

Effects of fluctuating hypoxia on benthic oxygen consumption in the Black Sea

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# Effects of fluctuating hypoxia on benthic oxygen consumption in the Black Sea (Crimean Shelf)

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Received: 6 April 2015 – Accepted: 7 April 2015 – Published: 30 April 2015

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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## Abstract

The outer Western Crimean Shelf of the Black Sea is a natural laboratory to investigate effects of stable oxic vs. varying hypoxic conditions on seafloor biogeochemical processes and benthic community structure. Bottom water oxygen concentrations varied between normoxic ( $175 \mu\text{mol O}_2 \text{ L}^{-1}$ ) and hypoxic ( $< 63 \mu\text{mol O}_2 \text{ L}^{-1}$ ) or even anoxic/sulfidic conditions within a few kilometres distance. Variations in oxygen concentrations between 160 and  $10 \mu\text{mol L}^{-1}$  even occurred within hours close to the chemocline at 134 m water depth. Total oxygen uptake, including diffusive as well as fauna-mediated oxygen consumption, decreased from  $> 15 \text{ mmol m}^{-2} \text{ d}^{-1}$  in the oxic zone to  $< 9 \text{ mmol m}^{-2} \text{ d}^{-1}$  in the hypoxic zone, correlating with changes in macrobenthos composition. Benthic diffusive oxygen uptake rates, comprising microbial respiration plus reoxidation of inorganic products, were around  $4.5 \text{ mmol m}^{-2} \text{ d}^{-1}$ , but declined to  $1.3 \text{ mmol m}^{-2} \text{ d}^{-1}$  at oxygen concentrations below  $20 \mu\text{mol L}^{-1}$ . Measurements and modelling of pore water profiles indicated that reoxidation of reduced compounds played only a minor role in the diffusive oxygen uptake, leaving the major fraction to aerobic degradation of organic carbon. Remineralization efficiency decreased from 100 % in the oxic zone, to 50 % in the oxic-hypoxic, to 10 % in the hypoxic-anoxic zone. Overall the faunal remineralization rate was more important, but also more influenced by fluctuating oxygen concentrations than microbial and geochemical oxidation processes.

## 1 Introduction

Hypoxia describes a state of aquatic ecosystems in which low oxygen concentrations affect the physiology, composition and abundance of fauna, consequently altering ecosystem functions including biogeochemical processes and sediment-water exchange rates (Middelburg and Levin, 2009). Coastal hypoxic zones often show reduced faunal abundances, biodiversity, and loss of habitat diversity below a threshold of  $63 \mu\text{mol O}_2 \text{ L}^{-1}$  (Diaz, 2001; Levin et al., 2009). In dynamic coastal hypoxic zones

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break (Stanev et al., 2013). This interface is stabilized by a halocline that separates the upper layer of brackish, oxic water (salinity < 17) from the saline, anoxic and sulfidic deep waters below (Tolmazin, 1985). Due to mixing processes by internal waves and eddies, the location of this interface zone is more dynamic along the margins of the Black Sea compared to the open sea. In the shelf region, hypoxic waters with oxygen concentrations < 63  $\mu\text{molL}^{-1}$  oscillate over > 70 m in water depth on time scales of hours to months (Stanev et al., 2013). On the outer Western Crimean Shelf, such strong vertical fluctuations affect a 40 km wide area of the slope (Friedrich et al., 2014; Luth et al., 1998).

Previous investigations on the consequences of hypoxia on benthic community structure on the Black Sea shelf focused on seasonally hypoxic coastal areas with water stagnation and a high organic carbon accumulation (Zaika et al., 2011), on shallow, active methane seeps with detrital-microbial mats (Zaika and Gulin, 2011) and on the effects of the basin-wide chemocline below the permanently hypoxic water column (Kolesnikova et al., 2014; Sergeeva et al., 2012, 2013; Zaika and Sergeeva, 2012). Sergeeva and Zaika (2013) reported that under permanently hypoxic conditions, some protozoa (Gromiida and Foraminifera) and some metazoa (Harpacticoida, Polychaeta, Nematoda) can complete full life cycles, depending on the water depth and the distance from the sulfidic zone. Some meiobenthos species even seem to prefer hypoxic conditions (Sergeeva and Anikeeva, 2014; Sergeeva et al., 2013).

Here we investigated processes on the outer Western Crimean Shelf to assess how natural fluctuations in bottom water oxygen concentrations influence biogeochemical processes such as respiration, organic matter remineralization and the distribution of benthic organisms. The questions addressed are to what extent the variability in oxygen concentration has an effect on (1) the remineralization rates, (2) the proportion of microbial vs. fauna-mediated respiration, (3) the community structure and (4) the share of anaerobic vs. aerobic microbial respiration pathways.

## 2 Methods

### 2.1 Study site on the outer Western Crimean Shelf

Investigations of bottom water oxygen concentrations and biogeochemistry of the underlying seafloor of the outer Western Crimean Shelf were carried out over a time period of 2 weeks (20 April–7 May 2010) during leg MSM 15/1 of R/V *Maria S. Merian*. The selected area on the outer shelf has a gentle slope and a maximum width of around 60 km until the shelf break at approx. 200 m water depth. The sediment and the water column were sampled along a transect from 95 to 207 m water depth within an area of about 100 km<sup>2</sup> (Fig. 1). Detailed information of all stations in the working area is given in Table 1. All biogeochemical data are deposited in the Earth System database www.PANGAEA.de and are available at <http://doi.pangaea.de/10.1594/PANGAEA.844879>.

### 2.2 Water column CTD and oxygen measurements

Bottom water oxygen concentrations were recorded repeatedly between 95 to 206 m water depth at different spatial and temporal scales with various sensors, which were all calibrated by Winkler titration (Winkler, 1888). A total of 26 casts were performed with a CTD/Rosette equipped with a SBE 43 oxygen sensor (Seabird Electronics, Bellevue, WA, USA). A mooring was deployed at 135 m water depth, equipped with a Seaguard current meter with CTD and a type 4330 oxygen optode (Aanderaa Data Instruments, Bergen, Norway) recording at 60 s intervals at a distance of 1.5 m above the sediment from the 30 April to the 7 May 2010. A second mooring was deployed for the same time period at 100 m water depth, with a CTD attached at 1.5 m above the sediment (type SBE 16, Seabird Electronics) to record density, salinity and temperature. CTD water column casts and the mooring at 135 m showed that oxygen concentrations strongly correlate with density ( $R^2 = 0.997$ ). Hence, oxygen concentrations at the 100 m mooring site were calculated from the density recordings at this site using a density-oxygen relationship (4th order polynomial fit) based on the compiled mooring/CTD data. Ad-

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ditionally, bottom water oxygen concentration was measured at the seafloor by oxygen optodes mounted on the manned submersible JAGO (GEOMAR, Kiel; optode type 3830), and to a Benthic Boundary Layer-Profiler (Holtappels et al., 2011) (type 4330). Furthermore, microprofilers equipped with oxygen microsensors were mounted on a lander and a crawler (see Sect. 2.5.1). For consistency with other hypoxia studies, we use the oxygen threshold of  $63 \mu\text{molL}^{-1}$  as upper boundary for hypoxia (Diaz, 2001). Sulfide concentrations were determined in bottom water collected with Niskin bottles during CTD casts and JAGO dives at 13 different locations between 135 and 218 m water depth. For all water column oxygen and sulfide concentrations a limit of  $2 \mu\text{molL}^{-1}$  was defined, below which concentrations were assumed to be zero.

### 2.3 Visual seafloor observations and micro-topography scans

To observe organisms, their traces of life, and the resulting micro-topography at the surface of the different seafloor habitats, a laser scanning device (LS) and the high-resolution camera MEGACAM were used on the benthic crawler MOVE (MARUM, Bremen). The LS consisted of a linear drive that moved a downward looking line laser together with a monochrome digital camera horizontally along a 700 mm long stretch of the seafloor. The position of the approx. 200 mm wide laser line in image-series recorded by the camera from an angle of  $45^\circ$  the 3-D micro-topography of the scanned area was determined on a  $1 \times 1 \text{ mm}^2$  horizontal grid at sub-mm accuracy (for a detailed description see Cook et al., 2007). The roughness of the sediment surface was quantified in three 700 mm long profiles extracted from the sides and along the center line of 7, 2, 6, and 2 micro-topographies scanned at 104, 138, 155, and 206 m water depth, respectively. Roughness was determined for different length scales by calculating mean absolute vertical differences to the same profile previously smoothed by applying moving average with 3 to 300 mm averaging window size.

The downward-looking MEGACAM was either attached directly to MOVE or added to the horizontal drive of the LS; the latter configuration facilitating imaging of larger sediment stretches by photo-mosaicking. In addition, visual seafloor observations were

carried out before pushcore sampling by JAGO. Dive videos were recorded with a type HVR-V1E HDV Camcorder (SONY, Tokyo, Japan) mounted in the center of JAGO's large front viewport during 19 dives. During each dive, video still images were captured by video-grabber from the running camera.

## 2.4 Faunal analyses

Meiofauna organisms were counted in 5 cm sediment horizons of 2–4 cores per station, with each core covering an area of 70.9 cm<sup>2</sup> (TVMUC) and 41.8 cm<sup>2</sup> (for JAGO pushcore) (Table 1, Fig. 1). The abundances were extrapolated to m<sup>2</sup>. Sediments were washed with distilled water through sieves with mesh sizes of 1 mm and 63 μm, and preserved in 75 % alcohol to conserve the morphological structures of the meiofauna. Subsequently, samples were stained with Rose Bengal, to separate living and dead/decaying organisms (Grego et al., 2013), and sorted in water under a microscope. Only organisms that strongly stained with Rose Bengal and showed no signs of morphological damage were considered as being alive at the time of sampling. All of the isolated organisms were counted and identified to higher taxa. In addition, macrofauna distribution was qualitatively assessed sieving sediments from several multicorer cores (area of 70.9 cm<sup>2</sup>) and JAGO pushcores (area of 41.8 cm<sup>2</sup>) (Table 1, Fig. 1) with a 2 mm size mesh. Statistical analyses of the similarity of fauna communities were conducted using the R package vegan (Oksanen et al., 2010) and performed in R (v. 3.0.1; <http://www.R-project.org>). Richness was calculated from species (taxa) presence/absence. A matrix based on Bray–Curtis dissimilarities was constructed from the Hellinger-transformed abundances for meiofauna taxa. The non-parametric Analysis of Similarity (ANOSIM) was carried out to test whether the communities (based on different bottom-oxygen zones) were significantly different (Clarke, 1993).

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## 2.5 Benthic exchange rates

### 2.5.1 In situ microsensor measurements

Vertical solute distributions were measured in situ at high resolution in sediment pore waters and the overlying waters with microsensors mounted on microprofiler units (Boetius and Wenzhöfer, 2009). In particular, Clark-type O<sub>2</sub> microsensors (Revsbech, 1989) and H<sub>2</sub>S microsensors (Jeroschewski et al., 1996) were used as well as microsensors for pH – either LIX-type (de Beer et al., 1997) or needle-type (type MI 408, Microelectrodes Inc., Bedford, NH, USA). A two-point oxygen sensor calibration was done in situ, using water column oxygen concentrations obtained from simultaneous oxygen recordings and zero readings in anoxic sediment layers. The H<sub>2</sub>S sensors were calibrated at in situ temperature on board at stepwise increasing H<sub>2</sub>S concentrations by adding aliquots of a 0.1 mol L<sup>-1</sup> Na<sub>2</sub>S solution to acidified seawater (pH < 2). pH sensors were calibrated with commercial laboratory buffers and corrected with pH obtained from water samples taken with Niskin bottles operated by JAGO.

Profiler units were mounted either on the benthic crawler MOVE (Waldmann and Bergenthal, 2010) or on a benthic lander (Wenzhöfer and Glud, 2002). The MOVE vehicle was connected to the ship via a fiber optic cable that allowed continuous access to video and sensor data. The maneuverability of the vehicle allowed to target spots of interest on the seafloor in the cm range. The profiler units were equipped with 3–4 O<sub>2</sub> microsensors, 2 H<sub>2</sub>S microsensors, and 1–2 pH sensors. Microprofiles across the sediment-water interface were performed at a vertical resolution of 100 μm and had a total length of up to 18 cm. During each deployment of the lander the microsensor array performed up to three sets of vertical profiles at different horizontal positions, each 26 cm apart.

From the obtained oxygen profiles the diffusive oxygen uptake (DOU) was calculated based on the gradients in the diffusive boundary layer (DBL) according to Fick's first

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law of diffusion,

$$J = \frac{dc}{dx} \times D_0 \quad (1)$$

where  $J$  is the oxygen flux,  $dc/dx$  is the concentration gradient, and  $D_0$  is the diffusion coefficient of oxygen in water ( $D_0 \text{O}_2 = 1.22 \times 10^{-4} \text{ m}^2 \text{ d}^{-1}$ , Broecker and Peng, 1974) at the ambient temperature (8 °C) and salinity (18–20). For each station, selected oxygen profiles were fitted using the software PROFILE (Berg et al., 1998) to determine oxygen consumption from the shape of the pore water gradient and to identify depth intervals of similar oxygen consumption based on statistical  $F$  testing.

### 2.5.2 In situ benthic chamber incubations

Total oxygen uptake (TOU) of sediments was measured by in situ benthic chamber incubations using 2 platforms: (1) two benthic chambers, each integrating an area of  $0.2 \times 0.2 \text{ m}$  (Witte and Pfannkuche, 2000) mounted to the same benthic lander frame used for microprofiler measurements (Wenzhöfer and Glud, 2002) and (2) a circular chamber ( $r = 0.095 \text{ m}$ , area =  $0.029 \text{ m}^2$ ) attached to the benthic crawler MOVE for video-guided chamber incubations. After positioning MOVE at the target area the chamber was lowered into the sediment, controlled by the video camera of MOVE and operated online through the MOVE-electronics. Both systems were equipped with a stirrer and syringe samplers that took up to 6 successive samples ( $V = 50 \text{ mL}$ ) from the 0.1–0.15 m high overlying bottom water. Benthic exchange rates were determined from the linear regression of oxygen solute concentration over time inside the enclosed water body that was continuously monitored for a period of 2 to 4 h by 1 or 2 oxygen optodes mounted in the chamber lid. The optodes were calibrated with a zero reading at in situ temperature on board and with bottom water samples, in which concentrations were determined either by Winkler titration (Winkler, 1888) or with a calibrated Aanderaa optode attached to the outside of the chamber. Oxygen concentrations in the chamber was the same as in in situ bottom water concentrations. During deploy-

ments in the hypoxic-anoxic zone, oxygen concentrations in the chambers were higher than in the surrounding bottom water, due to enclosure of oxygen-rich water during descent. These measurements were used to estimate potential TOU rates at intermittently higher oxygen concentration. To estimate the in situ ratio of TOU/DOU for the hypoxic-anoxic zone, we modeled the DOU based on the volumetric rate and the DBL thickness determined by the in situ microsensors profile.

## 2.6 Geochemical analyses of the sediments and sulfate reduction rates

Sediments for geochemical analyses were sampled with a video-guided multicorer (TV-MUC) at 4 stations between 104 and 207 m (Table 1). Pore water was extracted from sediment cores within 3 h after retrieval in 1 cm (upper 5 cm) or 2 cm (> 5 cm) intervals with Rhizons (type: CSS, Rhizosphere Research Products, pore size < 0.2  $\mu\text{m}$ ) at in situ temperature (8  $^{\circ}\text{C}$ ) in a temperature-controlled room, and fixed for Fe(II), Mn(II), sulfide and sulfate analyses as described in Lichtschlag et al. (2010). For ammonium analyses 3 mL of the samples were frozen at  $-20^{\circ}\text{C}$ . In addition, one sediment core from each station was sliced in 1 cm intervals (upper 10 cm) and 2 cm intervals (> 10 cm depth) for solid phase analyses. Aliquots were stored at 4  $^{\circ}\text{C}$  for porosity analyses and frozen at  $-20^{\circ}\text{C}$  for  $^{210}\text{Pb}$  and solid phase iron, manganese and elemental sulfur analyses.

Pore water constituents were analyzed by the following procedures: Dissolved Mn(II) and Fe(II) were measured with a Perkin Elmer 3110 flame atomic absorption spectrophotometer (AAS) with a detection limit of 5  $\mu\text{mol L}^{-1}$  for iron and manganese. Total sulfide concentrations ( $\text{H}_2\text{S} + \text{HS}^- + \text{S}^{2-}$ ) were determined with the diamine complexation method (Cline, 1969). A Skalar Continuous-Flow Analyzer was used for ammonium analyses following the procedures described in Grasshoff (1983), with a detection limit of 1  $\mu\text{mol L}^{-1}$ . Sulfate concentrations in pore water were determined by non-suppressed anion exchange chromatography (Metrohm 761 Compact IC) after filtration and dilution. To determine fluxes of iron, manganese, sulfide and ammonium the pore water profiles were fitted using the software PROFILE (Berg et al., 1998).

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Total zero-valent sulfur in sediments was extracted with methanol from sediment preserved in ZnAc (Zopfi et al., 2004) and analyzed by HPLC. Concentrations of acid volatile sulfide (AVS =  $\text{Fe}_3\text{S}_4$ , FeS) and chromium reducible sulfur (CRS =  $\text{FeS}_2$ , some  $\text{S}^0$ , remaining  $\text{Fe}_3\text{S}_4$ ) were determined on frozen sediment aliquots by the two-step Cr II distillation method (Fossing and Jørgensen, 1989). Solid phase reactive iron and manganese were extracted from frozen sediments after the procedure of Poulton and Canfield (2005) using sequentially Na-acetate, hydroxylamine-HCl, dithionite and oxalate. Manganese and iron concentrations were measured as described above.

Sulfate reduction rates were determined with the whole core incubation method described in Jørgensen (1978). On board  $10\ \mu\text{L}$  aliquots of an aqueous  $^{35}\text{SO}_4^{2-}$  tracer solution (activity  $11.5\ \text{kBq}\ \mu\text{L}^{-1}$ ) were injected into the sediments in 1 cm intervals and samples were incubated for up to 24 h at in situ temperature, until the sediments were sliced into 20 mL 20% ZnAc. Tracer turnover rates were determined with the single-step cold distillation method (Kallmeyer et al., 2004). Three replicates were measured per station and results were integrated over the upper 10 cm of the sediment.

Porosity and solid-phase density were determined by drying a wet sediment aliquot of known volume at  $105\ ^\circ\text{C}$  until constant weight and weighing before and after.

Sedimentation rates were determined from excess  $^{210}\text{Pb}$  activity ( $^{210}\text{Pb}_{\text{xs}}$ ) in frozen sediment aliquots of the upper 10 cm that were freeze-dried and homogenized by grinding. Activities of  $^{210}\text{Pb}$ ,  $^{214}\text{Pb}$ , and  $^{214}\text{Bi}$  were determined on 5–30 g aliquots by non-destructive gamma spectrometry using an ultra-low-level germanium gamma detector (EURISYS coaxial type N, Canberra Industries, Meriden, CT, USA). Sediment accumulation rates ( $\text{g}\ \text{cm}^{-2}\ \text{yr}^{-1}$ ) were calculated from the undisturbed part of the sediments from the change of the unsupported  $^{210}\text{Pb}_{\text{xs}}$  activity with sediment accumulation, expressed as cumulative dry weight ( $\text{g}\ \text{cm}^{-2}$ ) as described by Niggemann et al. (2007). This calculation is based on the assumption that the  $^{210}\text{Pb}_{\text{xs}}$  flux and sedimentation were constant over time.

### 3 Results

#### 3.1 Oxygen regime of the Outer Western Crimean Shelf

Recordings of bottom water oxygen concentrations ( $n = 85$ ) along the transect from 95 to 206 m water depth served to differentiate four zones of different bottom water oxygenation within a distance of more than 30 km (Table 1; Figs. 1 and 2):

The “oxic zone” at water depths of 95 to 130 m had oxygen concentrations of on average  $116 \pm 29 \mu\text{mol L}^{-1}$  (31 % air saturation at ambient conditions;  $8^\circ\text{C}$ , salinity of 19), and remained above the threshold for hypoxia ( $63 \mu\text{mol L}^{-1}$ ) throughout the period of our observations. Recordings from the mooring at 100 m water depth showed some fluctuations (Fig. S1a in the Supplement), with oxygen concentrations varying between  $100\text{--}160 \mu\text{mol L}^{-1}$  within 6 days. In this oxic zone, sediment surface color was brownish, and the seafloor looked rather homogenous, without ripple structures, but with faunal traces (Fig. S2a). The top 5 cm of the sediment comprised some shell debris of 2–6 mm diameter encrusted with a bright orange layer of up to 3 mm thickness, which most probably consisted of iron-oxides (Fig. S2b). During JAGO dives and MOVE deployments we recorded living fauna in the oxic zone such as clams, ascidians, phoronids, cerianthids, porifera and many fish. Traces of recent faunal activity at the seafloor included trails, worm borrows and feces (Fig. S2c). During our sampling campaign the horizontal distance to the oxic-anoxic interface (chemocline) was on average 13 km. The oxic zone served as reference for further comparisons of hypoxic effects on biogeochemical processes and faunal community composition.

In the “oxic-hypoxic zone” at water depths between 130 to 142 m, average bottom water oxygen concentrations were  $94 \pm 56 \mu\text{mol L}^{-1}$  (approx. 25 % air saturation at ambient conditions;  $8^\circ\text{C}$ , salinity of 20). However, we observed strong variations in oxygen concentrations with maxima of up to  $176 \mu\text{mol L}^{-1}$  and minima of  $9 \mu\text{mol L}^{-1}$ , respectively. Hypoxic conditions prevailed for 30 % of the observation period of 7 days, as recorded by the stationary mooring at 135 m water depth (Fig. S1b). Constantly rising oxygen concentrations over days were interspersed by a substantial drop from fully oxic to al-

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macrobenthos abundances in both the oxic and the oxic-hypoxic zone at around 129–138 m was related to an accumulation of cnidarians with abundances of up to  $54 \times 10^3$  individuals  $m^{-2}$  (Table S1). Also the two hypoxic zones were dominated by cnidaria. In accordance with the results from sampling, no larger macrofauna was documented during JAGO dives in these zones.

Meiobenthos was composed of similar groups and abundances in the oxic and oxic-hypoxic zone with densities of around  $200 \times 10^4$  individuals  $m^{-2}$  (Fig. 6, Table S2). A substantial decrease to  $50 \times 10^4$  individuals  $m^{-2}$  was observed between these two zones and the hypoxic-anoxic zone. The meiofaunal community structure changed according to the oxygenation regime (Fig. 7), showing significant differences between oxic and hypoxic-anoxic zones (ANOSIM-R = 0.7, Bonferroni corrected  $P$  value < 0.05) together with the highest dissimilarities (up to 50 %, Table S3). Nematodes dominated meiofauna composition in all oxic and hypoxic zones (Table S2). In the oxic zone ostracodes were the 2nd most abundant species. These were replaced by benthic foraminifera in the oxic-hypoxic and the hypoxic-anoxic zone. Altogether meiofaunal richness (taxa count, average  $\pm$  SD) was similar in the oxic zone and oxic-hypoxic zone ( $15 \pm 2$  and  $15 \pm 1$ ) and dropped to  $9 \pm 1$  in the hypoxic-anoxic zone.

### 3.3 Benthic oxygen fluxes and respiration rates

A total of 33 oxygen microprofiles were measured during seven deployments of the benthic crawler MOVE and the lander at water depths between 104 and 155 m. Oxygen penetration depths and dissolved oxygen uptake rates are summarized in Table 2. The shape of the profiles and the differences in oxygen penetration depth as shown in Fig. 3 reflect the spatial variations of oxygen bottom water concentrations and oxygen consumption rates. In the shallowest, oxic zone (104 m) clear signs of bioturbation were visible from the irregular shape of about 25 % of the profiles, occasionally increasing the oxygen penetration depth up to approximately 10 mm. Bioturbation activity was in accordance with a significant bioturbated surface layer and more pronounced roughness elements at the sediment surface at the shallowest site as compared to deeper

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duced (max.  $89 \mu\text{mol L}^{-1}$ , Fig. 5h), manganese concentrations were below detection (Fig. 5i), but free sulfide was still not present in the pore waters (Fig. 5j). In the hypoxic-anoxic zone dissolved iron and sulfide concentrations were below or close to detection limit (Fig. 5o and q), and some dissolved manganese was present in the lower part of the sediment (Fig. 5p). The station in the anoxic-sulfidic zone had no dissolved iron and manganese, but pore water concentrations of sulfide increased to up to  $1000 \mu\text{mol L}^{-1}$  at 30 cm sediment depth (Fig. 5v–x).

In solid phase extractions, reactive iron was elevated in the 0–1 cm interval of the oxic zone and iron oxides were present throughout the upper 30 cm of surface sediments (Fig. 5e). In contrast, concentrations of iron-oxides in the upper 10 cm of the oxic-hypoxic zone were clearly reduced and dropped to background concentrations below 10 cm. The same trend was observed in sediments of the hypoxic-anoxic and the anoxic-sulfidic zone (Fig. 5l, s, and z). Solid phase manganese concentration was only clearly elevated in the 0–1 cm interval of the oxic zone (Fig. 5f) and at or close to background concentration below 1 cm, as in all other zones (Fig. 5m, t and aa).

Although pore water concentrations of sulfide were below detection limit in the oxic to hypoxic-anoxic zones, the presence of reduced solid sulfide phases (AVS, CRS and  $\text{S}^0$ , Fig. 5g, n, u, and ab) and measured sulfate reduction rates indicate that sulfate reduction takes place below the oxygenated sediment. Sulfate reduction rates, integrated over the upper 10 cm of the sediment, represent gross sulfide production and compare well to net sulfide fluxes calculated from the pore water profiles in Table 3. Altogether, seafloor sulfate reduction rates were increasing nearly 40 fold from  $< 0.1 \text{ mmol m}^{-2} \text{ d}^{-1}$  in the oxic zone to  $3.7 \text{ mmol m}^{-2} \text{ d}^{-1}$  in the anoxic-sulfidic zone. In all cores sulfate concentrations were constant with  $16 \text{ mmol L}^{-1}$  over the upper 30 cm of the sediment and methane concentrations were close to or below detection limit (data not shown).

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### 3.5 Sediment accumulation and bioturbation

Sediment porosity was similar across all sites with  $0.9 \pm 0.03$  in the top cm and  $0.8 \pm 0.07$  averaged over the top 10 cm. Sediment accumulation rates, calculated from the decrease of  $^{210}\text{Pb}_{\text{xs}}$  with depth and cumulative dry weight, varied around  $1 \pm 0.5 \text{ mm yr}^{-1}$  for the upper 10 cm of the oxic-hypoxic and the hypoxic-sulfidic zone. Nearly constant  $\ln^{210}\text{Pb}_{\text{xs}}$  values in the upper 2 cm of the oxic zone indicate active sediment mixing by bioturbation. In all other zones, the linear decrease starting right below the sediment surface indicates a continuous decay and, hence, the absence of sediment mixing processes. A stronger bioturbation at the oxic site as compared to the oxic-hypoxic and hypoxic-anoxic site matches the micro-topographies observed at the different sites. Average absolute roughness heights at a water depth of 104 m were generally  $\sim 1.8$ ,  $\sim 3.2$ , and  $\sim 3.9$  times larger than at 138, 155, and 206 m depth, respectively, at all investigated length scales (i.e., averaging windows). At an averaging window of 50 mm, a horizontal scale that covers many biogenic roughness elements, e.g., fecal mounds or funnels of burrows, average absolute deviations from the smoothed surface were  $0.42 \pm 0.16 \text{ mm}$  at 104 m,  $0.23 \pm 0.03 \text{ mm}$  at 138 m,  $0.15 \pm 0.03 \text{ mm}$  at 155 m, and  $0.13 \pm 0.01 \text{ mm}$  at 206 m water depth. Fig. S3 shows example 3-D micro-topographies and extracted profiles (original and smoothed at 155 mm window size).

## 4 Discussion

### 4.1 Effect of oxygen availability on remineralization rates and reoxidation processes

Rates of benthic oxygen consumption are governed by a variety of factors including primary production, particle export, quality of organic matter, bottom water oxygen concentrations, and faunal biomass (Jahnke et al., 1990; Middelburg and Levin, 2009; Wenzhöfer and Glud, 2002). Here we investigated the effects of variable hypoxic con-

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by benthic fauna. The diffusive oxygen uptake (DOU), as calculated from microsensor profiles, represents mainly aerobic respiration of microorganisms or – although not relevant in our area (see above) – chemical reoxidation (Glud, 2008). In general, the DOU of the outer Western Crimean Shelf sediments was lower than in other shelf zones with seasonally hypoxic water columns (e.g., Glud et al., 2003), but in the same range as fluxes reported in other Black Sea studies (Table 4). Average DOU was similar in the oxic and oxic-hypoxic zone and only clearly reduced when oxygen concentrations were close to zero ( $20 \mu\text{mol L}^{-1}$ ). To test if lower fluxes at reduced bottom water oxygen concentrations rather reflect lowered efficiency of oxygen consumption processes (i.e., rate limitation), or decreased diffusional uptake (i.e., transport limitation), we calculated the highest possible oxygen fluxes in relation to bottom water oxygen concentration. For this we assumed complete consumption of oxygen at the sediment surface (i.e., oxygen penetration depth approaches zero and volumetric rates approaches infinity), and calculated the flux from measured  $\text{O}_2$  concentrations in the bottom water and the observed diffusive boundary layer thickness of  $500 \mu\text{m}$  using Ficks' first law of diffusion (Eq. 1). Maximum theoretical fluxes were  $4.3$  to  $36.4 \text{ mmol m}^{-2} \text{ d}^{-1}$  for the oxic-hypoxic zone and  $2.7$  to  $4.6 \text{ mmol m}^{-2} \text{ d}^{-1}$  for the hypoxic-anoxic zone (for oxygen concentrations see Table 4). Thus, while fluxes are generally not transport limited, the benthic uptake of oxygen approaches its potential maximum when bottom water oxygenation decreases.

TOU at the oxic-hypoxic zone was substantially lower as compared to the oxic zone despite bottom water oxygen concentrations mostly above the common threshold for hypoxia of  $63 \mu\text{mol L}^{-1}$  (Figs. 2 and 3). This indicates that total oxygen uptake is more sensitive to varying bottom water oxygen concentrations than diffusive uptake mediated by microorganisms. To quantify the extent to which benthos-mediated oxygen uptake (BMU) is affected by dynamic oxygen conditions, BMU was calculated from the difference between TOU and DOU (Glud, 2008; Wenzhöfer and Glud, 2004). BMU includes not only oxygen demand of the fauna itself but also oxygen consumption that is related to the increase in oxygen-exposed sediment area due to sediment ventilation and re-





pending on hydrographic conditions, ecosystem functioning could thus be negatively impacted in much larger areas adjacent to hypoxic ecosystems.

**The Supplement related to this article is available online at  
doi:10.5194/bgd-12-6445-2015-supplement.**

5 *Acknowledgements.* We thank the Captain and shipboard crew of the RV *Maria S. Merian*,  
the JAGO team (GEOMAR, Kiel) and shipboard scientists of the cruise MSM 15/1 for their  
excellent work at sea. We are grateful for technical assistance from Rafael Stiens, Martina  
Alich, Erika Weiz, and Kirsten Neumann. We thank the Sea-Tech technicians of the HGF MPG  
10 Joint Research Group for Deep-Sea Ecology and Technology (MPI-AWI) for the construction  
and maintenance of the in situ devices and the technicians of the Microsensor Group for the  
construction of microsensors. We thank Tim Ferdelman and Gail Lee Arnold for help with the  
sedimentation rate measurements. This project was financed by the EU 7th FP project HYPOX  
(In situ monitoring of oxygen depletion in hypoxic ecosystems of coastal and open seas, and  
land-locked water bodies) EC Grant 226213.

15 The article processing charges for this open-access publication  
were covered by the Max Planck Society.

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**Table 1.** Measurements and samples (including PANGAEA event labels) taken in zones with different oxygen regime. PUC = JAGO pushcores, MOVE = benthic crawler move (in situ microsensor measurements and/or benthic chamber deployment), TVMUC = video-guided multicorer, KAMM = lander (in situ microsensor measurements and/or benthic chamber deployment).

Zone	Water depth (m)	Station/PANGAEA event label	Position	Date	Device	Method
oxic zone < 130 m	101	MSM15/1_482_PUC 1, 3, 5, 6	44°49.00' N 33°09.37' E	3 May 2010	PUC	Macro- and meiobenthos
	104	MSM15/1_484-1	44°49.49' N 33°09.32' E	3 May 2010	MOVE	Benthic oxygen uptake
	104	MSM15/1_464-1	44°49.45' N 33°09.26' E	2 May 2010	TVMUC	Macro- and meiobenthos
	104	MSM15/1_462-1	44°49.45' N 33°09.26' E	2 May 2010	TVMUC	Geochemistry
	106	MSM15/1_469-1	44°49.46' N 33°09.67' E	2 May 2010	KAMM	Benthic oxygen uptake
	105	MSM15/1_444_PUC 1	44°49.32' N 33°09.46' E	1 May 2010	PUC	Macro- and meiobenthos
	117	MSM15/1_440_PUC 5, 6	44°40.49' N 33°05.53' E	1 May 2010	PUC	Macro- and meiobenthos
bottom water oxygen conc. > 63 $\mu\text{mol L}^{-1}$	120	MSM15/1_459-1, 2	44°40.48' N 33°05.53' E	2 May 2010	TVMUC	Macro- and meiobenthos
	129	MSM15/1_486_PUC 1, 7	44°39.13' N 33°01.78' E	4 May 2010	PUC	Macro- and meiobenthos
	136	MSM15/1_487-1	44°38.78' N 33°00.25' E	4 May 2010	TVMUC	Geochemistry
oxic-hypoxic (130–142 m)	137	MSM15/1_434-1	44°38.93' N 32°59.98' E	1 May 2010	KAMM	Benthic oxygen uptake
	137	MSM15/1_455-1	44°38.92' N 32°59.97' E	2 May 2010	MOVE	Benthic oxygen uptake
	138	MSM15/1_460_PUC-1	44°39.26' N 33°01.12' E	2 May 2010	PUC	Macro- and meiobenthos
bottom water oxygen conc. > 63 to > 0 $\mu\text{mol L}^{-1}$	138	MSM15/1_489- 1, 2	44°38.79' N 33°00.25' E	4 May 2010	TVMUC	Macro- and meiobenthos
	140	MSM15/1_499-1	44°38.80' N 33°00.26' E	5 May 2010	KAMM	Benthic oxygen uptake
hypoxic-anoxic (142–167 m)	145	MSM15/1_512-3	44°37.39' N 32°56.21' E	5 May 2010	PUC	Macro- and meiobenthos
	151	MSM15/1_372_PUC 1	44°37.46' N 32°54.91' E	25 Apr 2010	PUC	Macro- and meiobenthos
	154	MSM15/1_383-1	44°37.74' N 32°54.92' E	26 Apr 2010	KAMM	Benthic oxygen uptake
	155	MSM15/1_379-1	44°37.55' N 32°54.97' E	26 Apr 2010	TVMUC	Macro- and meiobenthos
	156	MSM15/1_386-1	44°37.58' N 32°54.97' E	26 Apr 2010	MOVE	Benthic oxygen uptake
	162	MSM15/1_374-1	44°37.07' N 32°53.49' E	25 Apr 2010	PUC	Macro- and meiobenthos
	163	MSM15/1_425-1	44°47.09' N 31°58.05' E	30 Apr 2010	TVMUC	Macro- and meiobenthos
anoxic-sulfidic zone (> 167 m) sulfide present in anoxic bottom water	164	MSM15/1_393-1	44°37.08' N 32°53.48' E	27 Apr 2010	TVMUC	Geochemistry
	207	MSM15/1_448-1	44°35.84' N 32°49.03' E	1 May 2010	TVMUC	Geochemistry

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**Table 2.** Diffusive oxygen uptake (DOU) rates, total oxygen uptake (TOU) rates and oxygen penetration depth under different oxygen regimes at the outer Western Crimean Shelf. Chamber measurements in the hypoxic-anoxic zone represent potential rates, scaled to a bottom water oxygen concentration of  $20 \mu\text{mol O}_2 \text{L}^{-1}$  (instead of  $70 \mu\text{mol O}_2 \text{L}^{-1}$ ).

Zone	DOU $J_{\text{O}_2} \pm \text{SD}$ ( $\text{mmol m}^{-2} \text{d}^{-1}$ )	TOU $J_{\text{O}_2} \pm \text{SD}$ ( $\text{mmol m}^{-2} \text{d}^{-1}$ )	DOU : TOU ration (%)	Oxygen penetration depth $\pm \text{SD}$ (mm)
<b>oxic zone</b> < 130 m bottom water oxygen conc. > $63 \mu\text{mol L}^{-1}$	$4.6 \pm 1.8$ range: 2.4 to 8.1, $n = 15$	$14.9 \pm 5.1$ range: 9 to 20.6, $n = 5$	30 : 70	$5.3 \pm 2.5$
<b>oxic-hypoxic</b> (130–142 m) bottom water oxygen conc. > 63 to $> 0 \mu\text{mol L}^{-1}$	$4.4 \pm 1.9$ range: 0.6 to 8.0, $n = 12$	$7.3 \pm 3.5$ range: 3.2 to 9.4, $n = 3$	60 : 40	$1.6 \pm 1.2$
<b>hypoxic-anoxic</b> (142–167 m) bottom water oxygen conc. $63\text{--}0 \mu\text{mol L}^{-1}$	$1.3 \pm 0.5$ range: 0.8 to 2.1, $n = 5$ (potential rate: 5.6)	$1.6 \pm 0.5$ <b>modeled</b>	80 : 20 <b>(modeled from potential rates)</b>	$0.4 \pm 0.1$

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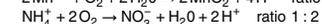
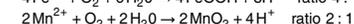
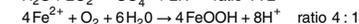
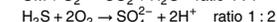
**Table 3.** Diffusive oxygen uptake compared to fluxes of reduced species, calculated from the modeled profiles (Fig. 5) or measured directly (SRR = Sulfate reduction rates). The sum in oxygen equivalents is calculated from the stoichiometry of the oxidation processes (respective formulas are displayed at the lower end of the table), and oxygen available for direct aerobic respiration is calculated by subtracting the potential oxygen demand from the available oxygen flux.

	Oxygen flux ( $\text{mmol m}^{-2} \text{d}^{-1}$ ) DOU ( $J_{\text{O}_2}$ ) see Table 2	Reduced species fluxes ( $\text{mmol m}^{-2} \text{d}^{-1}$ )					Diffusive oxygen consumption (direct aerobic mineralization : re- oxidation) in $\text{mmol}$ $\text{m}^{-2} \text{d}^{-1}$ and %
		$J_{\text{Fe}^{2+}}$	$J_{\text{Mn}^{2+}}$	$J_{\text{sulfide/SRR}}$	$J_{\text{NH}_4^+}$	SUM in oxygen equivalents	
<b>oxic zone</b> < 130 m, bottom water oxygen conc. > $63 \mu\text{mol L}^{-1}$	-4.6	0.1	< 0.1	$0^{\text{a}} / < 0.1$	0.1	0.23	4.38 : 0.23 95% : 5%
<b>oxic-hypoxic</b> 130–142 m, bottom water oxygen conc. > 63 to > $0 \mu\text{mol L}^{-1}$	-4.4	0.1	0	$0^{\text{a}} / 0.4$	< 0.1	< 0.1	4.36 : < 0.1 > 98% : < 2%
<b>hypoxic-anoxic</b> 142–167 m, bottom water oxygen conc. $63\text{--}0 \mu\text{mol L}^{-1}$	-1.3	0	0	$0^{\text{a}} / 0.2$	< 0.1	< 0.1	1.3 : < 0.1 > 92% : < 8%
<b>anoxic-sulfidic zone</b> > 167 m, sulfide present in anoxic bottom water	0	0	0	0.5/3.7	0.1	1.1	0 : $1.1^{\text{b}}$ 0% : 100%

Negative numbers denote downward flux, positive numbers upward flux.

<sup>a</sup> Bottom water sulfide was zero.

<sup>b</sup> Potential oxygen demand is higher than oxygen availability, thus reducing components are emitted.



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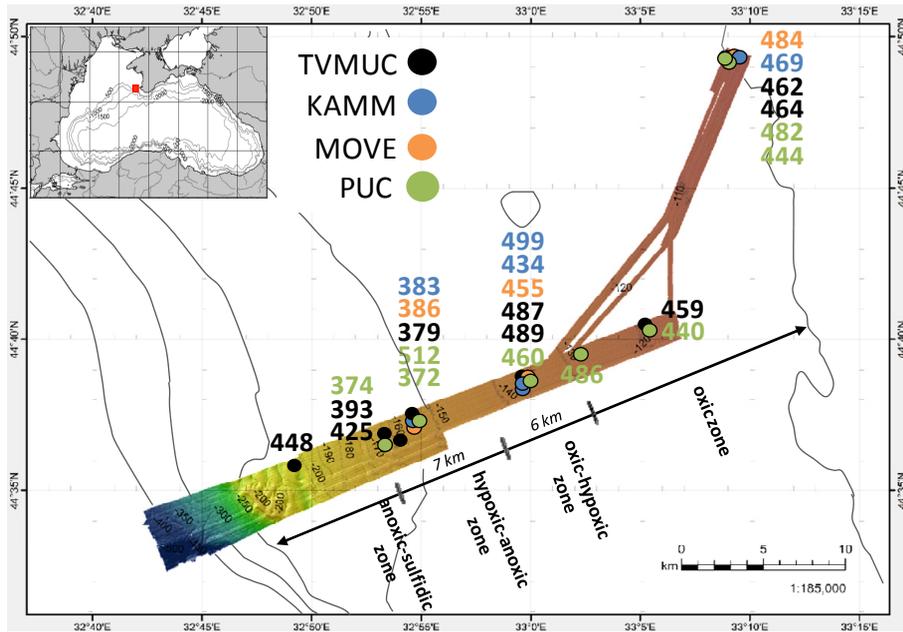
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**Table 4.** Oxygen consumption in hypoxic areas of the Black Sea, n.d. = not determined.

Area	Water depth (m)	Oxygen concentration ( $\mu\text{mol L}^{-1}$ )	TOU ( $\text{mmol m}^{-2} \text{d}^{-1}$ )	DOU ( $\text{mmol m}^{-2} \text{d}^{-1}$ )	Method	Fauna	Reference
Bay of Varna	24	230	33.3		in situ chamber (TOU)	living organisms living organisms living organisms no living organisms living organisms	Fridel et al. (1998)
Danube delta front	26	160	25.9				
Danube prodelta	27	0	5.7				
shelf edge	134	40					
shelf edge	142	30					
Romanian Shelf	62	211	39.8	11.9	in situ chamber (TOU)/ microsensors (DOU)	<i>Mytilus galloprovinciales</i> <i>Modiolus phaseolinus</i> <i>Modiolus phaseolinus</i> no macrofauna	Wenzhöfer et al. (2002)
	77	213	11.1	5.8			
	100	75	4.3	2.3			
	180	8	0	0			
NW Shelf	52	285	13.5, 10, 11.6		ex situ core incubations (TOU)	n.d.	Wijsman et al. (2001)
	54	314	11, 6.1				
	57	243	3.7				
	72	284					
	120	126					
	137	190					
Crimean Shelf	135	95	4.2–6		Eddy correlation		Holtappels et al. (2013)
Crimean Shelf	104	110–134	11.6	4.6	in situ chamber (TOU)/ microsensors (DOU)	living organisms living organisms living organisms, including fish	this study
	135	18–149	6.7	4.4			
	155	19–11	n.d.	1.3			



**Figure 1.** Sediment sampling locations (TVMUC = video-guided multicorer, PUC = JAGO pushcores) and deployment sites of benthic chamber and microprofiler with MOVE and lander (KAMM) along the transect from shallower (101 m) to deeper (207 m) water depth. Inset: working area on the outer Western Crimean Shelf (red square) in the Black Sea.

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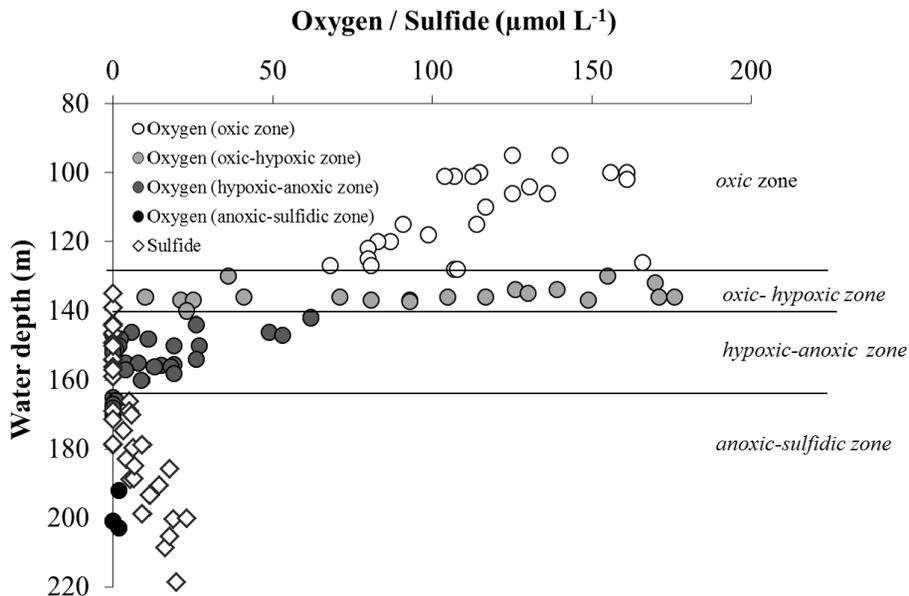
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**Figure 2.** Synthesis of oxygen concentrations in bottom water (circles) measured during the 2 weeks of the cruise ( $n = 85$ ). For continuously measuring instruments (BBL profiler, optode on JAGO, benthic lander, moorings) only an average value per deployment, dive or day was included. Maximum depth above the sediment was 12 m (CTD), minimum depth above the sediment was about 5 cm (Clark-type oxygen microelectrodes). Additionally, sulfide distribution in bottom waters during the same sampling period are shown (white diamonds,  $n = 43$ ). From depth distribution of oxygen and sulfide the distribution in (i) oxic, (ii) oxic-hypoxic, (iii) hypoxic-anoxic and (iv) anoxic-sulfidic zone was deduced.

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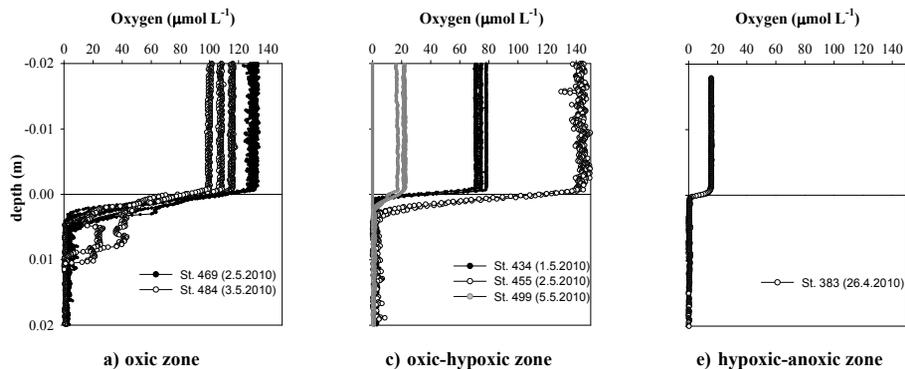
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**Figure 3.** Examples of high-resolution oxygen profiles under different oxygen regimes. Differences in bottom water oxygen concentrations (reflected in profile shape and oxygen penetration depth) are clearly visible between sites and deployments.

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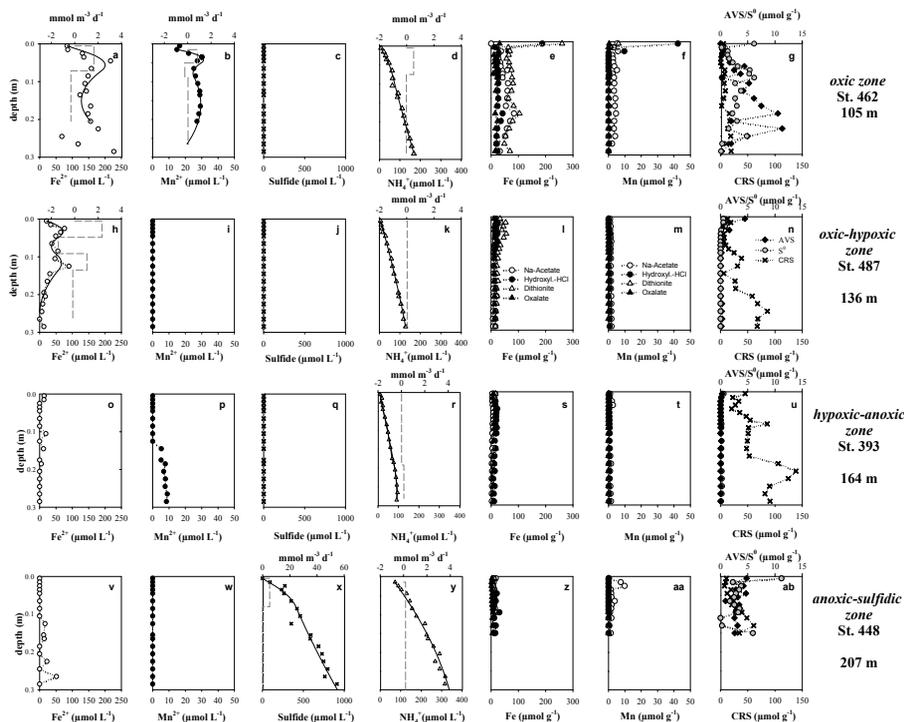
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oxic zone  
St. 462  
105 m

oxia-hypoxic  
zone  
St. 487  
136 m

hypoxic-anoxic  
zone  
St. 393  
164 m

anoxic-sulfidic  
zone  
St. 448  
207 m

**Figure 5.** Distribution of reduced pore water species and oxidized and solid phase iron and sulfur species along the depth transect in the upper 30 cm of the sediment (symbols with dotted lines). Solid lines are the model results and dashed lines represent production and consumption rates.

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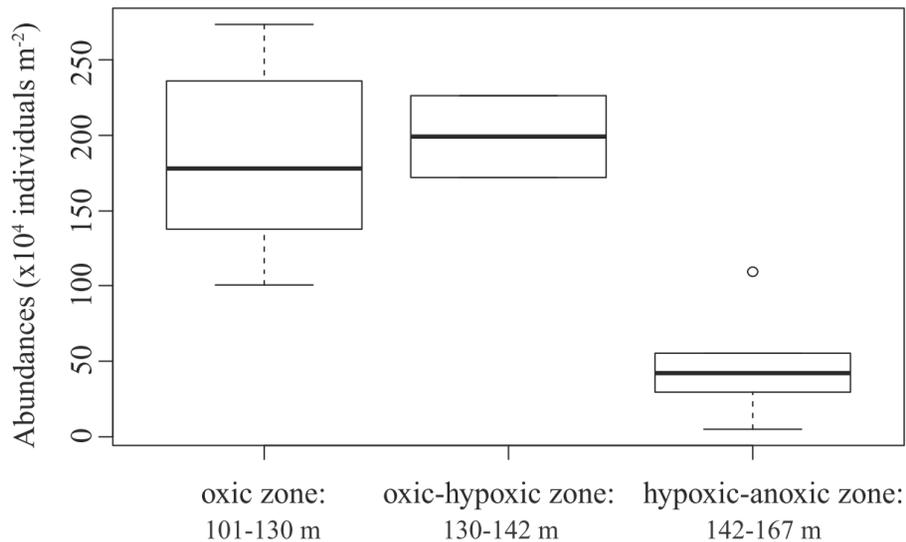
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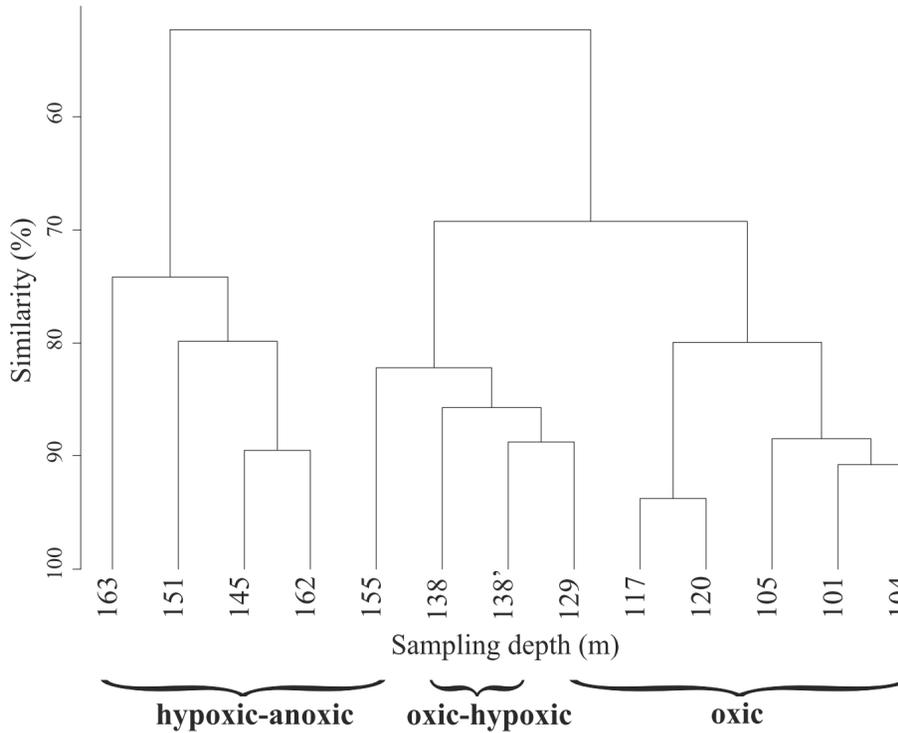
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**Figure 6.** Abundance of meiobenthos in the upper five centimeter of the sediment under different oxygen regimes. The middle line in each box depicts the median, while both whiskers and outliers indicate the distribution of remaining data points.



**Figure 7.** Cluster dendrogram of meiofauna abundances for different station depths based on the inverse of Bray–Curtis dissimilarity. Apostrophes denote stations with same depth.