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In situ-measured primary production in Lake Superior

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ABSTRACT

Water column primary production is a major term in the organic carbon cycle, particularly in large lakes with relatively reduced shoreline and near-shore influence. Presently, there is a large imbalance in the known inputs vs. outputs of organic carbon in Lake Superior. This study examined primary production in offshore Lake Superior using *in situ* incubations over a range of conditions representing an annual cycle. Primary producers were dominated by small (<20 μm) cells and included a relatively large abundance of small, spherical flagellates. During conditions with a warm surface layer, chlorophyll concentrations were two- to three-fold higher within the deep chlorophyll maximum (DCM) than at the surface. Volumetric production (mass L^{-1} d^{-1}) was maximal at 2-10 m depth, well above the typical DCM depth. On average, 22% of ^{14}C label appeared in the dissolved pool at the end of the incubation period with the rest appearing in GF/F-strained particles. A statistical model for volumetric production explained 93% of the variance in individual measurements for depths>2 m, using temperature and light as predictors. This model was applied to annual fields of temperature and light, and a new estimate for whole-lake annual primary production, 9.73 Tg y^{-1}, was derived. This combination of new measurements and modeling results brings the organic carbon cycle of Lake Superior closer to being balanced.

Introduction

A well-constrained organic carbon budget is foundational to understanding many aspects of the dynamics and biogeochemistry of any given ecosystem. As presently understood, Lake Superior's organic carbon budget is highly imbalanced. Cotner et al. (2004) estimated the inputs to be as follows: atmospheric deposition, 0.16–0.41, rivers, 0.54–0.62, and primary production, 5.3–8.2 (all in Tg y^{-1}). They estimated losses to be as follows: outflow, 0.08–0.1, respiration, 13–39, and burial, 0.48 (all in Tg y^{-1}). Urban et al. (2005) estimated inputs to be: precipitation, 0.1, rivers, 0.9, and production, 3–8 (all in Tg y^{-1}). They estimated losses to be as follows: outflow, 0.1, respiration, 13–81, and burial, 0.5 (all in Tg y^{-1}). According to these two budgets, respiration dominates all other fluxes and organic carbon losses exceed gains by as little as 1.5-fold or as much as 20-fold. The lack of balance in the organic carbon budget signals a significant gap in the present understanding of the dynamics of the Lake Superior ecosystem. Unless the lake's organic carbon budget is not in equilibrium, one or more terms needs to be revised (Cotner et al. 2004; Urban et al. 2005).

Primary production is thought to be the major source of organic carbon in Lake Superior. Over the past several decades, there have been only a few studies where primary production in Lake Superior was measured. Examination of the methodological details these studies used raises questions about relevance, representativeness, and appropriateness of the numbers that have been used to construct lake-wide, annual figures. The first attempt, a report by Putnam and Olson (1961), describes work conducted during 1960 and indicated that the O_2 evolution method was inadequate to measure production in this unproductive lake. These investigators switched to using the ^{14}C method and, in Putnam and Olson (1966), they reported the first values for primary production in Lake Superior. Their studies were performed on seven dates from July to September 1961 at one near-shore but deep water station in the western arm. Incubations were performed *in situ* for 6 to 9 h beginning at solar noon. Six depths to 20 m were studied. Values ranged from 0.6 to 42.8 mg C m^{-3} d^{-1} and from 76 to 507 mg C m^{-2} d^{-1}. Later, Olson and Odlaug (1966) returned to this "section of the lake" and measured primary production in nine depth profiles to 20 m during July and August 1964; data are presented graphically in somewhat stylized fashion making them difficult to use for any careful comparisons. Their information indicates a volumetric production of 1.8 to 8.4 mg C m^{-3} d^{-1} and a maximum areal production of 183 mg C m^{-2} d^{-1}.

Parkos et al. (1969) reported on results of 201 measurements from nine E–W transects performed on commercial shipping vessels. Water collected from the surface was incubated at a single light level at one temperature. There are some errors in the data presentation, whether units are mg C m^{-3} or mg C L^{-1}, for instance, but with some guesswork a range of volumetric production of 0.3 to 38.7 mg C m^{-3} d^{-1} (mean = 16.6, one very high outlier near the Duluth harbor omitted) can be reconstructed. Vollenweider et al. (1974)

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reported on a series of measurements performed during six cruises April–December 1973 based on incubator conditions at near-optimum light levels, "supplemented in each cruise by at least one *in situ* experiment" (no further details are given), and they used a model to integrate over the water column. Areal production was 330–350 mg C m^{-2} d^{-1}. Nalewajko et al. (1981) studied three sites during summer, 1979. Water was collected from the epilimnion and incubated at constant temperature. Mean volumetric production at optimum light was 63 mg C m^{-3} d^{-1}. Fahnenstiel and Glime (1983) measured *in situ* production ten times from May through October 1979 at a deep water station 25 km from shore. Incubations ran for 4 h during mid-day. Volumetric production ranged from <0.5 to >70 mg C m^{-3} d^{-1} with a prominent subsurface maximum, particularly in September and October. Nalewajko and Voltolina (1986) reported on data collected from 37 stations during six cruises from May 1980 to October 1981. Incubations were done in a light gradient at ambient temperature. Volumetric rates at optimal light averaged 24 mg C m^{-3} d^{-1} during stratified and 11 mg C m^{-3} d^{-1} during unstratified conditions.

Fee et al. (1992) studied primary production in Lake Superior at a single station near Isle Royal during 1990 and 1991. Reported rates represent June 1 to August 31. Areal rates were calculated from P vs. I curves, PAR extinction with depth, the level of PAR at the surface of the lake, and the depth of the mixed layer (based on temperature profile). Extracting data from their Figure 11 and converting units indicates a range of volumetric production of 11–22 mg C m^{-3} d^{-1} and a range of areal production of 100–200 mg C m^{-2} d^{-1}. Urban et al. (2005) studied a series of sites mostly within 20 km of the Keweenaw peninsula from May to July in 1998 and May to October in 1999. Most incubations were done at saturating light and application to the water column was made via eight P vs. I curves. Areal production was between <50 and 200 mg C m^{-2} d^{-1}. Although the above studies provide critical information on primary production in the lake, there are multiple shortcomings involved in scaling these observations up to an annual lake-wide value, as is needed to evaluate the organic carbon budget.

From the above it is apparent that there have been very few measurements performed offshore and fewer still done with *in situ* incubations. Measurements done in the lab or lake for less than one daylight period have to be extrapolated to an entire daylight period. Perhaps most critically, the stratified season represents only ~40–50% of the year (Austin and Colman 2008), and observations of production outside of that period are very rare. Finally, it is now understood that measurements of primary production are potentially subject to a variety of errors associated with contamination from trace metals or deleterious effects of rubber associated with sampling and incubations, which can substantially reduce observed rates (Fahnenstiel et al. (2002) provide a Great Lakes example). For all of these reasons, it is natural to question whether the imbalanced organic carbon cycle in Lake Superior results from inaccurate estimates of annual primary production.

Nearly all the above studies considered depths<20 m but during the stratified season there is a deep chlorophyll maximum below this depth; thus, a large proportion of the photosynthetic machinery has been left out of prior estimates. The highest concentration of chlorophyll in Lake Superior typically occurs below the surface mixed layer during the stratified season (Moll and Stoermer 1982; Fahnenstiel and Glime 1983; Barbiero and Tuchman 2001). Repeated offshore sampling over the past ~10 y (Sterner, unpublished) indicates that a deep chlorophyll maximum (DCM) is a persistent and predictable feature of the entire stratified season. Given the prominence of this feature of the photosynthetic biomass of Lake Superior, the activity of the phytoplankton within the DCM might play a large role in production dynamics of the lake. Lake Superior's DCM is thought to represent both an increased chlorophyll content of shade-adapted algae and a higher level of biomass (Barbiero and Tuchman 2001). The mechanisms behind the formation and maintenance of the DCM in Lake Superior are still not well worked out (Barbiero and Tuchman 2001). Relationships between CTD-measured fluorescence, chlorophyll measured on extractions from filtered samples, and biomass as determined microscopically or as particular organic carbon are complex and vary across the five Laurentian Great Lakes (Barbiero and Tuchman 2001). Fahnenstiel and Glime (1983) presented the most detailed information available to date on rates of production relative to the DCM in Lake Superior. They observed a correspondence between the development of the DCM and subsurface levels of primary production and concluded that *in situ* production was the principal process associated with the development of the DCM.

In terms of nutrients, Lake Superior algae are mainly P limited, with Fe deficiencies also noted when P is supplied, indicating that primary producers are near "the cusp" of macro- and micronutrient limitation (Sterner et al. 2004). Algal nutrient status (for example, as measured by C:P ratios) indicate greater nutrient content of algae at the DCM and below than in surface waters (Barbiero and Tuchman 2001). However, in spite of several careful examinations of distributions of very low dissolved phosphate in the lake (Baehr and McManus 2003; Field and Sherrell 2003; Anagnostou and Sherrell 2008), there is no clear evidence for nutrient gradients with depth that would support upwelling as a primary mechanism for DCM formation. Ammonium does show significant vertical structure offshore late in the season (Kumar et al. 2007), but it is highest at depths near the DCM rather than below it. Lower seston C:P at depth may reflect reduced photosynthesis (lowering C) as much as it may represent enhanced availability of nutrients (increasing P), so nutrient supply as a mechanism for DCM formation lacks unequivocal support. Loss rates as a function of depth have not yet been reported and losses are a potential mechanism for DCM formation and maintenance.

Detailed and comprehensive floristic study of Lake Superior indicated an importance of phytoflagellates (cryptophytes, chrysophytes, and dinophytes) and diatoms with small contributions by bluegreens and greens (Munawar and Munawar 1978). After methodology for studying picoplankton became available it soon became clear that this small size fraction was of great importance in this lake. Fahnenstiel et al. (1986) estimated that approximately 50% of autotrophic production of Lake Superior was attributable to phytoplankton that passed through a 3 μm screen. Large contribution of picoplankton production to the total was also noted by Ivanikova et al. (2007). Lake Superior harbors unusual and perhaps unique picocyanobacterial clades. Analysis of 16S rRNA genes of the Lake Superior autotrophic picocyanobacteria indicates that the majority of sequences clustered within the *Synechococcus* and *Prochlorococcus* clade, and that the most abundant species in the offshore are two new clusters of *Synechococcus*, which so far have not been described in any other environment (Ivanikova et al. 2007; Ivanikova et al. 2008). In contrast, picocyanobacteria in a Lake Superior bay corresponded to the cosmopolitan *Synechococcus* that has been found in numerous locations worldwide (Ivanikova et al. 2007).

In this study, primary production at offshore stations in Lake Superior over a range of stratified and unstratified conditions was measured using a standardized *in situ* protocol. Measurements were made to either 80 or 100 m depth, i.e. above, within and below the DCM. Precautions to minimize trace metal contamination were taken. Production was routinely measured as the incorporation of tracer into particles sampled on glass fiber filters at the end of the incubation. Because of the possibility that some ^{14}C tracer may cycle into the dissolved pool in <24 h, the total organic carbon incorporation including DOC as well as particles was measured in a subset of cruises. A predictive model for production as a function of light and temperature was used to scale "snapshot" measurements to an entire annual cycle. Although logistical difficulties still limited the manageable spatial and temporal coverage, the use of day-long, *in situ*

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incubations, offshore locations, extension through and below the DCM, and inclusion of measurements outside of the warm stratified period make this study unique compared to other studies of primary production in Lake Superior.

Methods

The two earliest deployments (one "deployment" is a single incubation of a cabled array of bottles incubated at eight different depths) occurred at sites CD-1 (47°3′54″N, 91°25′55″W) and EM (47°34′58.8″, 88°51′0″) (for a map, see Kumar et al. 2008). Beginning in July 2007, deployments were performed at station WM (47°20′0″, 89°48′0″). Temperature and other physical and biological parameters were measured via CTD (Supplementary Table 1). Water for incubations and for additional chemical analysis was collected using Niskin bottles modified to eliminate all rubber, latex, or metal in the internal parts. The central bungee was high-purity silicon pump tubing (food grade) and O-rings also were silicon.

Particulate nutrients were routinely prefiltered with 80-μm Nitex to eliminate the occasional large grazer from the sample. During the period of this study, algal biomass retained within routine 80-μm zooplankton nets was not visible, indicating that prefiltering did not remove a significant pool of photosynthetically active biomass from the present measurements. Beginning in July 2007, seston was measured in size fractions <2 μm, <10 μm, and <80 μm and chlorophyll was measured in size fractions <2 μm, <5 μm, <10 μm, <20 μm, <40 μm, and <80 μm. Particulate organic carbon (POC), particulate organic nitrogen (PON), and particulate phosphorus (PP) samples were collected by filtering 1 to 1.5 L of sample water onto a 0.7-μm GF/F filter (preashed at 450 °C for 4 h to remove residual carbon, PP filters then rinsed with 5 mL of 1% HCl and 50 mL of Millipore water). Samples were transported frozen then dried at 60 °C for 24 to 48 h and prepared for analysis. POC and PON samples were analyzed on a Perkin Elmer 2400 CHN analyzer calibrated with an acetanilide standard. PP samples were digested with potassium persulfate and analyzed using the ascorbic acid method. DIC and DOC samples were collected in preashed brown glass vials, prerinsed with sample water then filled to overflowing and capped with a septum and cap. Samples were analyzed within 4 days of collection on a Shimadzu TOC-Vcsh analyzer using a platinum catalyst.

Nitrate concentrations at numerous depths within the water column were measured on multiple cruises during 2005–2008. Unfiltered samples were collected in 1% acid cleaned HDPE bottles and frozen for transport and storage. Samples were analyzed using an OI Analytical FS 3000 automated chemistry analyzer (2005–2007) or a Lachat QuikChem® 8500 Flow Injection Analysis System (2007–2008) and a cadmium reduction column. Column reduction efficiency was routinely checked by comparing nitrite vs. nitrate recovery. These data were combined into a single seasonal trend to calculate the rate of nitrate drawdown in the mixed layer.

Phytoplankton samples were collected at all incubation depths beginning in July 2007, preserved with Lugol's, and kept under cold and dark conditions. Samples of 100 mL were settled in graduated cylinders for at least 20 h and the overlying 90 mL was removed by aspiration. These 10-mL concentrated samples were then placed in counting chambers and allowed to settle overnight. Samples were observed with an inverted microscope at 400× and cells >3 μm in at least one dimension were quantified. Randomly chosen grids were examined until at least 75 total cells (or, for some deep samples with very low algal density, 25 total cells) were enumerated. Taxa were identified using several keys and with reference to the species list compiled by Munawar and Munawar (1978). Much more intensive methods than this would be required for high accuracy taxonomic identifications, but this approach provides a general indication of the species composition of the larger algae encountered in this study.

In situ measurements of primary production followed the JGOFS protocols (Knap et al. 1996). The first deployment at CD-1 occurred from 1115 to 2130 and rates were adjusted to the full day-length period. For the remainder of deployments, samples were collected at least 1.5 h before sunrise (Table 1) from incubation depths. Trace-metal-cleaned 250-mL polycarbonate Nalgene bottles were rinsed 3× with lake water and filled to the brim. Four light and one dark bottle were filled at each depth. These were shielded from deck work lights and transferred into a radiation safety van where work continued under low levels of red light. Bottles were opened and spiked with 0.25 mL of $NaH^{14}CO_3$ (~20 μCi, MP Biomedicals no. 17441H25, specific activity 30–60 mCi/mmol, not chelex rinsed). At each depth, the entire contents of one light bottle was immediately filtered onto precombusted 25 mm GF/F filters to estimate T_0 ^{14}C uptake. Bottles were then capped, sealed with Parafilm® and cable-tied into wire baskets. These baskets were then suspended from a cable hanging from a float. A secondary float was tied to the main float and was equipped with a strobe light, radar reflector and PAR sensor (Onset S-LIA-M003) which measured light between 0° and 80° from vertical when pointing straight upwards.

PAR data was collected at 1-minute intervals from approximately 1 h before sunrise to approximately 1 h after sunset. The array of bottles drifted freely during the incubation period. At 1.5 h after sunset or later, bottles were retrieved and moved again into the radiation safety van where work continued under low levels of red light. Each bottle was opened, and 0.25 mL was removed and transferred into a scintillation vial containing 0.25 mL β-phenylethylamine and scintillation fluor to measure total radioactivity. In a subset of cruises, a second aliquot of 1 mL was removed and transferred into a vial with 250 μL of 6N HCl. These were shaken for >1.5 h to remove inorganic $^{14}CO_2$ and are referred to here as "total organic carbon" measurements. The remaining contents, or for some depths with high particle density, subsamples of the remaining contents, were then filtered onto 25-mm precombusted GF/F filters and transferred to scintillation vials. Vials containing filters were later acidified with 0.25 mL 0.5N HCl, evaporated to dryness, filled with

Table 1
Light conditions. Daily integrated PAR as measured on drifter array buoy (beginning in 2007). Apparent sunrise and sunset as calculated from http://www.srrb.noaa.gov/highlights/sunrise/sunrise.html/ without adjusting for daylight savings time. Extinction coefficient (K) taken from CTD profiles of PAR, eliminating data from near surface and depth to produce strong linear plot of log PAR vs. depth. Thermocline depth (*T*, m) was calculated by picking the midpoint of the two 1-m binned measurements of temperature associated with the greatest temperature gradient.

Date	PAR (photons m^{-2} d^{-1} × 10^{25})	Sunrise	Sunset	Conditions	K (m^{-1})	$Z_{1\%\ light}$ (m)	T (m)
June 19, 2006	n.d.	0410	2004	Clear, sunny	0.126	36.5	13.5
August 7, 2006	n.d.	0441	1921	Clear, sunny	0.115	40.0	18.5
July 31, 2007	2.50	0436	1934	Hazy sunshine	0.126	36.5	7.5
November 7, 2007	0.138	0653	1633	Cloudy throughout	0.114	40.4	66.5
April 30, 2008	2.41	0444	1910	Hazy sunshine	0.117	39.4	127.5[a]
July 31, 2008	2.71	0437	1933	Partly cloudy	0.127	36.3	8.5
September 17, 2008	2.16	0540	1806	Clear, sunny	0.161	28.6	16.5

[a] Early-season, reverse stratification.

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fluor and counted on a Beckman-Coulter LS 6500 liquid scintillation counter within 10 days of collection. Primary production using filter samples was calculated as:

$$\text{Particulate Production}\left(\text{mg C L}^{-1}\text{d}^{-1}\right) = (F/V)\cdot(0.00025C/T)\cdot(1.05/D) \quad (1)$$

where:

F = DPMs in filtered sample, corrected for T_0

V = volume filtered (L)

C = DIC concentration (mg C L^{-1})

T = total ^{14}C DPMs (in 0.25 mL)

D = incubation duration (= 1 day),

and with 0.00025 converting total DPMs to 1-L volume and 1.05 representing the correction for the lower uptake of ^{14}C compared to ^{12}C. Production rates were corrected for both T_0 and dark uptake. In general, T_0 DPMs were $\ll$1% of light sample DPMs for depth <20 m. For deep incubations, T_0 values were larger, sometimes 50% of sample DPMs.

Primary production from total organic carbon samples was calculated as

$$\text{Total Organic Production}\left(\text{mg C L}^{-1}\text{d}^{-1}\right) = (P/0.001)\cdot(0.00025C/T)\cdot(1.05/D) \quad (2)$$

where:

P = DPMs in 1-mL sample,

and with 0.001 converting mL to L.

OC samples were taken in light and dark bottles and were dark-corrected before comparison with particulate production numbers.

Column-integrated productivity was calculated using trapezoidal integration and extrapolating the rate measured for the shallowest depth to the surface. Volumetric production below the deepest measurement was assumed to be zero.

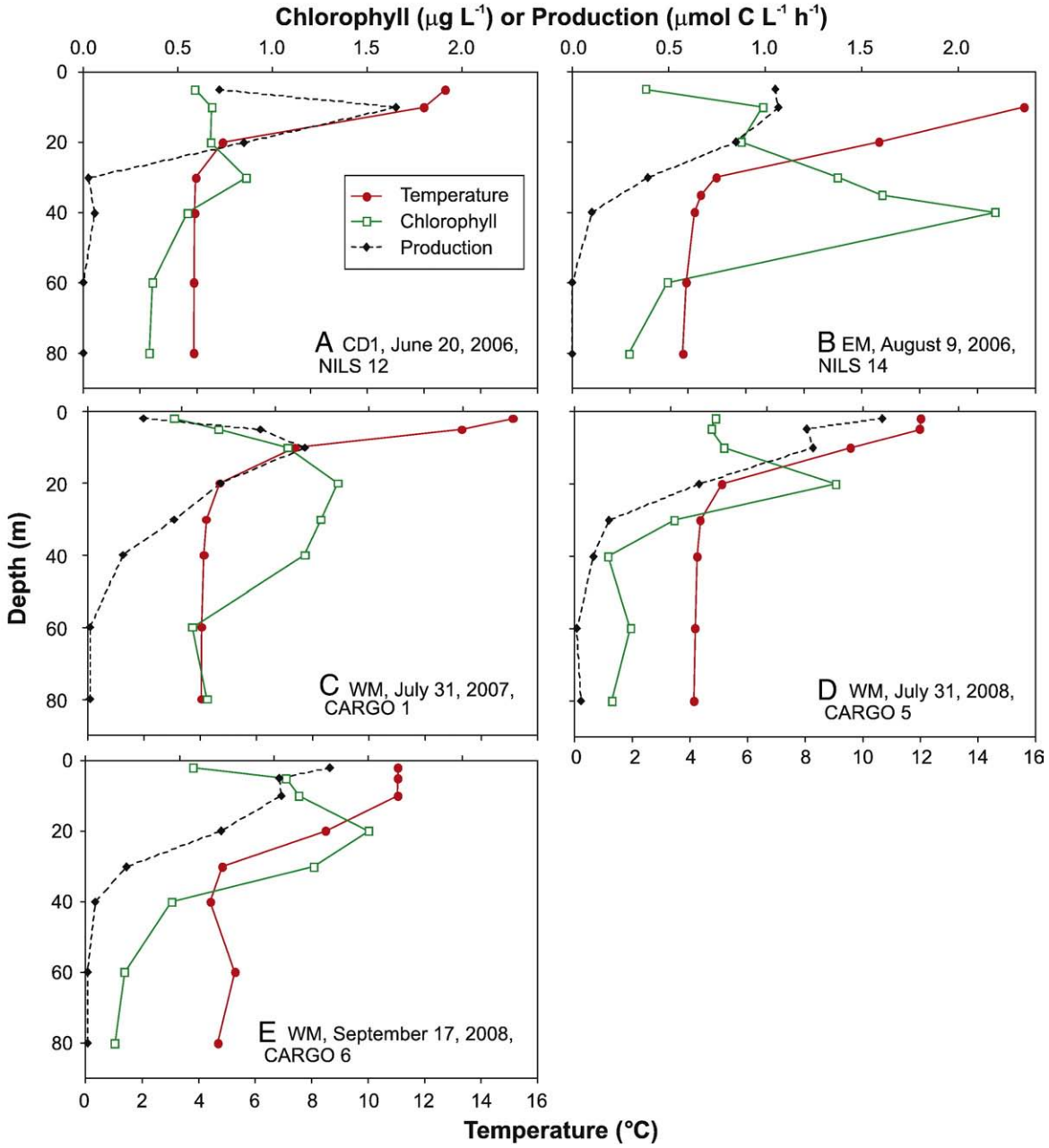

Fig. 1. Vertical profiles of temperature, chlorophyll, and primary production for cruises during warm mixed layer conditions.

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Results

Surface temperatures ranged from 1.8 to 18 °C, nearly the full range ever observed in the lake. During summer stratification, all variables associated with phytoplankton biomass (POC, PON, PP, and chl) normally exhibited mid-depth maxima (see Fig. 1 and Supplementary Fig. 1). Additional physical and chemical parameters measured at each incubation depth are given in Supplementary Table 1. The chl:C ratio under stratified conditions was typically greatest between 20 and 40 m depth (Supplementary Table 1). DOC levels were somewhat higher in November and April than under warmer conditions. Nitrate was always much higher in concentration than ammonium. Stoichiometric ratios of C:N and C:P were often highest near the surface. Daily incident photon flux ranged more than 10-fold from the lowest to the highest observed value (Table 1). The PAR extinction coefficient (K) on the other hand was similar from deployment to deployment, so that the depth of 1% surface light ranged only between 29 and 40 m (Table 1). The relatively small variation in K is a result of year-round low levels of chlorophyll in the lake. Thermocline depth varied greatly by deployment, from a minimum of 7.5 m to a maximum of almost 130 m (Table 1).

The size structure of photosynthesizing organisms was strongly skewed toward small organisms. Approximately half of the chlorophyll passed through a 2-μm filter, and approximately three quarters of the chlorophyll passed through a 5-μm filter (Fig. 2A). POC size fractions as a function of depth (Supplementary Fig. 1) also indicated an importance of small particles. Under stratified conditions, at depths < 50 m, more than half of the POC passed through a 2-μm filter. At greater depth, the relative importance of this small size fraction was typically even larger. Quantifiable algal taxa (Table 2) were diverse and their abundances were low. Consistent with the detailed floristic work done on the lake in the 1970s, small flagellates (*Ochromonas*, *Cryptomonas*, *Chroomonas*, and others) were relatively numerous. Previous authors have noted either a reduced abundance of centric diatoms in the metalimnion (Barbiero and Tuchman 2001) or an increased abundance of centric diatoms in the upper portion of the DCM (Fahnenstiel and Glime 1983). Relatively high abundance of centric diatoms was observed in the present study only on one date (September 17, 2008, not shown).

Dark volumetric $^{14}CO_2$ uptake for the first array deployment was clearly higher than the others, which likely is because it alone was begun during daylight and thus bottles received some illumination during deployment (Table 3). In other deployments, dark volumetric production was <1 mg C m^{-3} d^{-1}, with greatest values observed in the shallowest samples during stratified conditions (Table 3). Dark corrections were made where indicated below but were comparable to light production rates only at deepest incubation depth where production rates were low; thus, whether dark bottles are subtracted

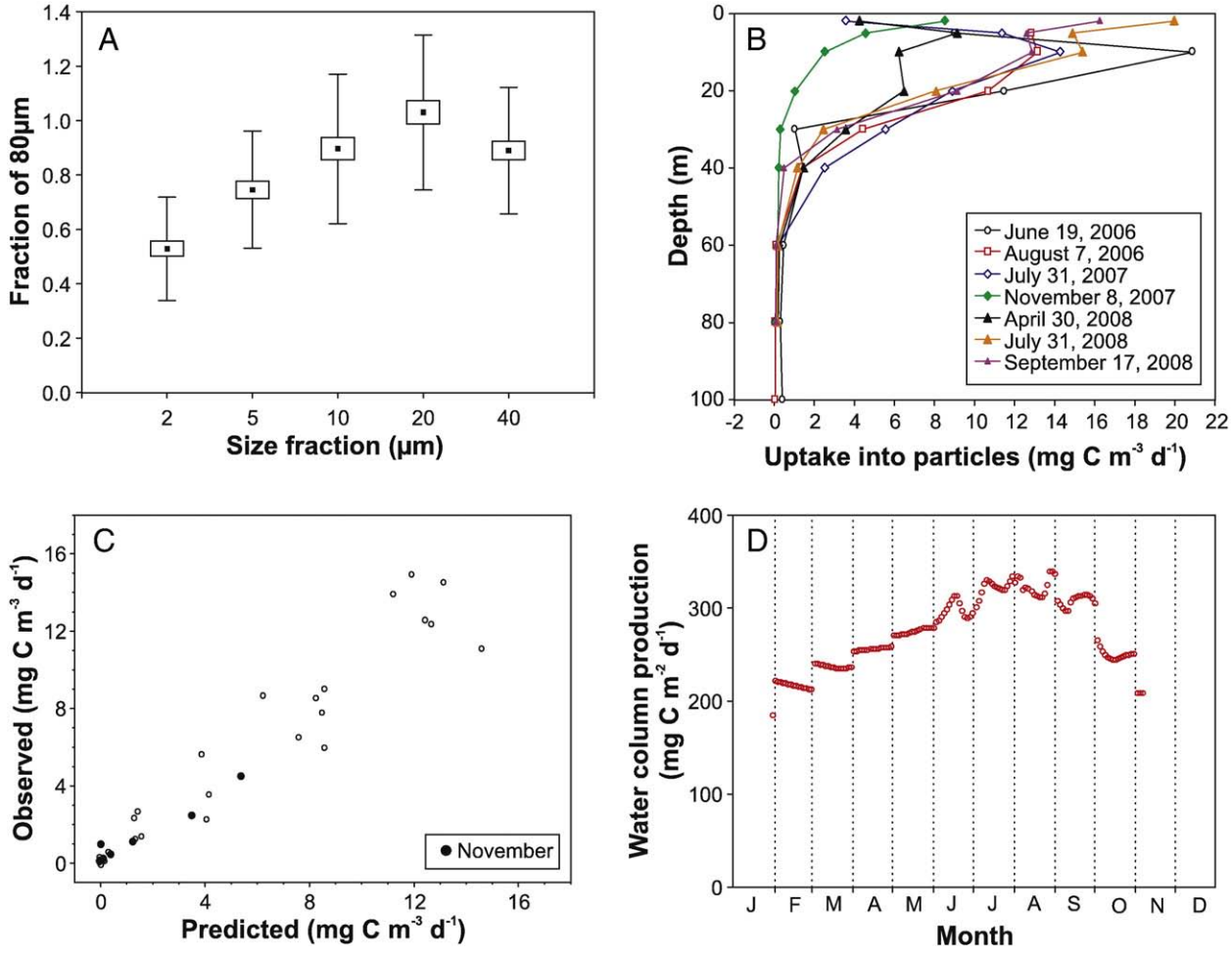

Fig. 2. (A) Chlorophyll size structure for all 2007 and 2008 cruises at all *in situ* incubation depths, given as the fraction of the chlorophyll measured in the largest size fraction (<80 μm) for that depth and date ($N = 40$ for all size fractions). Mean, SE (boxes), and SD (whiskers) all shown. (B) CO_2 uptake into particles (>0.07 μm) in light bottles for all *in situ* incubations (mean of 3 bottles incubated at each depth). See also Fig. 1 and Table 3. (C) Residual plot obtained from regression modeling of individual measurements (depth > 2 m) of production within *in situ* incubation bottles as a function of temperature and light (Eq. (3)). All cruises are included. November data are indicated by closed circles. (D) Modeled water column production (mg C m^{-2} d^{-1}) into particles as a function of day of year.

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Table 2
Abundances of algal taxa observed at all incubation depths at site WM (5 dates times 8 depths = 40 samples). Percent occurrence refers to the percent of the 40 samples in which that particular taxon was identified. "Taxon" refers to the most specific identity known, which was used during enumeration.

Taxon	Cells/ml	SE	Percent occurrence
Bacillariophyta			
Centric diatom	39.0	8.0	90
Synedra sp.	30.1	4.7	76
Asterionella formosa	4.5	2.4	14
Fragilaria sp.	2.3	1.2	10
Nitzschia sp.	0.8	0.8	2
Cymbella sp.	0.4	0.4	2
Melosira sp.	0.2	0.2	2
Navicula radiosa	0.2	0.2	2
Chlorophyta			
Scenedesmus ellipticus	42.8	13.5	55
Tetraedron sp.	4.2	1.4	24
Ankistrodesmus falcatus	2.3	1.0	17
Scenedesmus sp.	0.3	0.3	2
Cryptophyta			
Cryptomonas erosa	37.0	5.0	83
Chroomonas sp.	30.4	8.1	62
Cryptomonas ovata	1.2	0.6	12
Cyanobacteria			
Oscillatoria limmetica	119.9	33.0	67
Microcystis aeruginosa	4.6	4.3	5
Ochrophyta			
Dinobryon divergens	18.3	7.9	38
Rhizosolenia sp.	3.8	0.9	33
Dinobryon bavaricum	0.8	0.6	5
Dinophyta			
Gymnodinium sp.	1.5	1.3	5
Unassigned			
small spherical flagellates	186.7	28.6	100
Pseudokephyrion sp.	0.5	0.3	5

from light bottles or not plays little role in the areal production estimates.

Light volumetric $^{14}CO_2$ uptake profiles showed either an approximately exponential decline from surface downwards or a pronounced surface inhibition (Figs. 1 and 2B). The three deployments where surface inhibition was observed occurred during the early-mid portion of the season (June 2006, July 2007, and April 2008), whereas those without surface inhibition were performed in the mid-late portion of the season (August 2008, November 2007, July 2008, and September 2008). At depth ≥20 m, the five profiles studied during summer stratification exhibited a high degree of consistency from profile to profile.

Production expressed as a ratio to chlorophyll or POC concentration was always highest within the upper 10 m and usually was highest within the upper 5 m (Table 3). In several deployments, production to biomass (P/B) ratios exhibited reduced values in the shallowest depths. Summertime maximum P/B ratios expressed per unit carbon were in the range of 0.1 to 0.15 d^{-1}. However, P/B ratios at most depths were considerably lower. During stratified conditions, nearly all deployments showed highest P/B ratios at shallower depths than either the POC or chlorophyll peaks. There was up to a 20-m separation between highest production values (volumetric or P/B) and peak biomass. Neither the DCM nor the biomass peak generally occurred at the depth of most active production or biomass turnover gain due to primary production. There are significant complications with respect to P/B ratios calculated this way because POC includes non-autotrophic contribution. Given the heavy picoplankton dominance of the phytoplankton in Lake Superior, any attempt to calculate autotrophic biomass from routine microscopic counts would be fraught with error so was not made.

Water column-integrated production was lowest in the November deployment, higher in the April deployment, and highest and within a narrow range for all deployments under warm stratified conditions (Table 4). Total organic carbon production (dissolved plus particulate) values were usually higher than particulate production values (Table 5). There was no clear relationship between the ratio of total to particulate production as a function of depth or season. The average value of this ratio was 1.28, meaning 0.28/1.28 = 22% of total carbon fixed within a day appeared in the DOC pool at the end of that day.

To obtain an estimate for annual primary production from these observations, a statistical model was created predicting the rates of production measured in individual incubation bottles ($n = 40$) as a function of temperature and light. Only cruises with incident PAR measurements were included (5 cruises × 8 depths = 40 observations). Temperature came from CTD casts and daily integrated photon flux came from combining information from daily incident flux taken from the buoy with the extinction coefficient calculated from the CTD casts. This predictive model was then applied to annual cycles of light and temperature as a function of depth. A variety of temperature- and light-dependent models from the literature were tried and evaluated by examining r^2 values and plots of residuals. Both Eppley (1972) and Boltzmann (Gillooly et al. 2002) temperature dependence were examined as was a variety of growth-irradiance curves of different forms (Jassby and Platt 1976). Producing a successful model ($r^2 > 0.9$ and no sign of bias in residual plots) required elimination of observations from 2 m depth; these were sometimes high and sometimes low and no model successfully predicted them. Usually, more than 90% of measured water column production occurred at depths > 2 m, so removing those depths from the predictive model did not appear to be a serious shortcoming in calculating water column production. The predictive model so chosen was:

$$P = C \cdot e^{(-Ea/0.0000862*T)} \cdot P_{opt}\left(1 - e^{-\alpha I / P_{opt}}\right) \quad (3)$$

where:

P = volumetric production (mg C m^{-3} d^{-1}, light–dark)

C = constant (fit, = 1159, dimensionless)

E_a = activation energy (fit, = 0.283, eV)

8.62×10^{-5} = Boltzmann's constant (eV/K)

T = temperature (K)

P_{opt} = a factor associated with the optimal rate of production at high I (fit, = 836, mg m^{-3} d^{-1}) (note: this rate is not actually achieved because other terms in the equation ≠ 1)

α = a parameter giving light dependence of production (fit, = 7668, m^2 photons$^{-1} \times 10^{-25}$)

I = daily integral irradiance (photons $m^{-2} \times 10^{25}$)

The model had good predictive power for summer and winter samplings combined ($r^2 = 0.93$) and was unbiased (Fig. 2C). Surprisingly, models that included chlorophyll concentration as a predictor were always poorer from the standpoint of having lower r^2 and in terms of bias indicated in residual plots. The simpler model without chlorophyll therefore was preferable for the present purposes.

Eq. (3) was then applied to matrices of temperature and light as a function of day of year and depth. The temperature matrix was produced by combining data from 65 offshore cruises undertaken by the author's research group between 1996 and 2007. Dates spanned January 31 to November 8 although most cruises occurred within June–September. Observations of temperature were interpolated using the software program SurGe (http://www.geocities.com/miroslavdressler/surgemain.htm), which implements the ABOS approximation method (http://m.dressler.sweb.cz/ABOS.htm). Incident light as a function of month came from two sources, the Vegetation/Ecosystem Modeling and Analysis Project (http://www.cgd.ucar.edu/vemap/) and the National Renewable Energy Laboratory (http://www.nrel.gov/). Both sources provided modeled incident light at points on the Lake Superior shoreline near the sampling sites.

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Table 3
Volumetric production and productivity to biomass ratios. Values in bold signify the maximum observed value for that parameter for that date.

Date, Cruise	Depth (m)	Production (P)		Biomass	POC<80	P/chlorophyll	P/POC μmol C
		Light (μmol C L^{-1} d^{-1})	Dark	(μg chl L^{-1})	(μmol C L^{-1})	(μmol C μg chl^{-1} d^{-1})	(μmol C^{-1} d^{-1})
June 19, 2006, NILS12	5	0.75	0.04	0.593	**13.75**	1.21	0.052
	10	**1.74**	0.09	0.678	13.39	**2.43**	**0.123**
	20	0.96	0.10	0.672	11.15	1.27	0.077
	30	0.09	0.06	**0.863**	9.76	0.03	0.003
	40	0.12	0.06	0.551	7.79	0.11	0.008
	60	0.04	0.04	0.366	5.77	0.00	0.000
	80	0.02	0.03	0.348	5.71	−0.02	−0.001
	100	0.03	0.03	0.318	5.20	0.00	0.000
August 7, 2006, NILS14	5	1.07	0.02	0.380	7.31	**2.76**	**0.143**
	10	**1.09**	0.03	0.986	13.25	1.08	0.081
	20	0.89	0.04	0.875	15.05	0.97	0.057
	30	0.37	−0.02	1.376	**18.37**	0.28	0.021
	40	0.12	0.01	**2.192**	13.28	0.05	0.008
	60	0.01	0.01	0.492	6.38	−0.01	0.000
	80	0.00	0.01	0.294	5.29	−0.01	0.000
	100	0.00	0.01	0.257	5.46	−0.01	0.000
July 31, 2007, CARGO1	2	0.30	lost	0.462	8.63	0.64	0.034
	5	0.95	0.03	0.699	9.48	**1.32**	**0.097**
	10	**1.19**	0.04	1.065	**12.42**	1.09	0.093
	20	0.74	0.03	**1.332**	10.85	0.53	0.065
	30	0.46	lost	1.245	11.03	0.37	0.042
	40	0.21	0.02	1.155	7.69	0.17	0.025
	60	0.02	0.00	0.558	6.02	0.02	0.002
	80	0.00	0.00	0.636	5.70	0.00	0.000
November 8, 2007, CARGO3	2	**0.71**	0.00	0.716	11.79	**1.00**	**0.061**
	5	0.38	0.01	0.752	**12.10**	0.50	0.031
	10	0.21	0.01	0.872	11.09	0.23	0.018
	20	0.09	0.00	0.527	9.90	0.17	0.009
	30	0.03	−0.01	**0.914**	10.73	0.04	0.003
	40	0.02	0.00	0.586	10.19	0.03	0.002
	60	0.01	−0.06	0.350	10.89	0.23	0.007
	80	0.01	0.00	0.078	5.90	0.08	0.001
April 30, 2008 , CARGO4	2	0.36	0.00	**0.801**	8.07	0.44	0.044
	5	**0.76**	0.02	0.687	8.45	1.09	**0.088**
	10	0.52	0.02	0.617	**8.50**	0.80	0.058
	20	0.54	0.00	0.444	8.05	**1.22**	0.067
	30	0.30	0.01	0.456	7.35	0.64	0.040
	40	0.12	0.01	0.383	7.43	0.30	0.016
	60	0.02	0.01	0.768	7.48	0.01	0.001
	80	0.02	0.03	0.693	8.36	−0.02	−0.001
July 31, 2008, CARGO5	2	**1.66**	0.06	0.732	11.72	**2.19**	**0.137**
	5	1.24	0.04	0.710	11.04	1.70	0.109
	10	1.28	0.04	0.777	11.75	1.60	0.106
	20	0.67	0.02	**1.359**	**13.28**	0.48	0.049
	30	0.20	0.02	0.520	8.89	0.35	0.021
	40	0.10	−0.01	0.174	6.03	0.60	0.017
	60	0.01	0.00	0.289	6.65	0.04	0.002
	80	0.01	−0.01	0.192	6.71	0.13	0.004
September 17, 2008, CARGO6	2	**1.35**	0.05	0.574	11.97	**2.27**	**0.109**
	5	1.05	0.02	1.065	14.98	0.97	0.069
	10	1.07	0.03	1.134	**16.66**	0.92	0.063
	20	0.76	0.04	**1.503**	16.08	0.48	0.045
	30	0.26	0.04	1.212	12.01	0.18	0.019
	40	0.04	−0.01	0.456	7.03	0.10	0.007
	60	0.01	0.00	0.207	5.28	0.05	0.002
	80	0.01	0.00	0.157	4.67	0.03	0.001

These models were based on direct measurements at other stations coupled to locally observed meteorological information on parameters such as cloudiness. These generated nearly identical measures of production so only one is presented here. Incident solar radiation from these sources (kJ m^{-2} or kWh m^{-2} d^{-1}, depending on the data source) includes energy outside of the PAR band so radiation was

Table 4
Water column integrated primary production for each 1-d period. Tg y^{-1} is given to enable ready comparison to past estimates of annual primary production rates.

		June 19, 2006	August 7, 2006	July 31, 2007	November 8, 2007	April 30, 2008	July 31, 2008	September 17, 2008
Light	mg C m^{-2} d^{-1}	383.4	369.3	351.9	88.6	227.4	372.6	336.3
	Tg y^{-1}	11.5	11.1	10.6	2.7	6.8	11.2	10.1
Dark	mg C m^{-2} d^{-1}	62.3	17.2	15.2	1.2	11.2	12.6	13.7
	Tg y^{-1}	1.9	0.52	0.46	0.04	0.34	0.38	0.41
Light–dark	mg C m^{-2} d^{-1}	321.2	352.1	336.7	87.4	216.2	360.0	322.6
	Tg y^{-1}	9.62	10.6	10.1	2.62	6.48	10.8	9.67

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Table 5
Total organic carbon production (TOCP) and the ratio of total ("T") to particulate production ("P").

Depth	November 2007		July 2008		September 2008	
	TOCP (mg C m^{-3} d^{-1})	T:P	TOCP (mg C m^{-3} d^{-1})	T:P	TOCP (mg C m^{-3} d^{-1})	T:P
2	8.94	1.0	24.82	1.2	29.94	1.8
5	4.27	0.9	20.09	1.3	14.65	1.2
10	–	–	18.83	1.2	14.61	1.1
20	1.36	1.3	9.66	1.2	10.00	1.1
30	0.76	2.4	3.63	1.5	2.30	0.7

converted to PAR although both unit conversion and empirically adjusting the values for months when PAR from the incubation buoy was available. The empirical adjustment was 0.42 for VEMAP and 0.51 for NREL (PAR≈40–50% of total solar radiation). The seasonal minimum PAR was estimated to be 5.88×10^{24} photons m^{-2} (December) and the maximum seasonal PAR was estimate to be 3.09×10^{25} photons m^{-2} (July). Because of minimal seasonal variation in extinction coefficient observed in the present study, a single value (0.13 m^{-1}) was used.

Water column-integrated production modeled in this way is given in Fig. 2D. These calculations assume zero ice cover; we lack any certain information on how to estimate primary production under ice. Austin and Colman (2007; 2008) estimated that ice cover on Lake Superior has decreased from 23% to 12% (spatially and temporally averaged from Dec 1 to May 31) over the last century. According to this model, production ranges from ~200 to ~350 mg C m^{-2} d^{-1}. Finally, to obtain a single annual estimate, the values in Fig. 2D were summed with the earliest and latest values extrapolated to the first and last days of the year, respectively. These earliest and latest measured values are based on water column temperatures<4 °C and lowest or near-lowest monthly incident light and thus seem to be a reasonable basis for extrapolation, considering the information on incident light was monthly. The lake-wide, annual primary production value thus obtained was 93.7 g C m^{-2} y^{-1}. Multiplying by the surface area of the lake gives 7.6 Tg y^{-1}. These values, determined with standard JGOFS protocols, are values that are most comparable to other studies. Primary production channeled into particles is most relevant to considerations of energy flow directly from phytoplankton into upper trophic levels. However, consideration of the entire organic carbon cycle should also consider primary production that cycles quickly into the dissolved pool; this fraction is available for uptake by heterotrophic activity. Multiplying by the average increase in production due to ^{14}C label that cycles directly into the DOC pool within 1 day (1.28, Table 5), increases these annual estimates to 120 g C m^{-2} y^{-1}, or 9.73 Tg y^{-1}.

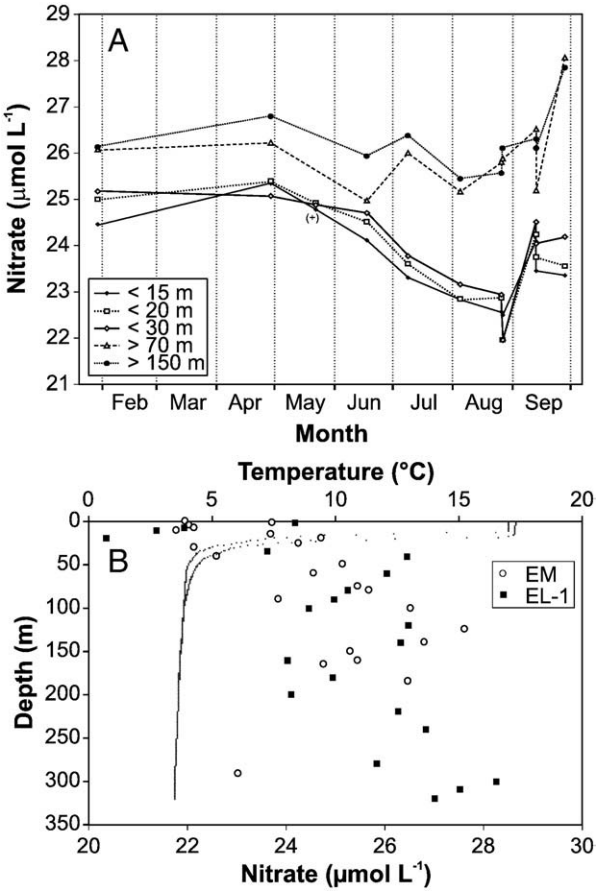

Fig. 3. (A) Seasonal NO_3^- concentration for different water column segments assembled from several sampling years. Two deep water observations with concentrations indicated by (+) were deemed to be outliers and were removed from the trends. (B) Late-summer profiles of [NO_3^-] and temperature in Lake Superior. Sampling locations were: EM, 47°35′59″, 88°51′0″ and EL-1, 47°30′0″, 87°0′0″. Both profiles from late August 2005 were chosen for display because they showed the greatest observed difference between surface and deep water.

Nitrate concentration in the upper part of the water column was lower than in the lower part of the water column, with an apparent steady mixed layer drawdown (Fig. 3). The high concentration observed in deep water on Oct 2, 2005 (site CD-1), seems anomalous or may indicate a localized, late-season sediment efflux. The period from April 29 to Aug 29 exhibits steady decline in nitrate concentration in surface waters with a rate of depletion of 1.35 nM NO_3^- d^{-1}. On average, NO_3^- uptake represents 22.7% of summertime total N uptake in Lake Superior (Table 1 in Kumar et al. 2008). Stable isotope dynamics indicates less importance of nitrate toward total N uptake in the winter (Kumar et al., submitted), although the calculations performed here are based only on summer dynamics. The average seston C:N ratios for depths≤30 m during the period of NO_3^- drawdown was 8.7 (molar, Supplementary Table 1). Combining the above information, one can arrive at an estimate of C incorporation associated with the NO_3^- drawdown in the upper 30 m of the water column:

$$1.35\ \text{nmol}\ NO_3^-\,(L\cdot d)^{-1}\cdot 1\,N/0.227\ NO_3^- \cdot 8.7C/N = 51.7\ \text{nmol C}\,(L\cdot d)^{-1}, \quad (4)$$

or 129 mg C m^{-2} d^{-1}. The carbon uptake associated with the seasonal nitrate drawdown thus is less than half of the production measured by the *in situ* ^{14}C method (compare to values in Table 4). A term not factored into the above calculation is any replenishment of the epilimnetic nitrate pools either via mixing of sub-thermocline waters into the epilimnion or water column nitrification. It is thus perhaps best to consider this estimate of production based on nitrate drawdown to be a minimum value. Reversing the chain of calculations, and estimating expected nitrate drawdown given the above assumptions plus the observed primary productivity, we would expect about twice the seasonal nitrate drawdown than what is observed, possibly indicating a supply of nitrate to surface waters from mixing or from nitrification or both approximately equal to the drawdown rate (~1.3 nmol NO_3^- L^{-1} d^{-1}).

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Discussion

Recent reviews have placed whole-lake, annual primary production in Lake Superior at between 5.3 and 8.2 Tg y^{-1} (Cotner et al. 2004) or between 3 and 8 Tg y^{-1} (Urban et al. 2005) and have pointed to a greatly imbalanced organic carbon budget, with outputs ≫ inputs. The present study revises the annual primary production number upwards to 9.73 Tg y^{-1}. Both Cotner et al. and Urban et al. estimated the allochthonous supply of organic C to be ~1 Tg y^{-1}. Thus, an estimate for total annual gains of organic production in Lake Superior is ~10 Tg y^{-1}. This value is closer to the minimum summed organic C losses (13.5 Tg y^{-1}) than previously indicated. The Lake Superior organic carbon budget remains unbalanced but gains and losses are closer together than they were before. The wide range of estimates of respiration in the lake (13 to 81 Tg y^{-1}) is still a large source of uncertainty in attempting to close Lake Superior's organic carbon budget. Furthermore, other fluxes such as riverine inputs, bear additional study and consideration. In addition, input of organic carbon from aerosols has not yet been estimated for Lake Superior and might be significant (Duarte et al. 2006).

Perhaps the greatest challenge in using direct measurements such as these to calculate a value for lake-wide, annual primary production suitable for budget purposes is spatial and temporal variability. An ideal study would utilize many deployments across the entire lake for the entire year, but this would be a highly impractical undertaking in Lake Superior. We therefore need to consider whether the scaling approach performed here, using a limited number of samplings, is adequate. Rate measurements of any kind in the offshore of Lake Superior during the winter have rarely been reported. The model developed here for volumetric production as a function of temperature and light was a good descriptor of summer, November and April conditions at all depths ≥ 5 m (Fig. 2C). The variability of factors that might affect primary production in this large lake is still incompletely characterized. Regarding spatial variation at any point in time, Barbiero and Tuchman (2001, 2004) provide information on lake-wide chlorophyll values with depth, and from their data, it is difficult to discern any stable spatial gradients or differences in the offshore chlorophyll levels across the lake. Thus, considering the lake as a single homogeneous system provides at least a provisional estimate, pending better information on spatial variation in the lake.

The model developed here suggests that light and temperature are key factors. A muted seasonal variability in chlorophyll levels points to an overriding importance of incident light in affecting the lake's light climate. Seasonal variation in incident light driven both by astronomical factors including solar angle and daylight, and by differences in cloudiness across seasons has been incorporated in the present model. Regarding temperature, the south shore often has higher temperatures and different stratification patterns than the rest of the lake early in the summer (Chen et al. 2001). The two sampling sites used here are well outside of that near-shore zone. The DCM is a potentially important component of spatial variability. The model developed here had good power to predict volumetric production with just temperature and light. The fact that including chlorophyll concentration worsened predictive power likely derives from two factors. First, the range of chlorophyll contents was not large. Offshore Lake Superior does not have wide seasonal swings in algal biomass (see Supplementary Table 1). Second, the DCM depth did not exhibit relatively high levels of production. A model for production lacking algal biomass is clearly not a mechanistic model, but the purpose here was to build a predictive model. The model should not be expected to operate outside of the range of conditions observed here. The estimate derived here, based as it is on still limited spatial and temporal coverage, rests on the finding that volumetric production is well predicted by light and temperature. It further assumes that the spatial variability in light and temperature can be overlooked so that they can be characterized across time with reasonable accuracy.

Allowing for rapid cycling of fixed organic carbon into the dissolved pool was partially responsible for the upward revision of primary production in this paper. Estimates of the percent of primary production in different lakes released by algae as DOC vary widely. There have not been many studies of algal DOC exudation in the Great Lakes. Laird et al. (1986) found 11 ± 9% (mean ± SD) for a study performed on epilimnetic Lake Michigan water. Lee and Nalewajko (1978) reported even lower values (1.2%, Lake Erie and 4.4%, Lake Ontario). Urban et al. (2005) on the other hand report a value of 35% for Lake Superior. The value for Lake Superior (22%) reported here is within the range of relevant reported values.

Based perhaps most of all on its high transparency, Lake Superior has often been described as "ultraoligotrophic". Classifying lakes into trophic categories is imprecise and is generally done only for convenience. However, the mean water column production of Lake Superior (in round numbers ~300 mg C m^{-2} d^{-1}, Fig. 2D) is actually at the more productive end of what Wetzel (2001, his Table 15-13) considered to be representative of "oligotrophic" systems, and it even extends into the lower end of his "mesotrophic" category. Therefore, in terms of primary production, Lake Superior should not be considered an "ultraoligotrophic." Lakes with lower estimated annual production than Lake Superior include high latitude lakes and ponds, high altitude lakes and a mid-latitude hardwater lake (Wetzel 2001, his Table 15-12). A potential 12-month growing season in Lake Superior (dependent on ice conditions) contributes to this perhaps higher than expected level of annual production. The ratio of maximum to minimum water column production is estimated to be only two (see Fig. 2D). These considerations strongly suggest that winter production is hardly negligible in consideration of the annual organic carbon budget and needs further study. The model suggests that the added production from the relatively warm and bright mixed layer in summertime conditions increases lake-wide annual production but not perhaps as much as would be expected.

Although this study suggests a somewhat higher value of primary production for Lake Superior than previous studies, the overall annual rate suggested here still remains less than values published for the other Laurentian Great Lakes. For example, studies on Lake Michigan have reported 325–350 mg C m^{-2} d^{-1} (annual, Cotner and Biddanda 2002) or 615–630 mg C m^{-2} d^{-1} (summertime, Fahnenstiel and Scavia 1987). These are higher than the 200–300 mg C m^{-2} d^{-1} reported here for Lake Superior prior to adjustment for total organic production (Fig. 2D). Studies on Lake Erie have measured 155–169 g C m^{-2} (summertime, Smith et al., 2005) and 320–370 g C m^{-2} (annual, Fitzpatrick et al. 2007). These are higher than the 93.7 g C m^{-2} reported here for Lake Superior for the entire year. The net primary production for the entire Laurentian Great Lakes Basin (land plus water) was recently estimated as 346 g C m^{-2} for the entire year (Karim et al. 2008). Alin and Johnson (2007) compiled carbon cycle information for 41 large lakes of the world and found that primary production was negatively related to latitude and mean depth and positively related to solar insulation, mean annual water temperature and the ratios of watershed–lake area. The primary production of Lake Superior, at 93.7 g C m^{-2} y^{-1} (particles) falls within the range of the global large lakes data (10–1900 g C m^{-2} y^{-1}).

The rate of production calculated here can be directly compared to certain oceanic studies because of the use of identical methodology. Karl et al. (1998) reported primary production at North Pacific Station ALOHA to average 472 mg C m^{-2} d^{-1} (SD = 125, N = 70). Even the summertime rates observed here for Lake Superior are among the lowest observed rates at Station ALOHA. Incorporation of DO^{14}C production potentially raises the ALOHA value to near 1 g m^{-2} d^{-1} (Karl et al. 1998) but raises the Lake Superior values to a lesser extent. The Lake Superior water column thus has a much lower rate of primary production than the North Pacific gyre. Production in the temporally more variable Bermuda Atlantic Time Series (BATS) station fall within a range of 180–810 mg C^{-2} d^{-1} with annual rates of 100–170 g C^{-2} y^{-1}

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(Michaels et al. 1994). The range of values of integrated production observed here for Lake Superior is similar to that observed during non-bloom conditions at BATS.

The DCM is a prominent photosynthetic feature of Lake Superior but its formation and maintenance are not yet well understood. Chlorophyll concentrations at mid-depth often exceed concentrations at the surface by factors of two- or three-fold (Fig. 1). The DCM is often though not always well below the thermocline (this study and unpublished data). The degree to which the DCM represents light/shade adaptation of algae, altering chlorophyll content, vs. changes in biomass is an important consideration, but can only be partially addressed because reliable estimates of biomass of photosynthesizing organisms are not available. Nevertheless, depth relations of POC, which includes heterotrophic and detrital carbon as well as autotrophic biomass (Supplementary Fig. 1) also indicate mid-depth maxima, suggesting that the DCM is not entirely due to light/shade adaptation. Depths of peak POC concentration are shallower than the DCM and are closer to the thermocline depth.

Fahnenstiel and Glime (1983), in the only other study that examined depth-dependent production relative to the DCM in Lake Superior, concluded that the DCM results from *in situ* production. They observed a correspondence between the DCM depth and the depth of maximum primary production. However, observations in the present study contradict those observations. It is possible that the factors affecting DCM formation and maintenance changed between the study of Fahnenstiel and Glime and the present study. Here, the DCM did not correspond to the stratum of highest productivity, either in terms of volumetric rates or in terms of productivity to biomass ratios. In most profiles during stratified conditions, the DCM was located well below the peak primary production (Table 3 and Fig. 1). The spatial disjunction of the DCM with the depths of maximum biomass production and the depth of maximal temperature gradient argues that, to understand the Lake Superior DCM, we need to look hard at loss factors including grazing.

Conclusions

Lake Superior is an oligotrophic lake with rates of water column production ranging from ~200 to 350 mg C m^{-2} d^{-1}. The phytoplankton community is dominated by small size classes and includes a large representation of small flagellated taxa. The annual rate of input of organic carbon to the lake by primary production is estimated here to be 9.73 Tg y^{-1}. This value is higher than previous estimates that have been used in constructing the whole-lake annual organic carbon budget, which helps to close the Lake Superior organic carbon budget.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jglr.2009.12.007.

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