

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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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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with fluctuating conditions as the Kattegat (Diaz, 2001), off the coast of New York/New Jersey (Boesch and Rabalais, 1991), or the Romanian Shelf of the Black Sea (Friedrich et al., 2014), mass mortality has been reported when oxygen concentrations drop below $22 \mu\text{mol L}^{-1}$ (0.5 mL L^{-1}) (Levin, 2003; Levin et al., 2009). In contrast, in regions under stable low-oxygen conditions faunal communities can be adapted to such physiologically challenging conditions, for example in long-term oxygen minimum zones in the SE-Pacific, tropical E-Atlantic and N-Indian Ocean (Levin et al., 2009). Here, the thresholds for faunal activity can reach much lower oxygen concentrations than in regions, which are facing periodic hypoxia.

Low faunal bioturbation rates in hypoxic zones limit sediment ventilation (Glud, 2008), decreasing oxygen availability for aerobic respiration. Hence, sediments underlying a low oxygen water column often show oxygen penetration depths of only a few millimeters (Archer and Devol, 1992; Glud et al., 2003; Rasmussen and Jørgensen, 1992). This increases the contribution of anaerobic microbial metabolism to organic matter remineralization at the expense of aerobic degradation by microbes and fauna as reported from the Romanian Shelf area of the Black Sea (Thamdrup et al., 2000; Weber et al., 2001), the Neuse River Estuary (Baird et al., 2004), and the Kattegat (Pearson and Rosenberg, 1992). Consequently, oxygen is channeled into the reoxidation of reduced substances produced during anaerobic degradation of organic matter. Even temporarily reduced bottom water oxygen concentrations can repress seafloor oxygen uptake that should become enhanced by algae blooms and temperature increases (Rasmussen and Jørgensen, 1992). However, depending on frequency and duration of oxygen oscillations, oxygen consumption following an anoxic event can also be significantly increased (Abril et al., 2010). Thus, overall not only the degree of oxygenation plays an important role in oxygen uptake, but also the frequency and persistency of the low oxygen conditions can shape faunal activity, biogeochemical processes, and the functioning of the ecosystem as a whole.

In the Black Sea, the depth of the oxic-anoxic interface increases from about 70–100 m in open waters (Friedrich et al., 2014) to depths of $> 150 \text{ m}$ above the shelf

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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 μmolL^{-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 km² (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° 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 cm² (TVMUC) and 41.8 cm² (for JAGO pushcore) (Table 1, Fig. 1). The abundances were extrapolated to m². 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 cm²) and JAGO pushcores (area of 41.8 cm²) (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 O₂ microsensors (Revsbech, 1989) and H₂S 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 H₂S sensors were calibrated at in situ temperature on board at stepwise increasing H₂S concentrations by adding aliquots of a 0.1 mol L⁻¹ Na₂S 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 O₂ microsensors, 2 H₂S 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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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 μm) 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°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°C for ^{210}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 = Fe_3S_4 , FeS) and chromium reducible sulfur (CRS = FeS_2 , some S^0 , remaining Fe_3S_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}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}Pb , ^{214}Pb , and ^{214}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°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°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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most anoxic conditions within < 3 h (Fig. S1b). Horizontal distance to the oxic-anoxic interface was on average 7 km during our expedition. In the oxic-hypoxic zone, only few fishes were observed, and video-observations of the seafloor showed a clear reduction of epibenthos abundance and their traces compared to those in the oxic zone.

In the “hypoxic-anoxic” zone between 142 and 167 m water depth sediments showed fluctuating hypoxic conditions between 0–63 $\mu\text{mol L}^{-1}$ (average $11 \pm 16 \mu\text{mol L}^{-1}$; 3 % air saturation at ambient conditions; 8 °C, salinity of 20). Unexpectedly, during a short period at these water depths, some fish (the sprattus *Sprattus phalericus* at 145 and 163 m water depth, and the whiting *Merlangius merlangus euxinus* at 145 m water depth, Zaika and Gulin, 2011) were observed when oxygen concentrations were as low as 20 $\mu\text{mol L}^{-1}$ (Fig. S2f). The seafloor was covered with fluffy greenish-brownish material and sediments showed a fine lamination (Fig. S2e). No epibenthic life was observed, nor borrows or other traces of bottom dwelling fauna.

Below 167 m, the bottom water was permanently anoxic during the time period of our campaign. Below 180 m sulfide was constantly present in the bottom water, with concentrations ranging between 5–23 $\mu\text{mol L}^{-1}$. In this “anoxic-sulfidic” zone sediments were dark green-blackish. Neither macrofauna, nor traces of bottom-dwelling infauna were observed.

3.2 Meiofauna composition and abundance

Abundance and composition of meiobenthos and macrobenthos > 2 mm as retrieved from the top 5 cm of pooled core samples were compared across the different zones of oxygen availability in Fig. 6 and Tables S1 and S2 in the Supplement. The macrobenthos abundances presented here are not quantitative for the entire size class, due to the limit in sample size available; they might represent mostly small types and juvenile stages. These decreased by more than one order of magnitude from the oxic zone (21×10^3 individuals m^{-2}) to the hypoxic-anoxic zone (1×10^3 individuals m^{-2}) (Table S1). In the oxic zone, cnidaria dominated the benthic community next to oligochaetes and polychaetes, also bivalves and gastropods were present. A peak in

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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 54×10^3 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 200×10^4 individuals m^{-2} (Fig. 6, Table S2). A substantial decrease to 50×10^4 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 ± 2 and 15 ± 1) and dropped to 9 ± 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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waters (see Sect. 3.5). In contrast, the shape of the oxygen profiles obtained in the oxic-hypoxic and the hypoxic-anoxic zone showed no signs of bioturbation. Small-scale spatial heterogeneity was low between parallel sensor measurements and within one deployment (area of 176 cm² sampled). However, strong temporal variations occurred in response to the fluctuations in bottom water oxygen concentration. For example, in the oxic-hypoxic zone a clear relation between oxygen penetration depth and bottom water oxygen concentration was detectable, with increased bottom water oxygen concentration leading to deeper oxygen penetration depth (Fig. 3a–c). Except where bioturbation led to slightly deeper penetration, oxygen was depleted within the first 0.4–3 mm of the surface layer (Fig. 3, Table 2).

Diffusive oxygen uptake (DOU) varied within an order of magnitude between all zones (Table 2). The highest DOU of 8.1 mmol m⁻² d⁻¹ was calculated from a profile obtained at 104 m water depth in the oxic zone, but the averages of all oxygen fluxes measured in the oxic and oxic-hypoxic zones were similar (averages of 4.6 ± 1.8 and 4.4 ± 1.9 mmol m⁻² d⁻¹, respectively, Table 2). The higher variability within the oxic-hypoxic zone, spanning from 0.6 to 8 mmol m⁻² d⁻¹ between measurements, matches the higher variability in bottom water oxygen concentrations observed for this zone (Fig. 3b). Diffusive oxygen uptake in that zone was lowest after a nearly anoxic event (~ 10 μmol O₂ L⁻¹; Fig. S1b). Highest fluxes in the oxic-hypoxic zone, however, were not recorded during a “normoxic event” (149 μmol O₂ L⁻¹), but at the typical intermediate bottom water oxygen concentration of approx. 90 μmol L⁻¹ (Fig. 4b and c, Fig. S1b). In the hypoxic-anoxic zone DOU was only 25 % of that in the oxic and oxic-hypoxic zones (average: 1.3 ± 0.5 mmol m⁻² d⁻¹).

In bottom waters of the hypoxic-anoxic zone high resolution measurements of pH indicated a pH of around 7.8, decreasing to values between 7.2–7.4 in the sediment. With the H₂S microsensors no free sulfide was detected in the pore waters of the oxic, oxic-hypoxic or hypoxic-anoxic zones. In the anoxic-sulfidic zone the microsensor measurements failed. Bottom water sulfide concentrations were > 5 μmol L⁻¹, and the

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 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 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 ± 0.03 in the top cm and 0.8 ± 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 ~ 1.8 , ~ 3.2 , and ~ 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 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-

working by faunal activity. Based on these calculations we assume that up to 70 % of the total oxygen uptake in the oxic zone, 40 % in the oxic-hypoxic zone and 20 % in the hypoxic-anoxic zone is due to benthos-mediated oxygen uptake. The remaining share (30, 60, 80 %, respectively) will mainly be channeled directly into the aerobic degradation of organic carbon by microbes (and potentially also some meiofauna). A BMU of 70 % ($10.3 \text{ mmol m}^{-2} \text{ d}^{-1}$) in the oxic zone was considerably higher than values of 15–60 % reported from shelf sediments underlying both normoxic (Glud et al., 1998; Heip et al., 2001; Moodley et al., 1998; Piepenburg et al., 1995) and hypoxic water columns (Archer and Devol, 1992; Wenzhöfer et al., 2002). A BMU of 40 % in the oxic-hypoxic zone was still well within the ranges of some normoxic water columns (Glud et al., 1998; Heip et al., 2001; Moodley et al., 1998; Piepenburg et al., 1995).

It has previously been shown that sediment-water exchange rates can be altered due to changes in fauna composition in response to different bottom water oxygenation (Dale et al., 2013; Rossi et al., 2008). Also in the outer Western Crimean Shelf area the overall reduction of BMU from the oxic zone to the oxic-hypoxic zone relates well with changes in macrobenthos composition. In the oxic zone the higher fauna-mediated uptake was probably partly caused by irrigation and bioturbation by polychaetes, bivalves, and gastropods (Table S1). Ventilation of the upper sediment layer is indicated by the presence of oxidized Fe and Mn solid phase minerals in the oxic zone and in the upper 10 cm of the oxic-hypoxic zone (Fig. 5). Decreased bioturbation in the other zones is due to reduced abundances of sediment infauna. Loss of sediment ventilation also explains changes in sediment biogeochemistry, in particular the ceasing of the iron and manganese cycle upon lower bottom water oxygen concentrations (Fig. 5). This is in accordance with previous studies that have shown that reoxidation of reduced iron and manganese is mainly stimulated by bioturbation, and thus recycling efficiency of the metals primarily depends on bottom-water oxygen levels and rates of bioturbation (Canfield et al., 1993b; Thamdrup et al., 2000; Wijsman et al., 2001).

The restriction of bivalves and gastropods to the upper oxic-hypoxic zone is surprising, as representatives of these groups are known to be able to maintain their respi-

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

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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)
oxic zone < 130 m bottom water oxygen conc. > $63 \mu\text{mol L}^{-1}$	4.6 ± 1.8 range: 2.4 to 8.1, $n = 15$	14.9 ± 5.1 range: 9 to 20.6, $n = 5$	30 : 70	5.3 ± 2.5
oxic-hypoxic (130–142 m) bottom water oxygen conc. > 63 to $> 0 \mu\text{mol L}^{-1}$	4.4 ± 1.9 range: 0.6 to 8.0, $n = 12$	7.3 ± 3.5 range: 3.2 to 9.4, $n = 3$	60 : 40	1.6 ± 1.2
hypoxic-anoxic (142–167 m) bottom water oxygen conc. $63\text{--}0 \mu\text{mol L}^{-1}$	1.3 ± 0.5 range: 0.8 to 2.1, $n = 5$ (potential rate: 5.6)	1.6 ± 0.5 modeled	80 : 20 (modeled from potential rates)	0.4 ± 0.1

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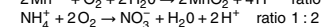
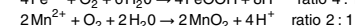
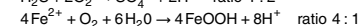
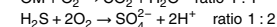
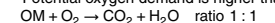
Table 3. Diffusive oxygen uptake compared to fluxes of reduced species, calculated from the modeled profiles (Fig. 5) or measured directly (SRR = Sulfate reduction rates). The sum in oxygen equivalents is calculated from the stoichiometry of the oxidation processes (respective formulas are displayed 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_{O_2}) see Table 2	Reduced species fluxes ($\text{mmol m}^{-2} \text{d}^{-1}$)					Diffusive oxygen consumption (direct aerobic mineralization : re- oxidation) in 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	
oxic zone < 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%
oxic-hypoxic 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%
hypoxic-anoxic 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%
anoxic-sulfidic zone > 167 m, sulfide present in anoxic bottom water	0	0	0	0.5/3.7	0.1	1.1	0 : 1.1^{b} 0% : 100%

Negative numbers denote downward flux, positive numbers upward flux.

^a Bottom water sulfide was zero.

^b Potential oxygen demand is higher than oxygen availability, thus reducing components are emitted.



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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			

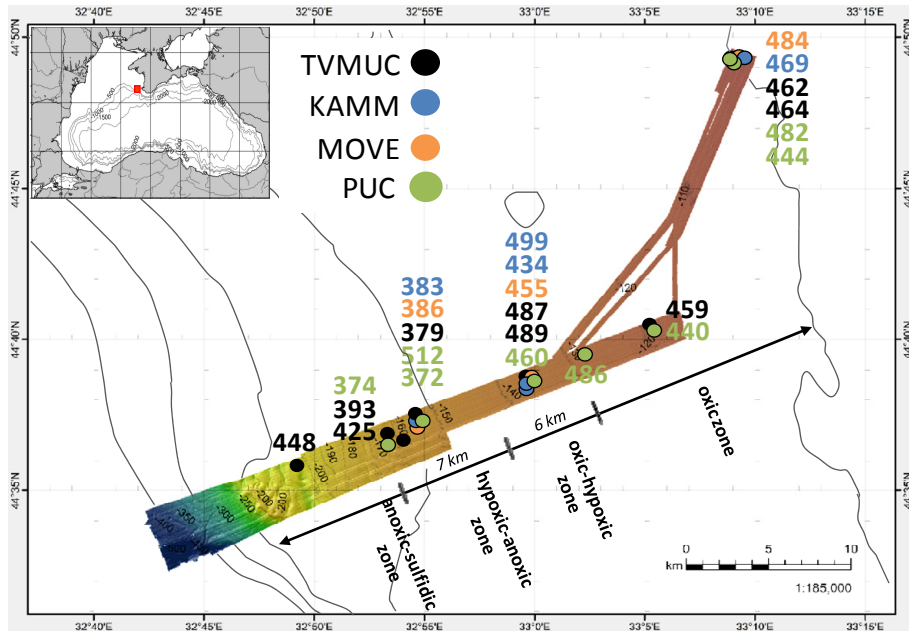


Figure 1. Sediment sampling locations (TVMUC = video-guided multicorer, PUC = JAGO pushcores) and deployment sites of benthic chamber and microprofiler with MOVE and lander (KAMM) along the transect from shallower (101 m) to deeper (207 m) water depth. Inset: working area on the outer Western Crimean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

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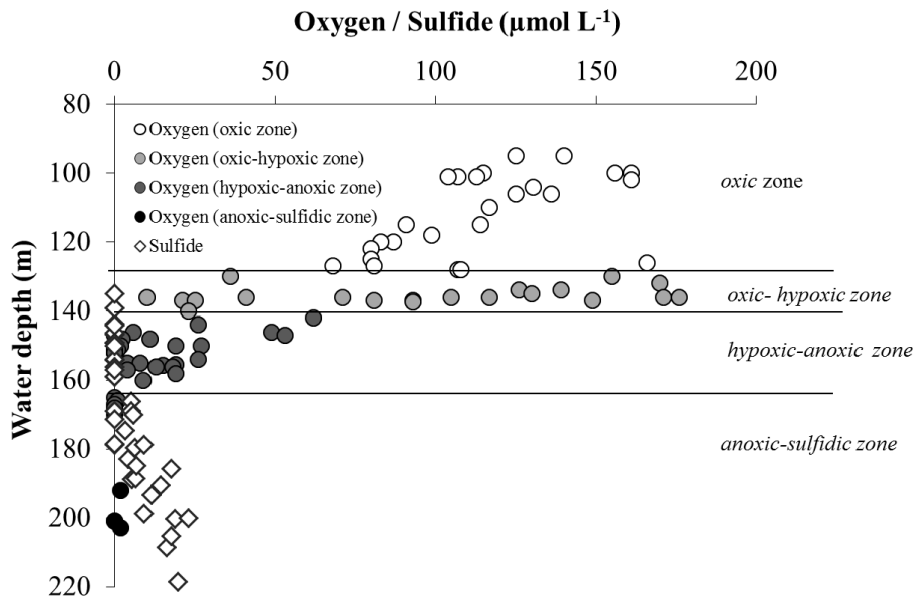


Figure 2. Synthesis of oxygen concentrations in bottom water (circles) measured during the 2 weeks of the cruise ($n = 85$). For continuously measuring instruments (BBL profiler, optode on JAGO, benthic lander, moorings) only an average value per deployment, dive or day was included. Maximum depth above 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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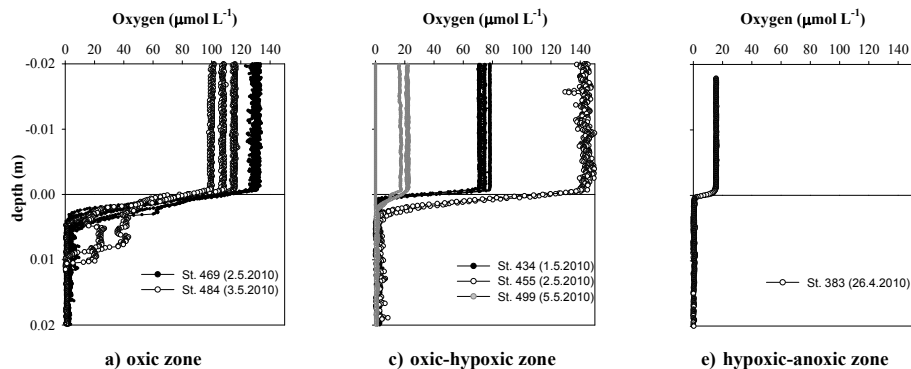


Figure 3. Examples of high-resolution oxygen profiles under different oxygen regimes. Differences in bottom water oxygen concentrations (reflected in profile shape and oxygen penetration depth) are clearly visible between sites and deployments.

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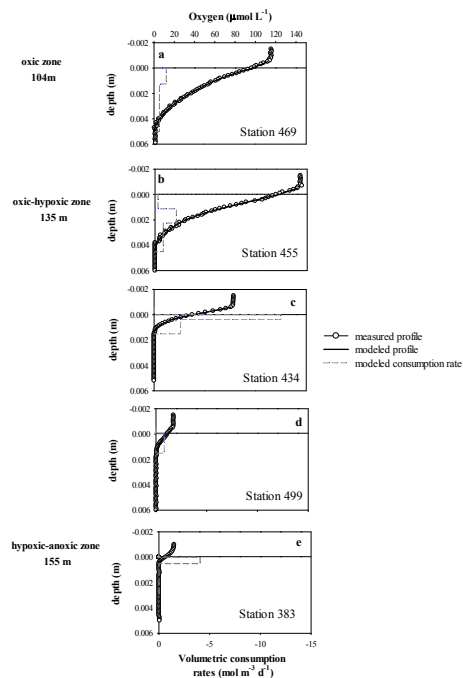


Figure 4. Examples of individual oxygen profiles measured in the sediment (white circles) and modeled with PROFILER (black lines). Volumetric rates are combined in discrete layers (dashed line) and exhibit different depths and degrees of oxygen consumption rates in different zones and under different bottom water oxygenation.

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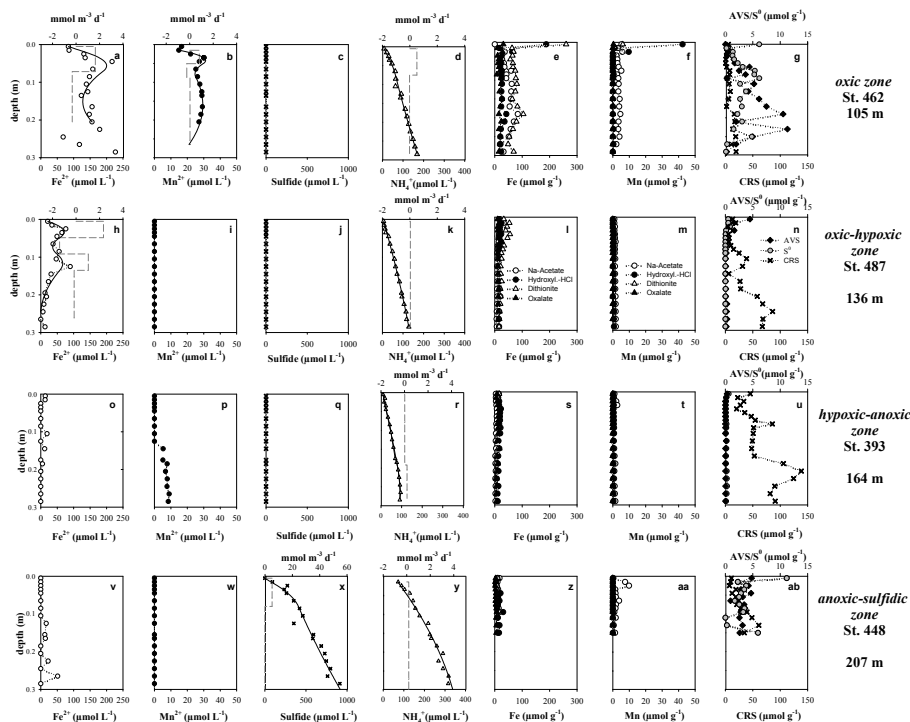


Figure 5. Distribution of reduced pore water species and oxidized and solid phase iron and sulfur species along the depth transect in the upper 30 cm of the sediment (symbols with dotted lines). Solid lines are the model results and dashed lines represent production and consumption rates.

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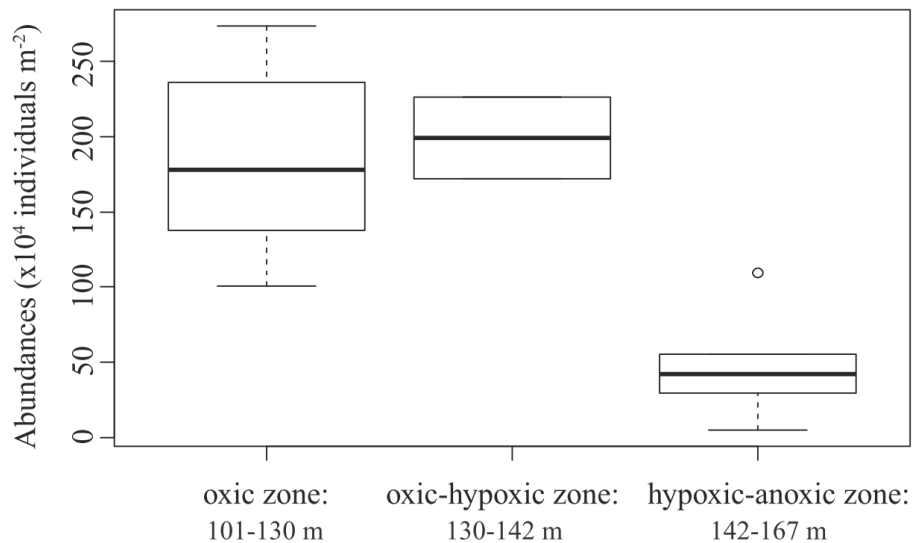


Figure 6. Abundance of meiobenthos in the upper five centimeter of the sediment under different oxygen regimes. The middle line in each box depicts the median, while both whiskers and outliers indicate the distribution of remaining data points.

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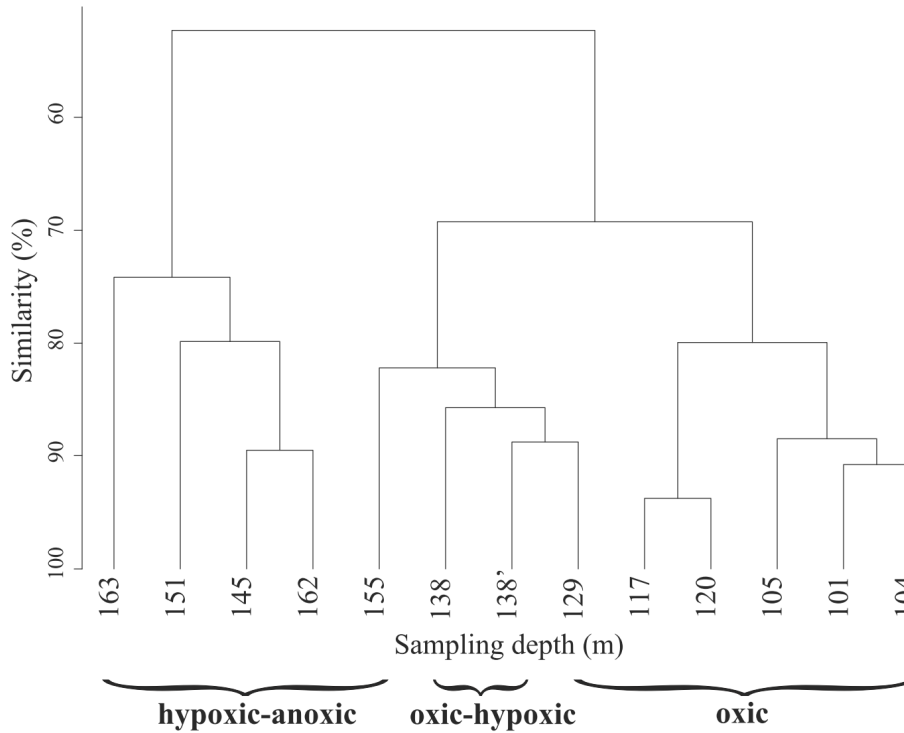


Figure 7. Cluster dendrogram of meiofauna abundances for different station depths based on the inverse of Bray–Curtis dissimilarity. Apostrophes denote stations with same depth.