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PHOTOSYNTHETIC CHARACTERISTICS OF PHYTOPLANKTON COMMUNITIES IN LAKES HURON AND MICHIGAN: P-I PARAMETERS AND END-PRODUCTS[1]

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ABSTRACT. Photosynthetic-irradiance (P-I) curves and partitioning of photosynthate into major end-products (protein, lipids, polysaccharides, and low molecular weight [LMW] metabolites) were examined for phytoplankton communities from Lakes Huron and Michigan. The mean and variance of P-I parameters and photosynthetic end-products were similar in both lakes. Mean P_M^B (maximum light saturated rate) and α (initial linear slope) values were 2.3 mg C·mg Chl^{-1}·h^{-1} and 5.5 mg C·mg Chl^{-1}·Einst^{-1}·m^2 for Lake Huron communities, and 2.4 mg C·mg Chl^{-1}·h^{-1} and 7.0 mg C·mg Chl^{-1}·Einst^{-1}·m^2 for Lake Michigan communities. The mean percent incorporation of $^{14}CO_2$ into proteins, lipids, polysaccharides, and LMW metabolites from short-term experiments (2-4 h) were 32.4, 21.3, 28.0, and 18.9, respectively, for Lake Huron communities and 34.8, 24.7, 24.5, and 15.8, respectively, for Lake Michigan communities. Over longer incubations the activity in each end-product increased linearly during the day; during the night the activity in the LMW and polysaccharide fractions decreased and the activity in the protein fraction increased. There were significant seasonal variation in P-I parameters and the photosynthetic end-products. In both lakes, phytoplankton communities from the late winter-spring isothermal period were characterized by lower P_M^B values, higher α values, significant susceptibility to photoinhibition, and less incorporation into protein, as compared to communities from periods when the lakes were thermally stratified.
ADDITIONAL INDEX WORDS: Primary productivity, light intensity, irradiation, proteins.

INTRODUCTION

Despite more than 20 years of primary production studies in the upper Great Lakes (Putnam and Olson 1961, 1966; Saunders *et al.* 1962; Parkos *et al.* 1969; Schelske and Callender 1970; Fee 1972; Schelske and Roth 1973; Watson *et al.* 1975; Parker *et al.* 1977; Fahnenstiel and Scavia 1987a), only limited data are available for comparisons of photosynthesis among the Great Lakes and with other aquatic environments (Vollenweider *et al.* 1974). This problem is not restricted to the Laurentian Great Lakes but is common in many other aquatic environments (Platt and Subba Rao 1975). The major causes of this problem are limited sampling, variable experimental protocol, and inconsistent data analysis and presentation. Restrictive temporal and/or spatial sampling often limit the application of results to specific sites or times (Vollenweider *et al.* 1974).

In the Great Lakes, measurements of photosynthesis have been made in 100- to 2,000-mL bottles, incubated for 1-24 h, and exposed to natural and artificial irradiance. In some cases, previous experimental conditions now are deemed unreliable and may produce artificially low production rates (Gieskes and Kraay 1984). Also, many incubations were performed at a single light intensity; because of the non-linear relationship between photosynthesis and irradiance, comparing results from different incubation conditions is difficult. Finally, investigators have reported rates of photosynthesis in areal, volumetric, or biomass units and rarely provided the additional data required to make conversions to other units. Because of such inconsistencies, it is difficult to characterize the general

[1]This paper is dedicated to the memory of Albert H. Fahnenstiel

patterns of photosynthesis in the upper Great Lakes.

An approach to the study of photosynthesis in aquatic systems that has not been extensively applied to the Great Lakes has been advanced by Platt and Jassby (1976) and Fee *et al.* (1987). This approach focuses on parameterizing photosynthesis-irradiance (P-I) curves rather than on measuring the instantaneous *in situ* rate. P-I curves have been used widely in oceanography (Platt and Jassby 1976, Côté and Platt 1983, Gallegos *et al.* 1983, Harrison and Platt 1986, Harding *et al.* 1986) and twice in the upper Great Lakes (Fee 1972, Fahnenstiel and Scavia 1987a) to study the patterns and controls of photosynthesis.

At least two parameters are required to describe P-I curves: P_M^B and α. P_M^B is the maximum photosynthetic rate at light saturation per unit of chlorophyll and is a function of the enzymatic reactions in photosynthesis. P_M^B has been demonstrated to be dependent on temperature (Harris and Piccinin 1977), nutrient availability (Senft 1978), light history (Sephton and Harris 1984), and phytoplankton community structure and composition (Dunstan 1973). P_M^B is equivalent to the assimilation number measured at saturating irradiances, which has been reported in several previous studies in the upper Great Lakes (Glooschenko *et al.* 1974, Parker *et al.* 1977, Fahnenstiel and Scavia 1987a). α is the initial linear slope of the P-I curve at low irradiance per unit of chlorophyll and is a measure of the photochemical processes of photosynthesis. α is dependent on previous light climate (Platt and Jassby 1976), phytoplankton community structure and composition (Harris 1973), and possibly on nutrient availability (Welschmeyer and Lorenzen 1981).

Two other less used parameters of the P-I curve are β and R^B. These two parameters are not suitable for all P-I curves but have special application and interpretation. β is the negative linear slope at high irradiances and is a measure of photoinhibition (Platt *et al.* 1980). R^B is the Y-intercept of the P-I curve and may estimate the phytoplankton respiration rate. Estimates of R^B are subject to a great deal of uncertainty both in terms of experimental error and interpretation (Platt and Jassby 1976).

The partitioning of photosynthate into major end-products such as proteins, lipids, polysaccharides, and low molecular weight metabolites may provide information on the physiological status and relative growth rate of phytoplankton communities (Morris *et al.* 1974, Li *et al.* 1980, DiTullio and Laws 1983, Priscu and Priscu 1984). Particularly, the percent incorporation into protein as compared to the percent incorporation into lipids and polysaccharides is a useful index of physiological condition of phytoplankton (Morris 1981). Substantial incorporation into protein suggests very good physiological condition with high relative growth rates, whereas low incorporation into protein suggests poor physiological condition with low relative growth rates.

In this paper we report on the photosynthetic characteristics of phytoplankton communities from Lakes Huron and Michigan. Our data were collected in 1983–1987 in Lake Michigan and 1986–1987 in Lake Huron. In the first part of this paper, we examine P-I parameters and their associated temporal and spatial variability. In the second part, we examine the temporal and spatial variability in the partitioning of photosynthate into major end-products. We hope that this paper will establish an initial data base for subsequent related studies of photosynthesis in the upper Great Lakes.

METHODS

Samples were collected at two offshore stations in Lake Huron (northern 45° 25′N 82°55′W, and southern 43°56′N 82°21′W) and at one offshore station in Lake Michigan (43°1′N, 86°37′W). The Lake Michigan station was sampled fourteen times from 1983 through 1987; the Lake Huron stations were sampled fifteen times from 1986 through 1987. On April 17 1986 three additional stations were sampled in Lake Michigan, corresponding to EPA stations number 23, 18, and 19 (Fig. 1).

Water samples were collected with 5- or 20-L PVC Niskin bottles. Surface mixing-layer water samples were collected at mid-depth if the surface mixing layer was < 20 m and at 5–10 m if the surface mixing layer was > 20 m. Temperature was measured with a electronic bathythermograph and a bucket thermometer. Underwater scalar irradiation was measured with a Licor LI-193SB sensor and LI-188B integrating meter. Chlorophyll concentrations were determined fluorometrically on 90% acetone extracted samples (Strickland and Parsons 1972).

Phytoplankton photosynthesis was estimated with the ^{14}C technique (Vollenweider 1974). Several modifications of the "clean techniques" were used for all ^{14}C experiments (Fahnenstiel and Scavia 1987a). Immediately after sample collection, incu-

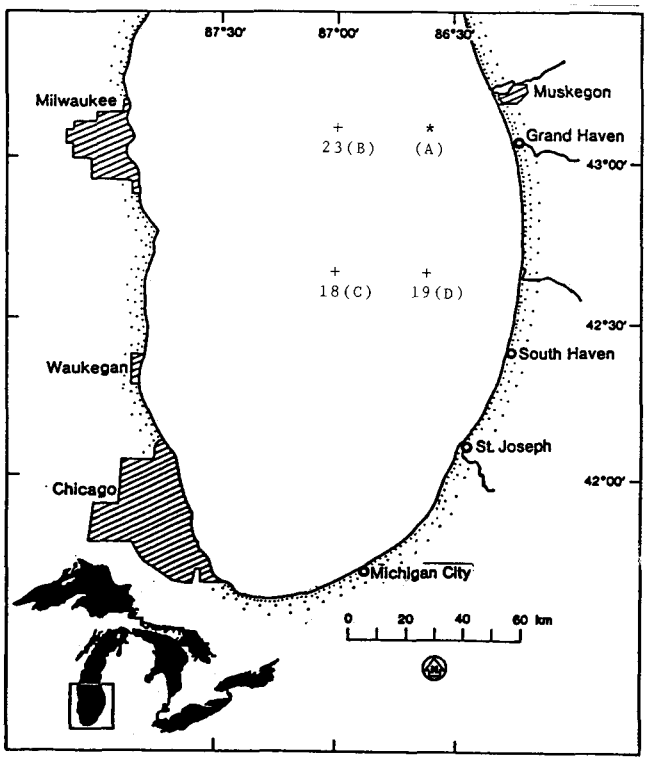

FIG. 1. Map of southern Lake Michigan indicating four stations that were sampled on 17 April 1986. Station A is main Lake Michigan station and stations B-D are EPA stations.

bation samples were dispensed into shaded 2-1 polycarbonate bottles. Incubation bottles were then inoculated with 111-1850 kBq of ^{14}C from a stock solution prepared as described in Fahnenstiel and Scavia (1987a). Bottles were incubated in a shipboard lakewater-cooled incubator with 8–12 light levels. Incubation temperature was maintained within 1°C of ambient lakewater temperature. The incubator consisted of a 1,000 W metal halide lamp attached at one end of a long box containing 8–12 compartments. Each compartment was separated by neutral density screens and the light received in each compartment was measured. To reduce heat and UV light from the light source, a piece of Plexiglass, 1.2 cm in thickness, was used in front of the forward compartment. In the lowest light compartment, an incubation bottle was spiked with DCMU and the uptake of ^{14}C in this bottle was subtracted from all light bottles (Legendre *et al.* 1983). The uptake of ^{14}C in this DCMU-spiked bottle never exceeded 5% of the light saturated rate. Total CO_2 was determined from alkalinity and pH measurements (Vollenweider *et al.* 1974). To minimize diurnal effects, most incubations were performed between 1400–1700 hours.

After a 1–2 h incubation, three subsamples from each bottle (with one exception) were filtered onto 0.45-μm Millipore filters, decontaminated with 0.5 mL of 0.5 N HCL for 4–6 h, placed in separate scintillation vials with scintillation cocktail, and counted with a scintillation counter. External standards were used to correct for quench. Also, after 2–4 h incubation, six subsamples from the remaining bottle were filtered onto GF/F Whatman filters, placed in amber glass vials, and frozen at -20°C for analysis of end-products. For surface mixing-layer samples, the incubation bottle from approximately 1.35 Ein·m^{-2}·h^{-1} was processed for end-products; for deep samples, the incubation bottle from approximately 0.07 Ein·m^{-2}·h^{-1} was processed.

Photosynthetic end-products were determined by differential solvent extraction (Li *et al.* 1980). This method separates photosynthetic end-products into four groups: methanol soluble-low molecular weight metabolites, chloroform soluble-lipids, hot TCA-soluble-polysaccharides, and hot TCA-insoluble-proteins. Our extraction protocol was similar to Li *et al.* (1980) with one exception: frozen filters with radio-labelled algae were stored dry rather than with 1.2 mL of distilled water. Distilled water was added to the filters after they were thawed. The efficiency of our extraction procedure was examined by comparing the sum of radioactivity in the four fractions to the radioactivity on unextracted filters containing an equivalent amount of radioactive algae. For 63 separate extractions, the sum of radioactivity in the recovery from the four fractions was very similar to the radioactivity on the unextracted filter ($\bar{x} \pm$ S.D., 98.7 ± 11.7%).

Photosynthetic rates, normalized to chlorophyll *a* from duplicate bottles in each compartment, were pooled to construct a single photosynthetic-irradiance (P-I) curve. The following equation was used to parameterize the P-I relationship (Platt *et al.* 1980):

$$P^B = P_S^B \cdot (1-e^{-\alpha i/P_S^B}) \cdot e^{-\beta i/P_S^B}$$

where P^B = specific photosynthetic rate at irradiance i (mg C·mg Chl^{-1}·h^{-1}), P_S^B = the maximum potential photosynthetic rate (same units as P^B),

α = the initial linear slope at low irradiances (mg C·mg Chl^{-1}·Einst^{-1}·m^2), β = the negative slope at high irradiances (same units as α). P_S^B is a scaling parameter that has little ecological significance. The more commonly used parameter, P_M^B, the maximum photosynthetic rate at light saturation, was determined from P_S^B with the following equation:

$$P_M^B = P_S^B \cdot [\alpha/(\alpha+\beta)] \cdot [\beta/(\alpha+\beta)]^{\beta/\alpha}$$

In the absence of photoinhibition, $P_M^B = P_S^b$. If $\beta > 0$, then $P_S^B > P_M^B$ and P_S^B represents the maximum obtainable photosynthetic rate in the absence of photoinhibition.

Two derived parameters are also of interest; I_K and I_β. I_K is the light saturation parameter (Talling 1957), defined as P_M^B/α with units of Einst^{-1}·m^2·h^{-1}. I_β is an index of photoinhibition (Platt *et al.* 1980), defined as P_S^B/β also with units of Einst^{-1}·m^2·h^{-1}.

A fourth parameter, R^B, the y-intercept, is often used in P-I models. Because R^B values were only significantly different than zero on a single date (April 17 1986), this parameter was excluded from our model. Thus, we constrained the model to pass through the origin.

A non-linear least squares estimation package from IMSL was used to determine the maximum likelihood estimates of the parameters and also the variance-covariance matrix. In many cases, the three-parameter model described above, including a photoinhibition parameter, may not be necessary to adequately fit P-I data (Platt *et al.* 1980). Many photoplankton communities do not exhibit significant photoinhibition at incubation irradiances, and the simple two-parameter model with P_M^B and α is adequate. Whether the photoinhibition parameter, β, should be included in our model was determined by the significance of β. If the 95% C.I. for β did not include zero then β was included in the model. If, however, the 95% C.I. for β included zero then β was excluded and the regression was repeated for the two parameter model.

RESULTS AND DISCUSSION

The P-I model reasonably described the relationship between photosynthesis and irradiance, with an average R^2 of 0.98. Examples of P-I curves from both Lakes Huron and Michigan are given in Figure 2. More than half (58%) of the P-I curves were adequately described with the two-parameter model (Tables 1 and 2). The average values and the spatial and temporal variability of each parameter are discussed below. Thermal stratification was divided into two periods based on epilimnetic temperature (Fahnenstiel and Scavia 1987a). Intermediate stratification refers to the period when epilimnetic temperature was >4°C but <15°C and mid-stratification refers to the period when epilimnetic temperatures were >16°C. The spring isothermal-mixing period refers to the period in the spring (March–June) when isothermal mixing temperatures are < 4°C.

Maximum Light Saturated Rate (P_M^B)

The average P_M^B values for Lakes Michigan and Huron were not significantly different (2.4 and 2.3 mg C· mg Chl^{-1}·h^{-1}, respectively, two-sample Kruskal-Wallis test, H = 1.7, P = 0.19). Our mean P_M^B values in 1983–1987 were higher than values reported previously from Lakes Huron and Michigan; however, given the limited amount of sampling, the significance of these differences is questionable. Glooschenko *et al.* (1974) reported a mean annual assimilation number (max. prod·chl^{-1}) of 1.7 mg C·mg Chl^{-1}·h^{-1} for Lake Huron in 1971, and Fee (1972) reported a mean P_M^B of 1.2 mg C· Chl^{-1}·h^{-1} for three offshore stations in Lake Michigan for the period July 1970–February 1971. Fee's mean P_M^B value for 1970–1971 and our mean annual P_M^B for 1983–1987 are not significantly different if the variation in annual P_M^B values from the 1983–1987 period is used as a measure of annual variation for both the 1970–1971 and 1983–1987 periods (T-test, T = 1.58, P>0.20). Part of the reason for lower values in the 1970s may be related to methodological differences between studies. The ^{14}C technique used by Fee (1972) and Glooschenko *et al.* (1974), which utilized relatively long incubations (4–5 h) in small bottles (100–150 mL), may produce artificially low rates of photosynthesis (Gieskes and Kraay 1984).

The average P_M^B values for Lakes Huron and Michigan are similar to annual mean assimilation numbers in Lakes Superior, Erie, and Ontario. Annual assimilation numbers averaged 1.5–3.0 mg C·mg Chl^{-1}·h^{-1} for Lake Ontario (Stadelman *et al.* 1974, Glooschenko *et al.* 1974), 3.0 mg C·mg Chl^{-1}·h^{-1} for Lake Erie (Glooschenko *et al.* 1974), and 2.4 mg C·mg Chl^{-1}·h^{-1} for Lake Superior (Fahnenstiel and Glime 1983). The general similarity in annual P_M^B and assimilation numbers from all the Great Lakes despite large differences in phytoplankton composition (Munawar and Munawar 1986) and trophic status (Vollenweider *et al.* 1974) has two important implications. First, physical

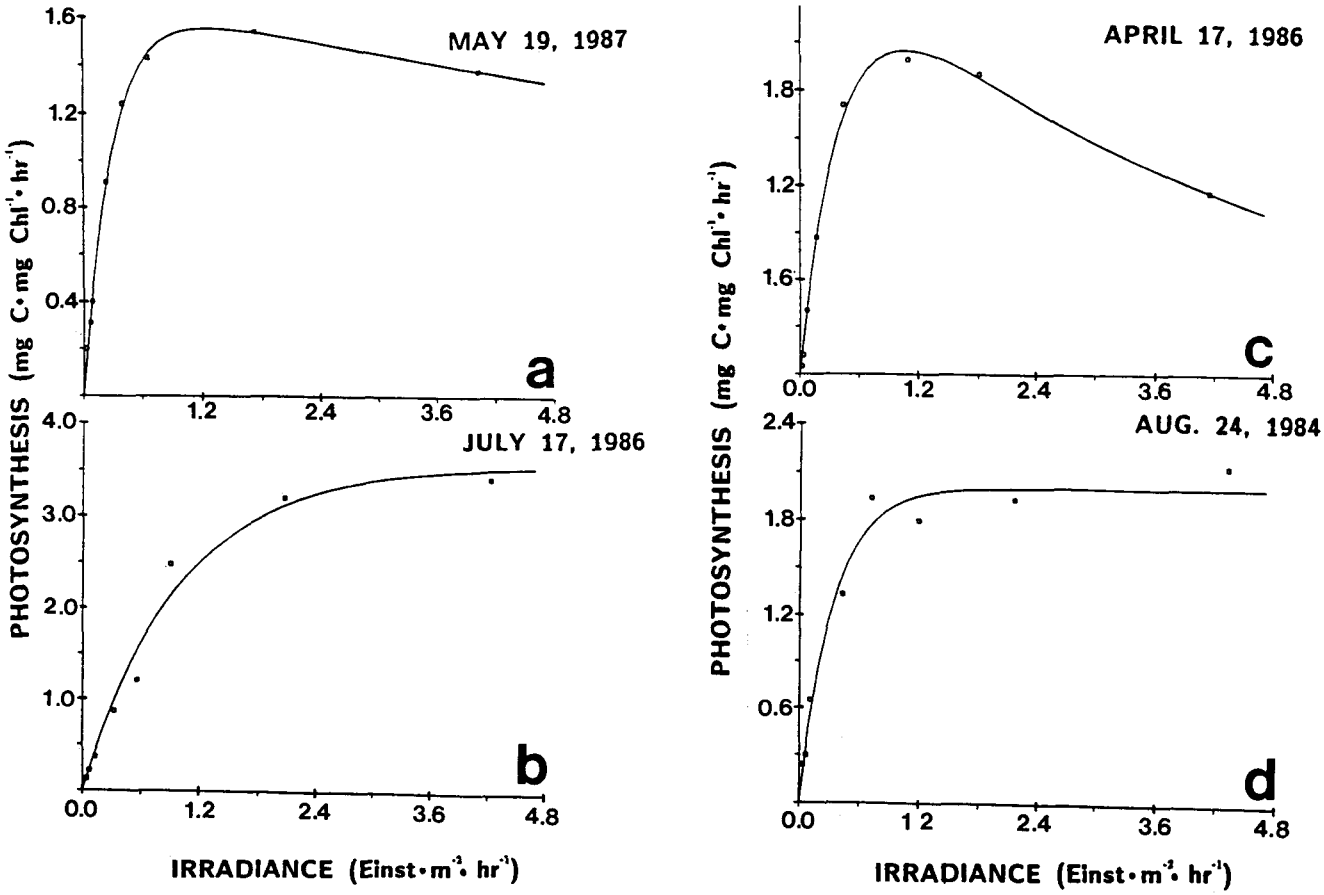

FIG. 2. Examples of P-I curves from Lake Huron (a-b) and Lake Michigan (c-d) during the spring isothermal mixing period and thermal stratification.

factors such as temperature and light play an important role in regulating annual primary production and may set a relatively narrow range for chlorophyll-specific production values. Second, provided the carbon:chlorophyll ratio is similar in all the Great Lakes, the turnover of algal carbon, i.e., growth rate, is relatively similar in all the Great Lakes.

The temporal variation in P_M^B was also similar in our two lakes. The coefficient of variations of P_M^B for the entire study period in Lakes Huron and Michigan were 47% and 37%, respectively. These coefficients of variability are also similar to the coefficients of variability of P_M^B reported for a temperate coastal community over a 2-year period (Harrison and Platt 1986).

Although our mean P_M^B values were not significantly different, P_M^B from the spring isothermal mixing period were significantly higher in Lake Michigan ($\bar{X}$ = 2.2) than in Lake Huron ($\bar{X}$ = 1.4) (Table 3, H = 9.00, P = 0.0027). Summer P_M^B values were not significantly different between the two lakes (H = 1.5, P = 0.2207).

Spatial variability was further examined by comparing P_M^B values for four stations in southern Lake Michigan on the same day. Because the P-I experiments were conducted at different times of the day (1000–2000 hours) any variability in P_M^B was due to a combination of spatial and diurnal variability. The resultant coefficient of variation of P_M^B was very low, 8%. Although it is possible that the effects of diurnal and spatial variability counteracted, the low coefficient of variation suggests that spatial and diel variability are not major contributors to the variability of P_M^B in Lake Michigan. This lack of major spatial variability in P_M^B is consistent

TABLE 1. Individual P-I curves for surface-mixing layer(S) and deep chlorophyll layer (25–30 m,D) phytoplankton communities from Lake Huron. P_m^B (mg C·mg Chl $^{-1}$·hr^{-1}), α (mg C·mg Chl^{-1}·Einst^{-1}·m^2), I_k (Einst·m^{-2}·hr^{-1}), I_{max} = maximum light intensity in incubator (Einst·m^{-2}·hr^{-1}), T = temperature of surface mixing-layer (°C), R^2 of regression and Chl. concentration (mg·m^{-3}) are given for each P-I curve. For communities with significant β values, P_s^B (same units as P_m^B), β (same units as α) and I_β (same units as I_k) are also provided. Error estimates are standard deviations.

Date	Zone	P_m^B	P_s^B	α	β	I_k	I_β	I_{max}	T	R^2	Chl
5 March/87	S	1.45	1.72±0.16	5.92±0.53	0.237±0.069	0.245	7.26	5.76	0.1	0.98	1.08
15 April/87	S	1.34	1.54±0.10	6.53±0.42	0.203±0.062	0.205	7.59	3.13	2.0	0.98	2.17
29 April/86	S	1.19	1.41±0.15	4.44±0.30	0.178±0.070	0.268	7.92	5.04	2.0	0.98	1.20
30 April/86	S	1.54	1.83±0.18	5.83±0.44	0.235±0.079	0.264	7.79	5.04	2.0	0.98	0.94
18 May/87	S	1.07	1.17±0.09	5.19±0.32	0.091±0.025	0.206	12.86	3.96	4.0	0.99	1.67
19 May/87	S	1.57	1.67±0.06	7.08±0.22	0.080±0.022	0.222	20.88	3.96	4.0	1.00	1.16
19 June/86	S	1.72±0.14	-	4.92±0.60	-	0.350	-	3.24	5.4	0.96	0.94
23 June/86	S	1.42±0.14	-	4.61±1.63	-	0.308	-	3.24	9.6	0.93	1.28
17 July/86	S	3.59±0.21	-	5.69±0.47	-	0.631	-	3.60	17.0	0.98	0.76
29 July/87	S	4.06±0.47	-	4.58±0.39	-	0.886	-	5.04	21.1	0.98	0.50
29 July/87	D	2.01±0.08	-	8.39±0.52	-	0.240	-	5.04	5.6	0.99	1.40
30 July/87	S	3.85±0.22	-	5.08±0.39	-	0.758	-	5.04	21.0	0.98	0.82
17 August/86	S	3.60±0.18	-	5.11±0.30	-	0.704	-	5.76	20.2	0.98	1.22
19 August/86	S	3.52±0.19	-	4.33±0.35	-	0.813	-	5.76	17.7	0.98	1.64
15 October/87	S	2.05±0.08	-	7.78±0.75	-	0.263	-	4.32	12.5	0.98	2.19
18 October/86	S	2.20±0.18	-	5.97±0.94	-	0.368	-	4.32	13.0	0.92	1.89

TABLE 2. Individual P-I curves for surface-mixing layer(S), deep chlorophyll layer (25–30 m,D), and hypolimnetic (50 m,H) phytoplankton communities from Lake Michigan. The four P-I curves on 17 April 1986 were from four different stations (See Fig. 1). Units for P-I parameters are same as in Table 1.

Date	Zone	P_m^B	P_s^B	α	β	I_k	I_β	I_{max}	T	R^2	Chl
17 April/86(A)	S	2.12	2.77±0.21	8.06±0.47	0.583±0.125	0.263	4.75	3.96	2.5	0.99	2.42
17 April/86(B)	S	2.00	2.57±0.18	7.44±0.39	0.497±0.101	0.269	5.17	3.96	2.5	0.99	2.44
17 April/86(C)	S	1.84	2.44±0.19	6.22±0.31	0.483±0.104	0.296	5.05	3.96	2.5	1.00	2.35
17 April/86(D)	S	2.25	2.92±0.34	8.53±0.78	0.597±0.200	0.264	4.89	3.96	2.5	0.99	2.41
1 May/87	S	2.95±0.16	-	9.00±0.91	-	0.328	-	3.96	3.8	0.97	2.54
16 May/83	S	1.61	2.14±0.36	7.53±0.94	0.330±0.087	0.214	6.48	3.24	4.0	0.96	2.28
21 May/84	S	2.58	3.29±0.33	7.11±0.44	0.456±0.145	0.363	7.21	4.32	3.3	0.99	2.27
18 June/84	S	1.81	2.06±0.14	7.25±0.49	0.204±0.065	0.250	10.10	4.32	7.0	0.99	2.57
22 June/87	S	2.69±0.09	-	3.61±0.14	-	0.745	-	4.32	18.0	1.00	0.85
10 July/83	S	1.74±0.15	-	4.75±0.58	-	0.366	-	3.24	18.5	0.95	0.96
10 July/83	D	0.91	0.99±0.06	5.75±0.40	0.100±0.040	0.158	9.90	3.24	6.0	0.98	6.2
10 July/83	H	0.56	0.58±0.02	6.36±0.41	0.048±0.016	0.088	12.08	3.24	4.7	0.98	6.3
21 July/87	S	4.36±0.45	-	5.89±0.69	-	0.740	-	2.88	21.8	0.97	0.76
21 July/87	D	2.89	4.16±0.72	11.33±1.00	1.269±0.278	0.255	3.28	2.88	8.7	0.98	1.39
23 July,84	S	2.58±0.11	-	5.58±0.45	-	0.462	-	3.96	19.0	0.98	0.98
20 August/87	S	3.51±0.16	-	6.42±0.58	-	0.547	-	2.88	22.4	0.98	0.99
24 August/84	S	2.01±0.09	-	7.36±0.87	-	0.273	-	4.32	22.3	0.98	1.37
25 August/86	S	3.46±0.19	-	6.39±0.75	-	0.541	-	5.76	20.8	0.96	1.38
17 September/83	S	1.76±0.04	-	6.92±0.40	-	0.254	-	3.24	19.0	0.99	1.73
3 November/87	S	3.61±0.07	-	11.30±0.47	-	0.319	-	3.24	10.8	1.00	2.86

TABLE 3. Summary P-I characteristics of surface-mixing layer phytoplankton communities from major thermal periods in Lakes Huron and Michigan. Major thermal periods, spring isothermal mixing, intermediate thermal stratification, and mid stratification, are defined in text. The range of surface-mixing layer temperatures (°C), number of P-I curves (N), P_m^B (mg C·mg Chl^{-1}·hr^{-1}), α (mg C·mg Chl^{-1}·Einst^{-1}·m^2), I_k (Einst·m^{-2}·hr^{-1}), and percent of P-I curves with significant β values (%β) are given for each thermal period.

Lake	T	N	P_m^B ($\bar{X}\pm$S.D.)	α ($\bar{X}\pm$S.D.)	I_k ($\bar{X}\pm$S.D.)	%β
Michigan						
Spring mixing 1983–87	2.5–4.0	7	2.19±0.45	7.78±0.94	0.285±0.049	86
Int. Strat. 1983–87	7.0–11.0	2	2.71±1.27	9.44±2.94	0.284±0.049	50
Mid strat. 1983–84	18.5–22.3	4	2.02±0.39	6.11±1.17	0.339±0.096	0
Mid strat. 1986–87	18.0–22.4	4	3.50±0.68	5.56±1.33	0.643±0.115	0
Huron						
Spring mixing 1986–87	0.1–4.0	6	1.37±0.20	5.85±0.97	0.235±0.028	100
Int. strat. 1986–87	5.4–13.0	4	1.85±0.35	5.89±1.39	0.322±0.047	0
Mid strat. 1986–87	17.0–21.0	5	3.72±0.23	5.00±0.53	0.758±0.098	0

with the general spatial homogeneity among other biological and chemical parameters in the upper Great Lakes (Kwiatkowski 1984).

Significant seasonal variability in P_M^B values was observed in both lakes (Table 3, Fig. 3). Previous studies of P_M^B in other temperate regions have also found significant temporal variability (Williams 1978, Harrison and Platt 1986, Fee *et al.* 1987). In 1986–1987 in both lakes, P_M^B values from the period of mid-stratification were significantly higher than P_M^B values from period of spring isothermal mixing (L. Huron, H = 7.5, P = 0.0062; L. Michigan, H = 4.86, P = 0.0275). P_M^B values from the period of intermediate stratification were between the spring and mid-stratification values (Table 3).

Unlike 1986–1987, no significant seasonal difference was found in P_M^B values for the 1983–1984 period in Lake Michigan (Table 3, Fig. 3). In these two years, mid-stratification P_M^B values were not significantly different than spring values (H = 0.06, P = 0.8143). The absence of a seasonal trend in 1983–1984 was due to lower summer P_M^B values. Mid-stratification P_M^B values in 1983–1984 were significantly lower than mid-stratification values in 1986–1987 (H = 5.33, P = 0.0209). This annual variability implies that chlorophyll measurements from a given year cannot reliably be extrapolated to estimates of primary production based on P_M^B values measured in a different year.

The rather low variability of P_M^B within each

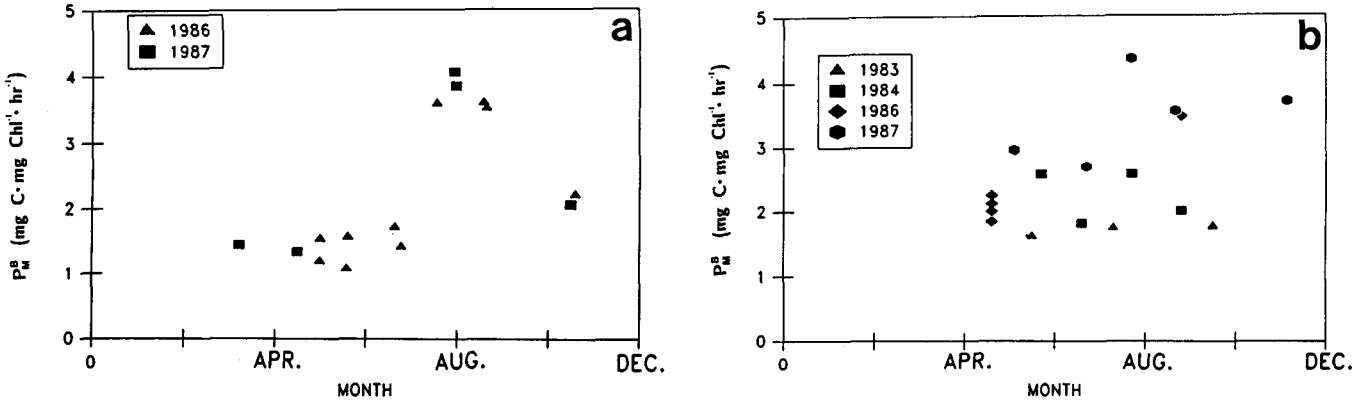

FIG. 3. Seasonal P_M^B values from surface-mixing layer communities in Lakes Huron (a) and Michigan (b).

major season suggests that seasonal sampling may provide a reasonable strategy for assessing annual variation of P_M^B. The mean coefficient of variation (c.v.) for the spring and summer sampling periods of each year averaged only 11.5%, which is only slightly higher than the variation (c.v. = 8%) attributable to diurnal and spatial variability.

Seasonal sampling must be conducted each year as the annual variation in P_M^B values is relatively high. The c.v. of annual mean P_M^B values for 4 years from Lake Michigan was 29%. Fee *et al.* (1987) suggested that large lakes may exhibit less annual variation in P-I parameters than small lakes. They reported a c.v. for annual mean P_M^B values of 34.5% for 8 years of sampling in the Experimental Lakes Area. Based on our limited sampling, the annual variation of P_M^B values appears to be similar in large and small lakes. It should be noted that the observed annual variation in P_M^B values from Lake Michigan may not reflect inherent variability within the lake. Rather, they may reflect recent management practices that have dramatically altered the ecosystem, such as fish manipulations and nutrient abatement (Scavia *et al.* 1986). A relatively unperturbed large lake may exhibit less annual variation in P-I parameters.

P_M^B values for subthermocline communities were considerably lower than values from comparable surface mixing-layer communities (Tables 1 and 2). For communities within the deep chlorophyll layer (25–30 m), P_M^B values averaged 56% of the values for comparable surface mixing communities. A P_M^B estimate for one upper hypolimnetic (50 m) community was much lower (Table 2). A reduction in P_M^B for subthermocline communities has been commonly observed (Platt and Jassby 1976, Harrison and Platt 1986) and is an indicator of a low-light adapted community (Beardall and Morris 1976).

Initial Linear Slope (α)

The mean α value from Lake Huron, 5.5 mg C·mg Chl^{-1}·Einst^{-1}·m^2, was significantly different than the mean value from Lake Michigan, 7.0 mg C·mg Chl^{-1}·Einst^{-1}·m^2, ($H = 7.23$, $P = 0.0072$), but both values are in the range of those reported from several other aquatic environments. Mean α values from Chesapeake and Delaware bays (Harding *et al.* 1986), the Experimental Lakes Area (Fee *et al.* 1987), and coastal Nova Scotia (Harrison and Platt 1986) were 8.3, 4.2, and 14.4 mg C·mg Chl^{-1}·Einst^{-1}·m^2, respectively.

Because no previous estimates of α exist for the Laurential Great Lakes, our comparisons are limited. However, quantum efficiencies reported for deep chlorophyll layer communities from Lake Superior (Fahnenstiel *et al.* 1984) can be converted to α estimates, where α is equal to the maximum quantum efficiency (ϕ_m) multiplied by the chlorophyll *a* specific absorption coefficient (K_C). In the Lake Superior study, the mean quantum efficiency was 0.04 moles C·Einst^{-1} and K_C was 0.017 m^2·mg Chl^{-1}. Thus an estimate of the mean α for deep Lake Superior phytoplankton is 8.23 mg C·mg Chl^{-1}·Einst^{-1}·m^2. This value is larger than the mean surface α values from Lakes Huron and Michigan but similar to the mean α value of 8.49 mg C·mg Chl^{-1}·Einst^{-1}·m^2 for deep chlorophyll layer communities from these two lakes (Tables 1 and 2).

The coefficients of variation of α values for Lakes Huron and Michigan were 22% and 27%, respectively, and were approximately 60% of the c.v. for P_M^B. Because α is a measure of the photochemical capacity of the phytoplankton, α values might be expected to be less variable than P_M^B values. However, previous observations have not supported this idea: Harrison and Platt (1986) and Fee *et al.* (1987) observed similar variability in P_M^B and α values for communities from coastal Nova Scotia and the Experimental Lakes Area.

The diurnal and spatial variability of α values was similar to diurnal and spatial variability of P_M^B values. The coefficient of variation for α estimates from four stations in southern Lake Michigan sampled on the same day was 13.2%. This variation is approximately half the total variation in α estimates found within either Lakes Huron or Michigan.

The seasonal variation in α values was not as pronounced as the seasonal variation in P_M^B values (Fig. 4 vs. Fig. 3). In Lake Michigan during midstratification the mean α value was significantly lower than the mean value from the spring isothermal mixing period ($H = 7.44$, $P = 0.0064$). In Lake Huron the mean values from these two thermal periods were not significantly different ($H = 3.08$, $P = 0.0793$). Subthermocline phytoplankton communities from both lakes always exhibited higher α values than comparable surface mixing-layer communities (Tables 1 and 2). Thus, subthermocline communities are more efficient at utilizing low light, which is probably a result of increased light absorption.

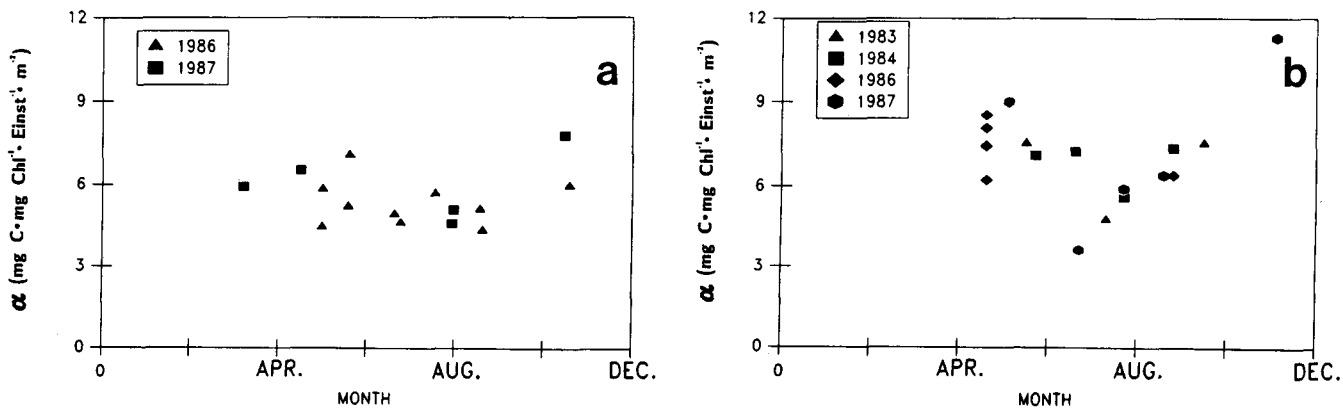

FIG. 4. Seasonal α values for surface-mixing layer communities in Lakes Huron (a) and Michigan (b).

Light Saturation Parameter (I_K)

I_K estimates have been used to characterize phytoplankton communities. Phytoplankton with lower I_K values were generally assumed to be more low-light adapted than phytoplankton with higher I_K values (Yentsch and Lee 1966). Adaptation to low-light results in lower P_M^B values and sometimes higher α values, thereby producing lower I_K values (Beardall and Morris 1976, Harris 1978). In Lakes Huron and Michigan, low-light adapted phytoplankton from subthermocline and spring mixing communities (as indicated by lower C:Chl ratios) generally exhibited lower I_K values (Tables 1–3). However, recent work has questioned the use of I_K as indicator of light adaptation (Harris 1978, Platt *et al.* 1982). Because low-light adapted communities in the Great Lakes also occur at low temperatures, it is difficult to attribute lower I_K values strictly to low light conditions.

Despite the uncertainty of I_K values as indicators of low-light adapted communities, I_K is useful in comparing phytoplankton communities from different environments. Harris (1978) reviewed I_K estimates from aquatic environments and noted that values generally fall between 0.14 and 0.72 Ein·m^{-2}·h^{-1}, with the most frequently observed estimates between 0.25 and 0.36 Ein·m^{-2}·h^{-1}. The mean I_K estimates from Lakes Huron and Michigan of 0.42 and 0.35 Ein·m^{-2}·h^{-1}, respectively, are consistent with previous estimates from freshwater and marine environments.

Negative Slope at High Irradiances and Index of Photoinhibition (β and I_β)

Photoinhibition was not a consistent feature of P-I curves in either lake. Phytoplankton communities from both lakes exhibited seasonal variation in the degree of photoinhibition. For surface mixing-layer communities, significant β estimates were found only during the periods of spring isothermal mixing and intermediate thermal stratification (Tables 1–3). Photoinhibition was especially pronounced during spring isothermal mixing, with 92% of the P-I curves exhibiting significant β values (Table 3). In only one case during the intermediate thermal mixing period were significant β values observed. However, as would be expected for low-light adapted phytoplankton, subthermocline phytoplankton communities exhibited significant photoinhibition in three-out-of-four cases (Tables 1 and 2).

The presence and intensity of photoinhibition may be a better indicator of low-light adapted communities than I_K (Harris 1978, Platt *et al.* 1982). Harris (1978) noted that low-light adapted communities (as indicated by lower C:Chl ratios and higher α values) were more suspectible to photoinhibition than high-light adapted communities. This relationship may be true for phytoplankton communities from Lakes Huron and Michigan. The communities that exhibited significant photoinhibition are the same communities that exhibited higher α values (Table 3) and lower C:Chl

TABLE 4. The mean percent of ^{14}C incorporated into proteins, lipids, polysaccharides, and low molecular weight (LMW) metabolites for surface-mixing layer communities determined from 25 short-term experiments.

	PROTEIN (%)	LIPID (%)	POLYSAC. (%)	LMW (%)
Lake Michigan	34.8	24.7	24.5	15.8
Lake Huron	32.4	21.3	28.0	18.9

ratios (Fahnenstiel and Scavia 1987b). As noted earlier, however, low temperatures co-occur with low light, and thus it is difficult to separate the role of light from temperature.

The degree or intensity of photoinhibition is indicated by the parameter I_β, with lower values indicating greater photoinhibition. Low values also have been used as an index of low-light adapted communities (Platt *et al.* 1982). In both lakes, the lowest I_β values were found during the late winter-early spring period (March–April); as spring isothermal mixing progressed, I_β values increased. Also, for similar time periods during spring isothermal mixing, Lake Michigan phytoplankton communities exhibited lower I_β values than comparable Lake Huron communities (Tables 1 and 2).

Photosynthetic End-Products

The mean percent of photosynthate incorporated into major end-products was similar in both lakes (Table 4). The protein fraction was the most significant, whereas the LMW metabolite fraction was the least significant (Table 4). These mean incorporation values are in the range of mean incorporation values from short-term experiments in other regions such as a Danish lake (Jensen 1985), a New Zealand coastal upwelling system (Priscu and Priscu 1984), the eastern Canadian arctic (Li and Platt 1982), and the coastal and oceanic regions of the Caribbean Sea and western Atlantic Ocean (Morris *et al.* 1981). In these systems, the range of mean incorporation values for various end-products were 22–43% for protein, 13–26% for lipids, 26–41% for polysaccharides, and 5–27% for LMW metabolites. However, our mean incorporation values were much different than incorporation values for Lake Ontario, where Cuhel *et al.* (1984) reported only 10% incorporation into protein but 38% incorporation into lipids.

As mentioned earlier, the percent incorporation into protein and storage products (lipids and polysaccharides) has been used to determine physiological status and relative growth of phytoplankton communities (Morris *et al.* 1974, DiTullio and Laws 1983). These data suggest that Lakes Huron and Michigan phytoplankton are in better physiological condition and have higher relative growth rates than Lake Ontario phytoplankton. Thus, although the *in situ* growth rates of phytoplankton communities in Lakes Huron, Michigan, and Ontario appear to be similar based on mean P_M^B values, relative growth rates as inferred by photosynthate allocation are not. This idea has interesting implications for potential production among the three lakes and should be examined in more detail.

The partitioning of photosynthetic end-products by deep chlorophyll layer (25–30 m) communities was relatively similar to values for surface mixing-layer communities on the same dates (Table 5). These results suggest that communities from the DCL region are in similar physiological condition to surface mixing-layer communities.

The importance of the various end-products varied seasonally. For surface mixing-layer communities in both lakes, the protein fraction increased considerably during summer stratification (Figs. 5 and 6). In both Lakes Huron and Michigan, mean percent protein incorporation increased from averages of 25% and 28%, respectively, during the spring mixing period to 39% and 38% during mid-stratification.

Lipids, polysaccharides, and LMW metabolites fractions changed less seasonally (Figs. 5 and 6). The mean percent incorporation into LMW metabolites decreased from 22% and 23% in Lakes Huron and Michigan, respectively, during mid-stratification to 15% and 14% during the spring mixing period. Mean values for lipid and polysaccharides were more variable. In both lakes, the lowest incorporation into polysaccharides was found during thermal stratification (Figs. 5 and 6).

Five time course experiments were performed to

TABLE 5. Photosynthate partitioning in surface mixing-layer (S) and deep chlorophyll layer (25–30 m, D) communities from Lakes Huron and Michigan. The mean percent of radioactivity incorporated into protein, lipid, polysaccharide, and LMW metabolites from short-term (2–4 h) experiments are listed below.

Date	Lake	Zone	Protein	Lipid	Polysac.	LMW Meta.
22 June 1987	Mich.	S	39.7	20.9	27.4	11.7
22 June 1987	Mich.	D	45.0	20.6	21.4	13.0
21 July 1987	Mich.	S	47.7	16.8	21.3	14.2
21 July 1987	Mich.	D	43.0	17.6	16.7	23.2
29 July 1987	Huron	S	42.5	17.2	28.4	12.0
29 July 1987	Huron	D	37.1	26.8	15.6	10.5

examine the relationship between short-term incorporation patterns and diel incorporation patterns. Throughout the day, the activity in each fraction increased linearly (Figs. 7 and 8), suggesting that results from short-term early afternoon experiments are reasonably representative of the entire day. During the night, the relative importance of most fractions changed markedly. Protein synthesis continued through the night in all five experiments, as evidenced by increased incorporation (Figs. 7 and 8). On the other hand, the incorporation into LMW metabolites decreased during the night in all five experiments. The polysaccharide fraction was variable, with 60% of the experiments exhibiting a decrease during the night and 40% exhibiting little change. The lipid fraction did not exhibit a marked change during the night in any of the experiments. Continued nighttime synthesis of protein at the expense of polysaccharides and LMW metabolites appears to a common feature of phytoplankton communities (Cuhel *et al.* 1984, Priscu and Priscu 1984).

After 24 h, the mean percent incorporated into protein, lipid, polysaccharide, and LMW metabolite fractions was 43, 30, 16, and 10, respectively. In nitrogen-limited cultures, a relationship has been observed between relative growth rate and percent protein incorporation after 24 h (DiTullio and Laws 1983). Although one would not expect a similar relationship between relative growth rate and protein incorporation for both nitrogen- and phosphorus-limited cells, the protein incorporation of both nitrogen- and phosphorus-limited cells decreases with nutrient limitation (Healey and

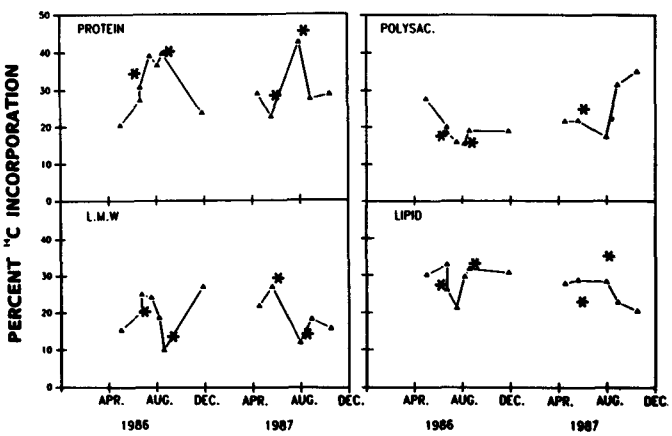

FIG. 5. Seasonal partitioning of major photosynthetic end-products for surface mixing-layer communities in Lake Huron. Triangles indicate samples from southern Lake Huron station and asterisks indicate samples from northern Lake Huron station.

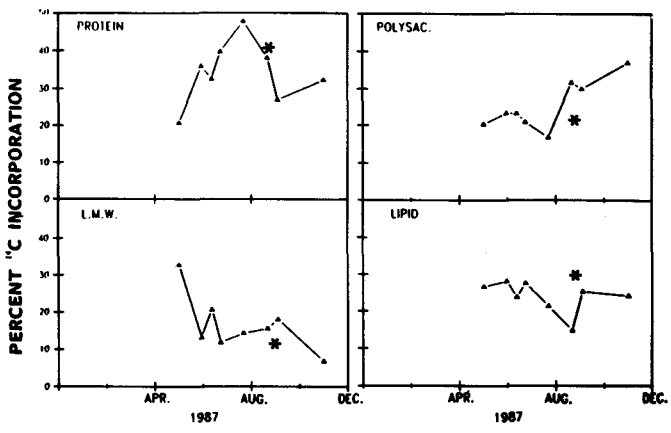

FIG. 6. Seasonal partitioning of major photosynthetic end-products for surface mixing-layer communities in Lake Michigan. Triangles indicate 1987 samples and asterisks indicate 1986 samples.

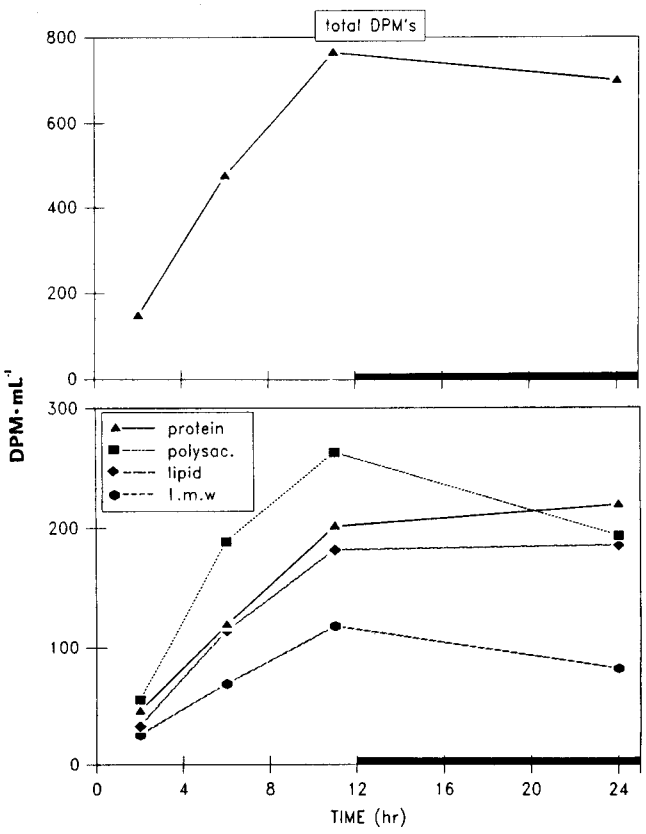

FIG. 7. Time courses of radioactivity in major end-products and on unextracted filter (total) from Lake Huron on 15 October 1987. Shaded bar indidcates the dark period.

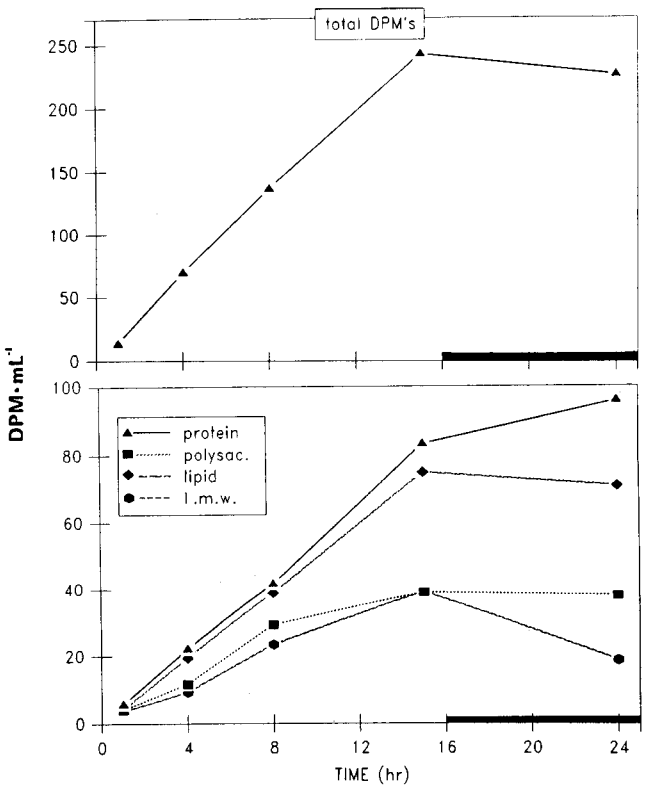

FIG. 8. Time course of radioactivity in major end-products and on unextracted filter (total) from Lake Michigan on 11 June 1987. Shaded bar indicates the dark period.

Hendzel 1979). If the relationship derived for nitrogen-limited cells is used (DiTullio and Laws 1983), phytoplankton communities from Lakes Huron and Michigan are growing at approximately 80% of their maximum rate, using an average protein incorporation rate of 43%. More work is needed to establish the specific relationship between protein incorporation and relative growth rate in phosphorus-limited systems.

CONCLUSIONS

There is great similarity in the photosynthetic characteristics of Lake Huron and Lake Michigan phytoplankton communities. Phytoplankton communities from both lakes exhibit similar means and variation of P-I parameters and partitioning of photosynthetic end-products. The similarity is not surprising given that Lake Michigan is a major source of water to Lake Huron. Although the growth rate of neither community is high, ca. 0.2–0.3 d^{-1} (Fahnenstiel and Scavia 1987a; G. Fahnenstiel, unpubl. data), both communities appear to be in relatively good physiological condition as indicated by a high incorporation into protein.

Significant seasonal variability was found in both P-I parameters and photosynthetic end-products. In both lakes, phytoplankton from the period of spring isothermal mixing were characterized by lower P_M^B (1.27–2.19 mg C· $Chl^{-1}\cdot h^{-1}$), some what higher α (5.85–7.78 mg C·mg $Chl^{-1}\cdot Einst^{-1}\cdot m^2$), less incorporation into protein (25–28%), and susceptibility to photoinhibition; by contrast phytoplankton communities from mid-stratification were characterized by higher P_M^B (2.0–3.7 mg C·mg $Chl^{-1}\cdot h^{-1}$), lower α (5.0–6.1 mg C·mg $Chl^{-1}\cdot Einst^{-1}\cdot m^2$), more incorporation into protein (38–39%), and no

susceptibility to photoinhibition (Table 3). Significant annual variation in P-I parameters was also noted in Lake Michigan. Several other studies from temperate regions have noted similar seasonal and annual variation in P-I parameters (Williams 1978, Harrison and Platt 1986, Fee *et al.* 1987). Subthermocline phytoplankton communities were more similar to surface communities from spring isothermal mixing than surface communities from mid stratification.

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REFERENCES

Beardall, J., and Morris, I. 1976. The concept of light intensity adaptation in marine phytoplankton: Some experiments with *Phaeodactylum tricornutum*. *Mar. Biol.* 37:377–387.

Côté, B., and Platt, T. 1983. Day-to-day variations in the spring-summer photosynthetic parameters of coastal marine phytoplankton. *Limnol. Oceanogr.* 28:320–344.

Cuhel, R. L., Ortner, P. B., and Lean, D. R. S. 1984. Night synthesis of protein by algae. *Limnol. Oceanogr.* 29:731–744.

DiTullio, G. R., and Laws, E. A. 1983. Estimates of phytoplankton N uptake based on $^{14}CO_2$ incorporation into protein. *Limnol. Oceanogr.* 28:177–185.

Dunstan, W. M. 1973. A comparison of the photosynthesis-light intensity relationship in phylogenetically different microalgae. *J. Exp. Mar. Biol. Ecol.* 13:181–187.

Fahnenstiel, G. L., and Glime, J. M. 1983. Subsurface chlorophyll maximum and associated *Cyclotella* pulse in Lake Superior. *Int. Revue ges. Hydrobiol.* 68:605–616.

_____, and Scavia, D. 1987a. Dynamics of Lake Michigan phytoplankton: Primary production and growth. *Can. J. Fish. Aquat. Sci.* 44:499–508.

_____, and Scavia, D. 1987b. Dynamics of Lake Michigan phytoplankton: the deep chlorophyll layer. *J. Great Lakes Res.* 13:285–295.

_____, Schelske, C. L., and Moll, R. A. 1984. *In situ* quantum efficiency of Lake Superior phytoplankton. *J. Great Lakes Res.* 10:339–406.

Fee, E. J. 1972. A numerical model for the estimation of integral primary production and its application to Lake Michigan. Ph.D. thesis, Univ. Wisconsin-Milwaukee.

_____, Hecky, R. E., and Welch, H. A. 1987. Phytoplankton photosynthesis parameters in central Canadian lakes. *J. Plankton Res.* 9:305–316.

Gallegos, C. L., Platt, T., Harrison, W. G., and Irwin, B. 1983. Photosynthetic parameters of arctic marine phytoplankton: Vertical variations and time scales of adaptation. *Limnol. Oceanogr.* 28:698–708.

Gieskes, W. W. C., and Kraay, W. 1984. State-of-the-art in the measurement of primary production. In M. J. Fasham (ed.), *Flows of Energy and Materials in Marine Ecosystems Theory and Practice*, pp. 171–190. New York: Plenum Press.

Glooschenko, W. A., Moore, J. E., and Vollenweider, R. A. 1974. Chlorophyll *a* distribution in Lake Huron and its relationship to primary productivity. In *Proc. 16th Conf. Great Lakes Res.*, pp. 40–49. Internat. Assoc. Great Lakes Res.

Harding, L. W., Jr., Meeson, B. W., and Fischer, T. R., Jr. 1986. Phytoplankton production in two east coast estuaries: photosynthesis-light functions and patterns of carbon assimilation in Chesapeake and Delaware Bays. *Est. Coastal and Shelf Sci.* 23:773–806.

Harris, G. P. 1973. Diel and annual cycles of net plankton photosynthesis in Lake Ontario. *J. Fish. Res. Board Can.* 30:1779–1787.

_____. 1978. Photosynthesis, productivity, and growth: The physiological ecology of phytoplankton. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 10:1–171.

_____, and Piccinin, B. B. 1977. Photosynthesis by natural phytoplankton populations. *Arch. Hydrobiol.* 80:405–457.

Harrison, W. G., and Platt, T. 1986. Photosynthesis-irradiance relationships in polar and temperate phytoplankton populations. *Polar Biol.* 5:153–164.

Healey, F. P., and Hendzel, L. L. 1979. Indicators of phosphorus and nitrogen deficiency in five algae in culture. *J. Fish. Res. Board Can.* 36:1364–1369.

Jensen, L. M. 1985. ^{14}C-labelling patterns of phytoplankton: specific activity of different product pools. *J. Plankton Res.* 7:643–652.

Kwiatkowski, R. E. 1984. Comparison of 1980 Lake Huron, Georgian Bay-North Channel surveillance data with historical data. *Hydrobiologia* 118:255–266.

Legendre, L., Demers, S., Yentsch, C. M., and Yentsch, C. S., 1983. The ^{14}C method: Patterns of dark CO_2 fixation and DCMU correction to replace the dark bottle. *Limnol. Oceanogr.* 28:996–1003.

Li, W. K. W., and Platt, T. 1982. Distribution of carbon among photosynthetic end-products in phytoplankton of the eastern Canadian Arctic. *J. Phycol.* 18:466–471.

_____, Glover, H. E., and Morris, I. 1980. Physiology of carbon assimilation by *Oscillatoria thiebautii* in the Caribbean Sea. *Limnol. Oceanogr.* 25:447–456.

Morris, I. 1981. Photosynthetic products, physiological state, and phytoplankton growth. In T. Platt (ed.), *Physiological Bases of Phytoplankton Ecology*, pp. 83–102. Can. Bull. Fish. Aquat. Sci., Ottawa.

_____, Glover, H. E., and Yentsch, C. S. 1974. Products of photosynthesis by marine phytoplankton: the effect of environmental factors on the relative rates of protein synthesis. *Mar. Biol.* 27:1–9.

_____, Smith, A. E., and Glover, H. E. 1981. Products of photosynthesis in phytoplankton off the Orinoco River and in the Caribbean Sea. *Limnol. Oceanogr.* 26:1034–1044.

Munawar, M., and Munawar, I. F. 1986. The seasonality of phytoplankton in the North American Great Lakes, a comparative synthesis. *Hydrobiologia* 138:85–115.

Parker, J. I., Conway, H. L., and Yaguchi, E. M. 1977. Seasonal periodicity of diatoms, and silicon limitation in offshore Lake Michigan, 1975. *J. Fish. Res. Board Can.* 34:552–558.

Parkos, W. G., Olson, T. A., and Odlaug, T. O. 1969. *Water Quality Studies on the Great Lakes on Carbon-14 Measurements on Primary Productivity*. Water Resources Res. Center, Univ. Minn. Bull. 17.

Platt, T., and Jassby, A. D. 1976. The relationship between phytosynthesis and light for natural assemblages of coastal marine phytoplankton. *J. Phycol.* 12:421–430.

_____, and Subba Rao, D. V. 1975. Primary production in marine microphytes. In Cooper, J. (ed.), *Photosynthesis and Productivity in Different Environments*. pp. 249–280. London: Cambridge Univ. Press.

_____, Gallegos, C. L., and Harrison, W. G. 1980. Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *J. Mar. Res.* 38:687–701.

_____, Harrison, W. G., Irwin, B., Horne, E. P., and Gallegos, C. L. 1982. Photosynthesis and photoadaptation of marine phytoplankton in the Arctic. *Deep-Sea Res.* 29:1159–1170.

Priscu, J. C., and Priscu, L. R. 1984. Photosynthate partitioning by phytoplankton in a New Zealand coastal upwelling system. *Mar. Biol.* 81:31–40.

Putnam, H. D., and Olson, T. A. 1961. *Studies on the Productivity and Plankton of Western Lake Superior*. School of Public Health, Univ. Minn. Duluth.

_____, and Olson, T. A. 1966. Primary productivity at a fixed station in Lake Superior. In *Proc. 9th Conf. Great Lakes Res.*, pp. 119–128. Internat. Assoc. Great Lakes Res.

Saunders, G. W., Trama, F. B., and Bachmann, R. W. 1962. *Evaluation of a Modified* ^{14}C *technique for Shipboard Estimation of Photosynthesis in Large Lakes*. Univ. Mich. Great Lakes Res. Div. Publ. 8:1–61.

Scavia, D., Fahnenstiel, G. L., Evans, M. S., Jude, D. J., and Lehman, J. T. 1986. Influence of salmonine predation and weather on long-term water quality trends in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 43:435–443.

Schelske, C. L., and Callender, E. 1970. Survey of phytoplankton productivity and nutrients in Lake Michigan and Lake Superior. In *Proc. 13th Conf. Great Lakes Res.*, pp. 93–105. Internat. Assoc. Great Lakes Res.

_____, and Roth, J. C. 1973. *Limnological Survey of Lakes Michigan, Superior, Huron* and *Erie*. Univ. Mich. Great Lakes Div. Publ. 17.

Senft, W. H. 1978. Dependence of light-saturated rates of algal photosynthesis on intracellular concentrations of phosphorus. *Limnol. Oceanogr.* 23:709–718.

Sephton, D. H., and Harris, G. F. 1984. Physical variability and phytoplankton communities. VI. Day to day changes in primary productivity and species abundance. *Arch. Hydrobiol.* 102:155–175.

Stadelmann, P., Moore, J. E., and Pickett, E. 1974. Primary production in relation to temperature structure, biomass concentration, and light conditions at an inshore and offshore station in Lake Ontario. *J. Fish. Res. Board Can.* 31:1215–1232.

Strickland, J. D. H., and Parsons, T. R. 1972. *A Practical Handbook of Seawater Analysis*, 2nd ed. Bull. Fish. Res. Bd. Can. No. 167.

Talling, J. F. 1957. Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater radiation. *New Phytologist* 56:29–50.

Vollenweider, R. A. (ed.) 1974. *A Manual on Methods for Measuring Primary Production in Aquatic Environments*, 2nd ed. IBP Handbook No. 12. Blackwell Scientific Publs.

_____, Munawar, M., and Stadelmann, P. 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. *J. Fish. Res. Board Can.* 31:739–762.

Watson, N. H. F., Nicholson, H. F., and Culp, L. R. 1975. Chlorophyll *a* and primary production in Lake Superior, May to November, 1973. *Can. Fish. Mar. Serv. Tech. Report* No. 525.

Welschmeyer, N. A., and Lorenzen, C. J. 1981. Chlorophyll-specific photosynthesis and quantum efficiency at subsaturating light intensities. *J. Phycol.* 17:283–293.

Williams, N. J. 1978. Annual variation of photosynthetic parameters in Lake Tahoe. *Verh. Internat. Verein. Limnol.* 20:419–425.

Yentsch, C. S., and Lee, R. W. 1966. A study of photosynthetic light reactions and a new interpretation of sun and shade phytoplankton. *J. Mar. Res.* 24:319–337.