Dynamics of Lake Michigan Phytoplankton: Primary Production and Growth[1]

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Primary production was measured with the ^{14}C technique during May through July–August 1982–84. ^{14}C experiments varied from short-term incubations (1–2 h) in a photosynthesis–irradiance (P–I) chamber to 24-h in situ incubations. The maximum assimilation number from six P–I experiments during thermal stratification averaged 2.1 mg C·mg Chl^{-1}·h^{-1} which agreed well with estimates from the 1970s. Chlorophyll-corrected P–I curves were combined with incident irradiation, chlorophyll concentrations, and extinction coefficients to estimate daily production (model estimate). Summer average integral production estimates in 1983 and 1984 were 615–630 mg C·m^{-2}·d^{-1}. Approximately 50% of summer primary production occurred below the epilimnion. Daily model production estimates were higher than 24-h in situ estimates at light intensities above I_k, the light saturation parameter, and similar at intensities below I_k. Comparisons of production estimates converted to growth rates suggest that 24-h in situ estimates provide a measure close to net production whereas model estimates provide a measure greater than net production. Summer epilimnetic growth rate estimates were low (range 0.06–0.60·d^{-1}), reflecting the limited availability of phosphorus.

La production primaire a été déterminée par la technique du ^{14}C de mai à juillet–août de 1982 à 1984. Ces essais ont comporté des incubations à court terme (1–2 h) en enceintes de photosynthèse par irradiance (P–I) et des incubations *in situ* de 24 h. Le taux maximal moyen d'assimilation de six essais P–I effectués en condition de stratification thermique s'élevait à 2,1 mg de C par mg de Chl par heure. Cette valeur correspond d'assez près à celles obtenues depuis les années 1970. Les courbes P–I corrigées pour la teneur en chlorophylle ont été utilisées de pair avec l'irradiation incidente, les concentrations de chlorophylle et les coefficients d'extinction afin d'estimer la production quotidienne (estimation du modèle). Les estimations de production intégrées des moyennes d'été de 1983 et 1984 s'élevaient à 615–630 mg·m^{-2}·j^{-1} de C. Environ 50 % de la production primaire d'été survenait en deçà de l'épilimnion. Les estimations de production quotidiennes du modèle étaient supérieures aux estimations *in situ* de 24 h aux intensités lumineuses supérieures à I_k, le paramètre de saturation lumineuse, mais semblables aux intensités inférieures à I_k. La comparaison des estimations de production converties en taux de croissance semble indiquer que l'estimation *in situ* de 24 h constitue une mesure se rapprochant de la production nette, les estimations par modèle donnant des valeurs supérieures. Les valeurs estimées du taux de croissance estival dans l'épilimnion étaient faibles (gamme de 0,06 à 0,60·j^{-1}), ce qui reflète le peu de disponibilité du phosphore.

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Estimates of primary production are critical to our understanding of aquatic ecosystems. In Lake Michigan alone, there have been at least a dozen investigations designed to measure primary production (for reviews see Tarapchak and Stoermer 1976; Parker et al. 1977). Most of the studies were conducted in the 1960s and early 1970s and used the ^{14}C technique as outlined by Steemann-Nielsen (1952) and Vollenweider (1974). Phytoplankton growth rates have also been estimated from ^{14}C production rates (Parker et al. 1977).

Subsequent to most of these investigations, concerns arose over the interpretation of results from ^{14}C-based experiments (Peterson 1980). It had been assumed generally that short-term ^{14}C uptake represents rates between net and gross production (Wetzel and Likens 1979). However, this may not be the case. ^{14}C uptake can range from gross underestimates of net production (Schulenberger and Reid 1981) to adequate measurements of gross production (Williams et al. 1983). This problem is also apparent in past work on the Great Lakes. In Lake Superior, photosynthetic rates calculated from pH shifts in light and dark bottles were an order of magnitude greater than ^{14}C-based photosynthetic rates (Verduin 1975). No consistent interpretation of results from ^{14}C-based experiments has been found. Thus, in an environment like Lake Michigan, where almost all productivity estimates were based on ^{14}C uptake, an evaluation is needed.

The purpose of this investigation was twofold: the first was to provide ^{14}C-based primary production measurements for comparison to previous estimates to determine if detectable changes have occurred in Lake Michigan primary production rate; the second was to evaluate results from ^{14}C-uptake experiments and clarify their usefulness as measurements of primary production and phytoplankton growth.

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Reasonable estimates of Lake Michigan primary production are needed to evaluate recent changes in the ecosystem (Scavia et al. 1986). Extensive salmonid stocking has changed the forage fish communities (Wells and Hatch 1984), which in turn have affected zooplankton (Evans and Jude 1986) and possibly even phytoplankton communities (Fahnenstiel and Scavia 1987). Spring total phosphorus concentrations also have decreased. Although these changes have had documented effects on summer water transparency and chlorophyll (Scavia et al. 1986), the effects on lake productivity have not been evaluated.

Methods

An offshore station, located 25 km from Grand Haven, Michigan (43°1′11″N, 86°36′48″W), was sampled 20 times from 1982 through 1984. The sampling periods were from late spring isothermal mixing (May) to midthermal stratification (July–August) of each year.

Temperature was measured with an electronic bathythermograph. Incident irradiation was recorded continuously with a Licor LI-190SB sensor connected to a printing integrator (LI-550B) or recorder. Underwater scalar irradiance was measured in 1983 and 1984 with a Licor LI-193SB sensor and LI-188B integrating meter. Downwelling and upwelling irradiances were measured in 1982 with a LI-192SB sensor and LI-185B meter and were combined to determine scalar irradiance (Spigel and Howard-William 1984).

Chlorophyll concentrations were determined fluorometrically on 90% acetone extracted samples (Strickland and Parsons 1972). Several times during thermal stratification, in vivo fluorescence was measured with a pumping system (Moll et al. 1984). Phytoplankton samples were preserved with Lugol's solution, settled (Crumpton and Wetzel 1981) or filtered (Stoermer and Kreis 1980) onto slides, and counted. Either half or the entire slide was enumerated under low magnification (150–240×) and at least one row of 20 mm under high magnification (840–1140×). Biovolumes for each species were calculated from estimates of cell dimensions. For abundant cells, a minimum of 50 measurements from at least two depths during each major sampling period was used to estimate biovolume. For less abundant cells, measurements were made during one or two sampling periods. These biovolume estimates were converted to carbon using the formulae of Strathman (1966). Separate conversions were used for diatoms and nondiatoms because of fundamental differences in the biovolume to carbon ratios (Sicko-Goad and Ladewski 1977).

Phytoplankton production was estimated with the ^{14}C technique (Vollenweider 1974). Several modifications of the "clean techniques" (Carpenter and Lively 1980; Fitzwater et al. 1982) were used for all ^{14}C experiments. Incubation samples were collected in PVC Niskin bottles and immediately dispensed into shaded 2-L polycarbonate bottles. Extreme care was taken to prevent light shock to the samples. Incubation samples were then inoculated with ^{14}C from a stock solution. This stock solution was purchased as a high-activity stock (i.e. 37 $MBq \cdot mL^{-1}$) from New England Nuclear and diluted to working strength (37–370 $kBq \cdot mL^{-1}$) with reagent-grade $NaHCO_3$ and distilled water. The working stock (pH 8.2–8.5) was then filtered through a 0.22-μm filter and stored in an acid-cleaned teflon bottle. The activity of each working stock was determined by adding small quantities of working solution to 12 m*M* $NaHCO_3$ (pH 8.5) and adding 0.5 mL of this solution to buffered scintillation cocktail. Depending on length of incubation, approximately 37–370 kBq was added to each incubation bottle. ^{14}C experiments varied in incubation length from <1 to 24 h. In situ experiments were carried out for 24 h starting at approximately 09:00 and short-term photosynthesis (P) versus irradiance (I) incubations were carried out for 1–2 h in an incubator with eight or nine light chambers, similar to the one described by Fee (1972). All short-term ^{14}C incubations were conducted between 13:00 and 16:00. Chlorophyll-corrected P–I curves were combined with incident irradiation, water column chlorophyll concentrations, and the extinction coefficient to estimate daily integral production (Fee 1973). During thermal stratification, P–I curves determined from the epilimnion and deep chlorophyll layer or hypolimnion were used for water column estimates. This production estimate will be referred to as the model estimate. ^{14}C uptake was combined with phytoplankton carbon estimates to determine exponential growth rates.

Phytoplankton growth rates were also determined from changes in phytoplankton carbon concentrations in diluted lakewater samples (SIG experiments). Small phytoplankton inocula (100–1000 mL) were added to between 1.9 and 3.0 L of 0.22-μm-filtered lake water and incubated in situ or in a rotating chamber in 2- or 4-L polycarbonate bottles for 1 or 4 d. For 4-d experiments, the ratio of inoculum to filtered water varied from 1:10 to 1:19, and for 1-d experiments the ratio varied from 1:3 to 1:4. Phytoplankton growth rates were calculated from phytoplankton counts, converted to phytoplankton carbon, at the beginning and end of the incubations.

Results

During spring mixing (May) when temperature and chlorophyll concentrations were uniform vertically, the maximum observed in situ volumetric rate of primary production (nP_{max}) occurred within the upper 10 m whereas below 10 m, the production rate decreased with depth (Fig. 1). nP_{max}, corrected for chlorophyll (P_{max}), also occurred in the upper 10 m and was strongly related to incident irradiation. Average incident irradiation was 233 and 256 $\mu E \cdot m^{-2} \cdot s^{-1}$ in May 1982 and 1983 and P_{max} was 10.3 and 12.16 mg $C \cdot mg\ Chl^{-1} \cdot d^{-1}$; however, in May 1984 incident irradiation increased to 494 $\mu E \cdot m^{-2} \cdot s^{-1}$ and P_{max} was 18.15 mg $C \cdot mg\ Chl^{-1} \cdot d^{-1}$. nP_{max} and P_{max} from short-term ^{14}C experiments ranged from 3.8 to 5.6 mg $C \cdot m^{-3} \cdot h^{-1}$ and from 1.7 to 2.4 mg $C \cdot mg\ Chl^{-1} \cdot h^{-1}$, respectively.

With the onset of thermal and chlorophyll stratification in June, subepilimnetic production was significant (Fig. 1). Subepilimnetic production contributed approximately 50% to water column production, with at least half of this production occurring within the deep chlorophyll layer (DCL) (Table 1). Over 30% of water column production was attributable to the DCL when it was located in the upper 50 m (June and July); however, when the DCL was located deeper than 50 m (August), only a small part (<19%) of total production was attributable to it. Production at 25–35 m was directly related to the amount of irradiance received at depth (Fig. 2).

For purposes of discussion, thermal stratification was divided into two periods based on epilimnetic temperatures. Early stratification applies to the period (primarily June) when epilimnetic temperatures were less than 15°C whereas midstratification applies to the period (July and August) when epilimnetic temperatures were greater than 17°C.

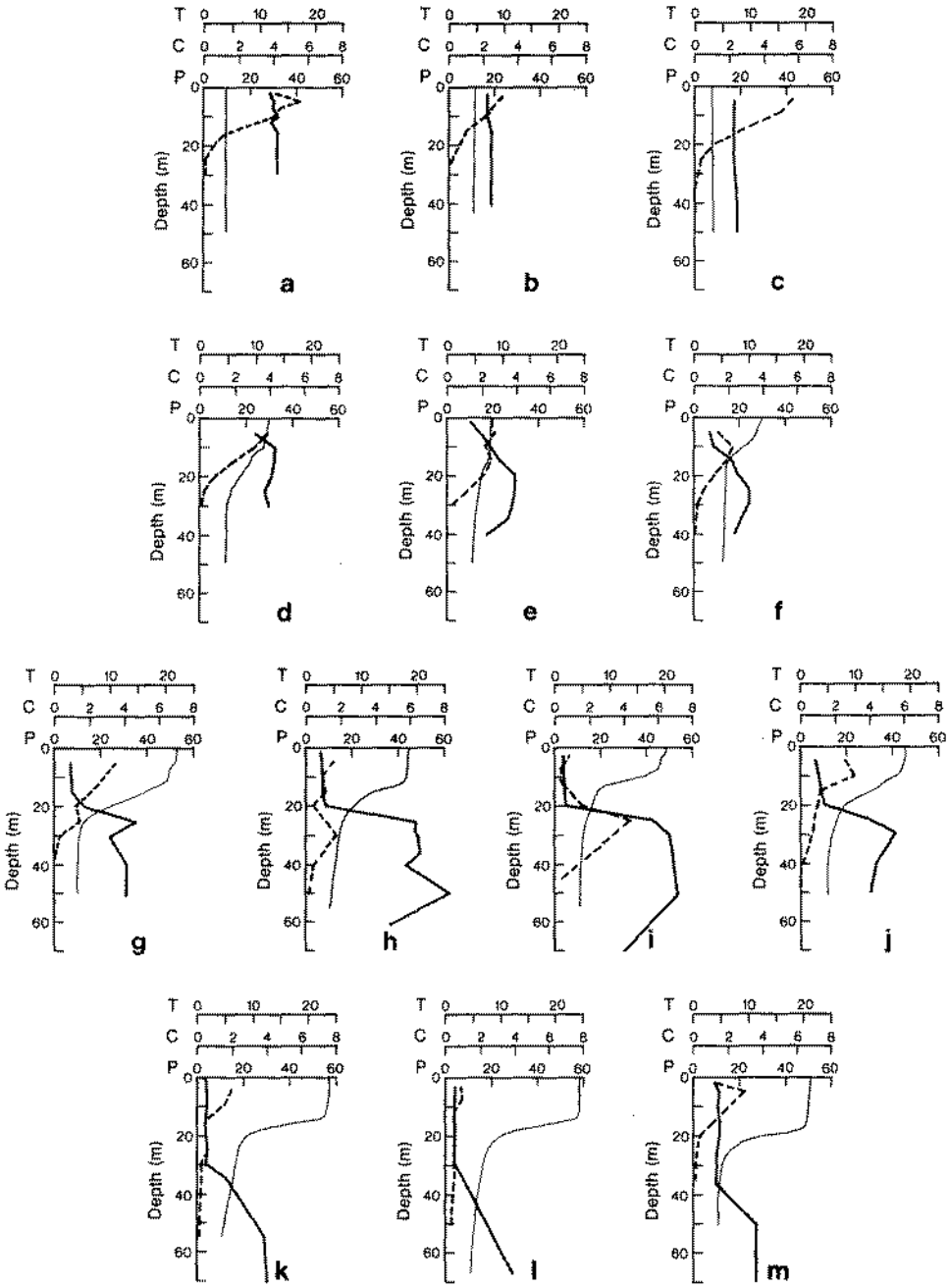

FIG. 1. Temperature (°C, T,—), chlorophyll a (mg·m^{-3}, C,—), and primary production (mg C·m^{-3}·d^{-1}, P,---) during (a–c) spring isothermal mixing, (d–f) early stratification, (g–j) July midstratification, and (k–m) August midstratification. (a) 22 May 1982, (b) 16 May 1983, (c) 21 May 1984, (d) 24 June 1982, (e) 9 June 1983, (f) 5 July 1984, (g) 22 July 1982, (h) 11 July 1983, (i) 13 July 1983, (j) 23 July 1984, (k) 2 August 1983, (l) 4 August 1983, (m) 23 August 1984.

Although significant subepilimnetic production was found during thermal stratification (Fig. 1), P_{max} occurred within the epilimnion in all but one case. P_{max} varied from 10.9 to 25.2 mg C·mg Chl^{-1}·d^{-1} during early stratification and from 14.0 to 27.8 mg C·mg Chl^{-1}·d^{-1} during midstratification. The maximum volumetric rate of production, nP_{max}, occurred below the epilimnion several times during thermal stratification. nP_{max} and P_{max} determined from short-term ^{14}C experiments during thermal stratification ranged from 1.8 to 4.4 mg C·m^{-3}·h^{-1} and from 1.7 to 2.7 mg C·mg Chl·h^{-1}, respectively.

Integral, euphotic zone (≥1% light level) production was determined by 24-h in situ experiments and by modelled short-term incubator experiments (Table 2). The lowest values for each year were found during thermal stratification, reflecting the large decrease in epilimnetic phytoplankton abundance. Model integral estimates were on average 1.43 times greater than in situ integral estimates (Table 2). The largest ratios of model to in situ production were found on the sunniest days during thermal stratification. Comparisons of individual profiles demonstrate that, in general, modelled and in situ volumetric rates are similar at low irradiances and that model rates are higher, relative to in situ rates, at higher irradiances (Fig. 3).

Several ^{14}C time-course experiments were performed to

TABLE 1. Proportion of total water column production found in various regions of the water column from 24-h in situ experiments. The deep chlorophyll layer (DCL) is the region where chlorophyll concentrations are ≥ 1.5 times the epilimnetic concentrations in early stratification and ≥2 times during midstratification.

Dates	% within epilimnion	% below epilimnion	% within DCL
	Early stratification		
9 June 83	42	58	39
23 June 82	62	38	36
24 June 82	63	37	36
25 June 84	38	62	38
5 July 84	31	69	34
	Midstratification, July		
11 July 83	35	64	51
13 July 83	8	92	74
21 July 82	68	32	13
22 July 82	53	47	16
23 July 84	50	50	22
	Midstratification, August		
2 August 83	67	33	8
4 August 83	39	61	19
24 August 84	75	25	4
Mean	49	51	30

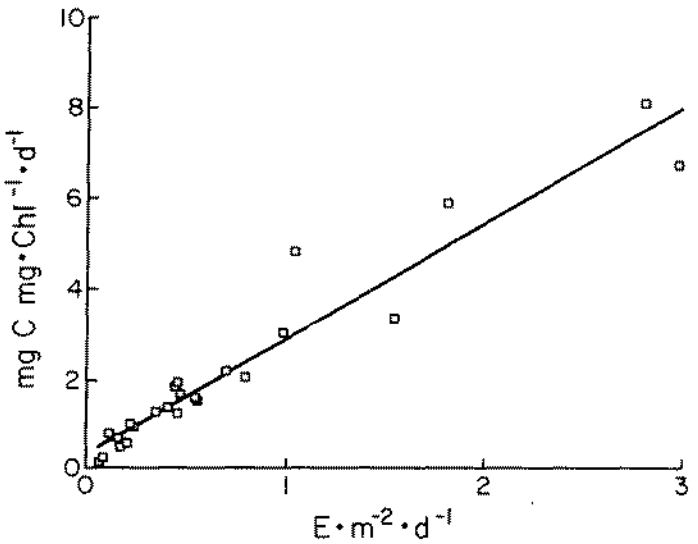

FIG. 2. In situ 24-h production and light received for populations at 25–35 m during thermal stratification (June–August). Light received at each depth during in situ incubations was calculated from measurements of incident and underwater irradiation. $y = 2.526x + 0.3768$ ($R^2 = 92.2$, $p < 0.0003$).

examine the relationship between short- and long-term ^{14}C incubations. ^{14}C uptake was linear for 6–12 h and became nonlinear (Fig. 4). The loss of ^{14}C during the dark period varied from 5 to 37% ($\bar{x} = 16\%$, $n = 9$) of the ^{14}C fixed during the previous light period.

Growth estimates exhibited as much variability within similar methods as between methods (Table 3). Differences of greater than 50% were found with comparisons based on the same method just a few days apart. For growth rates determined with the ^{14}C technique, model estimates were always higher than in situ estimates. Growth rates calculated from changes in phytoplankton carbon (SIG) exhibited good agreement with in situ 24-h ^{14}C estimates in some cases and relatively poor agreement in others. When SIG estimates were from 24-h incubations, generally good agreement was found with 24-h ^{14}C estimates.

In situ ^{14}C-based growth rates exhibited little seasonal pattern; mean epilimnetic (10 m in absence of thermal stratification) values were $0.38 \cdot d^{-1}$ (c.v. = 20%) during spring isothermy, $0.31 \cdot d^{-1}$ (c.v. = 14%) during early stratification, and $0.40 \cdot d^{-1}$ (c.v. = 42%) during midstratification. There was, however, a difference between growth rates from midstratification in 1983 (range $0.14-0.38 \cdot d^{-1}$) and in 1982 and 1984 (range $0.46-0.61 \cdot d^{-1}$).

Because all growth estimates were from experiments in which phytoplankton samples were enclosed in bottles, the effects of containment were evaluated by comparing chlorophyll and 1-h ^{14}C uptake before and after enclosure for 24 h (Table 4). Chlorophyll concentrations did not change significantly but some significant decreases were observed in ^{14}C uptake. Because ^{14}C-uptake rates were determined at the end of a 24-h incubation, they represent the maximum effect of containment on the 24-h ^{14}C experiments. In only one case (July 1983) was the difference between ^{14}C uptake before and after 24 h greater than 30%. The effects of containment increased with enclosure time as indicated by the results from the August 1984 experiment; ^{14}C uptake rates decreased 11% after 24 h and 39% after 48 h.

Discussion

Lake Michigan Primary Production: Past and Present

Most Lake Michigan primary production estimates have been based on short-term (2–6 h) ^{14}C experiments (see Tarapchak and Stoermer 1976; Parker et al. 1977; Moll et al. 1984). These estimates were determined from experiments that used a variety of experimental techniques and data reporting methods. Although comparisons among all investigations are not possible, there are sufficient similarities in some previous investigations to provide insight into primary production rates from 1970 to 1985. Several parameters, such as P_{max}, nP_{max}, A_{opt} (average daily rate at optimal depth), and ΣA (average daily integral rate) could be used for comparisons. However, many of these parameters have not been reported in previous investigations and, where reported, many assumptions were made in their calculations (see below). We believe that chlorophyll-specific parameters such as P_{max} and assimilation numbers are useful for comparisons of the Lake Michigan data set because they have been made in at least three published studies and are insensitive to phytoplankton biomass differences. Furthermore, because P_{max} represents the maximum photosynthetic response at optimum light levels, it is particularly useful for determining, the effect of environmental conditions on photosynthesis (Côté and Platt 1983)).

Three previous investigations have reported assimilation numbers from the offshore region of Lake Michigan. Fee (1972) reported nP_{max} and chlorophyll values from P–I incubations of surface populations and maximum assimilation numbers (P_{max}) can be calculated. The summer mean P_{max} from nine P–I experiments in 1970 from Fee's three offshore stations (Nos. 2–4) was 1.8 mg C · mg $Chl^{-1} \cdot h^{-1}$ which is similar to our summer mean P_{max} of 2.1 mg C · mg $Chl^{-1} \cdot h^{-1}$. Integral

TABLE 2. Euphotic zone (EZ) chlorophyll and integral production. The euphotic zone was defined as the portion of the water column where greater than 1% surface irradiance was received. Integral production estimates are from in situ and model experiments.

Date	EZ depth (m)	EZ Chl ($mg \cdot m^{-2}$)	Model production ($mg \cdot m^{-2} \cdot d^{-1}$)	In situ production ($mg \cdot m^{-2} \cdot d^{-1}$)	Model : in situ ratio
16 May 83	26	59.6	389	310	1.25
20 May 83	26	57.9	420	300	1.40
11 July 83	33	91.1	525	322	1.63
13 July 83	33	87.0	705	464	1.52
21 May 84	22	57.2	770	648	1.19
19 June 84	24	68.9	860	540	1.59
25 June 84	23	60.0	758	586	1.29
23 July 84	28	59.6	450	382	1.18
24 August 84	20	29.1	465	250	1.86

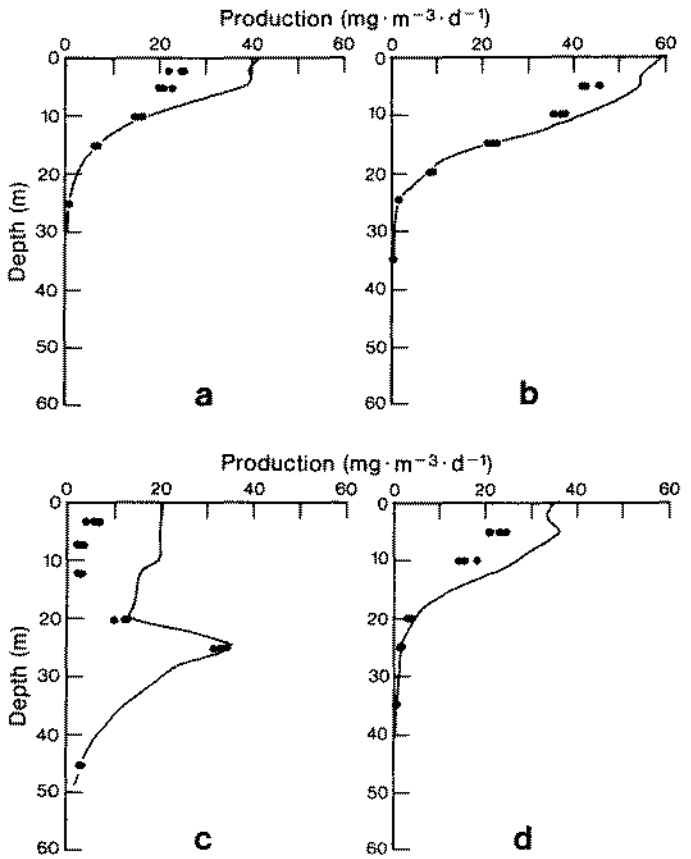

FIG. 3. Production from model experiments (solid line) and in situ experiments (dots) during spring isothermal mixing (a = 20 May 1983, b = 21 May 1984) and during thermal stratification (c = 13 July 1983, d = 24 August 1984).

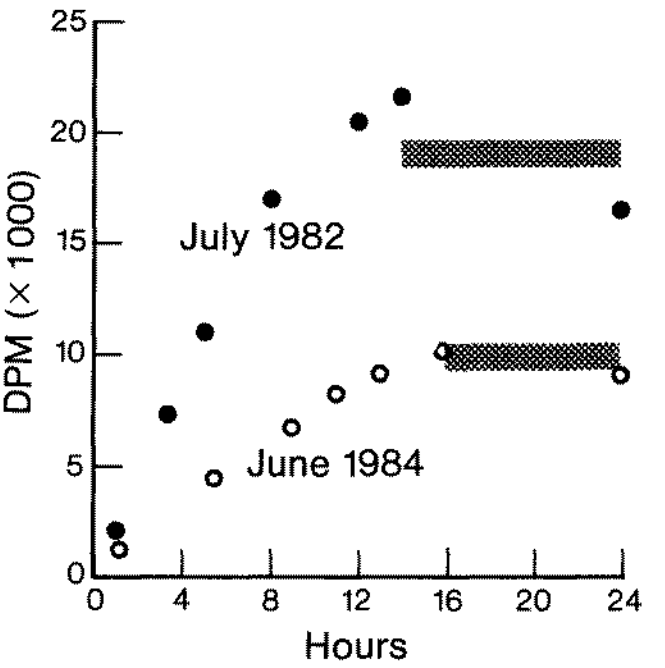

FIG. 4. Time courses of ^{14}C uptake during constant irradiance and dark periods. Dark period is represented by shaded bars.

euphotic zone assimilation numbers, calculated from integrated production and chlorophyll values, ranged from 6.9 to 14.0 mg $C \cdot mg\ Chl^{-1} \cdot d^{-1}$ with a mean of 9.7 for the period May–August in 1975 (Parker et al. 1977). We found similar euphotic zone assimilation numbers for the May–August period, ranging from 5.8 to 16.0 mg $C \cdot mg\ Chl^{-1} \cdot d^{-1}$ with a mean of 10.0. An exception to this general agreement is the work of Moll et al. (1984) in which euphotic zone production and chlorophyll were determined from short-term ^{14}C incubations during a 4-d period in July 1977. Their mean euphotic zone assimilation number was 16.9 mg $C \cdot mg\ Chl^{-1} \cdot d^{-1}$ which is significantly higher than Parker et al. and our mean values. This higher estimate is probably related to abnormally low chlorophyll estimates rather than to different assimilation values. Chlorophyll concentrations were estimated from in vivo fluorescence profiles and not from extracted samples as in the other investigations.

Although in vivo fluorescence is routinely used to estimate chlorophyll, extracted chlorophyll and in vivo fluorescence values may be significantly different (Cullen 1982). This suggestion is supported by comparisons of chlorophyll and phytoplankton carbon concentrations. While all investigators reported surface chlorophyll concentrations in the range of 0.5–1.2 $mg \cdot m^{-3}$, phytoplankton carbon concentrations were significantly different. Parker et al. (1977) and this study reported typical summer phytoplankton carbon concentrations of 20–35 mg $C \cdot m^{-3}$, whereas phytoplankton carbon concen-

TABLE 3. Growth rate (d^{-1}) estimates from different experiments. The experimental protocol is outlined in the methods section. Asterisk indicates 24-h SIG estimates.

Date and depth	In situ 24-h ^{14}C	Model ^{14}C	SIG
May 83 (upper 10 m)	0.34–0.38	0.47–0.55	0.31
June 83 (epilimnion)	0.37	—	0.29–0.32
June 84 (epilimnion)	0.24	—	0.22*
July 83 (epilimnion)	0.14–0.24	0.42–0.59	0.06
July 84 (epilimnion)	0.61	0.65	0.40
July 84 (25–30 m)	0.10	0.11	0.11
April 85 (incubator)	24-h ^{14}C: 0.41–0.43	—	0.41*

trations that we calculated with data from Moll et al. (1984) using phytoplankton biomass reported in Brahce (1980) and Strathman (1966) carbon conversion factors were approximately 100–130 mg $C \cdot m^{-3}$. This suggests that extracted chlorophyll concentrations during the study of Moll et al. were probably much higher than reported from in vivo fluorescence measurements and this would reduce their assimilation numbers. Furthermore, because the Moll et al. assimilation numbers were derived from one 4-d period, it is difficult to estimate a summer average.

Based on these results, Lake Michigan summer chlorophyll-specific production apparently has not changed since 1970. This is in marked contrast with trends in spring total phosphorus and summer Secchi disc depth (Scavia et al. 1986) which changed significantly from 1975 to 1984. Thus, although spring total phosphorus and summer Secchi disc depth have changed at least partially as a result of phosphorus load reductions, summer phytoplankton assimilation numbers (or potentially growth rate) are relatively insensitive to these reductions and more dependent on other factors, such as the efficiency of nutrient cycling.

Trends in average summer integral daily production were not as clear. This should not be surprising, since integral daily production is dependent on more variables than P_{max} and infrequent measurements are difficult to evaluate. Variability in incident or underwater irradiation, as well as phytoplankton biomass, are propagated to estimates of integral production. Our average summer integral daily production estimates from 1983 (615 mg $C \cdot m^{-2} \cdot d^{-1}$) and 1984 (633 mg $C \cdot m^{-2} \cdot d^{-1}$) were higher than averages from 1970 (380 mg $C \cdot m^{-2} \cdot d^{-1}$, Fee 1972) and 1975 (480 mg $C \cdot m^{-2} \cdot d^{-1}$, Parker et al. 1977) but lower than the average from 1977 (1160 mg $C \cdot m^{-2} \cdot d^{-1}$, Moll et al. 1984).

Methodological differences were responsible for most of the production differences. Fee's estimates were most likely low because he assumed a homogeneous vertical distribution of phytoplankton that was equal to the surface concentration and used an assumed extinction coefficient of underwater irradiation. We have found that the actual integral daily production from June to August would be underestimated by 35% if phytoplankton concentrations were assumed uniform and equal to the surface population with identical photosynthetic parameters. Therefore, Fee's estimate would have to be revised to at least 500 mg $C \cdot m^{-2} \cdot d^{-1}$, but the exact figure cannot be estimated, since vertical distributions of phytoplankton have not varied in a clear and predictable pattern. Parker's estimates may also be low because of assumptions that 50% of daily total irradiation was received during a 4-h incubation and the depth of the euphotic zone was fixed at 25 m. From our data, only 44% (range 35–50%) of daily summer irradiation was received during 4-h midday incubations. The depth of the euphotic zone probably was at times greater than 25 m in the mid-1970s (Liedle 1978) and significant production could have occurred below 25 m. As stated earlier, Moll et al.'s (1984) estimates were from only one 4-d period and probably are not adequate indicators of average summer productivity.

For this evaluation it is clear that no dramatic trend in summer-average integral production is apparent for 1970–84. Average summer production for this period was probably in the range of 500–650 mg $C \cdot m^{-2} \cdot d^{-1}$.

Further estimates of integral production should attempt to more accurately assess subepilimnetic production, as much of summer water column production occurs well below the epilimnion (Table 1). Subsurface production can be difficult to estimate accurately with in vivo experiments because of the effect of internal waves (G. Fahnenstiel, unpubl. data). Yet, these estimates need to be made if accurate knowledge of water column production is desired for lake assessment and management purposes. Nutrient abatement may reduce surface production, yet have little effect on water column production due to increases in subsurface production resulting from decreased surface chlorophyll and increased light penetration. This was found, for example, in 1982–84. However, there are little data to evaluate changes in subsurface production. From a 4-d study in July, Moll et al. (1984) reported that on average 63% of total production was found below the epilimnion. This value is similar to our average July value of 57%; however, because of the large variability found for our July estimates, 32–92%, little can be inferred from one comparison with a 4-d period.

Evaluation of ^{14}C Results and Estimates of Phytoplankton Growth

In the previous section we have compared results from ^{14}C experiments without considering differences in experimental protocol. The length of the ^{14}C incubation can influence estimates of integral daily production. Daily production estimates derived from short-term ^{14}C incubator experiments (model estimates) were consistently higher than daily production estimates from 24-h in situ experiments (Table 2). It has long been recognized that short-term (1–6 h) and long-term (24 h or longer) experiments do not yield the same production rates expressed either on a daily or hourly basis (Vollenwieder and Nauwerck 1961; Eppley and Sharp 1975; Li and Harrison 1982; Lancelot and Mathot 1985). We found that model estimates of daily integral euphotic zone production were on average 40% higher than 24-h in situ estimates. The ratio of model to in situ varied between 1.18 and 1.86, with the highest ratios found on the sunniest days. In general, irradiance was an important factor in comparisons of short and long ^{14}C incubations as demonstrated from all individual profiles. At low irradiances, model and in situ volumetric rates were similar; however, at increasing irradiances, model rates increased relative to in situ rates (Fig. 3).

TABLE 4. Containment effects determined by changes in short-term ^{14}C uptake (dpm) and chlorophyll *a* ($mg \cdot m^{-3}$) before and after enclosure for 24 h (significant differences, *t*-test, $\alpha = 0.05$, are indicated by an asterisk). Mean and standard deviations for each estimate are listed.

	^{14}C uptake		Chlorophyll	
Date and depth	Before	After	Before	After
May 1983	372±33	310±5*	2.1±0.2	2.0±0.2
June 1983 (epilimnion)	633±13	655±15	1.9±0.1	1.8±0.2
July 1983 (epilimnion)	1470±120	550±62*	1.2±0.3	0.6±0.3
July 1983 (25–30 m)	1223±19	940±65*	5.5±1.0	5.4±0.7
	296±28	222±30*	5.7±0.3	5.3±0.7
June 1984 (epilimnion)	720±19	710±29		
July 1984 (epilimnion)	217±10	168±30		
July 1984 (25–30 m)	437±13	410±23		
July 1984 (epilimnion)	368±13	315±8*		
August 1984 (epilimnion)	570±15	520±19*	^{14}C after 48 h: 350±18*	

This apparent relationship between irradiance and production ratio is similar to that found by Vollenweider and Nauwerck (1961). They found that the difference between cumulative short (4 h) and long (24 h) experiments decreased as irradiance decreased. Although the difference exhibited much variability, they suggested a possible correction factor of 1.25–1.30 for 24-h experiments. Our experiments would yield a somewhat similar correction factor of 1.43.

Several other investigators have also found a relationship between short and long incubations and irradiance. Harris and Piccinin (1977) and Marra (1978) found that, at low irradiances, short and long incubations gave similar results but at higher irradiances short incubations gave significantly higher results. The distinction between high and low irradiances was defined relative to the light saturation parameter, I_k, by Harris and Piccinin and equal to 60 $\mu E \cdot m^{-2} \cdot s^{-1}$ by Marra. Our results are similar. At irradiances up to approximately 45 $\mu E \cdot m^{-2} \cdot s^{-1}$, which is similar to the I_k for spring and subsurface phytoplankton populations, our model and in situ results agree. Because the difference between model and in situ estimates occurs well below the surface-mixing layer, this difference is strictly not an artifact of fixed-depth bottle incubations.

Thus, the portion of the P–I curve controlling production appears to be important in comparisons of short and long ^{14}C incubations. For populations that are light limited (below I_k), short and long incubations give similar results, but for populations that are nutrient limited (above I_k), short and long incubations give different results. These differences appear to be related to the type of photosynthetic limitation or light intensity as it relates to carbon metabolism within the cells (Harris and Piccinin 1977).

Although the exact details of carbon cycling within cells cannot be determined from this study, time course experiments at irradiances $> I_k$ can provide some insight. Prolonged exposure to saturating and inhibiting irradiances has resulted in nonlinear uptake of ^{14}C and this nonlinear uptake has been used to explain differences between results from short and long incubations (Harris and Piccinin 1977; Marra 1978). We found a consistent nonlinearity in ^{14}C uptake after 6–12 h at constant-irradiance incubations between 100 and 200 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fig. 4). This nonlinearity would partially explain the difference between model estimates, which assume constant photosynthetic parameters, and in situ rates. Although we did not perform time-course experiments at inhibiting irradiances, more severe nonlinearity at higher irradiances (Harris and Piccinin 1977; Marra 1978) would explain the larger differences we found at higher irradiances. The exact reason for this nonlinearity at saturating irradiances is not clear, but at least three factors may contribute: catabolic loss, containment effects, and foodweb interactions.

Dark loss of ^{14}C was also responsible for some of the difference between model and in situ estimates. Dark ^{14}C loss averaged 16%, range 5–37%, of daylight-fixed ^{14}C. Our average nighttime loss is similar to the average nighttime losses of 8–13% reported by Lancelot and Mathot (1985) and Smith (1977) but considerably less than the 40–50% reported by Eppley and Sharp (1975). The mechanisms contributing to dark loss are difficult to determine but may be similar to those for nonlinear uptake during the light period (i.e. catabolic loss, containment, and foodweb interactions).

Because of differences between short and long incubations, the interpretation of ^{14}C primary production estimates can be difficult. It has been suggested that ^{14}C-based experiments provide (1) a measure of gross production (Dring and Jewson 1982; Williams et al. 1983), (2) a measure between net and gross production (Harris and Piccinin 1977; Peterson 1978), (3) a measure of net production (Bell and Kuparinen 1984; Smith and Platt 1984), and (4) a severe underestimate of net production in the oligotrophic oceanic gyres and Lake Superior (Verduin 1975; Schulenberger and Reid 1981; Jenkins 1982). Much of this variance in interpretation can be attributed to recycling of ^{14}C within the cells and bottle. The general consensus is that short-term ^{14}C experiments (2–6 h) yield measurements between net and gross production (Harris 1980) and that longer incubations yield results closer to net production (Dring and Jewson 1982).

Results from field experiments are especially difficult to interpret because they are confounded by multispecies assemblages, foodweb interactions (Smith et al. 1984), and experimental artifacts (Venrick et al. 1975; Carpenter and Lively 1980). In field investigations, the most accepted approach for evaluating the ^{14}C technique has been to compare several independant estimates of production or growth (Laws et al. 1984; Sakamoto et al. 1984).

Only two studies in Lake Michigan have compared ^{14}C results with other independent production estimates. Verduin (1972) compared the ^{14}C technique to changes in CO_2 calculated from shifts in pH in light and dark bottles in short-term experiments (3–6 h) and found close agreement between the techniques. Because no correction could be made for light-dependent respiration, the CO_2 results probably measure something less than gross production. We compared growth rate estimates from short and long ^{14}C incubations to growth rate estimates from experiments that measured changes in algal carbon (Table 3). In general, our results suggest that 24-h ^{14}C experiments estimate net production and short-term ^{14}C experiments (model) estimate something greater than net production. For comparisons of similar length incubations, growth rates

from dilution experiments (SIG), which measured phytoplankton growth by changes in phytoplankton carbon, were in good agreement with growth rates from 24-h ^{14}C experiments. However, phytoplankton growth rates from 4-d SIG experiments were generally lower than 24-h ^{14}C growth estimates. These lower SIG estimates can be attributed to containment effects in the longer incubations (Table 4). Containment effects were usually not pronounced after enclosure for 24 h, but as incubation increased so did containment effects (Table 4). Thus, SIG estimates would be more likely to underestimate net production in longer incubations. This underestimation would be greatest during thermal stratification when containment effects were greatest.

Growth rate estimates for surface populations from short-term ^{14}C experiments (model estimates) were consistently higher than all other growth rates, suggesting that these short-term results are greater than net production. The degree to which short-term ^{14}C estimates provide an estimate of gross or net production is uncertain and potentially variable.

Since our manipulations and experimental designs were not always similar, the various techniques were not necessarily measuring the same production and therefore, our comparisons may be lacking in discrimination. For example, production of small particles (<1 μm) was measured with the ^{14}C technique but not with our dilution experiments that rely on phytoplankton counts. This problem would be particularly evident during July 1982 and 1984 when picoplankton (<1 μm) production exceeded 15% of total production (G. Fahnenstiel and D. Scavia, unpubl. data). Furthermore, growth rates from ^{14}C experiments are dependent on measurements of phytoplankton carbon which have potentially large errors associated with them. However, in spite of these difficulties, we feel that our conclusions, based on several comparisons at various times of the year, are justified.

These conclusions are based on similar in vitro experiments and may not be applicable as estimates of in situ rates. Although the 24-h experiments were conducted in situ, they represent rates obtained from samples confined in bottles. This is an important point that has not been adequately addressed in most investigations. An exception is the whole-lake radiocarbon experiment, where Hesslein et al. (1980) found that whole-lake photosynthetic rates were in agreement with in vitro estimates determined by the modelling technique of Fee (1973). There are no comparisons of in vitro and in situ measurements in Lake Michigan, but our estimated production rates are in the same general range as loss measurements due to sinking and zooplankton grazing (Scavia and Fahnenstiel 1987). These comparisons suggest that in vitro estimates may provide reasonable estimates of in situ rates in Lake Michigan, but more direct comparisons are needed to evaluate the use of in vitro measurements.

Evidence for Nutrient Limitation of Epilimnetic Lake Michigan Phytoplankton

An hypothesis has been advanced that phytoplankton growth in the mixing layer of the Great Lakes (Nalewajko et al 1981; Edgington 1984) and oceans (Goldman et al. 1979) may not be limited by nutrients. They postulated that phytoplankton may be growing at near maximal rates and/or limited by physical factors such as temperature and light. While physical factors are very important and may be limiting to phytoplankton growth during periods of very deep thermal mixing (Nalewajko and Voltolina 1986), it is our premise that phytoplankton growth during thermal stratification in Lake Michigan is limited by the availability of nutrients.

This premise is supported by three observations. First, during thermal stratification with an average mixing layer depth of 10–15 m, phytoplankton growth within that layer cannot be limited by light given measured extinction coefficients of $0.12-0.17 \cdot m^{-1}$ and measured I_k (light saturation parameter of Talling (1957)) values of $90-150\ \mu E \cdot m^{-2} \cdot s^{-1}$. Average irradiance received by a population in a 15-m mixing depth with a $0.17 \cdot m^{-1}$ extinction coefficient is 36% of incident light which corresponds to a daylight average of approximately $400\ \mu E \cdot m^{-2} \cdot s^{-1}$ on a clear sunny day. This average is clearly above the measured I_k values and even a population residing at 15 m for the entire day is in the range of measured I_k values. Second, in the absence of light limitation we would expect phytoplankton growth rates to be near the maximum for a given species and temperature. This is not the case, as community growth rates are much less than the maximum. In the absence of nutrient limitation and temperatures of 10–24°C, maximum growth rates for a community of phytoflagellates, blue-greens, and diatoms would be near or exceed $1.0 \cdot d^{-1}$ (Eppley 1972; Reynolds 1984). With average thermal stratification growth rates from 24-h in situ and SIG experiments of $0.32 \cdot d^{-1}$, it is clear that some other factor is important in regulating phytoplankton growth. Third, the factor that is most likely limiting phytoplankton growth is phosphorus, as indicated from field and laboratory experiments. Nutrient enrichment experiments (Schelske and Stoermer 1972; Schelske et al. 1986) have demonstrated that phosphorus additions stimulate phytoplankton growth in Lake Michigan water. Furthermore, from our field investigations (G. Fahnenstiel and D. Scavia, unpubl. data), the turnover time of ^{33}P decreased substantially from several hours during spring isothermal mixing to less than 30 min during midstratification. Turnover times of less than 1 h generally indicate that phosphorus is in limited supply (Lean et al. 1983).

In conclusion, we found no evidence that summer assimilation numbers have changed over the past 15 yr, in contrast with trends in total phosphorus and transparency (Scavia et al. 1986). Trends in summer integral daily production were not clear. Approximately half of summer production occurs below the epilimnion, and the deep chlorophyll layer accounts for approximately 30% of water column productivity. Model production estimates derived from short-term ^{14}C experiments and the modelling approach of Fee (1973) were always higher than 24-h in situ estimates. These short-term production estimates provide a measurement greater than net production whereas 24-h in situ estimates provide a measure of net production. Summer epilimnetic growth rates were relatively low ($0.06-0.60 \cdot d^{-1}$), reflecting the limited availability of phosphorus.

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