

rates, rendering zooplankton 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 zooplankton avoidance of the mesopelagic OMZ to set in if oxygen levels decline below approximately $20 \mu\text{mol O}_2 \text{ kg}^{-1}$. This may result in a positive feedback on the OMZ oxygen consumption rates, since zooplankton respiration within the OMZ as well as active flux of dissolved and particulate organic matter into the OMZ will decline.

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 centered 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 $40 \mu\text{mol O}_2 \text{ kg}^{-1}$ (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 diel 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

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concentrations) and vertically expand over the past decades and is predicted to further deoxygenate and expand laterally in the future (Stramma et al., 2008; Stramma et al., 2009) in the course of declining global oxygen inventories due to anthropogenic climate change (Cocco et al., 2013).

Submesoscale and mesoscale eddies (which in the tropics/subtropics comprise diameters on 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), translating even up to top predators (Tew Kai and Marsac, 2010). Their basin-wide relevance for biogeochemical cycles is increasingly recognized (e.g. Stramma et al., 2013). Numerous eddies spin off the productive Mauritanian and Senegalese coast (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., 2015a). Both eddy types propagate westward at about 4 to 5 km day^{-1} , passing the Cape Verde archipelago north or south. They can be tracked by satellite altimetry for up to nine months (Schütte et al., 2015b; Karstensen et al., 2015a). While “normal” anticyclones are usually relatively warm and unproductive (e.g. Palacios et al., 2006), both cyclonic and anticyclonic mode water 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., 2015a) has changed our view of current oxygen conditions in the ETNA. In that study, it had been observed that oxygen values $< 2 \mu\text{mol O}_2 \text{ kg}^{-1}$ 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 against surrounding water (a result of the rotation of the eddy) paired with enhanced respiration (a result of the high productivity and subsequent ex-

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port and degradation of particulate organic matter, Fischer et al., 2015), and introduced the term “dead-zone eddy” (Karstensen et al., 2015a). The so far lowest oxygen concentrations in such an eddy ($< 2 \mu\text{mol O}_2 \text{ kg}^{-1}$ 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 depth below the oxygenated mixed layer was observed. The acoustic backscatter signal received by the 300 kHz ADCP is largely created by organisms $> 5 \text{ mm}$ (thus missing a substantial part of the mesozooplankton) and does not enable 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) 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., 2015a; 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 the low oxygen eddies in the tropical North Atlantic, a dedicated field experiment (“eddy hunt”) north of the Cape Verde Archipelago was designed. In summer 2013, the identification and tracking of candidate eddies was started by combining remotely sensed data and Argo float profile data. In spring 2014, a candidate low oxygen eddy was identified and on-site sampling began covering genomics, physics, and biogeochemistry (see also Schütte et al., 2015b; Fiedler et al., 2015; Löscher et al., 2015; Karstensen et al., 2015b). Ship-based sampling (“site survey”) was carried out on 18 and 19 March 2014 during the RV *Meteor* cruise M105. Two ADCP sections

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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 2012 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 target strength 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 $< 2 \mu\text{mol kg}^{-1}$ (Karstensen et al., 2015).

2.1 ADCP

Underway current measurements were performed during cruise M105 using two vessel mounted Acoustic Doppler Current Profilers (vmADCP), 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 center 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 center. The second section was a perpendicular, northeast-to-southwest section through the location of lowest cross-sectional current velocity of the first section. The lowest cross-sectional velocity of the second section defines the eddy center.

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 4 beam design in Janus configuration with 20° opening. Based on accompa-

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nying hydrographic and pressure data each 4 m depth cell was allocated a discrete pressure/depth information as well as a sound speed profile (harmonic mean).

For vessel-mounted as well as moored ADCP, target strength was estimated for each beam and each depth cell by a recalculation of a simplified sonar equation (Deimes, 1999). Because we were not attempting to estimate biomass, no further calibration was applied. Moored ADCP data were recorded every 90 min. Target strength from the four ADCP beams was averaged and matched to the oxygen data. Only data from 1 January 2010 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 UTC 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.

2.2 CTD and UVP5

Oxygen concentration was measured using a SBE 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 in situ quantification of particles $> 60 \mu\text{m}$ and plankton $> 500 \mu\text{m}$ with high vertical resolution (Picheral et al., 2010). Thumbnails of all objects $> 500 \mu\text{m}$ 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 ten images were recorded per meter depth. The mean total sampling volume for the upper 600 m of the water column was $6.34 (\pm 0.99) \text{m}^3$. Volume-specific abundance was calculated in 5 m depth bins.

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2.3 Multinet

Zooplankton samples were collected with a Hydrobios multinet Midi (0.25 m² mouth opening, 5 nets, 200 μm mesh, equipped with flowmeters) hauled vertically from the maximum depth to the surface at 1m 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 the time series observations. As the NW-ward 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 O₂ concentration. Thus, the “eddy core day” haul is approximately 14 km away from the eddy center (Fig. 1). Depth intervals (600-300-200-120-85-0 m) were chosen according to the O₂ profile. When leaving the eddy, a second “day” haul was collected at the margin of the eddy, approximately 26 km from the eddy center, using the depth intervals from the eddy core station. Zooplankton samples were fixed in 100 mL Kautex[®] jars in 4% borax-buffered formaldehyde in 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 \times 29.7 cm (DIN-A4) size glass plate with a plastic frame. Scans were 8 bit grayscale, 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, $> 1000 \mu\text{m}$) and split using a Motoda plankton splitter if necessary. The $> 1000 \mu\text{m}$ fraction was scanned completely, whereas fractions comprising not more than approximately 1000 objects were scanned for the two other fractions.

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“Vignettes” and image characteristics of all objects were extracted with ZooProcess (Gorsky et al., 2010) and sorted into 39 categories using Plankton Identifier (Gasparini, 2007). Automated image sorting was then manually validated by experts.

3 Results

5 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 $3.75 \mu\text{mol } O_2 \text{ kg}^{-1}$ 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 $5 \mu\text{mol } O_2 \text{ kg}^{-1}$ were only found 10 within approximately 18 and 8 km from the center, respectively. For the purpose of this study, the four stations within 20 km to the eddy core (with minimum O_2 concentrations well below $20 \mu\text{mol } O_2 \text{ kg}^{-1}$) 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 $53 \mu\text{mol } O_2 \text{ kg}^{-1}$) and the CVOO station (M105 data 15 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 (centered around approximately 450 m depth) featured mean minimum oxygen concentrations of $70 \mu\text{mol } O_2 \text{ kg}^{-1}$).

3.2 Vertical distribution and DVM – acoustic observations

20 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 centered 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 center of the nighttime distribution outside the eddy ranged from approximately 30 to 130 m

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depth. During the day, lowest target strength 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.

5 A very different nighttime distribution was observed when traversing the eddy. The scatterers in the surface layer were 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 center). In the core of the shallow OMZ, below approximately $20 \mu\text{mol } O_2 \text{ kg}^{-1}$, an absolute minimum target strength was observed.

10 At the intersection of the two transects, the difference between the target strength in the surface at day and night suggests substantial vertical migration into/out of the surface layer, crossing the OMZ (Fig. 2b).

Reanalysis of acoustic backscatter and oxygen data from the CVOO mooring before and during the transit of an ACME in 2010 (Karstensen et al., 2015) shows that the 15 daytime target strength at the depth level of the oxygen sensor (around 50 m, depending on wire angle) is reduced below approximately $20 \mu\text{mol } O_2 \text{ kg}^{-1}$ (Fig. 3a, power function; $r^2 = 0.69$). For the nighttime data (Fig. 3b), the relationship between target strength and oxygen concentration is best described by a linear function ($r^2 = 0.94$). Analysis of dusk and dawn traces suggest that DVM species migrate through the OMZ 20 (Fig. S1 in the Supplement) even when the daily mean oxygen concentration is between 5 and $20 \mu\text{mol } O_2 \text{ kg}^{-1}$, since target strength in the subsurface increases around approximately 07:00 and 19:00 UTC.

3.3 Optical profiling

25 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

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collodaria appeared to avoid it. Not a single observation of shrimp-like micronekton (euphausiids and decapods, Fig. 4d) was made at oxygen concentrations lower than $28 \mu\text{mol O}_2 \text{ kg}^{-1}$. On the other hand, gelatinous zooplankton (comprising medusae, ctenophores, and siphonophores, Fig. 3e) were observed in the inner OMZ core. 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 $p < 0.001$) and “margin” ($p < 0.05$) stations. The integrated abundance of gelatinous plankton was significantly higher in the “core” stations than in the “outside” stations ($p < 0.05$). For the other groups, differences in integrated abundance were not significant.

3.4 Multinet

The multinet data provides 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. 6 E) and eucalanoid copepods (Fig. 6f) are all very abundant in the eddy’s surface layer during the night (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

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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 $151\,000 (\pm 34\,000) \text{ m}^{-2}$ in the eddy core and $101\,000 (\pm 15\,000)$ 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., 2015a) as well as increased nitrate levels in the eddy interior (autonomous gliders; Karstensen et al., 2015b; Fiedler et al., 2015) 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., 2015b; Schütte et al., 2015b), while the genomic characterization (Löscher et al., 2015) as well as the particle composition Fischer et al. (2015) indicate that the eddy has created a unique ecosystem that has not much in common with the coastal one it originated from.

The marked decrease in ADCP target strength 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 cm-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 organisms contributing most to the backscatter (e.g. mesopelagic fishes and other micronekton) may not be well quantified by the multinet and the UVP5 that mostly target organisms smaller than 10 mm.

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

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coastal systems under eutrophication-induced hypoxia (Mills, 2001). The UVP5 night-time section suggests that many gelatinous 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 preadaptation 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, highest ostracod abundances were found in the oxygenated surface layer, but consistent occurrence in the extreme OMZ ($< 5 \mu\text{mol O}_2 \text{ kg}^{-1}$) 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 *Poecobius meseres* (which was not observed in our samples).

Migration through the shallow OMZ core to better-oxygenated depths

To rigorously assess DVM reduction by the underlying OMZ, acoustic 24h-observations would be necessary to directly observe the migration pattern. Unfortunately, the dawn and dusk migration observations took place at the NE- and SW-margin of the eddy, respectively, just outside the $30 \mu\text{mol O}_2 \text{ kg}^{-1}$ boundary (Fig. 2). Nevertheless, it appears from the day/night difference in the shipboard ADCP target strength (at the intersection

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tion 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 meters 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 which, since it is well visible to 600 m depth, seems to resemble a massive export flux by sinking marine snow (see also Fischer et al., 2015 for sediment trap data of the 2010 ACME), which is available for higher trophic levels at greater depths. As an example, one of the few exclusively mesopelagic groups (only found deeper than approximately 200 m in UVP profiles), the integrated abundance of phaeodaria (in supergroup rhizaria) seemed to be positively affected by the eddy conditions, which may indicate favourable 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 caught sporadically outside the eddy were less abundant in the eddy core’s surface. It 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

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own mutations, selection forces, and genetic drift effects. Thus, they are not only hypothesized to play a central role in speciation of planktonic species (Bracco et al., 2000; Clayton et al., 2013), but 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 $20 \mu\text{mol } O_2 \text{ kg}^{-1}$. 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 the 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.

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References

- Andersen, V., Sardou, J., and Gasser, B.: Macroplankton and micronekton in the northeast tropical Atlantic: abundance, community composition and vertical distribution in relation to different trophic environments, *Deep-Sea Res. Pt. I*, 44, 193–222, 1997.
- Auel, H. and Verheye, H. M.: Hypoxia tolerance in the copepod *Calanoides carinatus* and the effect of an intermediate oxygen minimum layer on copepod vertical distribution in the northern Benguela Current upwelling system and the Angola–Benguela Front, *J. Exp. Mar. Biol. Ecol.*, 352, 234–243, 2007.
- Biard, T., Pillet, L., Decelle, J., Poirier, C., Suzuki, N., and Not, F.: Towards an Integrative Morpho-molecular Classification of the Collodaria (Polycystinea, Radiolaria), *Protist*, doi:10.1016/j.protis.2015.05.002, 2015.
- Böttger-Schnack, R.: Vertical structure of small metazoan plankton, especially noncalanoid copepods, I. Deep Arabian Sea, *J. Plankton Res.*, 18, 1073–1101, 1996.
- Bracco, A., Provenzale, A., and Scheuring, I.: Mesoscale vortices and the paradox of the plankton, *P. Roy. Soc. Lond. B Bio.*, 267, 1795–1800, 2000.
- Castillo, R., Antezana, T., and Ayon, P.: The influence of El Niño 1997–98 on pelagic ostracods in the Humboldt Current Ecosystem off Peru, *Hydrobiologia*, 585, 29–41, 2007.
- Clayton, S., Dutkiewicz, S., Jahn, O., and Follows, M. J.: Dispersal, eddies, and the diversity of marine phytoplankton, *Limnol. Oceanogr.*, 3, 182–197, 2013.
- Cocco, V., Joos, F., Steinacher, M., Frölicher, T. L., Bopp, L., Dunne, J., Gehlen, M., Heinze, C., Orr, J., Oschlies, A., Schneider, B., Segschneider, J., and Tjiputra, J.: Oxygen and indicators of stress for marine life in multi-model global warming projections, *Biogeosciences*, 10, 1849–1868, doi:10.5194/bg-10-1849-2013, 2013.

- Corbari, L., Carbonel, P., and Massabuau, J.-C.: How a low tissue O₂ strategy could be conserved in early crustaceans: the example of the podocopid ostracods, *J. Exp. Biol.*, 207, 4415–4425, 2004.
- Dagg, M., Cowles, T., Whittedge, T., Smith, S., Howe, S., and Judkins, D.: Grazing and excretion by zooplankton in the Peru upwelling system during April 1977, *Deep-Sea Res. Pt. I*, 27, 43–59, 1980.
- Deimes, K. L.: Backscatter Estimation Using Broadband Acoustic Doppler Current Profilers, Proceedings of the IEEE Sixth Working Conference on Current Measurement, San Diego, CA, 11-13 March 1999, 249–253, doi:10.1109/CCM.1999.755249, 1999.
- Fiedler, B., Karstensen, J., Hauss, H., Schütte, F., Grundle, D., Krahnemann, G., Santos, C., and Körtzinger, A.: Biogeochemistry of oxygen depleted mesoscale eddies in the open eastern tropical North Atlantic, *Biogeosciences Discuss.*, in prep., 2015.
- Fischer, J., Brandt, P., Dengler, M., Müller, M., and Symonds, D.: Surveying the upper ocean with the Ocean Surveyor: a new phased array Doppler current profiler, *J. Atmos. Ocean. Technol.*, 20, 742–751, 2003.
- Fischer, G., Karstensen, J., Romero, O., Baumann, K.-H., Donner, B., Hefter, J., Mollenhauer, G., Iversen, M., Fiedler, B., Monteiro, I., and Körtzinger, A.: Bathypelagic particle flux signatures from a suboxic eddy in the oligotrophic tropical North Atlantic: production, sedimentation and preservation, *Biogeosciences Discussions*, 2015.
- Gasparini, S.: Plankton identifier: a software for automatic recognition of planktonic organisms, available at: http://www.obs-vlfr.fr/~gaspari/Plankton_Identifier/index.php (last access: 11 September 2015), user manual, 2007.
- Godø, O. R., Samuelsen, A., Macaulay, G. J., Patel, R., Hjøllo, S. S., Horne, J., Kaartvedt, S., and Johannessen, J. A.: Mesoscale eddies are oases for higher trophic marine life, *PLoS One*, 7, e30161, doi:10.1371/journal.pone.0030161, 2012.
- Goldthwait, S. A. and Steinberg, D. K.: Elevated biomass of mesozooplankton and enhanced fecal pellet flux in cyclonic and mode-water eddies in the Sargasso Sea, *Deep-Sea Res. Pt. II*, 55, 1360–1377, 2008.
- Gorsky, G., Ohman, M. D., Picheral, M., Gasparini, S., Stemmann, L., Romagnan, J.-B., Cawood, A., Pesant, S., García-Comas, C., and Prejger, F.: Digital zooplankton image analysis using the ZooScan integrated system, *J. Plankton Res.*, 32, 285–303, 2010.
- Karstensen, J., Stramma, L., and Visbeck, M.: Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans, *Prog. Oceanogr.*, 77, 331–350, 2008.

18333

- Karstensen, J., Fiedler, B., Schütte, F., Brandt, P., Körtzinger, A., Fischer, G., Zantopp, R., Hahn, J., Visbeck, M., and Wallace, D.: Open ocean dead zones in the tropical North Atlantic Ocean, *Biogeosciences*, 12, 2597–2605, doi:10.5194/bg-12-2597-2015, 2015a.
- Karstensen, J., Schütte, F., Pietri, A., Krahnemann, G., Fiedler, B., Grundle, D., Hauss, H., Körtzinger, A., Löscher, C., and Viera, N.: Anatomy of open ocean dead-zones based on high-resolution multidisciplinary glider data, *Biogeosciences Discuss.*, in prep., 2015b.
- Kinzer, J. and Schulz, K.: Vertical distribution and feeding patterns of midwater fish in the central equatorial Atlantic, *Mar. Biol.*, 85, 313–322, 1985.
- Lethiers, F. and Whatley, R.: The use of Ostracoda to reconstruct the oxygen levels of Late Palaeozoic oceans, *Mar. Micropaleontol.*, 24, 57–69, 1994.
- Löscher, C. R., Fischer, M. A., Neulinger, S. C., Fiedler, B., Philippi, M., Schütte, F., Singh, A., Hauss, H., Karstensen, J., Körtzinger, A., Künzel, S., and Schmitz, R. A.: Hidden biosphere in an oxygen-deficient Atlantic open ocean eddy: future implications of ocean deoxygenation on primary production in the eastern tropical North Atlantic, *Biogeosciences Discuss.*, 12, 14175–14213, doi:10.5194/bgd-12-14175-2015, 2015.
- Marxen, J., Pick, C., Oakley, T., and Burmester, T.: Occurrence of Hemocyanin in Ostracod Crustaceans, *J. Mol. Evol.*, 79, 3–11, 2014.
- McGillcuddy, D. J., Anderson, L. A., Bates, N. R., Bibby, T., Buesseler, K. O., Carlson, C. A., Davis, C. S., Ewart, C., Falkowski, P. G., and Goldthwait, S. A.: Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms, *Science*, 316, 1021–1026, 2007.
- Menkes, C. E., Kennan, S. C., Flament, P., Dandonneau, Y., Masson, S., Biessy, B., Marchal, E., Eldin, G., Grelet, J., and Montel, Y.: A whirling ecosystem in the equatorial Atlantic, *Geophys. Res. Lett.*, 29, 48-41–48-44, 2002.
- Mills, C.: Jellyfish blooms: are populations increasing globally in response to changing ocean condition?, *Hydrobiologia*, 451, 55–68, 2001.
- Palacios, D. M., Bograd, S. J., Foley, D. G., and Schwing, F. B.: Oceanographic characteristics of biological hot spots in the North Pacific: A remote sensing perspective, *Deep-Sea Res. Pt. II*, 53, 250–269, 2006.
- Picheral, M.G., Stemmann, L., Karl, D.M., Iddaoud, G., Gorsky, G. The Underwater Vision Profiler 5: An advanced instrument for high spatial resolution studies of particle size spectra and zooplankton, *Limnol. Oceanogr.-Methods*, 8, 462–473, doi:10.4319/lom.2010.8.462, 2010.

18334

- Postel, L., da Silva, A. J., Mohrholz, V., and Lass, H.-U.: Zooplankton biomass variability off Angola and Namibia investigated by a lowered ADCP and net sampling, *J. Mar. Sys.*, 68, 143–166, 2007.
- Prince, E. D., Luo, J. C., Goodyear, P., Hoolihan, J. P., Snodgrass, D., Orbesen, E. S., Serafy, J. E., Ortiz, M., and Schirripa, M. J.: Ocean scale hypoxia based habitat compression of Atlantic istiophorid billfishes, *Fish. Oceanogr.*, 19, 448–462, 2010.
- Ressler, P. H.: Acoustic backscatter measurements with a 153kHz ADCP in the northeastern Gulf of Mexico: determination of dominant zooplankton and micronekton scatterers, *Deep-Sea Res. Pt. I*, 49, 2035–2051, 2002.
- Rutherford Jr, L. D. Thuesen, E. V.: Metabolic performance and survival of medusae in estuarine hypoxia, *Mar. Ecol.-Prog. Ser.*, 294, 189–200, 2005.
- Saltzman, J. and Wishner, K. F.: Zooplankton ecology in the eastern tropical Pacific oxygen minimum zone above a seamount: 2. Vertical distribution of copepods, *Deep-Sea Res. Pt. I*, 44, 931–954, 1997.
- Schütte, F., Brandt, P., and Karstensen, J.: Occurrence and characteristics of mesoscale eddies in the tropical northeast Atlantic Ocean, *Ocean Science Discussions*, submitted, 2015a.
- Schütte, F., Karstensen, J., Krahnemann, G., Fiedler, B., Brandt, P., Visbeck, M., and Körtzinger, A.: Characterization of “dead-zone eddies” in the tropical North Atlantic Ocean, *Biogeosciences Discuss.*, in prep., 2015b.
- Séguin, F.: Zooplankton community near the island of São Vicente in the Cape Verde archipelago: insight on pelagic copepod respiration, MSc Thesis, University of Bremen, 77 pp., 2010.
- Stramma, L., Johnson, G. C., Sprintall, J., and Mohrholz, V.: Expanding Oxygen-Minimum Zones in the Tropical Oceans, *Science*, 320, 655–658, 2008.
- Stramma, L., Visbeck, M., Brandt, P., Tanhua, T., and Wallace, D.: Deoxygenation in the oxygen minimum zone of the eastern tropical North Atlantic, *Geophys. Res. Lett.*, 36, L20607, doi:10.1029/2009GL039593, 2009.
- Stramma, L., Prince, E. D., Schmidtko, S., Luo, J., Hoolihan, J. P., Visbeck, M., Wallace, D. W., Brandt, P., and Körtzinger, A.: Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes, *Nature Climate Change*, 2, 33–37, 2012.
- Stramma, L., Bange, H. W., Czeschel, R., Lorenzo, A., and Frank, M.: On the role of mesoscale eddies for the biological productivity and biogeochemistry in the eastern tropical Pacific Ocean off Peru, *Biogeosciences*, 10, 7293–7306, doi:10.5194/bg-10-7293-2013, 2013.

18335

- Teixeira, M. C., Budd, M. P., and Strayer, D. L.: Responses of epiphytic aquatic macroinvertebrates to hypoxia, *Inland Waters*, 5, 75–80, 2014.
- Teuber, L., Schukat, A., Hagen, W., and Auel, H.: Distribution and ecophysiology of calanoid copepods in relation to the oxygen minimum zone in the eastern tropical Atlantic, *PLoS one*, 8, e77590, doi:10.1371/journal.pone.0077590, 2013.
- Tew Kai, E. and Marsac, F.: Influence of mesoscale eddies on spatial structuring of top predators’ communities in the Mozambique Channel, *Prog. Oceanogr.*, 86, 214–223, 2010.
- Thuesen, E. V. and Childress, J. J.: Metabolic rates, enzyme activities and chemical compositions of some deep-sea pelagic worms, particularly *Nectonemertes mirabilis* (Nemertea; Hoplonemertinea) and *Poebius meseres* (Annelida; Polychaeta), *Deep-Sea Res. Pt. I*, 40, 937–951, 1993.
- Thuesen, E. V., Rutherford, L. D., Brommer, P. L., Garrison, K., Gutowska, M. A., and Towanda, T.: Intralag oxygen promotes hypoxia tolerance of scyphomedusae, *J. Exp. Biol.*, 208, 2475–2482, 2005.
- Tremblay, N., Zenteno-Savín, T., Gómez-Gutiérrez, J., and Maeda-Martínez, A. N.: Migrating to the Oxygen Minimum Layer: Euphausiids, in: *Oxidative Stress in Aquatic Ecosystems*, John Wiley and Sons, Ltd, 89–98, doi:10.1002/9781444345988.ch6, 2011.
- Wiebe, P. and Flierl, G.: Euphausiid invasion/dispersal in Gulf Stream cold-core rings, *Aust. J. Mar. Freshw. Res.*, 34, 625–652, 1983.

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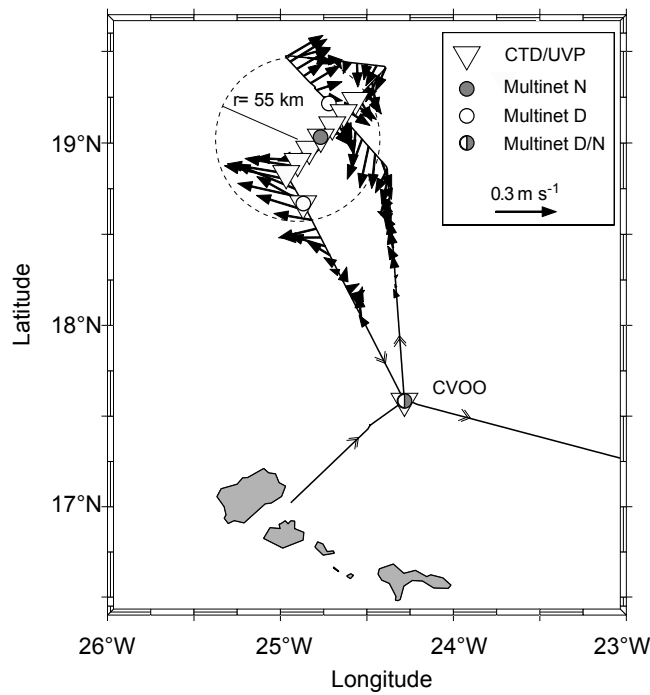


Figure 1. Cruise track (M105, only shown from 17 to 20 March 2014) with horizontal current velocities (arrows) and CTD/UVP sampling positions (triangles) as well as multinet stations (gray circles = night, empty circles = day). Large dashed circle indicates the estimated radius of the eddy based upon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

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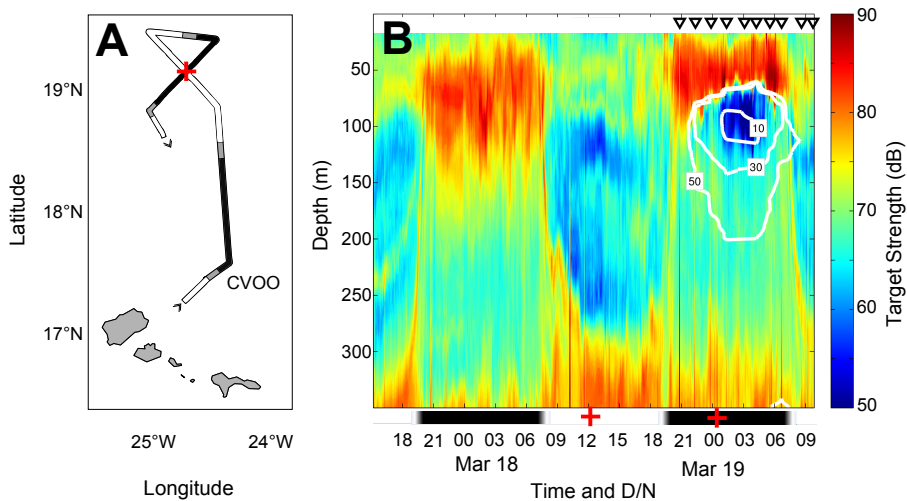


Figure 2. Cruise track with indicated day- and nighttime hours (a, red cross indicates intersection of day- and nighttime section) and Shipboard Acoustic Doppler Current Profiler (ADCP) target strength at 75 kHz (b, red crosses indicate the two profiles obtained at the intersection). White contour lines indicate oxygen concentrations interpolated from CTD profiles (triangles denote CTD stations).

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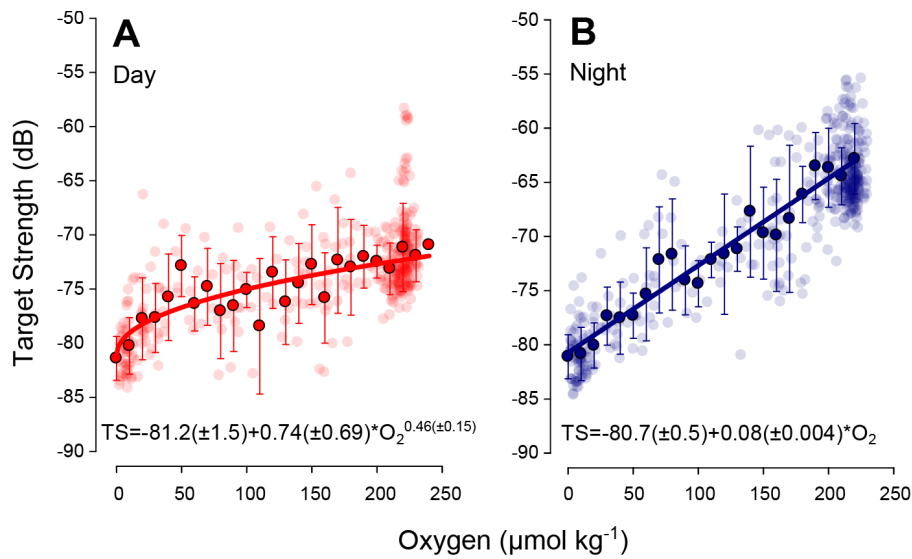
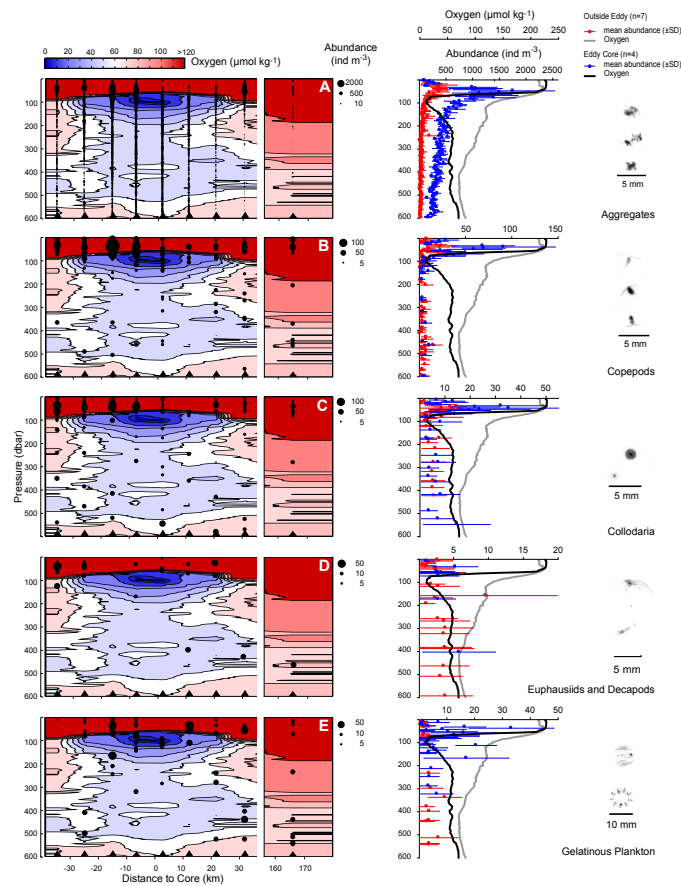


Figure 3. Moored ADCP (300 kHz, matched to depth of moored oxygen sensor) target strength (dB) as a function of oxygen concentration ($\mu\text{mol O}_2 \text{ kg}^{-1}$) during daytime (a) and nighttime hours (b). Higher target strength indicate a higher biomass of zooplankton and nekton. Transparent symbols are 1.5 hourly data, filled symbols are mean values (\pm SD) for $10 \mu\text{mol O}_2 \text{ kg}^{-1}$ bins. Data are from 1 January to 14 March 2010.

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Figure 4. Left column shows oxygen contours ($\mu\text{mol O}_2 \text{kg}^{-1}$) 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**), colpodaria (**c**), "shrimp-like" organisms (euphausiids and decapods, **d**), and gelatinous plankton (**e**). Note break in distance axis on section panels. Triangles denote CTD/UVP stations. Right column are profiles of mean ($\pm\text{SD}$) abundance within the eddy core ($n = 4$) and at the CVOO station ($n = 7$) along with mean oxygen profiles. For better visibility at low values, data with mean abundance = 0 are omitted.

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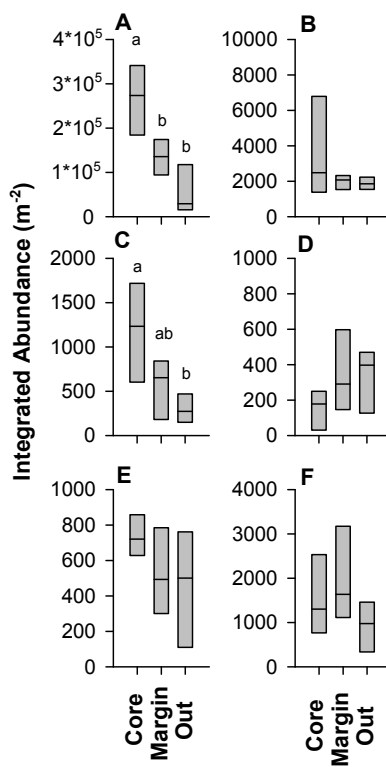
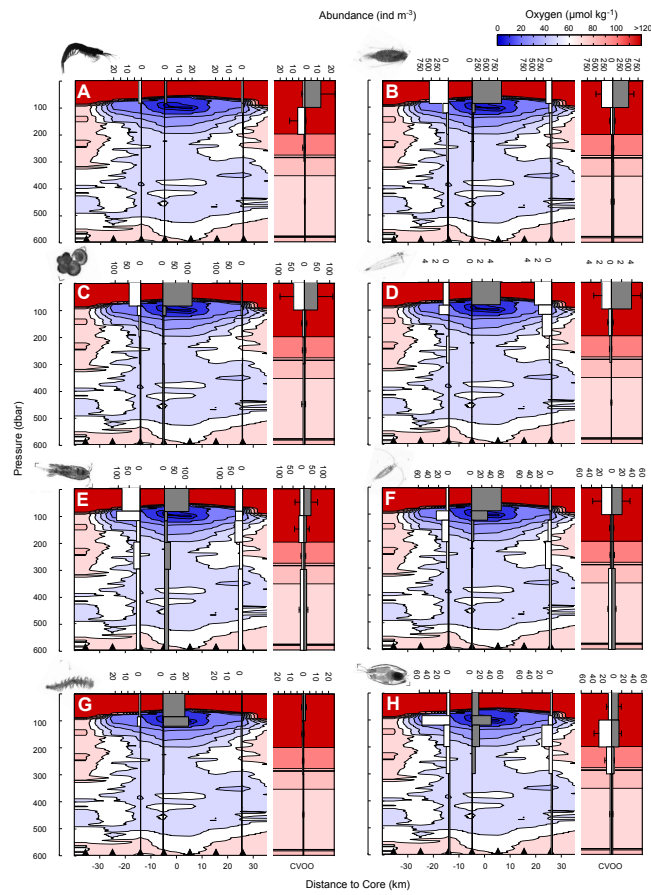


Figure 5. UVP5-derived integrated abundance (m^{-2} , upper 600 m) of large aggregates ($> 500 \mu\text{m}$, **a**), copepods (**b**), gelatinous plankton (**c**), shrimp-like micronekton (euphausiids/decapods, **d**), phaeodaria (**e**) and colpodaria (**f**) in the eddy core ($n = 4$ profiles), eddy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

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Figure 6. Oxygen contours ($\mu\text{mol O}_2 \text{ kg}^{-1}$) 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.

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