



1 Environmental factors influencing cold-  
2 water coral ecosystems in the oxygen  
3 minimum zones on the Angolan and  
4 Namibian margins  
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## 23 Abstract

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

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## 51 1. Introduction

52 Cold-water corals (CWCs) form 3D structures in the deep-sea, providing important habitats for dense  
53 aggregations of sessile and mobile organisms ranging from mega- to macrofauna (Henry and Roberts,  
54 2007;van Soest et al., 2007) and fish (Costello et al., 2005). Consequently, CWC areas are considered as  
55 deep-sea hotspots of biomass and biodiversity (Buhl-Mortensen et al., 2010;Henry and Roberts, 2017).  
56 Moreover, they form hotspots for carbon cycling by transferring carbon from the water column towards  
57 associated benthic organisms (Oevelen et al., 2009;White et al., 2012). Some framework-forming  
58 scleractinian species, with *Lophelia pertusa* and *Madrepora oculata* being the most common species in  
59 the Atlantic Ocean (Freiwald et al., 2004;White et al., 2005;Roberts et al., 2006;Cairns, 2007), are  
60 capable of forming large elevated seabed structures, so called coral mounds (Wilson, 1979;Wienberg  
61 and Titschack, 2017;Titschack et al., 2015;De Haas et al., 2009). These coral mounds, consisting of coral  
62 debris and hemipelagic sediments, commonly reach heights between 20 and 100 m and can be several  
63 kilometers in diameter. They are widely distributed along the Atlantic margins, being mainly restricted  
64 to water depths between 200-1000 m, while records of single colonies of *L. pertusa* are reported from a  
65 broader depth range of 50-4000 m depth (Roberts et al., 2006;Hebbeln et al., 2014;Davies et al.,  
66 2008;Mortensen et al., 2001;Freiwald et al., 2004;Freiwald, 2002;Grasmueck et al., 2006;Wheeler et al.,  
67 2007).

68 A global ecological-niche factor analysis by Davies et al. (2008) and Davies and Guinotte (2011),  
69 predicting suitable habitats for *L. pertusa*, showed that this species generally thrives in areas which are  
70 nutrient-rich, well oxygenated and affected by relatively strong bottom water currents. Other factors  
71 potentially important for proliferation of *L. pertusa* include chemical and physical properties of the  
72 ambient water masses (aragonite saturation state, salinity, temperature) and water depth (Davies et al.,  
73 2008;Dullo et al., 2008;Flögel et al., 2014;Davies and Guinotte, 2011). *L. pertusa* is most commonly  
74 found at temperatures between 4-12°C and a very wide salinity range between 32 and 38.8 (Freiwald et  
75 al., 2004). Although they occur in such a wide range of temperature and salinity, the link of *L. pertusa* to  
76 particular salinity and temperature within the NE Atlantic led Dullo et al. (2008) to suggest that they are  
77 restricted to a specific density envelope of sigma-theta ( $\sigma_\theta$ ) = 27.35-27.65 kg m<sup>-3</sup>. In addition, the  
78 majority of occurrences of live *L. pertusa* come from sites with dissolved oxygen concentrations (DO<sub>conc</sub>)  
79 between 6-6.5 ml l<sup>-1</sup> (Davies et al., 2008), with lowest recorded oxygen values being 2.1-3.2 ml l<sup>-1</sup> at CWC  
80 sites in the Gulf of Mexico (Davies et al., 2010;Schroeder, 2002;Brooke and Ross, 2014) or even as low as  
81 1-1.5 ml l<sup>-1</sup> off Mauritania where CWC mounds are in a dormant stage showing only scarce living coral  
82 occurrences today (Wienberg et al., 2018;Ramos et al., 2017). Dissolved oxygen levels hence seem to



83 affect the formation of CWC structures as also shown by Holocene records obtained from the  
84 Mediterranean Sea, which revealed periods of reef demise and growth in conjunction with hypoxia (with  
85  $2 \text{ ml l}^{-1}$  seemingly forming a threshold value for active coral growth; Fink et al., 2012).

86 Another essential constraint for CWC growth and therefore mound development in a generally food  
87 deprived deep-sea is food supply. *L. pertusa* is an opportunistic feeder, exploiting a wide variety of  
88 different food sources, including phytodetritus, phytoplankton, mesozooplankton, bacteria and dissolved  
89 organic matter (Kiriakoulakis et al., 2005; Dodds et al., 2009; Gori et al., 2014; Mueller et al.,  
90 2014; Duineveld et al., 2007). Transport of surface organic matter towards CWC sites at intermediate  
91 depths has been found to involve either active swimming (zooplankton), passive sinking, advection, local  
92 downwelling, and internal waves and associated mixing processes resulting from interactions with  
93 topography (Davies et al., 2009; van Haren et al., 2014; Thiem et al., 2006; White et al., 2005; Mienis et al.,  
94 2009; Frederiksen et al., 1992). Not only quantity but also quality of food particles is of crucial  
95 importance for the uptake efficiency as well as ecosystem functioning of CWCs (Ruhl, 2008; Mueller et  
96 al., 2014).

97 With worldwide efforts to map CWC communities, *L. pertusa* has also been found under conditions  
98 which seem environmentally stressful or extreme in the sense of the global limits defined by Davies et  
99 al. (2008) and Davies and Guinotte (2011). Examples are the warm and salty waters of the  
100 Mediterranean and the high temperature variations along the US coast (Cape Lookout; Freiwald et al.,  
101 2009; Mienis et al., 2014; Taviani et al., 2005). Environmental stress generally increases energy needs for  
102 organisms to recover and maintain optimal functioning, which accordingly increases their food demand  
103 (Sokolova et al., 2012). For the SW African margin one of the few records of living CWC come from the  
104 Angolan margin (at  $7^\circ$ ; Le Guilloux et al., 2009), which raises the question whether local environmental  
105 factors limit CWC growth due to the presence of an Oxygen Minimum Zone (OMZ; see Karstensen et al.  
106 2008), or data is lacking. Hydroacoustic campaigns nevertheless revealed extended areas off Angola and  
107 Namibia with structures that morphologically resemble coral mounds structures known from the NE  
108 Atlantic (M76-3, MSM20-1; Geissler et al., 2013; Zabel et al., 2012).

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



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

## 119 2. Material and Methods

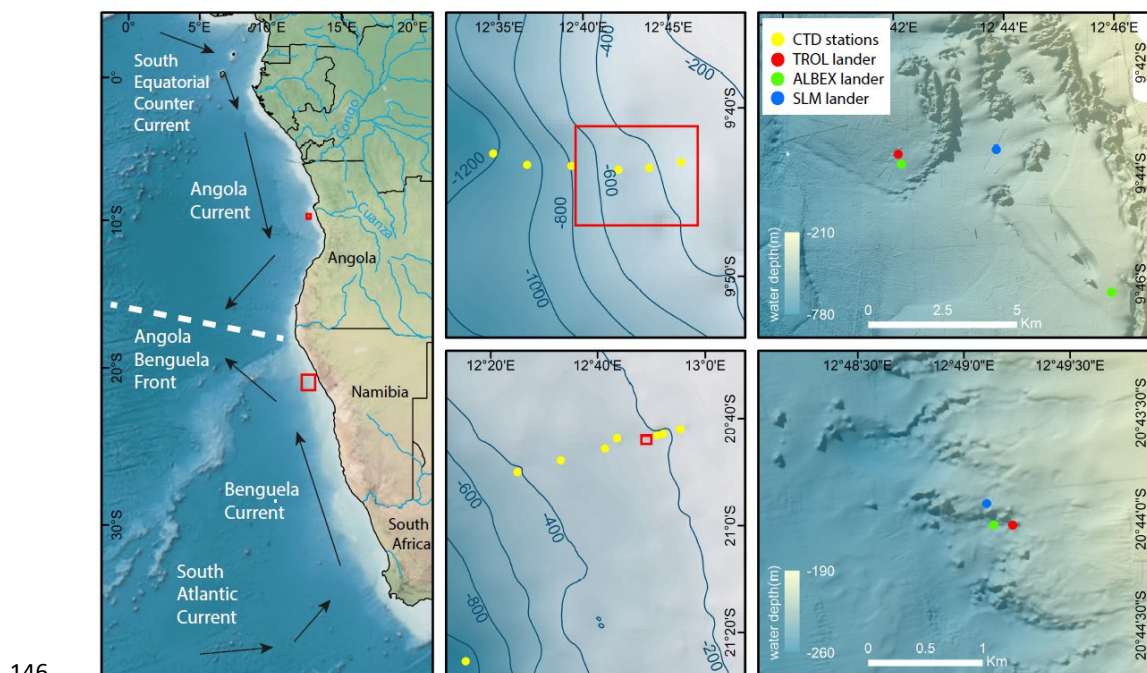
### 120 2.1 Setting

#### 121 2.1.1 Oceanographic setting

122 The SW African margin is one of the four major eastern boundary regions in the world and is  
123 characterized by upwelling of nutrient-rich cold waters (Shannon and Nelson, 1996). The availability of  
124 nutrients triggers a high primary production, making it one of the most productive marine areas  
125 worldwide with an estimated production of 0.37 Gt C/yr (Carr and Kearns, 2003). Remineralization of  
126 high fluxes of organic particles settling through the water column result in severe mid-depth oxygen  
127 depletion and an intense OMZ over large areas along the SW African margin (Chapman and Shannon,  
128 1985). The extension of the OMZs is highly dynamic being controlled by upwelling intensity which  
129 depends on the prevailing winds and two current systems along the SW African margin, i.e. the Benguela  
130 and the Angola currents (Kostianoy and Lutjeharms, 1999; Chapman and Shannon, 1987; Fig. 1). The  
131 Benguela Current originates from the South Atlantic Current, which mixes with water from the Indian  
132 Ocean at the southern tip of Africa (Poole and Tomczak, 1999; Mohrholz et al., 2008; Rae, 2005) and  
133 introduces relatively cold and oxygen-rich Eastern South Atlantic Central Water (ESACW; Poole and  
134 Tomczak 1999) to the SW African margin (Mohrholz et al., 2014). The Angola Current originates from the  
135 South Equatorial Counter Current and introduces warmer, nutrient-poor and less oxygenated South  
136 Atlantic Central Water (SACW; Poole and Tomczak 1999) to the continental margin (Fig. 1a). While the  
137 SACW flows along the continental margin the oxygen concentration is decreasing continuously due to  
138 remineralisation processes on the SW African shelf (Mohrholz et al., 2008). Both currents converge at  
139 around 14-16 °S, resulting in the Angola-Benguela Front (Lutjeharms and Stockton, 1987). In austral  
140 summer, the Angola-Benguela Front can move southward to 23 °S (Shannon et al., 1986), thus  
141 increasing the influence of the SACW along the Namibian coast (Junker et al., 2017; Chapman and  
142 Shannon, 1987), contributing to the pronounced OMZ due to its low initial oxygen concentration (Poole  
143 and Tomczak, 1999). ESACW is the dominant water mass at the Namibian margin during the main



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



146  
147 **Figure 1** (a) Overview map showing the research areas off Angola and Namibia (red squares) and main features of the surface  
148 water circulation (arrows) and frontal zone (dashed line) in the SE Atlantic as well as the two main rivers discharging at the  
149 Angolan margin. Detailed bathymetry maps of the Angolan (upper maps) and Namibian margins (lower maps) showing the  
150 position of (b) CTD transects (note the deep CTD cast down to 1000 m water depth conducted off Namibia) and (c) bottom  
151 lander deployments (red squares shown in (b) indicate the cutouts displayed in (c)).

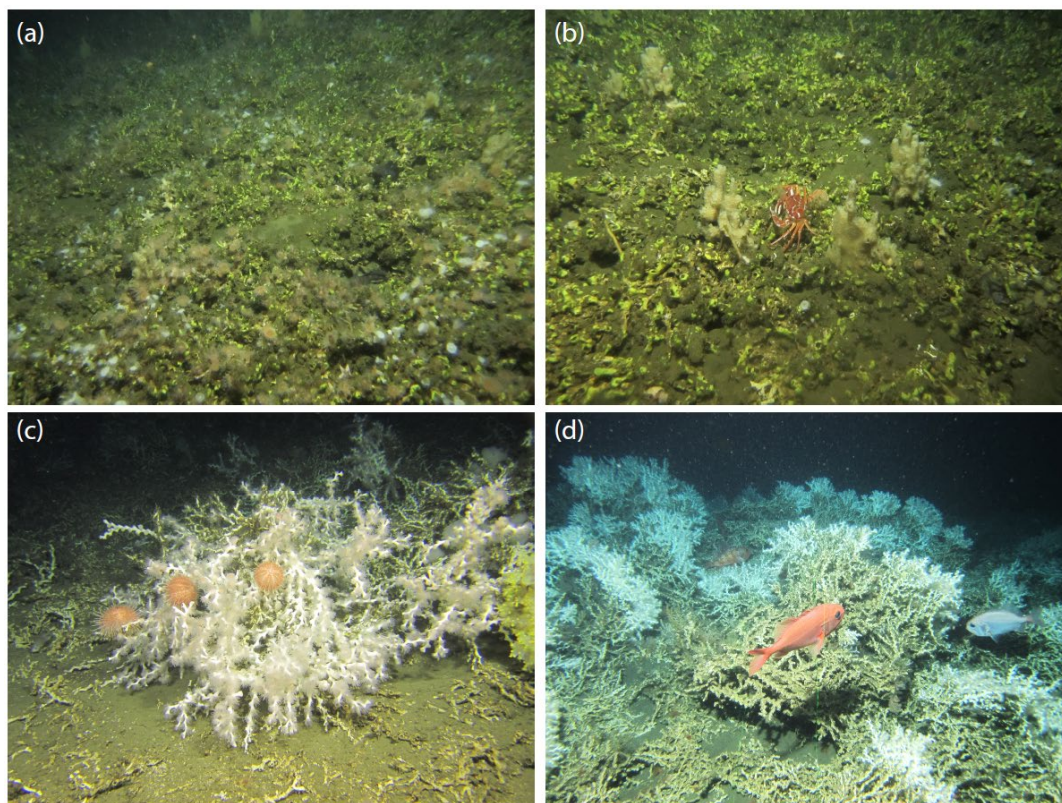
### 152 2.1.2. Coral mound provinces along the Angolan and Namibian margins

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



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

167 On the Angolan margin CWC structures varied from individual mounds to long ridges. Some mounds  
168 reached heights of more than 100 m above the seafloor. At shallow depths (~250 m) also some isolated  
169 smaller mounds are present (Hebbeln et al. 2017). All mounds showed thriving CWC cover, which was  
170 dominated by *L. pertusa* (estimated 99% relative abundance), *M. oculata* and solitary corals. Mounds  
171 with a flourishing coral cover were mainly situated at water depths between 330-470 m, whereas single  
172 colonies were found over an even broader depth range between 250-500 m (Figs. 2c, d; Hebbeln et al.,  
173 2017). Additionally to CWCs, large aggregations of hexactinellid sponges (*Aphrocallistes*, *Sympagella*)  
174 were observed. The scattered small mounds at shallower water depths were dominated by sponges and  
175 only sparsely covered with living coral. In these areas, active suspension feeders, like sponges were most  
176 commonly observed. First estimates for coral ages obtained from a gravity core records collected at one  
177 of the Angolan coral mounds revealed continuous coral mound formation during the last 34 ka until  
178 today (Wefing et al., 2017).



179

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

## 191 **2.2 Methodology**

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





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

### 196 *2.2.1 Lander deployments*

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

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

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

224



### 225 2.2.2 CTD transects

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

### 237 2.2.3 Hydrographic data processing

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

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

### 245 2.2.4 Suspended particulate matter

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

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



255 *C/N analysis and isotope measurements*

256 Filters from the in situ pump and sampled from the CTD/Rosette were freeze-dried before further  
257 analysis. Half of each filter was used for phytopigment analysis and a ¼ section of each filter was used  
258 for analyzing organic carbon, nitrogen, and their stable isotope ratios. The filters, used for carbon  
259 analysis, were decarbonized by vapor of concentrated hydrochloric acid (2 M HCl supra) prior to  
260 analyses. Filters were transferred into pressed tin capsules (12x5 mm, Elemental Microanalysis) and  
261  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$  and total weight percent of organic carbon and nitrogen were analyzed by a Delta V  
262 Advantage isotope ratio MS coupled on line to an Elemental Analyzer (Flash 2000 EA-IRMS) by a Conflo  
263 IV (Thermo Fisher Scientific Inc.). The used reference gas was purified atmospheric  $\text{N}_2$ . As a standard for  
264  $\delta^{13}\text{C}$  benzoic acid and acetanilide was used, for  $\delta^{15}\text{N}$  acetanilide, urea and casein was used. For  $\delta^{13}\text{C}$   
265 analysis a high signal method was exercised including a 70% dilution. Values are reported relative to v-  
266 pdb and the atmosphere respectively. Precision and accuracy based on replicate analyses and  
267 comparing international standards for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  was  $\pm 0.15$  ‰. The C/N ratio is based on the weight  
268 ratios between TOC and N.

269 *Phytopigments*

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

280 *2.2.5 Tidal analysis*

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

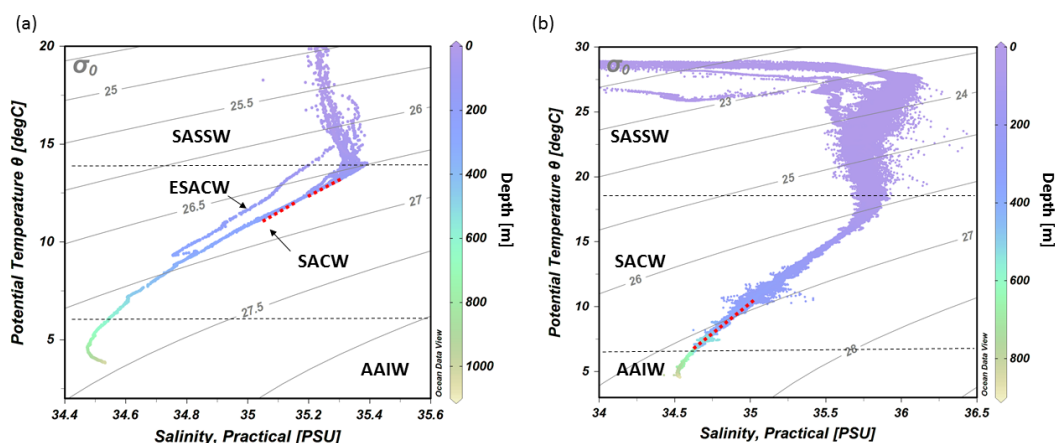


## 286 3. Results

### 287 3.1 Namibian margin

#### 288 3.1.1 Water column properties off Namibia

289 The hydrographic data obtained by CTD measurements along a downslope transect from the surface to  
290 1000 m water depth revealed distinct changes in temperature and salinity through the water column.  
291 These are ascribed to the different water masses in the study area (Fig. 3a). In the upper 85 m of the  
292 water column, temperatures are above 14°C and salinities are > 35.2, which corresponds to South  
293 Atlantic Subtropical Surface Water (SASSW). SACW is situated underneath the SASSW and reaches down  
294 to about 700 m. SCAW is defined by a linear relationship between temperature and salinity in the TS-  
295 plot (Shannon et al., 1987). The temperature in the layer of SCAW decreases from 14 to 7°C with depth  
296 and the salinity from 35.4 to 34.5 (Fig. 3a). The deep CTD cast about 130 km from the coastline recorded  
297 a water mass with the signature of ESACW, having a lower temperature (-1.3°C) and lower salinity (-0.2  
298 PSU) than SACW (in 200 m depth, not included in CTD transects of Fig. 4). Underneath these two central  
299 water masses Antarctic Intermediate Water (AAIW) was found with a temperature <7°C.



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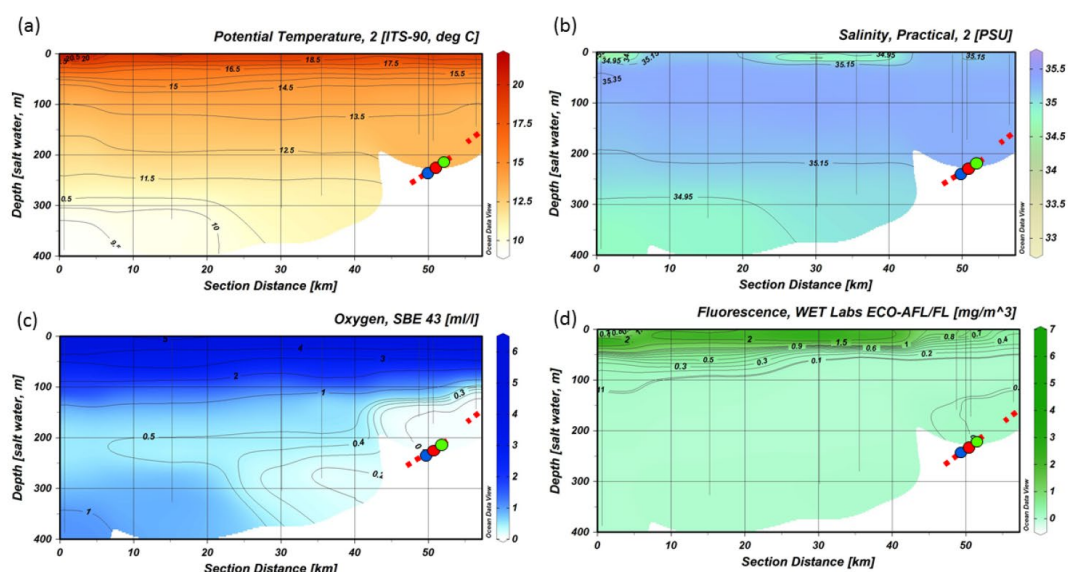
301 **Figure 3** TS-diagrams showing the different water masses being present at the (a) Namibian and (b) Angolan margins: South  
302 Atlantic Subtropical Surface Water (SASSW), South Atlantic Central Water (SACW) and Eastern South Atlantic Central water  
303 (ESACW), Antarctic Intermediate Water (AAIW)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

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



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

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



316

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

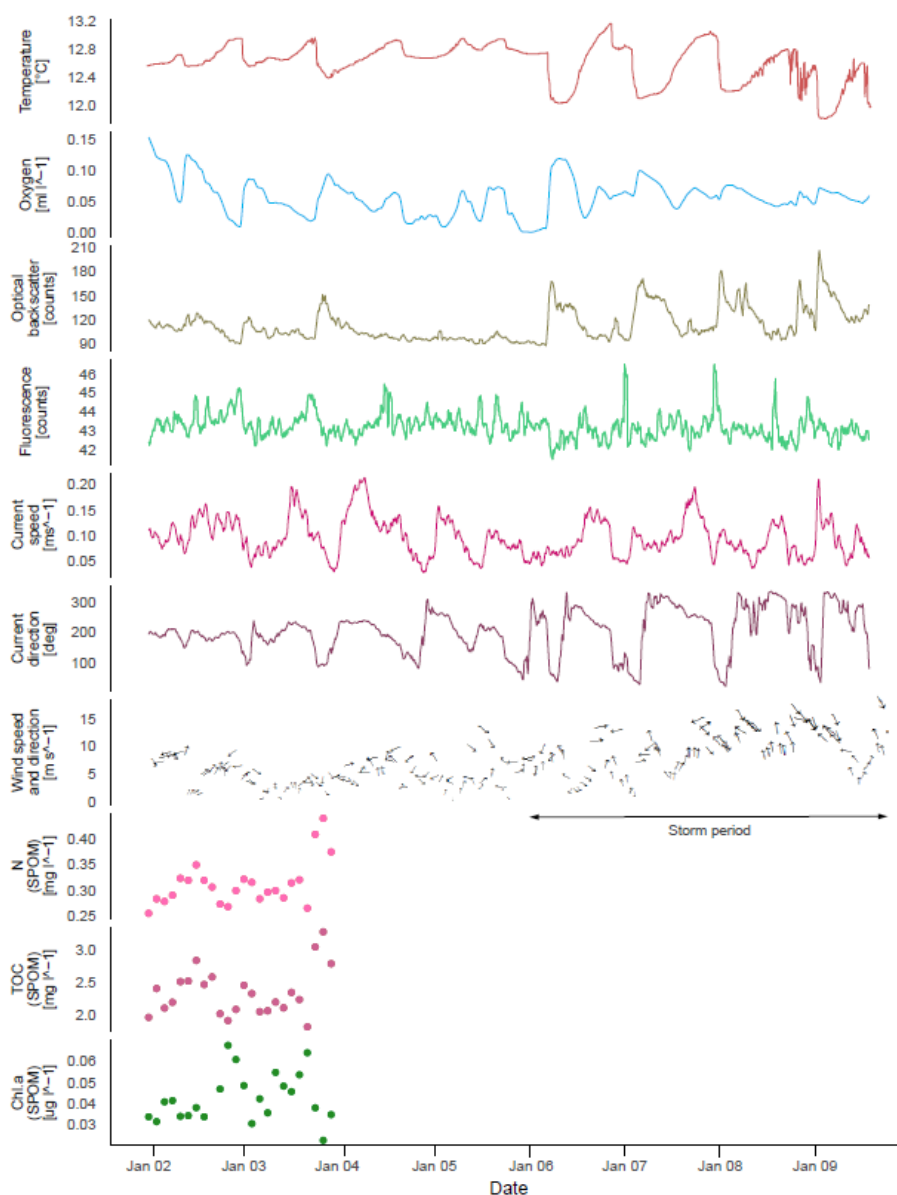
### 312 3.1.2 Lander time-series of physical data

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



327 correlated with oxygen concentration ( $r=-0.39$ ,  $p<0.01$ ) and also with turbidity (optical backscatter,  $r=-$   
328  $0.35$ ,  $p<0.01$ ). Turbidity was relatively low until it increased especially during the second half of the  
329 deployment, when wind speeds increased and also the current direction changed. The maximum current  
330 speeds measured during the deployment period were  $0.21 \text{ m s}^{-1}$ , with average current speeds of  $0.09 \text{ m}$   
331  $\text{s}^{-1}$  (Table 2). The tidal cycle explains  $>80 \%$  of the pressure fluctuations (Table 2), with a semidiurnal  
332 signal, M2, generating an amplitude of  $>0.35 \text{ dbar}$  and thus being the most important constituent.  
333 Before the 6<sup>th</sup> of January the current direction oscillated between SW and SE where after it changed into  
334 a dominating northern current direction. The current speed remained rather constant during the  
335 deployment period (Fig. 5). The wind speed, on the other hand, increased from  $10 \text{ m s}^{-1}$  to a maximum  
336 of  $17 \text{ m s}^{-1}$  on the sixth of January and remained high for the next six days. Wind direction changed from  
337 anticlockwise cyclonic rotation towards alongshore winds. The water current direction returned to SW-  
338 SE after the period of strong wind (not shown). During the strong wind period, colder water (correlation  
339 between wind speed and water temperature,  $r=-0.55$ ,  $p<0.01$ ), with a higher turbidity (correlation of  
340 wind speed and turbidity,  $r=0.42$ ,  $p<0.01$ ) and higher  $\text{DO}_{\text{conc}}$  was present. The SLM lander recorded an  
341 average pH of 8.01.

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



348

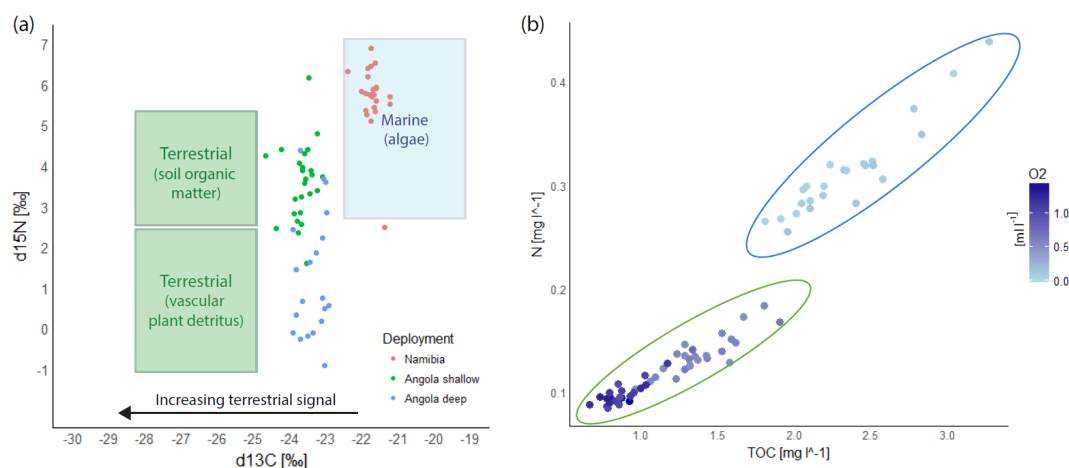
349 **Figure 5** Data recorded by the ALBEX lander (210 m) at the Namibian margin in January 2016. Shown are data for temperature  
350 (°C; red), dissolved oxygen concentrations ( $\text{ml l}^{-1}$ ; blue), optical backscatter (turbidity; moss green), fluorescence (counts per  
351 second green), current speed ( $\text{m s}^{-1}$ ; pink), current direction (degree: 0-360°; dark red) as well as nitrogen ( $\text{mg l}^{-1}$ ; pink dots),  
352 carbon ( $\text{mg l}^{-1}$ ; purple dots), and chlorophyll- $\alpha$  concentration ( $\mu\text{g l}^{-1}$ ; 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  $10 \text{ m s}^{-1}$  (stormy period indicated by black arrow).



## 356 3.1.3 Food supply

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

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



373

374 **Figure 6** Composite records of SPOM collected by the McLane pump of the ALBEX lander at the Namibian and Angolan margins  
375 during all three deployments. (a)  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotopic values at the Namibian (red dots) and Angolan (blue and green dots)  
376 margins. Indicated by the square boxes are common isotopic values of terrestrial and marine organic matter (Boutton 1991,  
377 Holmes et al. 1997, Sigman et al. 2009). The relative contribution of terrestrial material (green boxes) is increasing with a more





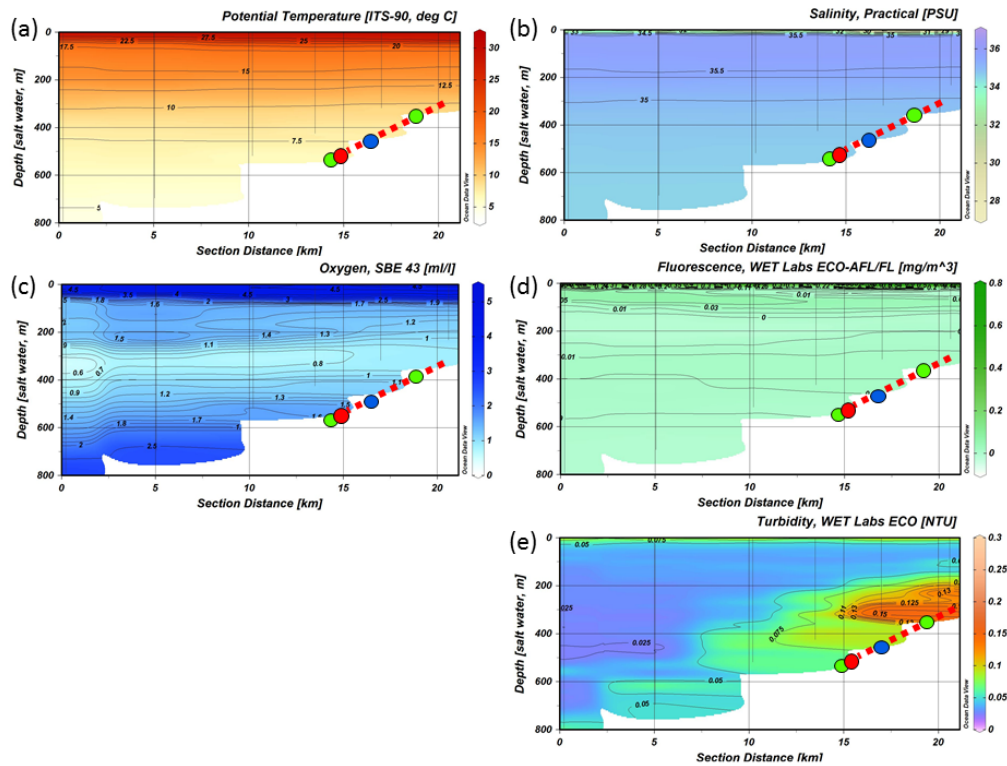
378 negative  $\delta^{13}\text{C}$  value. (b) Total organic carbon (TOC) and nitrogen (N) concentration of the SPOM. Values of the Namibian  
379 margin are marked by a blue circle (C/N ratio = 7.8), values of the Angolan margin are marked by a green circle (C/N ratio = 9.6).  
380 Dissolved oxygen concentrations are included to show the higher nutrient concentrations in less oxygenated water.

## 381 3.2 Angolan margin

### 382 3.2.1 Water column properties

383 The hydrographic data obtained by CTD measurements along a downslope transect from the surface to  
384 800 m water depth revealed distinct changes in temperature and salinity throughout the water column,  
385 related to four different water masses. At the surface a distinct shallow layer (>20 m) with a distinctly  
386 lower salinity (27.3-35.5) and higher temperature (29.5-27 °C, Fig. 3b) was observed. Below the surface  
387 layer, SASSW was recognized down to a depth of 70 m, characterized by a higher salinity (35.8). SACW  
388 was observed between 70-600 m, featuring the expected linear relationship between temperature and  
389 salinity. Temperature and salinity decreased from 17.5°C/35.8 to 7°C/34.6. At 700 m depth AAIW was  
390 recorded, characterized by a low salinity (<34.4) and temperature (<7°C, Fig. 3b).

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



402

403 **Figure 7** CTD transect across the Angolan margin. Shown are data for (a) potential temperature ( $^{\circ}\text{C}$ ), (b) salinity (PSU), (c)  
 404 dissolved oxygen concentration ( $\text{ml l}^{-1}$ ), (d) fluorescence ( $\text{mg m}^{-3}$ ), (e) turbidity (NTU) (data plotted using Ocean Data View  
 405 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  
 406 deployments are indicated by colored dots.

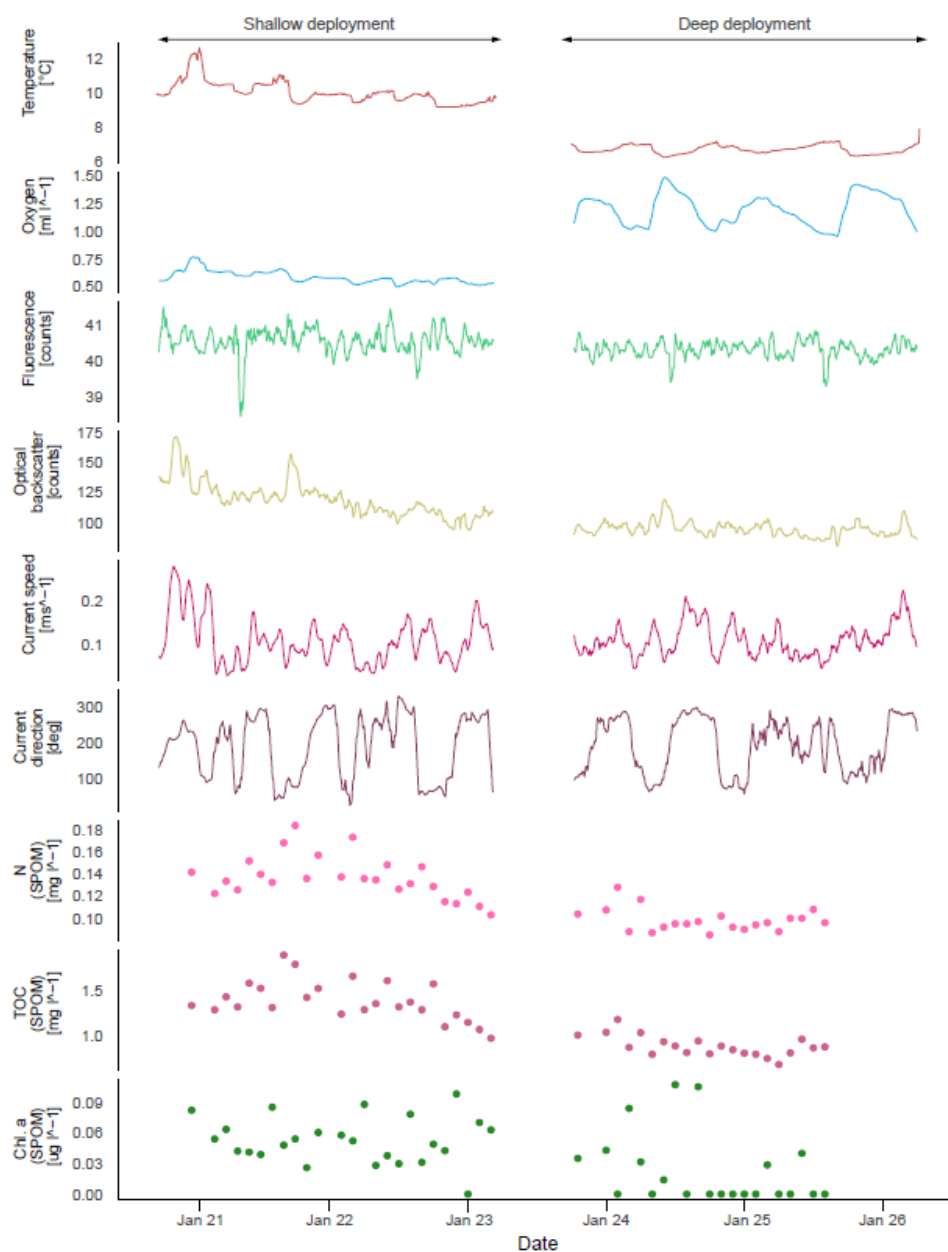
### 407 3.2.2 Lander time series physical data

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



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

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



431

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



### 437 3.2.3 Food supply

438 In general TOC and N concentrations of SPOM measured on the filters from the McLane pump were  
439 lower at the deep site. Nitrogen concentrations varied around  $0.14 \text{ mg l}^{-1}$  at 342 m and around  $0.1 \text{ mg l}^{-1}$   
440 at 532 m depth (Fig. 6b). The  $\delta^{15}\text{N}$  values of the lander time series of the shallow deployment ranged  
441 from 1.6 to 6.2 ‰ (3.7 ‰ average) and were even lower deeper in the water column, viz. range 0.3-3.7  
442 ‰ with an average of 1.4 ‰. The TOC concentrations were on average  $1.43 \text{ mg l}^{-1}$  at 342 m and  $0.9 \text{ mg l}^{-1}$   
443 at 532 m, with corresponding  $\delta^{13}\text{C}$  values ranging between -23.0 and -24.2 (average of -23.6 ‰) at the  
444 shallow and between -22.9 and -23.9 (average -23.4 ‰) at the deep site. The C/N ratio was relatively  
445 stable and on average 10.2 and 9 for the samples taken at the shallower and deeper site, respectively.

446 The chlorophyll- $\alpha$  concentrations of the SPOM collected by the McLane pump varied between 0.1 and  
447  $0.02 \mu\text{g l}^{-1}$ , with an average phaeopigments/chlorophyll- $\alpha$  ratio of 2.6 and 0.5 on the shallow and deep  
448 site, respectively. Phytopygments recorded by the shallow deployment included  $0.3 \mu\text{g l}^{-1}$  of fucoxanthin,  
449 while at the deep site only a concentration of  $0.1 \mu\text{g l}^{-1}$  was found. No zeaxanthin was recorded in the  
450 pigment fraction.

## 451 4. Discussion

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

### 460 4.1 Short-term vs long-term variations in environmental properties

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



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

478 Flow reversals were not observed during the lander deployments on the Angolan margin, where winds  
479 are reported to be weak throughout the year providing more stable conditions (Shannon, 2001). Instead  
480 river outflow seems to exert a strong influence on the oxygen concentration on the Angolan margin. The  
481 run-off of the Cuanza and Congo river reach their seasonal maximum in December and January (Kopte et  
482 al., 2017), intensifying upper water column stratification and transporting terrestrial organic matter to  
483 the margin. This stratification is restricting vertical mixing and thereby limits ventilation of the oxygen  
484 depleted subsurface water masses. The input of terrestrial organic matter is reflected by the isotopic  
485 signals of the SPOM, i.e. a  $\delta^{15}N$  values between 1.4 to 3.7‰. This range resembles a more terrestrial  
486 signal (-1 to 3‰; Montoya, 2007) and is well below the average isotopic ratio of the marine waters of  
487 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  
488 matter which is on average -27 ‰ in this area (Boutton, 1991; Mariotti et al., 1991). The C/N ratio of  
489 SPOM is higher compared to material from the Namibian margin, confirming admixing of terrestrial  
490 matter (Perdue and Koprivnjak, 2007). The combined effects of decreased vertical mixing and additional  
491 input of organic matter potentially result in the lowest  $DO_{conc}$  of the year during the investigated time  
492 period (January), since the highest river outflow and therefore strongest stratification is expected during  
493 this period.

#### 494 *4.2 Main stressors – Oxygen and temperature*

495 Environmental conditions marked by severe hypoxia and temporal anoxia (<0.17 ml l<sup>-1</sup>) likely explain the  
496 present-day absence of living CWCs along the Namibian margin. During the measurement period the  
497  $DO_{conc}$  off Namibia were considerably lower than the thus far recorded minimum concentrations near  
498 living CWCs (1-1.3 ml l<sup>-1</sup>), 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., submitted). 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  $0.06\text{--}0.18\text{ ml l}^{-1}$  (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  $DO_{conc}$  ( $0.02\text{ ml l}^{-1}$   
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 ( $0.5\text{--}1.5\text{ ml l}^{-1}$ ). 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 ( $<0.8\text{ ml l}^{-1}$ ) 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 limits<sup>3</sup> this could  
525 suggest a much higher tolerance of *L. pertusa* to low oxygen levels at least in a limited time-period as  
526 low as  $0.5\text{ ml l}^{-1}$  (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*.



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

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

### 553 *4.3 Food supply*

554 As mentioned above, environmental stress like high temperature or low  $DO_{conc}$  result in a loss of energy  
555 (Odum, 1971; Sokolova et al., 2012), which needs to be balanced by an increased energy (food) availability.  
556 Food availability therefore plays a significant role for faunal abundance under hypoxia or unfavorable  
557 temperatures (Diaz and Rosenberg, 1995). Above, we argued that survival of sponges and bryozoans on  
558 the relict mounds off Namibia and of CWCs and their associated fauna at the Angolan margin, may be  
559 partly due to a high input of high-quality organic matter, compensating the oxygen and thermal stresses.  
560 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  $\delta^{15}\text{N}$  and only slightly degraded pigments  
566 ( $\Sigma\text{phaeopigment}/\text{chlorophyll-}\alpha$  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- $\alpha$  concentrations coincide  
572 with low  $\text{DO}_{\text{conc}}$  which both are in line with downward movement of waters with a lower  $\text{DO}_{\text{conc}}$  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- $\alpha$   
583 concentration, lower  $\Sigma\text{phaeopigment}/\text{chlorophyll-}\alpha$  ratio) and the  $\delta^{15}\text{N}$ , TOC and N concentration of the  
584 SPOM was lower than off Namibia. However, here lower  $\delta^{15}\text{N}$  and higher  $\Sigma\text{phaeopigment}/\text{chlorophyll-}\alpha$   
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  $\text{DO}_{\text{conc}}$ , (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.

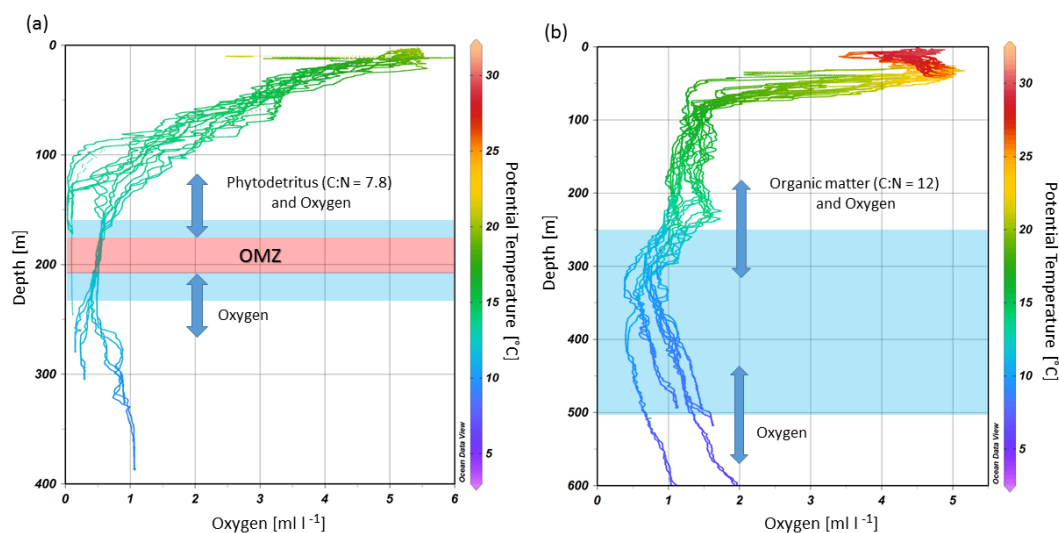


592 7e), which may represent a constant reservoir of fresh SPOM. This again indicates that CWCs can benefit  
593 from a constant source of high quality SPOM on the margin somewhat above the coral mound areas and  
594 are not exclusively depending on SPOM settling from the surface (like at the Namibian 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.



616

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

#### 621 **4.5 Implications**

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

#### 630 **5. Conclusions**

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



636 dropped below  $0.01 \text{ ml l}^{-1}$ , only fossil CWC mounds covered by a community dominated by sponges and  
637 bryozoans were found. This community survives as it receives periodically waters with slightly higher  
638  $\text{DO}_{\text{conc}}$  ( $>0.03 \text{ ml l}^{-1}$ ) due to regular tidal oscillations (semi diurnal) and erratic wind events (seasonal). At  
639 the same time, a high quality and quantity of SPOM sinking down from the surface water mass enables  
640 the epifaunal community to survive despite the oxygen stress and sustain its metabolic energy demand  
641 at the Namibian OMZ, while CWCs are not capable to withstand such extreme conditions. In contrast,  
642 thriving CWCs on the Angolan coral mounds were encountered despite the overall hypoxic conditions.  
643 The  $\text{DO}_{\text{conc}}$  were slightly higher than those on the Namibian margin, but nevertheless below the lowest  
644 threshold that was so far reported for *L. pertusa* (Ramos et al., 2017; Davies et al., 2010; Davies et al.,  
645 2008). In combination with temperatures, close to the upper limits for *L. pertusa*, metabolic energy  
646 demand probably reached a maximum. High energy requirements might have been compensated by the  
647 general high availability of fresh resuspended SPOM. Fresh SPOM is accumulated on the Angolan margin  
648 just above the CWC area and is regularly supplied due to mixing by semidiurnal tidal currents, despite  
649 the restricted sinking of SPOM from the surface due to the strong stratification.

## 650 6. Data availability

651 Data will be uploaded to Pangea after publication.

652

## 653 7. Author contribution

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

661

## 662 8. Competing interests

663 The authors declare that they have no conflict of interest.

664



## 665 9. Acknowledgements

666 We thank the Captain of the RV *Meteor* cruise M122, Rainer Hammacher, his officers and crew, which  
667 contributed to the success of this cruise. We also like to thank the scientific and technical staff for their  
668 assistance during the cruise and the work in the laboratory. Greatly acknowledged are the efforts from  
669 the German Diplomatic Corps in the German Embassies in Windhoek and Luanda and in the Foreign  
670 Office in Berlin. We thank the German Science Foundation (DFG) for providing ship time on RV *Meteor*  
671 and for funding the ROV *Squid* operations to investigate the cold-water coral ecosystems off Angola and  
672 Namibia. This work was further supported through the DFG Research Center/ Cluster of Excellence  
673 “MARUM – The Ocean in the Earth System”. UH is funded by the SponGES project, which received  
674 funding from the European Union's Horizon 2020 research and innovation program under grant  
675 agreement No 679849. FM is supported by the Innovational Research Incentives Scheme of the  
676 Netherlands Organisation for Scientific Research (NWO-VIDI grant 016.161.360). GJR is supported by the  
677 Netherlands Earth System Science Centre (NESSC), financially supported by the Ministry of Education,  
678 Culture and Science (OCW). We also thank the Norwegian Research Council (NRC) for funding. KJ is  
679 funded through the FATE project (Fate of cold-water coral reefs – identifying drivers of ecosystem  
680 change).

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## 936 11. Figure captions

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



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

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

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

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

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

968 **Figure 6** Composite records of SPOM collected by the McLane pump of the ALBEX lander at the Namibian and Angolan margins  
969 during all three deployments. (a)  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotopic values at the Namibian (red dots) and Angolan (blue and green dots)  
970 margins. Indicated by the square boxes are common isotopic values of terrestrial and marine organic matter (Boutton 1991,  
971 Holmes et al. 1997, Sigman et al. 2009). The relative contribution of terrestrial material (green boxes) is increasing with a more  
972 negative  $\delta^{13}\text{C}$  value. (b) Total organic carbon (TOC) and nitrogen (N) concentration of the SPOM. Values of the Namibian  
973 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).  
974 Dissolved oxygen concentrations are included to show the higher nutrient concentrations in less oxygenated water.



975 **Figure 7** CTD transect across the Angolan margin. Shown are data for (a) potential temperature ( $^{\circ}\text{C}$ ), (b) salinity (PSU), (c)  
 976 dissolved oxygen concentration ( $\text{ml l}^{-1}$ ), (d) fluorescence ( $\text{mg m}^{-3}$ ), (e) turbidity (NTU) (data plotted using Ocean Data View  
 977 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  
 978 deployments are indicated by colored dots.

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

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

## 988 12. Tables

989 **Table 1.** Metadata of lander deployments conducted during RV *Meteor* cruise M122 (ANNA) in January 2016. The deployment  
 990 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	$20^{\circ}44.03'$	$12^{\circ}49.23'$	210	7.8	+ particle pump
	20508-1	off-mound	TROL	01.- 09.01.16	$20^{\circ}44.03'$	$12^{\circ}49.14'$	220	7.8	
	20506-1	off-mound	SLM	01.- 16.01.16	$20^{\circ}43.93'$	$12^{\circ}49.11'$	231	12.5	
Angola	20921-1	off-mound	ALBEX	20.- 23.01.16	$9^{\circ}46.16'$	$12^{\circ}45.96'$	342	2.5	+ particle pump
	20940-1	off-mound	ALBEX	23.- 26.01.16	$9^{\circ}43.84'$	$12^{\circ}42.15'$	532	2.6	+ particle pump
	20916-1	off-mound	TROL	19.- 26.01.16	$9^{\circ}43.66'$	$12^{\circ}42.09'$	526	6.8	
	20915-2	off-mound	SLM	19.- 26.01.16	$9^{\circ}43.87'$	$12^{\circ}43.87'$	430	6.8	

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



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

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