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Dead zone or oasis in the open ocean? Zooplankton distribution and migration in low-oxygen modewater eddies

Helena Hauss[1], **Svenja Christiansen**[1], **Florian Schütte**[1], **Rainer Kiko**[1], **Miryam Edvam Lima**[2], **Elizandro Rodrigues**[2], **Johannes Karstensen**[1], **Carolin R. Löscher**[1,3], **Arne Körtzinger**[1,4], **and Björn Fiedler**[1]

[1]GEOMAR Helmholtz Centre for Ocean Research Kiel, Düsternbrooker Weg 20, 24105 Kiel, Germany
[2]Instituto Nacional de Desenvolvimento das Pescas (INDP), Cova de Inglesa, Mindelo, São Vicente, Cabo Verde
[3]Institute for General Microbiology, Kiel, Germany
[4]Christian Albrecht University Kiel, Kiel, Germany

Correspondence to: Helena Hauss (hhauss@geomar.de)

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Abstract. The eastern tropical North Atlantic (ETNA) features a mesopelagic oxygen minimum zone (OMZ) at approximately 300–600 m depth. Here, oxygen concentrations rarely fall below 40 µmol O_2 kg^{-1}, but are expected to decline under future projections of global warming. The recent discovery of mesoscale eddies that harbour a shallow suboxic (< 5 µmol O_2 kg^{-1}) OMZ just below the mixed layer could serve to identify zooplankton groups that may be negatively or positively affected by ongoing ocean deoxygenation. In spring 2014, a detailed survey of a suboxic anticyclonic modewater eddy (ACME) was carried out near the Cape Verde Ocean Observatory (CVOO), combining acoustic and optical profiling methods with stratified multinet hauls and hydrography. The multinet data revealed that the eddy was characterized by an approximately 1.5-fold increase in total area-integrated zooplankton abundance. At nighttime, when a large proportion of acoustic scatterers is ascending into the upper 150 m, a drastic reduction in mean volume backscattering (S_v) at 75 kHz (shipboard acoustic Doppler current profiler, ADCP) within the shallow OMZ of the eddy was evident compared to the nighttime distribution outside the eddy. Acoustic scatterers avoided the depth range between approximately 85 to 120 m, where oxygen concentrations were lower than approximately 20 µmol O_2 kg^{-1}, indicating habitat compression to the oxygenated surface layer. This observation is confirmed by time series observations of a moored ADCP (upward looking, 300 kHz) during an ACME transit at the CVOO mooring in 2010. Nevertheless, part of the diurnal vertical migration (DVM) from the surface layer to the mesopelagic continued through the shallow OMZ. Based upon vertically stratified multinet hauls, Underwater Vision Profiler (UVP5) and ADCP data, four strategies followed by zooplankton in response to in response to the eddy OMZ have been identified: (i) shallow OMZ avoidance and compression at the surface (e.g. most calanoid copepods, euphausiids); (ii) migration to the shallow OMZ core during daytime, but paying O_2 debt at the surface at nighttime (e.g. siphonophores, *Oncaea* spp., eucalanoid copepods); (iii) residing in the shallow OMZ day and night (e.g. ostracods, polychaetes); and (iv) DVM through the shallow OMZ from deeper oxygenated depths to the surface and back. For strategy (i), (ii) and (iv), compression of the habitable volume in the surface may increase prey–predator encounter rates, rendering zooplankton and micronekton more vulnerable to predation and potentially making the eddy surface a foraging hotspot for higher trophic levels. With respect to long-term effects of ocean deoxygenation, we expect avoidance of the mesopelagic OMZ to set in if oxygen levels decline below approximately 20 µmol O_2 kg^{-1}. This may result in a positive feedback on the OMZ oxygen consumption rates, since zooplankton and micronekton respiration within the OMZ as well as active flux of dissolved and particulate organic matter into the OMZ will decline.

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1 Introduction

The habitat of pelagic marine organisms is vertically structured by several biotic and abiotic factors, such as light, prey density, temperature, oxygen concentration and others. In the eastern tropical North Atlantic (ETNA), a permanent oxygen minimum zone (OMZ) exists in the mesopelagial. The core of this OMZ is centred at approximately 450 m, with the upper and lower oxyclines at approximately 300 and 600 m depth (Karstensen et al., 2008). Oxygen concentrations in this deep OMZ hardly fall below 40 μmol O_2 kg^{-1} (Karstensen et al., 2008), but are sufficiently low to exclude highly active top predators such as billfishes from the OMZ (Prince et al., 2010; Stramma et al., 2012). In the eastern tropical South Atlantic, with its more pronounced midwater OMZ, this layer may act as an effective barrier for some species (e.g. Auel and Verheye, 2007; Teuber et al., 2013), but seems to be diurnally crossed by others (Postel et al., 2007). Many zooplankton and nekton taxa perform diurnal vertical migrations (DVMs), usually spending the daylight hours in the mesopelagic OMZ and migrating into the productive surface layer at night. These taxa include for example euphausiids (Tremblay et al., 2011), sergestid and penaeid shrimp (Andersen et al., 1997), myctophid fishes (Kinzer and Schulz, 1985) as well as several large calanoid copepods (e.g. *Pleuromamma* species, Teuber et al., 2013). As DVM is a survival mechanism to evade predation, hindrance thereof could lead to substantial changes in ecosystem functioning. The ETNA OMZ has been observed to intensify (i.e. decrease in core O_2 concentrations) and vertically expand over the past decades and is predicted to further deoxygenate and expand laterally (Stramma et al., 2008, 2009) under future expectations of anthropogenic global warming (Cocco et al., 2013).

Submesoscale and mesoscale eddies (which in the tropics/subtropics comprise diameters of the order of 10^1 and 10^2 km, respectively) often represent hotspots (or “oases”) of biological productivity in the otherwise oligotrophic open ocean (e.g. Menkes et al., 2002; McGillicuddy et al., 2007; Godø et al., 2012), even translating up to top predators (Tew Kai and Marsac, 2010). Their basin-wide relevance for biogeochemical cycles has been increasingly recognized (e.g. Stramma et al., 2013). Numerous eddies spin off the productive Mauritanian and Senegalese coasts (between Cap Blanc and Cap Vert) throughout the year, with most anticyclones being generated in summer/autumn and most cyclones in winter/spring (Schütte et al., 2015). Both eddy types propagate westward at about 4 to 5 km day^{-1}, passing the Cabo Verde archipelago to the north or south. They can be tracked by satellite altimetry for up to 9 months (Schütte et al., 2016; Karstensen et al., 2015). While normal anticyclones are usually relatively warm and unproductive (e.g. Palacios et al., 2006), both cyclonic and anticyclonic modewater eddies (ACMEs) are characterized by a negative sea surface temperature (SST) and positive surface chlorophyll a (chl a) anomaly (Goldthwait and Steinberg; 2008; McGillicuddy et al., 2007). In particular, ACMEs were observed to exceed cyclones in terms of upwelled nutrients and productivity in the subtropical Atlantic (McGillicuddy et al., 2007).

The recent discovery of mesoscale eddies (cyclones and ACMEs) with extremely low oxygen concentrations just below the mixed layer (Karstensen et al., 2015) has changed our view of current oxygen conditions in the ETNA. In that study, it had been observed that oxygen values < 2 μmol O_2 kg^{-1} can be found in the shallow oxygen minimum. The authors concluded that the low oxygen concentrations were the result of isolation of the eddy core from surrounding water (a result of the rotation of the eddy) paired with enhanced respiration (a result of the high productivity and subsequent export and degradation of particulate organic matter; Fischer at al., 2015), and introduced the term “dead-zone eddy” (Karstensen et al., 2015). The lowest oxygen concentrations so far in such an eddy (< 2 μmol O_2 kg^{-1} at about 40 m depth) were observed in February 2010 at the Cape Verde Ocean Observatory (CVOO) mooring. During the eddy passage across the mooring, an almost complete lack of acoustic scatterers at depths below the oxygenated mixed layer was observed. The acoustic backscattering signal received by the 300 kHz acoustic Doppler current profiler (ADCP) is largely created by organisms > 5 mm (thus missing a substantial part of the mesozooplankton) and does not allow for the discrimination of different zooplankton groups.

Here, we characterize the ecology of zooplankton in response to the shallow OMZ within an ACME that was identified, tracked and sampled in spring 2014. We used acoustic (shipboard ADCP) and optical (Underwater Vision Profiler, UVP) profiling methods as well as vertically stratified plankton net hauls to resolve the vertical and horizontal distribution of zooplankton. Moreover, we used acoustic and oxygen time series data from the CVOO mooring of one extreme low oxygen eddy observed in February 2010 (Karstensen et al., 2015; Fischer et al., 2015) to derive a more general picture about the zooplankton sensitivity to low oxygen concentrations.

2 Materials and methods

In order to characterize the ecology, biogeochemistry and physical processes associated with low-oxygen eddies in the tropical North Atlantic, a dedicated field experiment (“eddy hunt”) north of the Cabo Verde archipelago was designed. In summer 2013, the identification and tracking of candidate eddies began by combining remotely sensed data and Argo float profile data. In spring 2014, a candidate low-oxygen eddy was identified and on-site sampling with gliders and research vessels began, covering genomics, physics and biogeochemistry (see also Löscher et al., 2015; Schütte et al., 2016; Fiedler et al., 2016; Karstensen et al., 2016). Ship-based sampling presented here was carried out on 18 and 19

March 2014 during the RV *Meteor* cruise M105. Two ADCP sections perpendicular to each other, a CTD/UVP5 cast section and five multinet hauls were conducted. To better characterize the average distribution of zooplankton during normal conditions in the investigation area (as compared to conditions within the eddy), we combined the single time point observation at the CVOO time series station with previously collected data at the same station. For the multinet data, we used three additional day/night casts (RV *Maria S. Merian* cruise MSM22: 25 October and 20 November 2012; RV *Meteor* cruise M97: 26 May 2013). For the UVP data, we used seven nighttime profiles (because the four eddy core stations were obtained during nighttime only) from cruises M105, MSM22, M97 and M106 (19/20 April 2014).

In order to evaluate in greater detail the critical oxygen concentrations that lead to avoidance behaviour, we used the mean volume backscatter (S_v) and oxygen time series data from the CVOO mooring. Here, we focus on the spring 2010 period that covered the transit of an extreme low oxygen eddy, with oxygen content $< 2\,\mu\mathrm{mol\,kg^{-1}}$ (Karstensen et al., 2015).

2.1 ADCPs

Underway current measurements were performed during cruise M105 using two vessel mounted ADCPs (vmADCPs), a 75 kHz RDI Ocean Surveyor (OS75) and a 38 kHz RDI Ocean Surveyor (OS38). Standard techniques (see Fischer et al., 2003) were used for data post-processing. Depending on the region and sea state, the ranges covered by the instruments are around 550 m for the OS75 and around 1000 m for the OS38. To locate the eddy centre from the observed velocities, two sections were conducted (Fig. 1). The first was a southeast-to-northwest section through the estimated (by remote sensing) eddy centre. The second section was a perpendicular, northeast-to-southwest section through the location of the lowest cross sectional current velocity of the first section. The lowest cross sectional velocity of the second section defines the eddy centre.

The ADCP installed at the CVOO mooring site in 109 m water depth was an upward looking 300 kHz Teledyne RDI workhorse instrument, recording data every 1.5 h. It has a four-beam design in Janus configuration with a 20° opening. Based on accompanying hydrographic and pressure data, each 4 m depth cell was allocated discrete pressure/depth information as well as a sound speed profile (harmonic mean). S_v from the four ADCP beams was averaged and matched to the oxygen data (i.e. backscatter values in the depth cell where the oxygen sensor was located were used, which varied around approximately 50 m, depending on the current strength). Only data from 1 January to 14 March 2010 were used for the analysis to avoid the influence of seasonal changes in scatterer abundance. Data collected from 11:00 to 18:00 and from 22:00 to 07:00 UTC were considered daytime and nighttime data, respectively. Apparent sunrise and sunset in the period of January to March are around 08:00 and 19:30 UTC, respectively.

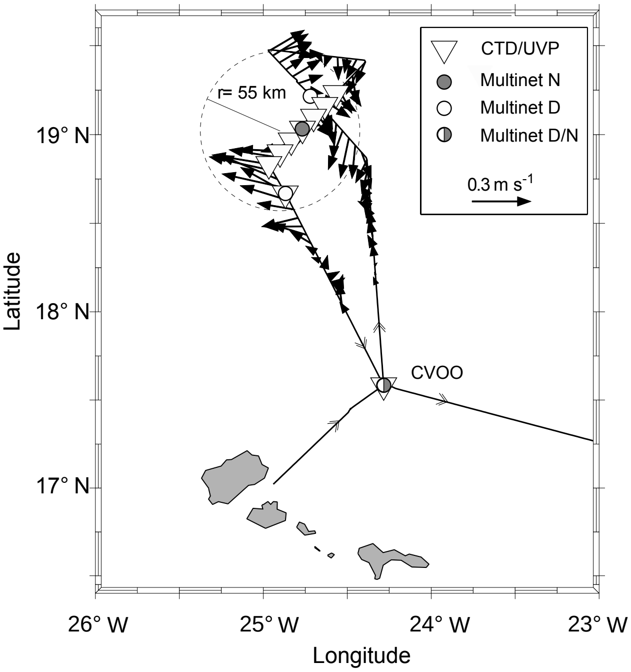

Figure 1. Cruise track (M105, only shown from 17 to 20 March 2014) with horizontal current velocities (arrows) and CTD/UVP sampling positions (triangles) as well as multinet stations (grey circles are night, empty circles are day). Large dashed circle indicates the estimated radius of the eddy based upon current structure.

For vessel-mounted as well as moored ADCPs, S_v (MacLennan et al., 2002) was estimated for each beam and each depth cell by a recalculation of a simplified sonar equation (Deimes, 1999). From the vessel-mounted ADCPs, only the OS75 was used to assess backscatter distribution. Since we were not attempting to estimate biomass, no further calibration was applied and S_v values are relative.

2.2 CTD and UVP5

Oxygen concentration was measured using a SBE (Sea–Bird Electronics) CTD with two SBE 43 oxygen sensors. The oxygen sensors were calibrated against 641 discrete oxygen samples measured by Winkler titration during cruise M105. Inside the CTD rosette, a UVP5 was mounted. This imaging tool allows for in situ quantification of particles > 60 µm and plankton > 500 µm with high vertical resolution (Picheral et al., 2010). Thumbnails of all objects > 500 µm were extracted using the ImageJ-based ZooProcess macro set (Gorsky et al., 2010) and sorted automatically into 41 categories using Plankton Identifier (Gasparini, 2007). Experts validated the automated image sorting. The observed volume of each image was 0.93 L and approximately 10 images were recorded per metre depth. The mean total sampling volume for the upper 600 m of the water column was 6.34 (±0.99) m^3. Volume-specific abundance was calculated in 5 m depth bins.

2.3 Multinet

Zooplankton samples were collected with a Hydrobios multinet Midi (0.25 m^2 mouth opening, five nets, 200 µm mesh, equipped with flowmeters) hauled vertically from the maximum depth to the surface at 1 $m\,s^{-1}$.

A full day/night multinet station was conducted well outside of the eddy at 17.3474° N and 24.1498° W at the CVOO site, where a set of physical and biogeochemical variables are measured on a monthly basis. For this reason, CVOO standard depths were used in this multinet haul (800–600–300–200–100–0 m) as it also served as the time series observation. As the northwestward eddy transect was conducted during daytime, the "eddy core day" multinet haul was collected on this transect (12:40 UTC) and the "eddy core night" haul was collected at 02:10 UTC during the second transect (for classification of stations, see hydrography results section), at the location of the CTD profile with the lowest O_2 concentration. Thus, the eddy core day haul is approximately 14 km away from the eddy centre (Fig. 1). Depth intervals (600–300–200–120–85–0 m) were chosen according to the O_2 profile. When leaving the eddy, a second day haul was collected at the margin of the eddy, approximately 26 km from the eddy centre, using the depth intervals from the eddy core station. Zooplankton samples were fixed in 100 mL Kautex® jars in 4 % borax-buffered formaldehyde in a seawater solution.

Zooplankton samples were analysed using a modification of the ZooScan Method (Gorsky et al., 2010), employing an off-the-shelf flatbed scanner (Epson Perfection V750 Pro) and a scan chamber constructed of a 21 cm × 29.7 cm (DIN-A4) size glass plate with a plastic frame. Scans were 8bit greyscale, 2400 dpi images (tagged image file format; *.tif). The scan area was partitioned into two halves (i.e. two images per scanned frame) to reduce the size of the individual images and facilitate the processing by ZooProcess/ImageJ. Samples were size fractionated by sieving into three fractions (<500, 500–1000 and >1000 µm) and split using a Motoda plankton splitter if necessary. The >1000 µm fraction was scanned completely, whereas fractions comprising no more than approximately 1000 objects were scanned for the two other fractions. "Vignettes" and image characteristics of all objects were extracted with ZooProcess (Gorsky et al., 2010) and sorted into 39 categories using a Plankton Identifier (Gasparini, 2007). Automated image sorting was then manually validated by experts.

3 Results

3.1 Hydrography

The site survey with RV *Meteor* succeeded in sampling the eddy core with CTD and UVP casts. The lowest measured O_2 concentration was 3.75 µmol O_2 kg^{-1} at 106 m depth. Based upon the current velocity, the eddy was approximately 110 km in diameter (Fig. 1), but oxygen concentrations below 20 and 5 µmol O_2 kg^{-1} were only found within approximately 18 and 8 km from the centre, respectively. For the purpose of this study, the four stations within 20 km of the eddy core (with minimum O_2 concentrations well below 20 µmol O_2 kg^{-1}) were considered "eddy core", while the four stations within 20 to 35 km from the eddy core were considered "eddy margin" (with minimum O_2 concentrations between 21 and 53 µmol O_2 kg^{-1}) and the CVOO station (M105 data complemented with data from previous cruises, $n = 7$ profiles; see methods) was considered to represent ambient conditions outside of the eddy. Here, a shallow OMZ was not present. The midwater OMZ (centred around approximately 450 m depth) featured mean minimum oxygen concentrations of 70 µmol O_2 kg^{-1}).

3.2 Vertical distribution and DVM – acoustic observations

During the M105 ADCP survey, several features were apparent in the vertical distribution and migration of scatterers outside of the eddy (Fig. 2). First, a deep scattering layer was detected centred between below 350 and 400 m depth. From this layer, part of the population started its ascent to the surface layer at about 18:00 UTC. The centre of the nighttime distribution outside the eddy ranged from approximately 30 to 130 m depth. During the day, the lowest S_v was recorded between 100 and 300 m depth, with a residual non-migrating population in the upper 100 m. The ascendant and descendent migration took place from approximately 18:00 to 20:00 UTC (16:15 to 18:15 solar time) and 07:00 to 09:00 UTC (05:15 to 07:17 solar time), respectively.

A very different nighttime distribution was observed when traversing the eddy. The scattering in the surface layer was located further up in the water column than outside the eddy and their lower distribution margin coincided with the upper oxycline (approximately 85 m in the eddy centre). In the core of the shallow OMZ, below approximately 20 µmol O_2 kg^{-1}, an absolute minimum S_v was observed.

The intersection of the two transects (see red crosses in Fig. 2) was visited shortly after 12:00 and 00:00 UTC, representing full day/night conditions, respectively. Here, the difference between S_v in the surface at daytime and nighttime suggests substantial vertical migration into/out of the surface layer, crossing the OMZ (Fig. 2b). Furthermore, the distribution of the surface daytime resident population (with S_v values of approximately 75 dB) is bimodal, peaking again at

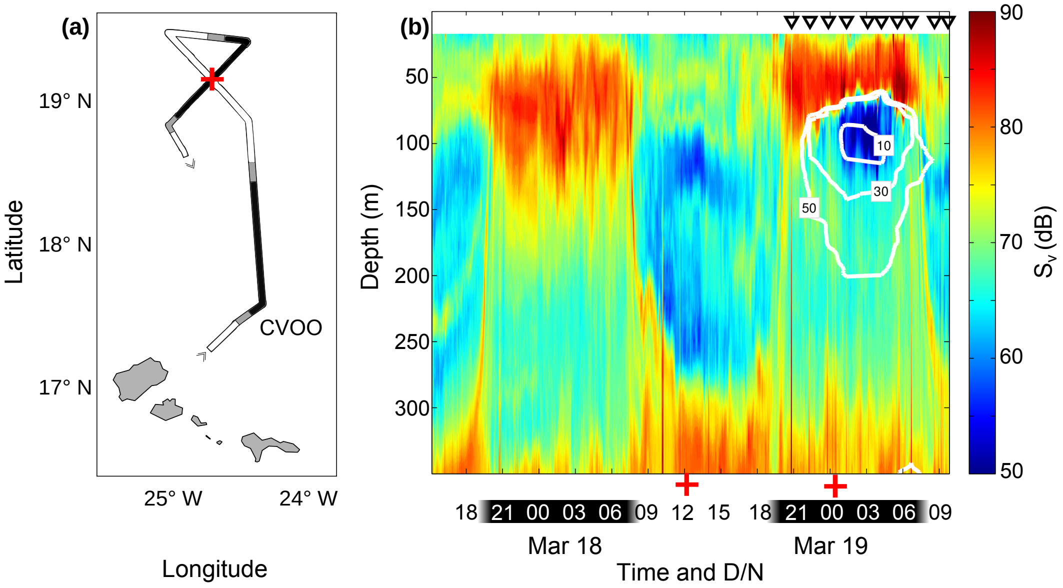

Figure 2. Cruise track with indicated day- and nighttime hours (panel **a**, red cross indicates intersection of day- and nighttime section) and shipboard acoustic Doppler current profiler (ADCP) mean volume backscatter S_V at 75 kHz (panel **b**, red crosses indicate the two profiles obtained at the intersection). White contour lines indicate oxygen concentrations interpolated from CTD profiles (triangles denote CTD stations).

approximately 90 m. This is well within the shallow OMZ (note that there are no O_2 isolines shown in the daytime transect in Fig. 2b since there were no CTD casts performed on the first transect).

Reanalysis of acoustic backscatter and oxygen time series data from the CVOO mooring before and during the transit of an ACME in 2010 (Karstensen et al., 2015) shows that the daytime S_V at the depth level of the oxygen sensor (around 50 m, depending on wire angle) is reduced below approximately 20 µmol O_2 kg^{-1} (Fig. 3a, power function; $r^2 = 0.69$). For nighttime data (Fig. 3b), the relationship between S_V and oxygen concentration is best described by a linear function ($r^2 = 0.94$). S_V in the subsurface increases around approximately 07:00 and 19:00 UTC (Supplement Fig. S1). These dusk and dawn traces suggest that DVM species migrate through the OMZ even when the daily mean oxygen concentration is between 5 and 20 µmol kg^{-1}.

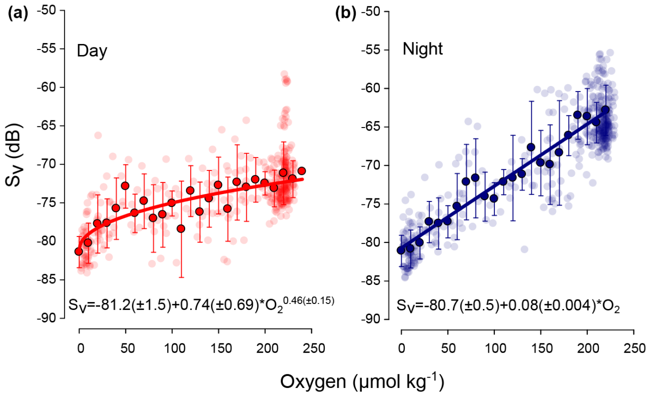

Figure 3. Moored ADCP (300 kHz, matched to depth of moored oxygen sensor, approximately 50 m) mean volume backscatter S_V (dB) as a function of oxygen concentration (µmol O_2 kg^{-1}) during daytime **(a)** and nighttime hours **(b)**. Higher S_V indicates a higher biomass of zooplankton and nekton. Transparent symbols are 1.5-hourly data, filled symbols are mean values (±SD) for 10 µmol O_2 kg^{-1} bins. Data are from 1 January to 14 March 2010.

3.3 Optical profiling

The UVP5 transect across the eddy revealed a pronounced increase of aggregates in the eddy core (Fig. 4a). This pattern was still evident at the maximum profile depth (600 m, below the midwater OMZ). At the same time, surface abundance of copepods (Fig. 4b) and, to a lesser degree, collodaria (Fig. 4c) is higher than in surrounding waters. Copepods were observed in substantial abundance within the OMZ, while collodaria appeared to avoid it. On the other hand, gelatinous zooplankton (comprising medusae, ctenophores and siphonophores; Fig. 3d) were observed in the inner OMZ core. Not a single observation of shrimp-like micronekton (euphausiids and decapods; Fig. 4e) was made at oxygen concentrations lower than 28 µmol O_2 kg^{-1}. Integrated abundance (upper 600 m; Fig. 5) of large aggregates was significantly higher in the core stations compared to the outside (one-way ANOVA, Tukey's HSD test $p < 0.001$) and margin ($p < 0.05$) stations. The integrated abundance of gelatinous plankton was significantly higher in the core stations than in

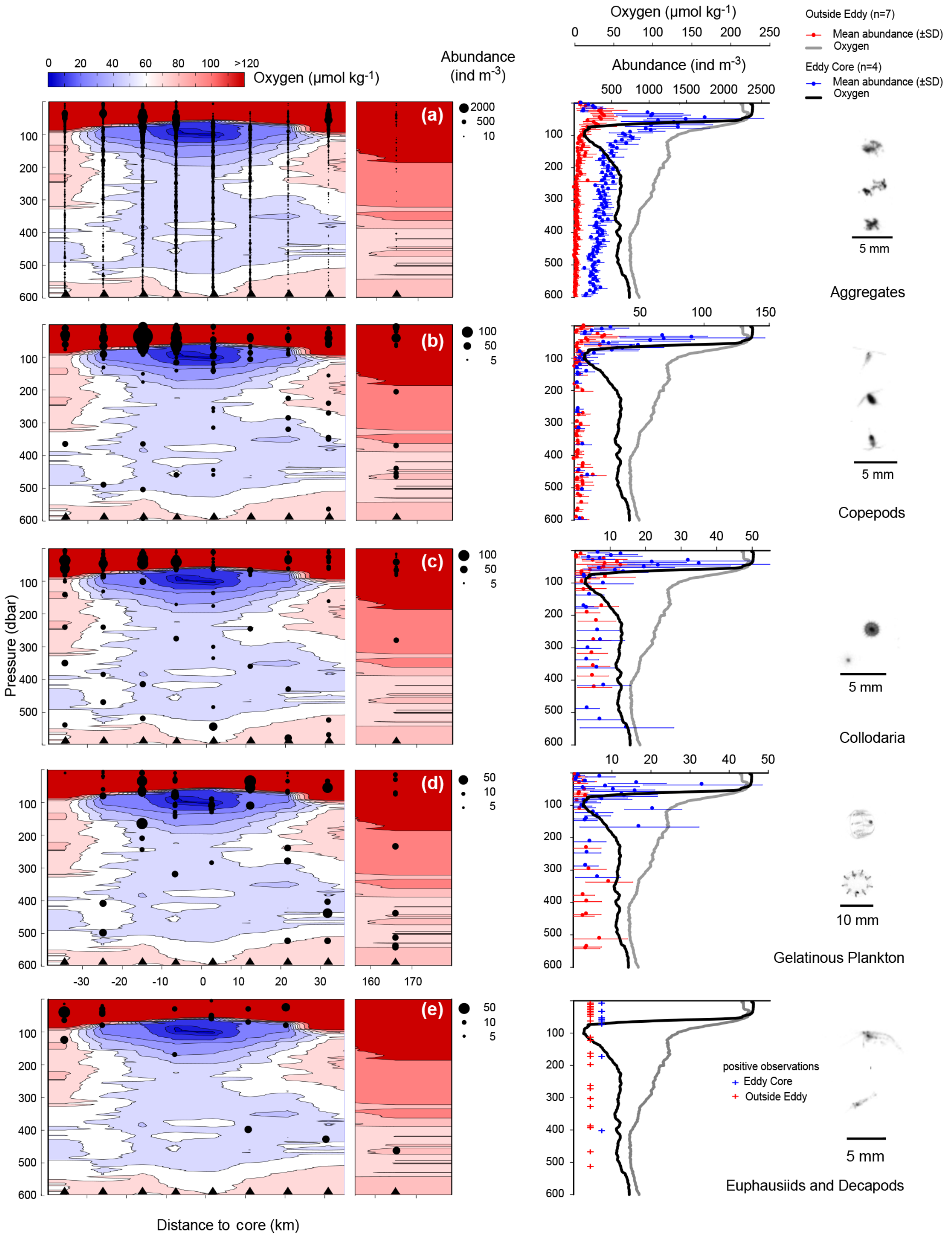

Figure 4. Left column shows oxygen contours (µmol O_2 kg^{-1}) across the eddy (from NE to SW) with superimposed bubble plots of UVP-based abundance (individuals m^{-3}, in 5 m depth bins) of aggregates **(a)**, copepods **(b)**, collodaria **(c)**, gelatinous plankton **(d)** and shrimp-like organisms (euphausiids and decapods) **(e)**. Note break in distance axis on section panels. Triangles denote CTD/UVP stations. Middle column are profiles of mean (±SD) abundance within the eddy core ($n = 4$) and at the CVOO station ($n = 7$) along with mean oxygen profiles with the exception of euphausiids and decapods **(e)**, where "+" denotes positive observations. For better visibility at low values, data with mean abundance = 0 are omitted. Right column shows representative images of the respective category.

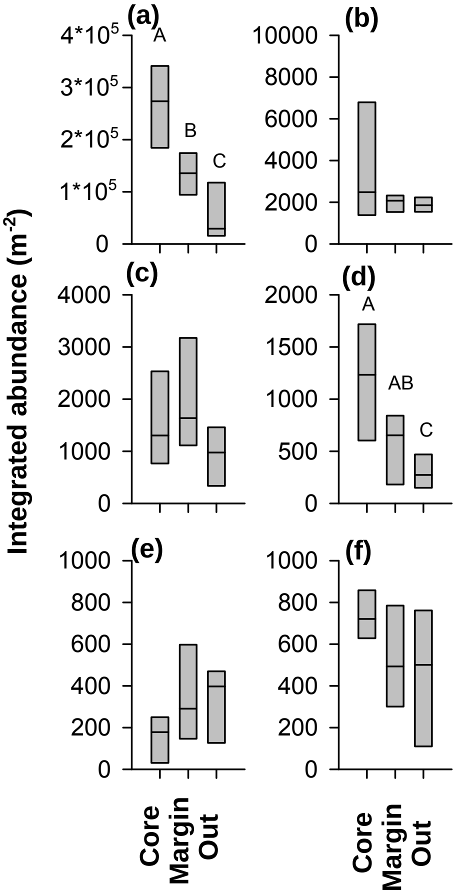

Figure 5. UVP5-derived integrated abundance (m^{-2}, upper 600 m) of large aggregates (> 500 µm) **(a)**, copepods **(b)**, collodaria **(c)**, gelatinous plankton **(d)**, shrimp-like micronekton (euphausiids/decapods) **(e)** and phaeodaria **(f)** in the eddy core ($n = 4$ profiles), eddy margin ($n = 4$) and outside of the eddy ($n = 7$). Different letters denote significant differences.

the outside stations ($p < 0.05$). For the other groups, differences in integrated abundance were not significant.

3.4 Multinet

The multinet data provide a higher taxonomic resolution, but lower spatial (horizontal and vertical) resolution than the optical profiles (UVP). In Fig. 6, the abundance and vertical distribution of eight conspicuous taxa are depicted, ordered by their apparent sensitivity to hypoxia. While euphausiids (Fig. 6a), calanoid copepods (Fig. 6b) and foraminifera (Fig. 6c) are abundant in the surface layer (exceeding the mean abundance at CVOO), they appear to avoid the shallow OMZ. Siphonophores (Fig. 6d), the poecilostomatoid *Oncaea* spp. (Fig. 6e) and eucalanoid copepods (Fig. 6f) are all very abundant in the eddy's surface layer during nighttime (with the latter also being observed in the shallow OMZ during nighttime) and appear to take refuge within the shallow OMZ during daylight hours. Two groups that appeared to favour the shallow OMZ even during nighttime hours were polychaetes (Fig. 6g) and ostracods (Fig. 6h), but also the harpacticoid copepod *Macrosetella gracilis* (Table S1 in the Supplement). Taxa that were more abundant in the surface layer of the eddy core compared to the mean outside eddy situation included eucalanoid and other calanid copepods, *Oithona* spp., *Macrosetella gracilis*, *Oncaea* spp., ostracods, decapods, siphonophores, chaetognaths, molluscs (mainly pteropods), polychaetes and foraminifera (Table S1). In contrast, taxa that were less abundant in the surface layer in the eddy were amphipods, salps and appendicularia. Although not sampled quantitatively by this type of net, this also seemed to be the case for fishes. In particular, no single individual was caught in the upper 200 m of the eddy core night station. Total area-integrated abundance of all zooplankton organisms in the upper 600 m was 151 000 (±34 000) m^{-2} in the eddy core and 101 000 (±15 000) at the outside station (Table S2).

4 Discussion

Already during the remote survey, it became apparent that the tracked mesoscale eddy was a hotspot of primary productivity. Lowered sea surface temperature and elevated surface chl *a* values (satellite imagery; Schütte et al., 2016) as well as increased nitrate levels in the eddy interior (autonomous gliders; Karstensen et al., 2016; Fiedler et al., 2016) indicate active upwelling and translate into substantially increased productivity (Löscher et al., 2015). During westward propagation, the hydrographic character was found to be remarkably constant (Karstensen et al., 2016; Schütte et al., 2016), while the genomic characterization (Löscher et al., 2015) indicated that the eddy had created a unique ecosystem that has not much in common with the coastal one it originated from. The present study is the first to observe the impact of such eddies on pelagic metazoans. Since process understanding and zooplankton production estimates are still lacking, we cannot conclude whether the system is ultimately bottom-up or top-down controlled and whether the seemingly high zooplankton productivity may be due to lacking higher trophic levels.

We deliberately chose not to attempt a direct comparison of methods (e.g. by trying to derive biomass from ADCP backscatter), but rather use the three methods complementary to each other: the acoustic survey reveals the horizontal and vertical fine-scale spatial distribution of scatterers (macrozooplankton and micronekton). It suggests a complete avoidance of the OMZ by these groups, whose identity remains somewhat unclear (see also Karstensen et al., 2015). The UVP has an excellent vertical and an intermediate horizontal (several profiles along transect) resolution, with restricted information regarding the identity of the organisms (limited by image resolution and sampling volume to more abundant mesozooplankton). The multinet has low vertical

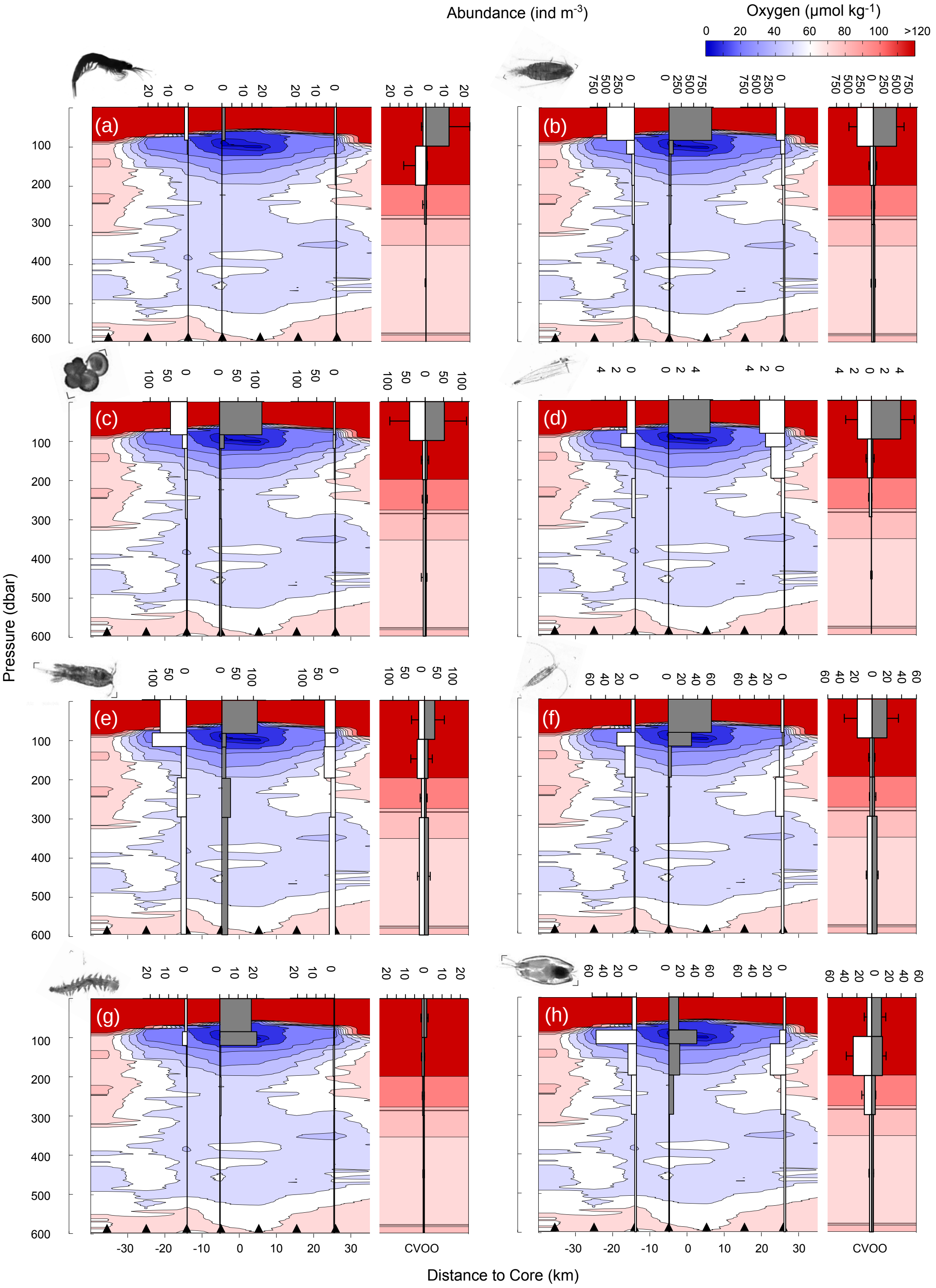

Figure 6. Oxygen contours (μmol O_2 kg^{-1}) across the eddy (from NE to SW) with superimposed bar plots of multinet-based abundance (individuals m^{-3}) of euphausiids **(a)**, calanoid copepods **(b)**, foraminifera **(c)**, siphonophores **(d)**, *Oncaea* sp. **(e)**, eucalanid copepods **(f)**, polychaetes **(g)** and ostracods **(h)**. White and grey bars indicate daylight and nighttime hauls, respectively. Triangles denote CTD stations used for the O_2 section. For the CVOO station (outside eddy situation), the mean (+SD) of four D / N samplings is shown and the distance to core is not calculated because data were combined from different cruises. Representative images are shown next to the respective category panel.

and horizontal resolution, and low catch efficiency for fast-swimming organisms. Its main asset is that it allows for a detailed investigation of zooplankton and some micronekton organisms. Since the samples are still intact after scanning, taxonomists interested in one of the groups presented here would even be able to proceed with more detailed work.

Using the shipboard and moored ADCP to investigate acoustic backscatter (rather than a calibrated scientific echosounder) resulted from the necessity to gather ADCP-derived current velocity data for eddy identification and localization of the core (see Fig. 1). It has to be noted that the backscatter signals from the 75 kHz shipboard ADCP and the 300 KHz moored ADCP are strictly not comparable, as for organisms that are small compared to the acoustic wavelengths, the backscatter strength increases rapidly with increasing frequency (Stanton et al., 1994). Also, smaller organisms contribute more to the 300 kHz signal than to the 75 kHz. Nevertheless, both instruments suggest that OMZ avoidance sets in at O_2 concentrations lower than approximately 20 µmol O^2 kg^{-1}.

The marked decrease in ADCP S_v in the shallow OMZ is only partly confirmed by the other two techniques. The animals that contribute most to the ADCP backscatter at a frequency of 75 kHz are targets in the centimetre-size range (75 kHz correspond to a wavelength of 20 mm), i.e. larger zooplankton and micronekton such as euphausiids, amphipods, small fish, pteropods, siphonophores and large copepods (Ressler, 2002). Thus, the community of organisms contributing most to the backscatter is not quantitatively (i.e. providing accurate abundance estimates) sampled by the multinet and the UVP5. Both mostly target organisms <10 mm in size and the sampling volume is small, in particular with the UVP5. Still, spatial observation patterns of these organisms derived from the multinet and UVP5 may help to provide explanations for the patterns observed in the ADCP, even though abundance estimates are to be taken with caution. For example, euphausiids contribute substantially to the backscatter at 75 kHz in this region (as observed through horizontal MOCNESS tows during dusk and dawn, resolving ADCP migration traces; Buchholz et al., unpublished data). Thus, the relative decrease of observed euphausiids in the OMZ (and in the eddy in general) in both multinet samples and UVP profiles suggests that they may be partly responsible for the lack of backscatter in the OMZ.

High-resolution profiles obtained by the UVP5 indicated OMZ avoidance by euphausiids and collodaria, while copepods (albeit at lower concentrations than in the surface layer) were observed in the OMZ core. Gelatinous zooplankton was even more abundant in the shallow OMZ than in surface waters. The multinet data (providing higher taxonomic resolution and larger sampling volume, but lower vertical resolution) suggest that there are four strategies followed by zooplankton in the eddy, which will be discussed below.

4.1 Shallow OMZ avoidance and compression at the surface

We ascribe this behaviour to euphausiids and most calanoid copepods as well as collodaria and foraminifera (from the supergroup rhizaria). While the total abundance of krill is probably underestimated by the comparatively slow and small plankton net, their vertical distribution in relation to the OMZ and the marked total decrease within the eddy compared to outside stations suggests that they are susceptible to OMZ conditions and may suffer from increased predation in the surface layer. This is in line with physiological observations, where a critical partial pressure of 2.4 and 6.2 kPa (29.6 and 64.2 µmol O_2 kg^{-1}) was determined at subsurface (13 °C) and near-surface temperatures (23 °C), respectively, in *Euphausia gibboides* in the ETNA (Kiko et al., 2015). Calanoid copepods represent the largest group in terms of abundance and biomass and comprise approximately 100 species in Cabo Verdean waters (Séguin, 2010) with a wide range of physiological and behavioural adaptations. Species most tolerant to low-oxygen conditions are vertically migrating species, such as *Pleuromamma* spp., while epipelagic species, such as *Undinula vulgaris*, are less tolerant (Teuber et al., 2013; Kiko et al., 2015). From the rhizaria supergroup, the fine-scale distribution pattern of solitary collodaria (a group that is abundant in surface waters of the oligotrophic open ocean; see Biard et al. 2015 and references therein) suggests OMZ sensitivity, but direct evidence from the literature is lacking. The foraminifera, which are mostly too small to be quantified well with the UVP5, but in contrast to other rhizaria are well preserved in buffered formaldehyde in seawater solution, were highly abundant in the surface of the eddy core. Here, the distribution shift likely also includes a community shift, since a marked dominance change from surface-dwelling to subsurface-dwelling species was found in sediment trap data during the transit of the 2010 ACME (Fischer et al., 2015). In that ACME, also an export flux peak by foraminifera was observed.

4.2 Migration to the shallow OMZ core during daytime

This strategy seems to be followed by siphonophores, *Oncaea* spp. and eucalanoid copepods.

Although it seems unlikely that siphonophores in this survey were contributing substantially to the ADCP backscatter, as those retrieved by the multinet were almost exclusively calycophorans (see Fig. 6d for a type specimen), which do not have a pneumatophore and, therefore, lack gas bubbles that are highly resonant in other siphonophore groups (e.g. Ressler, 2002). They may, however, contribute to the weak backscatter signal in the shallow OMZ during daytime (Figs. 2b and 6d). *Oncaea* spp. are particle-feeding copepods that are directly associated with marine snow (Dagg et al., 1980). They were observed in quite extreme OMZs in other oceanic regions (e.g. Böttger-Schnack, 1996; Saltzman and Wishner, 1997); however, our results suggest that at least in the tropical Atlantic biome they cannot permanently endure hypoxia but have to pay their oxygen debt during nighttime. The majority of adult eucalanoid copepods were *Rhincalanus nasutus*, a species that is frequently found in the midwater OMZ of the ETNA. In the eastern tropical Pacific, however, *R. nasutus* was reported to be excluded from the extreme midwater OMZ (500–1000 m depth, below approximately 22 µmol O_2 kg^{-1}), unlike the key OMZ-adapted eucalanoid species of that region (e.g. *Eucalanus inermis*), which are able to permanently inhabit the OMZ (Saltzman and Wishner, 1997). In our study, *R. nasutus* were also found in the shallow (extreme) OMZ of the eddy (well below 20 µmol O_2 kg^{-1}), indicating that this copepod species also may be able to cope with further deoxygenation of the midwater OMZ in the Atlantic. Both *Oncaea* and *Rhincalanus* are unlikely to be seen in the S_v signal at 75 kHz.

4.3 Residing in the shallow OMZ day and night

Contrary to most crustaceans, collodaria and euphausiids, a remarkable ability to endure OMZ conditions for prolonged periods of time seems to be present in ostracods, polychaetes, *Macrosetella gracilis* and gelatinous plankton. “Jellies” are a group of organisms of which several taxa, such as siphonophores, salps, hydromedusae and ctenophores, have been reported to tolerate hypoxic conditions much better than most crustacean zooplankton (Mills, 2001; Thuesen et al., 2005). In addition to reduced metabolic activity (e.g. Rutherford Jr. and Thuesen, 2005), using the mesoglea gel matrix as an oxygen reservoir was shown to be a strategy in scyphomedusae to temporarily survive anoxia (Thuesen et al., 2005). It has also been suggested that “jellyfish” (i.e. pelagic cnidarians and ctenophores) outcompete other planktonic groups in coastal systems under eutrophication-induced hypoxia (Mills, 2001). The UVP5 nighttime section suggests that many gelatineous organisms reside within the shallow OMZ even during nighttime. This is only partly confirmed by the multinet data; however, ctenophores and medusae are often destroyed during sampling and not well preserved in formaldehyde. For ostracods, it is known that several limnic (Teixeira et al., 2014) and marine (Corbari et al., 2004) benthic species tolerate hypoxia for prolonged periods of time (and preferentially select hypoxic habitats over oxygenated ones), which lead to the use of their abundance in sediment cores as a proxy for past ocean oxygenation (Lethiers and Whatley, 1994). In pelagic marine ostracods, however, there is little evidence for particular pre-adaptation to OMZ conditions. To the best of our knowledge, no physiological studies exist that describe the metabolic response of pelagic ostracods to hypoxia. Recently, it was found that the oxygen transport protein hemocyanin occurs in several groups within the class ostracoda, including planktonic species (Marxen et al., 2014). In the Arabian Sea, the highest ostracod abundances were found in the oxygenated surface layer, but consistent occurrence in the extreme OMZ (< 5 µmol O_2 kg^{-1}) was reported (Böttger-Schnack, 1996). In the eastern tropical Pacific, most species were reported to avoid the OMZ, with the notable exception of *Conchoecetta giesbrechti*, which is classified as an OMZ-adapted species (Castillo et al., 2007). For pelagic polychaetes, Thuesen and Childress (1993) even state that they may have the highest metabolic rates (and, thus, oxygen demand) in the meso- and bathypelagic zones of the oceans, with the exception of the aberrant species *Poeobius meseres*.

4.4 Migration through the shallow OMZ core to better-oxygenated depths

To rigorously assess DVM reduction by the underlying OMZ, acoustic 24 h observations would be necessary to directly observe the migration pattern. Unfortunately, the dawn and dusk migration observations took place at the northeast- and southwest-margin of the eddy, respectively, just outside the 30 µmol O_2 kg^{-1} boundary (Fig. 2). Nevertheless, it appears from the day/night difference in the shipboard ADCP S_v (at the intersection of the two transects) as well as from the moored ADCP data (Fig. S1) that at least part of the migrating population “holds its breath” and crosses the OMZ during ascent/descent. In this respect, the thin shallow OMZ seems to be different from the several hundred metres thick mesopelagic OMZ, which at low core oxygen concentrations can serve as a quite effective migration barrier (Auel and Verheye, 2007; Teuber et al., 2013).

The enhanced surface primary productivity of the eddy also resulted in an approximately 5-fold increase of large particles, well visible down to 600 m depth. This indicates a massive export flux by sinking marine snow (see also Fischer et al. (2015) for sediment trap data of the 2010 ACME), which is thus made available to higher trophic levels at greater depths. As an example, phaeodaria (in supergroup rhizaria) are one of the few exclusively mesopelagic groups (only found deeper than approximately 200 m in UVP profiles). Their integrated abundance seemed to be positively affected by the eddy conditions, which may indicate favourable feeding/growth conditions at depth.

In summary, mesozooplankton biomass was generally enhanced in the euphotic zone of the ACME, suggesting that it may represent an “oasis in the desert” sensu Godø et al. (2012), although the differences to outside conditions were not quite as large as those reported by Goldthwait and Steinberg (2008). On the other hand, subsurface hypoxia appears to be detrimental to some surface-dwelling as well as vertically migrating zooplankton taxa. We lack quantitative estimates of higher trophic levels (the multinet is too small and slow to efficiently sample fast-swimming nekton organisms), but it seems that the small migratory mesopelagic fishes, which were usually caught (albeit in low numbers) outside the eddy, were less abundant in the eddy core’s surface. To draw robust conclusions on the identity and whereabouts of acoustic scatterers, the additional use of several types of stratified nets is necessary (e.g. 10 m^2 MOCNESS in addition to a multinet or 1 m^2 MOCNESS) but was logistically impossible during the opportunistic sampling on M105. Since gelatinous plankton organisms appear to play a key role in these oceanic OMZs and are notoriously undersampled by nets and/or destroyed by fixatives, it even seems worthwhile to employ a dedicated camera system (with larger sampling volume than the UVP5) for such a survey. It also remains an open question whether the rich zooplankton prey field is exploited by epipelagic fishes and their predators (see, e.g., Tew Kai and Marsac (2010) for examples of tuna and seabird interaction with cyclonic eddies). By providing isolated bodies of water with distinct (and sometimes, like in our case, extreme) environmental conditions for many months, mesoscale eddies are important vectors of species dispersal and invasion (Wiebe and Flierl, 1983) and subject the population fragments they contain to their own mutations, selection forces and genetic drift effects. Thus, they not only are hypothesized to play a central role in speciation of planktonic species (Bracco et al., 2000; Clayton et al., 2013), but also may resemble a key mechanism to equip oceanic metapopulations with the range of physiological and behavioural adaptations deemed necessary to survive under global change.

5 Conclusions

Acoustic observations (shipboard ADCP) confirm previous observations (moored ADCP) of a sharp decrease in backscatter at O_2 concentrations below approximately 20 $\mu mol\, O_2\, kg^{-1}$. Euphausiids (which are known to contribute substantially to the ADCP backscatter) were not observed within the OMZ stratum of the eddy, and their integrated abundance was markedly reduced. Still, multinet and UVP5 data indicate that several zooplankton groups are surprisingly insensitive to these extreme OMZ conditions, and many taxa that avoid the OMZ even reach higher abundance in the productive surface environment of the eddy. However, it remains an open question if and how higher trophic levels (such as small pelagic forage fish and their predators) may benefit from the dense prey field. While the term “open ocean dead zone” may be an exaggeration, low-oxygen eddies in the ETNA in light of future deoxygenation might serve as a crystal ball (or, more appropriately, a “scrying pool”) to estimate the differential response of different plankton functional groups of the open ocean to global change.

Data availability

All data are publicly available in the PANGAEA database (doi:10.1594/PANGAEA.858323).

The Supplement related to this article is available online at doi:10.5194/bg-13-1977-2016-supplement.

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