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# Lake-wide phytoplankton production and abundance in the Upper Great Lakes: 2010–2013

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ABSTRACT

Lake-wide phytoplankton chlorophyll *a* concentrations and primary production were determined for lakes Huron, Michigan, and Superior in 2010–2013. Chlorophyll *a* concentrations were determined using MODIS imagery with a color-producing agent algorithm and primary production with the Great Lakes Production Model using remotely sensed and empirically derived input from the Upper Great Lakes. The new chlorophyll *a* and primary production estimates agreed well with field measurements. Lake-wide mean chlorophyll *a* concentrations determined from observations in all 12 months were highest in Lake Superior (mean = 0.99 mg/m$^3$), intermediate in Lake Michigan (mean = 0.88 mg/m$^3$), and lowest in Lake Huron (mean = 0.77 mg/m$^3$). In Lake Superior, a gradient in chlorophyll *a* concentrations was noted from the shallow zone (0–30 m, mean = 1.57 mg/m$^3$) to the deep-water zone (>150 m, mean = 0.94 mg/m$^3$). However, in Lake Michigan, no differences in mean chlorophyll *a* concentrations were noted in shallow-, mid-, or deep-water zones (means, 0.83, 0.86, 0.90 mg/m$^3$, respectively). Lake-wide areal integrated primary production rates in lakes Huron, Michigan, and Superior were not significantly different for the 2010–2013 period (means, 216, 259, and 228 mg C/m$^2$/d, respectively). Also, primary production in all depth zones (shallow, mid, and deep) were similar across lakes. Annual whole-lake phytoplankton carbon fixation values for 2010–2013 ranged from 4.4 to 5.7 Tg/y for Lake Huron, 5.0–7.2 Tg/y for Lake Michigan, and 6.4–9.5 Tg/y for Lake Superior.

## Introduction

The rate of primary production is a fundamental property of aquatic systems and measurements of primary production are critical to our understanding of the carbon cycle (Wetzel, 2001). In the Upper Great Lakes, the dominant primary producers are phytoplankton, and most primary production measurements have been made using the C-14 technique (Vollenweider et al., 1974). A variety of *in situ* and simulated *in situ* experiments have measured the rate of primary production in the Upper Great Lakes over the last 50 years. The first measurements were made in Grand Traverse Bay in 1959 (Saunders et al., 1962). *In situ* and simulated *in situ* experiments continued for the next 50 years as investigators sought to determine variations in primary production rates and the factors controlling rates (e.g., Parkos et al., 1969; Putnam and Olson, 1966; Schelske and Callender, 1970; Schelske et al., 1971; Verduin, 1972; Fee, 1973; Rousar, 1973; Vollenweider et al., 1974; Parker et al., 1977; Fahnenstiel and Scavia, 1987a; Lohrenz et al., 2004; Fahnenstiel et al., 2010). While *in situ* and simulated *in situ* experiments provided accurate estimates of primary production in small volumes of water (3 mL to 2 L), they may not be easily extrapolated to lake-wide estimates (Sterner, 2010). Moreover, these *in situ* and simulated *in situ* experiments provide an integrated measure of production that is dependent on many variables (e.g. phytoplankton biomass, light, temperature, etc.), thus limiting their predictive value.

Early lake-wide estimates of primary production for the Upper Great Lakes were summarized in Vollenweider et al. (1974). These earlier estimates (i.e., from 1950s to 1980s) may be biased because of deficiencies in traditional collection and incubation techniques. New trace-metal clean and non-toxic techniques for the measurement of primary productivity have been more recently developed and used (Carpenter and Lively, 1980; Fitzwater et al., 1982; Fahnenstiel et al., 2002). Because trace-metal limitation can occur in Great Lakes phytoplankton communities (Sterner et al., 2004; Twiss et al., 2004; North et al., 2007), the use of these new clean approaches is critical (Fahnenstiel et al., 2002), and thus, comparisons of results from the 1960–1970s to recent studies (e.g., Sterner, 2010) are fraught with uncertainty. It should be noted

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that not all recent studies have utilized the newer collection and incubation techniques (trace-metal free and non-toxic). For example, the only lake where multiple attempts have been made to estimate lake-wide phytoplankton production in the last 15 years is Lake Superior (Urban et al., 2005; Cotner et al., 2004; Sterner, 2010), but only one of these studies employed the newer clean techniques (Sterner, 2010). More measurements of phytoplankton productivity that utilize the clean techniques are needed in the Upper Great Lakes.

One promising technique for measuring primary production in large bodies of water is the application of satellite remote sensing-based measurements. Because remote sensing can provide high temporal and spatial resolution on a lake-wide basis (e.g., MODIS imagery), remote sensing may provide truly lake-wide estimates of primary production. Recent advances in the understanding of optical properties of the Great Lakes (Bergman et al., 2004; Lohrenz et al., 2008; Binding et al., 2012; Shuchman et al., 2013a), and new high-quality spectral sensors (SeaWiFS, MODIS, etc.) have recently allowed for accurate estimates of lake-wide primary production. Lesht et al. (2002), using SeaWiFS data for Lake Michigan estimated lake-wide chlorophyll concentrations and primary production (using a multiple regression model) to demonstrate the existence of a lake-wide phytoplankton bloom that accounted for 25% of annual primary production, but lasted only several weeks. Using both SeaWiFS and AVHRR imagery, Lohrenz et al. (2008) used a wavelength-resolved model to study the impact of river discharge and coastal sediments on primary production in the southeastern region of Lake Michigan. They noted the importance of sediment resuspension on regional primary production, and the significance of interannual variability, particularly as it relates to river discharge in the region. Moreover, they found good agreement between their remote sensing-based production estimates and those using an empirically based modeling approach (Fee, 1973) that has been used extensively in the Great Lakes (Fahnenstiel and Scavia, 1987a; Millard and Sager, 1994; Fahnenstiel et al., 1995; Millard et al., 1996; Lohrenz et al., 2004; Smith et al., 2005; Depew et al., 2006; Fahnenstiel et al., 2010). In more recent study, Warner and Lesht (2015) used a global remote sensing model to estimate lake-wide productivity in lakes Huron and Michigan from 1998 to 2008. Their estimates of total carbon fixation ranged from 9.5 to 13.6 Tg/y for Lake Michigan and from 7.7 to 11.0 Tg/y for Lake Huron.

It was the goal of this study to provide annual lake-wide estimates of phytoplankton production and biomass in the Upper Great Lakes from 2010 to 2013 using a consistent and novel approach (model and clean field measurements). Our model results were also used to evaluate primary production rates and phytoplankton biomass within different spatial regions of the lakes (e.g., north, south, shallow, deep, etc.). We used remote sensing and empirically derived relationships for input variables in a commonly used mechanistic model of primary production. While many simple models exist for estimating primary production with remote sensing input (Behrenfeld and Falkowski, 1997a), the mechanistic model of Fee has been widely used in the Great Lakes (see references above). This mechanistic model originally developed by Fee (1973) has been revised and termed the Great Lakes Production Model (Lang and Fahnenstiel, 1995), and more recently, the Great Lakes Primary Production Model (Shuchman et al., 2013b). Finally, given the recent changes in the lower food-web of lakes Huron and Michigan and the noted convergence of these lakes to Lake Superior (Fahnenstiel et al., 2010; Mida et al., 2010; Evans et al., 2011; Barbiero et al., 2012), we hypothesize that phytoplankton biomass and production would be similar across lakes. Moreover, given the high abundances of dreissenid mussels in the nearshore and mid regions of lakes Michigan and Huron and their effect in these regions (i.e., nearshore shunt and mid-depth sink, Hecky et al., 2004; Vanderploeg et al., 2010), we hypothesize that the gradients in phytoplankton abundance and production that have historically existed from nearshore to offshore regions (Fee, 1973; Glooschenko and Moore, 1973) now are greatly diminished.

## Methods

### Field

Three stations (43° 11.29′ and 86° 20.64′; 43° 12.37′ and 86° 26.98′; 43° 11.99′and 86° 34.19′) were sampled in southern Lake Michigan on an approximately monthly basis in 2010–2012 (Fig. 1). These three stations were the NOAA/GLERL monitoring sampling stations and ranged in depth from 15 to 110 m (Fahnenstiel et al., 2010; Pothoven and Fahnenstiel, 2013). Three stations (44° 30.98' and 86° 15.14'; 44° 30.11′ and 86° 20.62′; 44° 29.8′ and 86° 45.14') were sampled in northern Lake Michigan on three occasions in 2010 and ranged in depth from 15 to 110 m. Three stations (44° 47.82′ and 83° 00.68′; 44° 50.34′ and 83° 09.29′; 44°57.16′ and 83° 16.26′) were sampled in Lake Huron in May, July, and September 2012. These three stations ranged in depth from 18 to 86 m. In Lake Superior, six stations (47° 27.80′ and 88° 34.70′; 47° 38.95′ and 88° 34.74′; 48° 03.59′ and 88° 25.38′; 47° 50.88′ and 87° 48.77′; 47° 17.57′ and 87° 12.85′; 46° 53.80′ and 88° 24.79′) were sampled in 2013. Two stations were sampled approximately six times and the other four stations were sampled one–two times. These six stations ranged in depth from 70 to 230 m.

A Seabird CTD (conductivity, temperature, and depth) equipped with a chlorophyll fluorometer (Turner Designs), and photosynthetic active radiation (PAR) sensor (Biospherical) was lowered from the surface to just above the bottom. Secchi disk transparency was measured with a black/white or white 25-cm disk.

Discrete samples were taken with modified clean Niskin bottles (Fitzwater et al., 1982; Fahnenstiel et al., 2002). Typically, 6–12 depths were sampled during the thermally stratified period to characterize different regions (i.e., epilimnion, hypolimnion, deep chlorophyll layer, etc.). Chlorophyll *a* samples were filtered onto Whatman GF/F filters, extracted with N, N-dimethylformamide (Speziale et al., 1984) and analyzed fluorometrically.

Phytoplankton photosynthesis was measured with the clean, non-toxic C-14 technique in a photosynthesis–irradiance incubator at each station on each sampling date (Fitzwater et al., 1982; Fahnenstiel et al., 2000; Fahnenstiel et al., 2000). Experiments were conducted in a small-volume (3 ml samples) incubator for 1 h with 18 light levels (Fahnenstiel et al., 2000). After incubation, samples were filtered onto 0.45-μm Millipore filters, decontaminated with 0.5 ml of 0.5 N HCL for 4–6 h, placed in scintillation vials with scintillation cocktail, and counted with a liquid scintillation counter. Time-zero blanks were taken and subtracted from all light values. Total carbon dioxide was determined from alkalinity and pH measurements.

Photosynthetic rates, normalized to chlorophyll *a*, were used to construct a photosynthesis–irradiance (PE) curve using the methods outlined in Fahnenstiel et al., (1989). Two parameters were determined from this model: $P_{max}$, maximum photosynthetic rate at light saturation and alpha, initial linear slope at low irradiances. A third parameter, the photoinhibition parameter beta, was not included in our analysis because <10% of our experiments produced a significant value for this parameter when a three-parameter model was used. Moreover, to evaluate the effect of photoinhibition on Great Lakes phytoplankton, experiments with ultra-violet irradiance are needed (Marwood et al., 2000), and this was not done in our experiments.

Integral daily areal primary production (mg C/m$^2$/d) was determined using the Great Lakes Production Model-GLPM (Lang and Fahnenstiel, 1995), which is based on the model of Fee (1973). This model accounts for diel variations in surface irradiance, and depth variations in photosynthetic–irradiance parameters ($P_{max}$ and alpha), chlorophyll *a* concentrations, and the light extinction coefficient to estimate daily integrated primary production. This model has been used extensively by the authors to measure areal integrated water column phytoplankton production in the Great Lakes (e.g., Fahnenstiel and Scavia, 1987a; Fahnenstiel et al., 1995, 2000, 2010). Values for areal integrated production were calculated for each day of field sampling as

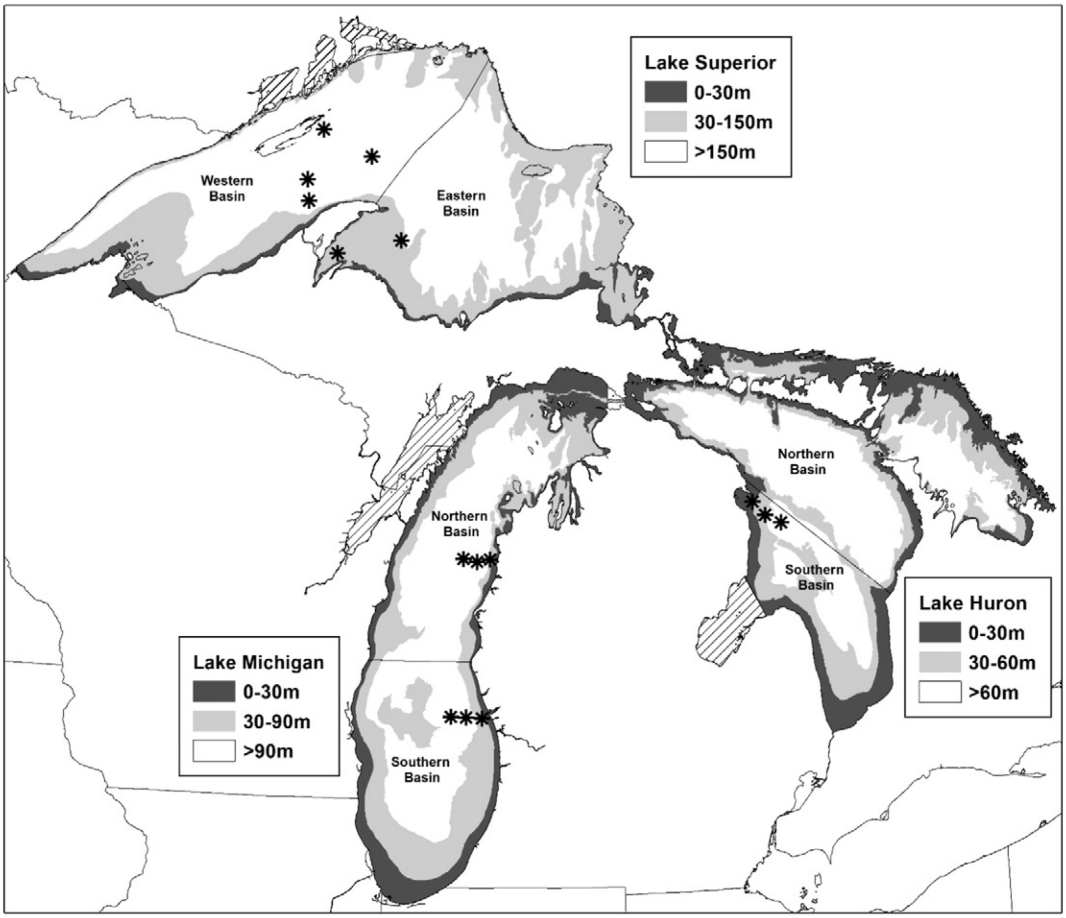

**Fig. 1.** Map of areas analyzed for phytoplankton production and biomass in lakes Huron, Michigan, and Superior. Hatched areas indicate areas not included in the analysis. Depth zones are indicated as follows: deep (white), mid (light gray), and shallow (darker gray)—see text for specific depth zones in each lake. Each lake was split into two regions indicated by the solid line. Asterisks indicate sampling stations.

well as for near coincident days (+1 day). These GLPM estimates with field measurements were only used to validate the new GLPM estimates which utilized remote sensing and empirically derived input values.

### *Remote sensing*

For remotely sensed data, our analysis used MODIS Aqua satellite imagery obtained from the NASA Ocean Biology Processing Group (OBPG) (http://oceancolor.gsfc.nasa.gov/cms/). Images were processed by the OBPG to level 2 using the standard atmospheric correction procedure (Gordon and Wang, 1994). Images were identified that intersected any part of each target's (Lake Michigan, Lake Huron, and Lake Superior) bounding box. This identified 2737 images intersecting Lake Michigan, 2718 for Lake Huron, and 2919 for Lake Superior for the MODIS Aqua mission period from January 1, 2010, to December 31, 2013. Each identified image was ordered from the OBPG subset to its respective bounding box to reduce file size.

Every image (8374) was processed by the Color-Producing Agent Algorithm (CPA-A) described by Shuchman et al., (2013a) to produce retrievals of chlorophyll *a*, suspended mineral concentrations, and CDOM absorption using remote sensing reflectance (Rrs) at MODIS bands 443, 490, 532, 547, and 667 nm. The 412 nm band was not used in CPA-A processing due to the high frequency of negative reflectance values after atmospheric correction. NASA Level 2 processing flags were used to create a mask to exclude pixels with low radiometric fidelity. The flags used were LAND (Pixel over land), HISATZEN (high-sensor view zenith angle), STRAYLIGHT (Straylight contamination is likely), and CLDICE (probable cloud or ice contamination).

On some occasions, multiple (up to three) MODIS Aqua overpasses exist for a single day due to the slight overlapping of neighboring swaths. CPA-A retrieval (chlorophyll *a*, suspended minerals, and CDOM) images were averaged where pixels overlap within a given day to produce daily CPA-A retrieval outputs.

Due to the presence of apparent outliers in several of the monthly mean chlorophyll *a* retrieval images particularly in the winter months (December–February), statistical rejection of outlier chlorophyll *a* values was applied using two filters. The first filter was used to reject all chlorophyll *a* values $<0.15$ mg/m$^3$ as this value is significantly lower than normal offshore chlorophyll values for lakes Huron and Michigan (EPA Surveillance/GLENDA data base, $p < 0.05$). April through September were identified as months where the standard deviation of chlorophyll *a* concentrations in the offshore zones(>mean depth) was low (<25% of the mean). For the second filter, chlorophyll *a* concentration values $\pm 7$ standard deviations from the computed means were rejected as statistical outliers. Because the lower threshold for this filter was below zero, it only affected high values. This statistical rejection scheme with the two filters resulted in the removal of 8% of pixels in Lake Superior, 4% in Lake Huron, and 7% in Lake Michigan. Mean monthly chlorophyll images were then recomputed with the remaining pixels after statistical rejection and monthly chlorophyll values from each year were analyzed. Great Lakes Surface Environmental Analysis (GLSEA) (Schwab et al., 1999) version 2 data set was used to generate monthly mean lake surface temperature geolocated grids with 2 by 2 km spatial resolution.

Underwater irradiance and photic zone depth were calculated from remotely sensed imagery. For this analysis, the diffuse attenuation coefficient at 490 nm, $Kd_{490}$, was estimated using a derivation of an approach proposed by Lee et al., (2005). This approach computes Kd at a given wavelength (490 nm in this case) as a function of bulk absorption, *a*, and bulk backscatter, $b_b$, and solar zenith angle. Both *a* and $b_b$ are dependent on CPA concentrations and can therefore be retrieved using the CPA-A. Both *a* and $b_b$ at 490 nm were retrieved for each daily CPA-A retrieval. The monthly mean images of *a* and $b_b$ were then computed for each lake. The derived hourly $Kd_{490}$ values were empirically converted to $Kd_{PAR}$ (400–700 nm) following the methods described by Saulquin et al. (2013). Hourly solar zenith angle was determined as a function of Julian date and latitude (Iqbal, 1983), which for this analysis was defined as the latitude at the geometric center of each Lake. The underwater PAR irradiance distribution in the photic zone (1% light level) was derived hourly (Lee et al., 2005).

The GLPM (Lang and Fahnenstiel, 1995) was used to estimate phytoplankton production with remotely sensed and empirically derived inputs. This approach is an improvement from Shuchman et al. (2013b) in that all parameters were directly estimated from remotely sensing or empirical relationships determined specifically from Great Lakes data (no mean or average values were used as model input), and a more thorough analysis was conducted. Incident irradiance, underwater irradiance, and chlorophyll concentrations were estimated directly from remotely sensed products. $P_{max}$ and alpha values were estimated from empirical relationships between measured values and temperature or month. The NOAA National Centers for Environmental Prediction (NCEP) Climate Forecast System version 2 (CFSv2) (Saha et al., 2014) incoming shortwave radiation flux product was used to estimate hourly PAR irradiance for every day in analysis period (January 1, 2010–December 31, 2013). Shortwave radiation (UV–VIS–NIR) flux was converted to PAR flux (VIS) using a conversion factor of 0.368 (McCree, 1981). PAR flux ($W/m^2$) was converted to photon flux ($E/m^2/s$) using a conversion factor of 4.56. Hourly PAR grids were generated with spatial resolution of 30 by 60 km. $Kd_{PAR}$ throughout the water column (1 m interval) was calculated as described above. For the GLPM, hourly production was calculated for each pixel through the photic zone using 1 m depth intervals assuming vertically uniform chlorophyll and $Kd_{PAR}$ values. When the calculated photic depth exceeded the water depth determined from NOAA bathymetric data, production was calculated only to bottom depth.

The GLPM was used to estimate phytoplankton areal integrated production on a pixel-by-pixel basis (1 km grid). On some clear days, over 80,000 pixels were analyzed for Lake Superior and over 50,000 for lakes Michigan and Huron. For each pixel, hourly values of incident irradiance, underwater irradiance attenuation coefficient (averaged over month), daily values of chlorophyll (averaged over month) and $P_{max}$ (from surface GLSEA temperature) and monthly values of alpha were used to calculate daily areal integrated primary productivity ($mg\ C/m^2/d$) for every day of the month. Daily production values for each pixel within a given month were averaged to provide monthly values of production. These monthly values were used to calculate mean production. During winter conditions partial lake-wide production estimates were produced because no satellite observations were possible through ice. Finally, because of recent similarities in $Kd_{PAR}$ and photic zone depths in the Upper Great Lakes (Barbiero et al., 2012), trends in volumetric production across the lakes would be similar to those of areal production.

To evaluate our new GLPM production estimates that used remotely sensed and empirically derived parameters to the more traditional approach that utilized field measurements (described in field methods section) as input, we compared both GLPM estimates from near coincident days (±1 day) of the field sampling dates. The same approach was used for comparisons of field measured and remotely estimated measures of chlorophyll *a* concentration. This one day window was used because many field observations were collected in the evening and ±1 day allowed for more comparisons between estimates. Finally, for comparisons between field and remotely sensed input variables, remotely sensed input values (chlorophyll, Kd, and irradiance) were determined in a 3 × 3 km grid around the sampling stations.

This new GLPM calculates phytoplankton primary production assuming vertically uniform phytoplankton abundance equal to the near-surface chlorophyll concentration determined from remote sensing (<1 optical depth or approximately 8–10 m). However, high concentrations of phytoplankton and chlorophyll concentrations can be found well below the surface in a deep chlorophyll layer (DCL) during thermal stratification in the Upper Great Lakes (Fahnenstiel and Glime, 1983; Fahnenstiel and Scavia, 1987b; Barbiero and Tuchman, 2004). To evaluate the effect of this DCL on our production estimates, we calculated primary production with the standard GLPM using a vertically uniform concentration of chlorophyll and photosynthetic parameters to a GLPM that utilizes the actual vertical distribution of chlorophyll in the Upper Great Lakes and a vertical variation in photosynthetic parameters (surface mixed layer and DCL values). Twenty-three vertical profiles of chlorophyll from 2010 to 2013 were used to construct an average vertical chlorophyll profile for the summer stratification period for each lake (June–August, lakes Huron and Michigan; July–September, Lake Superior) and these profiles were used with photosynthetic parameters from the surface mixed layer and DCL to estimate phytoplankton production. Because the DCL can vary by depth, we compared these two production estimates (vertically uniform and vertically stratified DCL) for each specific depth region (described below). In the mid-depth zone (LM >30–90 m, LH >30–60 m, LS >30–150 m), we calculated the percent difference between these two estimates for every segment of the depth region at 10 m depth intervals (e.g., Lake Michigan, 30, 40, 50, 60, 70, 80, and 90 m). In the deep region of each lake (LM >90 m, LH >60 m, and LS >150 m), only one comparison was made because the DCL was relatively consistent at the deep stations, and in the shallow water region (<30 m) no correction was made as the DCL was not found at these depths.

Because the number of useable remote sensing images varied throughout year (highest in summer and lowest in late fall/winter) and to eliminate the bias associated with our sampling frequency (daily), monthly mean values (chlorophyll and production) determined from the daily values were used for analyses. Monthly production data were log transformed to meet assumptions for parametric statistics. Simple parametric statistics were used to analyze means among regions, depth zones, lakes, or year using analysis of variance (ANOVA) with Tukey–Kramer post-hoc test (Zar, 2009). An alpha value of 0.05 was used for statistical significance in all tests. Each lake was partitioned into regional (2) and depth (3) zones based on mean depth and previous scientific studies (Fig. 1). For Lake Michigan, the regions were north and south and the depth zones were shallow (0–30 m), mid (>30–90 m), and deep (>90 m)(Nalepa et al., 2010; Yousef et al., 2014). For Lake Huron, the regions were north and south and the depth zones were shallow (0–30 m), mid (>30–60 m), and deep (>60 m) (Nalepa et al., 2007). Lake Superior was divided into west and east regions and shallow (0–30 m), mid (>30–150 m), and deep (>150 m) zones (Sierszen et al., 2011). In each lake, there were bays with complex optical properties (high chlorophyll concentrations and/or turbidity) and/or shoreline problems that were excluded from our analysis (Fig. 1). For Lake Superior, these areas were Thunder, Nipigon, and Black Bay. In Lake Huron, Saginaw Bay was excluded, and in Lake Michigan, Green Bay was excluded.

## Results

In order to estimate photosynthetic rate with the GLPM, two parameters that were not estimated by remote sensing were needed to determine production rates. These two parameters, $P_{max}$ and alpha, were estimated from empirical relationships. For the Upper Great Lakes, a strong relationship was noted between $P_{max}$ and sea surface temperature from GLSEA (Fig. 2a) and this relationship was used to estimate $P_{max}$ for the GLPM using GLSEA surface temperatures. For alpha values, a significant sine relationship was noted for alpha values by months

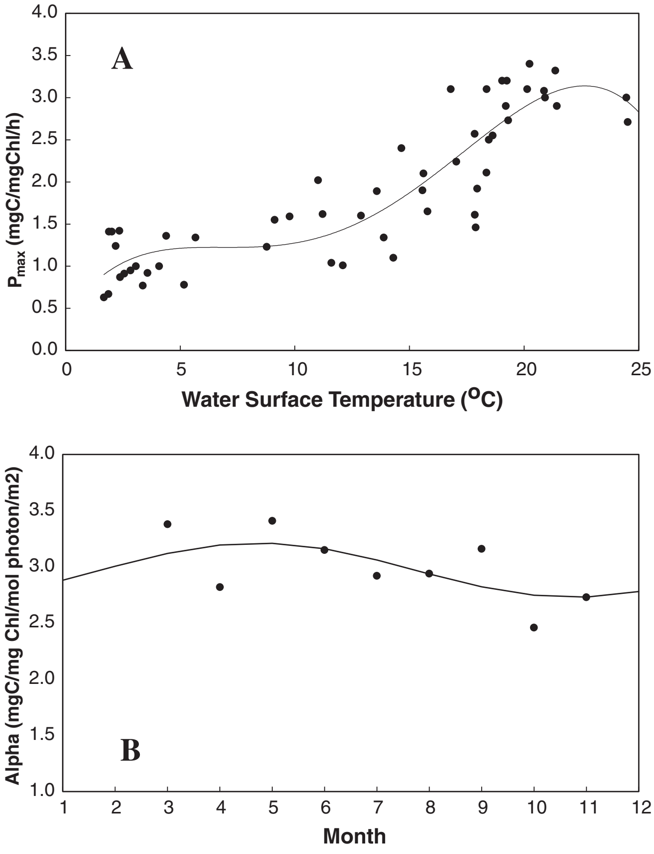

**Fig. 2.** A) Maximum photosynthetic rate ($P_{max}$) vs. surface temperature from lakes Michigan, Huron, and Superior in 2010–2013 ($y = -0.00009x^4 + 0.0044x^3 - 0.0651x^2 + 0.3845X + 0.4209$, $R^2 = 0.8$, $p < 0.01$). B) Initial linear slope (alpha) vs. month from lakes Michigan, Huron, and Superior in 2010–2013 (y = SIN ((Month − 1.73)/1.909)* 4.139 + 2.97; $R^2 = 0.41$, $p < 0.01$).

with data from the Upper Great Lakes (Fig. 2b). These monthly mean alpha values were used as input for the GLPM.

Chlorophyll *a* concentrations were used as an estimate of phytoplankton biomass and as input for the GLPM. CPA-derived satellite chlorophyll *a* from lakes Huron, Michigan, and Superior agreed well with near surface chlorophyll *a* concentrations from these lakes during the study period (Fig. 3, $y = 0.96\times + 0.04$, $r^2 = 0.83$, $p < 0.001$, $n = 55$). These remotely sensed chlorophyll *a* values were used to determine regional and lake-wide chlorophyll trends in the Upper Great Lakes for the 2010–2013 period.

Mean chlorophyll *a* concentrations from the three lakes were significantly different in 2010–2013 ($F = 19.3$, $p = <0.0001$, $df = 143$). Highest mean chlorophyll for the study period was found in Lake Superior (mean = 0.99 $\text{mg/m}^3$), intermediate mean value in Lake Michigan (mean = 0.88 $\text{mg/m}^3$), and lowest mean value was found in Lake Huron (mean = 0.77 $\text{mg/m}^3$; Fig. 4), and values were significantly different among lakes (LS vs LM, md = 0.12, p = 0.003, df = 143; LS vs. LH, md 0 = 23, p < 0.001, df = 143; LM vs. LH, md = 0.11, p = 0.008, df = 143). For lakes Huron and Superior, there was not a significant difference between basins (LS, west vs. east, t = −0.62, p = 0.53, df = 94; LH, north vs. south; t = 1.37, p = 0.17, df = 94), but in Lake Michigan, the northern basin values were significantly higher than southern basin values (N = 0.93 $\text{mg/m}^3$, S = 0.81 $\text{mg/m}^3$; t = 2.68, p = 0.009, df = 94).

Mean chlorophyll *a* values for the deep zone (>mean depth for each lake) were significantly different among lakes (F = 17.1, p < 0.0001, df = 143), with Lake Huron values (mean = 0.72 $\text{mg/m}^3$) significantly lower than lakes Michigan (mean = 0.90 $\text{mg/m}^3$; md = −0.17, p < 0.0001, df = 143) and Superior (mean = 0.94 $\text{mg/m}^{3;}$;

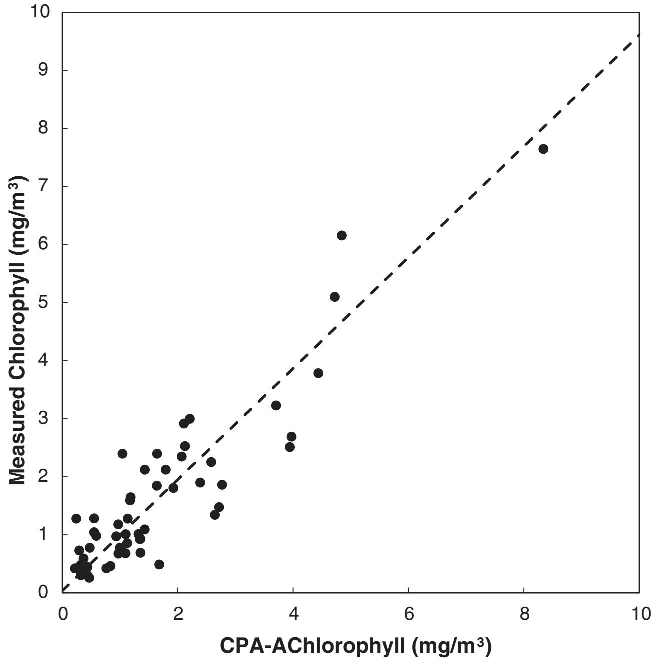

**Fig. 3.** Satellite (CPA)-derived chlorophyll concentrations ($\text{mg/m}^3$) vs. surface-mixed layer (5–10 m) chlorophyll a concentrations ($\text{mg/m}^3$) from lakes Huron, Michigan, and Superior (Type 2 Regression: $R^2 = 0.83$, $y = 0.96 + 0.04$, $p < 0.001$, $n = 55$).

md = −0.22, p < 0.0001, df = 143; Fig. 4). Mean values for lakes Michigan and Superior were not significantly different (md = −0.044, p = 0.50, df = 143). For the mid-depth zone (>30 to mean depth) in each lake, highly significant differences were noted (F = 30.6, p < 0.0001, df = 143) with Lake Superior mean value (mean = 1.06 $\text{mg/m}^3$) greater than both lakes Michigan (mean = 0.86 $\text{mg/m}^3$; md = 0.21, p < 0.0001, df = 143) and Huron (mean = 0.79 $\text{mg/m}^3$; md = 0.27, p < 0.0001, df 143). Mean values for lakes Michigan and Huron were not significantly different (md = 0.07, p = 0.17, df = 143). Similar differences were found in the shallow depth region (0–30 m; F = 121, p < 0.0001, df = 143) where the Lake Superior mean value (mean = 1.57 $\text{mg/m}^3$) was significantly different than lakes Michigan (mean = 0.91 $\text{mg/m}^3$; md = 0.74, p < 0.0001, df = 143) and Huron values (mean = 0.83 $\text{mg/m}^3$; md = 0.66, p < 0.0001, df = 143) which were not significantly different from each other (md = 0.08, p = 0.28, df = 143).

For Lake Superior, highly significant differences were noted for mean chlorophyll *a* values in all depth zones (F = 82, p < 0.0001, df = 143;

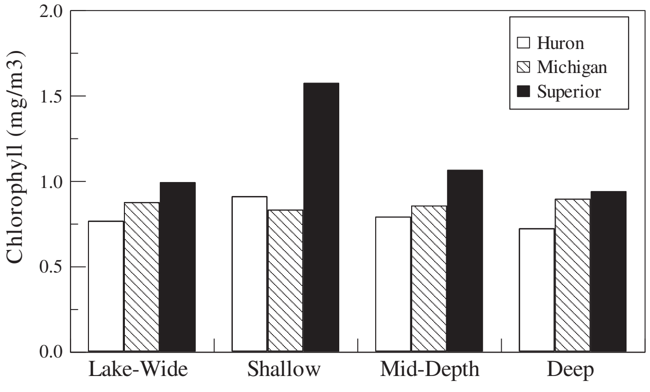

**Fig. 4.** Mean chlorophyll concentrations ($\text{mg/m}^3$) for the entire lake (lake-wide) and for each depth zone (shallow, mid, and deep—see text for specific depths) in lakes Superior, Huron, and Michigan.

Fig. 4). The shallow depth zone value was significantly different than mid and deep-water values (S vs. M, md = 0.51, $p < 0.0001$, df = 143; S vs D, md = 0.63, $p < 0.0001$, df = 143) and the mid zone value was different from the deep-water value (md = 0.12, p = 0.04, df = 143). For Lake Huron, the shallow-depth zone (<30 m) was significantly different from the mid-depth and deep-water regions (S vs M, md = 0.12, p = 0.002, df = 143; S vs D, md = 0.19, $p < 0.0001$, df = 143), but the mid-depth and deep zones were not significantly different from each other (md = 0.07, p = 0.14, df = 143). For Lake Michigan, there were no significant differences among depth zones (F = 1.2, p = 0.28, df = 143).

GLPM results using remotely sensed (incident and underwater PAR and chlorophyll) and empirically estimated ($P_{max}$ and alpha) parameters agreed well with GLPM results using field measured parameters from the Upper Great Lakes in 2010–2013 (Fig. 5, $y = 0.98x - 86$, $R^2 = 0.76$, $p < 0.0001$, n = 25). Removing the one high value still yielded a significant regression with relatively similar slope and intercept ($y = 0.92x - 66$, $R^2 = 0.44$, p = 0.004, n = 24). Thus, this approach using remotely sensed and empirically derived parameters in the GLPM can be used to provide accurate estimates of phytoplankton production in the Upper Great Lakes. For all subsequent analysis, phytoplankton production was estimated using this new approach in the 2010–2013 period.

Mean lake-wide production among the three lakes was relatively similar in 2010–2013 (F = 0.9, p = 0.4, df = 143; LS = 228 mg C/m$^2$/d, LH = 216 mg C/m$^2$/d, LM = 259 mg C/m$^2$/d; Fig. 6). There was no significant difference among years for all three lakes (LS, F = 0.59, p = 0.62, df = 47; LH, F = 0.41, p = 0.75, df = 47; LM, F = 0.48, p = 0.70, df = 47). Within each lake, production values were not significantly different among basins (LS-W vs E, t = 0.08, p = 0.93, df = 94; LH-N vs S, t = −0.03, p = 0.98, df = 94; LM-N vs S, t = 0.26, p = 0.8, df = 94). Also, all depth zones production values were similar across lakes (Shallow, F = 1.5, p = 0.22, df = 143; Mid, F = 0.9, p = 0.41, df = 143; Deep, F = 1.2, p = 0.31, df = 143; Fig. 6). For the shallow-water region (0–30 m), phytoplankton production was 183 mg C/m$^2$/d for Superior, 154 mg C/m$^2$/d for Huron, and 168 mg C/m$^2$/d for Michigan. For the mid-depth region (>30 m to mean depth) phytoplankton production was similar among all three lakes (LS = 222 mg C/m$^2$/d, LH = 215 mg C/m$^2$/d, LM = 257 mg C/m$^2$/d). Finally, for the deep-water region (> mean depth) similar values were found for all lakes (LS = 231 mg C/m$^2$/d, LH = 229 mg C/m$^2$/d, LM = 278 mg C/m$^2$/d). Within lakes Huron and Michigan there were notable differences among depths (LH, F = 6.2, p = 0.002, df = 143; LM, F = 10.6, $p < 0.0001$, df = 143). For lakes Huron and Michigan production in the shallow-water region was lower than that in the mid-depth and deep regions (Lake Huron S vs M, md = −0.16, p = 0.014, df = 143; S vs. D, md = −0.18, p = 0.003, df = 143: Lake Michigan S vs M, md = −0.22, p = 0.006, df = 143; S vs. D, −0.25, $p < 0.0001$, df = 143), but the mid-depth and deep regions had similar production (Lake Huron, md = −0.02, p = 0.91, df = 143; Lake Michigan, md = −0.03, p = 0.84, df = 143). However, in Lake Superior all depth regions exhibited similar production (F = 2.1, p = 0.13, df = 143).

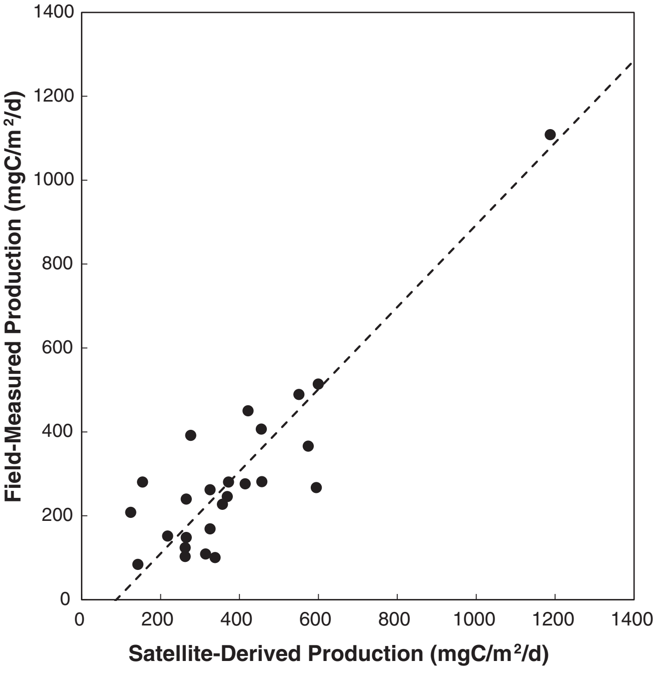

**Fig. 5.** Great Lakes Production Model output using measured parameters (field) vs. remotely sensed and empirically derived parameters (type II regression model $y = 0.98X - 86$, R2 = 0.76, $p < 0.001$, n = 25). Comparisons were limited to ±1 day of field sampling.

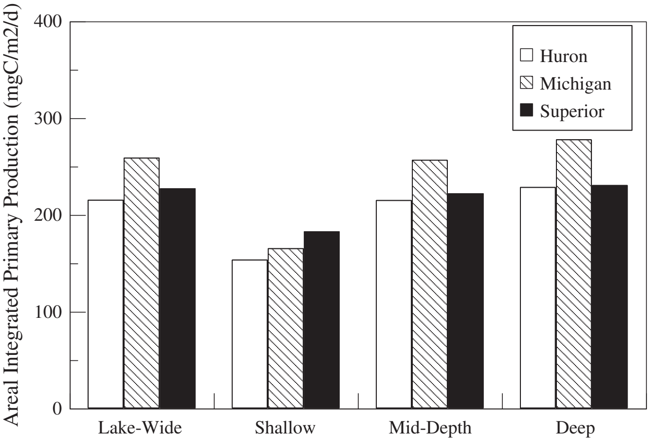

**Fig. 6.** Mean areal integrated phytoplankton production (mg C/m$^2$/d) for the entire lake (lake-wide) and for each depth zone (shallow, mid, and deep—see text for specific depths) in lakes Superior, Huron, and Michigan.

The summer is an interesting period to examine for annual trends because it is the period of greatest number of observations (most clear images) and of peak annual production (Parkos et al., 1969; Watson et al., 1975; Fahnenstiel et al., 1989). Production was calculated for both calendar (June–August) and meteorological summer (surface temperatures >10 °C) using daily production values (Fig. 7). The period of meteorological summer varied among lakes with the longest period for Lake Michigan (meteorological; mean = 163 days, range 151–177) and the shortest period for Lake Superior (meteorological; mean = 113 days, range = 101–128). Lake Huron (meteorological; mean = 157 days, range = 145–174) was more similar to Lake Michigan than to Lake Superior. Summer production differences were noted among lakes and years for both meteorological (F = 21.8, $p < 0.0001$, df = 1739) and calendar (F = 72.7, $p < 0.0001$, df = 1103) summers (Fig. 7). For meteorological summer, lowest value was found in Lake Huron (331 mg C/m$^{2}\cdot$d) with Lake Superior (359 mg C/m$^{2}\cdot$d) intermediate and Lake Michigan greatest (399 mg C/m$^{2}\cdot$d) and all mean values were significantly different (LS vs. LH, md = −.03, p = 0.02, df = 1739; LS vs. LM, md = 0.04, p = 0.003; LH vs. LM, md = −0.08, $p < 0.0001$, df = 1739). For calendar summer, the same pattern was found but the Lake Huron value (401 mg C/m$^{2}\cdot$d) was not significantly different from Lake Superior (mean = 417 mg C/m$^2$/d; md = −0.015, p = 0.17, df = 1103) and values from lakes Huron and Superior were significantly different from Lake Michigan (LM mean = 499 mg C/m$^2$/d; LH vs. LM, md = −0.09, $p < 0.0001$, df = 1103; LS vs. LM, md = 0.08, $p < 0.0001$, df = 1103). Lake Superior exhibited a greater range of meteorological summer production values (257–466 mg C/m$^2$/d) than lakes Huron (287–350 mg C/m$^2$/d) and Michigan (311–

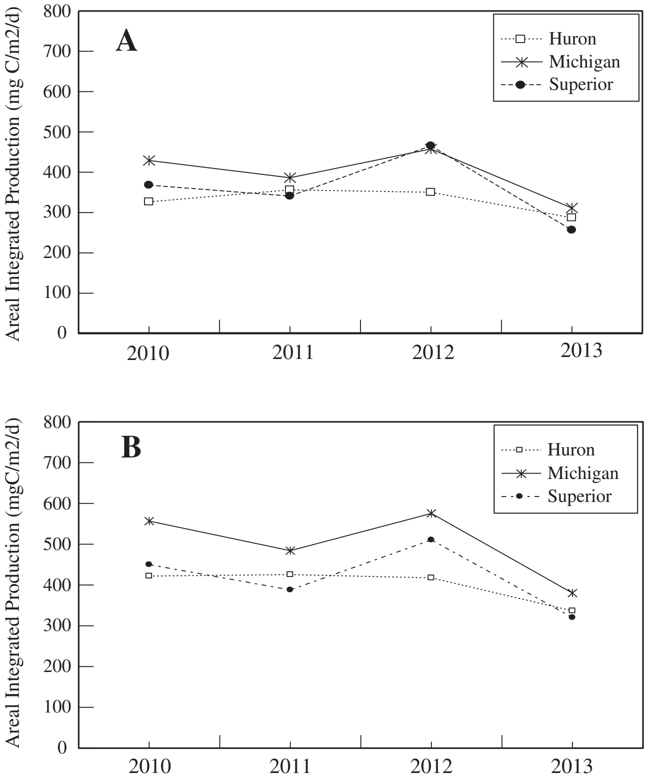

**Fig. 7.** Mean summer primary production (mg C/m$^2$/d) for lakes Superior, Huron, and Michigan during a) meteorological summer (surface temperatures >10 °C) and b) calendar summer (June–August).

458 mg C/m$^2$/d). In all three lakes, calendar and meteorological summer production values varied by year (LS, calendar, $F = 77$, $p < 0.0001$, $df = 367$, meterological, $F = 43$, $p < 0.0001$, $df = 451$; LH, calendar, $F = 20$, $p < 0.0001$, $df = 367$, meteorological, $F = 6.6$, $p = 0.0002$ $df = 636$; LM, calendar, $F = 82$, $p < 0.0001$, $df = 367$, meteorological, $F = 21$, $p < 0.0001$, $df = 650$). For all three lakes, the highest meteorological production values were found in 2012 and lowest in 2013. In Lake Superior, highest production values (both meteorological and calendar) were found in 2012 (257 and 320 mg C/m$^2$/d, respectively) and lowest values in 2013 (466 and 509 mg C/m$^2$/d, respectively), and values from both years were different from all other years (all $p < 0.0001$, $df = 451$ and 367).

Finally, a comparison of GLPM estimates with vertically uniform chlorophyll and photosynthetic parameters to GLPM estimates with vertically stratified chlorophyll (DCL) and photosynthetic parameters suggests that our new production estimates may underestimate actual primary production during thermal stratification depending on depth and lake. Using vertically stratified chlorophyll and photosynthetic parameters would increase summer production in the mid-depth region by 14% in Lake Superior, by 13% in Lake Huron, and by 15% in Lake Michigan. In the deep-water regions, using vertically stratified chlorophyll and photosynthetic parameters would increase summer production by 14, 19, and 17% in lakes Superior, Huron, and Michigan, respectively.

## Discussion

The usefulness of remotely sensed and empirically derived parameters as input for estimating phytoplankton production with the GLPM was demonstrated in this study. Previous investigators have found similar good agreement between remotely sensed and field-based estimates (Lohrenz et al., 2008; Shuchman et al., 2013b), but our use of both remotely sensed and empirically derived parameters for the GLPM will provide for more accuracy in estimating primary production in most regions of the Upper Great Lakes. Because of the high resolution of MODIS imagery (1 km spatial and 1 day temporal) and the application of our new approach, the ability to estimate and understand phytoplankton production in the Great Lakes should increase in the near future. In this study, the new approach provided many new insights into our understanding of phytoplankton dynamics in the Great Lakes and whole-lake estimates of phytoplankton production.

The similarity in mean annual phytoplankton production among lakes Michigan, Huron, and Superior in 2010–2013 was an important finding of this study. Phytoplankton production in the Upper Great Lakes ranged from 216 mg C/m$^2$/d in Lake Huron to 259 mg C/m$^2$/d in Lake Michigan with no significant differences found among lakes. The lakes have changed significantly in the last 15 years, and one cannot assume that prior trophic and limnological relationships still exist in these lakes. The similarity of phytoplankton production among the Upper Lakes observed in 2010–2013 was not observed by investigators studying the lakes in the 1960/70s. During this period, large differences in phytoplankton production were noted among lakes when utilizing relatively similar techniques. Parkos et al. (1969) noted that Lake Michigan annual primary production was approximately 2X Lake Superior production, and Lake Huron was 1.3X Lake Superior in 1967–1968. Similarly, for Lake Michigan, Fee (1973) noted annual production of 331–670 mg C/m$^2$/d in 1970/1971 whereas phytoplankton production in Lake Superior was approximately 190 mg C/m$^2$/d in the 1960s (Olson and Odlaug, 1966). In a review of primary production rates in the Great Lakes prior to 1974, Vollenweider et al. (1974) estimated annual primary production in Lake Superior as 50 g C/m$^2$/y, Lake Huron as 80–90 g C/m$^2$/y, and Lake Michigan as 140–150 g C/m$^2$/y. Watson et al. (1975) estimated the annual rate of primary productivity of Lake Superior to be 30 g C/m$^2$/y.

The similarity in areal rates of primary production in the three Upper Great Lakes noted in this study is consistent with the recent convergence of diatom production and related water quality parameters in the Upper Great Lakes. Mida et al. (2010) noted large decreases in phosphorus and chlorophyll *a* concentrations in Lake Michigan, and a similarity between recent Lake Michigan and Lake Superior values. Evans et al. (2011) noted large decreases in diatom production (silica utilization) in lakes Michigan and Huron after 2000 and the similarity to utilization rates in Lake Superior. Finally, Barbiero et al. (2012) noted the convergence of spring total P, water column transparency, and chlorophyll concentrations in lakes Superior, Huron, and Michigan in the early/mid 2000s.

Because primary production is strongly related to phytoplankton biomass (Fahnenstiel et al., 1989; Fahnenstiel et al., 2010), it is not surprising that lake-wide chlorophyll *a* concentrations in lakes Michigan and Huron also decreased compared to the 1960s and 1970s, but the extent of the decrease is surprising. In a review of phytoplankton biomass concentrations in the Great Lakes prior to 1974, Vollenweider et al. (1974) reported that Lakes Huron chlorophyll concentrations averaged 2.0 mg/m$^3$ and Lake Michigan averaged 2–3 mg/m$^3$ whereas Lake Superior concentrations were <1 mg/m$^3$. Watson et al. (1975) reported a mean annual chlorophyll concentration for Lake Superior of 1.1 mg/m$^3$. In the 2010–2013 period, Lake Superior chlorophyll *a* concentrations were similar to historical values (mean = 0.99 mg/m$^3$) but lakes Huron and Michigan chlorophyll values had declined to values significantly lower than Lake Superior. The Lake Huron mean value was 0.77 mg/m$^3$ and the Lake Michigan was 0.88 mg/m$^3$. These decreases are remarkable in that they represent a reduction over 50% from historical chlorophyll *a* values and in 2010–2013 the mean chlorophyll concentrations in lakes Huron and Michigan were significantly lower than in Lake Superior.

The cause of these large recent decreases in phytoplankton productivity and abundance in lakes Michigan and Huron is most likely filtering activities of invasive dreissenid mussels (Fahnenstiel et al., 2010; Mida et al., 2010; Kerfoot et al., 2010; Vanderploeg et al., 2010; Evans et al., 2011; Yousef et al., 2014; Rowe et al. in press) although other factors (phosphorus, climate change) may play a role (Warner and Lesht, 2015). The results from this study are consistent with the role of dreissenid mussels in causing recent changes in phytoplankton abundance in lakes Michigan and Huron. Not only did lakes Michigan and Huron exhibit large decreases in 2010–2013 consistent with large densities of mussels (Nalepa et al., 2010; T. Nalepa, pers.comm.), but in Lake Superior, where mussel populations are extremely low/absent (Grigorovich et al., 2008), no changes were noted in phytoplankton abundance from the 1960/1970s to the 2010/2013 period.

Another interesting change likely attributable to filtering activities of mussels is the relationship between nearshore (shallow zone) and offshore (deep zone) phytoplankton abundance and production in 2010–2013. Previously, higher phytoplankton abundance and production were noted in the nearshore region and it decreased in the offshore region (Schelske and Callender, 1970; Fee, 1973; Glooschenko and Moore, 1973; Rousar, 1973; Watson et al., 1975; Nalewajko and Voltolina, 1986). In 2010–2013, chlorophyll *a* concentrations were similar across all depth zones in Lake Michigan (mean zones = 0.83–90 mg/m$^3$) and only slightly increased in the shallow zone (0.91 mg/m$^3$) of Lake Huron as compared to mid-depth (0.79 mg/m$^3$) and deep-water (0.72 mg/m$^3$) zones. As expected, the non-mussel impacted Lake Superior exhibited a historically consistent significant gradient in phytoplankton abundance with highest chlorophyll concentrations found in the shallow zone (1.57 mg/m$^3$) and lowest in the deep zone (0.94 mg/m$^3$). The most surprising recent change in the shallow zone/nearshore regions of lakes Michigan and Huron was lower rates of primary production. In both lakes, primary production in the nearshore zone (0–30 m) in 2010–2013 is lower than in the offshore (deep) region by 33–40%. These results are particularly noteworthy when you compare them to those of Fee (1973). Fee's results are most comparable to ours because he used a similar mechanistic model for estimating primary production and he conducted year-round, cross-lake cruises which included both inshore and offshore stations in Lake Michigan. Fee sampled five stations: two nearshore (depths 20–25 m) and three offshore stations. His nearshore stations would be part of our shallow zone and his offshore stations would be in our deep-water zone. Primary production at Fee's nearshore stations was 62% higher than production at his offshore stations. This is a complete reversal of the pattern we observed in 2010–2013 and suggests that the nearshore region has exhibited much larger relative decreases in primary production in 2010–2013 than the offshore regions, and these changes are likely to influence ecological distributions of other organisms in that region as well (Turschak et al., 2014).

The larger decreases in shallow water/nearshore production in lakes Michigan and Huron are not only due to decreases in phytoplankton abundance but also to the increased photic zone now intersecting a greater portion of the bottom. Recent increases in light penetration have been noted in Lake Michigan and Lake Huron (Barbiero et al., 2009a, 2009b; Kerfoot et al., 2010; Yousef et al., 2014). With these increases in light penetration, the mean photic zone in the spring in Lake Michigan now exceeds the maximum depth of our shallow water zone (30 m) (Yousef et al., 2014), and the bottom can limit the depth of primary production in this zone (depth < photic zone). If we use our mean monthly $Kd_{PAR}$ values for the shallow zone and calculate primary production with and without bottom, the bottom effect can be determined. In Lake Michigan, consideration of the bottom reduces water column production by 28% in the shallow zone. This decrease is approximately 20% greater than would have been observed in 2002 (Yousef et al., 2014). However, with this increase in light at the bottom, benthic algae abundance and production may increase and significantly alter the ratio of pelagic:benthic algal production (Fahnenstiel et al., 1995).

Climate change may also affect phytoplankton production in the Upper Great Lakes (Warner and Lesht, 2015). Our results suggest that meteorology influenced areal integrated production in 2010–2013, which can be illustrated by the large variability noted in summer (both calendar and meteorological, >10 °C) production values. In the 4 years of our investigation, summer production in Lake Superior varied from 257 to 466 mg C/m$^2$/d for meteorological summer and from 320 to 510 mg C/m$^2$/d for calendar summer. Lowest values were found in 2013 and highest values in 2012. The length of both summers were not different (meteorological summer 113 vs. 110 days), but the temperatures for both meteorological and calendar summer were different. The lowest mean temperatures for meteorological and calendar summer were found in 2013 at 13.2 and 10.5 °C, respectively. On the other hand, the highest mean temperatures found for meteorological and calendar summer were in 2012 at 16.3 and 15.3 °C, respectively. Thus, in Lake Superior, which exhibits a relatively short period of summer stratification, summer production is sensitive to changes in mean summer temperature. Because Lake Superior has been affected by climate change (McCormick and Fahnenstiel, 1999; Austin and Coleman, 2007), large changes in summer temperatures will likely have profound impacts on summer phytoplankton production, and as a result overall biological production of the lake, as a disproportionate amount of primary and secondary production occurs during summer stratification (Watson et al., 1975; Watson and Wilson, 1978).

Finally, one of the more interesting aspects of this study is our ability to provide annual lake-wide estimates of phytoplankton production for the Upper Great Lakes based on the same approach. Because our primary production estimates were based on >2 million observations in lakes Michigan and Huron and >3 million observations in Lake Superior during all 12 months in 2010–2013, one might be inclined to believe they are accurate estimates of lake-wide phytoplankton production. While our estimates are unprecedented in terms of spatial and temporal observations within a given year, without a few additional corrections, our estimates are biased. We estimated particulate carbon fixation for ice-free regions of the Great Lakes assuming vertically uniform phytoplankton biomass and excluding select bays.

To provide truly lake-wide estimates of total phytoplankton production or whole-lake carbon fixation rates, we need to apply a few minor corrections to our estimates. First, we need to estimate primary production for the excluded bays (Fig. 1). Using the GLPM to determine preliminary production in the excluded bays and including these preliminary production estimates would increase production in each of the Upper Great Lakes, but the increases would be <5%. Second, during the summer, large deep chlorophyll layers (DCL) are found in the Upper Great Lakes (Fahnenstiel and Scavia, 1987b; Barbiero and Tuchman, 2004) and these layers can be responsible for significant primary production (Fahnenstiel and Scavia, 1987b). Correcting our annual production estimates for the DCL would increase annual production by 6–8%. Third, the effects of ice were not determined in our production estimates. Using the ice-coverage data for the Great Lakes in 2010–2013 (U.S. National Ice Center) and light attenuation determinations based on average Great Lakes ice conditions (December–March period, G. Leshkevich, pers. comm., R. Shuchman, pers. comm), our model can be used to estimate production under the ice. Consideration of ice reduces production in the Upper Great Lakes during the winter by 15–45% but only 2–5% on an annual basis. Finally, a correction to total carbon fixation which includes both particulate (estimated here) and dissolved components needs to be done. Previous work in Lake Michigan found that dissolved organic production was 11% of particulate production (Laird et al., 1986). In Lake Superior, during 2010–2013, dissolved organic carbon production was 9% of particulate carbon production (range 3–17%, n = 27, G. Fahnenstiel, unpubl. data). A 10% correction was used to correct particulate carbon fixation to total carbon fixation. It should be noted that these are simple corrections, and in particular, more work is needed to determine production in bays where optical properties can be very different from the main lake and our empirical relationships may not be robust, and under the ice where input parameters ($P_{max}$, chlorophyll, and Kd) can vary significantly from those assumed in the open water.

Applying these four corrections and summing primary production for the entire year, results in estimates of total phytoplankton production for the Upper Great Lakes ranging from 15.8 to 22.3 Tg C/y for 2010–2013 (Table 1). Lake Superior had the highest production rates, ranging from 6.4 to 9.5 Tg C/y, whereas Lake Huron had the lowest production rates, 4.4–5.7 Tg C/y. Lake Michigan values were 5.0–7.2 Tg C/y. Our estimates are lower than those of Warner and Lesht (2015) for lakes Michigan and Huron in 1998–2008. Warner and Lesht (2015) values ranged from 7.7 to 11.0 Tg C/y for Lake Huron and 9.5–13.6 Tg C/y for Lake Michigan. These differences might be explained by the different study periods (1998–2008 vs. 2010–2013), but this is unlikely because the range in values from either lake do not overlap for the 15 years of study. A more likely explanation is that results were influenced by the models used. As noted by Warner and Lesht (2015), the choice of primary production model can influence results.

There were notable differences between our approach and that of Warner and Lesht (2015). We used a mechanistic primary production model that used remote-sensing and empiricial relationships determined specifically from Upper Great Lakes phytoplankton communities as input for our model. Hundreds of measurements of phytoplankton abundance and productivity were made in the Upper Great Lakes during this study. Moreover, our model had high spatial (1 km) and temporal resolution (1 h) using every available pixel from every image for the study period (no interpolation). Production was calculated across the entire lake including the nearshore region (<30 m) and considered the effects of ice, vertical distribution of phytoplankton (DCL), and dissolved organic production.

Warner and Lesht (2015) used a global remote sensing model with generic oceanic algorithms to determine input parameters (standard NASA products for chlorophyll, Kd, and PAR; general oceanic for $P^B_{opt}$). These global models with standard input parameters have performed poorly in some environments (Ondrusek et al., 2001; McClain et al., 2002; Marra et al., 2003), and a regionally optimized model with regional inputs may be required to provide adequate results (Ondrusek et al., 2001). Standard oceanic NASA algorithms can perform poorly in Great Lakes (Li et al., 2004; Witter et al., 2009; Shuchman et al., 2013a), often underestimating actual chlorophyll concentrations (Lesht et al., 2013; Shuchman et al., 2013a). For example, the standard ocean NASA SeaWiFS algorithm used by Warner and Lesht (2015) did a poorer job predicting chlorophyll *a* concentrations in lakes Huron and Michigan than the Great Lakes specific algorithm used in this paper to predict chlorophyll *a* concentrations in the Upper Great Lakes (Fig. 8 vs. Fig. 3; $R^2 = 0.5$ vs. $R^2 = 0.8$). Another critical input parameter, the maximum photosynthetic rate ($P_{max}$ or $P^B_{opt}$), is much higher for oceanic phytoplankton than for Upper Great Lakes phytoplankton. $P_{max}$ values for Upper Great Lakes phytoplankton are 1.2 and 3.0 mg C/mg Chl/h at 10 and 20 °C, respectively (Fig. 2a), whereas oceanic values of $P^B_{opt}$ are 2.5 and 3.9 mg C/mg Chl/h at 10 °C and 4.6 and 6.6 mg C/mg Chl/h at 20 °C (Antoine and Morel, 1996, equation “A7”; Behrenfeld and Falkowski, 1997b, Eq. 7). Also, Warner and Lesht (2015) did not consider the effects of ice, vertical distribution of phytoplankton, nor apply their model to the nearshore regions (<30 m). Finally, Warner and Lesht used an automatic mapping or interpolation program (modified GLSEA; Schwab et al., 1999) to create data when no remote sensing observations were available.

Our estimates of whole-lake carbon fixation for Lake Superior can also be compared to recent values and used for determining the lake's carbon budget. Previous total carbon fixation estimates for Lake Superior range from 2 to 10 Tg C/y (Cotner et al., 2004; Urban et al., 2005; Sterner, 2010). Our annual estimates, ranging from 6.4 to 9.5 Tg C/y for 2010–2013, are on the upper end of this range but agree reasonably well with the most recent whole-lake carbon estimate of 9.7 Tg C/y (Sterner, 2010). Sterner (2010) used *in situ* measurements with clean techniques and a statistical model to estimate whole-lake carbon fixation. His slightly higher number is likely due to his use of a higher conversion factor for dissolved organic production. Sterner (2010) assumed 22% of total carbon fixation was dissolved organic whereas we assumed 10% of carbon fixation was dissolved. If Sterner (2010) used a 10% value for dissolved organic production, then his value for total carbon fixation would fall within the range of annual total carbon fixation rates observed in this study.

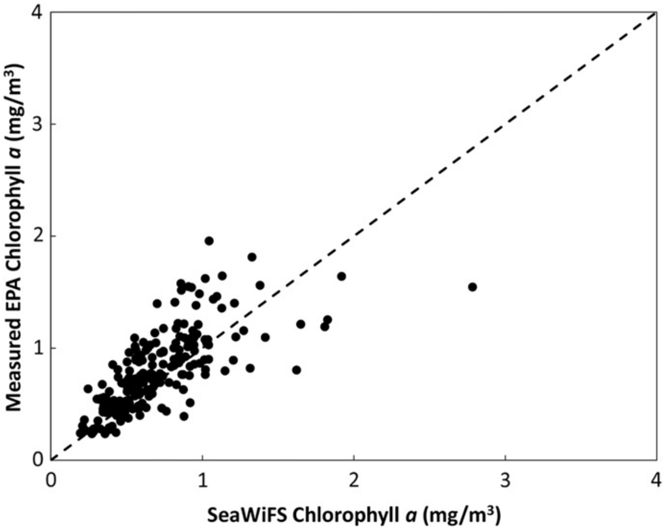

**Fig. 8.** SeaWiFS (standard NASA algorithm) estimated chlorophyll *a* concentrations vs. EPA measured chlorophyll *a* concentrations (EPA/GLNPO Surveillance Cruises, GLENDA database) from Lakes Michigan and Huron for the 2002–2008 period ($y = 1.02x + 0.08$, $R^2 = 0.50$, $p < 0.05$, $n = 204$). EPA chlorophyll were from spring and summer cruises, and only surface, individual, routine field samples were used (all correction factor samples were excluded). Satellite images ±1 day of field measurements were used for comparison. The mean SeaWiFS value in a 3-by-3 pixel window around field sampling stations was used where 6 or more out of 9 possible pixels were required to produce the chlorophyll value. Solid line is the 1:1 line.

**Table 1**
Annual whole-lake carbon fixation estimates for the Upper Great Lakes (Tg/y).

| Year | Lake Superior | Lake Huron | Lake Michigan | Upper Great Lakes |
|---|---|---|---|---|
| 2010 | 8.7 | 5.6 | 6.9 | 21.2 |
| 2011 | 7.9 | 5.5 | 6.0 | 19.3 |
| 2012 | 9.5 | 5.7 | 7.2 | 22.3 |
| 2013 | 6.4 | 4.4 | 5.0 | 15.8 |
| *Average* | *8.1* | *5.3* | *6.3* | *19.7* |

The new estimates of whole-lake carbon fixation do not change the carbon balance issues in Lake Superior. Even though our study corrected most of the deficiencies noted in Bennington et al. (2012) for previous carbon fixation estimates, our whole-lake carbon fixation estimates are in the range of previous values. Given that there is no overlap in years studied, it would be useful to use the GLPM with remote-sensed and empirically determined input values to calculate whole-lake production for all three lakes for the complete period (2002–present) in order to compare to previous work and to better understand interannual variability. Bennington et al. (2012), utilizing a modeling approach, noted that the source/sink nature of the carbon budget changed with season, and spatial heterogeneity of respiration was a major source of carbon budget uncertainty. More seasonal and spatial observations on important sink terms and long-term studies to assess interannual variation would greatly improve our ability to understand the Lake Superior carbon budget. Our work contributes to understanding of the carbon sink/source debate by providing accurate estimates of whole-lake carbon fixation for the 2010–2013 period.

Finally, our work highlights the value of remotely sensed products to characterize basin-wide parameters in large ecosystems. The insights gained in this study would not have been possible without the use of remotely sensed information, but these remotely sensed approaches will continue to need field validation. Future field studies are needed to evaluate algorithms and verify empirical relationships. This will be especially true if our model is applied to other environments. One particularly important model parameter, $P_{max}$, may vary among environments and this variability and the factors controlling this variability should be investigated.

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