Journal of Great Lakes Research 42 (2016) 1026–1035

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Estimating summertime epilimnetic primary production via in situ monitoring in an eutrophic freshwater embayment, Green Bay, Lake Michigan

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ARTICLE INFO

Article history:
Received 29 January 2016
Accepted 20 July 2016
Available online 16 September 2016

Communicated by Noel Urban

Index words:
Primary production
Net ecosystem production
Respiration
Diel oxygen
Observing systems

ABSTRACT

Quantifying rates of primary production and respiration is fundamental to understanding ecosystem function. This study utilized high-frequency time series, buoy-based sensor data to estimate daily primary production and respiration rates during the summers of 2012–2015 in southern Green Bay, Lake Michigan. Highly coherent diel oscillations of dissolved oxygen concentrations in epilimnetic waters were commonly observed for much of the summer via 30-min time intervals from the GLOS buoy (NOAA 45014) sensor array. Corrections for air–sea exchange based upon wind speed-derived gas exchange coefficients and saturation state, when combined with mixing depth, allow calculation of daytime net oxygen production and nighttime respiration. Thermistor string observations at 1-m intervals over the 13 m water depth showed the onset of thermal stratification, development of the thermocline, and occasional mixing events. For the summers of 2014 and 2015, during which a nearly continuous sensor record exists, gross primary production (GPP) and respiration (*R*) were estimated to be 342 ± 117 and 318 ± 83 mmol O_2 m^{-2} day^{-1} for GPP and −325 ± 120 and −306 ± 66 mmol O_2 m^{-2} day^{-1} for *R*, respectively. These results indicate that during most of the summer, southern Green Bay tends towards net autotrophy with production on average exceeding respiration by 9 ± 6% (SD). Cumulative net ecosystem production from June through September was estimated to be 3.2 and 1.3 mol C m^{-2} in 2014 (118 days) and 2015 (113 days), respectively, and is sufficient to drive a significant portion of benthic respiration, the principal cause of seasonal bottom water hypoxia.

Introduction

Gross primary production (GPP), ecosystem respiration (*R*) and net ecosystem production (NEP) have served as indicators of ecosystem function for many decades (Odum, 1957; Richey et al., 1978; Strayer, 1988; Woodwell and Whittaker, 1968). GPP is generally defined as the creation of biomass through carbon fixation by autotrophs over a given length of time (i.e. productivity), and ecosystem respiration as the fraction of this fixed carbon that is used by primary producers and remineralized back to carbon dioxide during cellular respiration (Odum, 1956). NEP, or the balance between production and respiration, is a measure of the net gain (or loss) in biomass for the ecosystem in question. Quantitatively, in aquatic ecosystems, GPP, *R*, and NEP are commonly estimated from the production and consumption of dissolved oxygen during diel cycles of photosynthesis and respiration (Collins et al., 2013; D'Avanzo et al., 1996; Staehr et al., 2010b).

Modern sensor technology has made it increasingly easier to collect in situ data for studying ecosystem processes, such as that required to calculate GPP and NEP. The measurements can now be made essentially continuously over an entire season and at multiple locations within one body of stratified water with a much lower investment in the time and expense usually needed for field sampling. Observing systems, such as the Great Lakes Observing System (GLOS; data.glos.us/obs) are increasingly being deployed as sensor platforms (Read et al., 2010). These systems collect long-term datasets that provide insights into temporal dynamics at significantly higher temporal resolution than previously possible. These observing systems are especially useful in highly variable systems in which isolated time points over a season are often a poor indication of mean conditions. The use of permanent moorings, such as GLOS buoys, has the potential to provide data relevant to understanding short-term (minutes to days), seasonal, and long-term (interannual) dynamics.

Such time series data have widespread application, particularly in eutrophic coastal regions, where human activities have accelerated the delivery of nutrients, stimulating excessive primary production, deteriorated water quality, nuisance algal blooms, and hypoxia (Zhou et al., 2014, 2013). One such area is Green Bay, Lake Michigan, an environment that has suffered hypereutrophic conditions for several decades, and has led, in part, to its designation as an Area of Concern (AOC). Loading data tabulated over 1967 to 2008 indicates that nutrient and sediment loading from the Fox River supports 70% of the annual

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http://dx.doi.org/10.1016/j.jglr.2016.07.028
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nutrient and sediment inputs to the bay and ~1/3 of the total phosphorous load to the entire Lake Michigan basin (Dolan and Chapra, 2012; Klump et al., 2009). These inputs drive a steep gradient in water quality from hyper-eutrophic conditions in the AOC to meso- to oligotrophic conditions at the northern, deeper portion of the bay that connects directly to Lake Michigan. Water quality varies along this gradient with Secchi depths ranging from <1 m to over 10 m and dissolved inorganic phosphorus concentrations ranging from ~1000 nmol L^{-1} in the lower Fox River to <20 nmol L^{-1} in northern Green Bay (Auer and Canale, 1986; Qualls et al., 2007; GBMSD, unpubl). Light-extinction coefficients, range from 1.3 m^{-1} in the southern end to 0.31 m^{-1} in the mid-upper region (Grunert, 2013) of the bay. These relatively high light-extinction coefficients limit primary production for much of the bay south of Chambers Island and are a likely cause of the benthic environment's minor contribution to the total primary production (Althouse et al., 2014). Quantifying the linkages among nutrient inputs, pelagic primary production and water clarity is an important management consideration in this system with one of the principal goals of the Remedial Action Plan (RAP) for the bay being the improvement in water clarity through reductions in algae and suspended sediment concentrations (WIDNR, 1988). Furthermore, as a consequence of the decomposition of both autochthonous and allochthonous organic matter, southern Green Bay also experiences seasonal hypoxia (Qualls et al., 2013; Valenta, 2013), typically during late summer (Qualls et al., 2013; Valenta, 2013).

Hyper-eutrophication and hypoxia concerns have led to two complimentary research areas—understanding the development of excessive algal production in regions of the Great Lakes (e.g. western Lake Erie, Saginaw Bay, and Green Bay (Davies and Hecky, 2005; Malkin et al., 2010; Maccoux et al., 2013)) and the deployment and use of long-term monitoring systems to understand ecosystem dynamics (Consi et al., 2007; Read et al., 2010; Rigosi et al., 2015; Watras et al., 2015). The main focus of this paper is the application of buoy based, high-frequency in situ time series data to investigate rates of primary production and respiration over summer season deployments in southern Green Bay between 2012 and 2015.

Methods

Study site and buoy-based measurements

Automated, in situ observations of dissolved oxygen, water temperature, conductivity, turbidity, and standard meteorological parameters, including wind speed and direction, solar radiation, and air temperature, were generated at 30-min intervals during portions or all of the period from early June to October in 2012, 2013, 2014, and 2015 using a Great Lakes Observing System (GLOS) buoy at a southern location in Green Bay, Lake Michigan. The buoy is a CB-1500 coastal monitoring buoy from Fondriest Environmental (Dayton, OH) with a 2 m met senor array, solar power system, and cellular communications for real-time data access. The buoy is anchored on a 2-point mooring holding a relatively constant directional orientation.

This GLOS buoy, also listed as NOAA 45014 (position 44°48.0′N, 87°45.6′W), is located in 13 m of water and is approximately 70 km northeast of the city of Green Bay, WI (Fig. 1). The buoy represents one of a series of standard GLOS deployments within the Great Lakes (Read et al., 2010) and is equipped with the following instruments: YSI 6600 series multi-parameter sonde measuring temperature, pH, turbidity, dissolved oxygen, and conductivity; Lufft WS501-UMB Compact Weather Station (Santa Barbara, CA) measuring temperature, relative humidity, global radiation, air pressure, mean wind speed and direction (over a 2 min period), and wind gust speed; a Nexsens (Dayton, OH) temperature string with thermistors every 1 m from 2 to 12 m; Nortek acoustic Doppler current profiler (ADCP) measuring x, y, and z velocities and amplitudes in 1 m bins. The sonde sensors, including oxygen and temperature sensors used here, are located ~1 m below the surface. Data is transmitted hourly to Nexsens iChart6 desktop software via a machine-to-machine cellular modem.

Meteorological and temperature data from NOAA 45014 are available online through the GLOS website Data Portal or Observation Explorer tools (see: http://glos.us/data-tools/observations-explorer).

The NOAA 45014 buoy is currently deployed during the recreational summer season, typically June through October (since July 2012; GLOS.org). Sondes were calibrated approximately monthly for dissolved oxygen (polarographic electrodes and optodes), pH, conductivity, and turbidity following the manufacturer's protocol, and were checked against separate measurements with sondes used for profiling on monthly buoy servicing cruises. Sensor failure, fouling, or buoy communication issues resulted in periods during which data were deemed unreliable and were excluded from calculations. GPP and R calculations were also only carried out for periods where DO concentrations exhibited coherent diel fluctuations indicating near steady state conditions in the epilimnion not confounded by advection or mixing (Fig. 2). For the purpose of this study, the relative changes in oxygen concentration are more critical than absolute change. Therefore, if the oxygen sensor is capturing the change between concentrations adequately, even if a small amount of drift in calibration has occurred, the rates of production and respiration calculated are not significantly affected. Corrections for drift were insignificant in 2014 and 2015 when optical oxygen sensors were employed.

Diel-based primary production rates

Rates of ecosystem productivity were estimated from the continuous YSI sonde data using the free-water accounting method outlined by Staehr et al. (2010a,b) with minor adaptations.

The general equation for changes in dissolved oxygen over a daily basis is

$$\frac{\Delta O_2}{\Delta t} = \mathrm{GPP} - R - J_{\mathrm{atm}} \pm A \tag{1}$$

where GPP is gross primary production, R is respiration, and J_{atm} is the atmospheric oxygen flux (defined as positive from the water to the atmosphere). A is a net term inclusive of other processes, e.g. advection. A is generally assumed to be negligible relative to other sources (Odum, 1956) and is not included in these calculations. All of the remaining terms in Eq. (1), except GPP, can be calculated with data measured on the buoy.

A classic GPP definition gives:

$$\mathrm{GPP} = \mathrm{NEP} + R \tag{2}$$

where the net ecosystem production (NEP) can be calculated after substitution into Eq. (1) for each time step using

$$\mathrm{NEP} = dO_2/dt + J_{\mathrm{atm}}/z_{\mathrm{mix}} \tag{3}$$

where z_{mix} is the depth of the epilimnion, which was determined from monthly temperature profiles and defined as the top of the thermocline in this study. Throughout the epilimnion, dissolved oxygen concentrations are relatively constant, meaning the water column in this region is well mixed and the sonde is assumed to be representative of the entire epilimnion.

Dissolved oxygen concentrations ($O_{2\mathrm{meas}}$), collected at 30-min intervals at 1 m depth, were used to calculate dO_2/dt. J_{atm} is determined as

$$J_{\mathrm{atm}} = k(O_{2\mathrm{meas}} - O_{2\mathrm{sat}}) \tag{4}$$

where k is the piston velocity, or coefficient of gas exchange between the water surface and atmosphere (Weiss, 1970) and $O_{2\mathrm{sat}}$, the saturated

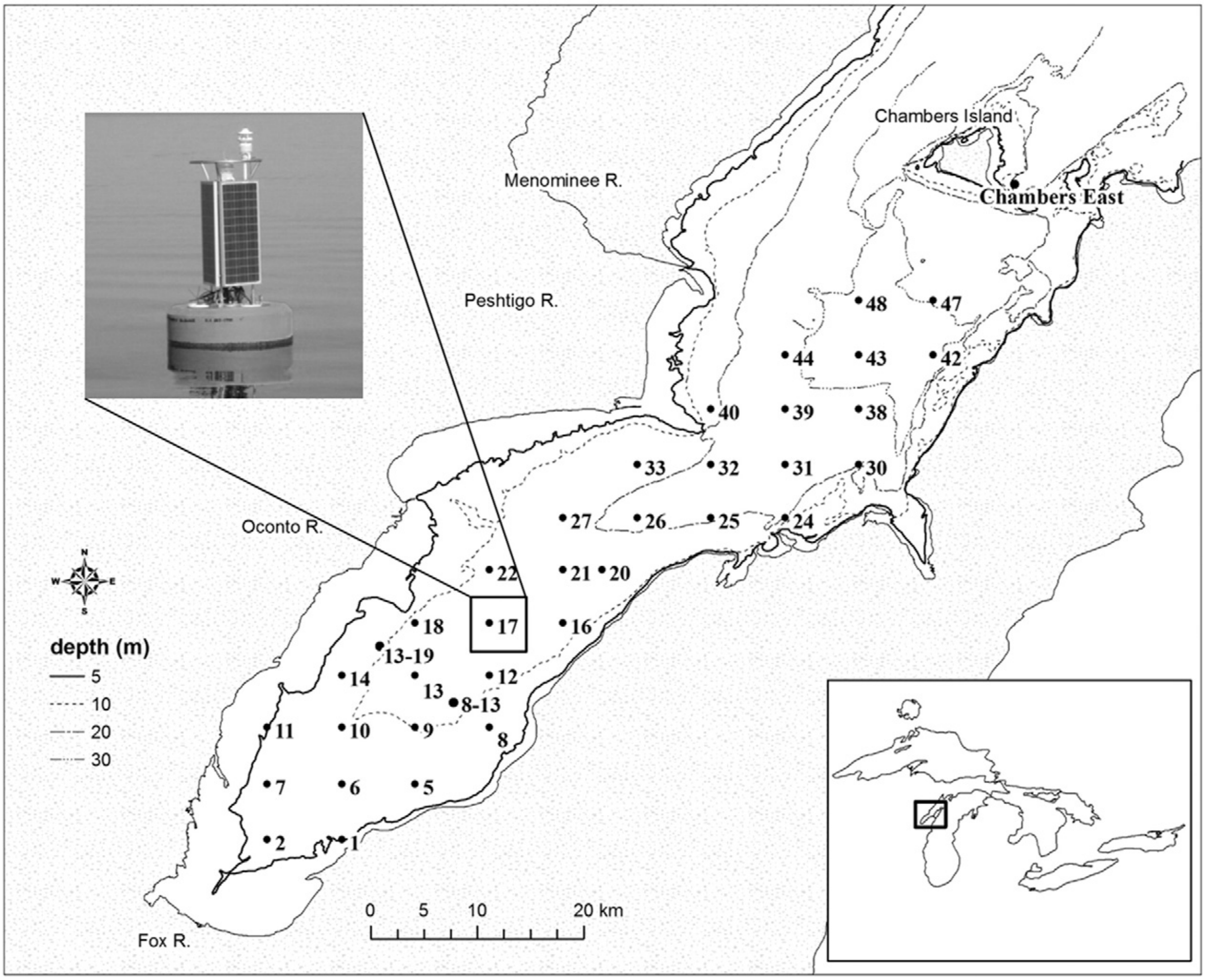

Fig. 1. Green Bay, Lake Michigan is a freshwater estuary. At GB17 (box) a Great Lakes Observing System (GLOS) buoy has been deployed seasonally since 2012.

oxygen concentration, is based on water temperature and atmospheric pressure. Piston velocity is calculated

$$k = k_{600}\left(\frac{Sc}{600}\right)^{-1/2} \tag{5}$$

where

$$k_{600} = \left(2.07 + .215U_{10}^{1.7}\right)/100 \tag{6}$$

(Cole and Caraco, 1998) and

$$Sc = 0.0476T^3 + 3.7818T^2 - 120.1T + 1800.6 \tag{7}$$

(Wanninkhof, 1992). U_{10} is wind speed at 10 m above the water surface and T is temperature in degrees Celsius. Wind speed was measured on

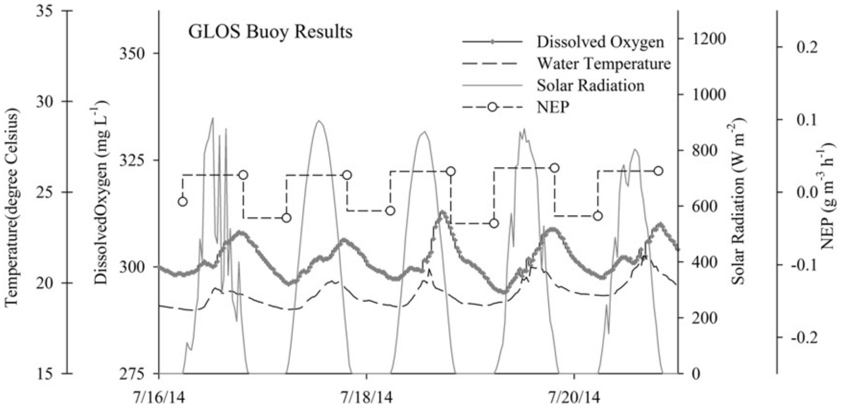

Fig. 2. An example of the data received from the buoy over a 5-day period in July 2014. The diel DO cycles are used to calculate primary production and respiration rates over the day. Daylight hours are determined from solar radiation values.

the buoy at 2 m above the water surface at 30-min intervals, then transformed using

$$U_{10} = 1.4125 \times U_z \times z^{-0.15} \tag{8}$$

(Smith, 1985) where U_z is wind speed at z height in meters.

NEP_{hr} was calculated for every 30-min time step using Eq. (3). NEP_{day} and R_{day} were calculated using NEP_{hr} and the number of daylight hours, or continuous periods of solar irradiance >0.0 W m^{-2}, over a 24-h period, as taken from the solar irradiance measurements on the buoy.

$$\text{NEP}_{\text{day}} = \text{mean NEP}_{\text{hr}} \text{ during daylight} \times \text{hours daylight} \tag{9}$$

and

$$R_{\text{day}} = \text{mean NEP}_{\text{hr}} \text{ during darkness} \times \text{hours daylight} \tag{10}$$

(Staehr et al., 2010a,b). We follow the usual assumption that NEP during the night represents the respiration rate for the entire 24-h period, although we recognize this may not always hold true (Hotchkiss and Hall, 2014; Tobias et al., 2007). There are also predictive model methods that use additional variables (e.g. photosynthetically active radiation, chlorophyll α) to better calculate daytime respiration rates (Hanson et al., 2008; McNair et al., 2013).

GPP can be computed using Eqs. (2), (9), and (10). NEP, GPP, and R values are initially calculated as volumetric rates, which can be converted to areal rates by multiplying by the epilimnetic mixed layer depth. The depth of the thermocline was taken from thermistor string data, monthly sonde profiles, or estimated from previous observations, when temperature and sonde data was lacking.

This study also assumes that changes in oxygen concentration due to advection and loss of oxygen through the thermocline are negligible. Thermocline diffusivities are assumed to be low (~10^{-8} m^2 s^{-1}, Edwards et al., 2005) because the thermocline is typically very steep (Hamidi et al., 2012). Oxygen diffusion into the thermocline would result in additional losses of oxygen from the mixed layer, making respiration seem larger than it actually is. To capture horizontal gradients in oxygen and spatially variable dynamics, such as advective water masses with differences in oxygen, a matrix of sensors would be needed (Van de Bogert et al., 2007). Average surface water velocities, measured by an ADCP on NOAA45014, are ~2.5 cm s^{-1}. Over an hour (two sampling time points), this corresponds to a sampling “footprint” for the sensor of just under 100 m radius or ~25,000 m^2. Cumulative NEP (NEP_{cum}) is the sum of daily NEP values and is also reported as monthly rates (Table 1). During those time periods when daily data are missing (2012 and 2013) average rates across the time period were used to estimate monthly rates. NEP_{cum} values were converted from mol O_2 m^{-2} to mol C m^{-2} using the molar ratio 138 mol O_2:106 mol C (Redfield et al., 1963).

Light–dark bottles

Light–dark bottle experiments were carried out at a range of stations during summers of 2013 as simple independent estimates of primary production rates. Water was collected in 20-L carboys from 1 to 2 m in depth, thoroughly mixed and distributed into triplicate standard 300 mL BOD bottles. In some instances when samples were collected late in the day, water was held in the carboy and aerated at ambient temperature overnight before incubation in light–dark bottles. Initial and final oxygen, temperature, and atmospheric pressure measurements were made using a YSI ProODO handheld sensor, calibrated in air immediately before initial readings. Bottles were placed in a circulating surface water bath continuously flushed in a flow-through system from the ship's surface water sampling pump to maintain in situ surface water temperature conditions. Bottles were incubated for eight to twelve hours during daytime in direct sunlight.

“Light” samples were incubated under 3 ambient light levels, 100%, 30%, and 11% by screening with multiple layers of nylon window screening. Dark samples were incubated in black-coated BOD bottles and used to estimate respiration rates. Rates are given as averages over the entire incubation period. Gross primary production is calculated as follows:

$$\text{GPP} = \text{NPP} + R \tag{11}$$

where NPP is the productivity rate from light bottles and R is the respiration rate from dark bottles. All bottle incubations were conducted in triplicate, sometimes quadruplicate subsamples. Light intensity for the various shading levels were measured using a HOBO Temperature and Light Logger that was attached to the neck of the bottles and placed under screening.

Results and discussion

The periods of data used for the free water calculations and some of the corresponding NOAA 45014 data are given in Table 1. The years 2012 and 2013 yielded partial results, approximately 77% and 57% of the deployment time period, respectively. For 2014 and 2015, the entire season (early June–September/October) of data was usable (Fig. 3). For months when data was discontinuous, the values from different periods were time-weight averaged to approximate a monthly value.

Table 1
GLOS buoy information for GB17 including sampling interval, number of samples (n) per time period, average wind speed (WS) ± standard deviation, range of wind speeds and average daily irradiance. * indicates that the value was taken from a different buoy than the GLOS buoy.

Time period	Sampling interval (min)	n	Thermocline depth (m)	WS (m s^{-1})	Range (m s^{-1})	Irradiance (W m^{-2})
8/21/12–8/31/12	6	2471	9.667	4.1*		n/a
9/1/12–9/8/12	6	1750	9.667	4.1*		n/a
9/26/12–9/30/12	30	203	9.667	4.24*		n/a
6/1/13–6/26/13	30	1210	11	4.26 ± 2.16	0–15.8	273.4
8/1/13–8/11/13	30	524	10	4.18 ± 1.70	0–11.4	408.9
8/20/13–8/27/13	30	357	6	4.83 ± 2.06	0–16.8	418.0
8/29/13–8/31/13	30	191	6	3.83 ± 2.21	0–8.7	353.3
9/1/13–9/7/13	30	334	12	5.37 ± 1.92	0.4–11.1	352.6
9/10/13–9/25/13	30	742	9.667	5.29 ± 2.23	0–11.3	331.6
6/4/14–6/30/14	30	1271	10	4.90 ± 2.40	0–13.6	419.8
7/1/14–7/31/14	30	1487	9	4.97 ± 2.29	0–12.3	427.4
8/1/14–8/31/14	30	1487	11	4.17 ± 2.17	0–13.3	360.6
9/1/14–9/30/14	30	1439	12	5.40 ± 2.60	0–14.8	284.1
6/3/15–6/30/15	30	1357	10	4.34 ± 2.13	0–12.1	424.8
7/1/15–7/31/15	30	1488	10	4.73 ± 2.10	0–13.8	496.5
8/1/15–8/31/15	30	1345	8	4.83 ± 2.32	0–16.7	345.7
9/1/15–9/30/15	30	1440	10	4.77 ± 2.20	0–12.4	314.0

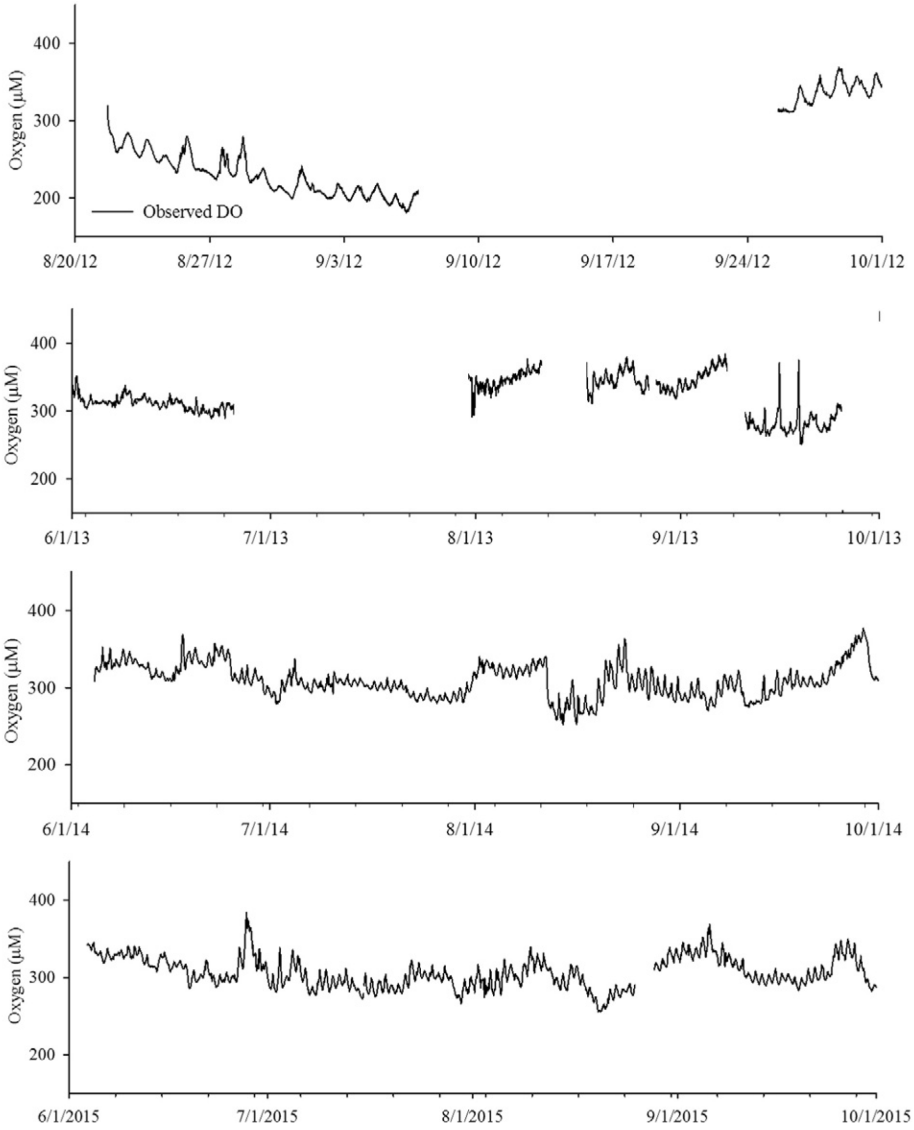

Fig. 3. Measurements of dissolved oxygen, at GB17 from the GLOS buoy, that were used for data analysis during (from top) 2012, 2013, 2014, and 2015.

Air–water gas exchange

For the 2013, 2014, and 2015 calculations, observed wind velocities were taken directly from the buoy anemometer. Average wind speeds were remarkably similar for all three years. In the first year of deployment, 2012, the meteorological station was not functioning properly, so wind speeds were acquired from the northern Lake Michigan buoy, NOAA Buoy 45,002 (ndbc.noaa.gov) and average values applied for the two time periods of data. The northern Lake Michigan buoy has been shown to be a reasonable surrogate for determining wind fields in Green Bay (Waples and Klump, 2002; Waples, 1998). The 2013 average wind speed over the useable data was 4.69 ± 0.5 m s^{-1}, with maximum speeds ranging from 11.1 to 16.8 m s^{-1}. In 2014, the average wind speed from June 4 to September 30 was 4.86 ± 0.5 m s^{-1} (Fig. 4), with the monthly maximums ranging from 13.6 to 18.8 m s^{-1}. In 2015, the average wind speed was 5.00 ± 2.3 m s^{-1} from June 3 to October 27 and the monthly maximums ranged from 14.2 to 28.8 m s^{-1}. The resulting piston velocities (*k*, Eq. (5)) ranged from 0.013 to 0.28 m h^{-1} in 2014 (Fig. 4) and from 0.011 to 0.289 m h^{-1} in 2015, using Eq. (6).

Over much of the 2013, 2014, and 2015 summertime deployments, oxygen concentrations in surface waters were at or above atmospheric equilibrium, driving gas exchange fluxes outward (positive), i.e. from the water to the atmosphere. Averaged atmospheric exchange (J_{atm}) ranged from −0.64 to +3.31 mmol O_2 m^{-2} h^{-1}. Only two time periods, both in late summer, exhibited average inward (negative) fluxes. These periods coincided with periods of water column mixing (Fig. 5), entraining hypoxic, hypolimnetic water with epilimnetic waters, lowering the overall oxygen saturation state of surface water below equilibrium with the atmosphere. Waples (1998) observed a similar trend in Green Bay for CO_2 uptake occurring throughout the summer, followed by a release during mixing and turnover in the fall.

In lower productivity waters, atmospheric exchange has the potential to contribute a relatively large fraction of O_2 flux to/from the overall surface water reservoir (Caffrey, 2004; Howarth et al., 1992) and choosing an appropriate piston velocity model can be quantitatively important. However, J_{atm} was generally <1% of the GPP; therefore, the choice of formulation for calculating piston velocity (e.g. Collins et al., 2013) would have <3% contribution to on the overall magnitude of GPP or *R* rates observed in Green Bay.

Monthly results

August and September sonde data were available for all 4 years of this study, allowing year to year comparisons for these two months. Over the

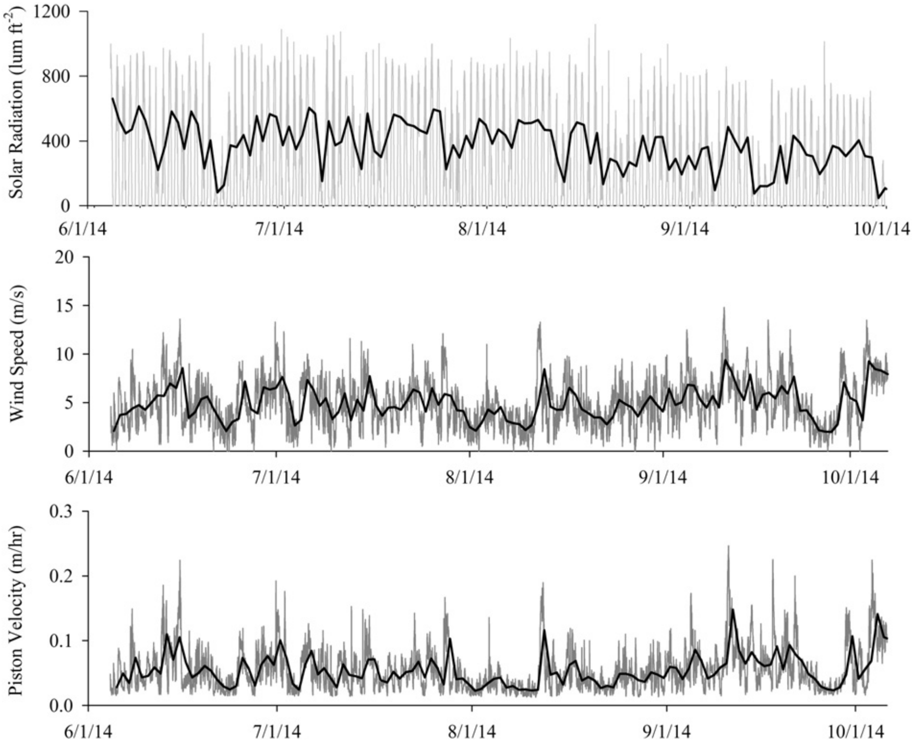

Fig. 4. Measured solar radiation (top), wind speed (middle), and calculated piston velocity (bottom) in 2014 from the GLOS buoy data, with daily averaged values in bold lines.

4-year period, the areal monthly NEP rate remained consistently close to zero, ranging from −80 to 77 mmol O_2 m^{-2} day^{-1} (Table 2). The epilimnion was slightly autotrophic in August and September, with net production ranging from 3.0 ± 64 to +9.9 ± 48 mmol O_2 m^{-2} day^{-1}, respectively. The August–September averages indicate that Green Bay tends towards net autotrophy during this period, although GPP and *R* are nearly balanced.

Daily GPP and *R* rates are relatively consistent over this 4-year deployment (Fig. 6). Both average GPP and *R* rates appear to decline slightly as the summer progresses from August to September. This decrease is

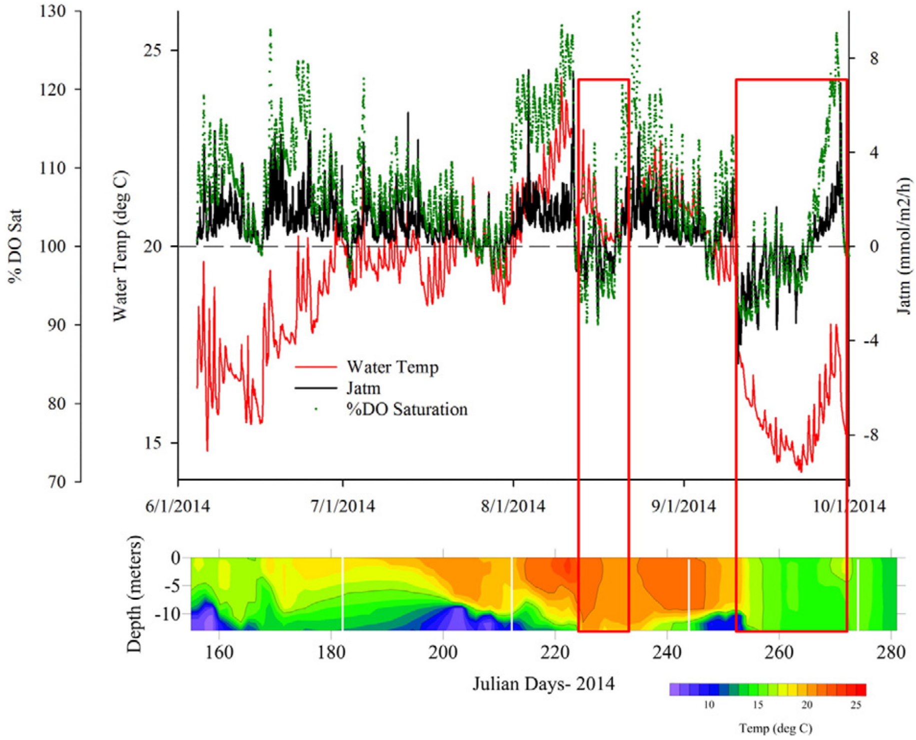

Fig. 5. 2014 comparisons of surface temperature (red), water column temperature (contour plot below), dissolved oxygen saturation (green) and atmospheric oxygen flux (black). The periods of inward, or negative, atmospheric flux coincide with periods of water column mixing.

Table 2
Monthly averaged net ecosystem production (NEP), gross primary production (GPP), and respiration (*R*). An average for August and September is also given to compare those two months which were present in the four years of the study. *These values represent averages over an incomplete dataset.

	June	July	August	September	Average for August and September
GPP (mmol O_2 m^{-2} day^{-1})					
2012	–	–	477*	472*	474.6*
2013	204	–	146	258	202.0
2014	360	244	499	263	380.8
2015	312	438	254	271	262.8
Respiration (mmol O_2 m^{-2} day^{-1})					
2012	–	–	−557*	−438*	−497.2*
2013	−207	–	−69	−193	−131.0
2014	−305	−209	−493	−293	−392.5
2015	−278	−398	−245	−302	−273.8
NEP (mmol O_2 m^{-2} day^{-1})					
2012	–	–	−80*	34*	−75.2*
2013	−3	–	77	65	68.2
2014	55	33	6	−29	16.3
2015	34	40	9	−31	12.9

possibly caused by declining phytoplankton growth due to shorter day length, cooler water temperatures, nutrient depletion, changes in nutrient availability, sedimentation, and/or grazing (Lohrenz et al., 1999; Wetzel, 2001). Regardless, despite a few outliers, these rates were remarkably constant over the course of the summer and from year to year. Primary production rate estimates from this oxygen monitoring system compare well with and generally fall within the range of similar regions within the Great Lakes and estuarine systems (Table 3). It should be noted that several experiments have shown that direct comparisons of GPP and *R* measurements by various techniques (e.g. ^{14}C, light–dark bottles, and free water O_2) yield varying results (Bender et al., 1987; Ostrom et al., 2005). However, carbon and oxygen measured fluxes are more likely to reach equilibrium as time periods approach phytoplankton generation time (Ostrom et al., 2005). Additionally, Hanson et al. (2003) found that over broad ranges in TP and DOC in aquatic systems, there was an almost 1:1 change in diel O_2 and CO_2 changes. GPP:*R* ratios are sometimes used to indicate the extent of external vs. internal sources of organic matter. Major inputs of allochthonous organic matter can drive a system to net heterotrophy and result in GPP:*R* ratios <1 (del Giorgio and Peters, 1993). For 2013–2015, the monthly averaged GPP to monthly averaged *R* ratio is ~1.09 ± 0.06 (SD), indicating net autotrophy at this site from June to September. On an annual basis, however, southern Green Bay tends towards net heterotrophy and carbon budgets are significantly influenced by organic matter inputs from the Fox River (Robertson and Saad, 2011; Klump et al., 2009; Waples, 1998).

Light–dark bottle incubation experiments conducted in 2013 with water from the same station as NOAA 45014 compare reasonably well to the monthly averaged in situ sonde data rates. August rates (GPP ~ 1.5–2.8 mmol m^{-3} h^{-1}) were higher for both bottle and in situ estimates than rates measured in June and July (~0.5–1.5 mmol m^{-3} h^{-1}, Fig. 7). Rates were also highest in the attenuated 25% ambient light bottles and lowest in the 100% ambient light bottles, probably as a result of photo-inhibition. In general, both 12% and 25% ambient light incubations gave similar results with slightly higher rates at the higher light level. The in situ diel-O_2 measured rates agree most closely with the 100% ambient light bottle incubations; however, the in situ rates were averaged over a

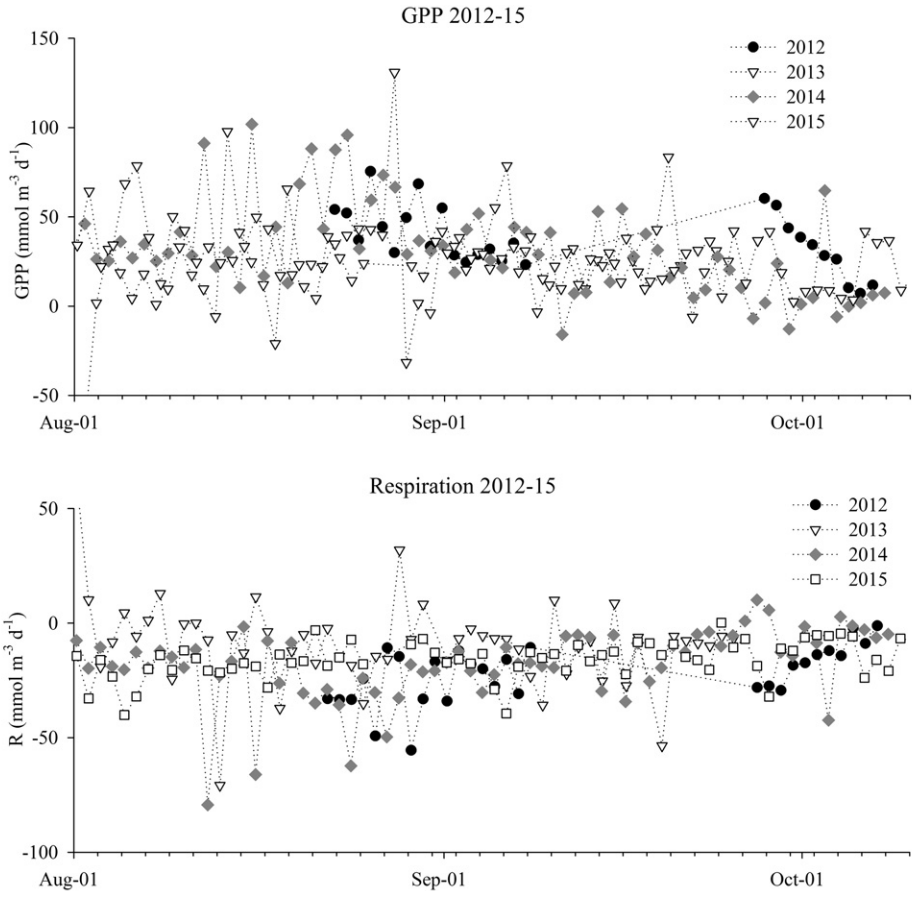

Fig. 6. Daily GPP versus *R* for the days included in the data analysis from 2012 to 2015.

Table 3
Gross primary production (GPP) comparisons between this study and other studies in similar systems including other Great Lakes

GPP value (mmol O^2 m^{-2} day^{-1})	System	Method	Year	Reference
31.5	Lake Superior	Carbon-14	Summers 2006–2008	Sterner, 2010
40.6–65.1	Saginaw Bay	C14 into a model	1989–1993	Fahnenstiel et al., 1995
64.1	Lake Michigan	Carbon-14	1970	Fee, 1973
73.4	Lake Michigan	Carbon-14	July to September 07–08	Fahnenstiel et al., 2010
65.1	Mid Green Bay, Lake Michigan	Carbon-14	June–August 1988	Millard and Sager, 1994
94–122	Sandusky Bay, Lake Erie	Light–Dark Bottles	July–August 2003	Ostrom et al., 2005
156	Colne Estuary—UK	Carbon-14	August 1995	Calculated from Kocum et al., 2002
168	Mid Green Bay	Model		Auer and Canale, 1986
193	Long Island Sound	Diel O2	May–August 2010	Collins et al., 2013
195	Lake Mendota	Carbon-14	Summer 1979–1981	Brock, 2012
203	**GB17**	**Diel O2**	**June-September 2013**	**This study**
342	**GB17**	**Diel O2**	**June-September 2014**	**This study**
319	**GB17**	**Diel O2**	**June-September 2015**	**This study**
358–412	Gulf of Mexico	Carbon-14	July–August 1990	Lohrenz et al., 1999
358–1258	Green Bay—Nearshore	Diel O2	2010–2011	Althouse et al., 2014
691–1071	Chesapeake Bay	Carbon-14	Summer 1969–1970	Taft et al., 1980

Boldface values indicate results from this study.

longer time period and the bottle incubations only represent 1 day. The monthly averaged in situ diel-O_2 calculated rates agree more closely with light/dark bottle incubations than the same day in situ rates, probably because diel calculated rates are relatively constant over periods of days to weeks. Individual days are subject to perturbations in mixing and short-term dynamics that often obscure a simple coherent diel signal that may be missed when a water sample is isolated in a bottle incubation.

Linking NEP and the benthos

The coupling between benthic and pelagic systems is a key process in understanding ecosystem function particularly in shallow aquatic environments (Renaud et al., 2008; Schindler and Scheuerell, 2002). Evidence suggests that recently deposited, relatively fresh organic matter settling out of the water column is largely responsible for driving benthic respiration resulting in steep oxygen gradients and oxygen depletion within millimeters of the sediment–water interface (Klump et al., 2009, unpub). Assuming the total net amount of organic material produced within the epilimnion (ΣNEP) settles through the thermocline and reaches the bottom, the extent of benthic respiration that can be supported from production within the overlying water can be estimated from aerobic benthic carbon metabolism assuming the Redfield stoichiometry for respiration in which 138 mol of oxygen are consumed for every 106 mol of carbon remineralized. Excess organic matter that is not respired may be exported, stored within the sediments, or remineralized anaerobically.

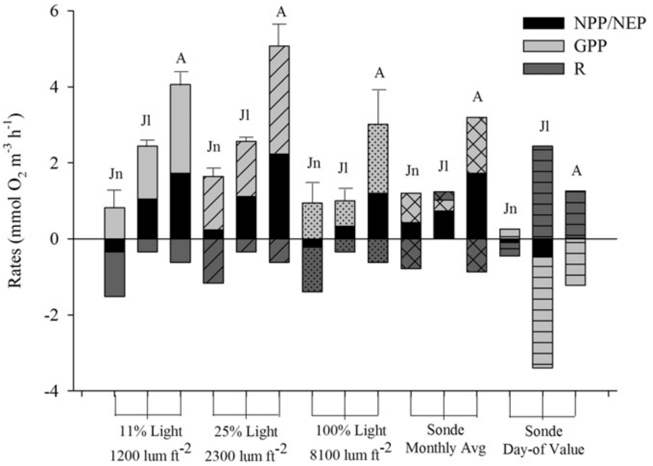

Fig. 7. Results of light–dark bottle experiments and diel sonde measurements in 2013. In each set of bottle treatments, there are 3 dates, represented by letters above the bars. Jn: 6/26/13; Jl: 7/31/13; and A: 8/25/13. The daily sonde values (rightmost bars) are from Jn: 6/25/13; Jl: 81/1/13; A: 8/25/13. Light for light–dark incubations was expressed as a percentage of the surface light as well as measured in lumens per square foot (1 lm per sq.ft. = 10.7 lm per sq. m.).

Over periods of deployment in 2014 and 2015, where a continuous record exists, cumulative NEP production is estimated at 4120 and 1660 mmol O_2 m^{-2} in 2014 and 2015, respectively, for the period June through September (Fig. 8). There is a relatively constant increase in net production throughout the season, with the exception of when mixing events occur, such as in August 2014. These cumulative production amounts do not capture the total net production in this system, since significant primary production likely occurs during fall, winter, and spring months that were not monitored here. Nevertheless, comparisons to other components of the carbon and oxygen budget of the bay may be made as a means of placing these measurements within the context of system mass balances. Klump et al. (2009) concluded that southern Green Bay was a net heterotrophic system that is subsidized by significant loading of fixed carbon from upstream reservoirs. It is estimated that 50%–60% of the total phosphorus loading delivered to the mouth of the Fox River is derived from the Lake Winnebago system, a highly eutrophic system in its own right, and delivered largely as fixed phosphorus in the form of algae (Dale Robertson, pers. comm.).

Cumulative net ecosystem production, i.e. that portion of primary production that may be lost from the epilimnion via deposition or advection, is estimated at 3.2 and 1.3 mol C m^{-2} over a 120-day period from June through September of 2014 and 2015, respectively or ~26.8 and 11.0 mmol C m^{-2} day^{-1}. The mean oxygen consumption rate within the sediments of southern Green Bay is estimated to be approximately 12 mmol O_2 m^{-2} day^{-1} (LaBuhn et al., in preparation). Rates measured at Station 17 average 9.1 mmol O_2 m^{-2} day^{-1}. This translates to a benthic carbon aerobic remineralization rate ~7 mmol C m^{-2} day^{-1}.

Largely because of its morphology, Green Bay is an extremely efficient sediment trap, sequestering 70%–80% of the total nutrient input in rapidly accumulating sediments mostly south of Chambers Island (Klump et al., 1997, 2009). Particle settling rates are also high (meters per day) and algal detritus can reach the sediments within hours to days, particularly under stratified conditions. The implication is that NEP helps fuel benthic respiration, and summertime carbon production could potentially support a significant fraction of the measured sediment respiration rates at this station. This is also consistent with the indirect calculations derived from hypolimnetic oxygen depletion conducted by Valenta (2013), which is based upon repeated profiling at numerous stations during the summer.

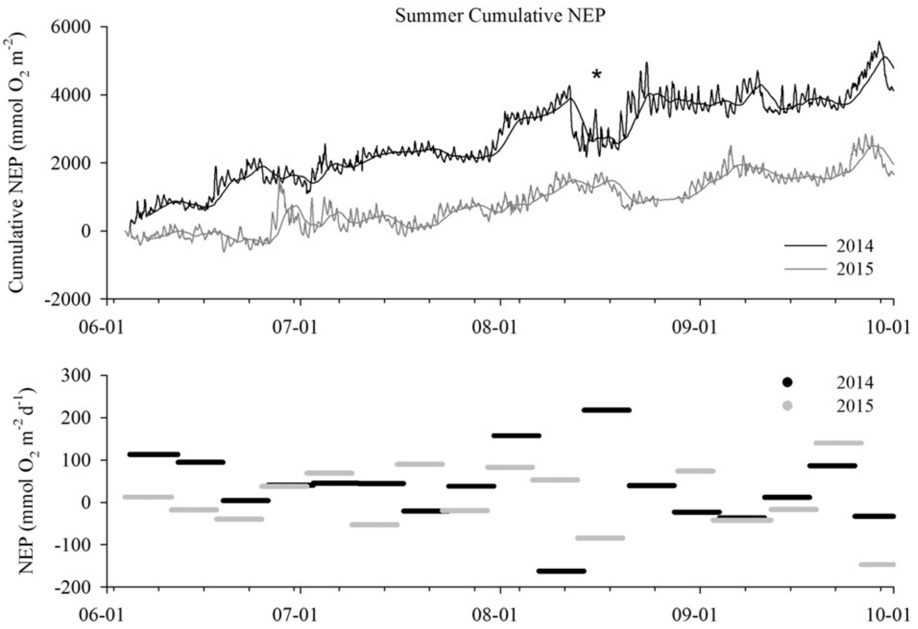

Fig. 8. Top: cumulative net ecosystem production for 2014 (black) and 2015 (gray) in 30-min intervals, with bold lines showing the 3-day running average. Bottom: weekly average NEP accumulation. *marks water column mixing event.

Conclusions

This study focused on using buoy-based, continuous, real-time in situ monitoring data collected as part of the GLOS observing network for the estimation of ecosystem primary production in the eutrophic waters of Green Bay. Daily GPP, *R*, and NEP rates were calculated over portions of the summer for 4 years (2012–2015), with a majority of the data collected in August and September. General trends include a tendency towards net autotrophy in the epilimnion, based on the August–September average NEP rate, although this was quite variable and the values remained close to zero. Primary production and respiration tended to be greater in August than in September, although this was not always the case.

Primary production rates will undoubtedly vary depending upon location within the trophic gradient, light attenuation, nutrient concentrations, algal speciation, and seasonal succession. In fact, it seems reasonable that a gradient in autotrophy/heterotrophy exists within the bay with distance from the major nutrient input at the mouth of the Fox River (Auer and Canale, 1986). Inherent limitations also exist when inferring whole lake production or metabolism from a single spatial location, despite having multiple time points. There can also be shifts in process rates with changes in depth that cannot be captured from a single point measurement. However, the estimated rates and fluxes in this study do imply that the water column and sediments are tightly coupled, and the system is efficient in turning over primary production through respiration and metabolism both in the water column and at the sediment–water interface.

Future work will include linking environmental drivers via ecosystem models to primary production, algal abundance, and the formation of hypoxia. Evaluating the role and form of external loading from the lower Fox River and Lake Winnebago would also be insightful since they are major contributors of total phosphorus to Green Bay. Although previous data suggests that perhaps as much as ~75% enters as fixed phosphorus (Klump et al. unpub), that may be changing with changing land use practices, especially in agriculture. Because water quality conditions vary greatly in Green Bay, single point estimates of primary production are somewhat limited spatial application or extrapolation. However, in conjunction with other observations, e.g. satellite imagery, nutrient loading, etc., buoy-based observations are extremely useful in verifying and calibrating hydrodynamic (Hamidi et al., 2015) and ecological models aimed at projecting the response of the system to changes in landscape processes and climate while also informing ecosystem restoration efforts.

Continuous buoy-based observations give high-frequency temporal datasets that are unobtainable in any other fashion and are extremely helpful in identifying system processes and variability that occurs in highly dynamic coastal systems. These observations are also valuable because they integrate broader scale processes than individual station by station point in time measurements or experiments. The advent of this technology should reveal unobserved temporal dynamics and assist in evaluating patterns and trends in environmental change.

Acknowledgements

We thank Kim Weckerly, Don Szmania, Brice Grunert, Dirk Koopmans, Jeff Houghton, R/V *Neeskay* Captain Gregory Stamatelakys, Geoffrey Anderson, and crew members for their assistance in the field, and Kim Weckerly, Brice Grunert, Joe Fillingham, and Dirk Koopmans for assistance during data processing and helpful comments during manuscript preparation. Comments by two anonymous reviewers also helped to improve this manuscript. This work was supported in part by grants Great Lakes Observing System (GLOS.us), from Wisconsin Sea Grant (R/HCE-12 to JVK), the NOAA CSCOR Coastal Hypoxia Research Program (Grant NA10NOS4780139 to JVK), the Michigan Water Center, the Erb Family Foundation, the CILER Graduate Student Fellowship and UWM Graduate Student Fellowships.

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