Estuaries and Coasts
https://doi.org/10.1007/s12237-024-01404-0

Effects of Diel Oxygen Cycling and Benthic Macrofauna on Sediment Oxygen Demand

Kara J. Gadeken[1,2] · **Kelly M. Dorgan**[1,2]

Received: 26 April 2023 / Revised: 9 July 2024 / Accepted: 9 July 2024

Abstract

This field study examined how sediment macroinfauna change patterns of sediment oxygen demand (SOD) throughout a diel oxygen cycle. Sediments with a greater faunal presence would be expected to have greater overall SOD, and at night may alter their behavior and influence SOD depending on their response to low-oxygen stress. Dynamic faunal bioturbation or bioirrigation behavior would also result in corresponding variation in SOD values on short time scales. In situ flow-through benthic metabolism chambers were used to measure SOD at a high temporal resolution in discrete sediment patches. Sediments with more macroinfauna had greater average SOD over the diel cycle, consistent with previous studies. Where more macroinfauna were present, they drove greater SOD during nightly low oxygen, presumably by enhancing their burrowing and irrigation activities. SOD was also more variable on a sub-diel timescale in sediments with more macroinfauna. Sediment oxygen demand is dynamic and highly sensitive both temporally, on very short timescales, and spatially, in terms of resident fauna, and their interaction produces heretofore unaccounted complexity in patterns of SOD particularly in shallow coastal systems. Extrapolations of temporally and spatially limited SOD measurements to a system-wide scale that do not account for the short-term and spatially variable effects of fauna may produce imprecise and misleading estimates of this critical ecosystem function.

Keywords Oxygen · Diel · Sediment · Macrofauna · SOD · Metabolism

Introduction

Benthic macroinfauna can significantly enhance the flux of dissolved oxygen across the sediment–water interface, here referred to as sediment oxygen demand (SOD). Faunal respiration and burrowing and irrigating activities oxygenate deeper sediments and enhance microbial respiration of organic matter (Aller 1978; Fenchel 1996; Banta et al. 1999; Timmermann et al. 2006; Norling et al. 2007). These functions are often lost when the dissolved oxygen (DO) concentration in the overlying water is persistently low, which drives faunal mortality and typically lower SOD (Diaz and Rosenberg 1995; Rosenberg et al. 2001; Middelburg and Levin 2009; Seitz et al. 2009; Lehrter et al. 2012; Sturdivant et al. 2012; Gammal et al. 2017). However, in shallow, productive coastal environments oxygen availability in the water can vary dramatically on short timescales (Wenner et al. 2004), often following a diel cycle with high DO concentrations during peak light periods due to high photosynthesis rates and low DO concentrations at night driven by respiration (Tyler et al. 2009). One study on diel changes in benthic metabolism in coral reef sediments found a positive relationship between DO concentration and SOD, with a 2.8-fold increase in flux between minimum and maximum DO (Clavier et al. 2008). Since it has become possible to measure sediment flux at high temporal resolution with the eddy correlation technique (Berg and Huettel 2008), oxygen fluxes in shallow, permeable sediments have been shown to have high variability between daytime and nighttime fluxes but also between successive measurements, taken on timescales of minutes to hours (Berg et al. 2013).

The influence of specific faunal taxa or constructed assemblages on SOD has been well studied using laboratory mesocosm experiments and has shown that the presence of

---

Communicated by Paul A. Montagna

Kara J. Gadeken
kgadeken@disl.org

[1] Dauphin Island Sea Lab, 101 Bienville Blvd,
Dauphin Island, AL 36528, USA

[2] University of South Alabama, Mobile, AL, USA

macroinfauna typically contributes to greater SOD (Banta et al. 1999; Vopel et al. 2003; Lohrer et al. 2004; Norling et al. 2007; Michaud et al. 2009). Though researchers rarely relate their in situ SOD measurements to the resident faunal community, studies which have examined this directly have found a positive relationship between total faunal biomass and SOD (Bolam et al. 2002; Clough et al. 2005). Total biomass is a useful but imperfect predictor as faunal taxa vary widely in their structure-forming, bioturbation, and bioirrigation activities, both in degree and in kind. Some taxa may have an outsized effect on SOD relative to their body size, such as small but abundant and highly active corophiid amphipods, or nereid worms that can construct and irrigate extensive burrow networks (Davey 1994; Zorn et al. 2006; De Backer et al. 2011; Kristensen et al. 2011).

A 2004 study by Wenzhofer and Glud investigated the relationship between the diurnal cycle and SOD in situ (Wenzhöfer and Glud 2004). They observed increased sediment oxygen uptake in benthic chambers at the onset of darkness which diminished throughout the night, in contrast to only minor diel changes in oxygen microprofiles. This difference, as well as diurnally fluctuating oxygen concentrations around faunal burrows observed with planar optodes, led the authors to attribute the changes in oxygen flux in part to light-driven diel rhythms of faunal activities. Specifically, the burrows of the sole faunal species found in the study sediments (the polychaete *Hediste diversocolor*) were intensively reworked and ventilated during nighttime hours. Though this and other studies have linked changing light to changes in both microphytobenthos-mediated oxygen fluxes and faunal behavior (Bartoli et al. 2003; Rosenberg and Lundberg 2004; Tang and Kristensen 2007), light exposure and oxygen availability have yet to be sufficiently decoupled and evaluated as drivers of diel-scale faunal activity.

Faunal responses to declining DO can be complex and their activities may not necessarily change directly with DO concentration. When DO is low but not lethal, many taxa will maintain or even increase their activity to manage the induced stress (Diaz and Rosenberg 1995; Riedel et al. 2014). For example, Gurr et al. found that the cardiac activity of the Atlantic bay scallop *Argopecten irradians* varied inversely with diel-cycling hypoxia, and that at moderately low DO (<5 mg O_2 L^{-1}), the scallop maintained its heart rate independent of DO concentration, but below 2 mg O_2 L^{-1} heart rate declined severely (Gurr et al. 2018). Infauna inhabiting sediments in shallow, productive waters where diel oxygen cycling occurs are likely acclimated to variability in oxygen availability, and particularly to short but repeating bouts of low DO. They may compensate by altering their irrigation, burrowing, and feeding activity, which may in turn affect sediment oxygen consumption over the day/night cycle. However, this variability remains largely undescribed since it is difficult to capture with existing methodologies.

In this field study, we examined how diel-varying oxygen concentrations and the presence of benthic macrofauna affect SOD throughout a diel cycle using a custom-built benthic chamber system to capture short-term temporal variability in adjacent sediments with differing faunal presence. We expected (H_1) that sediments with more infauna would exhibit greater SOD overall than less populated sediments. Further, we hypothesized that infauna would alter the relationship between DO and SOD; that either (H_{2A}) greater macroinfaunal presence would drive a more positive relationship between DO and SOD throughout the diel cycle, indicating that infauna decrease their activity (and their influence on SOD) during nightly low DO, or (H_{2B}) greater macroinfaunal presence would correspond to a flatter relationship between DO and SOD, indicating that infauna increase their activity during the nightly low DO. We also expected (H_3) that the presence of infauna would contribute to greater sub-diel variability in SOD, i.e., variability on the scale of minutes to hours, as behaviors can change on short time scales.

Methods

Experimental Design

We conducted the experiment at a shallow, sandy site in Bon Secour Bay, Mobile Bay, AL, (30.239478°, – 87.894094°), using custom-built in situ semi-flow-through benthic metabolism chambers (Gadeken et al. 2023). The site was subtidal (<1 m depth) and easily accessible from shore. Mobile Bay is a microtidal system with a mean diurnal tidal range of ~ 0.4 m (Webb and Marr 2016). The site is regularly exposed to strong wave action and the sediments in the shallow margin around Bon Secour Bay are clean, permeable sands (Ryan 1969; Davis 2017). Preliminary sampling at the site indicated there was a patchy community of infauna present, with large areas of sparsely populated sand dotted with tubes of the polychaete worm *Diopatra cuprea*.

A detailed description of the construction and operation of the in situ benthic chamber system is provided in Gadeken et al. 2023. The chamber setup consists of a central housing containing battery power and the electronics of the system and five replicate benthic chambers (Fig. 1). Each chamber encloses 0.017 m^2 of sediment surface area. When deployed, the chambers are pushed 15 cm vertically into the sediment with 5 cm protruding, which encloses 0.9 L of overlying water. The central housing controls and powers submersible pumps that are each attached to one of the chambers, as well as a pump that mixes the overlying water in the chambers. An Onset HOBO Dissolved Oxygen logger is secured through the lid of each chamber and takes DO measurements of the chamber overlying water every 2 min,

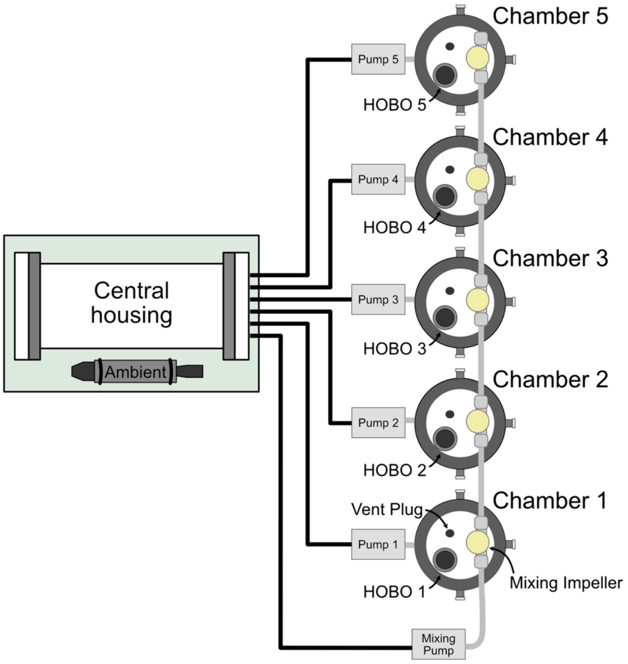


Fig. 1 Schematic of setup for custom-built flow-through chambers (reproduced from Gadeken et al. 2023). The central housing contains the batteries and electronics and the pumps are controlled via connections through a wet-mate bulkhead. The HOBO taking the Ambient DO measurement is secured to the platform with the chamber housing. During a measurement period, the flushing pumps (pumps 1–5) sequentially turn on to flush the overlying water in the chambers, and then the mixing pump is intermittently turned on to agitate the overlying water of all the chambers to prevent stagnation

and an additional HOBO DO logger is attached to the central housing platform and takes 2-min interval measurements of the ambient DO concentrations. The accuracy of DO measurements taken by the HOBO loggers is ± 6.25 µmol L^{-1} up to 250 µmol L^{-1}, and ± 15.6 µmol L^{-1} from 250 to 625 µmol L^{-1} (Johengen et al. 2016).

After being deployed, the chamber system is turned on. The system allows the chambers to incubate for a pre-set duration. Then, the overlying water enclosed in the chambers is flushed with water from the external environment, returning DO concentrations to the ambient level (as measured by the ambient DO logger). This repeats throughout the deployment and results in a sawtooth pattern in the DO concentrations within the chambers through time, with each tooth being a replicate incubation. The slopes of these incubations can be used to calculate SOD repeatedly and in association with a discrete area of sediment and the fauna within. SOD is influenced by many environmental, biological, and ecological processes, and given our research question and logistical constraints, there were limits on the factors that could be considered in the experimental design. Because the objective of this study was to isolate the effects of sediment fauna on SOD throughout the diel DO cycle, the chambers were shaded with a covering of opaque tape to prevent daytime photosynthesis within the chamber from confounding SOD measurements.

The chamber system was deployed midday and recovered the following day in three separate ~ 24-h deployments (7–8, 10–11, and 11–12 August 2021). All HOBO DO loggers were two-point calibrated before the first deployment. The chamber system was programmed to incubate the chambers for 20 min and then flush the chambers to begin a new incubation repeatedly for the duration of the 24-h deployments. In all three deployments, the flushing pump for chamber 1 malfunctioned by frequently failing to switch on at the start of a new incubation and flush the chamber with water, so data from that chamber were excluded from the analysis (Gadeken et al. 2023). This resulted in $n = 4$ per deployment, or $n = 12$ total. After each deployment, the chambers and the contained sediments (15 cm depth) were extracted and the contents of each chamber were sieved through a 1-mm mesh sieve in the field and preserved in 70% ethanol with Rose Bengal stain. Preserved samples were then sorted and infauna identified to the lowest practical taxonomic level and counted. The Shannon-Weiner Diversity index was calculated for each sample using PRIMER-e statistical software (Clarke and Gorley 2015). The total wet biomass of all fauna was measured for each chamber sample as well as the total biomass of each of the most dominant taxa. Faunal biomass was used as the metric for faunal presence in subsequent analyses.

Sandy sediment from the study site was analyzed for porosity and organic matter. During the first deployment, three 10-cm-diameter sediment cores were taken ~ 10 m away from the benthic chamber setup, vertically sectioned in 1-cm increments, and stored at − 20 °C until processing. Porosity was calculated from the conversion equation in Jackson and Richardson (2007) using weight lost after drying at 70 °C for > 24 h (Jackson and Richardson 2007), and percent organic matter content was calculated as loss-on-ignition after burning at 500 °C for 6 h. Samples were not acidified to remove $CaCO_3$ before burning. Measurements were averaged for each sectioned depth across the three sediment cores.

SOD Calculation and Analysis

SOD was calculated from the slope of the linear regression for each of the ~ 20-min incubation periods. Though many of the slopes were linear, some displayed an irregular pattern and were not useable. We removed low-quality data according to the criteria outlined in Gadeken et al. (2023). SOD calculated from slopes with R^2 values below 0.75 (unless determined to be linear but failed the threshold due to a shallow slope), slopes calculated from incubations shorter than 10 min, and measurements taken during incubations in which DO in the chamber decreased by more than 50% of the starting DO or had an overall positive slope were removed from the data set (Table S1).

The experiment was of a nested random design with repeated measures of SOD. To evaluate the effect of faunal presence on SOD throughout the diel cycle (H_1), a linear mixed effects model was performed on all measurements of SOD with DO and faunal biomass as fixed effects and deployment and sample as random effects. Nested model likelihood-ratio tests were performed by generating reduced models excluding DO and biomass as fixed effects and comparing between the full model and each of the reduced models. Further, we performed simple linear regressions of DO and SOD (hereafter SOD/DO) for each sample and regressed the resulting slopes against faunal biomass. Though this was necessary to compare the set of SOD/DO relationships among biomass values, it should be noted that this process essentially collapsed existing variance in the SOD/DO regressions into a single value, the slope, used for subsequent analyses. Test analyses were also performed using faunal abundance data and biomass from the most dominant taxa. These produced similar patterns to the analyses using total biomass but had less explanatory power, so total biomass was used as the best available metric of faunal presence.

Evaluating sub-diel variability in SOD was challenging because SOD was predicted to depend on DO, which varied over time. There were also numerous missing data points because not all chamber runs had usable slopes for every measurement period, which precluded several commonly used time series analysis methods that require very high coverage and consistent measurement intervals. To address these problems, we conducted a smoothing analysis. After detrending the SOD data for each sample using the sample mean, we used a weighted moving average to fit a smoothing curve to the time series of each sample's SOD measurements. The moving average was a lowpass filter using filter coefficients equal to the reciprocal of the span width. This analysis was performed iteratively on each sample's SOD data using increasing numbers of adjacent points for the moving average (hereafter "span size") to the data (Fig. S1). We then calculated the residual sum of squares (RSS) of the smoothed fit at each span size and examined the change in RSS with increasing span size. Smoothed fits were generated for odd-numbered span sizes from 1 to 29 points. A maximum span size of 29 was selected because all samples approached an asymptote at relatively small span sizes so calculations at greater spans were deemed unnecessary. If the SOD data contained high sub-diel variability, we expected a steep initial increase in RSS at small span sizes and a flat trend to emerge as span size increased. If infauna increase sub-diel variability, samples with more infauna would be expected to have a steeper initial slope.

Analyses were performed in Matlab R2021a and the R statistical software using custom scripts (R Core Team 2021; The MathWorks Inc. 2021).

Results

The ambient DO followed a diel cycle in all three deployments (Fig. 2). Both the maximum DO concentration and the time of day of maximum DO varied between deployments. The minimum DO concentration was similar among the three deployments (~ 3.4 mg L^{-1}); however, it occurred at different times in the nightly low DO period. Deployment 1 displayed an irregular pattern during the night-time hours, with a sudden, brief dip in DO beginning around 12 AM. Temperature data from the HOBO logger displayed a concurrent bump in temperature at this time (Fig. S2A), indicating that this may be the result of a water mass moving through the area.

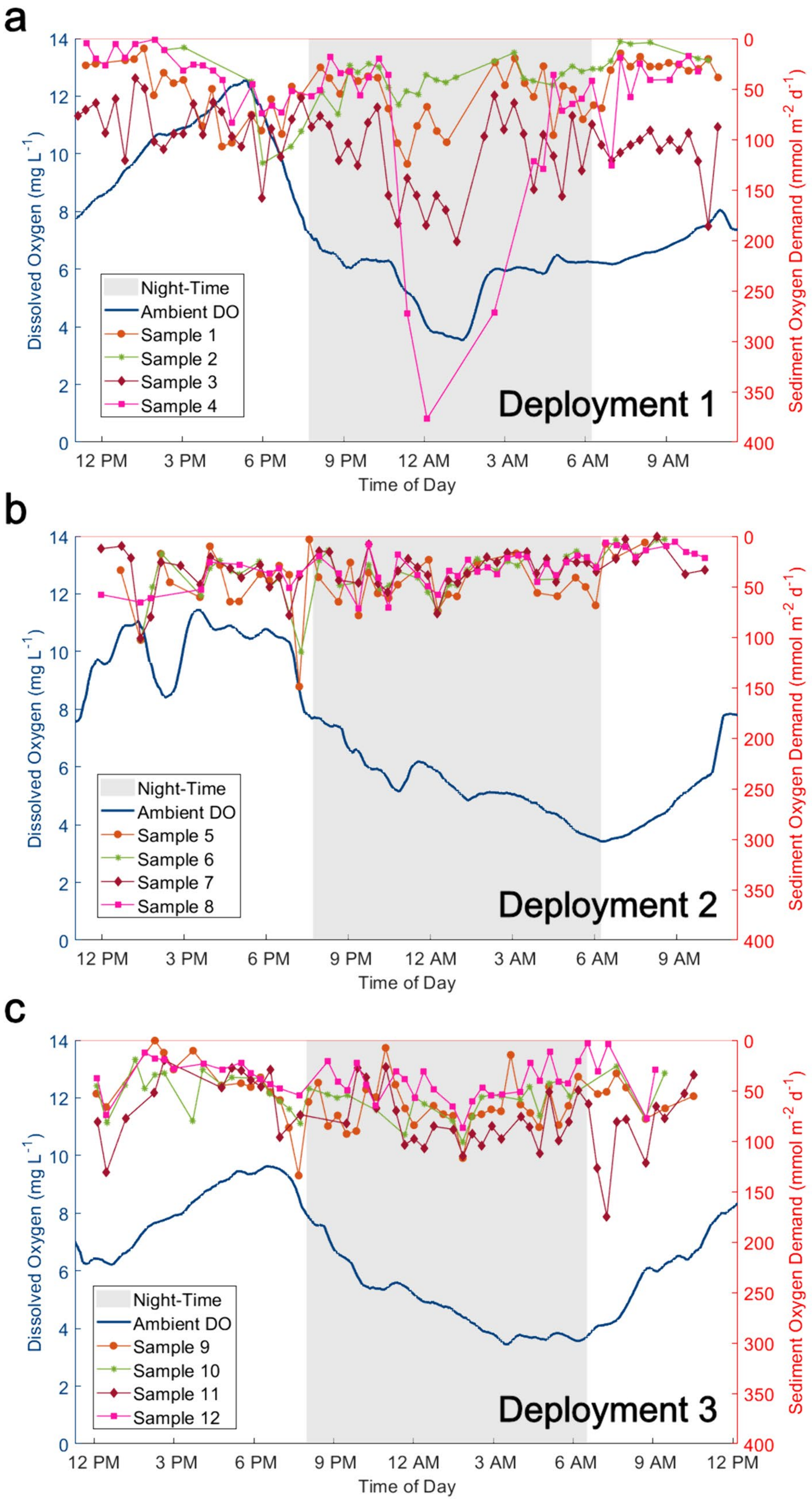
The most abundant infaunal taxa across all samples were mobile surface and subsurface deposit feeders in the polychaete families Nereididae, Capitellidae, Orbiniidae, and corophiid amphipods (Fig. 3a). Total faunal wet biomass ranged from 0.45 to 8.03 g m^{-2}, with both the maximum and minimum values found in samples from deployment 1 (Fig. 3b). Biomass was dominated by orbiniid and nereid worms. One of the chambers in the third deployment (Fig. 3, sample 11) had relatively low faunal abundance but contained a large burrowing wormfish (Microdesmidae) that contributed 62% of the biomass of that sample. We did not find any *D. cuprea* in the samples despite seeing their tubes when deploying the chambers and finding their tube caps in the preserved samples. However, *D. cuprea* can extend their tubes up to 1 m deep into the sediment (Woodin 1978), and we suspect that some may have been enclosed in the chambers but evaded collection by retreating deeper into the sediment than the chamber was able to sample.

The average porosity of all depths was 38%. Porosity was slightly higher in surface sediments but remained consistent with increasing depth, and organic matter content was consistently very low at all depths, with an average of 0.22% (Fig. S3).

SOD patterns throughout the diel cycle are shown for each sample in the three deployments in Fig. 2. The greatest individual measures of SOD were in samples 3 and 4 in deployment 1, which also had the greatest faunal biomass among all samples (Table 1). The highest SOD also occurred during the short dip in DO concentrations during that deployment. Deployment 2 displayed comparatively low SOD among all four samples (Table 1, Fig. 2b), while deployment 3 measures were moderately higher (Table 1, Fig. 2c).

The likelihood-ratio tests revealed that the model was significantly improved with the inclusion of

Fig. 2 Ambient DO and calculated SOD values for each sample throughout the three deployments (**a**–**c**). The shaded box indicates approximate night-time hours (sunrise and sunset times did not differ more than 5 min across deployments). Note that the axes for sediment oxygen demand are inverted. The ambient DO data have been smoothed using a moving average with a window size of 12 to increase readability



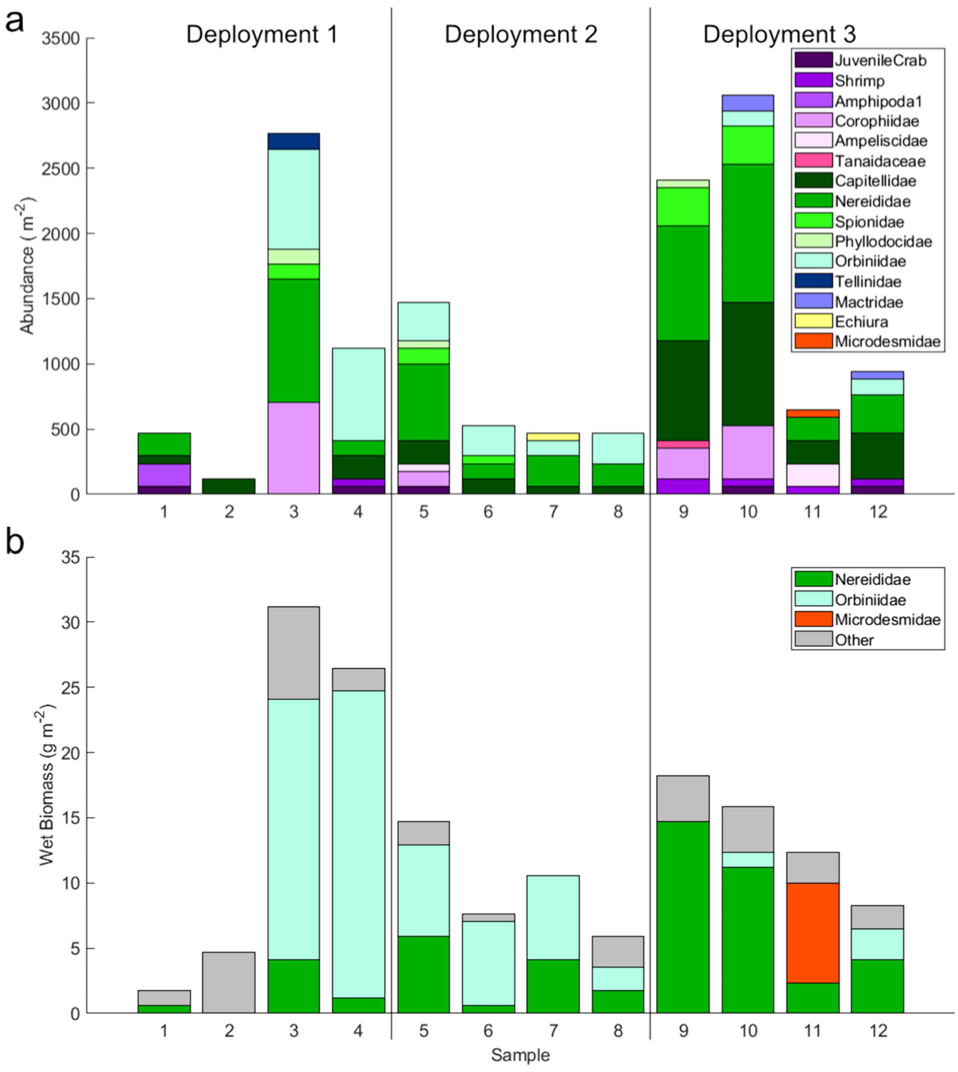


Fig. 3 **a** Faunal community composition by abundance and **b** faunal wet biomass by greatest contributing taxa, normalized to m^{-2} and g m^{-2}, respectively. The most abundant groups were the polychaete families Nereididae, Capitellidae, Orbiniidae, and corophiid amphipods. Orbiniids and nereids contributed most of the biomass in most samples, though in deployment 3, sample 11 contained a single burrowing wormfish (Microdesmidae) that made up the majority of biomass of that sample

Table 1 Summary data of SOD measurements and faunal community for each sample

Deployment	**Sample**	**n**	**Mean SOD ± Std Dev**	**Abundance**	**Biomass**	**Diversity**
1	1	57	51.2 (±28.6)	471	1.8	1.255
	2	36	39.0 (±26.9)	177	4.7	0.636
	3	65	104.9 (±36.0)	2765	31.2	1.474
	4	47	60.0 (±72.6)	1118	26.5	1.129
2	5	38	45.9 (±28.1)	1471	14.7	1.733
	6	42	36.6 (±22.9)	529	7.7	1.273
	7	49	34.1 (±19.8)	471	10.6	1.213
	8	46	31.8 (±17.5)	471	5.9	0.974
3	9	49	59.2 (±26.5)	2412	18.2	1.544
	10	39	55.7 (±19.1)	3059	15.9	1.628
	11	46	75.5 (±33.0)	647	12.4	1.499
	12	43	38.9 (±19.2)	941	8.2	1.511

n is the number of high-quality replicate incubations for each sample used in subsequent analyses. SOD is in units of mmol m^{-2}d^{-1}. Faunal abundance and biomass are normalized to m^{-2} and g m^{-2}, respectively, and diversity was calculated using the Shannon-Weiner method

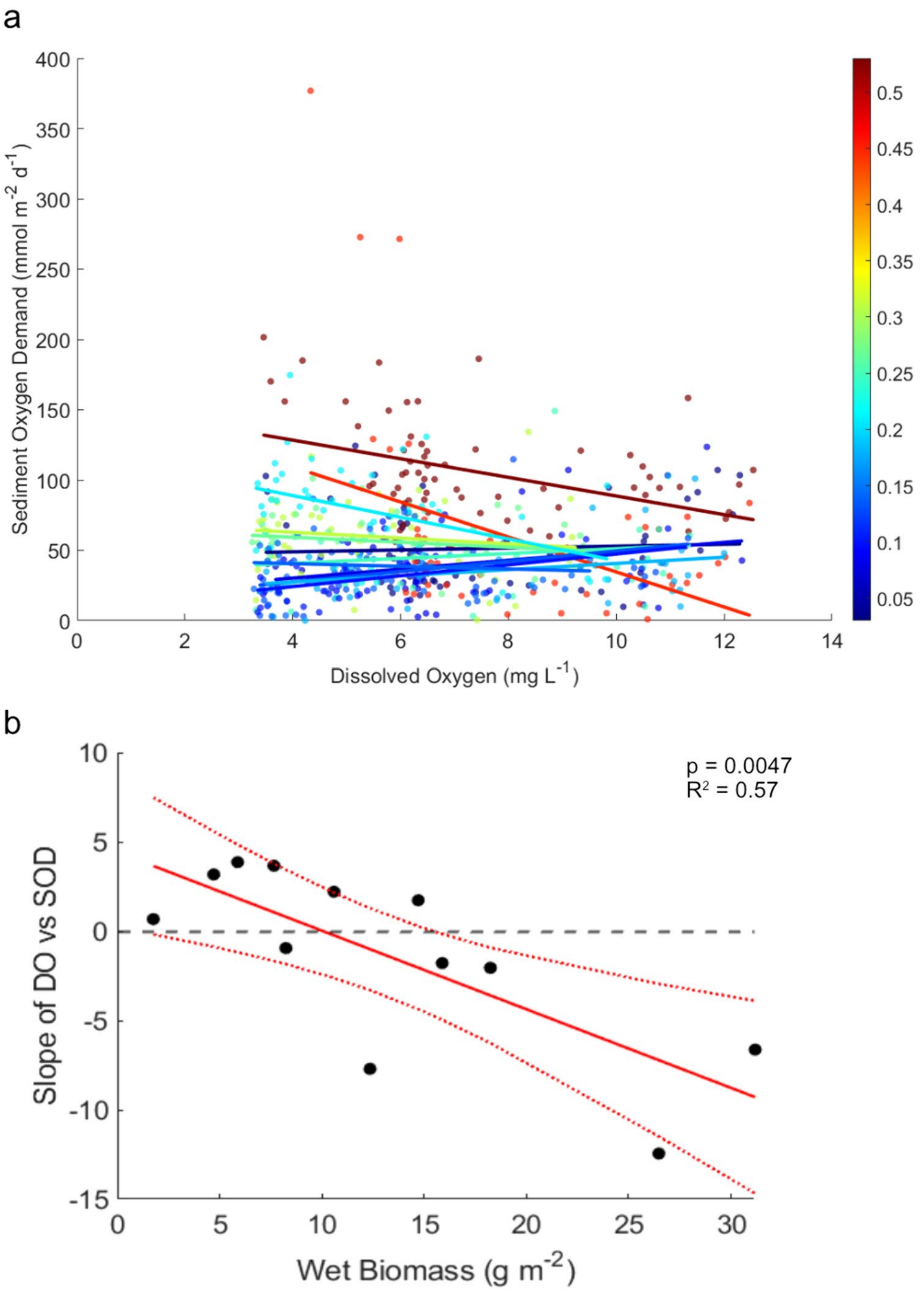


Fig. 4 **a** Regressions of DO and SOD for each sample, colored by sample biomass (g m^{-2}). Points are the individual SOD measurements and lines are the regressions among all incubations for that sample. **b** Simple linear regression of the slopes of DO vs SOD against faunal biomass for each sample. Solid red line is the regression, and dotted red lines are 95% confidence bounds. The dotted line at zero indicates where SOD shows no dependence on DO

faunal biomass ($p = 0.001$, $\Delta\text{df} = 1$), but not DO ($p = 0.09$, $\Delta\text{df} = 1$) as effects on SOD. Upon regressing the SOD/DO slopes (Fig. 4a, Table S2) against faunal biomass, we found a significant negative correlation ($p = 0.0047$, Fig. 4b), with SOD decreasing slightly or showing no relationship with decreasing DO at low faunal biomass but increasing with decreasing DO when faunal biomass was high.

We observed high variability in SOD measurements between and within samples (Fig. 2). In most samples, the RSS steeply increased as the span size widened, showing a sharp RSS increase when the span is widened from one to three adjacent points, and approached an asymptote as the span size increased (Fig. 5a). In all samples, RSS increased to greater than 50% of the sample's maximum as the span size increased to 7 points or 140 min (grey box in Fig. 5a). The linear initial slopes for each sample (a metric of high-frequency variability) were regressed against faunal biomass and revealed a significant relationship (Fig. 5b).

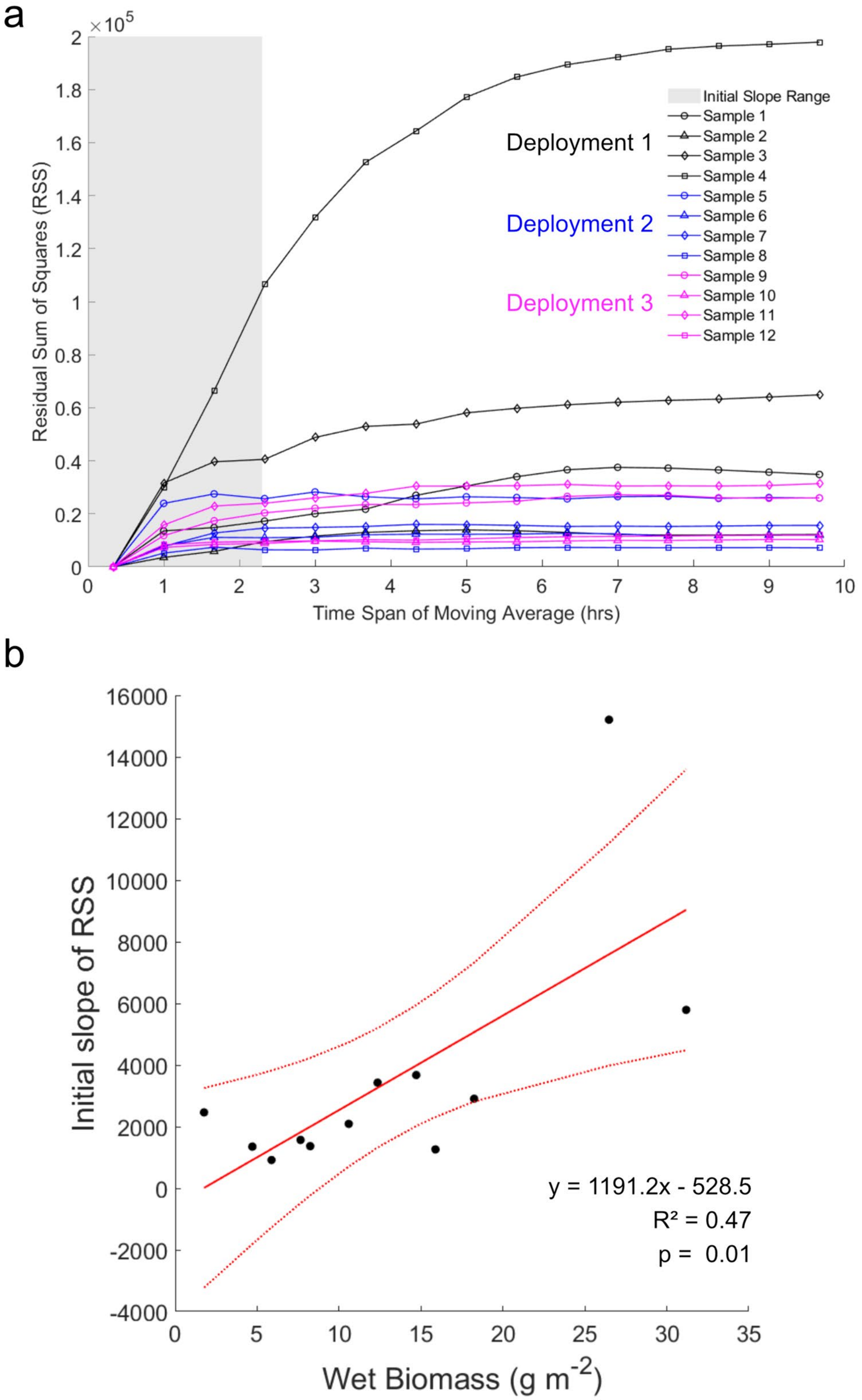


Fig. 5 Results of smoothing analysis assessing temporal variability. **a** Residual sum of squares (RSS) for smoothing fits performed with moving averages of an increasing number of points, converted into the amount of time the moving average covered. **b** the regression of initial slopes of RSS values over the smallest four span sizes (contained in the grey box in **a**) against faunal biomass

Discussion

Overall, SOD was greater in sediments with more fauna (H_1), consistent with previous studies (Aller 1988; Pelegri and Blackburn 1995; Waldbusser et al. 2004; Webb and Eyre 2004). In samples with low faunal biomass, SOD was relatively low throughout the diel cycle, which is not unexpected in sandy sediments low in organic content (Hargrave 1972;

Burdige 2006). Our measurements of SOD and the observed increase with faunal presence also agree well with chamber measurements from other studies in similar habitats. Banta et al. (1999) measured basal SOD rates of 30 mmol m^{-2} d^{-1} in lab microcosms with unpopulated sandy sediments, and the addition of the polychaete *Hediste diversicolor* (formerly *Nereis diversicolor*) inflated SOD by 80–90% (Banta et al. 1999). Likewise, Webb and Eyre found that burrowing thalassinid shrimp in in situ benthic chambers increased SOD by 80% compared to unoccupied sediments (Webb and Eyre 2004).

We found significant variability in SOD on two distinct temporal scales; diel variability driven by the presence of fauna and sub-diel variability on the scale of minutes to hours. The combined significant effects of DO and faunal biomass on SOD indicate that, where fauna were present, lowered DO drove shifts in their activity and behavior that increased SOD. This is consistent with our hypothesized response (H_{2B}), as well as the observations of Wenzhofer and Glud (2004), who found that the majority of nightly DO uptake could be attributed to faunal effects. Their variability in SOD appeared to be caused by light-driven circadian behaviors, and though our measurements were made in shaded chambers, the duration of our deployment was short enough that such behaviors cannot be eliminated as a potential driver. Though shading the chambers was necessary to isolate the effects of the resident fauna on sediment metabolism, shading also eliminated benthic photosynthesis which in shallow sediments can drive very high oxygen flux at the sediment surface (Sundbäck et al. 1991, 2000). In sediments exposed to their natural light regime, faunal contribution to sediment oxygen influx may be greater during daylight hours than at night but dampened or drowned out by high oxygen efflux from benthic productivity.

We hypothesized that fauna may flatten the relationship between DO and SOD (H_{2B}); however, in the regression of the DO vs SOD slopes against faunal biomass, increasing sediment faunal presence essentially inverted the relationship of DO and SOD throughout the diel cycle, surpassing even our hypothesized response. The regression of faunal biomass and the SOD/DO slope crosses zero which indicates that there exists some tipping point where increasing faunal presence begins to drive higher nightly SOD. Our data demonstrate that the presence of fauna changes SOD patterns considerably throughout the diel cycle, and in ways that could not be predicted from measurements at any single time point or even from daytime measurements alone.

Though we were unable to directly measure animal activity within the chambers during the deployments, the increase in SOD in more populated sediments at night was likely driven by fauna responding to low DO by increasing bioirrigation. Nereid worms irrigate their burrows (Wells and Dales 1951), and several common species are known to shift from oxygen conforming to regulatory behaviors at low DO concentrations (Kristensen 1983). However, the two samples with the highest nightly SOD values (samples 3 and 4) were dominated by orbiniids and had relatively little nereid biomass. Orbiniids are not known to construct and irrigate burrows like some nereids do (Jumars et al. 2015), so we would not have predicted that they drove the elevated SOD measurements. They are, however, active burrowers (Francoeur and Dorgan 2014) and have many dorsal external gills along their posteriors (Rouse and Pleijel 2001); irrigation during active burrowing may contribute more to bioirrigation than expected. A more likely explanation is that these samples may have contained individuals of the tube-dwelling Onuphid polychaete *D. cuprea* that evaded collection by retreating deep in their tubes when the sediment cores were extracted. *D. cuprea* tubes create subsurface habitat and refuge for other burrowing animals (Woodin 1978), and their irrigation activity is well documented (Mangum et al. 1968; Dales et al. 1970). Both the higher faunal abundance and the greater SOD measured in those samples may have been due to the presence of *D. cuprea*.

The short time scale of irrigation activity also explains the sub-diel variability in our measurements. In most of our samples, SOD varied substantially measurement-to-measurement, i.e., on ~ 20-min time scales, and samples with greater faunal presence exhibited greater high-frequency variability. Infauna typically irrigate intermittently in cycles of activity and rest which vary in intensity, rate, and duration and can be altered by DO availability (Wells and Dales 1951; Mangum et al. 1968; Kristensen 1983, 1989, 2001; Volkenborn et al. 2010, 2012; Camillini et al. 2019). The irrigation pattern depends on the taxon, however most irrigating infauna cycle through behaviors on a timescale of minutes or tens of minutes. On the timescale of our SOD incubations (~ 20 min), fauna intermittently irrigating likely contributed to the measurement-to-measurement variability. In sediments with large and complex faunal communities, intermittent irrigation would drive swings in SOD on very short timescales and depending on the resident fauna. Even accounting for diel variation by measuring SOD at maximum and minimum DO and interpolating measurements between them would not accurately describe SOD dynamics throughout the entire cycle and would still yield unreliable estimates of net SOD over time. This may be compounded by variation in daytime benthic primary production (Kwon et al. 2012), which was purposefully excluded in this study. And though our short, repeated incubations offer a far greater resolution of measurement than most batch-style benthic chambers, the selection of 20 min as the incubation period was a methodological trade-off between collecting sufficient DO measurements in each incubation to calculate SOD and capturing the changes driven by constantly varying DO. Were the incubation period shorter it may emerge that fauna drive more dramatic changes in SOD on even shorter timescales and our 20 min incubations, brief as they were, still smoothed the signal and reduced variance in the end data set.

It is common practice in sediment research to extrapolate single SOD measurements through time and space. SOD measurements taken in laboratory core incubations and with “batch” style benthic chambers are questionable in their representativeness, and the faunal effects that can substantially increase both the magnitude and the variability in SOD add important context to high-frequency eddy correlation SOD measurements. Measurement of SOD on small temporal and spatial scales has only recently become methodologically feasible but is proving potentially highly significant, and variability can now be captured but has yet to be fully explained. Our observed high spatial and temporal SOD variability, and their apparent interdependence, indicate that increasing resolution of SOD measurement in both dimensions may be not only beneficial but necessary to accurately characterize metabolic processes in these systems.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12237-024-01404-0.

Acknowledgements Thank you to Madeline Frey, Chesna Cox, and Lizi Byrd for help with sample collection and processing; Grant Lockridge for help with instrument fabrication; and Behzad Mortazavi, Sarah Berke, John Lehrter, and Brian Dzwonkowski for thoughtful discussions.

Funding This work was funded by the National Science Foundation OCE CAREER Grant 1844910 and Office of Naval Research Award N00014-18-1-2806 to KMD, the University of South Alabama Center for Environmental Resiliency, and the Southern Association of Marine Laboratories Student Support Program.

Data Availability Raw and processed data, metadata, and analysis scripts are available in the Biological and Chemical Oceanography Data Management Office database under the title FTC Field Study Dataset.

References

Aller, R. C. 1978. The effects of animal-sediment interactions on geochemical processes near the sediment-water interface. In Estuarine interactions, 157–172.

Aller, R. C. 1988. Benthic fauna and biogeochemical processes in marine sediments: The role of burrow structures. *Nitrogen cycling in coastal marine environments*: 301–338.

Banta, G.T., M. Holmer, M.H. Jensen, and E. Kristensen. 1999. Effects of two polychaete worms, Nereis diversicolor and Arenicola marina, on aerobic and anaerobic decomposition in a sandy marine sediment. *Aquatic Microbial Ecology* 19: 189–204.

Bartoli, M., D. Nizzoli, and P. Viaroli. 2003. Microphytobenthos activity and fluxes at the sediment-water interface: Interactions and spatial variability. *Aquatic Ecology* 37: 341–349. https://doi.org/10.1023/B:AECO.0000007040.43077.5f.

Berg, P., and M. Huettel. 2008. Monitoring the seafloor using the noninvasive eddy correlation technique. Oceanography 21. JSTOR: 164–167.

Berg, P., M.H. Long, M. Huettel, J.E. Rheuban, K.J. McGlathery, R.W. Howarth, K.H. Foreman, A.E. Giblin, and R. Marino. 2013. Eddy correlation measurements of oxygen fluxes in permeable sediments exposed to varying current flow and light. *Limnology and Oceanography* 58: 1329–1343. https://doi.org/10.4319/lo.2013.58.4.1329.

Bolam, S.G., T.F. Fernandes, and M. Huxham. 2002. Diversity, biomass, and ecosystem processes in the Marine Benthos. *Ecological Monographs* 72: 599–615. https://doi.org/10.1890/0012-9615(2002)072[0599:DBAEPI]2.0.CO;2.

Burdige, D.J. 2006. *Geochemistry of marine sediments*. Geochemistry of Marine Sediments: Princeton University Press. https://doi.org/10.1515/9780691216096.

Camillini, N., M. Larsen, and R. Glud. 2019. Behavioural patterns of the soft-shell clam Mya arenaria: Implications for benthic oxygen and nitrogen dynamics. *Marine Ecology Progress Series* 622: 103–119. https://doi.org/10.3354/meps13004.

Clarke, K.R., and R.N. Gorley. 2015. PRIMER v5, v6 & v7: User manual/tutorial. *PRIMER-e, Plymouth UK* 91: 192–296.

Clavier, J., L. Chauvaud, P. Cuet, C. Esbelin, P. Frouin, D. Taddei, and G. Thouzeau. 2008. Diel variation of benthic respiration in a coral reef sediment (Reunion Island, Indian Ocean). *Estuarine, Coastal and Shelf Science* 76: 369–377.

Clough, L.M., P.E. Renaud, and W.G. Ambrose Jr. 2005. Impacts of water depth, sediment pigment concentration, and benthic macrofaunal biomass on sediment oxygen demand in the western Arctic Ocean. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 1756–1765. https://doi.org/10.1139/f05-102.

Dales, R.P., C.P. Mangum, and J.C. Tichy. 1970. Effects of changes in oxygen and carbon dioxide concentrations on ventilation rhythms in onuphid polychaetes. *Journal of the Marine Biological Association of the United Kingdom* 50: 365–380.

Davey, J.T. 1994. The architecture of the burrow of Nereis diversicolor and its quantification in relation to sediment-water exchange. *Journal of Experimental Marine Biology and Ecology* 179: 115–129.

Davis, R. 2017. Sediments of the Gulf of Mexico. In Habitats and biota of the Gulf of Mexico: Before the deepwater horizon oil spill. 165–215. https://doi.org/10.1007/978-1-4939-3447-8_3.

De Backer, A., F. Van Coillie, F. Montserrat, P. Provoost, C. Van Colen, M. Vincx, and S. Degraer. 2011. Bioturbation effects of Corophium volutator: Importance of density and behavioural activity. *Estuarine, Coastal and Shelf Science* 91: 306–313. https://doi.org/10.1016/j.ecss.2010.10.031.

Diaz, R.J., and R. Rosenberg. 1995. ine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and marine biology An Annual Review* 33: 245–303.

Fenchel, T. 1996. Worm burrows and oxic microniches in marine sediments. 1 Spatial and Temporal Scales. *Marine Biology* 127: 289–295.

Francoeur, A. A., and K. M. Dorgan. 2014. Burrowing Behavior in Mud and Sand of Morphologically Divergent Polychaete Species (Annelida: Orbiniidae). In *The Biological Bulletin 226*, 131–145. The University of Chicago Press. https://doi.org/10.1086/BBLv226n2p131.

Gadeken, K.J., G. Lockridge, and K.M. Dorgan. 2023. An in situ benthic chamber system for improved temporal and spatial resolution measurement of sediment oxygen demand. *Limnology and Oceanography: Methods* 21: 645–655. https://doi.org/10.1002/lom3.10571.

Gammal, J., J. Norkko, C.A. Pilditch, and A. Norkko. 2017. Coastal hypoxia and the importance of benthic macrofauna communities for ecosystem functioning. *Estuaries and Coasts* 40: 457–468.

Gurr, S.J., J. Goleski, F.P. Lima, R. Seabra, C.J. Gobler, and N. Volkenborn. 2018. Cardiac responses of the bay scallop Argopecten irradians to diel-cycling hypoxia. *Journal of Experimental Marine Biology and Ecology* 500: 18–29.

Hargrave, B.T. 1972. Aerobic decomposition of sediment and detritus as a function of particle surface area and organic content. *Limnology and Oceanography* 17: 583–586. https://doi.org/10.4319/lo.1972.17.4.0583.

Jackson, D., and M. Richardson. 2007. High-frequency seafloor acoustics. Springer Science and Business Media.

Johengen, T., G. J. Smith, D. Schar, H. Purcell, D. Loewensteiner, Z. Epperson, M. Tamburri, G. Meadows, S. Green, and F. Yousef. 2016. Performance Verification Statement for Onset's HOBO U26 Dissolved Oxygen Sensors. 013. Alliance for Coastal Technologies.

Jumars, P.A., K.M. Dorgan, and S.M. Lindsay. 2015. Diet of worms emended: An update of polychaete feeding guilds appendix a family-by-family updates. *Annual Review of Marine Science* 7: 497–520.

Kristensen, E. 1983. Ventilation and oxygen uptake by three species of Nereis (Annelida: Polychaeta). I. Effects of hypoxia. *Marine Ecology Progress Series* 12: 289–297.

Kristensen, E. 1989. Oxygen and carbon dioxide exchange in the polychaete Nereis virens: Influence of ventilation activity and starvation. *Marine Biology* 101: 381–388. https://doi.org/10.1007/BF00428134.

Kristensen, E. 2001. Impact of polychaetes (Nereis spp. and Arenicola marina) on carbon biogeochemistry in coastal marine sediments. *Geochemical Transactions* 2: 92.

Kristensen, E., T. Hansen, M. Delefosse, G.T. Banta, and C.O. Quintana. 2011. Contrasting effects of the polychaetes Marenzelleria viridis and Nereis diversicolor on benthic metabolism and solute transport in sandy coastal sediment. *Marine Ecology Progress Series* 425: 125–139. https://doi.org/10.3354/meps09007.

Kwon, B.-O., J. S. Khim, J. Park, J. Ryu, S.-G. Kang, and C.-H. Koh. 2012. Short-term variability of microphytobenthic primary production associated with in situ diel and tidal conditions. *Estuarine, Coastal and Shelf Science* 112. Assessing Ecological Quality in Estuarine and Coastal Systems – Functional Perspective: 236–242. https://doi.org/10.1016/j.ecss.2012.07.029.

Lehrter, J.C., D.L. Beddick, R. Devereux, D.F. Yates, and M.C. Murrell. 2012. Sediment-water fluxes of dissolved inorganic carbon, O 2, nutrients, and N 2 from the hypoxic region of the Louisiana continental shelf. *Biogeochemistry* 109: 233–252.

Lohrer, A. M., S. F. Thrush, and M. M. Gibbs. 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* 431. Nature Publishing Group: 1092–1095. https://doi.org/10.1038/nature03042.

Mangum, C.P., S.L. Santos, and W.R. Rhodes. 1968. Distribution and feeding in the onuphid polychaete, Diopatra cuprea (Bosc). *Marine Biology* 2: 33–40.

Michaud, E., G. Desrosiers, R. Aller, F. Mermillod-Blondin, B. Sundby, and G. Stora. 2009. Spatial interactions in the Macoma balthica community control biogeochemical fluxes at the sediment-water interface and microbial abundances. *Journal of Marine Research* 67: 43–70. https://doi.org/10.1357/002224009788597926.

Middelburg, J.J., and L.A. Levin. 2009. Coastal hypoxia and sediment biogeochemistry. *Biogeosciences* 6: 1273–1293.

Norling, K., R. Rosenberg, S. Hulth, A. Grémare, and E. Bonsdorff. 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Marine Ecology Progress Series* 332: 11–23.

Pelegri, S.P., and T.H. Blackburn. 1995. Effect of bioturbation by Nereis sp., Mya arenaria and Cerastoderma sp. on nitrification and denitrification in estuarine sediments. *Ophelia* 42: 289–299.

R Core Team. 2021. R: a language and environment for statistical computing (version 4.1.2). Vienna: R Foundation for Statistical Computing.

Riedel, B., T. Pados, K. Pretterebner, L. Schiemer, A. Steckbauer, A. Haselmair, M. Zuschin, and M. Stachowitsch. 2014. Effect of hypoxia and anoxia on invertebrate behaviour: Ecological perspectives from species to community level. *Biogeosciences* 11: 1491–1518.

Rosenberg, R., and L. Lundberg. 2004. Photoperiodic activity pattern in the brittle star Amphiura filiformis. *Marine Biology* 145: 651–656.

Rosenberg, R., H.C. Nilsson, and R.J. Diaz. 2001. Response of benthic fauna and changing sediment redox profiles over a hypoxic gradient. *Estuarine, Coastal and Shelf Science* 53: 343–350.

Rouse, G., and F. Pleijel. 2001. Polychaetes. Oxford university press.

Ryan, J. J. 1969. A sedimentologic study of Mobile Bay, Alabama. Contribution 30. Sedimentology Research Laboratory, Florida State University, Department of Geology, Tallahassee, FL, USA.

Seitz, R.D., D.M. Dauer, R.J. Llansó, and W.C. Long. 2009. Broad-scale effects of hypoxia on benthic community structure in Chesapeake Bay, USA. *Journal of Experimental Marine Biology and Ecology* 381: S4–S12.

Sturdivant, S.K., R.J. Díaz, and G.R. Cutter. 2012. Bioturbation in a declining oxygen environment, in situ observations from Wormcam. *PLoS ONE* 7: e34539.

Sundbäck, K., V. Enoksson, W. Granéli, and K. Pettersson. 1991. Influence of sublittoral microphytobenthos on the oxygen and nutrient flux between sediment and water: A laboratory continuous-flow study. *Marine Ecology Progress Series* 74. Inter-Research Science Center: 263–279.

Sundbäck, K., A. Miles, and E. Göransson. 2000. Nitrogen fluxes, denitrification and the role of microphytobenthos in microtidal shallow-water sediments: An annual study. *Marine Ecology Progress Series* 200: 59–76. https://doi.org/10.3354/meps200059.

Tang, M., and E. Kristensen. 2007. Impact of microphytobenthos and macroinfauna on temporal variation of benthic metabolism in shallow coastal sediments. Journal of experimental marine biology and ecology 349. Elsevier: 99–112.

Timmermann, K., G.T. Banta, and R.N. Glud. 2006. Linking Arenicola marina irrigation behavior to oxygen transport and dynamics in sandy sediments. *Journal of Marine Research* 64: 915–938.

The MathWorks Inc. 2021. MATLAB (version 9.10.0.1710957 (R2021a) Update 4). Natik, Massachusetts.

Tyler, R.M., D.C. Brady, and T.E. Targett. 2009. Temporal and spatial dynamics of diel-cycling hypoxia in estuarine tributaries. *Estuaries and Coasts* 32: 123–145.

Volkenborn, N., C. Meile, L. Polerecky, C.A. Pilditch, A. Norkko, J. Norkko, J.E. Hewitt, S.F. Thrush, D.S. Wethey, and S.A. Woodin. 2012. Intermittent bioirrigation and oxygen dynamics in permeable sediments: An experimental and modeling study of three tellinid bivalves. *Journal of Marine Research* 70: 794 Sears Foundation for Marine Research: 794–823.

Volkenborn, N., L. Polerecky, D.S. Wethey, and S.A. Woodin. 2010. Oscillatory porewater bioadvection in marine sediments induced by hydraulic activities of Arenicola marina. *Limnology and Oceanography* 55: 1231–1247.

Vopel, K., D. Thistle, and R. Rosenberg. 2003. Effect of the brittle star Amphiura filiformis (Amphiuridae, Echinodermata) on oxygen flux into the sediment. *Limnology and Oceanography* 48: 2034–2045. https://doi.org/10.4319/lo.2003.48.5.2034.

Waldbusser, G.G., R.L. Marinelli, R.B. Whitlatch, and P.T. Visscher. 2004. The effects of infaunal biodiversity on biogeochemistry of coastal marine sediments. *Limnology and Oceanography* 49: 1482–1492.

Webb, A., and B. Eyre. 2004. Effect of natural populations of burrowing thalassinidean shrimp on sediment irrigation, benthic metabolism, nutrient fluxes and denitrification. *Marine Ecology Progress Series* 268: 205–220. https://doi.org/10.3354/meps268205.

Webb, B.M., and C. Marr. 2016. Spatial variability of hydrodynamic timescales in a broad and shallow estuary: Mobile Bay, Alabama. *Journal of Coastal Research* 32: 1374 The Coastal Education and Research Foundation: 1374–1388.

Wells, G.P., and R.P. Dales. 1951. Spontaneous activity patterns in animal behaviour: The irrigation of the burrow in the polychaetes Chaetopterus variopedatus Renier and Nereis diversicolor OF Müller. *Journal of the Marine Biological Association of the United Kingdom* 29: 661–680.

Wenner, E., D. Sanger, M. Arendt, A.F. Holland, and Y. Chen. 2004. Variability in dissolved oxygen and other water-quality variables within the national estuarine research reserve system. *Journal of Coastal Research* 100: 17–38.

Wenzhöfer, F., and R.N. Glud. 2004. Small-scale spatial and temporal variability in coastal benthic O2 dynamics: Effects of fauna activity. *Limnology and Oceanography* 49: 1471–1481.

Woodin, S.A. 1978. Refuges, disturbance, and community structure: A marine soft-bottom example. *Ecology* 59: 274–284.

Zorn, M.E., S.V. Lalonde, M.K. Gingras, S.G. Pemberton, and K.O. Konhauser. 2006. Microscale oxygen distribution in various invertebrate burrow walls. *Geobiology* 4: 137–145.