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# Environmental factors influencing cold-water coral ecosystems in the oxygen minimum zones on the Angolan and Namibian margins

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## Abstract

Fossil cold-water coral mounds overgrown by sponges and bryozoans were observed in anoxic conditions on the Namibian margin, while mounds colonized by thriving cold-water coral reefs were found in hypoxic conditions on the Angolan margin. These low oxygen conditions do not meet known environmental ranges favoring cold-water corals and hence are expected to provide unsuitable habitats for cold-water coral growth and therefore reef formation. To explain why the living fauna can nevertheless thrive in both areas, present day environmental conditions at the southwestern African margin were assessed. Downslope CTD transects and the deployment of bottom landers were used to investigate spatial and temporal variations of environmental properties. Temporal measurements in the mound areas recorded oscillating low dissolved oxygen concentrations of 0-0.17 ml $l^{-1}$ (≙ 0-9 % saturation) on the Namibian and 0.5-1.5 ml $l^{-1}$ (≙ 7-18 % saturation) on the Angolan margin, which were associated with relatively high temperatures (11.8-13.2°C and 6.4-12.6°C respectively). Semi-diurnal barotrophic tides were found to interact with the margin topography producing internal waves with excursions of up to 70 and 130 m for the Namibian and Angolan margins, respectively. These tidal movements temporarily deliver water with more suitable characteristics to the coral mounds from below and above the hypoxic zone. Concurrently, the delivery of high quantity and quality of suspended particulate organic matter was observed, which serves as a food source for cold-water corals. On the Namibian slope organic matter indicates a completely marine source and originates directly from the surface productive zone, whereas on the Angolan margin the geochemical signature of organic material suggest an additional mechanisms of food supply. A nepheloid layer observed above the cold-water coral mound area on the Angolan margin may constitutes a reservoir of fresh organic matter, facilitating a constant supply of food particles by tidal mixing. This suggests that the cold-water coral communities as well as the associated fauna may compensate unfavorable conditions induced by low oxygen levels and high temperatures with an enhanced availability of food. With the expected expansion of oxygen minimum zones in the future due to anthropogenic activities, this study provides an example on how ecosystems could cope with such extreme environmental conditions.

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# 1. Introduction

Cold-water corals (CWCs) form 3D structures in the deep-sea, providing important habitats for dense aggregations of sessile and mobile organisms ranging from mega- to macrofauna (Henry and Roberts, 2007;van Soest et al., 2007) and fish (Costello et al., 2005). Consequently, CWC areas are considered as deep-sea hotspots of biomass and biodiversity (Buhl-Mortensen et al., 2010;Henry and Roberts, 2017). Moreover, they form hotspots for carbon cycling by transferring carbon from the water column towards associated benthic organisms (Oevelen et al., 2009;White et al., 2012). Some framework-forming scleractinian species, with *Lophelia pertusa* and *Madrepora oculata* being the most common species in the Atlantic Ocean (Freiwald et al., 2004;White et al., 2005;Roberts et al., 2006;Cairns, 2007), are capable of forming large elevated seabed structures, so called coral mounds (Wilson, 1979;Wienberg and Titschack, 2017;Titschack et al., 2015;De Haas et al., 2009). These coral mounds, consisting of coral debris and hemipelagic sediments, commonly reach heights between 20 and 100 m and can be several kilometers in diameter. They are widely distributed along the Atlantic margins, being mainly restricted to water depths between 200-1000 m, while records of single colonies of *L. pertusa* are reported from a broader depth range of 50-4000 m depth (Roberts et al., 2006;Hebbeln et al., 2014;Davies et al., 2008;Mortensen et al., 2001;Freiwald et al., 2004;Freiwald, 2002;Grasmueck et al., 2006;Wheeler et al., 2007).

A global ecological-niche factor analysis by Davies et al. (2008) and Davies and Guinotte (2011), predicting suitable habitats for *L. pertusa,* showed that this species generally thrives in areas which are nutrient-rich, well oxygenated and affected by relatively strong bottom water currents. Other factors potentially important for proliferation of *L. pertusa* include chemical and physical properties of the ambient water masses (aragonite saturation state, salinity, temperature) and water depth (Davies et al., 2008;Dullo et al., 2008;Flögel et al., 2014;Davies and Guinotte, 2011). *L. pertusa* is most commonly found at temperatures between 4-12°C and a very wide salinity range between 32 and 38.8 (Freiwald et al., 2004). Although they occur in such a wide range of temperature and salinity, the link of *L. pertusa* to particular salinity and temperature within the NE Atlantic led Dullo et al. (2008) to suggest that they are restricted to a specific density envelope of sigma-theta (σΘ) = 27.35-27.65 kg $m^{-3}$. In addition, the majority of occurrences of live *L. pertusa* come from sites with dissolved oxygen concentrations ($DO_{conc}$) between 6-6.5 ml $l^{-1}$ (Davies et al., 2008), with lowest recorded oxygen values being 2.1-3.2 ml $l^{-1}$ at CWC sites in the Gulf of Mexico (Davies et al., 2010;Schroeder, 2002;Brooke and Ross, 2014) or even as low as 1-1.5 ml $l^{-1}$ off Mauritania where CWC mounds are in a dormant stage showing only scarce living coral occurrences today (Wienberg et al., 2018;Ramos et al., 2017). Dissolved oxygen levels hence seem to

affect the formation of CWC structures as also shown by Holocene records obtained from the Mediterranean Sea, which revealed periods of reef demise and growth in conjunction with hypoxia (with 2 ml $l^{-1}$ seemingly forming a threshold value for active coral growth; Fink et al., 2012).

Another essential constraint for CWC growth and therefore mound development in a generally food deprived deep-sea is food supply. *L. pertusa* is an opportunistic feeder, exploiting a wide variety of different food sources, including phytodetrius, phytoplankton, mesozooplankton, bacteria and dissolved organic matter (Kiriakoulakis et al., 2005;Dodds et al., 2009;Gori et al., 2014;Mueller et al., 2014;Duineveld et al., 2007). Transport of surface organic matter towards CWC sites at intermediate depths has been found to involve either active swimming (zooplankton), passive sinking, advection, local downwelling, and internal waves and associated mixing processes resulting from interactions with topography (Davies et al., 2009;van Haren et al., 2014;Thiem et al., 2006;White et al., 2005;Mienis et al., 2009;Frederiksen et al., 1992). Not only quantity but also quality of food particles is of crucial importance for the uptake efficiency as well as ecosystem functioning of CWCs (Ruhl, 2008;Mueller et al., 2014).

With worldwide efforts to map CWC communities, *L. pertusa* has also been found under conditions which seem environmentally stressful or extreme in the sense of the global limits defined by Davies et al. (2008) and Davies and Guinotte (2011). Examples are the warm and salty waters of the Mediterranean and the high temperature variations along the US coast (Cape Lookout; Freiwald et al., 2009;Mienis et al., 2014;Taviani et al., 2005). Environmental stress generally increases energy needs for organisms to recover and maintain optimal functioning, which accordingly increases their food demand (Sokolova et al., 2012). For the SW African margin one of the few records of living CWC come from the Angolan margin (at 7°; Le Guilloux et al., 2009), which raises the question whether local environmental factors limit CWC growth due to the presence of an Oxygen Minimum Zone (OMZ; see Karstensen et al. 2008), or data is lacking. Hydroacoustic campaigns nevertheless revealed extended areas off Angola and Namibia with structures that morphologically resemble coral mounds structures known from the NE Atlantic (M76-3, MSM20-1; Geissler et al., 2013;Zabel et al., 2012).

Two such mound areas on the margins off Namibia and Angola were visited during the RV *Meteor* cruise M122 'ANNA' (ANgola/NAmibia) cruise in January 2016 (Hebbeln et al., 2017). During this cruise fossil CWC mound structures were observed near Namibia, while flourishing CWC reef covered mound structures were observed on the Angolan margin. The aim of the present study was to assess present-day environmental conditions at the southwestern African margin that enable cold-water coral growth

in this low oxygen environment. To identify key parameters influencing CWC growth and therefore mound development, hydrographic parameters as well as chemical properties of the water column were measured, characterizing environmental conditions and food supply. These data are used to provide new insights in susceptibility of CWCs towards extreme oxygen limited environments, in order to improve understanding of the fate of CWC mounds in a changing ocean.

# 2. Material and Methods

## *2.1 Setting*

### *2.1.1 Oceanographic setting*

The SW African margin is one of the four major eastern boundary regions in the world and is characterized by upwelling of nutrient-rich cold waters (Shannon and Nelson, 1996). The availability of nutrients triggers a high primary production, making it one of the most productive marine areas worldwide with an estimated production of 0.37 Gt C/yr (Carr and Kearns, 2003). Remineralization of high fluxes of organic particles settling through the water column result in severe mid-depth oxygen depletion and an intense OMZ over large areas along the SW African margin (Chapman and Shannon, 1985). The extension of the OMZs is highly dynamic being controlled by upwelling intensity which depends on the prevailing winds and two current systems along the SW African margin, i.e. the Benguela and the Angola currents (Kostianoy and Lutjeharms, 1999;Chapman and Shannon, 1987; Fig. 1). The Benguela Current originates from the South Atlantic Current, which mixes with water from the Indian Ocean at the southern tip of Africa (Poole and Tomczak, 1999;Mohrholz et al., 2008;Rae, 2005) and introduces relatively cold and oxygen-rich Eastern South Atlantic Central Water (ESACW; Poole and Tomczak 1999) to the SW African margin (Mohrholz et al., 2014). The Angola Current originates from the South Equatorial Counter Current and introduces warmer, nutrient-poor and less oxygenated South Atlantic Central Water (SACW; Poole and Tomczak 1999) to the continental margin (Fig. 1a). While the SACW flows along the continental margin the oxygen concentration is decreasing continuously due to remineralisation processes on the SW African shelf (Mohrholz et al., 2008). Both currents converge at around 14-16 °S, resulting in the Angola-Benguela Front (Lutjeharms and Stockton, 1987). In austral summer, the Angola-Benguela Front can move southward to 23 °S (Shannon et al., 1986), thus increasing the influence of the SACW along the Namibian coast (Junker et al., 2017;Chapman and Shannon, 1987), contributing to the pronounced OMZ due to its low initial oxygen concentration (Poole and Tomczak, 1999). ESACW is the dominant water mass at the Namibian margin during the main

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upwelling season in austral winter, expanding from the oceanic zone about 350 km offshore, further inshore. (Mohrholz et al., 2014).

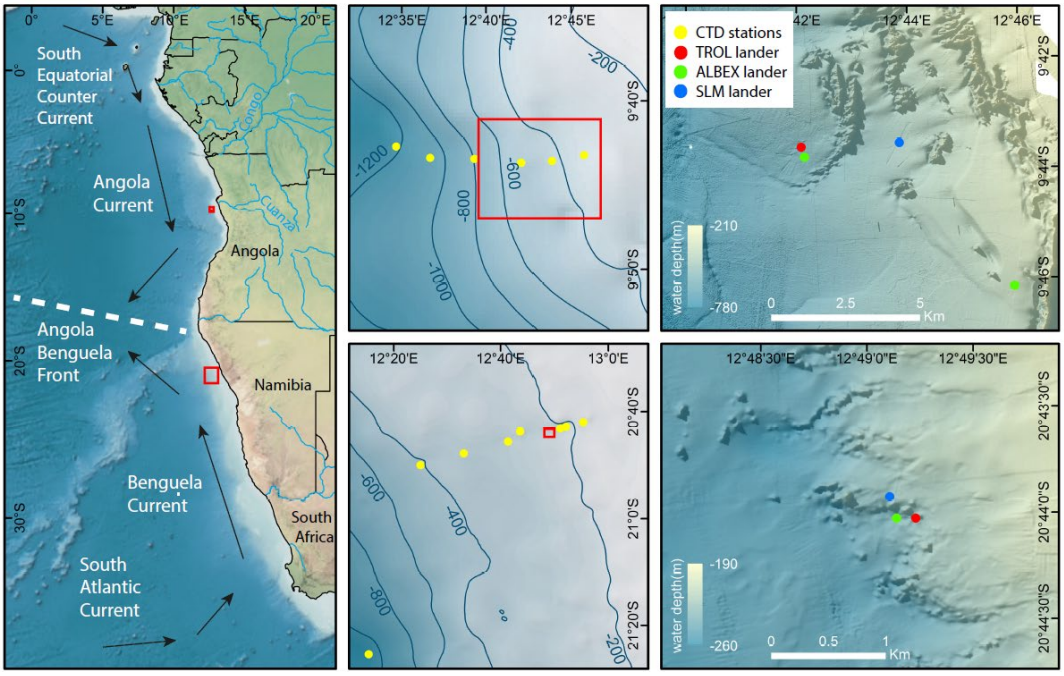


**Figure 1** (a) Overview map showing the research areas off Angola and Namibia (red squares) and main features of the surface water circulation (arrows) and frontal zone (dashed line) in the SE Atlantic as well as the two main rivers discharging at the Angolan margin. Detailed bathymetry maps of the Angolan (upper maps) and Namibian margins (lower maps) showing the position of (b) CTD transects (note the deep CTD cast down to 1000 m water depth conducted off Namibia) and (c) bottom lander deployments (red squares shown in (b) indicate the cutouts displayed in (c)).

### *2.1.2. Coral mound provinces along the Angolan and Namibian margins*

During RV *Meteor* cruise M122 in 2016, over 2000 coral mounds were observed between 160-260 m water depth on the Namibian shelf (Hebbeln et al., 2017). All mounds were densely covered with coral rubble and dead coral framework (entirely consisting of *L. pertusa*), while no living corals were observed in the study area (Hebbeln et al., 2017; Figs. 2a, b). Few species were locally very abundant, viz. a yellow cheilostome bryozoan which was the most common species, and five sponge species. The bryozoans were encrusting the coral rubble, whereas some sponge species reached heights of up to 30 cm (Fig. 2a, b). The remaining CWC community consisted of an impoverished fauna overgrowing *L. pertusa* debris. Commonly found sessile organism were actiniarians, zoanthids, hydroids, some thin encrusting sponges, serpulids and sabellid polychaetes. The mobile fauna comprised asteroids, ophiuroids, two shrimp



species, amphipods, cumaceans and holothurians. Locally high abundances of *Suffogobius bibarbatus*, a fish that is known to be adapted to hypoxic conditions, were observed in cavities underneath the coral framework (Hebbeln, 2017). Corals collected from the surface of various Namibian mounds date back to about 5 ka BP, pointing to a simultaneous demise of these mounds during the mid-Holocene (Tamborrino et al., sumbitted).

On the Angolan margin CWC structures varied from individual mounds to long ridges. Some mounds reached heights of more than 100 m above the seafloor. At shallow depths (~250 m) also some isolated smaller mounds are present (Hebbeln et al. 2017). All mounds showed thriving CWC cover, which was dominated by *L. pertusa* (estimated 99% relative abundance), *M. oculata* and solitary corals. Mounds with a flourishing coral cover were mainly situated at water depths between 330-470 m, whereas single colonies were found over an even broader depth range between 250-500 m (Figs. 2c, d; Hebbeln et al., 2017). Additionally to CWCs, large aggregations of hexactinellid sponges (*Aphrocallistes, Sympagella*) were observed. The scattered small mounds at shallower water depths were dominated by sponges and only sparsely covered with living coral. In these areas, active suspension feeders, like sponges were most commonly observed. First estimates for coral ages obtained from a gravity core records collected at one of the Angolan coral mounds revealed continuous coral mound formation during the last 34 ka until today (Wefing et al., 2017).

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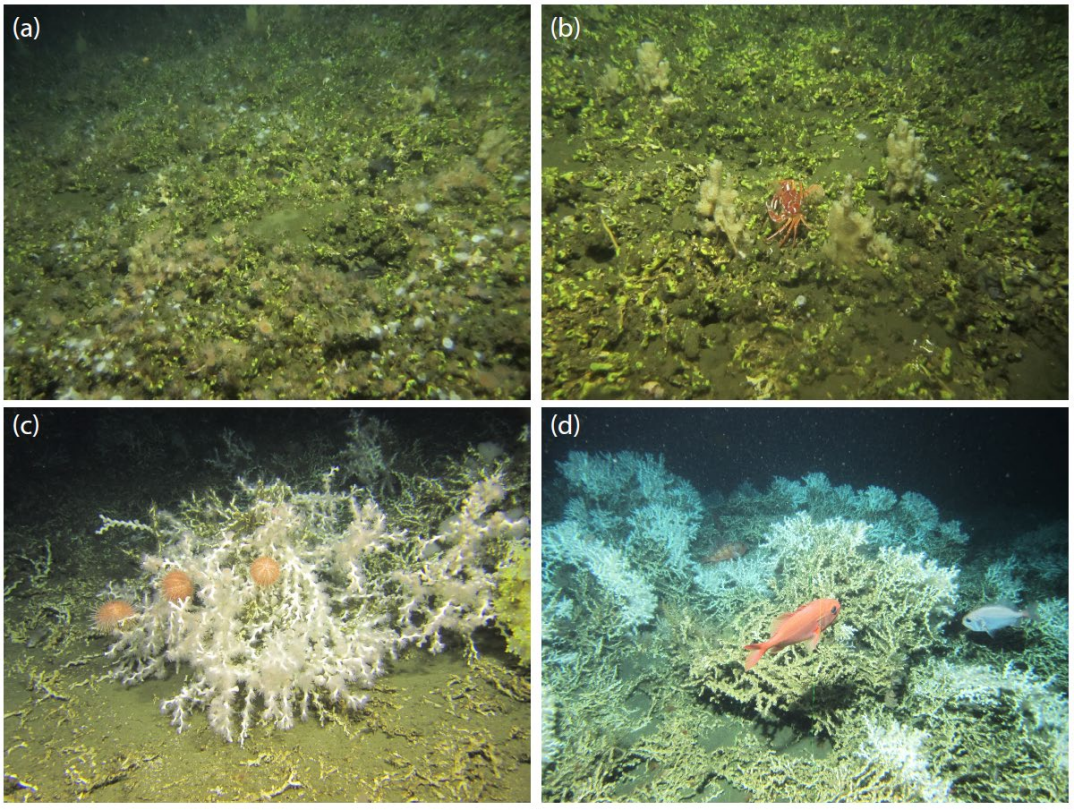


**Figure 2** ROV images (copyright MARUM ROV SQUID, Bremen, Germany) showing the surface coverage of cold-water coral mounds discovered off Namibia (a, b) and Angola (c, d). Images were recorded and briefly described for their faunal composition during RV *Meteor* cruise M122 "ANNA" (see Hebbeln et al. 2017). (a) Sylvester mound, 225 m water depth. Dead coral framework entirely consisting of *Lophelia pertusa*. The framework is intensely colonized by the yellow bryozoan *Metropriella* sp., zoanthids, actiniarians and sponges. Vagile fauna consists of asteroids and gobiid fishes (*Sufflogobius bibarbatus*) that hide between hollows underneath the coral framework. (b) Sylvester mound, 238 m water depth. Dense coral rubble (*L. pertusa*) heavily overgrown by *Metropriella* sp. and sponges. Note the decapod crab *Macropipus australis* (center of the image). (c) Valentine mound, 238 m water depth. Live *Lophelia* colony being grazed by echinoids. Note the sponge *Aphrocallistes* sp. with its actiniarian symbionts (right side of the image). (d) Buffalo mound, 345 m water depth. Living CWC reef observed on top of an Angolan coral mound. Many fishes are present around the reef (*Helicolenus dactylopterus*, *Gephyroberyx darwinii*).

## *2.2 Methodology*

During RV *Meteor* expedition M122 in January 2016, two CTD transects and five short-term bottom lander deployments (Table 1, Fig. 1) were carried out to measure near-bed environmental conditions

potentially influencing benthic habitats. In addition, weather data were continuously recorded by the RV *Meteor* weather station, providing real-time information on local wind speed and wind direction.

### *2.2.1 Lander deployments*

Sites for deployment of the NIOZ designed landers (ALBEX and TROL) were selected based on multibeam bathymetric data. In each area, two landers were deployed simultaneously. On the Namibian margin one lander was deployed on top of a mound structure (water depth 220 m), while the other lander was deployed in close vicinity but off-mound (Fig. 1, Table 1). As both landers show similar trends for all measured physical properties, only the dataset recorded by the ALBEX lander is presented here (see Table 1). Off Angola, mounds with live corals were observed over a large depth zone (250-500 m). To obtain as much information as possible over the entire mound zone, one lander (ALBEX) was first deployed in the relatively shallow part of the mound zone at 340 m water depth, and after retrieval redeployed in the deeper part of the zone at 530 m. A second lander (TROL) was deployed at the deeper part of the zone (530 m) for the full time period (Fig. 1, Table 1). Since the records of the ALBEX and TROL landers obtained during the simultaneous deployment at the deep mound site (~530 m) did not show significant differences, only the data of the ALBEX lander are here presented (Table 1). These data are compared with ALBEX lander data obtained during its deployment in the shallow part of the mound zone at ~340 m (Table 1). Deployment times varied from 2.5 to 8 days (Table 1).

Both, the ALBEX and TROL lander consist of an aluminum tripod for this experiment equipped with 13 glass benthos floats, two IXSEA acoustic releasers and a single 260 kg ballast weight. Oceanographic data were obtained by different sensors: an ARO-USB oxygen sensor (JFE-Advantech™) which also recorded temperature, a combined OBS-fluorometer (Wetlabs™) and an Aquadopp (Nortek™) profiling current meter. The ALBEX lander was furthermore equipped with a Technicap PPS4/3 sediment trap with 12 bottles (allowing daily samples) and a McLane particle pump (24 filter units for each 7.5 L of seawater, two hour interval) to sample particulate organic matter in the near-bottom water (40 cm above bottom).

Additionally, a GEOMAR Satellite Lander Module (SLM) was deployed off-mound close to the NIOZ landers (Fig. 1, Table1). The SLM was equipped with a 600 kHz ADCP Workhorse Sentinel 600 from RDI, a CTD (SBE SBE16V2™), a combined fluorescence and turbidity sensor (WET Labs ECO-AFL/FL), a dissolved oxygen sensor (SBE™) and a pH sensor (SBE™) (Hebbeln et al., 2017). From the SLM only pH measurements are used here, complementing the data from the NIOZ landers.



### *2.2.2 CTD transects*

Vertical profiles of principal hydrographic parameters in the watercolumn, viz. temperature, conductivity, oxygen and turbidity, were obtained using a Seabird CTD/Rosette system (Seabird SBE 9 plus). The additional sensors on the CTD were a dissolved oxygen sensor (SBE 43 membrane-type DO Sensor) and a combined fluorescence and turbidity sensor (WET Labs ECO-AFL/FL). The CTD was combined with a rosette water sampler consisting of 24 Niskin® water sampling bottles (10 L) that were electronically triggered to close at given depths during the up-cast. CTD casts were carried out along two downslope CTD transects (Fig. 1). Off Angola, the downslope transect covered a distance of 20 km reaching down to a depth of 800 m, whereas the main transect in Namibia covered a distance of 60 km and maximum depth of 400 m. In order to measure deeper water masses, one deep CTD cast was conducted at a distance of about 130 km from the shallowest CTD, going down to about 1000 m depth (Figs. 1 and 3).

### *2.2.3 Hydrographic data processing*

The CTD dataset was processed using the processing software Seabird data SBE 11plus V 5.2 and data were visualized using the program Ocean Data View (Schlitzer 2011; Version 4.7.8). Turbidity data were only collected on the Angolan slope.

Hydrographic data recorded by the CTD and landers were analyzed and plotted using the program R (Team, 2017). Data from the different instruments (temperature, turbidity, current speed, oxygen concentration, fluorescence) were averaged over a period of 1.5 h to remove shorter tem trends and occasional spikes. Correlations between variables were assessed by Spearman's rank correlation tests.

### *2.2.4 Suspended particulate matter*

With each upcast of the CTD/Rosette, water samples were taken as close to the seabed as possible, at mid-water depth, and in the chlorophyll-maximum. From each depth, two 5 L water samples were subsequently filtered over pre-combusted (450 °C) and pre-weighted GF/F filters (47 mm, Whatman™). Filters were stored at -20 °C until further analysis at the NIOZ.

Near-bottom suspended particulate organic matter (SPOM) was additionally sampled by means of a phytoplankton sampler (McLane PPS) mounted on the ALBEX lander. The PPS was fitted with 24 GF/F filters (47 mm Whatman™ GF/F filters pre-combusted at 450 °C). A maximum of 7.5 L was pumped over each filter during a 2h period yielding a time series of near bottom SPOM supply and its variability over a period of 48 hours.

*C/N analysis and isotope measurements*

Filters from the in situ pump and sampled from the CTD/Rosette were freeze-dried before further analysis. Half of each filter was used for phytopigment analysis and a ¼ section of each filter was used for analyzing organic carbon, nitrogen, and their stable isotope ratios. The filters, used for carbon analysis, were decarbonized by vapor of concentrated hydrochloric acid (2 M HCl supra) prior to analyses. Filters were transferred into pressed tin capsules (12x5 mm, Elemental Microanalysis) and $\delta^{15}N$, $\delta^{13}C$ and total weight percent of organic carbon and nitrogen were analyzed by a Delta V Advantage isotope ratio MS coupled on line to an Elemental Analyzer (Flash 2000 EA-IRMS) by a Conflo IV (Thermo Fisher Scientific Inc.). The used reference gas was purified atmospheric $N_2$. As a standard for $\delta^{13}C$ benzoic acid and acetanilide was used, for $\delta^{15}N$ acetanilide, urea and casein was used. For $\delta^{13}C$ analysis a high signal method was exercised including a 70% dilution. Values are reported relative to v-pdb and the atmosphere respectively. Precision and accuracy based on replicate analyses and comparing international standards for $\delta^{13}C$ and $\delta^{15}N$ was ± 0.15 ‰. The C/N ratio is based on the weight ratios between TOC and N.

*Phytopigments*

Phytopigments were measured by reverse-phase high-performance liquid chromatography (RP-HPLC) with a gradient based on the method published by (Kraay et al., 1992). For each sample half of a GF/F filter was used and freeze-dried before extraction. Pigments were extracted using 95% methanol and sonification. All steps were performed in a dark and cooled environment. Pigments were identified by means of their absorption spectrum, fluorescence and the elution time. Identification and quantification took place as described by Tahey et al. (1994). The absorbance peak areas of chlorophyll-α were converted into concentrations using conversion factors determined with a certified standard. The ∑Phaeopigment/ Chlorophyll-α ratio gives an indication about the degradation status of the organic material, since phaeopigments form as a result of bacterial or autolytic cell lysis and grazing activity (Welschmeyer and Lorenzen, 1985).

*2.2.5 Tidal analysis*

The barotropic (due to the sea level and pressure change) and baroclinic (internal „free waves“ propagating along the pycnoclines) tidal signals obtained by the Aquadopp (Nortek™) profiling current meter were analysed from the bottom pressure and from the horizontal flow components recorded 6 m above the sea floor, usinf the harmonic analysis toolbox t_tide (Pawlowicz et al., 2002). The data mean and trends were subtracted from the data before analysis.

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# 3. Results

## *3.1 Namibian margin*

### *3.1.1 Water column properties off Namibia*

The hydrographic data obtained by CTD measurements along a downslope transect from the surface to 1000 m water depth revealed distinct changes in temperature and salinity through the water column. These are ascribed to the different water masses in the study area (Fig. 3a). In the upper 85 m of the water column, temperatures are above 14°C and salinities are > 35.2, which corresponds to South Atlantic Subtropical Surface Water (SASSW). SACW is situated underneath the SASSW and reaches down to about 700 m. SCAW is defined by a linear relationship between temperature and salinity in the TS-plot (Shannon et al., 1987). The temperature in the layer of SCAW decreases from 14 to 7°C with depth and the salinity from 35.4 to 34.5 (Fig. 3a). The deep CTD cast about 130 km from the coastline recorded a water mass with the signature of ESACW, having a lower temperature (-1.3°C) and lower salinity (-0.2 PSU) than SACW (in 200 m depth, not included in CTD transects of Fig. 4). Underneath these two central water masses Antarctic Intermediate Water (AAIW) was found with a temperature <7°C.

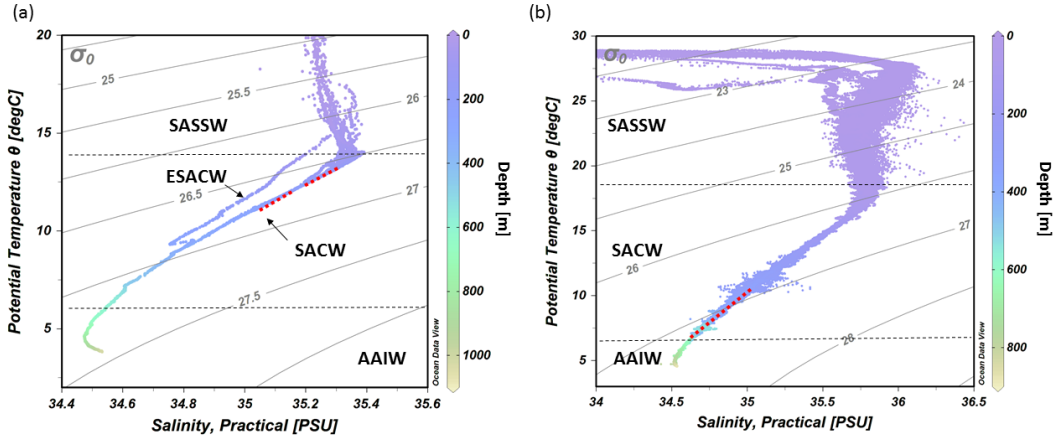


**Figure 3** TS-diagrams showing the different water masses being present at the (a) Namibian and (b) Angolan margins: South Atlantic Subtropical Surface Water (SASSW), South Atlantic Central Water (SACW) and Eastern South Atlantic Central water (ESACW), Antarctic Intermediate Water (AAIW) (data plotted using Ocean Data View v.4.7.8; http://odv.awi.de; Schlitzer, 2011). Red dotted line indicates the depth range of cold-water coral mound occurrence.

The CTD transect showed decreasing $DO_{conc}$ from the surface (6 ml $l^{-1}$) towards a minimum in 150-200 m depth (0 ml $l^{-1}$). Lowest values for $DO_{conc}$ were found on the continental margin between 100-335 m water depth. The $DO_{conc}$ in this pronounced OMZ ranged from <1 ml $l^{-1}$ down to 0 ml $l^{-1}$ (≙ 9-0 %

saturation, respectively). The zone of low $DO_{conc}$ (<1 ml $l^{-1}$) was stretching horizontally over the complete transect towards at least 100 km offshore (Fig. 4c). The upper boundary of the OMZ was relatively sharp compared to its lower limits and corresponds with the border between SASSW at the surface and SACW below.

Within the OMZ, a small increase in fluorescence (0.2 mg $m^{-3}$) was recorded, whereas fluorescence was otherwise not traceable below the surface layer (Fig. 4d). Within the surface layer highest surface fluorescence (>2 mg $m^{-3}$) was found ~40 km offshore. Above the center of the OMZ fluorescence reached only up to 0.4 mg $m^{-3}$.

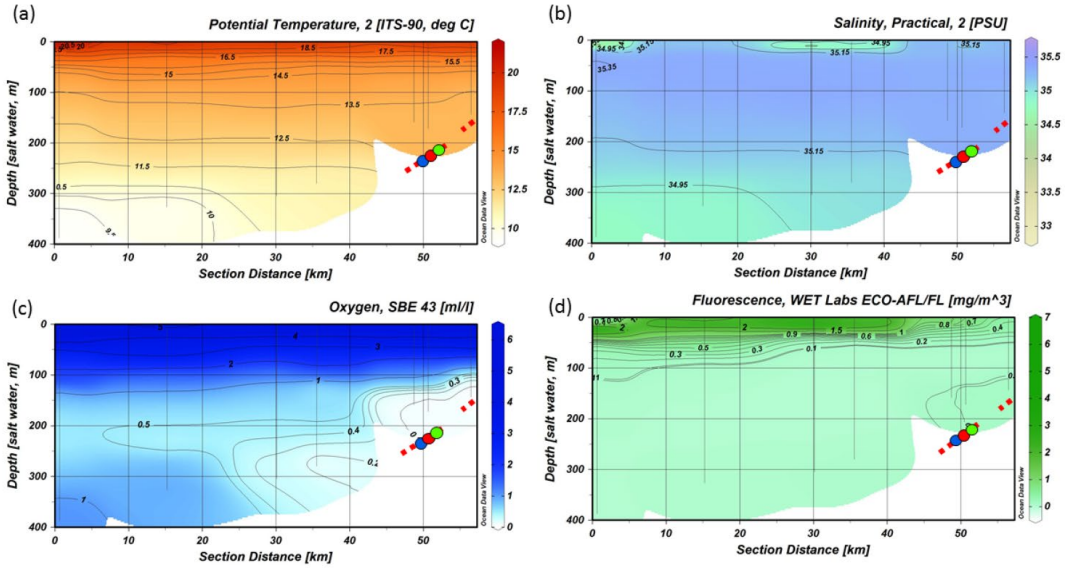


**Figure 4** CTD transect across the Namibian margin. Shown are data for: (a) potential temperature (°C),( b) salinity (PSU), (c) dissolved oxygen concentrations (ml $l^{-1}$), note the pronounced oxygen minimum zone (OMZ) between 100-335 m water depth, and d) fluorescence (mg $m^{-3}$) (data plotted using Ocean Data View v.4.7.8; http://odv.awi.de; Schlitzer, 2011). The occurrence of fossil CWC mounds is indicated by a red dashed line, colored dots indicate bottom lander deployments.

### *3.1.2 Lander time-series of physical data*

Bottom temperature ranged from 11.8 to 13.2°C during the deployment of the ALBEX lander (Table 1) showing oscillating fluctuations with a maximum semidiurnal (Δt ~ 6h) change of ~1°C (on 9.1.2018). The $DO_{conc}$ fluctuated between 0-0.15 ml $l^{-1}$ and was negatively correlated with temperature (r=-0.39, p<0.01). Fluorescence ranged from 42 to 45 NTU during the deployment and was positively correlated with temperature (r=0.38, p<0.01). Hence, both temperature and fluorescence were negatively

correlated with oxygen concentration (r=-0.39, p<0.01) and also with turbidity (optical backscatter, r=-0.35, p<0.01). Turbidity was relatively low until it increased especially during the second half of the deployment, when wind speeds increased and also the current direction changed. The maximum current speeds measured during the deployment period were 0.21 m $s^{-1}$, with average current speeds of 0.09 m $s^{-1}$ (Table 2). The tidal cycle explains >80 % of the pressure fluctuations (Table 2), with a semidiurnal signal, M2, generating an amplitude of >0.35 dbar and thus being the most important constituent. Before the 6$^{th}$ of January the current direction oscillated between SW and SE where after it changed into a dominating northern current direction. The current speed remained rather constant during the deployment period (Fig. 5). The wind speed, on the other hand, increased from 10 m $s^{-1}$ to a maximum of 17 m $s^{-1}$ on the sixth of January and remained high for the next six days. Wind direction changed from anticlockwise cyclonic rotation towards alongshore winds. The water current direction returned to SW-SE after the period of strong wind (not shown). During the strong wind period, colder water (correlation between wind speed and water temperature, r=-0.55, p<0.01), with a higher turbidity (correlation of wind speed and turbidity, r=0.42, p<0.01) and higher $DO_{conc}$ was present. The SLM lander recorded an average pH of 8.01.

The observed fluctuations in bottom water temperature at the deployment site imply a vertical tidal movement of around 70 m. This was calculated by comparing the temperature change recorded by the lander to the respective temperature-depth gradient based on water column measurements (CTD site GeoB20553, 12.58 °C at 245 m, 12.93°C at 179 m). Due to these vertical tidal movements, the oxygen depleted water from the core of the OMZ is regularly being replaced with somewhat colder and slightly more oxygenated water (up to 0.2 ml $l^{-1}$).

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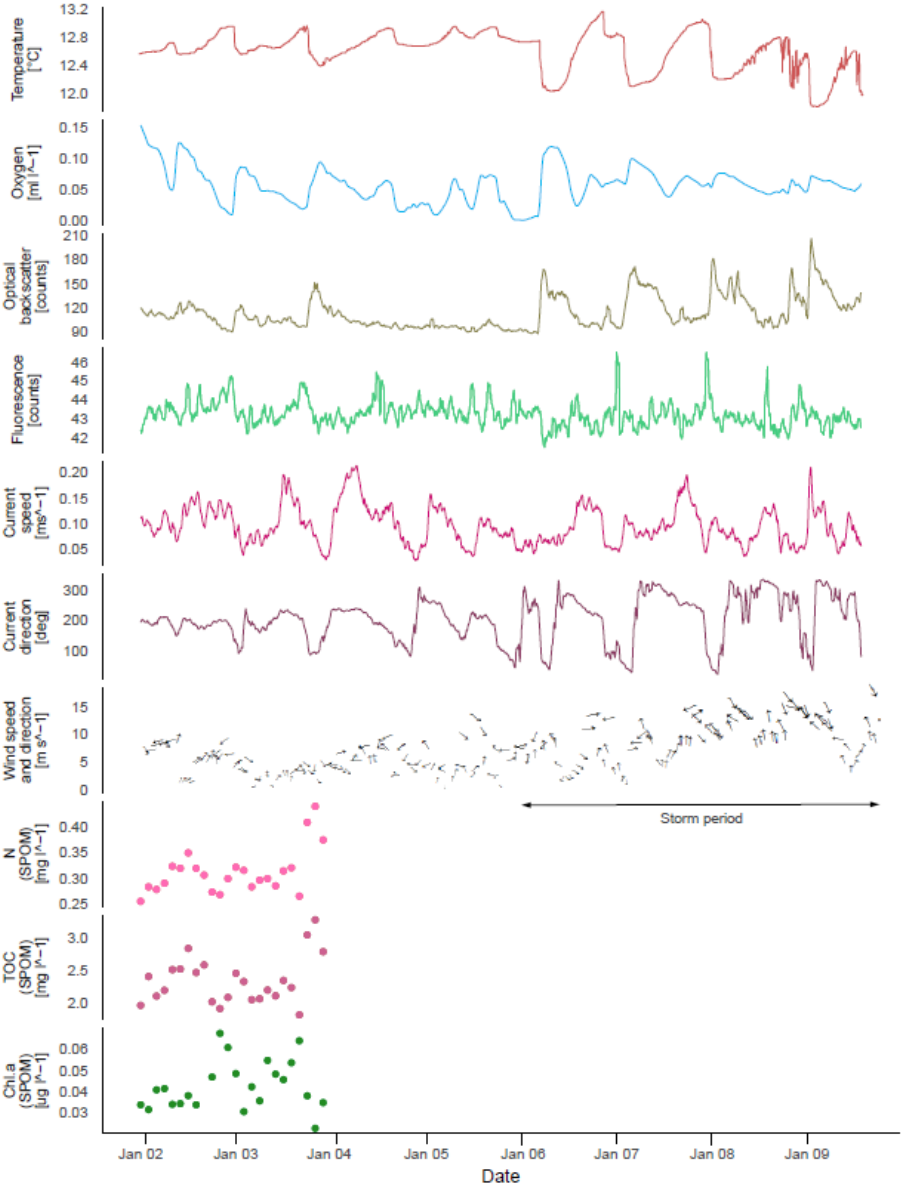


348

349 **Figure 5** Data recorded by the ALBEX lander (210 m) at the Namibian margin in January 2016. Shown are data for temperature
350 (°C; red), dissolved oxygen concentrations (ml $l^{-1}$; blue), optical backscatter (turbidity; moss green), fluorescence (counts per
351 second green), current speed (m $s^{-1}$; pink), current direction (degree: 0-360°; dark red) as well as nitrogen (mg $l^{-1}$; pink dots),
352 carbon (mg $l^{-1}$; purple dots), and chlorophyll-α concentration (µg $l^{-1}$, green dots) of SPOM collected during the first 48h by the
353 McLane pump. These data are supplemented by wind speed and direction (small black arrows) recorded concurrently to the
354 lander deployment by ship bound devices. Note that current directions changed from a generally south-poleward to an
355 equatorward direction when wind speed exceeded 10 m $s^{-1}$ (stormy period indicated by black arrow).

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### *3.1.3 Food supply*

The nitrogen (N) concentration of the SPOM measured on the filters of the ALBEX lander McLane pump fluctuated between 0.25 and 0.45 mg $l^{-1}$ (Fig 5). The highest N concentration corresponded with a peak in turbidity (r=0.42, p<0.01). The $\delta^{15}N$ values of the lander time series fluctuated between 5.1 and 6.9 with an average value of 5.7 ‰. Total Organic Carbon (TOC) showed a similar pattern as nitrogen, with relative concentrations ranging between 1.8-3.5 mg $l^{-1}$. The $\delta^{13}C$ value of the TOC increased during the surveyed time period from -22.39 to -21.24‰ with an average of -21.7 ‰ (Fig. 6a). The C/N ratio ranged from 8.5 to 6.8 and was on average 7.4 (Fig. 6b). During periods of low temperature and more turbid conditions TOC and N as well as the $\delta^{13}C$ values of the SPOM were higher.

Chlorophyll-α concentrations in the SPOM collected with the lander in situ pump were on average 0.042 µg $l^{-1}$ and correlated with the record of the fluorescence sensor on the Seabird CTD (r=0.43, p=0.04). A six times higher amount of chlorophyll-α degradation products were found during the lander deployment (0.248 µg $l^{-1}$) compared to the amount of chlorophyll-α, giving a ∑Phaeopigment/ Chlorophyll-α ratio of 6.5 (not shown). Additionally, carotenoids (0.08-0.12 µg $l^{-1}$) and fucoxanthin (0.22 µg $l^{-1}$) were found as major components of the pigment fraction, which are common in diatoms. Zeaxanthin, indicating the presence of prokaryotic cyanobacteria, was only observed in small quantities in the SPM (0.066 µg $l^{-1}$).

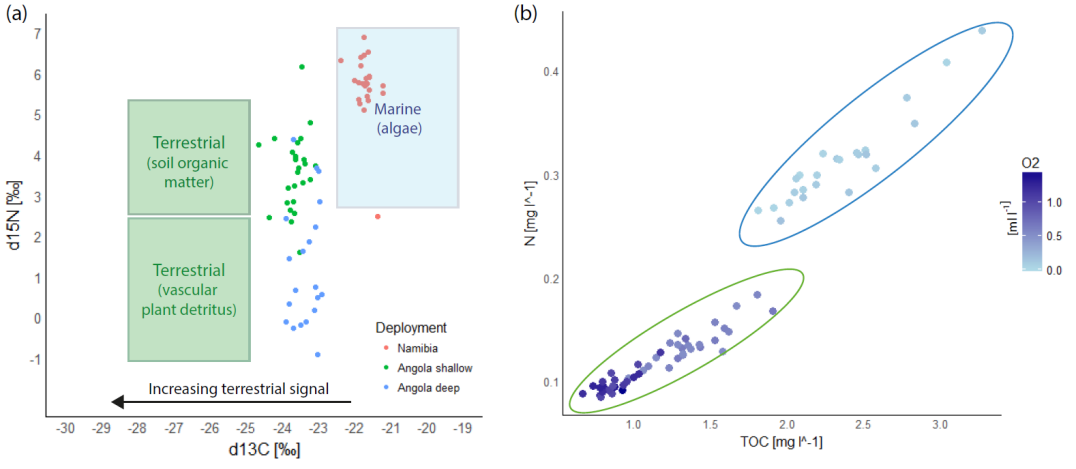


**Figure 6** Composite records of SPOM collected by the McLane pump of the ALBEX lander at the Namibian and Angolan margins during all three deployments. (a) δ15N and δ13C isotopic values at the Namibian (red dots) and Angolan (blue and green dots) margins. Indicated by the square boxes are common isotopic values of terrestrial and marine organic matter (Boutton 1991, Holmes et al. 1997, Sigman et al. 2009). The relative contribution of terrestrial material (green boxes) is increasing with a more

negative δ13C value. (b) Total organic carbon (TOC) and nitrogen (N) concentration of the SPOM. Values of the Namibian margin are marked by a blue circle (C/N ratio = 7.8), values of the Angolan margin are marked by a green circle (C/N ratio = 9.6). Dissolved oxygen concentrations are included to show the higher nutrient concentrations in less oxygenated water.

## 3.2 Angolan margin

### 3.2.1 Water column properties

The hydrographic data obtained by CTD measurements along a downslope transect from the surface to 800 m water depth revealed distinct changes in temperature and salinity throughout the water column, related to four different water masses. At the surface a distinct shallow layer (>20 m) with a distinctly lower salinity (27.3-35.5) and higher temperature (29.5-27 °C, Fig. 3b) was observed. Below the surface layer, SASSW was recognized down to a depth of 70 m, characterized by a higher salinity (35.8). SACW was observed between 70-600 m, featuring the expected linear relationship between temperature and salinity. Temperature and salinity decreased from 17.5°C/35.8 to 7°C/34.6. At 700 m depth AAIW was recorded, characterized by a low salinity (<34.4) and temperature (<7°C, Fig. 3b).

The CTD transect shows a sharp decrease in the $DO_{conc}$ underneath the SASSW from 5 to <2 ml $l^{-1}$ (Fig. 7). $DO_{conc}$ was further decreasing until a minimum of 0.6 ml $l^{-1}$ at 350 m and subsequently increasing to >3 ml $l^{-1}$ at 800 m depth. Lowest $DO_{conc}$ were not found at the slope but 70 km offshore in the center of the zone of reduced $DO_{conc}$ between 200-450 m water depth (<1 ml $l^{-1}$). Compared to the Namibian margin (see Fig. 4), the hypoxic layer was hence situated further offshore, slightly deeper and overall $DO_{conc}$ were higher (compare Fig. 4c). Also, the boundaries of the hypoxic zone were not as sharp. Salinity underneath the surface layer decreased linearly from 35.75 to 34.5 in 800 m and did not show any specific features likewise as the temperature which decreased from 16 to 5°C. Fluorescence near the sea surface was generally low (around 0.2 with small maxima of 0.78 mg $m^{-3}$) and not detectable deeper than 150 m depth. The OBS signal showed a distinct zone of enhanced turbidity on the continental margin between 200-350 m water depth.

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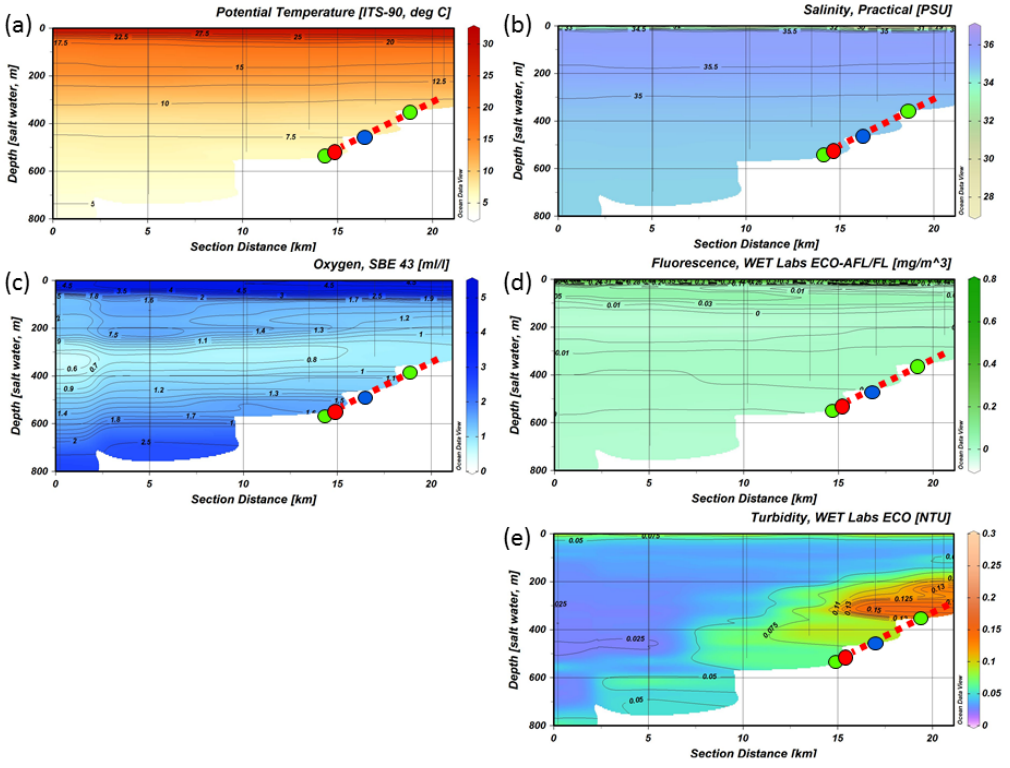


**Figure 7** CTD transect across the Angolan margin. Shown are data for (a) potential temperature (°C), (b) salinity (PSU), (c) dissolved oxygen concentration (ml $l^{-1}$), (d) fluorescence (mg $m^{-3}$), (e) turbidity (NTU) (data plotted using Ocean Data View v.4.7.8; http://odv.awi.de; Schlitzer, 2011). The depth occurrence of CWC mounds is marked by a red, dashed line, the lander deployments are indicated by colored dots.

### *3.2.2 Lander time series physical data*

Mean bottom water temperatures varied from the deepest to the shallowest site between 6.73-10.06 °C (Fig. 8). The maximum semidiurnal (Δt ~ 6h) temperature change varied between 0.82 to 1.60 °C at the deepest and shallowest site respectively. At the shallow site, the maximum short-term temperature change was 2.4 °C (Fig. 8). $DO_{conc}$ at the deep site were a factor of two higher than those at the shallow site, i.e. 0.9-1.5 *vs*. 0.5-0.8 ml $l^{-1}$respectively (≙ range between 4-14% saturation of both sites), where also the range of diurnal fluctuations was much smaller compared to the shallow site. $DO_{conc}$ were negatively correlated with temperature at the deep site ($r=-0.99$, $p<0.01$) while positively correlated at the shallow site ($r=0.91$, $p<0.01$). Fluorescence was overall low during both deployments and showed only small fluctuations whereas it was slightly higher at the shallow site (between 38.5 and 41.5 NTU at both sites). Current speeds were relatively high (between 0–0.3 m $s^{-1}$, average 0.1 m $s^{-1}$) and positively

correlated with temperature at the shallow site (r=0.31, p<0.01) and negatively correlated at the deep site (r=-0.22, p<0.01). Analysis of the tidal cycle showed, that it explains 29.8-54.9% of the horizontal current fluctuations. The M2 (principal lunar semi-diurnal) amplitude was 0.06-0.09 m $s^{-1}$ and was the most important signal (Table 2). The OBS measurements showed a decreasing turbidity during the deployment at the shallow station. This station was located directly below the turbidity maximum between 200-350 m depth as observed in the CTD transect (Fig.7). In contrast, a relative constant and low turbidity was observed for the deep deployment. Turbidity during both deployments was positively correlated to $DO_{conc}$ (r=0.47, p<0.01, shallow and r=0.50, p<0.01, deep). The SLM lander was deployed at a depth of 440 m and recorded an average pH of 8.12.

The short-term temperature fluctuations imply a vertical tidal movement of around 130 m, based on comparing the temperature range measured by the lander and the temperature versus depth gradient based on CTD measurements (12.9-9.1 °C measured by lander ≙ 218-349 m depth in CTD above lander at station GeoB20966).

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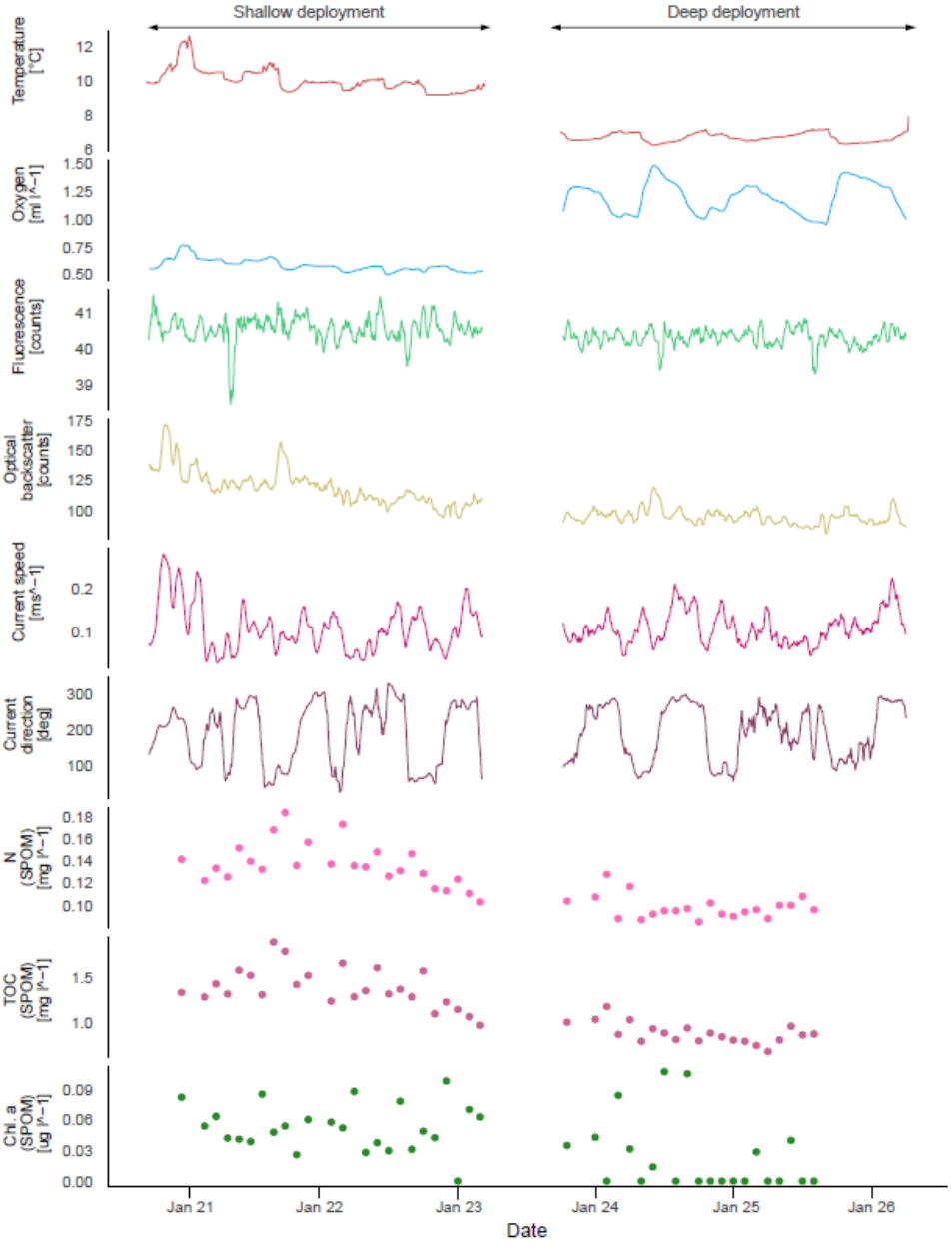


**Figure 8** Lander data (ALBEX) recorded during the shallow (~340 m water depth) and deep deployments (~530 m water depth) off Angola (January 2016). Shown are temperature (°C; red), dissolved oxygen concentration (ml $l^{-1}$; blue), fluorescence (counts per second; green), optical backscatter (turbidity; yellow), current speed (m $s^{-1}$; pink) and current direction (degree: 0-360°; purple) as well as nitrogen (mg $l^{-1}$; pink dots), carbon (mg $l^{-1}$; purple dots), and chlorophyll-α concentration (µg $l^{-1}$, green dots) of SPOM collected during the both deployments by the McLane pump.

*3.2.3 Food supply*

In general TOC and N concentrations of SPOM measured on the filters from the McLane pump were lower at the deep site. Nitrogen concentrations varied around 0.14 mg $l^{-1}$ at 342 m and around 0.1 mg $l^{-1}$ at 532 m depth (Fig. 6b). The $\delta^{15}N$ values of the lander time series of the shallow deployment ranged from 1.6 to 6.2 ‰ (3.7 ‰ average) and were even lower deeper in the water column, viz. range 0.3-3.7 ‰ with an average of 1.4 ‰. The TOC concentrations were on average 1.43 mg $l^{-1}$ at 342 m and 0.9 mg $l^{-1}$ at 532 m, with corresponding $\delta^{13}C$ values ranging between -23.0 and -24.2 (average of -23.6 ‰) at the shallow and between -22.9 and -23.9 (average -23.4 ‰) at the deep site. The C/N ratio was relatively stable and on average 10.2 and 9 for the samples taken at the shallower and deeper site, respectively.

The chlorophyll-α concentrations of the SPOM collected by the McLane pump varied between 0.1 and 0.02 µg $l^{-1}$, with an average phaeopigments/chlorophyll-α ratio of 2.6 and 0.5 on the shallow and deep site, respectively. Phytopigments recorded by the shallow deployment included 0.3 µg $l^{-1}$ of fucoxanthin, while at the deep site only a concentration of 0.1 µg $l^{-1}$ was found. No zeaxanthin was recorded in the pigment fraction.

# 4. Discussion

Even though the ecological-niche factor analysis of Davies et al. (2008) and Davies and Guinotte (2011) predict *L. pertusa* to be absent on the oxygen-limited southwestern African margin, two CWC mound ecosystems were observed along the Namibian and Angolan margins. The coral mounds on the Namibian shelf host no living CWCs, instead dead coral framework covering the mounds was overgrown with fauna dominated by bryozoans and sponges. Along the slope of the Angolan margin an extended coral mound area with thriving CWC communities was encountered. Differences between the areas indicate different environmental conditions influencing faunal assemblages present in both areas. The potential impact of the key environmental factors will be discussed below.

## *4.1 Short-term vs long-term variations in environmental properties*

On the Namibian margin, seasonality has a major impact on local-mid-depth oxygen concentration due to the periodically varying influence of the Angola current and its associated low $DO_{conc}$. The lowest $DO_{conc}$ are expected from February to May when SACW is the dominating water mass on the Namibian margin and the contribution of ESAC water is smaller. Due to this seasonal pattern, the $DO_{conc}$ measured in this study (January; Figs. 4) most likely do not represent minimum concentrations, which are expected to occur in the following months (February to May; Mohrholz et al., 2014). Interestingly, we captured a flow reversal from a southward to an equatorward current direction during high wind conditions on the

Namibian margin (Fig. 5), leading to an intrusion of ESACW with higher $DO_{conc}$ (+0.007 ml $l^{-1}$ on average) and lower temperatures (-0.23°C on average, Fig. 5) than the SACW after the 6th of January, leading to an temporal relaxation of the oxygen stress. This shows that variations in the local flow field have the capability to change water properties on relatively short time scales, which might provide an analogue to the water mass variability related to the different seasons. Such relaxations are likely important for the survival of the abundant invertebrate fauna present on the relict coral mounds under the conditions generally considered unsuited for them. Other seasonal changes, like riverine outflow do not have decisive impacts on the margin ecosystem since only relatively small rivers discharge from the Namibian margin. This is also reflected by the dominant marine isotopic signature of the isotopic ratios of $\delta^{15}N$ and $\delta^{13}C$ of the suspended particulate matter at the mound areas (Fig. 6, cf. Tyrrell and Lucas, 2002).

Flow reversals were not observed during the lander deployments on the Angolan margin, where winds are reported to be weak throughout the year providing more stable conditions (Shannon, 2001). Instead river outflow seems to exert a strong influence on the oxygen concentration on the Angolan margin. The run-off of the Cuanza and Congo river reach their seasonal maximum in December and January (Kopte et al., 2017), intensifying upper water column stratification and transporting terrestrial organic matter to the margin. This stratification is restricting vertical mixing and thereby limits ventilation of the oxygen depleted subsurface water masses. The input of terrestrial organic matter is reflected by the isotopic signals of the SPOM, i.e. a $\delta^{15}N$ values between 1.4 to 3.7‰. This range resembles a more terrestrial signal (-1 to 3‰; Montoya, 2007) and is well below the average isotopic ratio of the marine waters of 5.5‰ (Meisel et al., 2011). Also $\delta^{13}C$ values of -23.5‰ are in line with the $\delta^{13}C$ values of terrestrial matter which is on average -27 ‰ in this area (Boutton, 1991;Mariotti et al., 1991). The C/N ratio of SPOM is higher compared to material from the Namibian margin, confirming admixing of terrestrial matter (Perdue and Koprivnjak, 2007). The combined effects of decreased vertical mixing and additional input of organic matter potentially result in the lowest $DO_{conc}$ of the year during the investigated time period (January), since the highest river outflow and therefore strongest stratification is expected during this period.

### *4.2 Main stressors – Oxygen and temperature*

Environmental conditions marked by severe hypoxia and temporal anoxia (<0.17 ml $l^{-1}$) likely explain the present-day absence of living CWCs along the Namibian margin. During the measurement period the $DO_{conc}$ off Namibia were considerably lower than the thus far recorded minimum concentrations near living CWCs (1-1.3 ml $l^{-1}$), which were found off Mauritania where only isolated living CWCs are found



499 (Ramos et al., 2017). Age dating of the Namibian fossil coral framework shows that CWCs disappeared
500 about 5 ka BP, which coincides with an intensification in upwelling and therefore most likely a decline of
501 $DO_{conc}$ (Tamborrino et al., sumbitted). This is supporting the assumption that the $DO_{conc}$ is responsible for
502 the demise of CWCs on the Namibian margin. Although no living corals were observed on the Namibian
503 coral mounds, we observed a dense living community dominated by sponges and bryozoans (Hebbeln et
504 al., 2017). Several sponge species have been reported to survive at extremely low $DO_{conc}$ within OMZs.
505 For instance, along the lower boundary of the Peruvian OMZ sponges were found at $DO_{conc}$ as low as
506 0.06-0.18 ml $l^{-1}$ (Mosch et al., 2012). Mills et al. (2018) recently found a sponge (*Tethya wilhelma*) to be
507 physiologically almost insensitive to oxygen stress and to respire aerobically under low $DO_{conc}$ (0.02 ml $l^{-1}$
508 ). Sponges can potentially stop their metabolic activity during unfavorable conditions and re-start their
509 metabolism when some oxygen becomes available, for instance during diurnal irrigation of water with
510 somewhat higher $DO_{conc}$. The existence of a living sponge community off Namibia might hence be
511 explained by the diurnal baroclinic tides occasionally flushing the sponges with more oxic water enabling
512 them to metabolize, when food availability is also highest (pulse of suspended particulate matter with a
513 higher amount of TOC and N during oxygenated conditions, Figs. 5, 8). Increased biomass and
514 abundances in these temporary hypoxic-anoxic transition zones were already observed for macro- and
515 mega-fauna in other OMZs and is referred to as the "edge effect" (Mullins et al., 1985;Levin et al.,
516 1991;Sanders, 1969). It is very likely that this mechanism plays a role for the benthic communities on the
517 Angolan margin.

518 Along the Angolan margin low oxygen concentrations apparently do not restrict the proliferation of
519 thriving CWC reefs even though $DO_{conc}$ are considered hypoxic (0.5-1.5 ml $l^{-1}$). The $DO_{conc}$ measured off
520 Angola are well below the lower $DO_{conc}$ limits for *L. pertusa* based either on habitat suitability modelling
521 (Davies et al., 2008) or on laboratory experiments and earlier field observations (Schroeder, 2002;Brooke
522 and Ross, 2014). The $DO_{conc}$ encountered at the shallow mound sites (<0.8 ml $l^{-1}$) are even below the so far
523 lowest limits known for single CWC colonies from the Mauritanian margin (Ramos et al., 2017b). Since in
524 the present study, measured $DO_{conc}$ were even lower than the earlier established lower limits3 this could
525 suggest at a much higher tolerance of *L. pertusa* to low oxygen levels at least in a limited time-period as
526 low as 0.5 ml $l^{-1}$ (4% $O_2$ saturation), which was measured by the ALBEX lander as well as the CTD during
527 the cruise in 2016. Even though concentrations at the Angolan margin showed to be relatively stable, it
528 should be emphasized that the observation period was limited and long-term (year-long) observations
529 remain necessary to confidently extend the lower limit of oxygen deficiency tolerance by *L. pertusa*.



In addition to the oxygen stress, heat stress is expected to put additional pressure on CWCs. Temperatures at the CWC mounds off Angola ranged from 6.4 to 12.6 °C, which are close to their reported maximum temperatures (~12-14.9 °C; Davies and Guinotte 2011) and are hence expected to impair the ability of CWCs to form mounds (see Wienberg and Titschack 2017). In most aquatic invertebrates respiration rates roughly double with every 10 °C increase ($Q_{10}$ temperature coefficient = 2-3, e.g. Coma 2002), which at the same time doubles energy demand. Dodds et al. (2007) found a doubling of the respiration rate of *L. pertusa* with an increase at ambient temperature of only 2 °C (viz. $Q_{10}$=7-8). This would limit the survival of *L. pertusa* at high temperatures to areas where the increased demand in energy (due to increased respiration) can be compensated by high food availability. Higher respiration rates also imply that enough oxygen needs to be available for the increased respiration.

Survival of *L. pertusa* under hypoxic conditions along the shallow Angolan CWC areas is probably positively influenced by the fact that periods of highest temperatures coincide with highest $DO_{conc}$ during the tidal cycle, which stands in contrast to mounds on the Namibian margin or the deeper Angolan mound area. Probably the increase of one stressor is compensated by a reduction of another stressor in the shallow Angolan mound areas. On the Namibian margin or the deeper Angolan mound sites we found the opposite pattern, with highest temperatures during lowest $DO_{conc}$. The occurrence of *L. pertusa* at the the deeper Angolan mound sites is possibly related to the fact that $DO_{conc}$ are anyway higher and temperatures more within a suitable range compared to the shallow sites (0.9-1.5 ml $l^{-1}$, 6.4-8 °C, Fig. 8). Additionally it was shown by ex situ experiments that *L. pertusa* is able to survive periods of hypoxic conditions similar to those found along the Angolan margin for several days, which could be crucial in periods of most adverse conditions during one tidal period or also slightly longer time periods (Dodds et al., 2007). However, oxygen stress leads to a loss of energy which and associated increased energy demand like in other aquatic invertebrates (Sokolova et al., 2012).

### *4.3 Food supply*

As mentioned above, environmental stress like high temperature or low $DO_{conc}$ result in a loss of energy (Odum, 1971;Sokolova et al., 2012), which needs to be balanced by an increased energy (food) availability. Food availability therefore plays a significant role for faunal abundance under hypoxia or unfavorable temperatures (Diaz and Rosenberg, 1995). Above, we argued that survival of sponges and bryozoans on the relict mounds off Namibia and of CWCs and their associated fauna at the Angolan margin, may be partly due to a high input of high-quality organic matter, compensating the oxygen and thermal stresses. The importance of the food availability for CWCs was already suggested by Eisele et al. (2011), who



561 mechanistically linked CWC mound growth periods with enhanced surface water productivity and hence
562 organic matter supply. Here we found evidence for high quality and quantity of SPOM in the vicinity of
563 the coral mounds on the Namibian as well as on the Angolan margin. Indicators for the high quality of
564 food in the SPOM at both sites were high TOC and N concentrations (Figs. 6, 10) in combination with a
565 low C/N ratio (Fig. 7), a low isotopic signature of $\delta^{15}N$ and only slightly degraded pigments
566 (∑phaeopigment/ chlorophyll-α ratio of on average 6.5 and 3.2 off Namibia and Angola, respectively).

567 The Namibian margin is known for its upwelling cells, where phytoplankton growth is fueled by nutrients
568 from deeper water layers producing high amounts of phytodetritus (Chapman and Shannon, 1985), which
569 subsequently sinks down to the relict mounds on the slope. This high flux and accumulation of fresh SPOM
570 towards the reefs is evident as a slightly increased fluorescence deeper in the water column around the
571 mound sites (Fig. 4d). Furthermore, the increased fluorescence and chlorophyll-α concentrations coincide
572 with low $DO_{conc}$ which both are in line with downward movement of waters with a lower $DO_{conc}$ from the
573 OMZ above (Fig. 5). The higher turbidity during lower current speeds provides additional evidence that
574 the material settling from the surface is not transported away with the strong currents (Fig. 5). Mounds
575 off Namibia occur at relatively shallow depths, hence downward transport of SPOM from the surface
576 waters is rapid and hence time for decomposition of the sinking particles in the water column is limited.
577 This fast delivery of SPOM over short depth intervals appears to be linked to both, high primary
578 productivity (high surface fluorescence, Fig. 4d) and reduced decomposition due to low oxygen
579 concentrations (Pichevin et al., 2004;Cavan et al., 2017), leads to a generous food supply for several
580 benthic organisms thus enabling them to survive under hypoxic conditions.

581 At the Angolan coral mounds, SPOM appeared to have a signature corresponding to higher quality organic
582 matter compared to off Namibia. The phytopigments were less degraded (i.e. higher chlorophyll-α
583 concentration, lower ∑phaeopigment/ chlorophyll-α ratio) and the $\delta^{15}N$, TOC and N concentration of the
584 SPOM was lower than off Namibia. However, here lower $\delta^{15}N$ and higher ∑phaeopigment/ chlorophyll-α
585 ratio are likely connected to terrestrial OM input, which constitutes a less suitable food source for CWCs.
586 On the other hand the riverine input delivers nutrients, which can support the growth of phytoplankton,
587 indirectly influencing food supply (Kiriakoulakis et al., 2007;Mienis et al., 2012). Moreover the food quality
588 at the shallow Angolan reefs was not coupled to periods of other environmental stressors and variations
589 were relatively small during this study. At the Angolan margin we see a rather constant delivery of SPOM.
590 The slightly higher turbidity during periods of highest $DO_{conc}$, (Fig. 8) suggest that the SPOM on the Angolan
591 margin originates from the bottom nepheloid layer on the margin directly above the CWC mounds (Fig.

592 7e), which may represents a constant reservoir of fresh SPOM. This again indicates that CWCs can benefit
593 from a constant source of high quality SPOM on the margin somewhat above the coral mound areas and
594 are not exclusively depending on SPOM settling from the surface (like at the Namibian margin), since the
595 strong stratification inhibits mixing of the different water masses. This is also supported by the fact, that's
596 increased fluorescence off Angola was not as strongly correlated with the downward currents as off
597 Namibia.

598 *4.4 Tidal currents*

599 The semidiurnal tidal currents observed probably play a major role in the survival of benthic fauna on the
600 southwestern African margin. On the Namibian margin internal waves deliver oxygen from the surface
601 and deeper waters semi-diurnally about 70 m towards to the inside the OMZ and thereby enable benthic
602 fauna on the fossil coral framework to survive in hypoxic conditions (Fig. 9a). At the same time these
603 currents are likely responsible for the delivery of fresh SPOM from the surface productive zone to the
604 communities on the margin.

605 On the Angolan margin internal tides produce slightly faster currents and vertical excursions of up to 130
606 m which are twice as high as those on the Namibian margin. Similar to the Namibian margin these tidal
607 excursions deliver oxygen from shallower and deeper waters to the mound zone (Fig. 9b). Internal tides
608 are also responsible for the formation of a bottom nepheloid layer in 200-350 m depth (Fig. 7e). This layer
609 is formed by bottom erosion due to the intensification of near-bottom water movements, which is
610 indicated by maxima of the buoyancy frequency $N^2$ in 225 and 300 m depth (GeoB20977-1, not shown).
611 Tidal waves will be amplified due to a critical match between the characteristic slope of the internal M2
612 tide and the bottom slope of the Angolan margin, as is known from other continental slope regions
613 (Dickson and McCave, 1986;Mienis et al., 2007). As argued above, this turbid layer is likely important for
614 the nutrition of the slightly deeper situated CWC mounds, since vertical mixing is hindered by the strong
615 stratification.

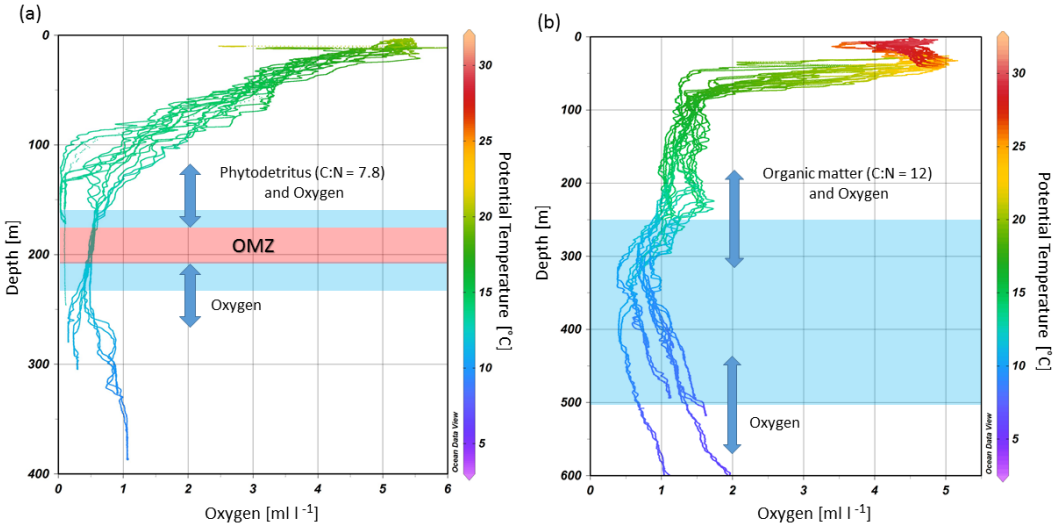


**Figure 9** Depth range of cold-water coral mound occurrences (blue shaded areas) at the (a) Namibian and (b) Angolan margins in relation to the dissolved oxygen concentrations and potential temperature. Diurnal tides are delivering mainly phytodetritus (shown in (a) and organic matter from the benthic nepheloid layer (shown in (b) as well as oxygen from above, and from below to the mound sites (indicated by blue arrows, the length of which indicate the tidal ranges).

### *4.5 Implications*

CWC and sponge communities are known to play an important role as a refuge, feeding ground and nursery for commercial fishes (Miller et al., 2012) and have a crucial role in the marine benthic pelagic coupling (Cathalot et al., 2015). CWCs and their ecosystem services are threatened by the expected expansion of OMZs due to anthropogenic activities like rising nutrient loads and climate change (Breitburg et al., 2018). This study showed that CWCs are able to cope with low oxygen levels as long as sufficient high quality food is available. Further, reef associated sponge grounds, as encountered on the Namibian margin could play a crucial role in taking over the function of CWCs in marine carbon cycling as well as in providing a habitat for associated fauna, when conditions become unsuitable for CWCs.

## 5. Conclusions

Different environmental properties and different relations between these properties explain the dissimilar present conditions of CWCs on the southwestern African margin including temperature, $DO_{conc}$, food supply and tidal movements. The $DO_{conc}$ likely defines the state of the CWCs along the Namibian and the Angolan margin, whereas high temperatures constitute an additional stressor by increasing the respiration rate and therefore energy demand. On the Namibian margin, where $DO_{conc}$

dropped below 0.01 ml $l^{-1}$, only fossil CWC mounds covered by a community dominated by sponges and bryozoans were found. This community survives as it receives periodically waters with slightly higher $DO_{conc}$ (>0.03 ml $l^{-1}$) due to regular tidal oscillations (semi diurnal) and erratic wind events (seasonal). At the same time, a high quality and quantity of SPOM sinking down from the surface water mass enables the epifaunal community to survive despite the oxygen stress and sustain its metabolic energy demand at the Namibian OMZ, while CWCs are not capable to withstand such extreme conditions. In contrast, thriving CWCs on the Angolan coral mounds were encountered despite the overall hypoxic conditions. The $DO_{conc}$ were slightly higher than those on the Namibian margin, but nevertheless below the lowest threshold that was so far reported for *L. pertusa* (Ramos et al., 2017;Davies et al., 2010;Davies et al., 2008). In combination with temperatures, close to the upper limits for *L. pertusa*, metabolic energy demand probably reached a maximum. High energy requirements might have been compensated by the general high availability of fresh resuspended SPOM. Fresh SPOM is accumulated on the Angolan margin just above the CWC area and is regularly supplied due to mixing by semidiurnal tidal currents, despite the restricted sinking of SPOM from the surface due to the strong stratification.

## 6. Data availability

Data will be uploaded to Pangea after publication.

## 7. Author contribution

UH analyzed the physical and chemical data, wrote the manuscript and prepared the figures with contributions of all authors. FM, GD and ML designed the lander research. DH and CW led the cruise and wrote the initial cruise plan. FM and ML collected the data during the research cruise. WCD was responsible for water column measurements with the CTD. AF and ML provided habitat characteristics, including species identification of both CWC areas. KJ performed the tidal analysis and provided together with SF data of the SML lander. All authors contributed to the data interpretation and discussion of the manuscript.

## 8. Competing interests

The authors declare that they have no conflict of interest.



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## 11. Figure captions

**Figure 1** (a) Overview map showing the research areas off Angola and Namibia (red squares) and main features of the surface water circulation (arrows) and frontal zone (dashed line) in the SE Atlantic as well as the two main rivers discharging at the

Angolan margin. Detailed bathymetry maps of the Angolan (upper maps) and Namibian margins (lower maps) showing the position of (b) CTD transects (note the deep CTD cast down to 1000 m water depth conducted off Namibia) and (c) bottom lander deployments (red squares shown in b indicate the cutouts displayed in c).

**Figure 2** ROV images (copyright MARUM ROV SQUID, Bremen, Germany) showing the surface coverage of cold-water coral mounds discovered off Namibia (a, b) and Angola (c, d). Images were recorded and briefly described for their faunal composition during RV *Meteor* cruise M122 "ANNA" (see Hebbeln et al. 2017). (a) Sylvester mound, 225 m water depth. Dead coral framework entirely consisting of *Lophelia pertusa*. The framework is intensely colonized by the yellow bryozoan *Metropriella* sp., zoanthids, actiniarians and sponges. Vagile fauna consists of asteroids and gobiid fishes (*Sufflogobius bibarbatus*) that hide between hollows underneath the coral framework. (b) Sylvester mound, 238 m water depth. Dense coral rubble (*L. pertusa*) heavily overgrown by *Metropriella* sp. and sponges. Note the decapod crab *Macropipus australis* (center of the image). (c) Valentine mound, 238 m water depth. Live *Lophelia* colony being grazed by echinoids. Note the sponge *Aphrocallistes* sp. with its actiniarian symbionts (right side of the image). (d) Buffalo mound, 345 m water depth. Living CWC reef observed on top of an Angolan coral mound. Many fishes are present around the reef (*Helicolenus dactylopterus*, *Gephyroberyx darwinii*).

**Figure 3** TS-diagrams showing the different water masses being present at the (a) Namibian and (b) Angolan margins: South Atlantic Subtropical Surface Water (SASSW), South Atlantic Central Water (SACW) and Eastern South Atlantic Central water (ESACW), Antarctic Intermediate Water (AAIW) (data plotted using Ocean Data View v.4.7.8; http://odv.awi.de; Schlitzer, 2011). Red dotted line indicates the depth range of cold-water coral mound occurrence.

**Figure 4** CTD transect across the Namibian margin. Shown are data for: (a) potential temperature (°C),( b) salinity (PSU), (c) dissolved oxygen concentrations (ml $l^{-1}$), note the pronounced oxygen minimum zone (OMZ) between 100-335 m water depth, and d) fluorescence (mg $m^{-3}$) (data plotted using Ocean Data View v.4.7.8; http://odv.awi.de; Schlitzer, 2011). The occurrence of fossil CWC mounds is indicated by a red dashed line, colored dots indicate bottom lander deployments.

**Figure 5** Data recorded by the ALBEX lander (210 m) at the Namibian margin in January 2016. Shown are data for temperature (°C; red), dissolved oxygen concentrations (ml $l^{-1}$; blue), optical backscatter (turbidity; moss green), fluorescence (counts per second green), current speed (m $s^{-1}$; pink), current direction (degree: 0-360°; dark red) as well as nitrogen (mg $l^{-1}$; pink dots), carbon (mg $l^{-1}$; purple dots), and chlorophyll-α concentration (µg $l^{-1}$, green dots) of SPOM collected during the first 48h by the McLane pump. These data are supplemented by wind speed and direction (small black arrows) recorded concurrently to the lander deployment by ship bound devices. Note that current directions changed from a generally south-poleward to an equatorward direction when wind speed exceeded 10 m $s^{-1}$ (stormy period indicated by black arrow).

**Figure 6** Composite records of SPOM collected by the McLane pump of the ALBEX lander at the Namibian and Angolan margins during all three deployments. (a) δ15N and δ13C isotopic values at the Namibian (red dots) and Angolan (blue and green dots) margins. Indicated by the square boxes are common isotopic values of terrestrial and marine organic matter (Boutton 1991, Holmes et al. 1997, Sigman et al. 2009). The relative contribution of terrestrial material (green boxes) is increasing with a more negative δ13C value. (b) Total organic carbon (TOC) and nitrogen (N) concentration of the SPOM. Values of the Namibian margin are marked by a blue circle (C/N ratio = 7.8), values of the Angolan margin are marked by a green circle (C/N ratio = 9.6). Dissolved oxygen concentrations are included to show the higher nutrient concentrations in less oxygenated water.

**Figure 7** CTD transect across the Angolan margin. Shown are data for (a) potential temperature (°C), (b) salinity (PSU), (c) dissolved oxygen concentration (ml $l^{-1}$), (d) fluorescence (mg $m^{-3}$), (e) turbidity (NTU) (data plotted using Ocean Data View v.4.7.8; http://odv.awi.de; Schlitzer, 2011). The depth occurrence of CWC mounds is marked by a red, dashed line, the lander deployments are indicated by colored dots.

**Figure 8** Lander data (ALBEX) recorded during the shallow (~340 m water depth) and deep deployments (~530 m water depth) off Angola (January 2016). Shown are temperature (°C; red), dissolved oxygen concentration (ml $l^{-1}$; blue), fluorescence (counts per second; green), optical backscatter (turbidity; yellow), current speed (m $s^{-1}$; pink) and current direction (degree: 0-360°; purple) as well as nitrogen (mg $l^{-1}$; pink dots), carbon (mg $l^{-1}$; purple dots), and chlorophyll-α concentration (µg $l^{-1}$, green dots) of SPOM collected during the both deployments by the McLane pump.

**Figure 9** Depth range of cold-water coral mound occurrences (blue shaded areas) at the (a) Namibian and (b) Angolan margins in relation to the dissolved oxygen concentrations and potential temperature. Diurnal tides are delivering mainly phytodetritus (shown in (a) and organic matter from the benthic nepheloid layer (shown in (b) as well as oxygen from above, and from below to the mound sites (indicated by blue arrows, the length of which indicate the tidal ranges).

# 12. Tables

**Table 1.** Metadata of lander deployments conducted during RV *Meteor* cruise M122 (ANNA) in January 2016. The deployment sites are shown in Figure 1.

| | Station no. (GeoB ID) | Area | Lander | Date | Latitude [S] | Longitude [E] | Depth [m] | Duration [days] | Devices |
|---|---|---|---|---|---|---|---|---|---|
| **Namibia** | 20507-1 | on-mound | ALBEX | 01.-09.01.16 | 20°44.03' | 12°49.23' | 210 | 7.8 | + particle pump |
| | 20508-1 | off-mound | TROL | 01.-09.01.16 | 20°44.03' | 12°49.14' | 220 | 7.8 | |
| | 20506-1 | off-mound | SLM | 01.-16.01.16 | 20°43.93' | 12°49.11' | 231 | 12.5 | |
| **Angola** | 20921-1 | off-mound | ALBEX | 20.-23.01.16 | 9°46.16' | 12°45.96' | 342 | 2.5 | + particle pump |
| | 20940-1 | off-mound | ALBEX | 23.-26.01.16 | 9°43.84' | 12°42.15' | 532 | 2.6 | + particle pump |
| | 20916-1 | off-mound | TROL | 19.-26.01.16 | 9°43.66' | 12°42.09' | 526 | 6.8 | |
| | 20915-2 | off-mound | SLM | 19.-26.01.16 | 9°43.87' | 12°43.87' | 430 | 6.8 | |

**Table 2** Tidal analysis of the ALBEX lander from 6 m above the sea floor. Depth, mean current speed, polarization ratio, mean current direction, tidal prediction of pressure fluctuations, two most important harmonics with amplitude, tidal prediction of horizontal current field, two most important harmonics with semi-major axis' amplitude.

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| | Station no. (GeoB ID) | Depth (m) | Mean current speed (cm $s^{-1}$) | Polarization ratio | Current direction (°) | Tides [%] (p) | Const. [dbar] | Tides [%] (u) | Const. [cm $s^{-1}$] |
|---|---|---|---|---|---|---|---|---|---|
| **Namibia** | 20507-1 | 433 | 9.34 | 0.18 | 221.6 | 81.8 | M2: 0.37 | 10.5 | M2: 3.1<br>M3: 0.8 |
| **Angola** | 20921-1 | 532 | 9.96 | 0.42 | 247.9 | 91.6 | M2: 0.59<br>M3: 0.04 | 36 | M2: 7.8<br>M8: 0.7 |
| | 20940-1 | 228 | 8.92 | 0.86 | 275.6 | 86.8 | M2: 0.60<br>M8: 0.02 | 50.9 | M2: 8.6<br>M3: 3.7 |

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