Seiche- and storm-driven benthic oxygen uptake in a eutrophic freshwater bay determined with aquatic eddy covariance

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Abstract: Oxygen depletion in bottom waters of lakes and coastal regions is expanding worldwide. To examine the causes of hypoxia, we quantified the drivers of benthic oxygen uptake in Green Bay, Lake Michigan, USA, using 2 techniques, aquatic eddy covariance and sediment core incubation. We investigated benthic oxygen uptake along a gradient in C deposition, including shallow water near the riverine source of eutrophication and deeper waters of lower Green Bay where high net sediment deposition occurs. Time-averaged eddy covariance oxygen uptake was high near the source of eutrophication (11.5 mmol m^{-2} d^{-1}) and at the shallower of the high deposition sites (9.8 mmol m^{-2} d^{-1}). The eddy covariance technique revealed a decrease in benthic oxygen uptake with depth at the high deposition sites. These patterns were consistent with benthic uptake being driven by the deposition of autochthonous production. Additionally, eddy covariance revealed a nearly proportional relationship between benthic oxygen uptake and current velocity at all sites. Specifically, because of the lake seiche, water velocity typically varied $3\times$ at a site and caused a $3\times$ variation in benthic oxygen uptake. A summer storm also doubled bottom-water velocities and caused a further doubling of uptake to 28 mmol m^{-2} d^{-1}. This high sensitivity of benthic oxygen uptake to seiche-driven water velocities indicates that redox conditions in surficial cohesive sediments are highly dynamic.
Key words: oxygen flux, benthic uptake, cohesive sediment, eddy covariance, water velocity, storm, redox oscillation

Benthic organic matter mineralization is a source of biologically available nutrients and a sink for oxygen in aquatic ecosystems, with consequences including phytoplankton blooms and hypoxia. Because of the capacity of sediments to store and mineralize organic matter, summertime phytoplankton blooms can be fueled by nutrients delivered to an estuary months or years after their introduction (Boynton et al. 2008, Lebo et al. 2012, Bruesewitz et al. 2013). The remineralized nutrients may be more important than external loading in determining the timing and severity of blooms (Burger et al. 2008, Wu et al. 2017). Where stratification inhibits the resupply of oxygen to the hypolimnion, benthic mineralization can lead to hypolimnetic hypoxia (<63 µM O$_2$). Hypoxia causes the collapse of benthic biotic communities (Vaquer-Sunyer and Duarte 2008, Riedel et al. 2012). It can be highly dynamic (e.g., Biddanda et al. 2018),

and it is expanding in freshwater and coastal systems because of eutrophication and climate change (Diaz and Rosenberg 2008, Jenny et al. 2014, Schwefel et al. 2016). Hypolimnetic hypoxia also greatly enhances the release of biologically available N and P from freshwater sediments (Mortimer 1941, Nürnberg 1988, Malecki et al. 2004), further contributing to phytoplankton blooms (Petkuviene et al. 2016). Our limited understanding of the mechanisms driving benthic organic matter mineralization limits our ability to predict shallow-water phytoplankton blooms and benthic hypoxia.

Oxygen flux across the interface from water to sediments can be driven from the sediment side, by benthic oxygen consumption, or from the water side, by turbulence or water column oxygen concentration. In both cases, a net benthic oxygen uptake occurs. The drivers of the sediment-side

control, benthic organic matter mineralization, are spatially and temporally variable. Ultimately, benthic organic matter supply limits the rate of its mineralization (Arndt et al. 2013). On shorter time scales, benthic organic matter mineralization is also affected by macrofauna (Glud et al. 1998), organic matter quality (Sobek et al. 2009), water temperature (Gudasz et al. 2010), sediment grain size (e.g., Rauch and Denis 2008), and oxygen exposure time (Sobek et al. 2009). In cohesive sediments, changes in water velocity can cause changes in benthic oxygen uptake, but these changes may not reflect changes in benthic organic matter mineralization. Cohesive sediments rely on diffusion for the delivery of oxidants (i.e., oxygen, nitrate, and sulfate) that are reduced during organic matter mineralization. Diffusion rates, in turn, are affected by water velocity. Near the sediment surface, overlying water velocities are attenuated gradually to 0 by friction with the bed. The lowest part of this layer (typically 0.2–1 mm thick) is the diffusive boundary layer. Within this region, molecular diffusion is the dominant transport process (Caldwell and Chriss 1979, Jørgensen and Des Marais 1990). The thickness of the diffusive boundary layer is driven by turbulence (Lorke et al. 2003, Bryant et al. 2010a), and oxygen transport into sediments is influenced by the thickness of this layer (Jørgensen and Revsbech 1985). As the thickness of the diffusive boundary layer diminishes, the delivery of oxygen to sediments increases, which increases oxygen concentration in surficial sediments and increases the oxidation of accumulated reduced species (e.g., NH_4^+, Fe^{2+}, Mn^{2+}). Where organic matter mineralization is ultimately limited by its supply, rather than oxygen availability, this temporary increase in measured oxygen uptake, even if made permanent, may have little effect on long-term rates of benthic oxygen uptake (Glud et al. 2007, Brand et al. 2009). Instead, oxygen penetration of sediments would adjust toward a new equilibrium determined by the balance of oxygen supply and its consumption (e.g., Higashino et al. 2004, Bryant et al. 2010a, b). This suggestion is supported by evidence that oxygen uptake by cohesive marine sediments is similar whether the diffusive boundary layer is thin or thick (Tengberg et al. 2004). An exception can occur in cases of high organic matter loading and low hydrodynamic forcing, conditions that are more commonly observed in lakes and reservoirs, where slow oxygen transport across a thick diffusive boundary layer can limit organic matter oxidation (Wüest and Lorke 2003).

Benthic oxygen uptake is frequently assessed through the use of benthic chambers and incubated sediment cores, but these methods may introduce biases to measurements of benthic oxygen uptake under certain conditions. Where oxygen transport across a thick diffusive boundary layer limits organic matter mineralization, stirring of overlying water in chambers or sediment cores may alter the thickness of the diffusive boundary layer and give biased results. Other technique-dependent factors can also cause biases in measurement of uptake. For instance, oxygen uptake determined with incubated sediment cores can be 2 to 3× lower than that measured with in-situ benthic chambers (Archer and Devol 1992, Glud et al. 1998), likely because of exclusion or disturbance of macrofauna (Glud 2008). Sediment disturbance during core collection can also alter the dissolved oxygen profiles in sediments, altering the measured oxygen flux (Reimers et al. 1986).

The aquatic eddy covariance technique makes disturbance-free measurements of oxygen flux under in-situ hydrodynamic conditions (Berg et al. 2003). To examine benthic organic matter mineralization, measurements are made in the tens of centimeters above the sediment surface, where water velocity is diminished by friction with the bed. This portion of the water column is called the benthic boundary layer. Turbulence is the primary mechanism responsible for the transfer of dissolved substances through this layer (Boudreau 2001). The eddy covariance technique quantifies the vertical flux of dissolved oxygen through this layer as the product of turbulent fluctuating components of vertical velocity and oxygen concentration (Berg et al. 2003). The resulting fluxes reflect benthic processes occurring over an area of tens of square meters (Berg et al. 2007). Despite the popularity of aquatic eddy covariance, it has not yet been compared to oxygen uptake measured with benthic chambers or incubated sediment cores in cohesive, freshwater sediments.

We undertook the current study to determine benthic oxygen uptake in a dynamic freshwater embayment of the Great Lakes (Green Bay, Lake Michigan, USA). The primary goal was to examine spatial and hour-to-hour temporal variability in benthic oxygen uptake as a driver of recurring summertime hypolimnetic hypoxia. A secondary goal was to evaluate the effectiveness of the core incubation technique at reproducing in-situ rates of benthic oxygen uptake. To meet these goals, we measured oxygen uptake using the eddy covariance and core incubation technique at each of our sampling stations. This paired approach allowed us to resolve station-to-station variability in uptake, hydrodynamic forcing as a driver of uptake, and the effectiveness of core incubation at reproducing in-situ eddy covariance measurements.

METHODS
Study site
To address our research goals, we quantified oxygen uptake with the aquatic eddy covariance technique and with sediment core incubation during hypoxia monitoring cruises in Green Bay, an embayment of Lake Michigan, USA (Fig. 1). Green Bay covers an area of 4200 km^2, has a volume of ~67 km^3, and a maximum depth of 53 m. The Fox River, which enters Green Bay at the southern end, enriches the bay with nutrients and organic material (Manchester-Neesvig et al. 1996, Klump et al. 2009). As a result, Green Bay has persistent water quality problems, including dense phytoplankton
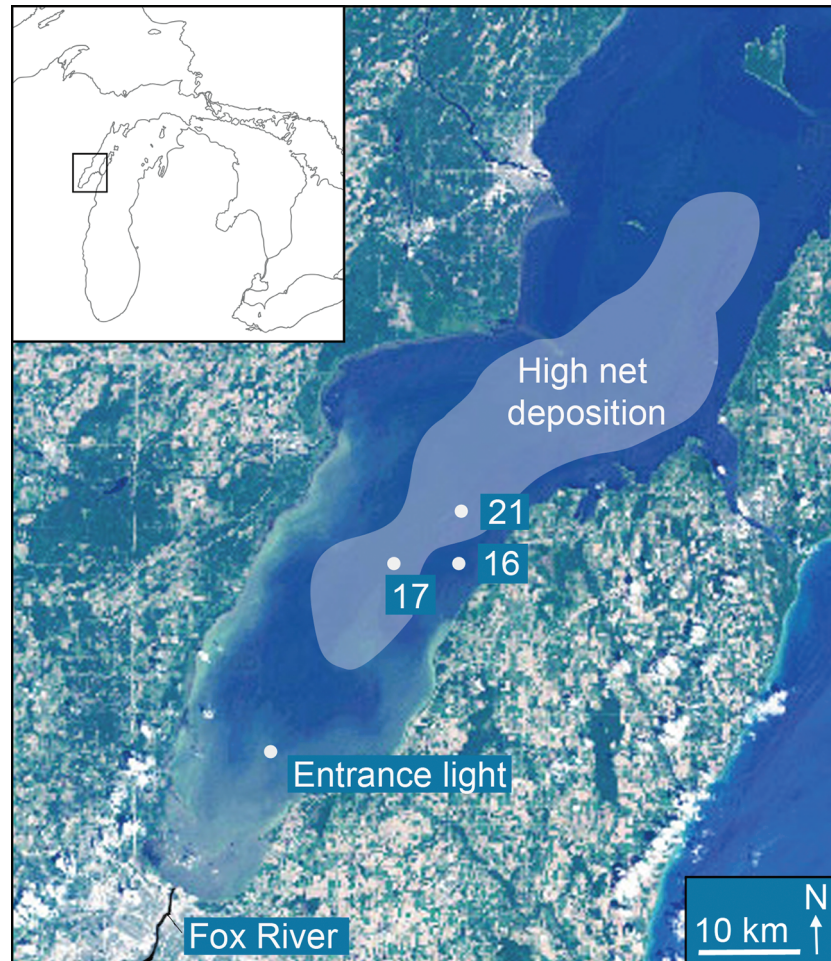
Figure 1. Landsat true color image of Green Bay, Lake Michigan, USA, in July of 2014 (courtesy of NASA Goddard Space Flight Center and the United States Geological Survey). Inset shows the study location in the Great Lakes region of North America. The city of Green Bay, Wisconsin, is on the Fox River at the bottom left. The 4 benthic flux stations used in this study are labelled. In the area of high net deposition (in white), C burial in sediments exceeds 1 mol m^{-2} y^{-1} (replotted from Klump et al. 2009).

blooms (LaBuhn and Klump 2016) and hypoxia (Klump et al. 2018). Exceptionally strong summertime thermal stratification can result from wind-induced upwelling of cold Lake Michigan bottom waters into the northern end of Green Bay (Hamidi et al. 2015). As this bottom water flows south, the concentration of dissolved oxygen within it is depleted. Consequently, hypoxia (<63 μM O$_2$) is observed in bottom waters of lower Green Bay nearly 25% of the period between late June and early September (Klump et al. 2018), causing the loss of benthic invertebrates throughout lower Green Bay (Kaster et al. 2018) and contributing to the decline of what was once a highly productive fishery.

Despite the high nutrient loading and exchange of water with the rest of Lake Michigan, Green Bay is an effective nutrient and sediment trap. It retains 70 to 90% of P inputs (Klump et al. 1997), buries or respires 60% of C inputs, and retains or denitrifies 50% of N inputs (Klump et al. 2009). Shallow water depths, high particle loads, and a large fetch make sediment resuspension common in the lower portions

of the Bay. Organic C resuspension of the upper 2 cm of Green Bay sediments is 10 to 70× greater than net accumulation (DePinto et al. 1993). High net sediment deposition occurs in the central portion of lower Green Bay (Fig. 1). As depth increases from the shipping channel entrance light to deep waters off of Sturgeon Bay, the cohesive sediments grade from erosive sandy silts to depositional porous muds.

We present oxygen fluxes that were determined during deployments at 4 stations in Green Bay (1 deployment at each of the 3 northern stations, 2 deployments at the southernmost station; Table 1). We selected the stations from a grid of over 100 stations established for the Contaminant Mass Balance Study sponsored by the United States Environmental Protection Agency (USEPA 1989). They were chosen to include a shallow site close to the Fox River mouth and deeper sites where high net sediment deposition occurs. The station at the shipping channel entrance light (Entrance light), the only non-permanent station, was located 13 km to the north of the Fox River mouth (Fig. 1) at 7.8 m depth.

Table 1. Environmental characteristics of the 4 stations where we determined benthic oxygen uptake in Green Bay, Lake Michigan, USA. The station names and measurement start dates are given. The mean bottom water temperature (Temp), mean oxygen concentration ([O_2]), and the mean water velocity (U) were determined over time during eddy covariance measurements. The range of hourly mean water velocities during each deployment is also given. Differences in temperature and oxygen concentration over time at each station were small relative to differences between stations. Organic C content at the sediment surface and C deposition were determined in a prior study (Klump et al. 2009).

Station	Measurement date	Depth (m)	Temp (°C)	[O_2] (μmol/L)	U (cm/s; range)	Organic C (weight %)	C deposition (mol m^{-2} y^{-1})
Entrance light	16 September 2014	7.8	15.6	296	4.2 (3.6–4.7)	–	1.21[a]
Entrance light	25 August 2015	7.8	15.9	273	3.1 (2.4–5.2)	–	–
Station 16	15 July 2015	11.5	14.4	60	3.5 (2.0–5.9)	1.0	0.42
Station 17	25 August 2014	13.5	16.6	101	2.4 (0.8–7.2)	8.2	2.99
Station 21	28 August 2014	16	12.5	166	2.1 (1.2–3.5)	7.8	3.38

[a] C deposition was determined at Station 6, which is located 1.5 km from our entrance light station.

Three additional stations are located 39 to 46 km northeast of the Fox River mouth. Station 16, located 5 km from the edge of the bay, is characterized by low mean annual C deposition (Klump et al. 2009). The other 2 northern stations, 17 and 21, have high mean annual C deposition. Water depths at the 3 northern stations increase from 11.5 m at Station 16 to 16 m at Station 21. The study was conducted between July and September in 2014 and 2015. The timing of the field study coincided with the time of year during which bottom water hypoxia is observed (Hamidi et al. 2015, Grunert et al. 2018, Zorn et al. 2018), allowing us to investigate the drivers of hypoxia as it occurred.

Eddy covariance measurements

The eddy covariance technique requires simultaneous high-frequency measurement of water velocity and dissolved oxygen concentration at the same point in the water column. To obtain these measurements, we built a lightweight stainless steel tripod to support eddy covariance instruments in the benthic boundary layer. We positioned the measurement volume height 30 cm above the bottom of the tripod feet. During some deployments, the feet submerged into particularly soft sediments. As a result, our measurement volume heights ranged from 15 to 30 cm above the sediment surface. An acoustic Doppler velocimeter (Vector; Nortek-AS, Rud, Norway) measured water velocity at 16 Hz in a discrete measurement volume (~2 cm^3). An optode minisensor (FireSting UHS-430; PyroScience GmbH, Aachen, Germany) determined dissolved oxygen for eddy covariance calculations. The minisensor is composed of a fiber-optic cable with a 430-μm diameter sensing tip. The cable end of the sensor is connected through an optical port in a submersible housing to an electronic module with an illumination source and a fluorescence detector (FireSting mini, PyroScience GmbH). We positioned the sensing tip 1 cm outside of the measurement volume of the velocimeter to avoid interfering with the velocity measurements. The

90% response time of the minisensor was 0.39 s (Fig. S1). We optimized the module settings for high frequency (15 Hz) measurement (i.e., the LED illuminated the oxygen-sensitive membrane at the tip of the sensor 15×/s). For future deployments, the sensor life may be improved with minimal losses of high frequency flux contributions by adjusting sampling frequency to 5 Hz (e.g., Koopmans et al. 2020). The velocimeter provided power for the minisensor module and logged the analog dissolved oxygen signal.

We made supporting measurements of the gradient in dissolved oxygen in the benthic boundary layer, of photosynthetically active radiation (PAR), and of thermal stratification of the water column. We arranged 3 logging optodes (miniDOT; Precision Measurement Engineering, Vista, California) vertically on the eddy covariance frame at 10, 30, and 60 cm above the feet of the tripod. These optodes recorded temperature and dissolved oxygen concentration every minute. We positioned the middle optode at the height of the velocimeter measurement volume and used this optode to calibrate the eddy covariance minisensor. We used the remaining 2 optodes to identify oxygen gradients that could occur because of density stratification. We determined PAR with a submersible logging sensor (Odyssey PAR Logger; Dataflow Systems, Christchurch, New Zealand). Prior to instrument deployment, we determined water-column conductivity, temperature, and depth profiles with a conductivity-temperature-depth logger equipped with a polarographic probe for dissolved oxygen measurement (YSI-600; Yellow Springs Instruments, Yellow Springs, Ohio). Wind speed at Station 17 was determined 2 m above the water surface by a National Oceanic and Atmospheric Administration monitoring buoy (www.ndbc.noaa.gov/station_page.php?station=45014).

To examine if sediment resuspension was enhanced when a storm caused a sudden increase in water velocities during 1 deployment, we used acoustic backscatter measured by the acoustic Doppler velocimeter. Backscatter increases logarithmically with the concentration of cohesive sediments for

a given sediment type (Ha et al. 2009). We did not calibrate backscatter strength for this study, however, so we report only an increase or decrease in backscatter as a proxy for an increase or decrease in particle suspension.

Eddy covariance data analysis

We analyzed eddy covariance data using the EddyFlux software package (version 2.0; PB, unpublished). We divided the continuous data into 1-h intervals for the following data processing steps. First, the observed velocity field was rotated to align the x-axis of the acoustic Doppler velocimeter with the mean current, nullifying average velocities in both the transverse and vertical axes. This correction may be unnecessary at low water velocities (i.e., at a mean velocity of <5 cm/s). Next, benthic O_2 flux was calculated as the mean of the product of the fluctuating components of vertical velocity (w') and oxygen (O_2'):

$$O_2 \text{ flux} = \overline{w'O_2'} \qquad \text{(Eq. 1)},$$

where the over bar indicates averaging. w' and O_2' were determined by Reynolds decomposition. The mean components were determined by a 3-min running average to the observations. Then, instantaneous fluxes were cumulated over the hourly intervals for flux calculations. Optode minisensors made in excess of 1 million measurements every 24 h. Because of this intense use, there was some photobleaching of the sensor over time, which causes an apparent drift in oxygen concentration due to the degraded effectiveness of the fluorophore response to oxygen. The maximum signal change due to photobleaching was 8% at the end of a 48-h deployment. We made a 1st-order correction for photobleaching by dividing the observed minisensor oxygen concentration by the extent of photobleaching over time (e.g., dividing by 1.08 at an 8% signal change). Net oxygen flux into sediments is reported as oxygen uptake with a positive value. We calculated the time-averaged eddy covariance oxygen uptake at each station as the mean of the hourly oxygen uptake observed over time.

Eddy covariance data quality assurance

We made a total of 15 deployments of eddy covariance equipment in Green Bay for this study, during which we measured 255 h of turbulent fluctuations in velocity and dissolved oxygen. Of that dataset we include only 5 deployments, comprising 46 h of measurements, in our analyses. We removed most of the eddy covariance observations (46%) because of thermal stratification of the benthic boundary layer during a portion of the deployment, which commonly resulted in spuriously large oxygen fluxes due to the transport of oxygen across the thermocline, which is also an oxycline. We excluded 22% of the remaining eddy covariance observations because of particle interference in flux measurement and 20% because of damage to the optode

minisensor. We identified particle interference in flux measurement as an abrupt change in the cumulative flux, which commonly co-occurred with a spike or baseline shift in eddy covariance oxygen measurement. Inconsistent cumulative fluxes typically followed. As a result of removing these inconsistencies, some of our hourly measurements of uptake include less than a complete hour of observations. Particle-induced errors routinely affect eddy covariance measurements (e.g., Rheuban et al. 2014, Koopmans and Berg 2015). A robust eddy covariance optode has been developed to address this issue (Berg et al. 2016), but it was not used in this study. Despite the challenges of stratification and particle suspension, we found that optode minisensors made reproducible measurements of oxygen flux at the Entrance light and Stations 16, 17, and 21 (Figs S2–S5).

Assessment of benthic uptake with eddy covariance oxygen flux

We also examined the data to test for the presence of sufficient turbulent mixing in the benthic boundary layer. Seiche-driven oscillations in bottom-water velocities in lakes can allow for periods of near-bed density stratification. As a result, a time series of oxygen flux in the benthic boundary layer can underestimate benthic oxygen uptake during periods of stratification and overestimate when turbulent mixing recurs (Brand et al. 2008). To ensure that the time-varying eddy covariance oxygen fluxes reported during this study were assessments of time-varying benthic oxygen uptake, we removed time periods during which we observed near-bed stratification. Additionally, where turbulent mixing is insufficient to fully mix the parcel of water between the eddy covariance measurement volume and the sediment surface, eddy covariance fluxes may not represent benthic uptake. However, we found that turbulent contributions to vertical flux occurred even at minimal velocities and were sufficient to drive turbulent mixing of dissolved oxygen (Figs S6 and S7). In a final check of our data, we examined the fluxes that result from the velocity-induced redistribution of dissolved oxygen in the benthic boundary layer. Briefly, at low stable water velocities (e.g., <2 cm/s), dissolved oxygen is depleted from waters within a few centimeters of the sediment surface. As water velocities increase, turbulence mixes this oxygen-depleted water upwards, causing a transient downward oxygen flux. Under conditions similar to those in our study (water velocities from 2–10 cm/s, benthic uptake of 10 mmol m^{-2} d^{-1}), this process causes a small (20%) increase in the magnitude of the downward oxygen flux at the onset of an increase in velocity (Holtappels et al. 2013). The effect is small and disappears with further increases in water velocity (Fig. S8). This effect likely contributes to noise in the relationship between oxygen flux and water velocity at the lowest water velocities (<2.5 cm/s), but it cannot explain the wide range over which velocity drives oxygen flux in our study. Therefore, we report the time-varying eddy covariance oxygen

fluxes that we observed in this study as measurements of time-varying benthic oxygen uptake.

Oxygen uptake by sediment core incubation

We lowered a Soutar-type box corer to the lake bottom to collect sediments for core incubation 200 m from each of the eddy covariance deployment sites. The box corer was counter-weighted to reduce the speed at which it penetrated sediments and to reduce disturbance of the sediment–water interface. The surface area of sediment retrieved by the box corer was 30 × 30 cm. The retrieved sediments were typically 40 to 80 cm thick. On retrieval of the box corer, we inserted three 7.5-cm diameter plastic core liners into the box corer to collect subcores for incubation. Ten cm of overlying water from the box corer were retained over the subcores to maintain in-situ oxygen exposure. Each subcore was fitted with a top-mounted mechanical stirrer and combined oxygen and temperature sensor to monitor change in dissolved oxygen over time (Digital Oxygen Meter 21800-022; Traceable® Products, Webster, Texas). Air was excluded, and the liner and sensors were sealed against gas exchange. Water enclosed in the subcore was stirred at 20 rpm, an adequate rate to mix the enclosed water without disturbing the sediment–water interface, thereby generating reproducible measurements of benthic uptake (Tengberg et al. 2004). We placed sediment subcores in a shipboard temperature incubator to maintain in-situ temperatures. We determined oxygen uptake in each sediment subcore with a least-squares linear fit to the change in oxygen inventory in overlying water over time during the 24 to 48-h incubation (e.g., Fig. 2). We calculated the rate of uptake for each station as the mean uptake of the 3 incubated sediment
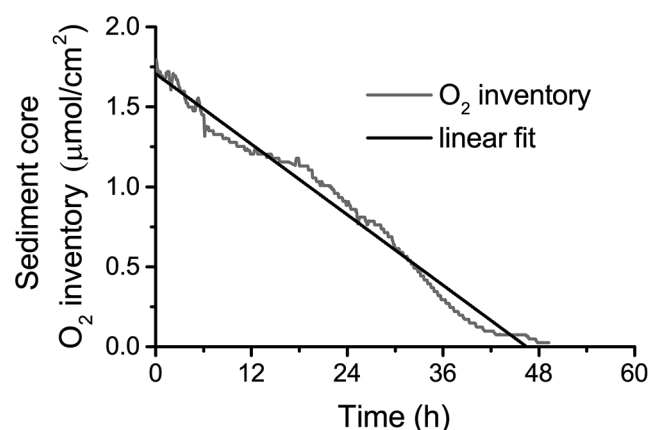

Figure 2. An example calculation of benthic oxygen uptake determined by core incubation at Station 17 in Green Bay, Lake Michigan, USA, in August of 2014. Uptake is calculated from a least-squares linear regression fit to the change in oxygen inventory in water overlying the incubated sediment core over time. In this case, oxygen uptake was 8.9 mmol m^{-2} d^{-1}, calculated as 1.71 μmol O_2/cm^2 divided by 46.2 h.

cores. Details on our approach are given by LaBuhn (2016). Dadi et al. (2015) provide further details for improving the accuracy of measurements of benthic uptake with core incubation.

Statistical analyses

To test for an effect of water velocity on eddy covariance oxygen uptake, we used a least-squares linear regression of hourly flux observations as a function of water velocity at each station.

To test for station-to-station differences in oxygen uptake, we examined the eddy covariance and core incubation datasets separately by performing a 1-way analysis of variance (ANOVA) on each dataset. We then used Tukey's honestly significant difference (HSD) tests to quantify the strength of the differences in uptake between stations in multiple pairwise comparisons. The ANOVA assumption that measurements are independent within groups is not explicitly met by data from the eddy covariance technique because our measurements are correlated over time. To minimize the impact of this correlation on our analyses, we determined eddy covariance fluxes during a wide range of flow velocities at each site. Where possible, we also pooled together short time series from a station so that no station was represented by <8 h of data. We also aggregated measurements over 1-h time intervals, as opposed to 15-min time intervals, to reduce dependence on time. This approach would be improved with more measurements, but it has previously been used for eddy covariance datasets (e.g., Berg et al. 2003). We used the Shapiro–Wilk test to examine the assumption that measurements were normally distributed within groups, and we used Levene's test to examine the assumption that there was equal within-group variance. Following guidance of Wasserstein et al. (2019), we use exact p-values as a measure of effect strength. All of the tests were calculated using OriginPro® 2015 (OriginLab® Corporation, Northampton, Massachusetts).

RESULTS
Environmental setting

During our hypoxia monitoring cruises on Green Bay, the top of the thermocline was typically 10 m in depth. Its presence allowed dissolved oxygen to become depleted in bottom water at our deeper stations. We observed very low dissolved oxygen, 20% of saturation (60 μmol/L), at Station 16. Dissolved oxygen was also depleted at Station 17 (101 μmol/L) and at Station 21 (166 μmol/L; Table 1). Bottom-water oxygen concentrations remained high at the Entrance light station because the shallower depth placed the sediments above the thermocline during our measurements there. Because of suspended material, very little PAR penetrated to the sediment surface at Entrance light (0 to 6 μE m^{-2} s^{-1}). No measurable light reached the sediment surface at the other stations.

Benthic oxygen uptake determined with aquatic eddy covariance

Time-varying benthic oxygen uptake at all stations increased with increases in water velocity. At Station 17, we happened to capture the effect of a summer storm on benthic oxygen uptake with the eddy covariance technique. In the early morning of 27 August 2014, wind speed over the meteorological buoy at that station increased to >8 m/s for 2.5 h because of the storm. This storm caused bottom-water velocities to increase 3× from a seiche-driven velocity of 2.2 cm/s to a maximum of 7 cm/s (Fig. 3A–C). During this time, benthic oxygen uptake doubled. The amplitude of acoustic backscatter measured by the velocimeter increased in the hours following the onset of high water velocities, consistent with sediment resuspension. As water velocities decreased from their storm-enhanced peak, oxygen uptake returned to a pre-storm rate (Fig. 4). At all stations, the increases in oxygen uptake had a linear relationship with water velocity (Fig. 5; least-squares linear regression). Further, the increases in uptake were close to proportional with increases in water velocity at Stations 17, 21, and Entrance light. For example, a doubling of water velocity at each of these stations caused a doubling of benthic oxygen uptake.

To examine differences in eddy covariance benthic oxygen uptake across stations, we excluded the storm-enhanced uptake observed at Station 17 from the rest of the observations at that station. This exclusion resulted in a mean uptake of 9.8 ± 1.0 mmol m^{-2} d^{-1} ($n = 16$ hourly intervals) for Station 17, which was slightly lower than the mean uptake determined from eddy covariance observations across the 2 deployments at Entrance light (11.5 ± 0.9 mmol

m^{-2} d^{-1}, $n = 9$ hourly intervals; Fig. 6). The lowest uptake was observed at Station 16 (3.2 ± 0.7 mmol m^{-2} d^{-1}, $n = 8$ hourly intervals), and uptake was intermediate at Station 21 (5.1 ± 0.7 mmol m^{-2} d^{-1}, $n = 12$ hourly intervals). Despite the strong dependency of time-varying benthic oxygen uptake on water velocity at each station, velocity was not the primary driver of time-averaged benthic oxygen uptake across stations. For example, time-averaged uptake at Station 16 was lower than at Station 21, yet the average water velocity at Station 16 was 1.7× greater than at Station 21 (Table 1, Fig. 5).

Comparison of techniques

Averaged over time at each station and across stations, eddy covariance benthic oxygen uptake agreed with core incubation benthic oxygen uptake (Fig. 6). The across-station mean eddy covariance uptake was 7.8 ± 2.3 mmol m^{-2} d^{-2} ($n = 4$ stations). The across-station mean core incubation uptake was 8.2 ± 1.7 mmol m^{-2} d^{-1} ($n = 4$ stations). Station to station, however, there were differences between the techniques. The time-averaged eddy covariance uptake was 30% lower than the average core incubation uptake at Stations 16 and 21, although we are not confident that this difference is real given the measurement uncertainties. Both techniques agreed on the relatively high uptake at Entrance light and on the lowest uptake at Station 16. Importantly, the eddy covariance technique revealed a greater difference in benthic oxygen uptake between Stations 17 and 21 than did the core incubation technique. Eddy covariance uptake at Station 17, excluding the storm-enhanced intervals, was twice as high as
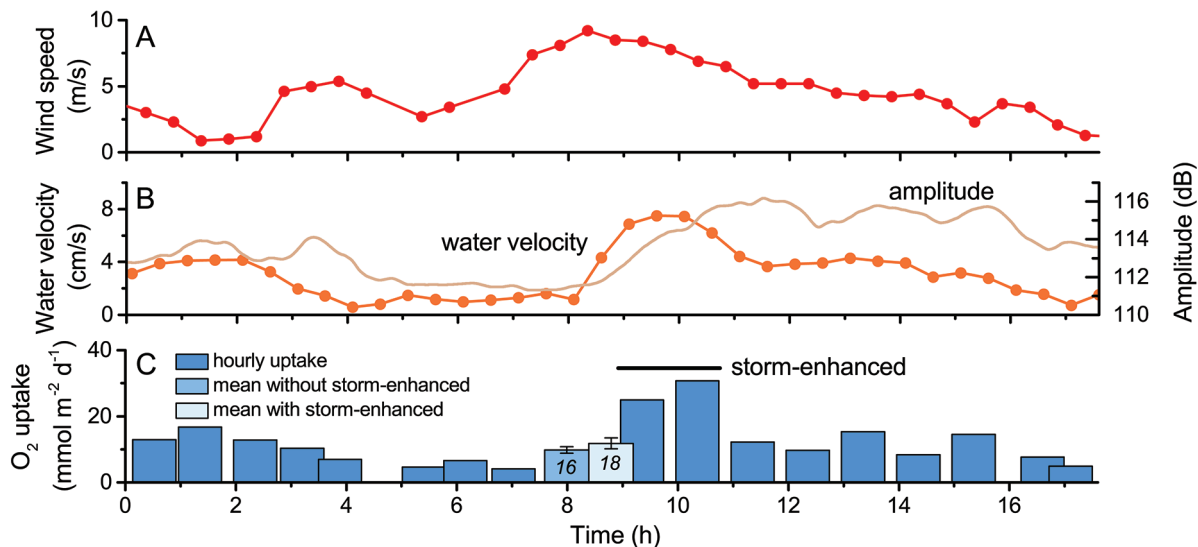

Figure 3. A storm caused a transient increase in benthic oxygen uptake determined with eddy covariance at Station 17 in Green Bay, Lake Michigan, USA, in August of 2014. Time series of wind speed (A), bottom water velocity, and acoustic amplitude as a proxy for sediment suspension (B). Oxygen uptake increased with the storm-enhanced increase in water velocity (C). Excluding storm-enhanced fluxes, the mean (±SE) uptake was 9.8 ± 1.0 mmol m^{-2} d^{-1}, $n = 16$ hourly intervals. Including storm-enhanced fluxes, the mean uptake was 11.8 ± 1.7 mmol m^{-2} d^{-1}, $n = 18$ hourly intervals.
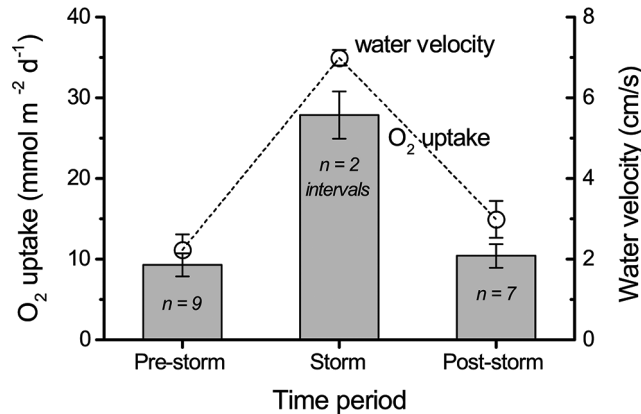
Figure 4. The effect of a storm on bottom water velocities and benthic oxygen uptake at Station 17 in Green Bay, Lake Michigan, USA, in August of 2014. During the period of enhanced velocity (Storm) oxygen uptake was enhanced (mean ± SE = 27.9 ± 2.9 mmol m^{-2} d^{-1}, with n equal to the number of hourly flux intervals) relative to Pre-storm (9.3 ± 1.4 mmol m^{-2} d^{-1}) and Post-storm (10.4 ± 1.4 mmol m^{-2} d^{-1}).

at Station 21 (Tukey's HSD, $p = 0.001$; Fig. 6). In contrast, the mean core incubation uptake at Station 17 was only 30% greater than at Station 21, but with a Tukey's HSD p-value of 0.907, we are not confident that the difference is real.

DISCUSSION

The novel aspect of our work was the combined use of aquatic eddy covariance and core incubation to quantify benthic oxygen uptake in a freshwater environment with cohesive sediments. Our primary goal was to examine spatial and hour-to-hour variability in uptake as a driver of hypolimnetic hypoxia. We found that uptake was high in the southern portion of the bay, closer to the outlet of the Fox River. Among the 3 northern sites, uptake was higher at the shallower of the high deposition sites. More surprisingly, eddy covariance revealed high variability in benthic oxygen uptake over time, with increases and decreases in water velocity at each station causing increases and decreases in uptake. A summer storm, observed during eddy covariance measurements at Station 17, caused even greater uptake at greater water velocities. Our secondary goal was to evaluate the effectiveness of core incubation at reproducing in situ rates of uptake. Broadly, time-averaged eddy covariance uptake and core incubation uptake agreed well. In the following sections, we first discuss the variation in dissolved oxygen uptake over time at each station, its implication for redox cycling in sediments, and how its net effect on organic matter mineralization may nevertheless be limited. We then examine time-averaged eddy covariance uptake and compare it to core incubation uptake to consider strengths of the techniques, explanations for the general pattern of uptake in the bay, and a 1st-order examination of the contribution of benthic oxygen uptake to hypolimnetic hypoxia.

Velocity-dependent oscillations in oxygen uptake

Eddy covariance oxygen fluxes responded dynamically to water velocity at all stations. Seiche-driven oscillations in water velocity caused approximately proportional increases and decreases in oxygen flux (Fig. 5). A further increase in bottom-water velocity during a summer storm caused a further doubling of eddy covariance oxygen flux at Station 17 (Fig. 4). Eddy covariance measures a water-column dissolved oxygen flux, yet we suggest that the time-varying oxygen flux was caused by time-varying benthic oxygen uptake based on the presence of turbulent contributions to flux even when turbulent contributions were at a minimum (Figs S6, S7). Our analysis also suggests that variations in the storage of oxygen in the water column could not explain the variations in flux that we observed (further details in Methods; Fig. S8). Ours is not the only study to find that oxygen uptake in cohesive sediments is highly dynamic. A similar dependence of oxygen uptake in cohesive sediments on water velocity occurs in other lakes (Lorke et al. 2003, Brand et al. 2008, Bryant et al. 2010a) as well as rivers (Murniati et al. 2015), sea lochs (Glud et al. 2016), and deep-sea sediments (Donis et al. 2016). This dependence has also been reproduced in models of the effect of seiche-induced oscillations in diffusive boundary layer thickness on benthic oxygen uptake (Brand et al. 2009). Our results confirm theoretical and laboratory investigations indicating that benthic oxygen uptake is linearly dependent on water velocity at water velocities <10 cm/s (Nakamura and Stefan 1994, Mackenthun and Stefan 1998).

We would expect increases in water velocity to cause a particularly strong increase in benthic oxygen uptake where benthic organic matter mineralization is limited by oxygen availability. We can examine if this scenario was the case in our study by comparing the residence time of oxygen in
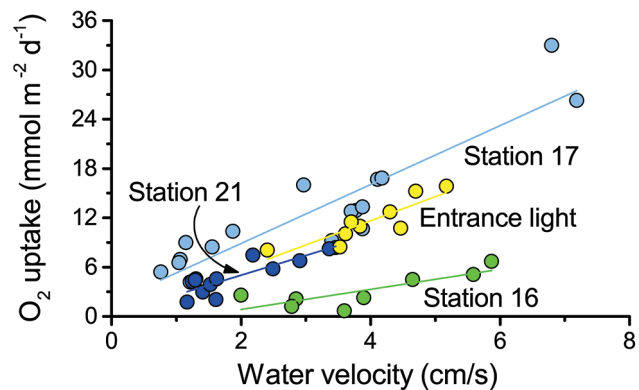

Figure 5. Hourly eddy covariance benthic oxygen uptake at 4 stations in Green Bay, Lake Michigan, USA, plotted as a function of water velocity. The least-squares linear regressions of the Entrance light, Station 16, Station 17, and Station 21 have $p = 0.002$, $p = 0.014$, $p < 0.001$, and $p < 0.001$, respectively, and have adjusted R^2 between 0.61 (Station 16) and 0.83 (Station 17).
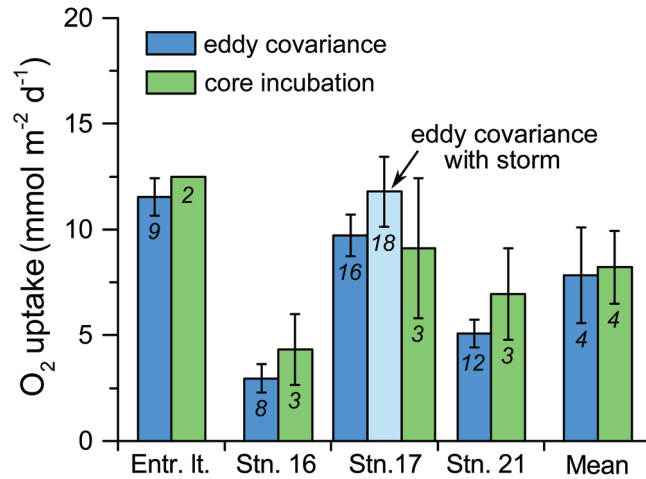
Figure 6. Comparison of benthic oxygen uptake determined with time-averaged eddy covariance and core incubation at 4 stations in Green Bay, Lake Michigan, USA (±SE, n is the number of hourly eddy covariance flux intervals or the number of cores incubated). Mean represents the mean across stations, where n refers to the number of stations. Eddy covariance with storm is the time-averaged uptake including 2 h of storm-enhanced uptake.

sediments to its transport time through the diffusive boundary layer. The residence time is calculated as the areal oxygen content of sediments divided by uptake. Based on oxygen microsensor profiles in Green Bay sediments determined by Klump et al. (2009), the oxygen penetration depth at Stations 9 (12 km NE of Entrance light), 17, and 21 were 4, 5, and 15 mm, respectively. The areal oxygen content of these 3 stations was 0.30, 0.45, and 1.12 mmol O_2/m^2, respectively. Based on time-averaged eddy covariance oxygen uptakes of 11.5 mmol m^{-2} d^{-1} at Entrance light, 9.8 mmol m^{-2} d^{-1} at Station 17 (excluding storm-enhanced uptake), and 5.1 mmol m^{-2} d^{-1} at Station 21 (Fig. 6), the residence times of dissolved oxygen in sediments were 37, 66, and 316 min, respectively. The oxygen residence time may have been shorter during our study because of the low concentration of dissolved oxygen in the hypolimnion that we observed. Nevertheless, because the transport time of dissolved oxygen through the diffusive boundary layer of cohesive sediments is only 1 to 9 min (Jørgensen and Revsbech 1985), these 1st-order calculations indicate that organic matter mineralization was not limited by the thickness of the diffusive boundary layer in our study.

An explanation for why oxygen does not appear to limit organic matter mineralization in Green Bay is that this effect is most likely to occur where C deposition is high and oxygen penetration depths are at a minimum (Wüest and Lorke 2003). The mean C deposition at our high deposition stations (Stations 17 and 21, 3.2 mol C m^{-2} y^{-1}; Table 1) is not particularly high for freshwater. An example of a very high C deposition site is at the Rhine inflow of Lake Con-

stance on the border of Switzerland and Germany, where deposition is 26 mol C m^{-2} y^{-1} (Sobek et al. 2009). In Lake Constance sediments, the oxygen penetration depth is 2 mm, and oxygen uptake matches our study. Therefore, the residence time of dissolved oxygen in those surficial sediments would be much shorter than we observed in Green Bay, making C mineralization in those sediments more likely to be limited by oxygen availability.

In Green Bay sediments, the increased benthic oxygen uptake at increased water velocity (Fig. 5) can be explained by transient changes in the distribution and consumption of dissolved oxygen in sediments. At a given water velocity and diffusive boundary layer thickness, an equilibrium dissolved-oxygen profile develops in sediments because of the balance of sediment oxygen consumption and the supply of oxygen through the diffusive boundary layer. As water velocity increases and the diffusive boundary layer is compressed, dissolved oxygen supply increases, and the dissolved oxygen profile is altered, with enhanced oxygen penetration into surficial sediments. This series of events, in turn, can increase biotic and abiotic oxidation of reduced compounds (e.g., NH_4^+, H_2S, Fe^{2+}). In Lake Alpnach, Switzerland, water velocities falling from 1.5 to 0.5 cm/s caused oxygen penetration depths to diminish from 2.3 to 0.9 mm (Bryant et al. 2010a). The maximum oxygen concentration in sediments fell from 55 to 5 μmol/L. At the same time, benthic oxygen uptake, determined from dissolved oxygen microprofiles across the sediment–water interface, diminished from 6.8 to 1 mmol m^{-2} d^{-1}. That variation in uptake is similar to what we observed at Station 16. We would expect greater oscillations in oxygen penetration of sediments to occur to drive the greater variations in uptake at Entrance light and Station 17. These large variations in oxygenation of sediments could be supported by processes other than diffusion. For example, periodic replacement of water at the sediment–water interface by turbulent sweep and eject motions would deliver oxygen to surficial sediments more rapidly than by diffusion alone (Røy et al. 2002, Hondzo et al. 2005, O'Connor and Hondzo 2008). However, where organic matter mineralization is not oxidant limited, as appears to be the case in our study sites, the net effect of greater oxygenation on time-averaged organic C mineralization may be minimal (Glud et al. 2007, Brand et al. 2009). That prediction is supported by the general agreement that we observed between time-averaged eddy covariance oxygen uptake and core incubation oxygen uptake. If organic C mineralization was limited by oxygen delivery to sediments, we would expect that the differences in hydrodynamic conditions in situ versus in incubated cores could cause substantial differences in measured rates of uptake. Instead, the results of the measurements were generally similar.

Despite a general lack of evidence from the current study, counter evidence from other studies suggests that oscillations in benthic oxygen uptake and co-occurring oscillations in

oxygenation of surficial sediments may affect net benthic organic matter mineralization. The burial efficiency of organic C in freshwater and marine systems diminishes with oxygen exposure time (Hartnett et al. 1998, Sobek et al. 2009). In lakes, Sobek et al. (2009) found that a $10\times$ increase in oxygen exposure would yield a 15% increase in remineralization efficiency of allochthonous C. This effect is small, but in specific cases the effects of varying oxygen exposure may be greater. For instance, oxygen exposure substantially enhances the degradation rate of refractory and degraded organic matter (Kristensen et al. 1995, Burdige 2007, Middelburg and Levin 2009). Phytoplankton-derived particulate organic C can be mineralized $5\times$ faster under oxic than anoxic conditions (Harvey et al. 1995). Hypolimnetic hypoxia can reduce benthic organic matter mineralization by 50% (Jessen et al. 2017). Furthermore, oxic–anoxic oscillations enhance C and N cycling in cohesive marine sediments (Aller 1994, Gilbert et al. 2016), enhance organic matter mineralization in fluid muds (Abril et al. 1999, 2010), increase chloropigment degradation (Sun et al. 1993), and increase organic matter mineralization where it is limited by bacterial production (Dauwe et al. 2001). Finally, seiche-driven oscillations in bottom-water velocity can cause transient N-species flux deviations of 60% (Brand et al. 2008).

Effect of storms on ecosystem metabolism

Lake ecosystem metabolism is generally determined from measurements of dissolved oxygen in surface waters and calculation of gas exchange across the water surface (Staehr et al. 2010, Solomon et al. 2013). These measurements capture the effect of the net transfer of low-oxygen water in the hypolimnion to the epilimnion, but they may miss the effect of storms on respiration within the hypolimnion. Based on prior studies of lake ecosystem metabolism, storms cause a shift toward net heterotrophy that is fueled by an increase in external inputs (Tsai et al. 2008, Klug et al. 2012, Vachon and Del Giorgio 2014). Through our use of the eddy covariance technique, we found that a storm also greatly enhanced the flux of oxygen into hypolimnion sediments (Fig. 4). However, the enhanced uptake did not diminish the concentration of oxygen within the hypolimnion (Fig. S5), which is likely because the elevated water velocities enhanced the exchange of dissolved oxygen across the thermocline. These observations are consistent with enhanced benthic oxygen uptake caused by oxidation of reduced species during resuspension events (Almroth et al. 2009, Toussaint et al. 2014).

Eddy covariance vs core incubation

The difference between benthic oxygen uptake determined by eddy covariance and by core incubation was not substantial at any station. The similarity between the 2 techniques is consistent with observations that the diffusive boundary layer thickness does not strongly affect benthic

uptake in sediment cores (Tengberg et al. 2004). Prior comparisons of eddy covariance and chamber/core incubation techniques in cohesive marine sediments have also generally found that the 2 techniques agreed with each other. In Danish coastal bays, eddy covariance oxygen flux exceeded benthic chamber fluxes by 15 to 40% (Berg et al. 2003). In other comparisons, mean eddy covariance uptake has been 2 to 20% lower than the mean uptake determined with benthic chambers, although statistical analyses indicate the differences may not be real (Berg et al. 2009, Reimers et al. 2012, Donis et al. 2016, Glud et al. 2016). Differences that do exist may result from disturbance of sediment (Reimers and Smith 1986), disturbance of macrofauna (Glud 2008), or other alterations of in-situ conditions that occur when inserting chambers into sediments or collecting sediment cores for incubation.

We can examine if the disturbance of macrofauna could have contributed to the differences in uptake between the 2 techniques. The primary macrofauna in Green Bay sediments are benthic invertebrates of the Chironimidae and Nematoda families (Kaster et al. 2018). At high density, chironimids enhance benthic oxygen uptake (Svensson and Leonardson 1996). In Green Bay, we identified chironimids and determined their density by observation of the number of their emergent tubes in box cores collected at the sites. In Green Bay, chironimids are abundant near Entrance light (1000–2000 ind./m^2; Kaster et al. 2018), but we did not observe any of their emergent tubes in sediment collected there. However, emergent chironomid tubes were present in box-core sediment collected at Station 16 at a density of ~300 ind./m^2, and a few were included in sediment-core incubations. At both Entrance light and Station 16, the mean time-averaged core-incubation uptake agreed with, or was slightly greater than, uptake determined with eddy covariance. Therefore, core incubation of sediments with chironimids did not diminish oxygen uptake relative to eddy covariance measurements. Further work would be needed to determine if other macrofauna may have had an effect.

Spatial pattern of benthic oxygen uptake

The broad pattern of benthic oxygen uptake in Green Bay determined by eddy covariance was of similarly high uptake in the shallow waters of Entrance light and at Station 17 but with uptake at ≤½ this rate at Stations 21 and 16 (Fig. 6). Station 16 is the shallowest of the 3 northerly stations, and it sits outside of the area of high C deposition (Fig. 1). The lower uptake at that station is likely due to the lower deposition of organic material, but low dissolved oxygen concentrations in the hypolimnion could also contribute (e.g., Lichtschlag et al. 2015). The explanation for the lower uptake at Station 21 than at Station 17 is not clear from the data that we collected. However, a potential explanation for this difference is the heterogeneous deposition of phytoplankton-derived organic material. In a coastal bay

with substantial terrestrial input, the mineralization of labile, plankton-derived material may nevertheless account for almost all of benthic oxygen consumption (Hedges et al. 1988). The highest abundance of phytoplankton in Green Bay is commonly near the Fox River mouth and in shore-parallel flow along the west and east sides of the bay (Fig. 1). On cell death, phytoplankton-derived particulate organic material would be preferentially transported down-slope towards depositional areas in the lower bay, passing through Station 17 before Station 21. The turnover time of phytoplankton-derived particulate organic C is short, between 20 and 30 d under oxygenated conditions (Harvey et al. 1995), which is similar to the travel time (22 d) for water between the 2 stations (calculated from the observed net northward current of 0.44 cm/s at Station 21). Therefore, the fraction of plankton-derived organic material that is labile at Station 17 may be degraded by the time it reaches Station 21. This explanation is consistent with more widespread observations in Green Bay that uptake is driven by recent deposition, as tracked by beryllium-7 (^{7}Be) (JVK, unpublished). The long distance (39 km) between the source of eutrophication at the Fox River mouth and the high rate of uptake at Station 17 is consistent with other eutrophic environments with a strong depositional gradient. In Lake Erie and Chesapeake Bay, for instance, benthic oxygen uptake in the central basin often exceeds that closer to the riverine sources of eutrophication (Cowan and Boynton 1996, Matisoff and Neeson 2005). These patterns support the evidence that organic matter lability is important in driving sediment oxygen demand (Grant and Hargrave 1987).

Comparison of oxygen uptake across systems

The range of benthic oxygen uptake in Green Bay was consistent with the range observed in Lake Erie's western and central basins (Matisoff and Neeson 2005) and exceeded uptake in nearby Lake Superior (Li et al. 2012). Li et al. (2012) demonstrate that benthic organic C mineralization in Lake Superior occurs at a similar rate as in marine pelagic and hemipelagic sediments exposed to similar sedimentation rates (using data from Canfield 1989, 1994, Burdige 2007). That uptake in autochthonous freshwater sediments can be predicted using a relationship between uptake and sedimentation rate determined in marine environments is broadly supported across a wide range of sedimentation rates in lakes dominated by autochthonous inputs (Sobek et al. 2009). In Green Bay, sedimentation is predominantly allochthonous (~81%; Klump et al. 2009), and the mean sedimentation rate of the Green Bay stations was 0.05 g C cm^{-2} y^{-1} (Klump et al. 2009). A rate of deposition of 0.05 g C cm^{-2} y^{-1} in coastal marine systems, where sedimentation is autochthonous, would be expected to yield uptake on the order of 3.5 mol m^{-2} y^{-1}, equivalent to 10 mmol m^{-2} d^{-1} (Li et al. 2012). However, the similarity of this estimate to our observed mean eddy covariance uptake of 7.8 ± 2.3 mmol m^{-2} d^{-1} (across stations) is not as close as it appears, once the influence of temperature is considered. Bottom-water temperatures at the stations in our study range from 2°C in winter to 15°C in summer, and benthic organic matter mineralization is strongly temperature dependent. To generate an annual mineralization rate with a mean of 10 mmol m^{-2} d^{-1}, uptake at peak temperatures in July, August, and September would need to be ~2× greater than the observed value (for temperature dependence of organic matter mineralization in Green Bay sediments see Klump et al. 2009). The high contribution of allochthonous, less-labile material in Green Bay may contribute to the relatively low rate of uptake that we observed.

Contribution to hypolimnetic hypoxia

The primary goal of our study's measurements was to investigate the contribution of benthic oxygen uptake to the development of hypolimnetic hypoxia. Based on 1st-order estimates, uptake appears to be adequate to drive hypolimnetic hypoxia in waters where the hypolimnion is only a few meters thick. As an example, hypolimnetic oxygen depletion can be estimated from monthly observations of hypolimnetic dissolved oxygen. Based on prior work, in July 2011, a hypoxic (<63 µmol O$_2$/L) region of 150 km^2 formed in the hypolimnion on the east side of Green Bay (Klump et al. 2018). A month prior, dissolved oxygen had been near saturation (225 µmol O$_2$/L). Given a hypolimnion thickness of 1 m, and a 1st-order assumption that no oxygen was transferred from the epilimnion to the hypolimnion during the month, the areal oxygen consumption would have to be 5.4 mmol m^{-2} d^{-1} to drive this event. That value represents 70% of the mean eddy covariance benthic uptake (7.8 mmol m^{-2} d^{-1} across sites) found in the current study, indicating that benthic uptake is sufficient to drive hypolimnetic hypoxia, at least at relatively shallower depths.

Hypolimnetic hypoxia also occurs to the north of our stations at greater water depths, where the hypolimnion thickness is greater than a few meters. Our results, in combination with companion measurements of benthic oxygen uptake by core incubation at other stations (LaBuhn 2016), suggest that benthic uptake alone is insufficient to drive hypolimnetic hypoxia at those greater depths. Benthic uptake at greater depths is similar to what we observed in this study. The development of hypolimnetic hypoxia would require an additional oxygen sink to deplete dissolved oxygen at a similar rate from the substantially thicker hypolimnion. These observations are consistent with evidence that the thickness of the hypolimnion contributes substantially to the development of hypolimnetic hypoxia in lakes (Müller et al. 2012, Bouffard et al. 2013). These findings suggest that oxygen is removed from the deeper waters because of the combination of benthic oxygen uptake and oxygen consumption in the water column of the hypolimnion.

Study limitations

Among the limitations of our study are the low number of observations that were made and also a scarcity of measurements to support the suggested implications of our work. The similarity of benthic oxygen uptake near the Fox River mouth and in shallower water of the depositional area is based on measurements at single stations. Likewise, the observation of an increase in uptake with depth at the high deposition stations was based on measurements at single stations. Without additional stations, the confidence one can have in drawing inferences about patterns of oxygen uptake in Green Bay is limited. Additionally, all of our measurements were made in August or September, and 3 of the 4 stations were visited only once. We (SB and VK) address these shortcomings in a companion study in which the core incubation technique was used to quantify benthic oxygen uptake at dozens of stations in lower Green Bay, with many station revisits during spring, summer, and autumn across years (LaBuhn 2016).

An additional limitation is our lack of independent measurements to confirm that these oscillations in water velocity can drive such substantial oscillations in benthic oxygen uptake in Green Bay sediments. In support of that suggestion, many prior studies have documented substantial changes in benthic oxygen uptake as a function of water velocity (or diffusive boundary layer thickness; Mackenthun and Stefan 1998, Røy et al. 2002, Hondzo et al. 2005). Our confidence in making this assertion also relies on the strength of in-situ studies in Lake Alpnach, Switzerland, where seiche-driven oscillations in water velocity cause $4\times$ variations in oxygen uptake (Bryant et al. 2010a, b). Bryant et al. (2010a) found remarkable variations in oxygen availability in sediments (a $10\times$ decrease in dissolved oxygen concentration in surficial sediments) as water velocities dropped from 1.5 to 0.5 cm/s. Nevertheless, our study would benefit from time series measurements of dissolved oxygen in Green Bay sediments.

Conclusions

Benthic oxygen uptake determined from hour-to-hour with eddy covariance was highly dynamic, responding to seiche-driven oscillations in bottom-water velocity and doubling during a summer storm. These variations in uptake are likely due to oscillations in the dissolved-oxygen penetration of surficial sediments as well as exposure of chemically reduced sediments by sediment resuspension during the storm. Therefore, these results suggest that the anoxic–oxic boundary in cohesive sediments is not static but fluctuates with oscillations in water velocity. Velocity oscillations are ubiquitous over freshwater and marine cohesive sediments, yet the effect of these processes on net solute fluxes is poorly understood. The time-averaged oxygen uptake determined with aquatic eddy covariance generally matched uptake determined with core incubation. Nevertheless, the eddy covariance technique revealed a difference that was not revealed with the core-incubation technique. As a result, eddy covariance improved our understanding of the drivers of benthic oxygen uptake in cohesive sediments in this study.

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