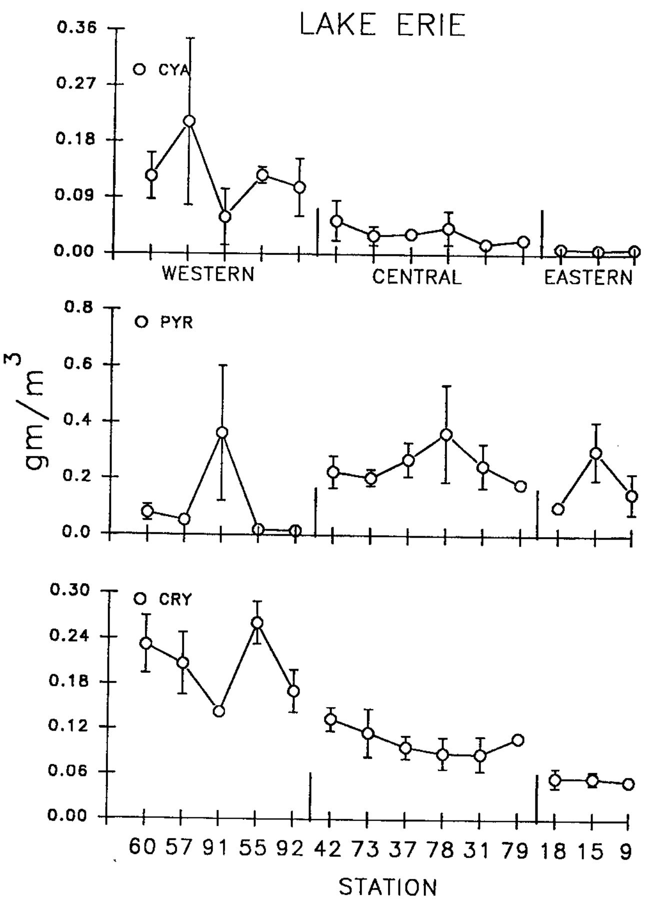

FIG. 6. Geographical distribution of Cyanophyta (CYA), Pyrrophyta (PYR), and Cryptophyta (CRY) biomass in Lake Erie, 1983–87. Spring and summer data only. Values are the mean ±S.E.

Cyclotella stelligera (Cl. & Grun) V.H. and *Rhizosolenia eriensis*, two species present in the 1930s and '40s in large numbers in the western basin, had almost disappeared by the 1960s (Hohn 1969) and 1970s (Munawar and Munawar 1976). During 1983 to 1987, *C. stelligera* remained uncommon in the western basin, never reaching an abundance of greater than 0.5% of the total cells or biomass. However, abundance of *R. eriensis* averaged 259 cells/mL from 1983-87 with a maximum of 671 cells/mL in 1983 in the western basin.

Stephanodiscus alpinus Hust., although not observed in 1970 (Munawar and Munawar 1976), was a dominant species (e.g., maximum abundance in 1965 = 4,600 cells/mL) in the 1960s and was present in low numbers in the 1930s and '40s (Hohn 1969). During the 1983-87 period, *S. alpinus* was present in the western basin in fairly abundant numbers. For example, a maximum density of 120 cells/mL was observed in April (Station 55) with an average of 16 cells/mL for the period (range 4.5-35 cells/mL) in the western basin.

Although abundance was variable from 1983 to 1987, it is apparent that mesotrophic species such as *Asterionella formosa* and perhaps *Rhizosolenia eriensis*, once common in the lake, have returned to densities comparable to those during the 1930s and '40s. In the case of *S. alpinus*, a species that was historically common is once again present in the lake after a period of absence.

EUTROPHIC SPECIES: *Fragilaria capucina* was a dominant, western basin diatom in 1961 (Verduin 1964), but not in 1970 (Munawar and Munawar 1976). During the 1983-87 period, *Fragilaria capucina* was the most abundant diatom (absolute abundance) in the western basin (Table 3) due to exceedingly high populations in the western basin during 1986 (mean = 991 cells/mL, 6.9% of the total abundance).

In the western basin in 1970, *Stephanodiscus niagarae, S. tenuis, S. hantzschii,* and *S. binderanus* made up 5% or more of the total biomass in spring and summer cruises (Munawar and Munawar 1976). These eutrophic species were not present or were observed only occasionally in the 1940s and '50s (Hohn 1969). During the 1983-87 period, *S. tenuis, S. hantzschii,* and *S. binderanus*, although present, never reached 5% of the total biomass on any given cruise as in 1970. Similarly in 1987, *S. niagarae* biomass never was greater than 5% of the biomass for a cruise.

In general, occurrences of common species in 1970 and 1983-87 were similar; but dramatic decreases in abundance of many species were evident. This pattern was evident in all three basins. For example, a 70 to 98% reduction in biomass of *Stephanodiscus binderanus, S. niagarae, S. tenuis, Aphanizomemon flos-aquae,* and *Rhodomonas minuta* was evident (Table 8).

Historical Changes in Phytoplankton Community Biomass

Between 1927 and 1964, a large and consistent increase in the total quantity of phytoplankton of the central basin had occurred (Davis 1964, 1969). Nichols *et al.* (1977) observed that a decline in

TABLE 8. Mean maximum biomass of selected common phytoplankton species in 1970, 1983–1987, Lake Erie. Data from Munawar and Munawar (1976) and this study. 1970 data-graphical accuracy. Percent reduction is from 1970 to the average of 1983–85 and 1986–87. W = Western basin; C = Central basin; E = Eastern basin.

		April-November			Spring and Summer	
	BASIN	1970 g/m^3	Mean 83–85 g/m^3	Percent Reduction	Mean 86–87 g/m^3	Percent Reduction
Actinocyclus normanii f. *subsalsa*	W	4.7	0.34	93	0.71	85
Stephanodiscus niagarae	E	1.4	0.58	59	0.06	96
	C	2.3	1.44	37	0.23	90
	W	0.6	0.54	11	0.19	68
Stephanodiscus tenuis	W	1.8	.006	99	0.007	99
Stephanodiscus binderanus	W	0.5	0.07	85	0.11	78
Fragilaria crotonensis	E	1.0	0.19	81	0.08	92
	C	3.4	0.12	96	0.12	96
	W	7.9	0.25	97	0.33	96
Fragilaria capucina	C	2.4	0.14	94	0.06	97
	E	0.4	0.02	95	0.01	97
Peridinium aciculiferum	E	1.0	0.03	97	0.22	78
Ceratium hirundinella	C	1.8	0.28	84	0.25	86
	E	2.0	0.24	88	0.44	78
Rhodomonas minuta	E	1.6	0.03	98	0.002	99
	C	0.4	0.08	80	0.006	98
Cryptomonas erosa	W	2.0	0.39	81	0.11	94
Pediastrum simplex	C	0.4	0.06	86	0.00	100
Staurastrum paradoxum	C	0.4	0.02	94	0.00	100
Aphanizomenon flos-aquae	W	2.0	0.22	89	0.16	92

TABLE 9. Average basin abundance (cells/mL) of* Asterionella formosa, *1983–87, Lake Erie.

	Western	Central	Eastern	Weighted average
1983	31	2	3	10
1984	38	165	51	99
1985	40	14	9	18
1986	49	59	11	46
1987	61	12	5	21

nearshore phytoplankton of the western basin occurred between 1967 and 1975. However, Gladish and Munawar (1980) discounted this finding and suggested that no realistic conclusion could be drawn from a comparison of biomass between 1970 and 1975.

A comparison of biomass between 1970 and 1983-1987 suggests a decline in biomass in all three basins (Fig. 7). A 52 to 89% reduction in mean basin-weighted algal biomass had occurred in offshore waters of Lake Erie from 1970 to 1983-87 depending on the basin. This reduction in biomass was evident for all seasons of the year (Fig. 8). The historically highly productive western basin (Munawar and Burns 1976) had a decrease in community phytoplankton biomass from 1958 to 1985 (Fig. 9). This decrease in algal biomass correlated well (r = 0.74) with the decrease in total phosphorus (Makarewicz *et al.* 1989). As mentioned earlier, dramatic reductions in the biomass of various species were evident (Table 8).

Based on maximum biomass concentrations (Vollenweider 1968), Munawar and Munawar (1976) classified the western basin as highly eutrophic, the eastern basin as mesotrophic, and the central basin between the mesotrophic and eutrophic conditions. Using the same classification system of Vollenweider (1968) (ultra-oligotrophic: <1 g/m^3, mesotrophic: 3 to 5 g/m^3, highly eutrophic: >10 g/m^3), the

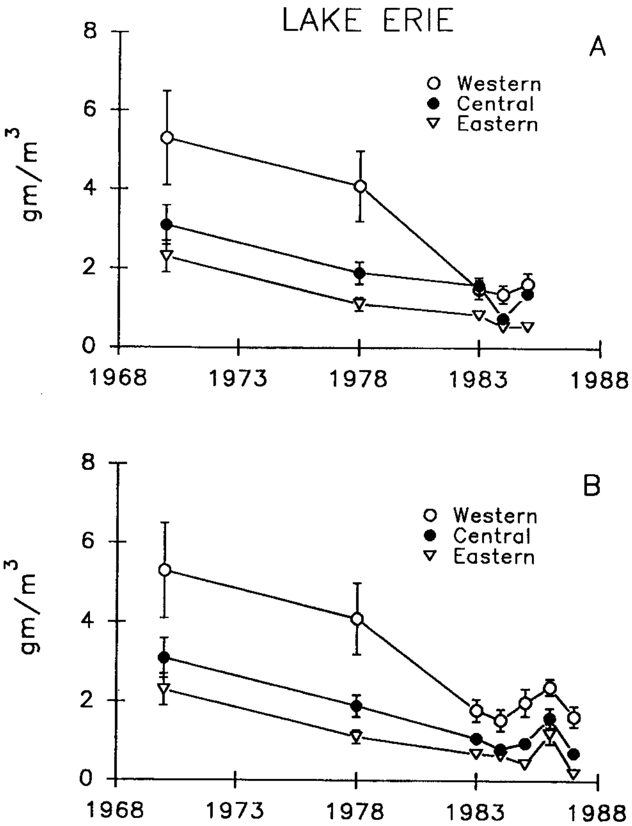

FIG. 7. Historical offshore phytoplankton biomass trends in Lake Erie. (A) April-November data. (B) Spring and summer data only for 1983–87. Values are the mean ± S.E. The 1970 and 1978 data are from Munawar and Munawar (1976) and Devault and Rockwell (1986).

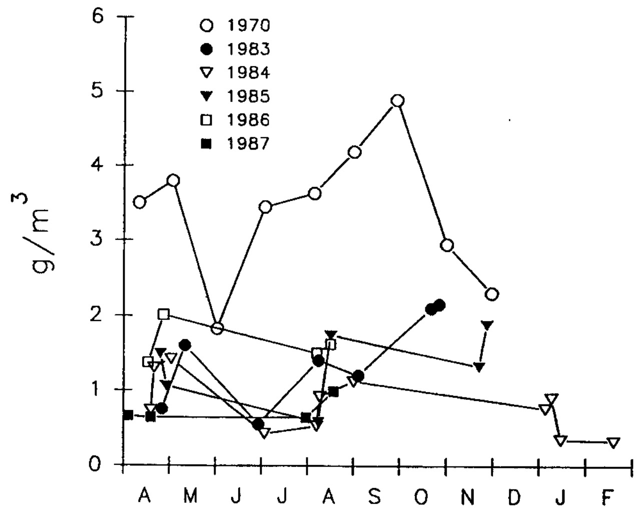

FIG. 8. Seasonal fluctuation of weighted mean phytoplankton biomass in 1970 and 1983–87, Lake Erie. 1970 data modified from Munawar and Munawar (1976). Values are corrected by weighting factors of 15.6%, 59.6%, and 24.6% for the western, central, and eastern basins (after Munawar and Munawar 1976).

TABLE 10. Maximum and mean phytoplankton biomass (g/m³) observed in each basin.

	Western		Central		Eastern	
	Max	Mean	Max	Mean	Max	Mean
1970	—	5.3	—	3.1	—	2.3
1978	—	4.1	—	1.9	—	1.1
1983	4.5	1.8	3.1	1.1	1.4	0.70
1984	6.6	1.6	3.0	0.83	2.0	0.64
1985	5.3	2.0	4.6	0.96	1.6	0.43
1986	4.1	2.4	8.8	1.6	3.4	1.2
1987	5.8	1.6	3.4	0.72	0.41	0.20

western and central basins for the 1983-87 period would be classified as mesotrophic and the eastern basin would be between oligotrophic and mesotrophic. Similarly, the classification scheme of Munawar and Munawar (1982), based on mean phytoplankton biomass, suggested an improvement in water quality between 1970 and 1983-87. In 1970, the eastern and central basins were classified as mesoeutrophic (2.0-4.0 g/m^3) and the western basin as eutrophic (4.0-8.0 g/m^3). Considering mean phytoplankton biomass from 1983 to 1987, most of the basins were mesotrophic (1.0-2.0 g/m^3) and occasionally oligotrophic (0.5-1.0 g/m^3) or mesoeutrophic (2.0-4.0 g/m^3)(Table 10).

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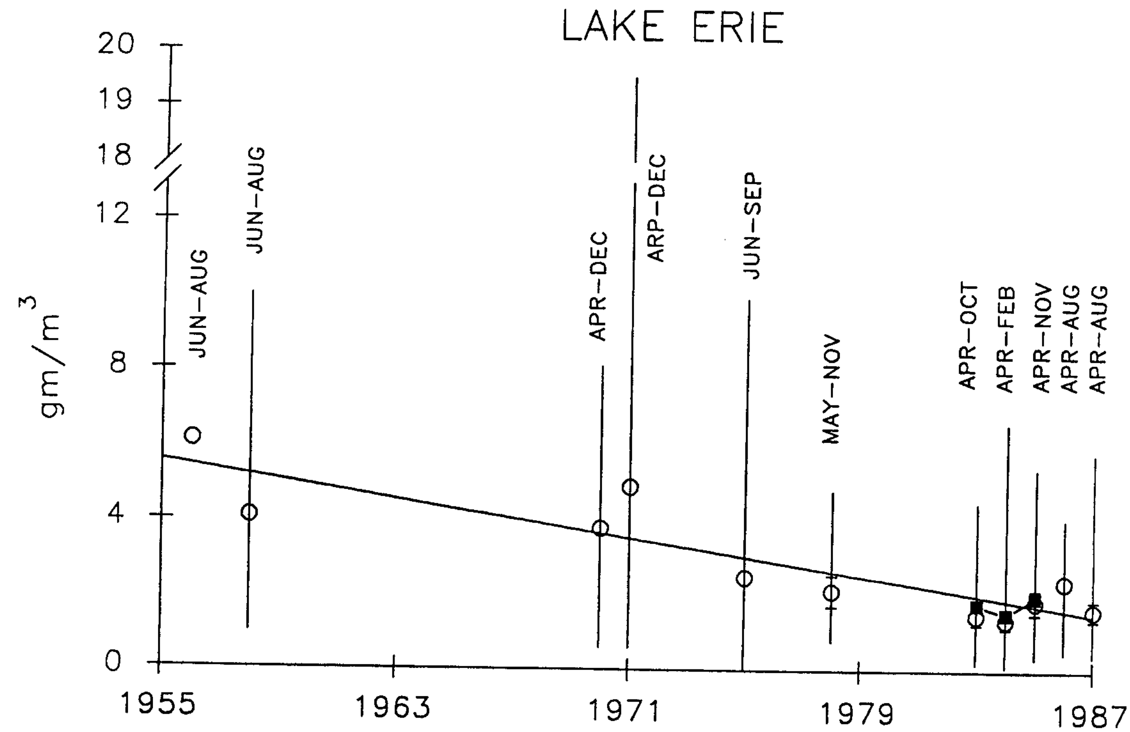

FIG. 9. Regression (r^2 = 0.79) of phytoplankton biomass versus time in the western basin of Lake Erie. Modified from Gladish and Munawar (1980). 1956–58 data are from the Bass Island region. 1970 data from Point Pelee and near the mouth of Detroit River. 1975–76 data are from northern portions of the western basin. 1978 data are from similar geographical areas as 1970 (Devault and Rockwell 1986). 1979 data are not included because of a reduced sampling regime and other technical difficulties (Devault and Rockwell 1986). 1983–87 data are from Stations 55, 57, and 60. Except for the 1956 and the 1957–58 data sets, all enumeration was by the Utermöhl technique. In 1956 and 1957-58, a settling technique was used, but counts were not made on an inverted microscope. Vertical lines are the range. Horizontal lines represent the standard error. Square symbols represent the mean of the spring and summer data from 1983 to 1985.

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