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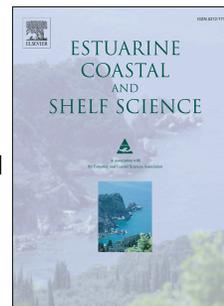


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Journal Pre-proof

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Benthic oxygen dynamics and implication for the maintenance of chronic hypoxia and ecosystem degradation in the Berre lagoon (France)

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Abstract

Chronic hypoxia and anoxia have strong impacts on coastal ecosystems worldwide. In shallow coastal ecosystems, such situations are essentially driven by high benthic oxygen (O_2) demand resulting from organic matter mineralization in surface sediment and amplified by a low mixing of the water column. However, the benthic O_2 demand may greatly vary according to the O_2 availability, sediment biogeochemical properties, and bioturbation by macrobenthic fauna. Here we examined how the sediment O_2 demand varies in response to seasonal and long-lasting (pluri-decadal) hypoxia in the Berre lagoon, a coastal ecosystem impacted by chronic hypoxia events since 60 years. Oxygen penetration depth, diffusive and total O_2 fluxes were measured *in situ* using a microelectrode autonomous profiler and benthic chamber deployments at three sites impacted by quite-permanent (PA), seasonal (PI) and occasional (PO) hypoxia in August 2016. They were seasonally repeated at site PI between August 2015 and August 2016. Additional physical and chemical characteristics were also measured in surface sediment. Sediment profile images and characteristics of benthic macrofauna communities enabled to estimate the quality of the benthic ecosystem. The highest benthic O_2 demand was observed after seasonal anoxia in relation to the important accumulation of reduced chemical species in surface sediment. Interestingly, both pluri-decadal hypoxia and normoxia produced relatively high benthic O_2 demand related to a higher accumulation of organic matter and to the presence of reduced chemical species at site dominated by hypoxia, and to the presence of fresher organic matter and active bioturbating macrofaunal communities in normoxic site. The low benthic O_2 demand at site seasonally impacted by hypoxia likely resulted from the degraded state of the macrofaunal community and from the lower accumulation of reduced chemical species. The occurrence of hypoxia and anoxia situations in the Berre lagoon was predicted from the competition between kinetics of benthic O_2 demand and water column reoxygenation events induced by strong wind. The good agreement between the measured and predicted hypoxia/anoxia occurrence clearly indicates that the chronic deoxygenation events in the Berre lagoon, and the resulting degraded ecological state of the benthic ecosystem are driven both by the benthic O_2 demand and by the intensity and duration of the water column stratification.

Keywords

Oxygen, Coastal hypoxia, Biogeochemistry, Sediment-water interface, Benthic habitat quality, Berre lagoon

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1. Introduction

The health of aquatic ecosystems and the associated functions and services they provide directly depend on dissolved oxygen (O_2) concentrations. It is well established that O_2 concentrations depend on a tight balance between its physical inputs (e.g., water mass transport and mixing, water-atmosphere exchanges), biological production (i.e., photosynthesis) and its removal processes (biological respiration and chemical reactions; Zhang et al., 2010; Levin, 2018; Fennel and Testa, 2019). In many coastal environments, excessive inputs of nutrients of anthropogenic origins generate an important production of organic matter (OM) that mostly deposits onto surface sediment. Its mineralization is related to the consumption of large amount of O_2 by sediments, that when combined with water column stratification, induces a decrease of bottom water O_2 concentrations. Aquatic organisms start to be affected when O_2 concentration drops below $63 \mu\text{M}$ (defined as hypoxia) and can drive to a mass mortality in case of complete depletion (i.e., anoxia), leading to the formation of “dead zones” with large ecological and socioeconomic consequences (Rabalais et al., 2002; Schmidtke et al., 2017).

Sediments are thus known as one of the main O_2 sink in coastal areas (Glud, 2008). The benthic O_2 demand (BOD) is mainly driven by aerobic respiration of freshly deposited OM and oxidation of accumulated reduced chemical species in the surface sediment (i.e., NH_4^+ , Mn^{2+} , Fe^{2+} , H_2S). The BOD thus generally varies at seasonal scale in relation with the seasonal cycle of pelagic productivity and fresh OM deposition onto sediments. However, the occurrence of hypoxia events modifies the biogeochemical processes occurring at the sediment-water interface (SWI) and thus is expected to modify the BOD. Firstly, for a given sediment characteristic, the O_2 fluxes to the sediment are expected to be dependent to the O_2 concentrations in the water column (i.e., the higher is the O_2 availability, the higher is the flux). This suggests that the BOD should be lower in areas impacted by intense hypoxia events. In contrast, the BOD may increase with the duration of hypoxia because of the accumulation of reduced chemical species in the surface sediment over time (Lichtschlag et al., 2015). Thus, in areas where hypoxia/anoxia events are frequent, the inputs of O_2 may generate significant higher BOD because of the presence of large amount of OM and reduced species in the surface sediment (Morse and Eldrige, 2007), thereby supporting or even intensifying hypoxic conditions. It has also been reported in sites seasonally or episodically impacted by hypoxia that changes of O_2 concentrations in the water column directly impacted the macrobenthic community (Diaz and Rosenberg, 1995; Gooday et al., 2009; Levin et al., 2009; Riedel et al., 2012; Levin, 2018), which are involved in bioturbation processes (i.e.,

sediment reworking and bioirrigation). This is expected to modify the rates of biogeochemical reactions in surface sediments and the nature and extent of O_2 exchanges at the SWI (Middelburg and Levin, 2009). The mass mortality of benthic organisms that occur during anoxic period can be responsible for important BOD due to the massive input of fresh OM from dead organisms. It has also been observed in coastal areas where light reaches the sediment surface that the photosynthetic activity of microphytobenthos and macrophytes may reduce, and even reverse in some cases, the net flux of O_2 at the SWI during daytime (e.g., Hochard et al., 2010; Rigaud et al., 2018). Here, we consider the BOD as being a net demand in O_2 , which can be positive when respiration exceeds photosynthesis or negative when photosynthesis exceeds respiration. Benthic photosynthetic activity may hence limit the bottom water deoxygenation. Thus, hypoxia events in shallow coastal areas are mainly initiated by the O_2 consumption by sediments, while temporal changes of the O_2 concentration in the water column drive the O_2 availability for biogeochemical reactions and macrofaunal communities, which in turn control the O_2 consumption kinetics by sediment. Both water column O_2 content and sediment O_2 consumption therefore tightly depend on each other. The identification of factors affecting this relationship remains challenging in the prospect to better understand the duration, intensity and frequency of coastal hypoxia events and their consequences on the functioning of coastal ecosystems.

The Berre lagoon (Figure 1) is a Mediterranean lagoon strongly affected by eutrophication and impacted by recurrent hypoxia for several decades. These hypoxia events are largely favored by a strong haline stratification of the water column due to massive freshwater inputs from a hydroelectric power plant since 1966 (Nerini et al., 2000). These events show different temporal dynamics depending on the depth in the lagoon. Hypoxia events are quasi-permanent in the deeper areas (> 7.5 m), mostly absent in shallow areas (< 4 m), and seasonal in intermediate depth zones. These variable deoxygenation conditions generate a strong gradient in macrobenthic communities which are absent in the deepest areas, relatively functional close to the shore and severely affected in the intermediate zones (GIPREB, 2016; Figure 1). The Berre lagoon is thus a natural laboratory suitable to investigate the interactions between deoxygenation events and the BOD, and their implications in the conservation of chronic hypoxia and ecological degradation of the lagoon ecosystem.

The present study has two main objectives: (1) To characterize the drivers involved in O_2 exchanges at the SWI in a context of both seasonal and long-lasting (i.e., pluri-decadal)

deoxygenation events. The drivers more specifically considered here were the oxygen availability in the water column, the organic matter amount and quality in surface sediment, and the characteristics of the benthic macrofaunal community. (2) To evaluate if the measured BOD is sufficiently important to be responsible of the occurrence of the hypoxia/anoxia events in the Berre lagoon.

2. Material and methods

2.1. Study sites and sampling strategy

The Berre lagoon is located on the French Mediterranean coast. It is 155 km² large and present a maximum depth of 9 m. Three sampling sites were chosen in order to cover the three main areas with respect to the ecological status of macrobenthic communities and to hypoxia characteristics (i.e., intensity, duration, and frequency), that have been prevailed over the last six decades (for details see GIPREB 2016). Site PO (43°30.992' N, 5°4.271' E; 3.8 m depth) is characterized by the absence of hypoxia and the presence of an active macrobenthic community. Site PI (43°30.244'N, 5°4.233'E; 6.0 m depth) presents seasonal hypoxia events and degraded macrobenthic community, and site PA (43°27.688'N, 5°5.606'E; 8.9 m depth) is impacted by quasi-permanent hypoxic/anoxic conditions and the absence of any macrobenthic organisms (Figure 1). In August 2016, the three stations (PO, PI, PA) were sampled in order to obtain information on the influence of long-lasting hypoxia. During the 2015-2016 period, four field campaigns (i.e. August 2015, January, May and August 2016) were conducted on site PI in order to observe the influence of seasonal hypoxia.

2.2. *In situ* measurements of water column parameters

Continuous measurement by autonomous probes were carried out in these three sites over the entire study period. *In situ* autonomous probes (SeaBird SBE19+ on site PI and U20, U24, U26 and UA002 Hobo data loggers, Onset on sites PO, PI and PA) were moored at about 50 cm above the sediment surface in order to continuously monitor the O₂ concentration, temperature, salinity, water pressure (i.e., depth) and light radiation with a 10 minutes (SBE19+) and 30 minutes (HOBO data loggers) time resolution (Figure 2a). Continuous measurements were initiated in summer 2015 at site PI and in summer 2016 at site PO and PA, and were maintained until December 2019. In addition, photosynthetically active radiation (PAR) was monitored during each field campaign using a SPAR data logger (NKE Instruments) equipped with a flat LI-192 sensor (LI-COR Corporate). The precisions of

measurements were $\pm 5\%$ for O_2 , 0.1°C for temperature, 0.1 for salinity and 0.1 m for water depth.

During field campaigns, vertical profiles of physicochemical parameters (i.e., O_2 concentration, temperature, salinity, turbidity, fluorescence, light radiation) were carried out at 8 sites localized along a depth gradient (i.e., North-South transect, Figure 1) allowing to collect information on the spatial extend of the physicochemical conditions at the scale of the lagoon.

2.3. In situ measurements of oxygen micro-profiles and diffusive flux computations

Vertical distributions of O_2 concentration at the SWI were measured *in situ* using an autonomous miniprofiler MP6 system (*Unisense A/S*) (Figure 2b). This benthic miniprofiler is a 6-channels system equipped with a resistivity sensor for sediment surface detection, three O_2 sensors (100 μm tip), one pH sensor and one H_2S sensor. All sensors were from *Unisense A/S*. Profiling sequence was programmed to provide vertical O_2 profiles with 0.1 mm vertical resolution from 1 cm above the SWI and to -2 cm below the interface. Once the sequence completed, sensors returned to their initial position, moved horizontally by about 2 cm and started the next profiling sequence. Oxygen sensors were calibrated using the O_2 concentration measured *in situ* a few cm above the SWI with an U26 HOBO data loggers (Onset) and the zero-oxygen concentration in the anoxic sediment. Oxygen profiles were treated and the diffusive fluxes at the SWI (J_{dif} , $\text{mmol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) were computed with the ProbeFlux program software, a modified version of the PRO2FLUX program software (Deflandre and Duchêne, 2010) using Fick's law:

$$J_{\text{dif}} = -\phi D_s \frac{\delta O_2}{\delta z} \quad \text{Equation 1}$$

where ϕ is the porosity, D_s ($\text{m}^2\cdot\text{d}^{-1}$) is the O_2 molecular diffusion coefficient corrected for sediment temperature and tortuosity (Boudreau, 1997) and $\frac{\delta O_2}{\delta z}$ ($\text{mmol}\cdot\text{m}^{-4}$) is the measured O_2 concentration gradients at the sediment-water interface. Sediment porosity was assessed during each campaign on small sediment cores from the mass differences between fresh and freeze-dried sediment after correction for salt content, and assuming a sediment density of $2.65 \text{ g}\cdot\text{cm}^{-3}$. Total number of exploitable profiles at site PI were 4, 7, 17 and 25 for August 2015, January 2016, May 2016 and August 2016, respectively, whereas they were 14 and 16 in August 2016 at sites PO and PA, respectively.

2.4. In situ deployments of benthic chambers and total oxygen fluxes computations

Benthic chambers were deployed in order to quantify *in situ* total O₂ fluxes at the SWI. They were composed of a cylindrical base of 37 cm diameter and 11 cm height that were introduced into the sediment and closed with a hemispherical dome fixed above with elastics (Figure 2c). The corresponding surface sediment incubated and the volume of water enclosed, were 1074 cm² and about 20 L. The bases of benthic chambers were introduced into the sediment by scuba divers at least one day before the start of the first incubation in order to minimize the influence of sediment perturbation. The domes were equipped with a magnetic stirrer to homogenize the water within the chamber during the incubation period. Stirring was adjusted to avoid any sediment resuspension. During each campaign, clear and dark domes were used in order to assess the influence of photosynthetic processes. Four identical benthic chambers were deployed simultaneously in order to have three replicates and one control. Control benthic chambers, a classical chamber with a plexiglass plate positioned between the base and the dome, were used in order to correct for the influence of eventual water column process. The temporal evolution of O₂ concentration within the chambers was recorded every minute using a SDOT300 data logger (NKE instrument) equipped with an Aanderaa optode 3835 directly inserted into the dome. Incubation periods were adjusted to limit the relative decrease of O₂ concentration during the incubation period to 20%, i.e. 2 hours in August 2015 and 2016, 6 hours in May 2016 and 8 hours in January 2016. Overall, 4 clear and 3 dark deployments were performed in August 2015 and 2 clear and 2 dark deployments were performed in January, May and August 2016.

The total O₂ fluxes at the SWI, J_{tot} (mmol.m⁻².d⁻¹), was then calculated using

$$J_{tot} = (\alpha - \alpha_c) \frac{V}{S} \quad \text{Equation 2}$$

where α and α_c (mmol.m⁻³.d⁻¹) were the variation of O₂ concentration in the benthic chamber and control during the incubation experiment, respectively, V (m³) is the volume enclosed in the benthic chamber and S (m²) is the surface of sediment enclosed in the benthic chamber.

2.5. Sediment characteristics

During each campaign, sediment cores were collected in duplicate or triplicate by scuba divers using 15 cm inner diameter plexiglass tubes. Cores were sliced and each sediment layer was transferred to pre-weighed plastic vials for granulometry, porosity and solid-phase composition analyses. The surface sediment characteristics refer here to the upper 0-0.5 cm layer.

Grain size analysis was carried out using laser granulometry (LS13320, Beckman coulter) following the elimination of organic matter at 450°C for 4 hours and sample dispersion into defloculant ((NaPO₃)₆, 3‰). Porosity was assessed as previously indicated (see section 2.3). An aliquot of sediment was freeze-dried for measurements of total organic carbon (TOC), total nitrogen (TN) and corresponding isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) using a Carlo Erba elemental analyzer coupled to a Sercon Integra CN mass spectrometer for stable isotope ratio measurements (Kristensen & Andersen 1987). Another aliquot of the fresh sediment was frozen at -20°C for chlorophyll analysis. Sediment samples were extracted overnight (4°C in darkness) in 5 mL of 90% acetone (final concentration taking into account the water content of sediments). Fluorescence measurements were then performed using a Perkin Elmer® LS55 spectrofluorometer according to Neveux and Lantoiné (1993). This allowed for the quantification of chlorophyll-a (*Chl-a*), chlorophyll-b (*Chl-b*) and phaeophytin-a (*Phaeo-a*) expressed in µg/g dry weight. The (*Chl-a*)/(*Chl-a* + *Phaeo-a*) ratio (in %) was computed to indicate the freshness of chlorophyll-related pigments.

2.6. Benthic macrofauna features

The species richness and abundance of benthic macrofauna were determined from 4 sediment samples collected using an orange peel grab (total surface area of 0.08 m²), directly sieved on board on a 1.0 mm mesh. Collected organisms were kept frozen until analysis. Sediment Profile images (SPI) were collected using an Ocean Imaging® system. Up to 12 deployments were carried out at each station in August 2016. SPIs were analyzed using the SpiArcBase software (Romero-Ramirez et al. 2013) to determine the apparent redox potential discontinuity (aRPD) and the benthic habitat quality index (BHQ; Nilsson and Rosenberg, 1997), which has been shown to correlate closely with benthic faunal successional stages in response to a gradient in oxygen saturation (Rosenberg, 2001). The BHQ index is typically used to assess the ecological quality of the benthic habitat.

2.7. Statistical analysis

The existence and the significance of spatial (i.e., between PO, PI and PA stations in August 2016) and temporal (i.e., between seasonal campaigns at site PI) variations were tested for Oxygen Penetration Depth in sediment, diffusive and total oxygen fluxes and SPI data (aRPD and BHQ). Differences were tested using Univariate One-Way PERMANOVAs (Anderson, 2001), with untransformed data and Euclidean distance as (dis)similarity measure. Prior to each test, permutational analysis of dispersion homogeneities (PERMDISP; Anderson, 2004)

were used to assess the existence of significant differences in inter-replicate variability. All statistics were performed using the PRIMER 6 package (Clarke and Warwick, 2001) and its PERMANOVA add-on (Anderson, 2001).

3. Results

3.1. Oxygenation level of the bottom water before and during field campaigns

The O₂ concentration in the water column generally decreased with depth, reaching minimum values near the sediment (Figure 3; corresponding salinity data is reported in supplementary material). During summer campaigns, hypoxic/anoxic situations were present in the deepest part of the lagoon. So that a strong O₂ gradient was observed in August 2016 from PO, PI and to PA (from oxic to anoxic water). Such gradient also occurred during the 30-days periods before this field campaign: site PO was well oxygenated with only 9% of the time with hypoxic conditions, site PA was strongly impacted by hypoxia (46% of the time) and anoxia (18% of the time), while site PI was intermediately impacted by hypoxia (36% of the time).

During seasonal campaigns carried out at site PI, bottom water was always oxygenated, between 90 and 320 µM (40-100% O₂ saturation), the lowest concentrations being found during the summer campaigns. However, averaged O₂ concentration during the 30-days period previous field campaigns showed important seasonal variations: no or low (<15% of the time) hypoxia events in May 2016 and January 2016, and large hypoxic events during both summer periods (i.e., corresponding to 42% and 36% of the time in August 2015 and August 2016, respectively; Figure 3). The main difference between August 2015 and August 2016 at site PI is the occurrence of an important period of anoxia (22% of the time) in August 2015.

3.2. Surface sediment characteristics

Surface sediments in all stations consisted of silty-clay sediments (silt: 74-88%, clay: 6-23%, sand: 3-10%) with a porosity of 0.82-0.90. Overall, surface sediments showed high organic content (2.4-3.2% dw) with the highest content found in PA (4.0% dw; Figure 4a). Isotopic signature of TOC was homogeneous along sites and dates ($\delta^{13}\text{C} = -23.2$ to -23.9‰) excepted for site PA that showed the highest value (-22.8‰). Molar C/N ratios were relatively homogeneous (6.5-8.2; Figure 4b). Both Chl-*a* and Phaeo-*a* contents decreased with depth from PO, PI to PA in August 2016 while concentrations at site PI slightly changed across seasons (Figure 4c). The Chl-*b* content also decreased with depth from PO, PI to PA in August 2016 whereas temporal changes at site PI highlighted the highest content in January

2016 decreasing seasonally till August 2016. The (Chl-*a*)/(Chl-*a* + Phaeo-*a*) ratio was the highest in PO, the lowest in PA and intermediate with seasonal changes at site PI (Figure 4d).

3.3. Macrobenthic community and benthic ecosystem quality

The abundance and species richness of the macrobenthic community were characterized in August 2016 along the depth transect (Figure 5a). The benthic fauna was generally sparse with a maximum of 9 species observed in site PO with the dominance of the small polychaete *Hediste succinea* and the bivalve *Musculista senhousia*, which gradually decreased with depth up to their disappearance in the anoxic site PA. The macrofauna abundance and species richness exhibited seasonal changes at site PI (Figure 5a). The benthic macrofauna was absent in August 2015 after a mass mortality caused by an anoxia event but the sediment was quickly recolonized a few months later as demonstrated by the relatively high abundance and specific richness measured in January 2016.

The Sediment Profile Images were collected along the depth transect during the August 2016 campaign (Figure 5bc). They clearly indicated an increasing impact of O₂ deficiency on sediment biogeochemical characteristics and fauna with water depth. Sediments at site PA was laminated and very dark without any presence of fauna and an apparent redox potential discontinuity (aRPD) not visible. The site PI had an intermediate and discontinuous aRPD of 36 mm with the presence of biological structures (i.e. oxid voids, burrows, tubes and feeding pits) whereas a continuous and oxidized layer was clearly observed at the shallowest site PO with aRPD of 51 mm and the presence of numerous burrows and oxid voids, suggesting a higher bioturbation activity. The number and depth of biological structures in the sediment were thus well related to the benthic community found in the sites PO, PI and PA (Figure 5ab). The corresponding BHQ index indicated that the quality of these benthic habitats was "Good/Moderate" at sites PO and PI, and "Bad" at site PA.

3.4. Oxygen penetration depth in the sediment

The O₂ penetration depth in the sediment (z_{O_2}) measured in August 2016 significantly ($p < 0.001$) decreased with water column depth from 2.7 ± 1.6 mm at PO, 1.5 ± 0.4 mm at PI and < 0.1 mm at PA (Figures 6 and 7). At site PI, z_{O_2} ranged from 0.7 to 2.5 mm depth over the seasonal surveys. The lowest z_{O_2} were observed in summer, especially in August 2015 after the anoxia event. Interestingly, z_{O_2} was positively correlated with O₂ concentrations in bottom waters ($r^2 = 0.812$; $p < 0.0001$). The presence of O₂ deeper in sediment depth was punctually

observed at site PO in August 2016 (up to 2.1 cm depth) and at site PI in May and August 2016 (up to 1.7 cm depth) due to the presence of tubes inhabited by sediment-dwelling organisms (e.g. *Hediste succinea*) (Figure 6). Such features were absent in August 2015 and January 2016.

3.5. Diffusive and total oxygen fluxes

The diffusive O₂ fluxes (J_{dif}) were similar ($\sim 15 \text{ mmol.m}^{-2}.\text{d}^{-1}$) at sites PI during the 2016 campaigns but was two times higher in August 2015 (Figure 7). At site PA, where the lowest O₂ concentration was measured, J_{dif} was not significantly different from 0. It is worth noting that the high variability of the diffusive fluxes measured at site PO, is associated to the presence of negative diffusive fluxes (i.e., from the sediment to the water column) that were punctually measured in association to photosynthetic activity occurring at the sediment surface during daytime (Figure 6). This is related to the significantly higher light intensity that reached the sediment surface at PO (up to 8000 Lux) in comparison to sites PI and PA (up to 1500 and 600 Lux, respectively) during the August 2016 campaign (data not shown).

The total O₂ fluxes (J_{tot}) measured by dark chambers showed the highest values at site PO, the lowest values at site PA and intermediate values at site PI, although seasonal variation was observed (Figure 7). Total fluxes obtained from clear chambers were similar to those measured with dark chamber excepted at site PI in May 2016 and at site PO where fluxes in clear chamber were lower. At site PO, the flux in clear chamber is not significantly different from 0 and is due to the presence of negative flux (i.e., from the sediment to the water column) in 2 of the 6 benthic chambers. This is attributed to a significant photosynthetic activity in sediment surface in this shallowest site as also observed from O₂ microprofiles (Figure 6). The lower flux measured in clear chambers at site PI in May 2016 may also be due to the presence of benthic photosynthetic activity, although in this deeper site, this doesn't allow to invert the O₂ fluxes at the SWI.

The total/diffusive O₂ fluxes ratios ($J_{\text{tot}}/J_{\text{dif}}$) were only significantly higher than unity at site PI in May and August 2016 and at site PO in August 2016.

4. Discussion

The sampling strategy deployed in this study allowed to intercept contrasted environmental conditions, which were related directly and indirectly to the temporal variations of deoxygenation events. Firstly, the O₂ concentrations measured in the water column at the selected sites during the field campaigns showed increasing magnitude, frequency and

duration of hypoxia/anoxia with depth in addition to seasonal variations (Figure 3). Those conditions are well representative to the situation that are known to occur in the Berre lagoon over the last decades (GIPREB, 2016). Secondly, the macrobenthic community and associated ecological status of the benthic ecosystems found during sampling campaigns, appeared to be directly related to that trend in hypoxia/anoxia occurrence. Indeed, the density and species richness and quality of the benthic habitat decreased with depth and during hypoxic/anoxic summer period (Figure 5). Thirdly, the characteristics of the surface sediment (grain size, porosity, TOC, $\delta^{13}\text{C}$) in the three investigated sites indicated that the nature and origin of the sediment were similar. The various rivers around the Berre lagoon clearly constitutes a major source of particulate matter with discharges of 45 kt.yr^{-1} with an additional discharges of the St-Chamas hydroelectrical power plant estimated between 45 and 525 kt.yr^{-1} (Fiandino, 2004; Rigaud et al., 2011). Such large continental inputs may enrich the OM concentration in surface sediment but their contribution seems to decrease with depth (i.e. from PO to PA) as indicated by the Chl-*b* content lowering southward from 13.9 to $5.3 \mu\text{g/g dw}$ from sites PO to PA, respectively (Figure 4). The temporal variability of Chl-*b* content suggests that the contribution of continental OM inputs at site PI evolved with seasons with the highest content as expected in winter. Surface sediments appeared however to be mainly exposed to local production of marine phytoplankton since both molar C/N and $\delta^{13}\text{C}$ values in surface sediments clearly indicated that OM was mainly composed of marine planktonic origins (Thornton & McManus 1994; Cathalot et al., 2013). The higher TOC concentrations found at site PA, together with a higher C/N ratio and lower $\delta^{13}\text{C}$ indicated a higher marine OM accumulation in the deepest part of the lagoon characterized by quasi-permanent hypoxia. This is in agreement with others studies indicating that hypoxia reduces the efficiency of OM remineralization, resulting in higher OM accumulation in sediment (Middelburg and Levin, 2009; Lichtschlag et al., 2015). However, results also indicated that the freshness of chloropigments, and thus its lability, was decreasing with depth in August 2016 (Figure 4). This is likely due to the higher residence time of particles in the deeper water column before to settle onto sediment surface.

Consequently, the sampling strategy carried out in the Berre lagoon, based on seasonal (site PI) or spatial (sites PO, PI, PA) approaches, thus allowed to intercept contrasted oxygenation situations in the water column and related sediment and benthic community characteristics. Here we use this original compiled dataset to characterize the BOD and involved drivers with respect to both seasonal variations and contrasted long-term oxygenation situations, and

then to assess if the BOD can be responsible of the occurrence the hypoxia/anoxia events in the Berre lagoon.

4.1. Impact of seasonal hypoxia on the benthic oxygen demand

The four field campaigns carried out at site PI allowed to intercept the seasonal dynamic of hypoxia at the same site and its influence on the BOD. The August 2015 field campaign occurred few weeks after an anoxia event that induced an important mass mortality of macrobenthic organisms (Figure 5). The three following campaigns were conducted during the following year that was characterized by the continuous presence of O₂ in the water column, which allowed the recolonization of the sediment by the macrobenthic community.

The August 2015 campaign was characterized by the lowest z_{O₂}, the highest J_{dif} and a high J_{tot} (Figure 7). This indicated that the preceding anoxia event promoted the O₂ consumption at the sediment surface while O₂ reappeared in the water column. Such higher BOD could be the consequence of organism's mass death that constitute an important input of fresh OM and related high O₂ consumption for its mineralization. However, the OM content in surface sediment was roughly similar to that of other campaigns (Figure 4). At the time of the sampling survey, few weeks after the anoxia event, most of the deposited OM was already mineralized as organism soft tissues could not be seen on the surface sediment (pictures not shown). In agreement with the observation of high concentrations of H₂S, NH₄⁺ or Mn²⁺ in surface porewaters in August 2015 (Rigaud et al., in prep.), the high BOD rate was rather related to the oxidation of those reduced chemical species accumulated in the surface sediment porewaters. Such high BOD associated to the "oxygen debt" of sediment agreed with previous findings (Morse and Eldrige, 2007; Seitaj et al., 2017).

The J_{dif} measured during the three following campaigns was two times lower and constant, while the J_{tot} increased. The resulting J_{tot}/J_{dif} was close to unity in August 2015 and January May 2016, indicating that the major process controlling O₂ fluxes at SWI was the molecular diffusion. In May and August 2016, J_{tot}/J_{dif} was higher than unity indicating that other transport processes governed the O₂ fluxes at the SWI. The macrofaunal determination showed the presence of bivalve (*Musculista senhousia*) and polychaete (*Hediste succinea*) in the sediment, which are known to actively bioturbate the surface sediment (Quéiros et al., 2013). Those organisms were then likely responsible of the biogenic structures observed in the surface sediment (Figure 5). The activity of sediment dwelling organism, such as *Hediste succinea*, was further supported by the presence of oxygenated tubes observed up to 2 cm depth in O₂ microprofiles of May and August 2016 (Figure 6). Bioturbating activity thus

could explain the 2 to 3 times higher O_2 consumption by sediment observed between total and diffusive fluxes in May and August 2016 (Figure 7).

Thus, in coastal zone impacted by seasonal hypoxia/anoxia, the BOD appeared highly variable over time (Figure 8b). The seasonal hypoxia/anoxia phenomenon was responsible of an important increase of BOD due to the large accumulation of reduced chemical species in surface sediment associated to the anoxia event itself. But, as anoxia generated the massive mortality of the macrobenthic community, the O_2 consumption was only driven by its molecular diffusion through the SWI. The progressive recolonization of the sediment by macrofaunal organisms then progressively increased the BOD in sediment surface in relation to the bioturbating activity of benthic organisms.

4.2. Impact of pluri-decadal hypoxia on the benthic oxygen demand

The field campaign carried out at sites PO, PI and PA in August 2016 allowed to observe the influence of pluri-decadal lasting hypoxia on the BOD. The most important differences between the three stations were the water column O_2 concentrations (i.e., high at PO, very low at PA and intermediate at PI; Figure 3) and related benthic macrofaunal community (i.e., relatively diversified and abundant at PO, degraded at PI and absent at PA; Figure 5). The relation between O_2 concentration and benthic ecosystem quality was further confirmed by an ecological index (i.e., BHQ), which was decreasing with depth (Figure 5b). It is also worth noting that even at the site PO, the less impacted by hypoxia, the density and specific richness of the macrobenthic community is relatively poor in comparison to similar Mediterranean lagoons (e.g., Thouzeau et al., 2007), reflecting the general degraded state of the benthic ecosystem of the Berre lagoon. In addition, the macrobenthic community is dominated by opportunistic species with short cycle life (i.e., *Musculista senhousia*; *Hediste succinea*), characteristic of degraded ecosystems (Crooks, 1992; Magni et al., 2004). These observations were in agreement with the surveys carried out by the GIPREB management board over the last decades (GIPREB, 2016) and could be directly related to the increase of the frequency, duration and intensity of the hypoxia events in relation with increasing depth in the Berre lagoon.

The z_{O_2} as well as the diffusive and total O_2 fluxes at the SWI decreased from PO, PI to PA (Figure 7) in direct relation with the O_2 concentration in bottom waters. This suggested that, in areas subjected to long-term contrasted oxygenation conditions, the most important driver of the BOD was firstly the O_2 availability in the water column.

The $J_{\text{tot}}/J_{\text{dif}}$ ratios at site PO (dark benthic chamber) higher than unity (Figure 7) indicated a significant contribution of the macrofaunal activity to the BOD. Such contribution can increase between 2 and 5 times the diffusive BOD at this station. This agreed with commonly found proportion of the benthos mediated fluxes reported in other normoxic coastal areas (e.g., Glud, 2008; Lichtschlag et al., 2015, Gammal et al., 2016). Although the $J_{\text{tot}}/J_{\text{dif}}$ ratio could not be calculated at site PA because of the difference in O_2 concentration in the water column during the microprofiler and the benthic chambers deployments, the absence of macrofaunal organisms at PA made unlikely any contribution of biota to the BOD, that was thus only controlled by diffusion.

The low water depth at site PO also favoured the light irradiance at the bottom that promotes photosynthetic activities by microphytobenthos as observed from O_2 microprofiles in surface sediments and the significant differences of O_2 fluxes between clear and dark benthic chambers. This indicated that in euphotic zones of coastal areas, the BOD can be significantly reduced and potentially inverted due to photosynthetic organisms activity, as previously reported (e.g., Thouzeau et al., 2007). The depth of the euphotic layer, which is related to the water turbidity in eutrophicated aquatic system such as the Berre lagoon, must thus also be an important driver to be considered when focussing on the O_2 budget in the benthic compartment. For example, we calculated that an increase of the mean euphotic layer (i.e., depth where 10% of the incident light radiation is measured, 4.9 m depth; GIPREB, 2010) by 1 m depth, will allow an increase by 9% of the Berre lagoon area where sediment may be concerned by photosynthetic activity.

Thus, the BOD at sites that have been impacted by long-lasting hypoxia appeared primarily limited by O_2 concentration in the water column (Figure 8 a and c): lower was the O_2 concentration, lower was its penetration depth in sediment and lower was its consumption by the sediment. In areas where dominant long-term hypoxia/anoxia occurs, the absence of macrofaunal organism further limited the BOD to its diffusion process.

4.3. Role of the benthic oxygen demand on the hypoxia and anoxia occurrence in the Berre lagoon

The role of the BOD on the occurrence of hypoxia and anoxia in the water column involved three steps calculations based on the total O_2 fluxes measured during the benthic chamber deployments:

1) *Determination of the first-order kinetic constant of O₂ consumption by the sediment (k_{O₂})*

Assuming that the decrease of O₂ concentration over time in the water of benthic chambers is governed by a first-order reaction, the k_{O₂} (m. d⁻¹) can be obtained using:

$$k_{O_2} = \frac{J_{tot}}{[O_2]_{t_0,BC}} \quad \text{Equation 3}$$

where J_{tot} is the total O₂ flux (mmol.m⁻².d⁻¹) measured during benthic chamber deployments and [O₂]_{t₀,BC} is the initial O₂ concentration (mmol.m⁻³) within the benthic chamber.

2) *Determination of the time (t) to reach hypoxia or anoxia in the bottom water*

If we consider (i) the initial O₂ concentration ([O₂]_{t₀}) in an homogeneous and isolated water mass of a height z (in m) overlying the sediment surface, and that (ii) the decrease of O₂ concentration in this isolated water mass is only controlled by the benthic consumption (i.e., negligible pelagic consumption, negligible input of O₂ from vertical mixing or lateral displacement of water masses), the O₂ concentration at any time ([O₂]_t) can be calculated in this water mass using

$$[O_2]_t = [O_2]_{t_0} e^{-\frac{k_{O_2}t}{z}} \quad \text{Equation 4}$$

The previous assumptions are supported in the Berre lagoon by our dataset. The negligible input of O₂ from vertical mixing in the bottom water is mostly prevented by the thermohaline stratification. The contribution of pelagic O₂ consumption in the total benthic O₂ consumption (from control benthic chamber) was found to be low (i.e., between 0 and 16%) in all stations.

Equation 4 can then be transformed in order to isolate the time needed to reach a specified O₂ concentration:

$$t = \frac{z}{k_{O_2}} \ln \left(\frac{[O_2]_{t_0}}{[O_2]_t} \right) \quad \text{Equation 5}$$

Equation 5 was then used to calculate the time to reach hypoxia ([O₂]_t < 63 μM) or anoxia ([O₂]_t < 2 μM) in a 1 m height water column above sediments for each station and season. This water height is associated to water haline stratification typically observed in the Berre lagoon (e.g., Figure 3). The initial O₂ concentration in the water column ([O₂]_{t₀}) corresponded to the typical O₂ saturation calculated from the average temperature and salinity measured in each station for each period. In order to represent diurnal variations in total O₂ fluxes, the k_{O₂} obtained in dark and in clear chambers were successively applied for night and day conditions, respectively.

3) Determination of the occurrence rate of hypoxia ($OR_{hypoxia}$) and anoxia (OR_{anoxia}) events:

The times calculated to reach hypoxia and anoxia could finally be compared to the occurrence period of the strong wind events in the Berre lagoon able to generate a full mixing of the water column (whatever the stratification), resulting in a reoxygenation of the bottom water. The comparison between the O_2 concentration in bottom water measured at sites PO, PI and PA with the wind speed measured at the Marignane meteorological station (dataset corresponded to 10 minutes-averaged wind speed every three hours available at <https://donneespubliques.meteofrance.fr>) indicated that a reoxygenation of the water column occurred for wind speed events >10 m/s at sites PO and PI and >12 m/s at site PA. Then a strong wind event was defined by at least two consecutive 10 minutes-averaged of a given wind speed measured during a 6 hours period. Based on the MeteoFrance 1996-2018 dataset for the Marignane station, the average periods between two 10 m/s wind events were 5.5 ± 1.1 d in winter (January-March), 7.6 ± 2.1 d in spring (April-June) and 7.9 ± 1.7 d in summer (July-September), while it was 12.6 ± 3.6 d in summer for >12 m/s wind events. By assuming that the O_2 concentration in the bottom water was only controlled by benthic consumption and reoxygenation by strong wind events, the occurrence rate of hypoxia/anoxia ($OR_{hypoxia}$ and OR_{anoxia} , respectively) events could be calculated as follows:

$$OR_{hypoxia} = \frac{t_{wind} - t_{hypoxia}}{t_{wind}} \quad \text{Equation 6}$$

$$OR_{anoxia} = \frac{t_{wind} - t_{anoxia}}{t_{wind}} \quad \text{Equation 7}$$

Where t_{wind} was the average period between each strong wind events (in d) and t_{anoxia} and $t_{hypoxia}$ were the time to reach anoxia and hypoxia (in d) respectively, calculated using Equation 5.

The averaged kinetic constant rate of benthic O_2 consumption (k_{O_2}) values, corresponding time to reach hypoxia/anoxia in the last meter of the water column and corresponding occurrence of hypoxia/anoxia in the Berre lagoon were reported in Figure 9. The highest k_{O_2} values were observed at site PI in August 2015 indicating that the highest BOD in a site seasonally impacted by anoxia was related to the reoxygenation of reduced species accumulated in sediment after the anoxia events. Such kinetics were several folds lower during the other campaigns at site PI, although it increased from January to August 2016 likely due the progressive recolonization of sediment by benthic macro-organisms. In comparison to PI in August 2016, k_{O_2} was higher in PO (dark chamber, for clear chamber see below) and PA. The

high k_{O_2} value in PO (dark chamber) was driven by both fresher organic matter (Figure 4) and the presence of bioturbating fauna (Figure 5). In PA it could be linked to the presence of higher OM contents, even if less labile, and oxidation of accumulated reduced chemical species.

The derived time to reach hypoxia/anoxia events from an O_2 saturated water mass, when only considering the local benthic consumption, was largely variable according to seasons and sites (Figure 9). This time was very short in summer after a seasonal anoxia at site PI (1.3/5.2 d) and at site PA, impacted by pluri-decadal and frequent anoxia (2.0/7.0 d). At site PO and other seasons at site PI, these times were longer and ranged between 5-14/20-42 d.

Comparing these times to reach hypoxia/anoxia with the average periods between strong wind events (>10 m/s at sites PO and PI and >12 m/s at site PA) give precious information about the probability of hypoxia/anoxia occurrence in the Berre lagoon. We thus found that hypoxia/anoxia occurrence were 84%/44% in summer at site PA and 83/35% at site PI during summer after an anoxia event (Figure 9). Anoxia is not expected to occur at site PO and in others seasons at site PI, but hypoxia is expected to occur in summer at site PI (30%) and at site PO (12%). Those predictions match very well with field observations on the occurrence of hypoxia/anoxia measured in the Berre lagoon during the last seasons where dissolved O_2 was measured (from summer 2015 to winter 2019) (Figure 9). This indicates that BOD and strong wind were the two most important competing drivers of the hypoxia/anoxia occurrence in the bottom water of the Berre lagoon.

5. Conclusion

The BOD in the Berre lagoon was found to be driven by both biogeochemical (i.e., photosynthesis, aerobic respiration and chemical oxidation) and transport (i.e., diffusive and biological) processes. However, the relative importance of these processes varies with respect to the time-scale (i.e., seasonal and long-term) of the hypoxia/anoxia events. We showed that the availability of O_2 (i.e., its concentration) in the water column was the first driver of the BOD as higher O_2 concentration generated higher O_2 flux. The kinetic constant rate of benthic O_2 consumption, that account for the difference in O_2 availability in the water column, indicated that the highest BOD was generated by the oxidation of the reduced chemical species accumulated in sediment after anoxia events at site seasonally impacted by hypoxia. However, as anoxia induced the mortality of macrofaunal organisms, this O_2 demand was only controlled by diffusive transport. After the reoxydation of reduced chemical species, the BOD reached low values, and then increased progressively over the following months in

relation to the recolonization of sediment by bioturbating macrofauna. In area impacted by pluri-decadal hypoxia/anoxia, the BOD was strengthened, although only controlled by diffusive transport, due to the accumulation of both higher amount of organic matter and reduced chemical species. In shallower areas rarely impacted by hypoxia, the BOD was greatly enhanced by fresh OM deposition in surface sediment and bioturbating activity. However, as light irradiance may reach the sediment surface, the photosynthesis activity could partly reduce, and in some cases, reverse the net O_2 consumption fluxes, the sediment potentially becoming a O_2 source for the water column, hence limiting the deoxygenation.

Based on a simplified representation of the Berre lagoon oxygenation, considering merely the BOD as the O_2 sink and strong wind events as the O_2 source in the bottom water, we were able to predict the occurrence of hypoxia/anoxia in the Berre lagoon. The reduction of the occurrence of hypoxia/anoxia events in the Berre lagoon and associated ecosystem rehabilitation in the future necessarily imply to act both on the increase of the O_2 inputs by reducing water column stratification and on the decrease of the BOD. It is also worth noting, that an increase of the euphotic layer by reducing water turbidity may also increase the area where microphytobenthos may act as an important O_2 inputs, limiting hypoxia to the deepest areas. As our results indicated that the highest BOD were generated by hypoxia/anoxia, this supports that the hypoxia was self-sustaining in the Berre lagoon. Therefore, only management efforts to reduce eutrophication and water column stratification, and likely turbidity, will allow the Berre lagoon ecosystem rehabilitation.

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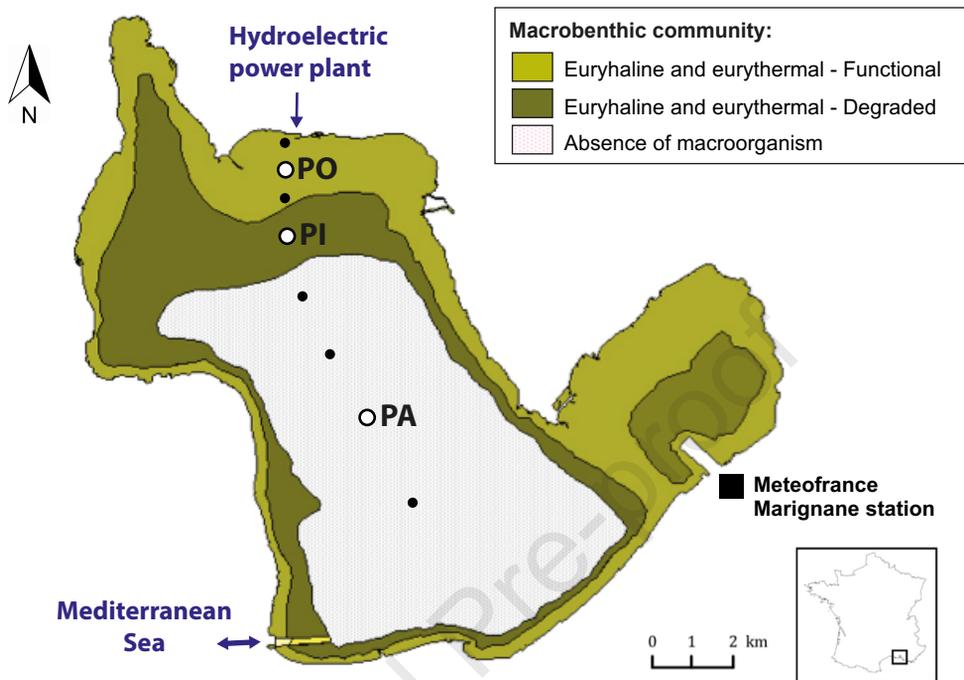


Figure 1: Map showing the position of sampling sites in the Berre lagoon: PO (3.8 m depth), PI (6.0 m depth) and PA (8.9 m depth). Note that stations were positioned with respect of the ecological status of macrobenthic communities (GIPREB, 2016). Their status (functional, degraded or absent) is associated with the increasing frequency, intensity and duration of hypoxia events that has been lasted over the last decades. The black dots correspond to additional stations used to carry out the vertical CTD profiles along the North-South transect during field campaigns as shown in Figure 3. The location of the MeteoFrance meteorological station in Marignane is also reported.

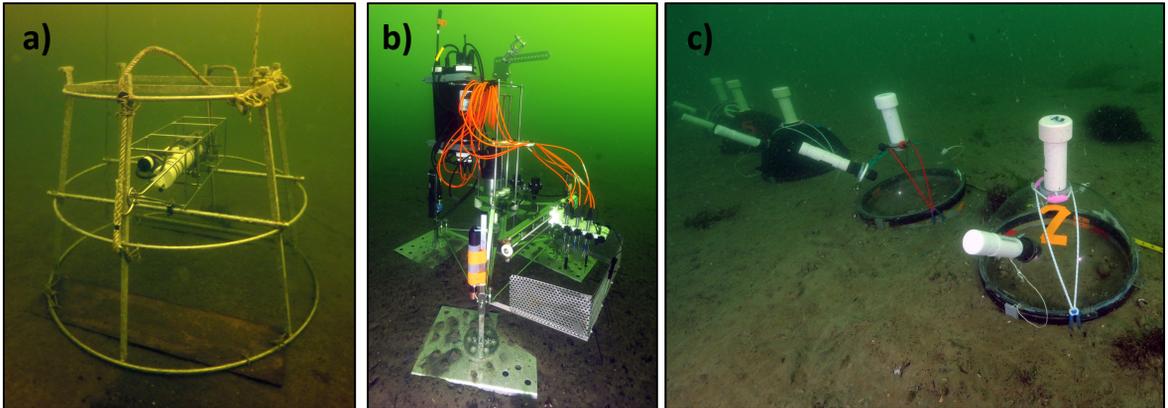


Figure 2: Pictures showing a) the moored structure with CTD SB19+ for time series measurement of physicochemical parameters in the bottom water, b) the MP6 miniprofiler system, c) the benthic chambers.

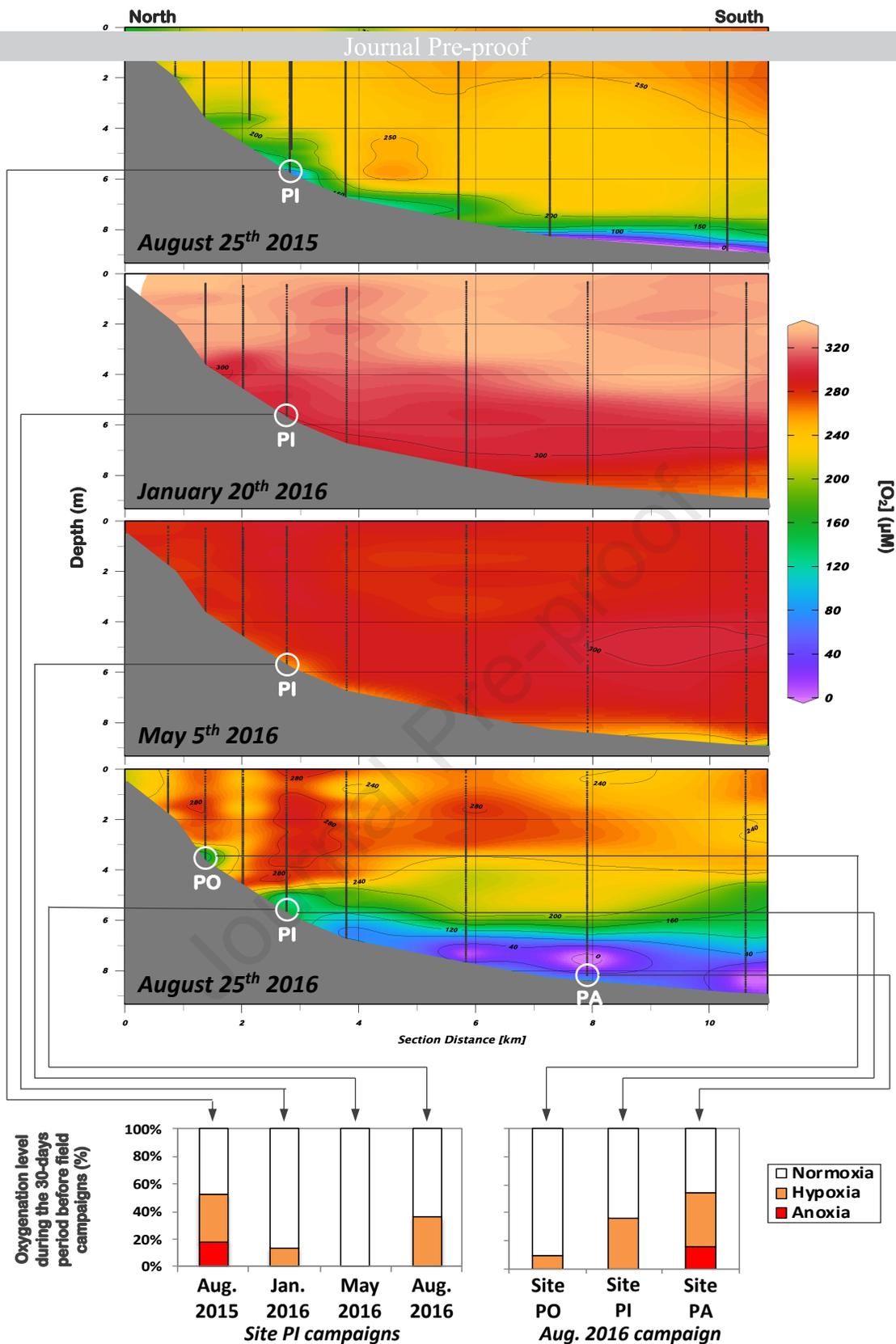


Figure 3: Examples of 2D North-South section of dissolved oxygen (O_2) concentrations measured in the water column of the Berre lagoon during the field campaigns. Sites PO, PI and PA, where experimental works were conducted, are reported with white circles. The bottom figure reports on the proportion of time normoxia ($[\text{O}_2] > 63 \mu\text{M}$), hypoxia ($[\text{O}_2] < 63 \mu\text{M}$) and anoxia ($[\text{O}_2] < 2 \mu\text{M}$) occurred in the bottom water in sites PO, PI and PA during the 30-days period before the campaigns. The 2D mapping was carried out using the DIVA Gridding mode on the ODV software (Schlitzer, 2014).

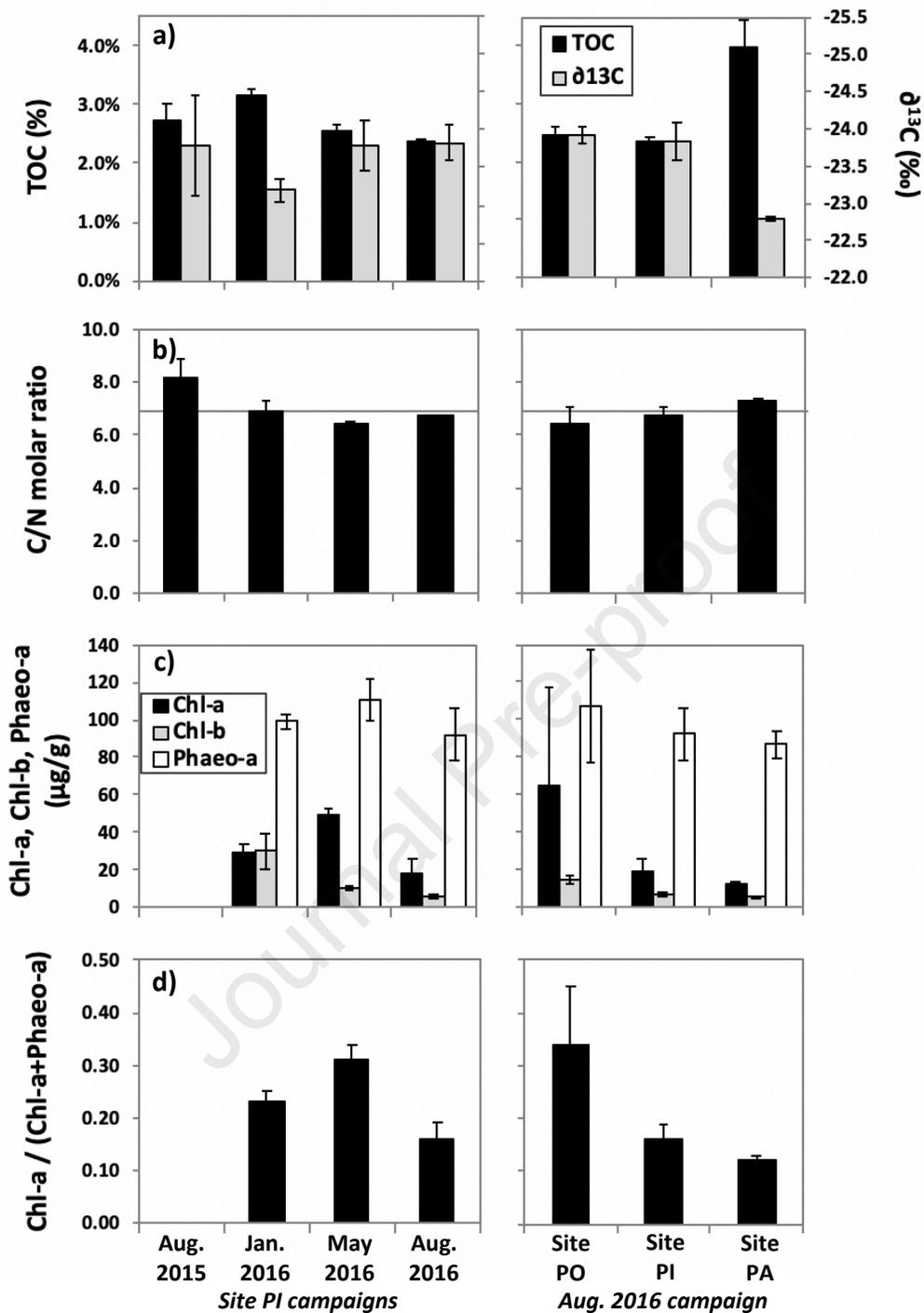


Figure 4: Total organic carbon (TOC), $\delta^{13}C$ isotopic composition of TOC, molar C/N ratio and pigments values (Chl-a: Chlorophyll a; Chl-b: Chlorophyll b; Phaeo-a: phaeophytin-a). The (Chl-a)/(Chl-a + Phaeo-a) ratio is a proxy of the freshness of chlorophyll-related pigments. The horizontal grey line correspond to the Redfield ratio. Data reported correspond to the average \pm 1 standard-deviation on the analysis of replicate surface (0-0.5 cm) sediment layer (n=2). Left panels: in site PI during the August 2015, January 2016, May 16 and August 2016 field campaigns. Right panels: in sites PO, PI and PA during the August 2016 campaign.

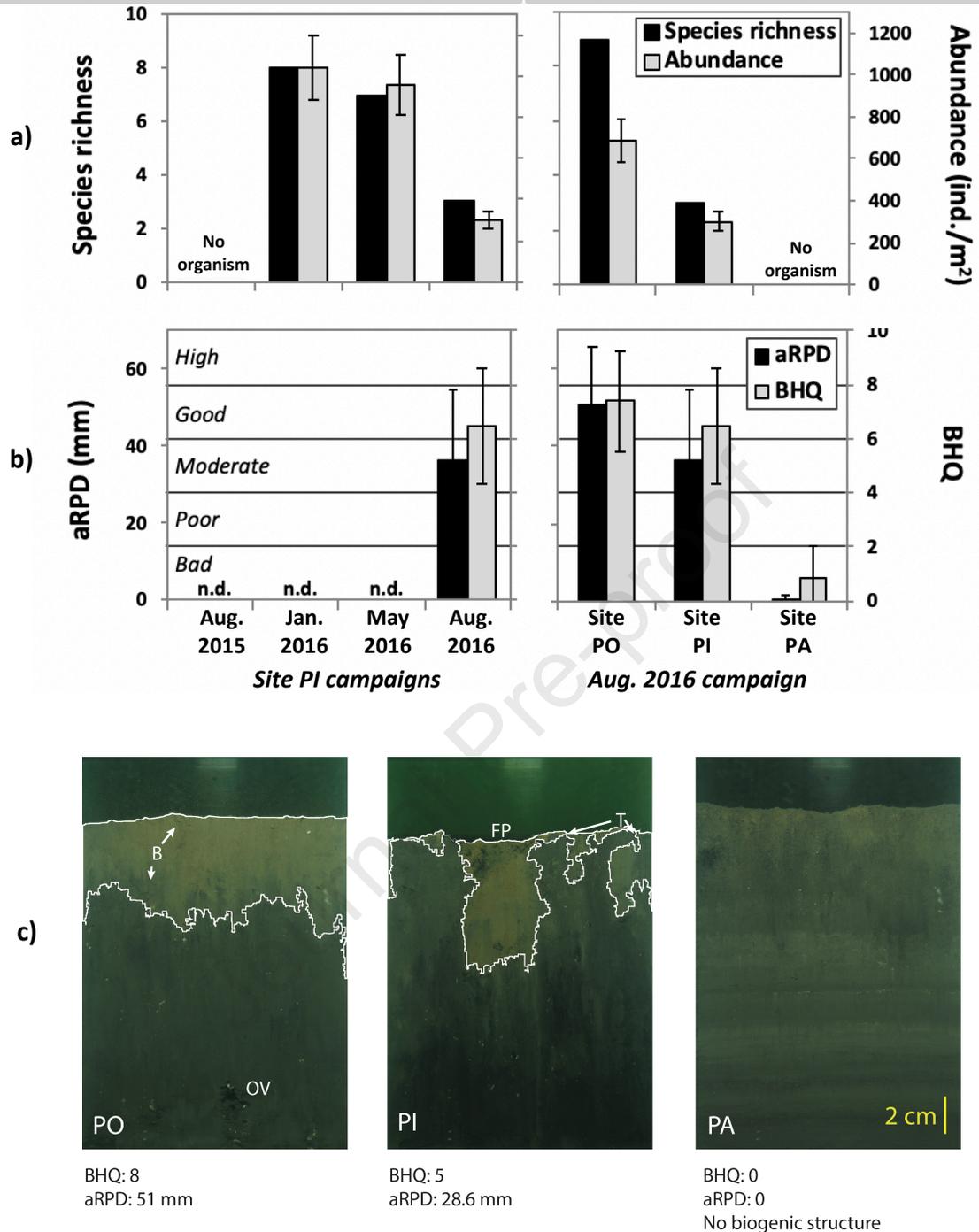


Figure 5: a) Macrobenthic species richness and abundance obtained from surface sediment sampling. b) Average and standard deviation of apparent Redox potential discontinuity (aRPD) and Benthic Habitat Quality index (BHQ) obtained from Sediment Profile Imaging. Corresponding BHQ status are also reported. c) Examples of sediment profiles images obtained from the sites PO, PI and PA in August 2016. The white line corresponds to the aRPD. OV: oxenic void; B: burrow; FP: feeding pit; T: tube.

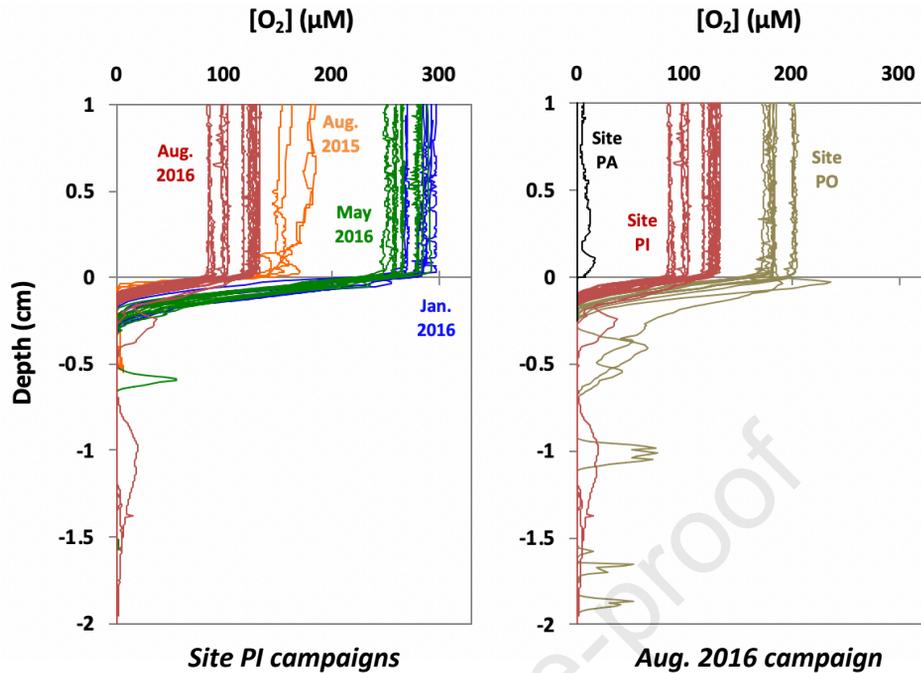


Figure 6: Dissolved oxygen profiles measured with the MP6 miniprofiler. Left panels: in site PI during the August 2015, January 2016, May 16 and August 2016 field campaigns. Right panels: in sites PO, PI and PA during the August 2016 campaign. The presence of oxygen peaks in anoxic sediment in site PI in May and August 2016 and in site PO in August 2016 indicate the presence of active burrows. The oxygen peaks at the sediment-water interface in site PO in August 2016 is associated to the activity of microphytobenthos activity.

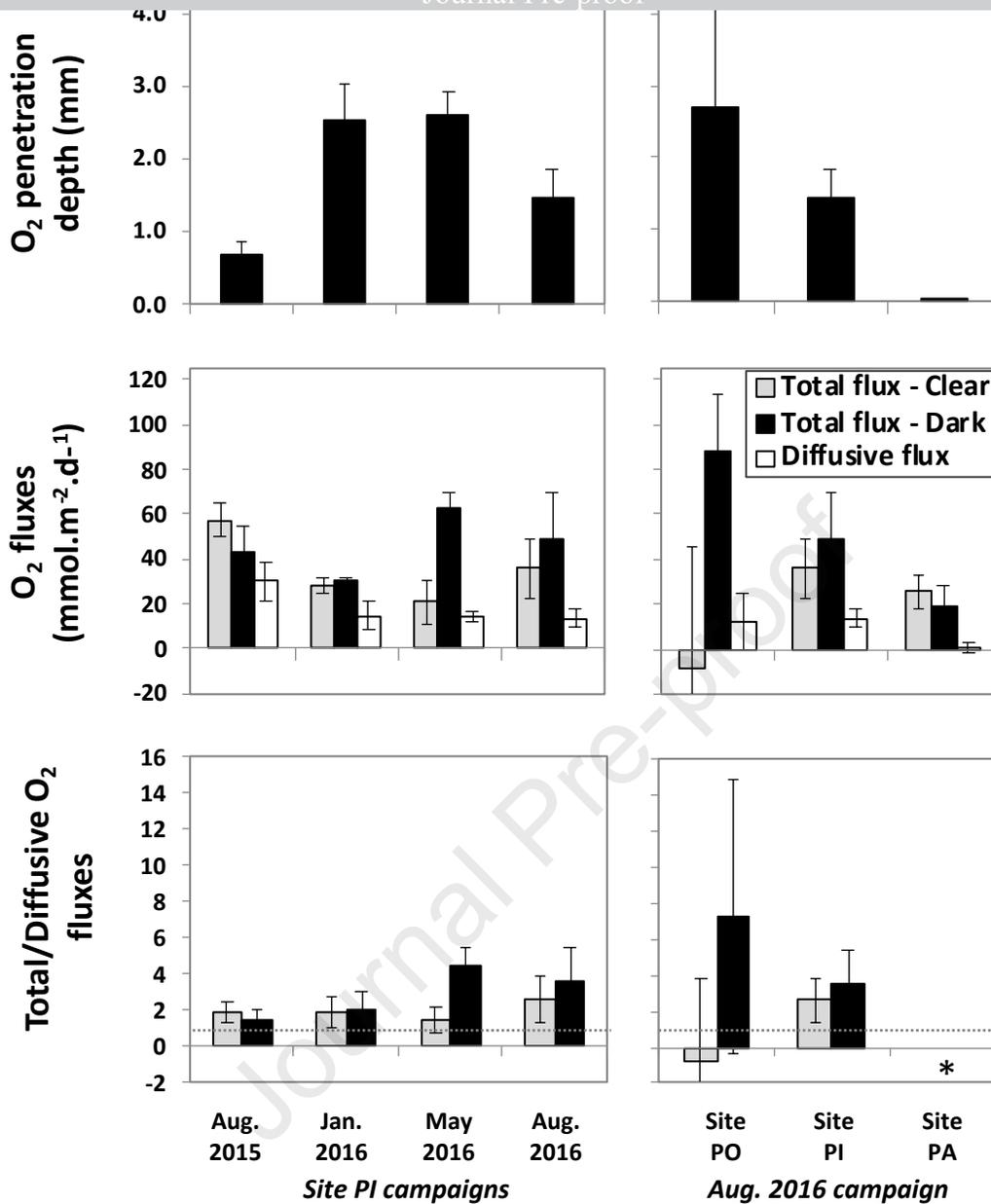
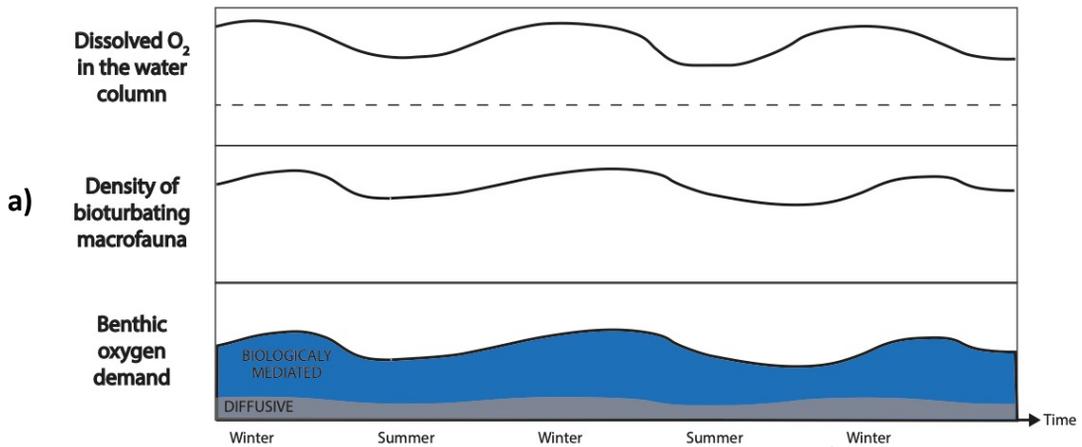


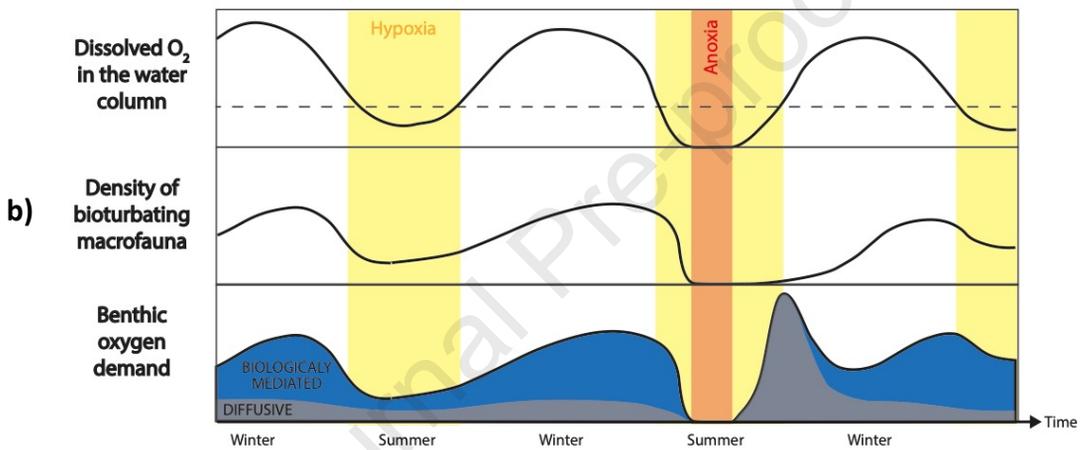
Figure 7: O₂ penetration depth in sediment and diffusive and total O₂ fluxes and corresponding total/diffusive O₂ fluxes ratios. Left panels: in site PI during the August 2015, January 2016, May 16 and August 2016 field campaigns. Right panels: in sites PO, PI and PA during the August 2016 campaign. The horizontal dashed line corresponds to a total/diffusive O₂ fluxes ratio = 1.

* No total/diffusive O₂ fluxes ratio can be reported in site PA in August 2016 because total and diffusive fluxes were measured within two days interval corresponding of two contrasted oxygenation conditions.

Permanently well oxygenated zone



Seasonally hypoxic/anoxic zone



Permanently hypoxic zone

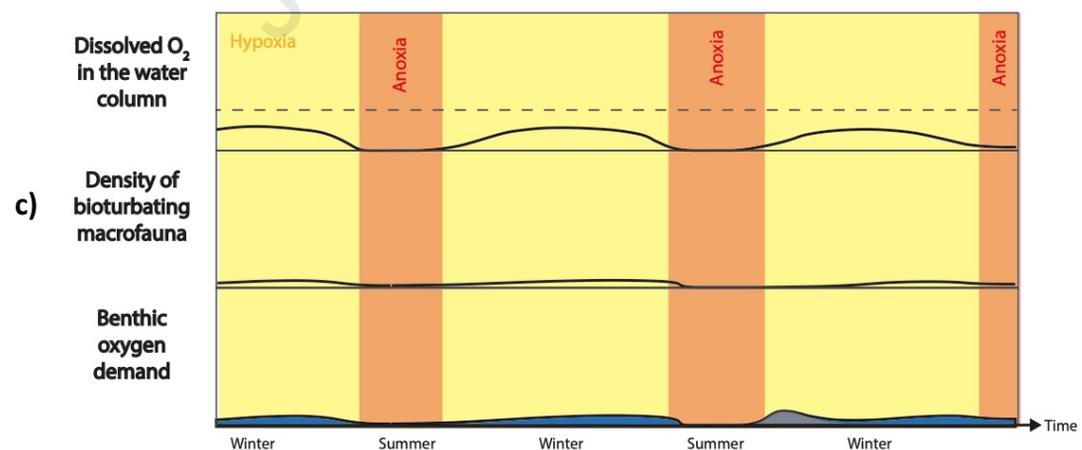


Figure 8: Conceptual representation of the temporal variation of the Benthic Oxygen Demand with respect to contrasted oxygenation situation in the coastal zone. The contribution of diffusive and biologically mediated fluxes are represented.

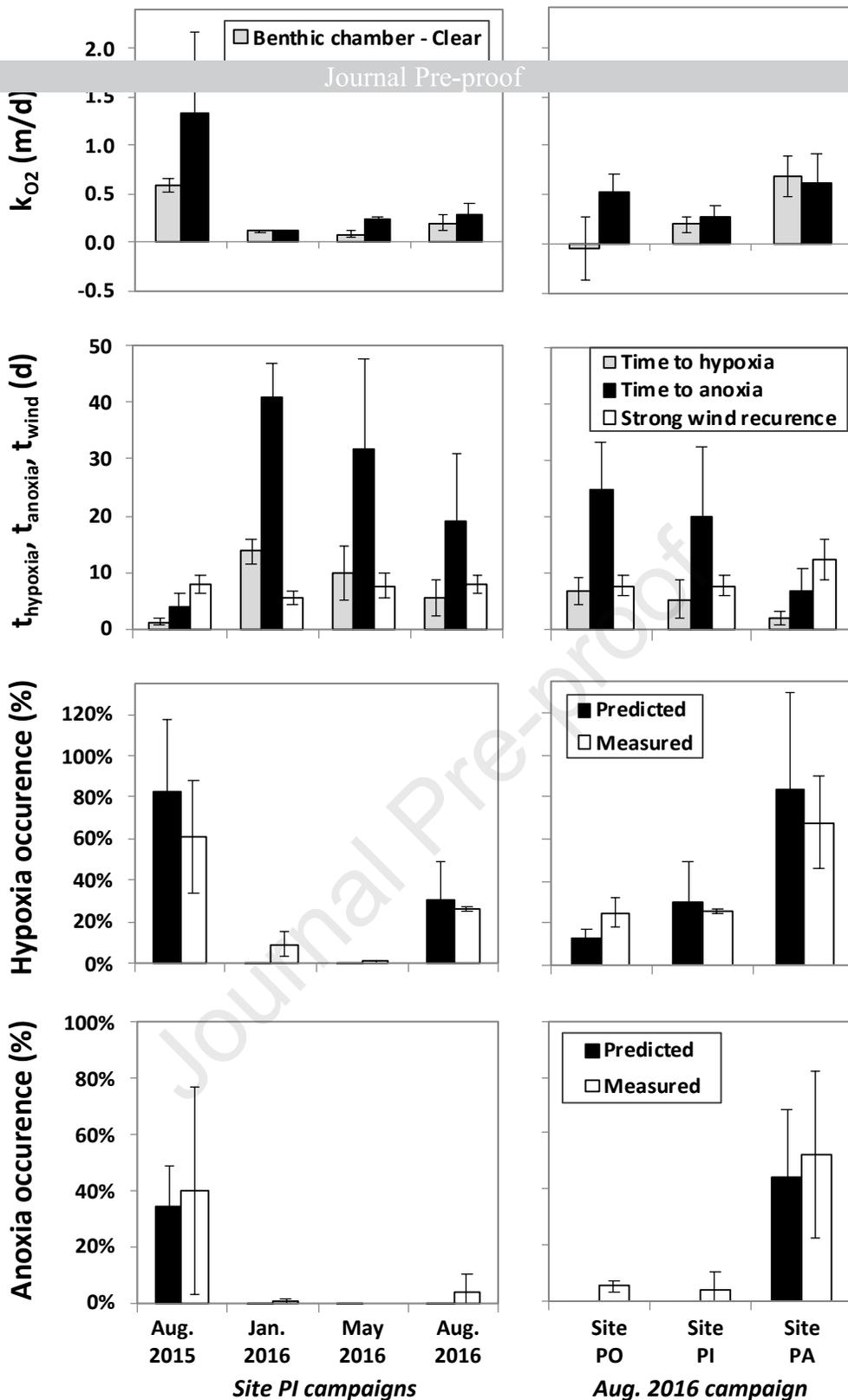


Figure 9: First-order kinetic constant rate of O_2 consumption (k_{O_2}) measured from clear and dark benthic chamber experiments, corresponding time to reach hypoxia (t_{hypoxia}) or anoxia (t_{anoxia}) in the last meter of the water column and recurrence period of strong wind events (>10 m/s at sites PO and Pi and >12 m/s at site PA), recognized to fully mix the water column in the Berre lagoon, and predicted and measured occurrence of hypoxia and anoxia in the Berre lagoon. Measured occurrence are based on continuous measurement of dissolved oxygen in the bottom water in the three investigated sites between summer 2015 and winter 2019. The strong wind recurrence and probability of occurrence of hypoxia and anoxia are reported for the season corresponding to each measurement: August = Summer (July-Sept period), January = Winter (Jan.-March period) and May = Spring (April-June period).

HIGHLIGHTS

- > The benthic oxygen demand (BOD) varies with seasonal and long-lasting deoxygenation events
- > BOD is firstly driven by oxygen availability in the water column
- > Hypoxia generates highest BOD for the oxidation of accumulated reduced chemical species
- > Mass mortality of benthic organism during anoxia limits the BOD to diffusive process.
- > Long-lasting normoxia generates high BOD because of high bioturbation and fresher organic matter
- > BOD can be reduced and inverted when light irradiance reach surface sediment
- > BOD and water column stratification are responsible of the chronic deoxygenation in the Berre lagoon

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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