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Primary production in lakes Huron and Michigan: *in vitro* and *in situ* comparisons

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Abstract. Oxygen- and carbon-14-based primary production estimates from 9–16 h *in vitro* incubations were compared in lakes Huron and Michigan. For surface mixing layer comparisons, gross $O_2/^{14}C$ photosynthetic quotients (gross PQ) averaged 2.2, and net $O_2/^{14}C$ photosynthetic quotients (net PQ) averaged 1.4. The mean gross PQ is consistent with a theoretical PQ based on the CO_2 and NO_3 assimilation ratio. However, within the deep chlorophyll layer, gross PQ and net PQ averaged 4.9 and 2.8 respectively. These higher values were likely due to excess NO_3 reduction at the expense of CO_2 uptake. Thus, during short experiments under low light conditions, oxygen evolution and CO_2 uptake may not be tightly coupled. *In vitro* and *in situ* O_2-based production estimates were compared in four diurnal (dawn to dusk) experiments in Lake Huron. *In situ* production estimates were determined by measuring water-mass oxygen changes and oxygen transfer across the air-water interface. *In situ* production estimates were approximately twice *in vitro* production estimates for both surface mixing layer and deep chlorophyll layer comparisons. The difference between estimates was attributable to containment effects manifest in 13–16 h bottle incubations. Short-term (1–2 h) *in vitro* production was also compared to diurnal *in vitro* production. Rates of short-term production were ~1.6 times higher than rates of diurnal production, suggesting that short-term *in vitro* production experiments may provide reasonable estimates of *in situ* primary production.

Introduction

Although the ^{14}C technique has been used for three decades, some questions remain whether this method provides reasonable estimates of primary production. Criticisms of the ^{14}C technique have come from a wide range of studies (Verduin, 1975; Gieskes *et al.*, 1979; Goldman *et al.*, 1979; Tijssen, 1979; Shulenberger and Reid, 1981; Jenkins, 1982). Despite these criticisms, there is also a large body of recent work suggesting that the technique can provide reasonable estimates of primary production (Williams *et al.*, 1979; Davies and Williams, 1984; Gieskes and Kraay, 1984; Laws *et al.*, 1984, 1987; Bowers *et al.*, 1987).

A significant part of the controversy concerns problems that are not unique to the ^{14}C technique but are common to *in vitro*-based (bottle incubation) production rates. These problems include containment and manipulation effects, proper incubation of samples and even proper sampling strategy. Some of the most convincing challenges to the ^{14}C technique may fall into this category, such as the challenges based on *in situ* water column changes in O_2, POC and CO_2 (Tijssen, 1979; Postma and Rommets, 1979; Shulenberger and Reid, 1981).

Because of this potential uncertainty in production estimates, we compared *in vitro* ^{14}C uptake and *in vitro* and *in situ* O_2 evolution. *In vitro* comparisons of

oxygen evolution and ^{14}C uptake were used to evaluate errors specific to the ^{14}C technique, whereas *in situ* and *in vitro* comparisons of oxygen evolution were used to evaluate *in vitro* experiments. Our *in vitro* ^{14}C and O_2 comparisons were not unlike those conducted in more eutrophic freshwater environments (Jewson, 1977; Harris and Piccinin, 1977; Bell and Kuparinen, 1984). Recent modifications of the Winkler technique (Bryan *et al.*, 1976) allow detection of relatively small oxygen changes even in oligotrophic Lake Huron. Our diurnal (dawn to dusk) *in vitro* and *in situ* O_2 comparisons accounted for water mass movement and oxygen transfer across the air–water interface to estimate *in situ* production.

Methods

Sampling was conducted at two offshore stations in Lake Huron (43°56′N, 82°21′W; 45°25′N, 82°55′W) and one in Lake Michigan (43°1′N, 86°37′W) between March 24 and August 19, 1986. The Lake Huron stations were chosen because of their close proximity to National Oceanic and Atmospheric Administration weather buoys. Water samples were collected from two regions of the water column: surface mixing layer and deep chlorophyll layer (30 m).

For all experiments, water samples were collected early in the morning (05.00–07.00 h) with 5- to 10-l PVC Niskin bottles. Immediately after collection, BOD bottles (300 ml) were filled by overflowing their volume three times, taking care to minimize water temperature changes. If air temperature was >2°C different than the water temperature, BOD bottles were filled in a lakewater incubator. In general, 8–14 light oxygen BOD bottles, 4–7 dark oxygen BOD bottles and 4 ^{14}C BOD bottles were filled from each sampled depth. Half the light oxygen bottles were fixed with Winkler reagents (see below) immediately after collection and served as measures of initial oxygen concentration. The remaining sample bottles were placed in a fluorescent light or screened natural light incubator for 9–16 h, or back in the lake until sunset (13–16 h). Although some of these samples were incubated *in situ*, the production estimates from the above described experiments are considered *in vitro* production estimates because samples were incubated in bottles.

When bottles were incubated in the lake, a satellite-tracked drifter with window-shade drogue was placed in the lake immediately after initial sample collection to follow the sampled water mass throughout the day. Details of the drifter design and ability to track a water mass are described elsewhere (McCormick *et al.*, 1985; Scavia and Fahnenstiel, 1987). During the day (12.00–14.00 h) and at the end of bottle incubations (20.00–21.00 h), water samples were taken at the location of the satellite-tracked drifter, where BOD bottles were filled as outlined above and immediately fixed with Winkler reagents. Thus, the diurnal changes in water column oxygen concentration provided an estimate of production without enclosing the sample (*in situ* production estimate).

Oxygen analysis of water samples was performed by a modified Winkler technique (Carpenter, 1965; Carritt and Carpenter, 1966; Bryan *et al.*, 1976). Filled BOD bottles were fixed with 2.0 ml of $MnCl_2$ followed by 2.0 ml of alkali-

iodide (Carpenter, 1965). Bottles were shaken and allowed to settle twice and then placed in a cooler or incubator until titration. Titrations were performed generally within 1–3 h after sample collection. Twenty to thirty minutes before titration, 2.0 ml of sulfuric acid was added to the BOD bottles. Whole bottles were titrated with 0.5 N sodium thiosulfate using the end-point detection system described by Bryan *et al.* (1976). Standardization of thiosulfate and blank determinations were performed during each experiment as outlined in Carpenter (1965) and Carritt and Carpenter (1966).

Our 9–16 h *in vitro* incubations were longer than the traditional 1–4 h *in vitro* production incubations and these longer incubations may limit the general application of our comparisons. The precision of our analytical oxygen technique and the low production rates in lakes Huron and Michigan dictated the use of long incubations (>6 h). Prior to the initiation of our field experiments, the precision of our analytical oxygen technique was compared to the rates of primary production in lakes Huron and Michigan. The coefficient of variation (CV) of oxygen titrations ranged between 0.1 and 0.2%. If we assume a CV of titrations of 0.1%, ambient oxygen concentrations of 10 mg l^{-1}, four replicates of initial and final oxygen concentrations, an RQ of 0.8, then the precision of our oxygen technique at the 95% confidence level is ~6 μg C l^{-1} (see Bryan *et al.*, 1976, for details of calculations). Maximum summer productivity rates in Lakes Huron and Michigan can be as low as 1 μg l^{-1} h^{-1} (Fee, 1972; Glooschenko *et al.*, 1973). Thus, with our oxygen technique an incubation of at least 6 h is needed to detect statistically significant production.

Primary production was also estimated with the ^{14}C technique, an account of which is given by Fahnenstiel and Scavia (1987). Incubation bottles were similar to those of the *in vitro* oxygen productivity experiments. At the end of the ^{14}C experiment, two samples from each bottle were filtered under low vacuum through a 0.45-μm pore size Millipore filter. Before the addition of scintillation cocktail, filters were decontaminated with 0.5 N HCl for 4–6 h in scintillation vials. Radioactivity was assayed with a Packard Tricarb scintillation counter (model 460). Counts per minute were converted to disintegrations per minute with external standards.

Two approaches were used to examine the effects of our longer *in vitro* incubations. On June 21 and August 17 the rate of ^{14}C uptake in 300-ml bottles from 13–16 h incubations in a constant-light incubator (~250 μE m^{-2} s^{-1}) was compared to the rate of ^{14}C uptake from 1–2 h incubations. Short-term ^{14}C uptake was determined twice during each day, morning and afternoon, and the mean value was used for comparisons. Additionally, on July 16, ^{14}C uptake from 1 h incubations in 300-ml bottles before and after containment for 16 h were compared.

Corrections for movement of oxygen across the air–water interface are critical if diurnal surface *in situ* oxygen changes are to be attributed to photosynthetic oxygen production. The movement of oxygen across the air–water interface was modelled with the following equation:

$$T = K(O_s - O_w)$$

where T is the transfer rate (g O_2 m^{-2} h^{-1}), K the transfer coefficient (m h^{-1}), O_w the oxygen concentration in surface water (g O_2 m^{-3}) and O_s the saturation oxygen concentration in surface water (g O_2 m^{-3}). If T is negative, oxygen moves from the water to the atmosphere. Hourly wind speed data from a NOAA weather buoy were used to estimate transfer coefficients (Liss and Merlivat, 1986). The saturation oxygen concentration was estimated from atmospheric pressure taken from observations at the NOAA weather buoy and water temperature (Golterman *et al.*, 1978). Hourly transfer rate estimates were summed for the length of the *in situ* experiment. Any exchange of oxygen between the air and water was assumed to mix instantaneously to 2 m so the effect on our 2-m samples could be determined. The assumption of instantaneous mixing to 2 m could result in an overestimate of air–water exchange, because any resistance to mixing caused by diel stratification in the upper 2 m would be ignored (Lang and Scavia, 1986).

Results

In vitro O_2 and ^{14}C comparisons

In the first set of experiments, O_2 and ^{14}C production estimates in similar bottle incubations (*in vitro* experiments) of similar duration (9–16 h) were compared. Gross oxygen production (light bottle minus dark bottle) was on average 58% higher than net oxygen production (light bottle minus initial water concentration) (Table I).

For surface mixing layer communities, gross oxygen production (μM O_2 l^{-1} h^{-1}) was significantly higher than ^{14}C-based production (μM C l^{-1} h^{-1}) (paired t-test, $t = 8.35$, $n = 11$, $P = 0.0001$). The photosynthetic quotient (PQ = mol O_2 evolution/mol carbon fixation) ranged from 1.58 to 2.78 with a mean of 2.21 (Table I). Net oxygen production estimates were also significantly greater than ^{14}C-based production estimates (paired t-test, $t = 3.53$, $n = 11$, $P = 0.0055$) and PQ values ranged from 1.00 to 2.14 with a mean of 1.38 (Table I).

PQs for deep chlorophyll layer (DCL) communities were approximately twice surface values. The mean photosynthetic quotients for gross O_2/^{14}C-based and net O_2/^{14}C-based were 4.90 and 2.84 respectively (Table II).

Evaluation of in vitro experiments

To examine the effect of *in vitro* containment, diurnal *in vitro* O_2 concentration changes (light bottle minus initial water column concentration) were compared to diurnal *in situ* O_2 concentration changes (final water column concentration minus initial water column concentration). *In vitro* light bottles were incubated at the depth of sampling.

Except in one case, diurnal *in situ* oxygen concentration changes were higher than *in vitro* oxygen concentration changes (Table III; paired t-test, $t = 1.83$, $n = 8$, $P = 0.109$). The one exception was from 2 m on June 23, probably as a result of the influence of air–water oxygen exchange (see below). Highly significant differences between *in situ* and *in vitro* oxygen changes were found

Table I. *In vitro* O_2 and ^{14}C-based production estimates (μmol O_2 or C l^{-1} h^{-1}) and photosynthetic quotients (O_2/C) from the surface waters of lakes Huron and Michigan

Date	Z (m)	Net O_2	Gross O_2	^{14}C	Gross PQ	Net PQ
March 24	S	0.11 ± 0.01	0.23 ± 0.08	0.11 ± 0.010	2.09	1.00
April 29	S	0.15 ± 0.02	0.27 ± 0.03	0.12 ± 0.001	2.25	1.25
April 30	S	0.13 ± 0.04	0.24 ± 0.05	0.10 ± 0.004	2.40	1.30
June 23	2	0.30 ± 0.05	0.39 ± 0.06	0.14 ± 0.004	2.78	2.14
	5	0.26 ± 0.06	0.41 ± 0.06	0.15 ± 0.005	2.73	1.73
	8	0.21 ± 0.05	0.35 ± 0.07	0.15 ± 0.001	2.33	1.40
July 15	S	0.09 ± 0.03	0.16 ± 0.08	0.09 ± 0.001	1.78	1.00
August 5	S	0.08 ± 0.04	0.12 ± 0.05	0.05 ± 0.003	2.40	1.60
August 19	2	0.26 ± 0.07	0.38 ± 0.07	0.24 ± 0.003	1.58	1.08
	5	0.22 ± 0.05	0.33 ± 0.06	0.17 ± 0.044	1.94	1.29
	8	0.28 ± 0.04	0.41 ± 0.06	0.20 ± 0.004	2.05	1.40
					$\bar{X}$ = 2.21 ± 0.11	1.38 ± 0.10

Production estimates for samples collected from the surface mixing layer and incubated in a shipboard or shore incubator are indicated by S, whereas samples collected at a specific depth and incubated at that depth are indicated. Error estimates are standard errors.

Table II. *In vitro* O_2 and ^{14}C-based production estimates (μmol O_2 or C l^{-1} h^{-1}) and photosynthetic quotients from the deep chlorophyll layer in Lake Huron

Date	Z (m)	Net O_2	Gross O_2	^{14}C	Gross PQ	Net PQ
July 17	30	0.21 ± 0.07	0.36 ± 0.04	0.07 ± 0.002	5.14	3.0
August 17	30	0.08 ± 0.04	0.14 ± 0.05	0.03 ± 0.004	4.67	2.67
					$\bar{X}$ = 4.90	2.84

Error estimates are standard errors.

Table III. Diurnal *in vitro* O_2 and *in situ* O_2 production estimates (μmol O_2 l^{-1} h^{-1}) from Lake Huron

Date	Z (m)	*In situ*	*In vitro*	r
June 23	2	−0.03 ± 0.08	0.30 ± 0.05	−0.10
	5	0.39 ± 0.04	0.26 ± 0.06	1.50
	8	0.56 ± 0.07	0.22 ± 0.05	2.54
August 19	2	0.74 ± 0.03	0.26 ± 0.07	2.85
	5	0.42 ± 0.05	0.22 ± 0.05	1.91
	8	0.56 ± 0.03	0.28 ± 0.04	2.00
July 17	30	0.30 ± 0.03	0.21 ± 0.07	1.43
August 17	30	0.14 ± 0.04	0.08 ± 0.04	1.75

r is the ratio of *in situ* to *in vitro* production. Error estimates are standard errors.

(paired *t*-test, $t = 3.96$, $n = 7$, $P = 0.007$) when the 2-m June 23 data were excluded. If surface mixing layer comparisons are averaged and the 2-m comparison on June 23 is excluded, *in situ* oxygen changes were ~2.15 times higher than *in vitro* changes. For DCL communities, *in situ* oxygen changes were 1.60 times higher than *in vitro* changes.

Because surface mixing layer oxygen changes can also be attributed to oxygen transfer across the air–water interface, the flux of oxygen across the air–water

interface was estimated. On June 23, wind speeds averaged 4 m s^{-1}, and the loss of oxygen from the upper 2 m of water was calculated to be −0.78 μmol O_2 l^{-1} h^{-1}; this flux is comparable to *in situ* oxygen changes at 5 and 8 m (Table III). Any increase in oxygen concentration due to photosynthesis at 2 m would have been lost to the atmosphere. Thus, based on the calculated loss rate and the observed diurnal change, an estimate of photosynthetic oxygen production in this region is ~0.75 μmol O_2 l^{-1} h^{-1}. This large loss of oxygen from the water column was not observed in the August experiment, when the wind speed averaged only 1.6 m s^{-1} and the oxygen flux from the upper 2 m was only −0.01 μmol O_2 l^{-1} h^{-1}. This loss is small compared to the observed *in situ* oxygen changes (Table III) and suggests that the diurnal oxygen changes on this date equal photosynthetic oxygen evolution.

Results from short-term (1–2 h) *in vitro* experiments may be more comparable to results from *in situ* experiments. Rates of ^{14}C uptake from short-term incubations were on average 1.6 times higher than rates of ^{14}C uptake from diurnal incubations (dawn to dusk). This 1.6-fold increase is similar to the 2-fold increase of diurnal *in situ* to diurnal *in vitro* production estimates. The decrease in ^{14}C uptake with longer incubations appears to be primarily the result of containment. The rate of ^{14}C uptake from a 1 h experiment after enclosure for 16 h was 50% less than rate of ^{14}C uptake from a 1 h experiment prior to enclosure for 16 h.

Discussion

Oxygen and carbon-14 comparisons

Primary production estimates were evaluated in two parts; the first evaluated the ^{14}C technique and the second evaluated bottle or *in vitro* experiments. Based on our results, ^{14}C-based production provides reasonable estimation of *in vitro* primary production. For comparisons from surface waters, oxygen evolution and ^{14}C-based particulate carbon production estimates yielded a mean gross PQ of 2.2 and a mean net PQ of 1.4. PQs of this magnitude have been found in a variety of freshwater environments. Mean net PQs ranged between 1.0 and 2.2 (Lewis, 1974; Harris and Piccinin, 1977; Bell and Kuparinen, 1984) and gross PQs between 2.0 and 2.4 (Bell and Kuparinen, 1984; Megard *et al.*, 1985).

The experimental PQ can be quite variable depending on the source of nitrogen used by the phytoplankton and the photosynthetic end products (Myers, 1949). If photosynthetically generated reductant is required for the reduction of nitrate and/or production of very reduced end-products (i.e. lipids), then higher PQs may be expected. Theoretical PQs can be calculated if NO_3 and CO_2 assimilation ratios are known (Davies and Williams, 1984). During thermal stratification, Lake Michigan epilimnetic phytoplankton have a CO_2 production/NO_3 depletion molar ratio of 11 (Scavia and Fahnenstiel, 1987; Laird *et al.*, 1988), suggesting a theoretical quotient of 1.43. Because this theoretical PQ refers to total carbon fixation and not to particulate carbon as measured in our experiments, the theoretical PQ must be increased to ~1.63 to account for

excretion of fixed carbon (Laird *et al.*, 1986). Given the discrimination of our comparisons (Smith *et al.*, 1984), our experimentally determined PQ of 2.2 is in reasonable agreement with the theoretical PQ of 1.63.

Previous work on Lake Michigan also suggests that ^{14}C-based production estimates provide reasonable estimates of *in vitro* primary production. Twenty-four-hour ^{14}C production estimates agreed reasonably well with particulate carbon increases determined from changes in phytoplankton abundance (Fahnenstiel and Scavia, 1987) and short-term ^{14}C uptake agreed well with CO_2 changes (Verduin, 1972). However, the same has not been found in Lake Superior; ^{14}C-based production estimates were about an order of magnitude less than corresponding CO_2 changes (Verduin, 1975). Although it is possible that problems with the ^{14}C technique may have occurred in Lake Superior and not lakes Huron and Michigan, this is not likely for several reasons. First, a large percentage of Lake Huron water is supplied from Lake Superior and relatively similar chemical and biological conditions exist (Schelske and Roth, 1973). Secondly, in other freshwater environments where direct comparisons have been made, results from the ^{14}C technique were in reasonable agreement with results from other techniques (Harris and Piccinin, 1977; Jewson, 1977; Bell and Kuparinen, 1984).

Good agreement between O_2 and ^{14}C estimates was not found in the region of the DCL in Lake Huron. PQs in this region were approximately twice the surface values, with a mean gross PQ of 4.9 and a mean net PQ of 2.8. Although these PQs may seem high, PQs of this magnitude have been found in other low light environments (Andersen and Sand-Jensen, 1980; Megard *et al.*, 1985). In Lake Kinneret, surface phytoplankton incubated at the base of the euphotic zone exhibited a PQ of 5 (Megard *et al.*, 1985). Likewise, PQs for phytoplankton near the base of the euphotic zone ranged from 2 to 4 in a small eutrophic lake, and from 3 to 8 for cultures of *Selenastrum capricornutum* incubated under low light (Andersen and Sand-Jensen, 1980).

One explanation for these high PQs is that NO_3 reduction competes with CO_2 reduction, and NO_3 reduction is favored under low light conditions (Megard *et al.*, 1985). Thus, most of the photosynthetically generated reductant preferentially reduces NO_3 rather than CO_2, as NO_3 has a higher affinity for reductant under low light (Hatori, 1962; Priscu, 1984). This preferential reduction of NO_3 may occur in the DCL region of lakes Huron and Michigan. Nitrate is the dominant nitrogenous nutrient with concentrations of ~15–20 μM, whereas NH_4 concentrations are generally <0.5 μM (Lesht and Rockwell, 1985; Laird *et al.*, 1988). Furthermore, concentrations of NO_2, a possible by-product of NO_3 use, were reported as high as 0.7 μM in the region of the Lake Michigan DCL (Mortonson and Brooks, 1980).

However, PQs of 3–6 require excessive amounts of nitrate reduction. If growth is balanced by nutrient uptake, then PQs of 3–6 would produce phytoplankton with low C/N ratios. With balanced growth a PQ of 3.25 would produce a C/N ratio of 1/1 and a PQ of 5.25 would produce a C/N ratio of 0.5/1 (Davies and Williams, 1984). It is unlikely that such low C/N ratios are found in lakes Huron and Michigan. Rather, it is more likely that PQs determined from

relatively short incubations (9–16 h) do not reflect balanced growth. Over short incubations, phytoplankton uptake of CO_2 and evolution of O_2 may not be diametrically coupled as balanced growth is more likely to apply to time periods approaching the generation time of the phytoplankton (4–10 days). Even over the diurnal cycle, photosynthetic quotients have been found to vary by a factor of three (Nihei *et al.*, 1954).

Whatever the explanation for high PQs, they appear to be common under certain low light conditions. Whether these PQs are applicable to longer time periods is uncertain but potentially important (Shulenberger and Reid, 1981; Megard *et al.*, 1985). Although oxygen- and carbon-based estimates over the short time periods of our incubation were different, they may each provide accurate estimates of primary production; oxygen evolution may measure energy flux and ^{14}C uptake carbon flux. Only in environments where the reductant generated during oxygenic photosynthesis is used solely for CO_2 reduction would we expect a PQ of 1.0–1.3.

Evaluation of in vitro experiments

In our comparisons, diurnal *in situ* oxygen changes were approximately twice diurnal *in vitro* changes, suggesting that *in vitro* experiments underestimate *in situ* production. The difference between *in situ* and *in vitro* estimates is due to containment effects manifested during prolonged containment of phytoplankton in small bottles. A large (50%) reduction in ^{14}C uptake was found for Lake Huron phytoplankton enclosed in bottles for 16 h. A similar reduction in ^{14}C uptake was found for Lake Michigan phytoplankton after containment in 2-l bottles for 24 h in July 1983 (Fahnenstiel and Scavia, 1987). These containment effects would cause *in vitro* production estimates to underestimate *in situ* production.

Our results do not imply that previous estimates of primary production are underestimates of *in situ* production. Rather, the containment effects found in our experiments should alert investigators to the significant effect that containment can have under certain conditions. Containment effects are not a consistent problem in the Great Lakes (Fahnenstiel and Scavia, 1987) or other environments (Laws *et al.*, 1987), as they appear to depend on several factors such as size of the containers (Gieskes *et al.*, 1979), length of incubation (Fahnenstiel and Scavia, 1987), phytoplankton composition (Venrick *et al.*, 1977), nutritional status of the phytoplankton (Li and Goldman, 1981) and incubation conditions (e.g. adequate representation of *in situ* conditions) (Marra, 1978). It is difficult to extrapolate our results to different lakes or even the same lake under different conditions. Also, the incubations used in our diurnal oxygen and carbon comparisons were significantly longer than traditional production incubations (1–4 h). However, one promising approach for minimizing containment effects is the use of short-term incubations (1–2 h) in large containers (2 l or larger).

It is very likely that results from short-term incubations may provide reasonable estimation of *in situ* production in the Laurentian Great Lakes and

other environments. Rates of ^{14}C uptake from short-term *in vitro* experiments (1–2 h) were 1.6 times higher than rates of ^{14}C uptake from diurnal *in vitro* experiments (13–16 h). Although several factors such as catabolic losses and foodweb cycling may cause lower rates of ^{14}C uptake in longer incubations (Fahnenstiel and Scavia, 1987), the lower rate found in this study was due to containment. Thus, the 1.6-fold increase of short-term ^{14}C uptake to diurnal ^{14}C uptake is comparable to the 2-fold increase of diurnal *in situ* to diurnal *in vitro* production estimates. Further support for the applicability of short-term ^{14}C uptake as a measure of *in situ* production comes from the work of Bowers *et al.* (1987), in which results from short-term ^{14}C experiments were in reasonable agreement with results from whole lake radiocarbon additions.

In conclusion, for surface mixing layer communities, the ^{14}C technique provides reasonable estimates of *in vitro* primary production. *In vitro* primary production estimates may not accurately estimate *in situ* production, as containment effects can be significant. Thus, the investigator should be as concerned about experimental manipulation and containment effects as the method used for estimating primary production. Short-term production experiments (1–2 h) appear to provide reasonable estimates of *in situ* production. For samples from the region of the DCL, ^{14}C uptake and oxygen evolution were not tightly coupled and large differences in production estimates resulted. Such discrepancies seem to reflect differences between carbon and energy flux.

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