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SPECIAL ISSUE-LETTER

Oxygen dynamics control the burial of organic carbon in a eutrophic reservoir

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Scientific Significance Statement

Oxygen concentrations are changing in lakes and reservoirs globally, which may have substantial consequences for the balance of organic carbon (OC) burial and respiration in these ecosystems. However, the vast majority of previous studies on the control of oxygen on OC cycling have been conducted in the laboratory or in mesocosms, so the ecosystem-level effects of changing oxygen dynamics at the daily or weekly scale on OC burial and respiration are unknown. A whole-reservoir oxygenation experiment and mass balance model demonstrate that short-term variability in oxygen availability at the sediment–water interface can have major effects on OC fate, resulting in ecosystem-scale OC burial alternating between positive and negative rates.

Abstract

Organic carbon (OC) mineralization in freshwaters is dependent on oxygen availability near the sediments, which controls whether OC inputs will be buried or respired. However, oxygen dynamics in waterbodies are changing globally due to land use and climate, and the consequences of variable oxygen conditions for OC burial are unknown. We manipulated hypolimnetic oxygen availability in a whole-reservoir experiment and used a mass balance OC model to quantify rates of OC burial. Throughout summer stratification, we observed that OC burial rates were tightly coupled to sediment oxygen concentrations: oxic conditions promoted the mineralization of "legacy" OC that had accumulated over years of sedimentation, resulting in negative OC burial. Moreover, our study demonstrates that fluctuating oxygen conditions can switch ecosystem-scale OC burial in a reservoir between positive and negative rates. Consequently, changing oxygen availability in freshwaters globally will likely have large implications for the role of these ecosystems as OC sinks.

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Author Contribution Statement: CCC and PCH developed the idea for this study. CCC led the whole-ecosystem experiment with the assistance of JPD and RPM, and PCH developed the OC model. CCC, JPD, and RPM analyzed field data. CCC led the interpretation of the data and writing of the manuscript; all co-authors contributed to writing.

Data Availability Statement: Data are available in the Environmental Data Initiative (EDI) repository at https://doi.org/10.6073/pasta/10545e44a05b1a688c1561d602ca8a62.

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Freshwaters receive and process a vast amount of organic carbon (OC), which can be buried in the sediments or mineralized to carbon dioxide (CO_2) or methane (CH_4) after it is deposited onto the sediment surface (Downing et al. 2008; Knoll et al. 2014). While burial is typically a small part of the OC budget in lakes and reservoirs and often overlooked in process-based models, burial governs the role freshwaters play in long-term C cycling (Buffam et al. 2011). Therefore, understanding the controls of OC burial in freshwater ecosystems is paramount for constraining the global C budget. However, there are significant gaps in our knowledge of the factors controlling OC burial (Hanson et al. 2015): in particular, little is known about how changes in oxygen dynamics near the sediments alter ecosystem-scale OC burial in lakes and reservoirs (Bastviken et al. 2004; Maerki et al. 2009; Sobek et al. 2009).

Global changes in oxygen availability in the hypolimnia of lakes and reservoirs due to climate and land use may have major implications on long-term OC balance in freshwaters. At the decadal scale, many waterbodies are exhibiting increased seasonal hypolimnetic anoxia as a result of eutrophication, warmer temperatures, and stronger thermal stratification (Marcé et al. 2010; Jenny et al. 2016). Simultaneously, many waterbodies are experiencing more powerful summer storms at the daily scale that initiate mixing and trigger rapid changes in oxygen availability (e.g., Klug et al. 2012). For example, monitoring of Lake Erie demonstrates that storms can alleviate anoxia at the sediments and drive substantial variability in hypolimnetic oxygen (Perello et al. 2017). As a result, many lakes and reservoirs will increasingly experience large and rapid shifts in hypolimnetic oxygen conditions during the summer stratified period. Prior studies have primarily examined this topic in the laboratory (e.g., Bastviken et al. 2004); thus, it remains unknown how rapid changes in oxygen availability, independent of changes in temperature or stratification, will interact to alter seasonal OC balance at the whole-ecosystem scale.

The interplay between hypolimnetic oxygen concentration and duration of sediment oxygen exposure is a crucial determinant of OC burial vs. mineralization. Oxygen concentrations and sediment exposure duration help determine the dominant pathways and rates of C mineralization, which in turn govern OC burial (Hedges et al. 1999; Bastviken et al. 2004; Maerki et al. 2009; Sobek et al. 2009). Under anoxic conditions, alternate terminal electron acceptors such as NO_3^-, Mn^{4+}, Fe^{3+}, SO_4^{2-}, and DIC/CO_2 become coupled with C mineralization, depending on their availability (Stumm and Morgan 1996). These anaerobic electron-accepting processes exhibit much lower OC mineralization rates than aerobic respiration (LaRowe and Van Cappellen 2011). Studies on sediment OC mineralization integrate the hypolimnetic oxygen concentration with the duration of oxygen contact time at the sediments by using a metric called oxygen exposure time (OET), calculated as the depth of oxygen penetration into the sediments divided by sedimentation rate (following Hartnett et al. 1998). OET has been shown to be positively correlated to OC mineralization (Hedges et al. 1999; Maerki et al. 2009; Sobek et al. 2009), but it remains unclear which component of OET—oxygen concentration or duration—is a more important determinant of OC burial.

We are interested in exploring oxygen–OC interactions in reservoirs (human-made lakes) because they are ubiquitous in the landscape and may bury up to 0.6 Pg yr^{-1} of OC globally (Dean and Gorham 1998; Regnier et al. 2013). This rate represents 20% of the combined terrestrial and freshwater C sink (Le Quéré et al. 2015) and 4× the annual burial rate in oceans (Ciais et al. 2013). Given that reservoirs usually have much larger catchments relative to naturally formed lakes (Doubek and Carey 2017), resulting in large inputs of OC, reservoir sediments provide a major, potentially persistent OC sink during anoxic conditions. However, an increase in oxygen availability at the sediments due to e.g., storm-driven mixing, an increase in oxygen in cold water inflows, or turnover, may promote the aerobic mineralization of "new" OC that has recently entered an ecosystem as well as "legacy" OC that has accumulated over years of sedimentation.

Here, we conducted a whole-ecosystem manipulation of hypolimnetic oxygen concentrations in a reservoir to study OC dynamics in both oxic and anoxic states. A whole-ecosystem manipulation provides an unparalleled opportunity to determine the in situ effects of oxygen on ecosystem-scale OC cycling. We used our observational data to calibrate a mass balance OC model that estimated the reservoir OC budget during the summer stratified period. The goals of the model were: (1) quantify important ecosystem rates (e.g., seasonal OC burial) that could not be characterized directly from field observations; (2) evaluate uncertainty in ecosystem rates and model predictions; (3) determine the relative importance of different drivers affecting OC burial (e.g., oxygen concentration and duration, temperature); and (4) explore the consequences of varying oxygen conditions for OC burial. We integrated the field experiment with model scenarios to address our overarching question: How do variable hypolimnetic oxygen conditions affect seasonal OC burial in a eutrophic reservoir?

Methods

Study site

We studied OC cycling in Falling Creek Reservoir (FCR), a small, eutrophic reservoir in a forested catchment in Vinton, Virginia, U.S.A. (37°18′12″N, 79°50′14″W; Fig. 1). FCR has a surface area of 0.12 km^2, a maximum depth of 9.3 m, and is primarily fed by one upstream tributary (Gerling et al. 2014, 2016). FCR has accumulated sediments since its construction in 1898 and has never been dredged (Supporting Information File 1).

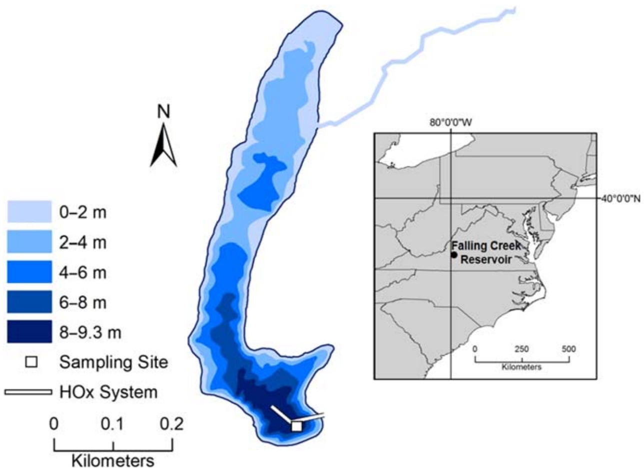

Fig. 1. Bathymetry and location of Falling Creek Reservoir (FCR), Virginia, U.S.A. The hypolimnetic oxygen (HOx) system is shown by the line on the map.

Whole-ecosystem experimental manipulation

FCR is a drinking water source managed by the Western Virginia Water Authority (WVWA), which installed a hypolimnetic oxygenation (HOx) system in the reservoir in 2012 (Supporting Information File 1; Gerling et al. 2014). HOx operation can increase oxygen concentrations in the bulk hypolimnion without altering thermal stratification or temperature (Gerling et al. 2014). We manipulated the hypolimnetic oxygen concentrations in FCR in 2014 by sequentially activating and deactivating the HOx system throughout the summer stratified period (10 June–06 October; Supporting Information File 1). We monitored FCR's thermal structure, oxygen, OC concentrations and loads, and water budget one to three times per week in summer 2014 following standard methods (Supporting Information File 1).

Mass balance OC model

We used a mass balance approach to quantify sources, sinks, and transformations of OC in FCR. For the whole reservoir, changes in OC through time can be represented as:

$$dOC/dt = \text{Allochthony} + \text{Autochthony} - \text{Respiration} - \text{Burial} - \text{Export} \quad (1)$$

where Allochthony represents all external sources of OC, including surface inflow and aerial inputs, Autochthony is net primary production within the reservoir, Respiration is all mineralization of OC to inorganic C, Burial is long-term burial in sediments, and Export is export via surface outflow (after Hanson et al. 2014).

We modeled the epilimnion (Supporting Information File 1: Table 2, Eq. 1) and hypolimnion (Supporting Information File 1: Table 2, Eq. 2) separately because oxygen conditions at the sediments during thermal stratification were a focus of this study. OC dynamics at the sediment–water interface were also modeled separately (Supporting Information File 2: Table 2, Eq. 3), thus allowing a relatively simple model to represent fluxes across the sediment–water interface for both epilimnetic and hypolimnetic strata. Rather than track sediment state variables, we modeled oxygen, OC, and CO_2 fluxes across the sediment–water interface and tracked the accumulation of these fluxes. Net OC burial was determined as the difference between sedimentation of OC and CO_2 efflux from the sediments (Supporting Information File 1: Table 2, Eq. 3e). Given the short duration of the simulation period, we assumed the OC sediment pool would not be depleted. While our approach obviates the need for modeling the complexities of sediment diagenesis, it constrains our inferences to the manifestations of sediment processes and how they contribute to balancing ecosystem-scale OC budgets. Because high oxygen availability elevates OC mineralization (Stumm and Morgan 1996), we included a sediment respiration enhancement term as a function of oxygen concentration (Supporting Information File 1: Table 2, Eq. 3f). We did not presume oxygen enhancement to be significant, but rather used the experimental design of this study, which included controlled periods of oxic and anoxic conditions, to fit the enhancement parameters and evaluate their significance. We also fit a water column dissolved OC (DOC) respiration parameter so that we could balance the relative contributions of sediment OC respiration and water column DOC respiration to dissolved gas and DOC concentrations (Supporting Information File 1: Table 3).

We used the mass balance model to estimate OC burial in FCR during the experimental manipulation. In addition, we estimated what burial rates would have been if oxygen was continuously added to the hypolimnion throughout the monitoring period and if no oxygen was added. Model constants, parameters, driver data, and uncertainty assessment are in Supporting Information File 1.

Model scenarios

We forced the calibrated mass balance model with different oxygenation scenarios to compare the relative importance of oxygen addition and duration at the sediments for OC burial in FCR. We examined the response of seasonal OC burial to three different sets of scenarios: the first set of $n = 2976$ scenarios compared the effects of oxygen addition vs. duration; the second set of $n = 2830$ scenarios examined the consequences of oxygenation timing to disentangle the effect of temperature at the sediments from oxygen concentration on OC burial; and the third set of 10,000 scenarios were bootstrapped from a uniform distribution of oxygen addition rates. Each season-long scenario consisted of varying oxygen addition, oxygenation duration, and oxygenation timing conditions throughout the summer stratified period with the same observed weather, hydrology, and temperature conditions in FCR (Supporting Information File 1). We calculated seasonal OC budgets for all simulations and

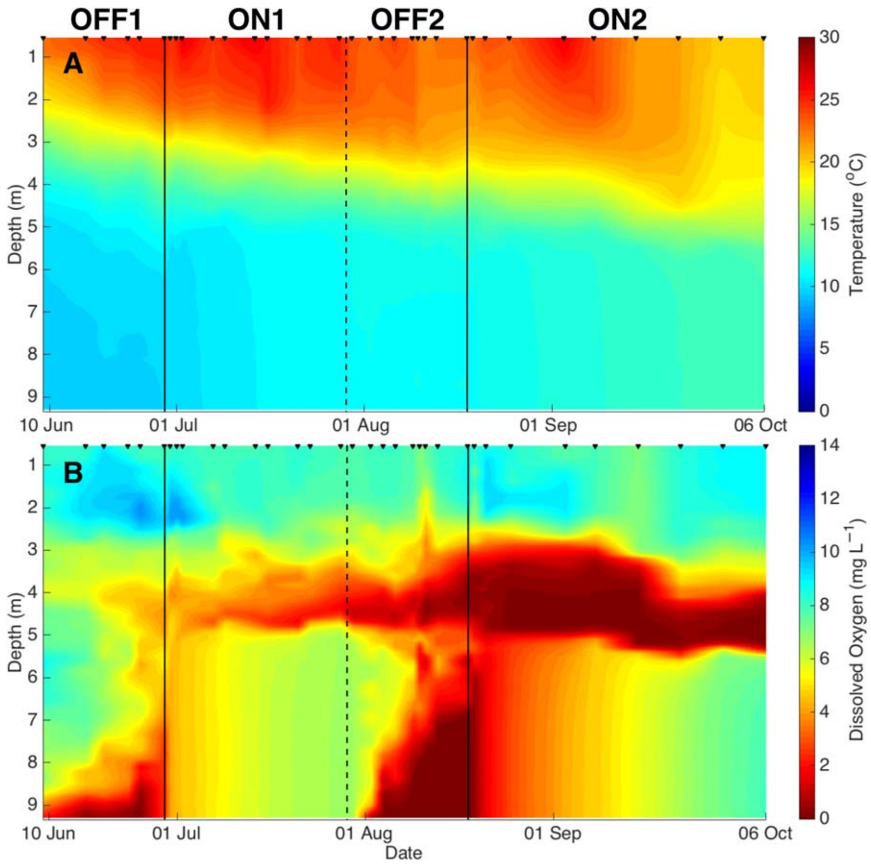

Fig. 2. Water temperature (**A**) and dissolved oxygen (**B**) profiles of Falling Creek Reservoir throughout the monitoring period. ON and OFF denote periods when the oxygenation system was activated and deactivated, respectively, and are separated by solid and dashed lines on the plots. The triangles on the top of the plots show sampling days; the intervening days were interpolated.

analyzed the output with multiple linear regression analysis and model selection (following Snortheim et al. 2017; Supporting Information File 1).

Results

Whole-ecosystem experimental manipulation

Oxygen concentrations in the hypolimnion responded rapidly to HOx system activation and deactivation (Fig. 2B). At the beginning of the monitoring period, the water just above the sediments was anoxic (< 1 mg L^{-1}), with hypoxia (< 2 mg L^{-1}) throughout the entire hypolimnion before the HOx was activated on 29 June 2014 (OFF1). Activation of the HOx immediately increased oxygen concentrations above 5 mg L^{-1} in the hypolimnion, which was well-mixed throughout the first oxygenation period (ON1). Anoxia at the sediments developed 3 d after oxygenation was deactivated in late July (OFF2). In the absence of oxygenation, DO depletion in the lower hypolimnion was much greater than in the upper hypolimnion, resulting in a metalimnetic oxygen minimum. The re-activation of oxygenation in mid-August homogenized the hypolimnion and resulted in uniformly increasing oxygen concentrations in August and September (ON2). It took $\sim$ 2 weeks longer for oxygen concentrations at the sediments to increase to 5 mg L^{-1} during ON2 than ON1, likely because the entire hypolimnion exhibited anoxia prior to ON2, vs. hypoxia prior to ON1. The thermal structure of the water column was not affected by oxygenation, with a mean thermocline depth of 3.4 ± 0.9 m (1 SD) throughout the summer (Fig. 2A). The metalimnetic oxygen minimum persisted until turnover in mid-October, after our monitoring ended.

Mass balance OC model

The mass budget OC model generally captured the observed oxygen, CO_2, and DOC dynamics (Fig. 3; RMSE values in Supporting Information File 2). Modeled hypolimnetic oxygen responded strongly to the deactivation of the HOx system, especially during the OFF2 period (Fig. 3A), and in general, CO_2 dynamics mirrored oxygen dynamics (Fig. 3C). Hypolimnetic DOC concentrations increased from a baseline of $\sim$ 2 mg L^{-1} during the ON periods to $\sim$ 3 mg L^{-1} during the OFF periods; the model replicated the observed pattern but underestimated DOC increases (Fig. 3E). In comparison

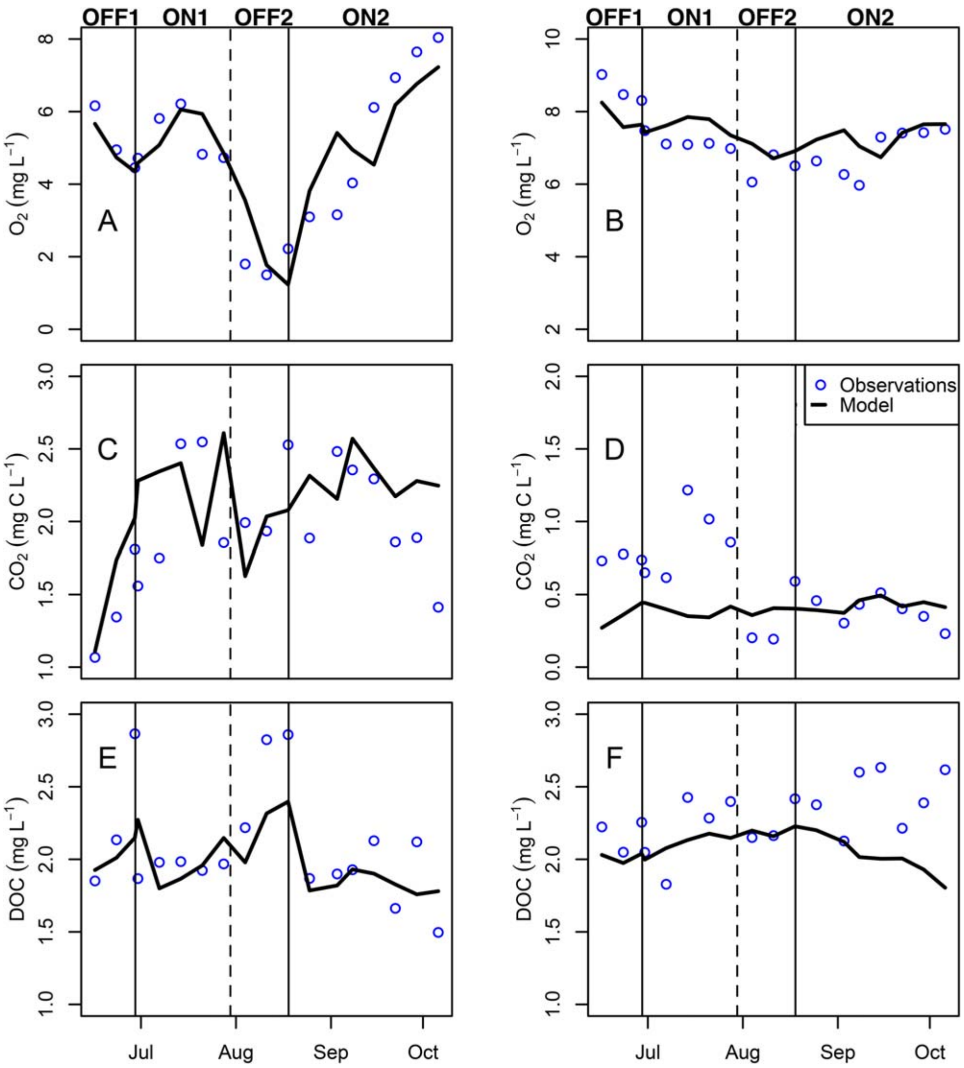

Fig. 3. Modeled (black line) and observed (blue circles) time series of oxygen (O_2, panels **A**, **B**), carbon dioxide (CO_2, panels **C**, **D**), and dissolved organic carbon (DOC, panels **E**, **F**) concentrations in the hypolimnion (left column) and epilimnion (right column) of Falling Creek Reservoir. ON and OFF denote periods when the oxygenation system was activated and deactivated, respectively, and are separated by solid and dashed lines on the plots.

to the hypolimnion, the observed epilimnetic oxygen and DOC concentrations did not substantially vary throughout the summer, which was replicated by the model (Fig. 3B,F). Observed epilimnetic CO_2 was more dynamic than what the model predicted, and elevated concentrations in early summer could not be explained by model processes (Fig. 3D).

During the experimental manipulation (black line in Fig. 4A; note that units are daily burial rates and not cumulative burial), daily OC burial rates varied between negative and positive values, primarily in response to changes in OC loads, export, and respiration. Negative OC burial indicates that more OC from the sediments (including accumulated “legacy” OC) was respired than was buried, whereas positive burial indicates OC storage in sediments. The effect of oxygen addition is demonstrated clearly by the contrast of observed OC daily burial rates with the burial rates that would have occurred if oxygen was continuously added throughout the simulation period (red line) or if no oxygen was added (blue dotted line). For example, during the OFF1 period, observed daily OC burial rates were mostly negative (black line; mean -0.04 ± 0.007 g m^{-2} d^{-1}, 1 SE). In comparison, if oxygen was always on, mean daily burial rates would have been approximately three times more negative than observed due to elevated sediment respiration (red line). The “oxygen always off” (blue line) is not visible during OFF1 because this scenario and the observed conditions exhibit identical daily burial rates. When the oxygen was activated in ON1, the daily burial rates for the “oxygen always on” scenario and the observed conditions become

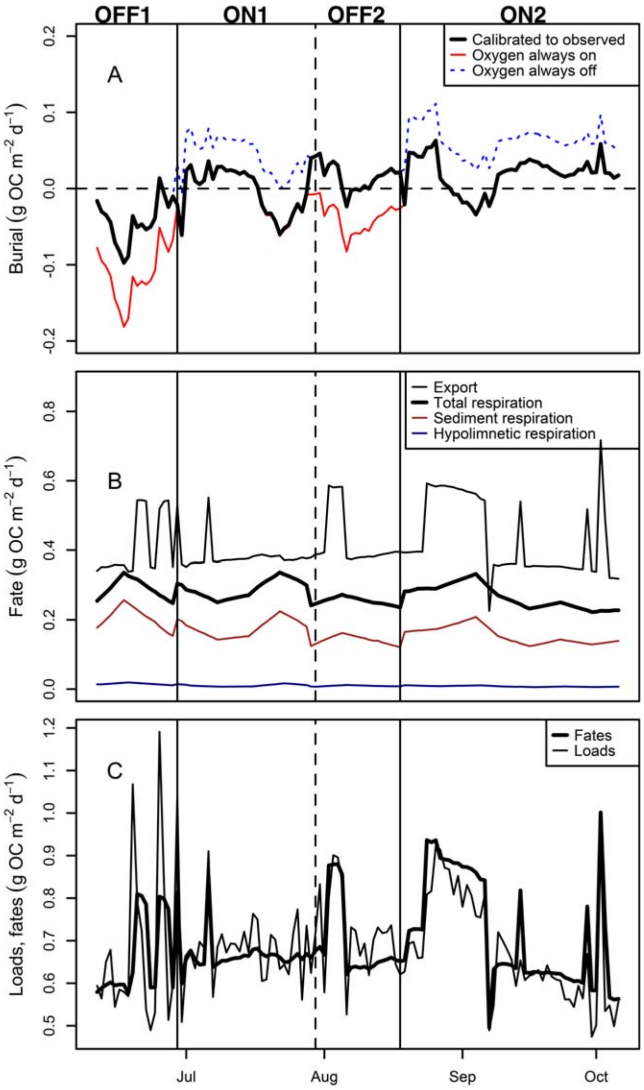

Fig. 4. The loads and fates of organic carbon (OC) in Falling Creek Reservoir. (**A**) Comparison of daily OC burial rates for observed conditions with alternating periods of oxygenation (black), if oxygen was continuously added to the hypolimnion throughout the simulation (red), and if no oxygen was added (dotted blue); (**B**) daily rates of export and respiration fate (total respiration is divided into sediment and hypolimnetic rates; the difference between total—(sediment + hypolimnetic) is due to epilimnetic respiration); and (**C**) total fates and total loads. ON and OFF denote periods when the oxygenation system was activated and deactivated, respectively, and are separated by solid and dashed lines on the plots.

identical, and are approximately seven times lower than in the "oxygen always off" scenario. This divergence highlights how much greater burial would have been if oxygen had not been added. Both the observed and "oxygen always on" daily burial rates become more positive during the onset of the ON1 period, but this was not due to changes in respiration, but rather due to changes in other components of the budget (Eq. 1), e.g., decreases in export (Fig. 4B).

The model predicted slightly positive cumulative OC burial summed across the study period (0.35 g m^{-2} or 1.07 g m^{-2} yr^{-1}). In comparison, if the reservoir was continuously oxygenated, seasonal burial would have been negative (−2.09 g m^{-2} or −6.41 g m^{-2} yr^{-1}), and if the reservoir was not oxygenated, seasonal burial would have been 11-fold higher than observed (3.96 g m^{-2} or 12.2 g m^{-2} yr^{-1}; Fig. 4A). Throughout the summer, the two dominant fates of OC in FCR were export downstream (50.4 ± 0.022 g m^{-2}) and respiration (30.8 ± 0.023 g m^{-2}; Fig. 4B). A comparison of total loads with total fate shows that the loads exceeded fate during all periods except for ON2, when the highest rate of oxygen was injected into the reservoir (Fig. 4C).

Estimates for the three model parameters were well constrained and significantly different from zero (Supporting Information File 1: Table 4). Sediment respiration increased at the initiation of both ON periods and represented 51–76% of whole-ecosystem respiration. Throughout the simulation period, sediment respiration was 13–22× higher than hypolimnetic respiration and 1.1–4.2× higher than epilimnetic respiration (Fig. 4B).

Model scenarios

The scenarios indicate that oxygen concentration was more important than oxygen duration in controlling OC burial in FCR (Fig. 5, Supporting Information File 3). For example, in the first set of scenarios, any simulation in which 150 kg of oxygen was added into FCR's hypolimnion over any time period lasting between 52 and 109 d resulted in similar seasonal OC burial (~ 3 g m^{-2}; Fig. 5), despite that the oxygen contact time was more than twice as long for the 109-d oxygenation simulation than the 52-d oxygenation simulation. Oxygen addition contributed 3–39% more variation in OC burial than oxygen duration across the three sets of simulations (Fig. 5, Supporting Information File 3).

Interestingly, the scenarios also reveal that temperature played a much less important role in controlling OC burial than oxygen addition, duration, or hypolimnetic surface area: in the second set of simulations, temperature at the hypolimnetic sediments only explained 10% of the variation in OC burial and was negatively correlated with mineralization rate (Supporting Information File 3). In contrast, hypolimnetic sediment surface area, which varied fourfold throughout the summer due to changes in the thermocline depth (Fig. 2A), explained 20% of the variation in OC burial and was positively correlated with mineralization rate. Altogether, oxygen addition, duration, and hypolimnetic area were the most important variables explaining OC burial in FCR.

Discussion

Increasing variability of oxygen concentrations in freshwaters may have implications for the global C budget by altering OC balance. Our modeling and field data suggest that oxic

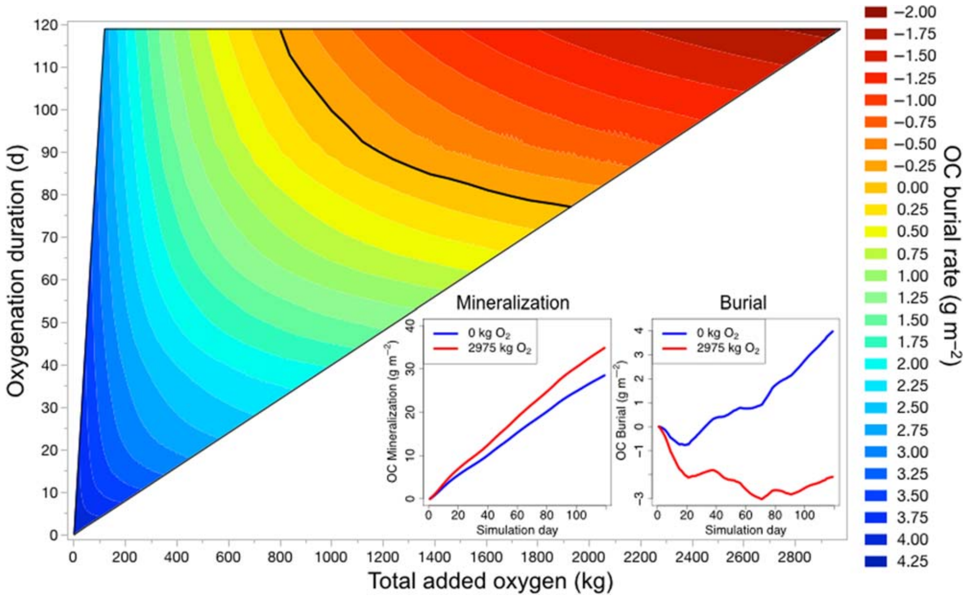

Fig. 5. Data from the first set of scenarios ($n = 2976$ unique season-long simulations total) indicate that seasonal organic carbon (OC) burial increased with total oxygen addition (kg) and oxygenation duration (d). The black line on the contour plot separates positive seasonal burial (blue, green, and yellow colors) from negative burial (red colors), in which legacy OC that had previously accumulated in the reservoir is respired. In the inlay plots, the time series of two contrasting scenarios are compared: the blue line refers to a scenario in which 0 kg of oxygen was added over the simulation period, resulting in cumulative OC burial of 4 g m^{-2}, and the red line refers to a scenario in which 2975 kg of oxygen was added, resulting in cumulative OC burial of −2 g m^{-2}. The left inlay plot shows cumulative mineralization and the right inlay plot shows cumulative burial throughout the simulation for both scenarios.

conditions promote not only the mineralization of "new" OC that has recently entered an ecosystem, but also "legacy" OC accumulated over years of sedimentation, resulting in negative OC burial. Conversely, increasing anoxia may lead to greater positive OC burial. Aggregated across summer 2014, FCR exhibited net positive OC burial, but as a result of whole-ecosystem oxygenation, we were able to transition the reservoir back and forth between negative and positive daily OC burial rates. Strikingly, our study indicates that short-term fluctuations in oxygen concentrations at the sediments can play a large role in controlling OC burial.

The mass budget model served a critical role in allowing us to evaluate the relative importance of different drivers affecting OC burial and generally replicated observed dynamics. In the absence of oxygenation, the model predicted ~ 12 g m^{-2} yr^{-1} of OC burial in FCR, which is within the observed range of other north temperate waterbodies: 0.22–1140 g m^{-2} yr^{-1} (Downing et al. 2008; Sobek et al. 2009; Knoll et al. 2014), but on the low end, likely because FCR is located in a forested catchment (Gerling et al. 2016). Similarly, our modeled FCR mineralization rates (varying from no oxygen added to continuous oxygenation: 87–107 g m^{-2} yr^{-1}) are within the observed range of 7–197 g m^{-2} yr^{-1} (Müller et al. 2005; Sobek et al. 2009). Integrating a whole-reservoir manipulation with an ecosystem model provided a powerful approach for quantifying whole-ecosystem OC stocks in the field under different oxygen conditions, and then quantifying whole-ecosystem rates (with their uncertainties) that cannot be directly measured with the model (e.g., oxygen enhancement of OC mineralization). Moreover, the integrated model and experiment, which examined the effects of oxygen on OC mineralization separately from temperature, enables scaling mineralization rates from FCR to other freshwater ecosystems on oxygen and temperature gradients by providing unbiased estimates of rate constants.

We used the oxygen scenarios to disentangle the effects of multiple drivers of OC respiration and burial, including oxygen concentration and duration. Our results indicate that observed relationships between OET and OC accumulation in sediments (e.g., Hedges et al. 1999; Maerki et al. 2009; Sobek et al. 2009) may be more driven by oxygen concentrations above the sediments than the length of time that the sediments have been exposed to oxygen, though both factors are important.

Interestingly, the scenarios indicate that sediment temperature was a less important driver of OC burial than hypolimnetic sediment surface area, likely because the temperature gradient was small (10–13.5°C) during the monitoring period. Throughout June–October, the thermocline depth ranged from 0.8 m to 5.3 m, which resulted in the hypolimnetic sediment surface area varying from $\sim$ 14,000 to 53,000 m^2 (mean $24{,}000 \pm 9000$ m^2, 1 SD). Increasing the sediment substrate area had a large positive effect on OC respiration during oxygenated conditions, and resulted in a surprising negative relationship between temperature and OC respiration because the periods with the warmest temperatures at the sediments in late summer coincided with when hypolimnetic sediment surface area was the smallest (Supporting Information File 3). As sediment surface area decreased, OC respiration decreased and burial increased, regardless of temperature. If we modeled the reservoir throughout the year, not just in the summer, we likely would have detected a positive effect of temperature on respiration, as expected (e.g., Gudasz et al. 2010).

Because of the inherent design of our experimental manipulations in FCR, our study has some limitations that may affect scaling to other systems. For example, the bathymetry of FCR—specifically, its long shallow upstream arm at approximately the depth of the thermocline (Fig. 1)—resulted in large changes in hypolimnetic sediment surface area when the thermocline fluctuated. Hence, the important role of physics in governing OC burial in FCR may not be observed in natural lakes with less dendritic morphometry. In addition, because our research question was focused on the summer stratified period, OC rates may not be reflective of whole-year integrated averages, though we note that OC processing in the summer, when primary production and temperatures peak, likely dominates the yearly budget. Other limitations to our study include that we did not take into account microbial community dynamics, mixing by benthic organisms, OC chemical composition, and the effects of oxygen on the flux of reduced substances (e.g., ammonium) from the sediments, which indirectly alters OC mineralization (Hedges et al. 1999; Steinsberger et al. 2017).

Conclusions

Our study indicates that lakes and reservoirs experiencing increasing hypolimnetic anoxia due to land use and climate (e.g., Marcé et al. 2010; Jenny et al. 2016) will exhibit increasing OC burial rates in the future, providing a critically important C sink in the landscape. However, even short periods of increased oxygen at the sediments can significantly increase respiration rates, quickly reversing any gains in burial experienced during anoxia and potentially switching the waterbody from an OC sink to OC source. Consequently, the strong control of transient fluctuations in oxygen over OC cycling in FCR suggests that increasing short-term variability in oxygen conditions at the sediments may have substantial implications for long-term OC burial in many freshwater ecosystems.

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