Interactive comment on “Environmental factors influencing cold-water coral ecosystems in the oxygen minimum zones on the Angolan and Namibian margins” by Ulrike Hanz et al.

First of all we would like to thank the reviewer for the positive and helpful comments. We carefully went through all the comments and suggestions. We have adjusted the manuscript according to the comments made. Below we provide a description of the adjustments made, addressing the reviewers remarks.

Kind regards,

Ulrike Hanz (corresponding author)

Anonymous Referee #1

Received and published: 15 May 2019

The manuscript by Hanz et al. titled ‘Environmental factors influencing cold-water coral ecosystems in the oxygen minimum zones on the Angolan and Namibian margins’ report observations of live and extinct coral mounds and associated fauna along the southwestern margin of Africa (South Atlantic). The authors contrast 2 areas showing distinct cold-water corals patterns, one barren (Namibian margin) and one thriving (Angolan margin). The authors couple these observations with oceanographic properties in the vicinity of these mounds acquired with benthic landers and CTD. The authors report interesting findings: cold-water corals (and associated fauna) are not thought to occur at such low oxygen concentrations, and therefore is provided a detailed rationale of the various physical processes that could maintain the existence of these corals in (perhaps short-lived) hypoxic conditions. The manuscript is well written and provide interesting insights and details on the ecology and physiology of cold-water corals, here the scleractinian Lophelia pertusa. Given that observations of other megafauna are reported – e.g. along the Namibian margin on extinct coral mounds – this study is also broadly relevant to deep-sea biology, especially in the context of the presence of Oxygen Minimum Zones.
I enjoyed reading the manuscript and consider it an important contribution to the field of deep-sea biology. It is very relevant to obtain this ecological information to more accurately forecast impacts of a changing ocean and constrain habitat suitability models.
I do not have major comments on the content of the manuscript. My comments are very specific (needed clarifications) and most relate to technical corrections.

Reply on specific comments:

L291-293: The South Atlantic Subtropical Surface Water (SASSW) is not described in Section 2.1.1. Oceanographic setting. Could you add a short specification about the origin of this water mass to situate the reader?

A short description of SASSW was added.

Figure 4: Please specify geographic orientation relative to land (i.e. on the right?). I’m also confused by the statement at L309 that the OMZ was stretching at least 100 km offshore. Only 50 km is shown in the figure. Is this accurate or am I misunderstanding the figure?

This is a misunderstanding coming from the Figure. Figure 4 does not show the 50 km closest to the shore, but the shore is about 45 km further to the east (right).

Technical corrections:

L35: ‘barotropic’
Changed.

L104: What does the 7_ refer to? Geographic coordinates, temperature? Please specify.
It refers to the geographical coordinate. We changed it to 7° S.

Figure 1: There is no a, b and c on the figure.
The figure was changed accordingly.

L211: No comma after ‘Both’.
The comma was removed.

L226: water column in 2 words.
Changed.

L242: The citation for R should read ‘R Core Team, Year’.
The citation was updated.

L243: ‘shorter term trends’
Changed.

L281: “free waves”
Changed.

L284: using
Changed.

L323: Is the date accurate? Year is 2018?
Indeed this is not accurate. It should be 2016. We modified the text.

L470: a temporal
Changed.

L517: Did you mean Namibian margin?
Yes we did. The text was changed accordingly.

L524: limits3
Changed.

L577: no comma after both
The comma was removed.

L595: that
Changed.

Interactive comment on "Environmental factors influencing cold-water coral ecosystems in the oxygen minimum zones on the Angolan and Namibian margins" by Ulrike Hanz et al.

We wish to thank the reviewer for the efforts and input provided. We carefully went through all the comments and suggestions and have adjusted the manuscript accordingly. Below we provide a description of the adjustments made, addressing the reviewers remarks.

Kind regards,

Ulrike Hanz (corresponding author)

Anonymous Referee #2
Received and published: 24 July 2019

This paper, according to the title, is about environmental factors influencing cold-water coral ecosystems in the oxygen minimum zones on the Angolan and Namibian margins. It describes results from a cruise off the southwest coast of the continent of Africa carried out in 2016. Specifically the cruise targeted two areas where previous work has suggested the presence of cold-water coral reef structures, one off the coast of Namibia and one further north off the coast of Angola. At each of the 2 sites landers were deployed, and across each site transects of CTD casts were made. There are numerous problems with the manuscript as it is written, many of which could easily be rectified. The first is that the paper is not really about cold-water coral ecosystems. The structures sampled in the Namibian sector are home to a deep water assemblage which just happens to have grown on the relict remains of a cold-water reef that died thousands of years ago. It could just have easily grown on emerging bed-rock, an oil platform or a relatively recent wreck. While what was found may be informative about hard-substrate dwelling assemblages, it tells us nothing about cold-water corals.

We agree that the ecosystem on the Namibian margin is not a cold-water coral ecosystem. We have emphasized in the text that it is a deep-water assemblage of sponges and bryozoans that is growing on cold-water coral remains, which grows in extremely low oxygen concentrations. We also have adapted the title of the manuscript.

The findings from the Angolan sector, on the other hand, do contain information relevant to our knowledge about cold-water corals, specifically extending our knowledge about the environmental envelope within which reefs may be able to survive, with some limited evidence for mechanisms which may assist their survival. Overall the question that the manuscript raises is why there are no living corals off Namibia, given that the conditions off Angola are not highly different and all the factors that apparently mitigate low oxygen there, such as abundant high quality food and tidal excursions replenishing depleted oxygen, are also present off Namibia where they support a different assemblage.
Much of the manuscript is unfocussed and over-detailed. It reads like a cruise report. A large proportion of the information given is presented in formats that are difficult to digest and are ultimately irrelevant in the context of the paper. We do not need to know that 2 landers were deployed but only the data from one is used here, for example.

We have shortened the Materials and Method section and went through the manuscript to remove unnecessary information.

Samples for particulates and photo-pigments may have been collected from the CTDs, but there is no evidence analyses of these samples are used in the manuscript.

We have removed this from the manuscript, see comment above.

And so on. Several pages of text could be replaced by a table and/or as supplementary material, allowing the reader to focus on the portions of the data and interpretation that are directly relevant to the subject of the paper, namely factors influencing deepwater hard-substratum assemblages and supporting their survival in zones of reduced oxygen availability.

Specific comments:

P2 L35 Barotropic not barotrophic
Changed.

P2 L37-39 Dead coral mounds are not CWCs, so a complete rewrite with consistent nomenclature is recommended
It was changed in all relevant sections of the manuscript.

P2 L45 'Compensate' should be followed by 'for'
We have added "for".

P3 L54 et seq. Spacing among references is needed
A spacing was added to all relevant references.

P3 L72 If aragonite saturation is important why is it not mentioned in the rest of the manuscript, and why was it not measured in this study?
In this study we did not focus on the aragonite saturation even though it is an important factor. It is expected to not be a limiting factor in the Atlantic at these depths.

P3 L77 If a specific density envelope is important why is it not mentioned in the rest of the manuscript, and why was it not measured?
The appearance of CWCs in relation to the density envelope has been added to the discussion (L653ff).

P5 L114-118 Are key parameters influencing CWC growth and therefore mound development really the focus of this investigation? What do the surveys from Namibia tell us about CWC growth? There are no living CWCs there. What are the new insights into susceptibility?
The focus of this manuscript is on benthic communities growing on coral mounds in oxygen depleted environments. We agree with the reviewer that the communities on the Namibian margin are no CWC ecosystems. We adapted the manuscript accordingly (see comment above).

P5 L127 All acronyms (here OMZ) should be defined on first occurrence in the manuscript.
OMZ was defined in L117.

P6 L152-P7 L166 There were no CWCs at the Namibian site, only dead rubble with limited deep-water hard-bottom assemblages.
We have changed the description of the benthic community to avoid confusion.

P8 L180-190 Important records and details of the biological communities were recorded, begging the question why more was not made of this data in the paper. Many fish species were recorded in the Angolan reefs, which presumably aren't all OMZ specialists.
This was unfortunately not the focus of this manuscript, whereas we do agree that this information is very interesting. These data will be part of other manuscripts.

P9 et seq. Methods and results. We do not need complete details of everything that was done on the cruise, the cruise report is already referenced, we only need the sampling and analysis details for the variables of relevance to this paper. Much could be done to condense text into a table or SI, to considerably shorten and focus the manuscript.
We do agree with the reviewer. We have shortened the text to only focus on relevant information.

P10 L240 Why was turbidity data only collected from Angola, and were the data used?
Unfortunately no turbidity data were collected on the Namibian margin, due to technical issues with the sensor on the CTD. The data is shown in Figure 5 (CTD transect across the Angolan margin).

P10 L274 What instrument was used to analyse the absorbtion spectrum etc?
A Waters Acquity UPLC system was used (was added to material and methods L300)

P11 L284-285 'unsinf' - ? Why were the data mean and trends removed?
The tidal analysis outcome will not change in respect of significant constituents or their amplitudes whether or not the means and trends are within the input data. It belongs to the standard procedure of tidal analysis.

P12 L294 Why was 'SASSW' not discussed in the section describing water masses earlier? SCAW should presumably be SACW. The definition of SACW belongs in that section, not in the results.
A short description of SASSW and AAIW was added (L 160ff) and the definition of SACW was moved to section 2.1.1.

P12 L297 Temperature differences must not be confused with actual temperatures. The -1.3 and -0.2 here are differences but they are reported as a values. This is a problem throughout the manuscript. AAIW was not mentioned in the section on water masses, and should have been.
We agree that this might be confusing. Temperature differences are now reported as Δ values. AAIW is now mentioned in section 2.1.1. (L164).

P12 L305 et seq. Why DOconc and not simply DO, or even DO2? Abbreviations should be defined on first use.
DO_{conc} is the shortest abbreviation for dissolved oxygen (DO) concentration. The definition was added.

P13 L321 Table 1 is only metadata. A table of actual data would be helpful and reduce the need for a lot of text.

An additional table with values from the lander deployments at the Angolan and Namibian margin was added (Table 2).

P13 L324 et seq. Are the r values Spearman rank correlations? What is the justification for this approach? Are values truly independent? Would a more multivariate approach not have been more appropriate? Why do correlations between temperature and DO switch from negative to positive?
Spearman rank correlations were used because they show a general statistical correlation of two variables (water characteristics). Oxygen concentrations for example are not independent from temperature, whereas these dependencies are not strongly influencing the outcome since we were not investigating underlying causes for the correlations, but wanted to show how the separate variables correlate.
Correlations did not switch from negative to positive. Both datasets from Angola come from two separate deployments in two separate depths and therefore show to separate correlations. We have indicated this more clearly in Fig 7.

P14 L331 It is unclear to this non-expert what several of the variables in Table 2 actually are/mean.
I removed the polarization ratio. Other variables are explained in the table caption.

P14 L333 'whereafter', not 'where after'
Changed.

P14 L327-341 Does this section not simply describe what is well known about the forces (e.g. along-shore winds) driving upwelling along this coast? Why is what is known not reviewed or discussed in more detail in this manuscript?
Yes, it serves as an example how the seasonal variations change the water characteristics at the margin. It is reviewed in section 4.1.

P14 L342-347 Isn't this the key (and only really relevant) result? More should be made of it. Is the method appropriate for calculating such incursions?
It would of course be much nicer to be able to capture these incursions with for example a mooring comprising the whole water column, but unfortunately we were not able to use a mooring in this study. We think that this method is the best method we can use with the available data. We are aware that this is an estimation.

P16 L356-372 Was CTD data not used?
Not used in this manuscript. (Changed in the method section, L275ff).

P16 L374 The figure encapsulates all that we need to know about POM inputs, so the text should describe what it shows and the authors are encouraged to leave out much of the irrelevant details elsewhere in the manuscript. The figure also combines details from both sites. The authors could shorten the manuscript by producing combined sections comparing and contrasting the sites, rather than describing the 2 sites separately.
We have changed the result section according to the recommendation made and combined both sites.

P16 L386 What is this surface water layer – a river plume? Should it not be described in the section about hydrography?
The river influence is now described in section 2.1.1. (L164f).

P18 L408 Should this not read 'from the shallowest to the deepest'? Some of this section is confusing.
The paragraph was changed to remove eventual confusion.

P19 L425 What does 'p<0.01, deep' mean?
It means that the correlation of turbidity and oxygen concentration during the deep deployment is significant. We changed the description to make it more clear.

P19 L427-430 This is the result of relevance and should be focused on.
It is focused on in section 4.4 and Figure 9. We have tried to stress the importance slightly more by adapting the text in section 4.4.

P21 L438 Would lower TOC and N in deeper waters not be expected? Could some of this text not be replaced with a figure, or is it repeating what is already in the figure?
Yes, it is expected. It is a description of what is shown in Figure 8.

P21 L454 I do not accept that what was observed off Namibia can be regarded as a CWC.
We have made the changes throughout the whole manuscript, see also response above.

P21 L461 Who says seasonality has a major impact? Reference(s)? A better review and incorporation of what is known about this coast needs to be included in the manuscript.
Relevant references were added to section 4.1.

P21 L465 If the measurements made in this study are not the relevant ones, what is the point of the whole manuscript?
These are the first records of environmental factors in these two specific areas. These data provide valuable insight about daily environmental fluctuations even though it is a short term record. Main outcome is that the boundaries previously described on CWC oxygen tolerance need to be adapted. Indeed the data only provides a snapshot in time and ranges can be even larger. However, this does not devaluate the measurements. We still measured the lowest ever recorded oxygen concentrations for *L. pertusa*.

P22 L468 What is ESACW? This wasn't mentioned before.
ESACW was mentioned in L147.

P22 L470 'a temporal' not 'an temporal'
Changed.

P22 L472-477 References are needed for all the statements in this paragraph (and elsewhere in the manuscript).
References were added.

P22 L484 Some of this paragraph belongs in the results.
Specific values were removed.

P22 L495 How can the authors, based on limited cruise data, possibly determine what determines the absence of living CWCs from the Namibian margin?
We can not determine what determines the absence of living CWCs but we can hypothesize, since it is accepted that environmental conditions changed at the same time with the CWCs disappearance (Tamborrino et al. accepted).

P23 L517 ‘Namibian’ not ‘Angolan’?
Yes, Corrected.

P23 L518 DO is an input to habitat suitability modelling, not an output, surely?
It is only an input. Corrected.

P23 L524 Not ‘limits3’
Corrected.

P24 L530-539 The conclusion appears to be drawn that increased food availability compensates for decreased oxygen or higher temperature. Is it not the case that increased food in the water column is actually one of the main causes of decreased oxygen availability in these regions? This doesn’t seem to be mentioned anywhere.
We agree with the reviewer and have adapted the text accordingly (L661ff).

P24 L551 What does ‘loss of energy which and associated increased energy demand like’ mean?
It should be ‘loss of energy with an associated increased energy demand’. Corrected.

P24 L555 ‘an’ before ‘energy (food) availability’ unnecessary.
‘An’ was removed.

P25 L563 If high quality food is available off Namibia but there are no living corals how can it be concluded that the presence of the SPOM promotes and/or supports coral growth?
It can not be concluded for CWCs at the Namibian margin. It can only be suggested for the benthic fauna which is associated to the dead cold-water coral framework, since it still survives in otherwise stressful conditions.

P25 L579 ‘leading to’ not ‘leads to’
Corrected.

P25 L581-584 Some of this information belongs in the results section.
Information was removed from this section.

P25 L585 Why does terrestrial POM constitute a less suitable food source, and who says so (references)?
Because terrestrial matter includes carbon rich polymeric material (cellulose, hemicellulose and lignin) which cannot easily be taken up by marine organisms (Hedges and Oades, 1997). A reference and explanation was added (L605ff).

P25 L589 Delivery rates of SPOM were not measured, only the presence of POM with speculation as to its source(s).
True, the presence of SPOM was meant, corrected.

P26 L592 What is the source of this fresh POM?
It is directly sinking as well as advected organic matter from the surface ocean. Explanation added (L723f).

P26 L595 ‘fact that’ not ‘fact, that’s’
Corrected.

P26 L603 How are these currents likely to be responsible for the delivery of fresh SPOM from the surface productive zone?
Currents lead to mixing of the water layers, which allows material from the surface water layer to sink down to the mound sites. Explanation was added to the manuscript (736f)

P26 L610 I do not understand how the nepheloid layer is formed by bottom erosion due to the intensification of near-bottom water movements, which is indicated by maxima of the buoyancy frequency N2 in 225 and 300 m depth. Explain and provide evidence.
The interaction of internal waves with the margin topography will intensify currents and therefore mixing. These internal waves can move on density gradients which are indicated by buoyancy frequency maxima. The manuscript was changed and a better explanation was added.

P27 L622 et seq. The examples of ecological roles of CWCs are not applicable in OMZs.
The benthic communities on the cold-water coral rubble were meant. We have changed the text.

P27 L626-627 CWCs are sometimes able to cope with low oxygen levels (there are none off Namibia).
This is due to the fact that oxygen levels are too low at the Namibian margin.

The line numbers refers to the track changes document.

List of relevant changes

Spacing was added between all relevant references through the whole manuscript. Figures were moved and numbers were changed in all relevant cases.

P1 L2f Title was adapted

P2 L24f Abstract was adapted in order to stress that mounds on the Namibian margin do not include living CWCs. Non relevant information was removed from the abstract (L40f).

P2 L39 “Barotropic” was corrected.

P2 L52 “Compensate for” was corrected.

P5 L115: Geographical location (° S) was added to make clear that it is a geographical coordinate.

P6 L126 The absence of CWC at the Namibian margin was stressed.

P6 L150f The definition of SACW was moved to this section.

P7 L160ff A description of the water masses (SASSW and AAIW) and the influence of major rivers at the Angolan margin was added.

P8 Figure 1 a), b) and c) was added to the Figure.

P9 L182 CWC were changed to “community” to stress the absence of alive CWC.

P9 L187 It was stressed that only dead CWC were found at the Namibian margin.

P11 L221ff Non relevant information about the lander deployments was removed.

P11 L240 Text was changed in order to remove unnecessary information.

P11 L255 “Water column” was corrected.

P12 L255ff Non relevant information about the CTD transects was removed.

P12 L261 Explanation why turbidity was not measured at the Namibian margin was added.

P12 L270f Citation was corrected.

P12 L272 “Short term trends” was corrected.

P12 L275ff Non relevant information about the SPOM collection was removed.

P13 L299f Instrument name was added.

P14 L310 “Free waves” was corrected.

P14 L313 “Using” was corrected.

P14 L316ff Result section was changed according to the suggestion of referee 2. Environmental characteristics of the Namibian and Angolan margin are now presented consecutively.

P14 L323f Definition of SACW was moved to section 2.1.1. “SACW” was corrected.

P14 L327 Differences are now marked as delta values.

P15 L335 Abbreviation of DO was added.

P15 L339 and L347: Position of transect in regard to the coastline was described better.

P16 L352: CTD transects of the Angolan margin are now described before the results of other measurements.

P17 Figure 5 is now the CTD transect of the Angolan margin.

P17 L376ff Near bottom environmental data of both regions are now described consecutively.

P17 L380 Differences are now marked as delta values.

P18 L381 Date was corrected.

P18 L387ff Sentences were moved to stress the influence of wind on water characteristics on the Namibian margin.

P18 L397 “~~Where~~after” was corrected

P18 L407 The inaccuracy of the method was stressed.

P18 L411 Delta was added.

P19 L413 Number of figure was changed.

P20 L420 Near bottom environmental data of Angola was moved.

P21 L442 Figure was moved.

P22 L467 Paragraph was slightly changed to avoid confusion about the shallow and deep deployment.

P23 L480 Figure number was changed.

P27 L561ff Text was changed in order to stress that there are no CWC on the Namibian margin.

P27f References were added to section 4.1.

P28 L582 “A temporal” was corrected.

P28 L598ff Specific values were removed from the discussion.

P28 L605ff Description of the influence of terrestrial organic matter was added.

P29 L636 Namibian margin was added.

P30 L639 Oxygen concentration as a model output was removed.

P30 L643 “Limits” was corrected.

P30 L653 Density envelope was added to the discussion.

P30 L661ff Explanation of a negative feedback of high food availability on the oxygen concentration was added.

P31 L676ff Sentence was removed.

P31 L681 “An” removed.

P31f L688ff Text was shortened and specific values were removed from the discussion.

P32 L720 Delivery was replaced by availability.

P32 L724 Unnecessary text was removed.

P33 L736 Short description of how currents are responsible to mix the water masses and therefore are responsible in delivering SPOM to the mound areas.

P33 L743ff Section was changed to explain the function and location of the internal waves.

P34 L758ff Implications were fused with the conclusion.

P34 L769ff Text was changed to stress the absence of living CWCs on the Namibian margin.

P41 L1047 Reference was updated.

P44f L1159 Table with environmental properties of the Namibian and Angolan margin was added to the manuscript.

P45 L1163 Polarization ratio was removed from table 3.

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

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Abstract

Thriving benthic communities were observed in the oxygen minimum zones along the southwestern African margin. On ~~T~~the Namibian margin ~~was characterized by the presence of~~ fossil cold-water coral mounds were overgrown by sponges and bryozoans, while ~~on~~ the Angolan margin was characterized by cold-water coral mounds covered by a living coral reef ~~were observed~~. ~~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~~benthic ~~fauna~~ communities ~~can nevertheless thrive~~differ in both areas, present day environmental conditions ~~at the southwestern African margin~~ were assessed, using ~~. Downslope~~ CTD transects and ~~the deployment of~~ bottom landers ~~were used~~ to investigate spatial and temporal variations of environmental properties. ~~Temporal~~ Near-bottom measurements ~~in the mound areas~~ recorded ~~oscillating~~ low dissolved oxygen concentrations on the Namibian margin of 0-0.~~17~~ 15 ml l^{-1} (≙ 0-9 % saturation) ~~on the Namibian~~ and on the Angolan margin of 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 barotrop~~h~~ic 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~~benthic communities from below and above the ~~hypoxic~~ zone of low oxygen. Concurrently, the delivery of high quantity and quality ~~of suspended particulate~~ organic matter was observed, ~~which serves as a~~ being an important food source for ~~cold-water corals~~the benthic fauna. On the Namibian ~~slope~~ margin organic matter ~~indicates a completely marine source and~~ originate~~s~~d directly from the surface productive zone, whereas on~~, whereas on~~ the Angolan margin the geochemical signature of organic ~~material~~ matter suggested~~s~~ an additional mechanism~~s~~ of food supply. A nepheloid layer observed above the cold-water corals ~~mound area on the Angolan margin~~ may constitute~~s~~ a reservoir of ~~fresh~~ organic matter, facilitating a constant supply of food particles by tidal mixing. ~~in both areas~~~~This~~Our data suggest~~s~~ that the benthic fauna on the Namibian margin as well as ~~that~~ the cold-water coral communities ~~as well as the associated fauna~~ on the Angolan margin may compensate for unfavorable conditions ~~induced by~~ of low oxygen levels and high temperatures with ~~an~~ enhanced availability of food~~.~~, while ~~O~~ anoxic conditions on the Namibian margin are at present a limiting factor for cold-water coral growth. ~~With the expected expansion of oxygen~~

~~minimum zones in the future due to anthropogenic activities, t~~This study provides an example ~~on~~ of how benthic ecosystems ~~could~~ can cope with such ~~such~~ extreme environmental conditions~~,~~ since it is~~.~~ expected that oxygen minimum zones will expand in the future due to anthropogenic activities.

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 North 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, like ~~(~~ for example aragonite saturation state, salinity and~~,~~ 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, t~~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* comes 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 was 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 the deep-sea ~~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 phytodetritus, 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). 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).Transport of surface organic matter towards CWC sites at intermediate water 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~~ was also ~~been~~ found under conditions which ~~seem~~ are 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 bottom water temperatures ~~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 comes from the Angolan margin (at 7° S; (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 whether this is related to a ~~data is lacking~~lack of data. Hydroacoustic campaigns ~~nevertheless~~ revealed extended areas off Angola and Namibia with structures that morphologically resemble coral mound~~s~~ structures known from the NE Atlantic (M76-3, MSM20-1; ~~(~~Geissler et al., 2013; Zabel et al., 2012).

~~Two~~ Therefore two of 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~~ found 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 to identify why ~~cold-water corals~~CWCs thrive on the Angolan margin and are absent on the Namibian margin~~. that enable cold-water coral growth in this low oxygen environment~~. ~~To identify k~~Key parameters influencing CWCs ~~growth and therefore mound development~~, hydrographic parameters as well as chemical properties of the water column were measured~~,~~ to ~~characterizing~~ characterize the difference in 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.

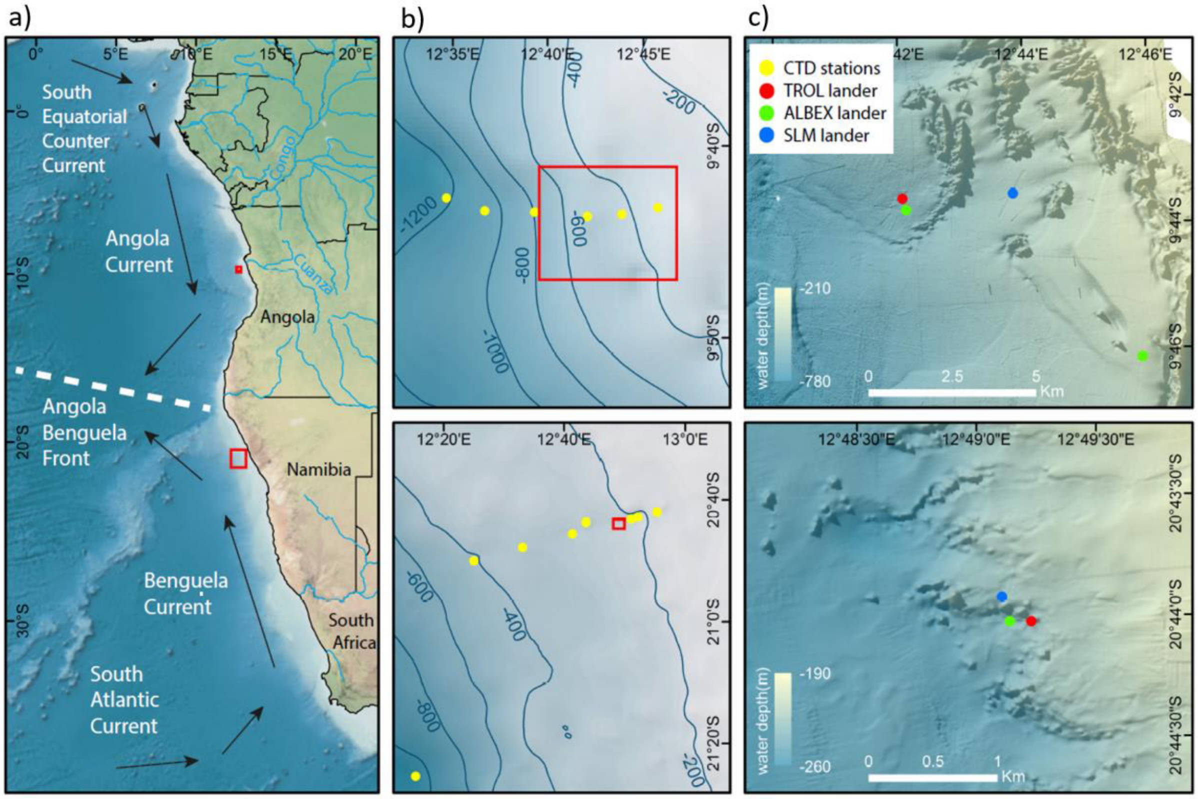
2. Material and Methods

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 results 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). SACW is defined by a linear relationship between temperature and salinity in a T-S~~-~~ plot (Shannon et al., 1987).

While the SACW flows along the continental margin the oxygen concentration is decreasing ~~c~~continuously due to remineralisation processes of organic matter 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 upwelling season in austral winter, expanding from the oceanic zone about 350 km offshore, further in-shore. (Mohrholz et al., 2014). The surface water mass at the Namibian margin is a mixture of sun warmed upwelled water and water of the Agulhas Current, which mixes in complex eddies and filaments and is called South Atlantic Subtropical Surface Water (SASSW) (Hutchings et al., 2009). At the Angolan margin the surface water is additionally influenced by water from the Cuanza and Congo rivers (Kopte et al., 2017, Fig. 1). Antarctic Intermediate Water (AAIW) ~~can be was~~is situated~~-~~ in deeper areas at the African continental margin and ~~can be~~~~was~~can be identified as the freshest water mass around 700-800 m depth (Shannon and Nelson, 1996).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Angola Benguela Front
Benguela Current
South Atlantic Current
Congo
Cuanza
Angola
Namibia
South Africa
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12°45'E
9°40'S
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CTD stations
TROL lander
ALBEX lander
SLM lander
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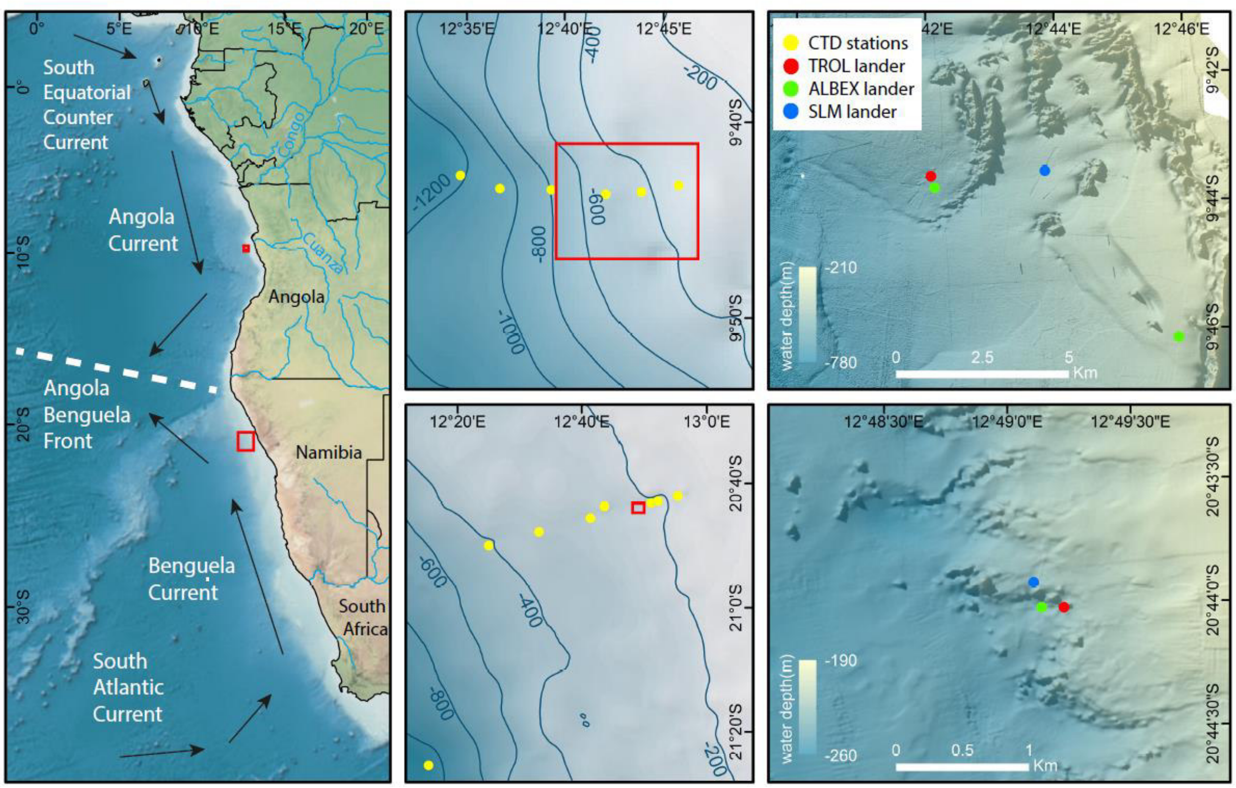
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South Atlantic Current
Congo
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Angola
Namibia
South Africa
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CTD stations
TROL lander
ALBEX lander
SLM lander
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Figure 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 mounds ~~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). Dead c~~C~~orals 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., accepted).

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~~ were present (Hebbeln et al. 2017). All mounds showed a 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).

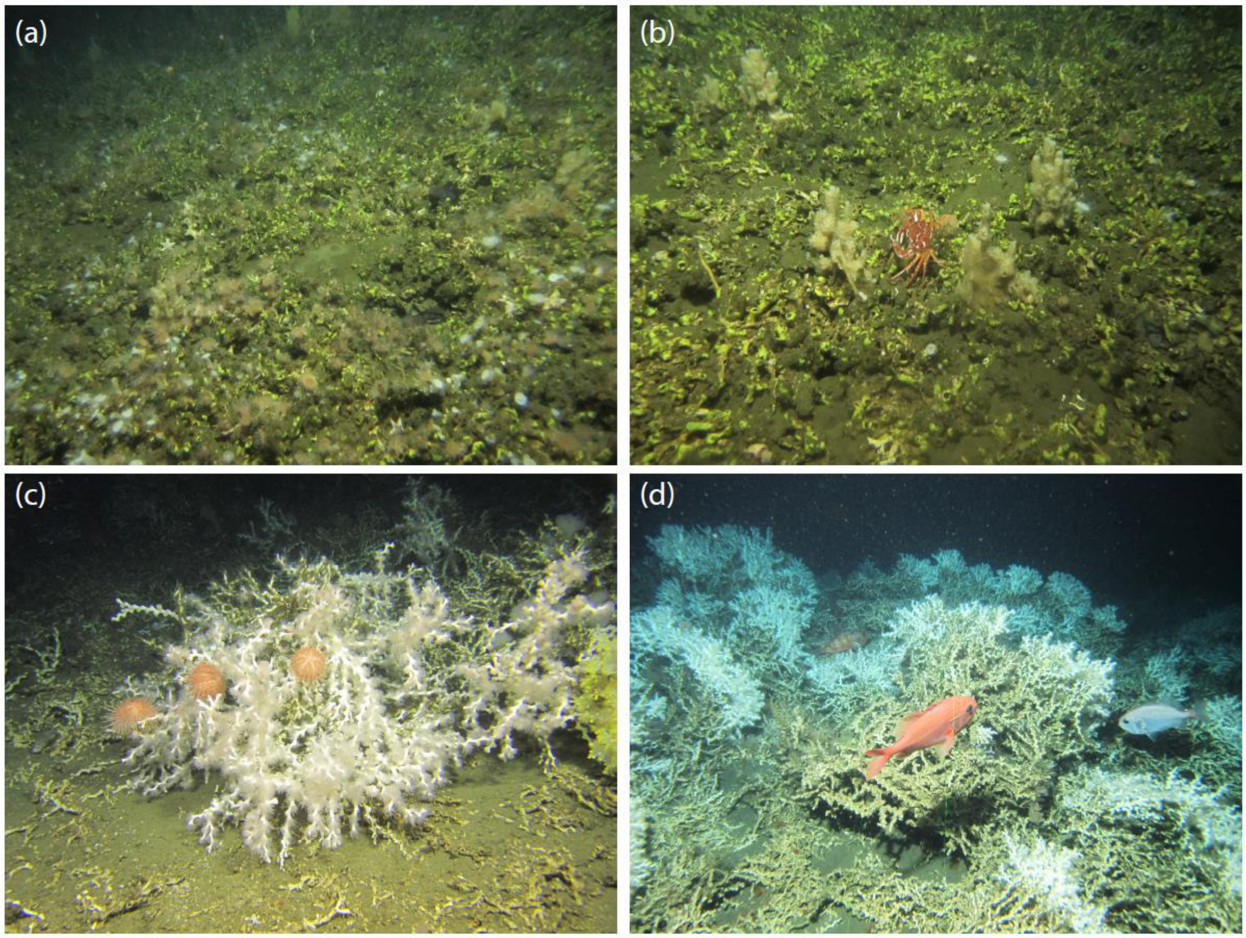

Figure 2 ROV images (copyright MARUM ROV SQUID, Bremen, Germany) showing the surface coverage of cold-water coral mounds discovered off Namibia (a, b) and Angola (c, d). Images were recorded and briefly described for their faunal composition during RV *Meteor* cruise M122 "ANNA" (see Hebbeln et al. 2017). (a) Sylvester mound, 225 m water depth. Dead coral framework entirely consisting of *L.~~ophelia~~ 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 *L. pertusa~~ophelia~~* 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~~ three 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 lander~~s~~ (ALBEX~~and TROL~~) were selected based on multibeam bathymetric data. ~~In each area, two landers were deployed simultaneously.~~ On the Namibian margin ~~one~~ the bottom 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~~the lander ~~(ALBEX)~~ was ~~first~~ deployed in the relatively shallow part of the mound zone at 340 m water depth and in the~~, and after retrieval redeployed in the deeper part of the zone at 530 m.~~while the ~~A second lander (TROL) was deployed at~~ in ~~the~~ deeper part ~~of the zone (~~at 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).~~ A second lander (TROL) was deployed simultaneously to the ALBEX lander during two deployments, whereas recorded data was very similar to the ALBEX data and is not shown here. Additionally, a GEOMAR Satellite Lander Module (SLM) was deployed off-mound in 230 m depth at the Namibian margin and at 430 m depth at the Angolan margin~~close to the NIOZ landers~~ (Fig. 1, Table 1).

~~Two landers were deployed on the Namibian and Angolan margin around mound structures (see Table 1). Both, the ALBEX and TROL lander~~ The lander ~~harbored~~w~~ere~~as equipped with ~~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 lander.~~s.~~

2.2.2 CTD transects

Vertical profiles of ~~principal~~ hydrographic parameters in the water column, 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). Turbidity data were due to technical problems only collected on the Angolan slope.~~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 data~~set~~ ~~was~~ were 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 (R Core 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 term 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~~phytoplankton sampler ~~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, Waters Acquity UPLC) 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~~analyzed from the bottom pressure and from the horizontal flow components recorded 6 m above the sea floor, ~~usinf~~ using the harmonic analysis toolbox t_tide (Pawlowicz et al., 2002). The data mean and trends were subtracted from the data before analysis.

3. Results

3.1 Water column properties~~Namibian margin~~

3.1.1 ~~Water column properties off Namibia~~Namibian margin

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 throughout 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~~ were above 14 °C and salinities ~~are~~ > 35.2, which correspond~~s~~eds to South Atlantic Subtropical Surface Water (SASSW). SACW ~~is~~ was situated underneath the SASSW and reaches down to about 700 m~~.~~, characterized by ~~SCAW is defined by a linear relationship between temperature and salinity in the TS-plot . The~~ a temperature ~~in the layer of SCACW decreases~~ from 14 ~~to~~ -7 °C ~~with depth~~ and ~~the~~ a salinity from 35.4 ~~to~~ -34.5 (Fig. 3a). ~~The~~ A deep CTD cast about 130 km from the coastline recorded a water mass with the signature of ESACW, having a lower temperature (Δ -1.3 °C) and lower salinity (Δ -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.

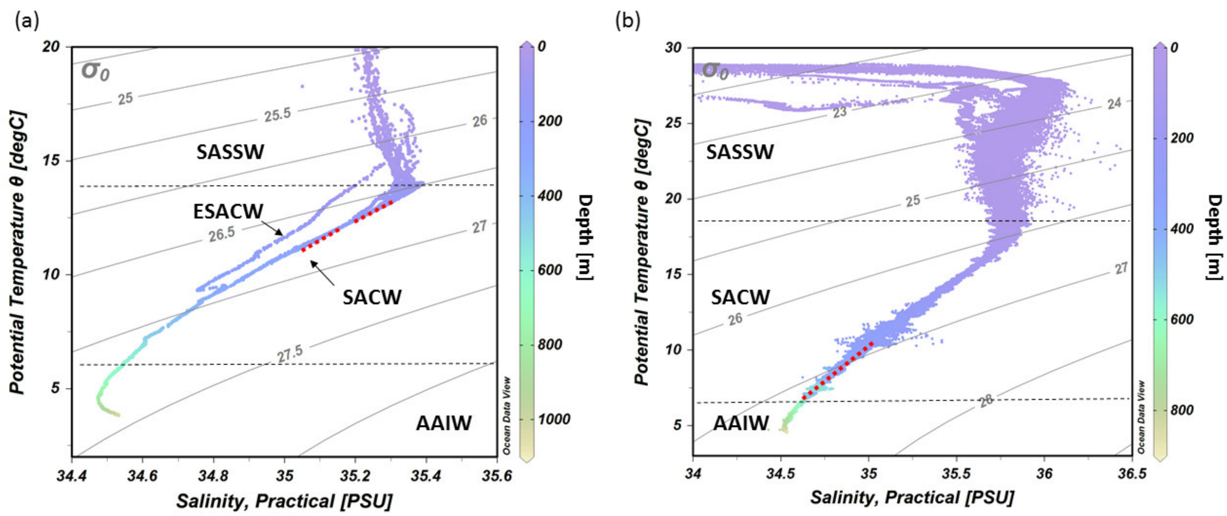

Figure 3 TS-diagrams showing the different water masses being present at the (a) Namibian and (b) Angolan margins: South Atlantic Subtropical Surface Water (SASSW), South Atlantic Central Water (SACW) and Eastern South Atlantic Central water (ESACW), Antarctic Intermediate Water (AAIW) (data plotted 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~~ (dissolved oxygen) concentration~~)~~ 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 from about 50 towards at least 100 km offshore (Fig. 4c). The upper boundary of the OMZ was relatively sharp compared to its lower limits and correspond~~s~~ed 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}.

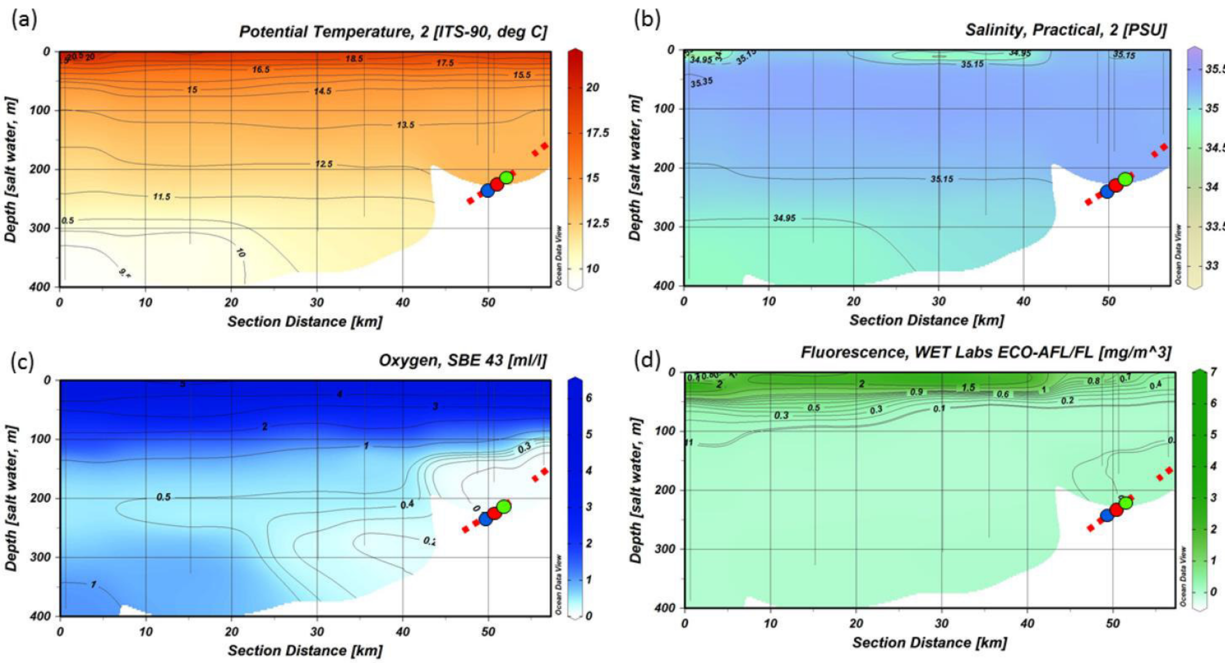

Figure 4 CTD transect across the Namibian margin from west to east towards 50 km from the coastline. ~~Shown are d~~Data are presented for: (a) potential temperature (°C),(b) salinity (PSU), (c) dissolved oxygen concentrations (ml l^{-1}), note the pronounced oxygen minimum zone (OMZ) between 100-335 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 Angolan margin

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 found down to a depth of 70 m, characterized by a higher salinity (35.8). SACW was observed between 70-600 m, showing 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 showed a sharp decrease in the DO_{conc} underneath the SASSW from 5 to <2 ml l^{-1} (Fig. 5). 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 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. 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. A distinct zone of enhanced turbidity was observed on the continental margin between 200-350 m water depth.

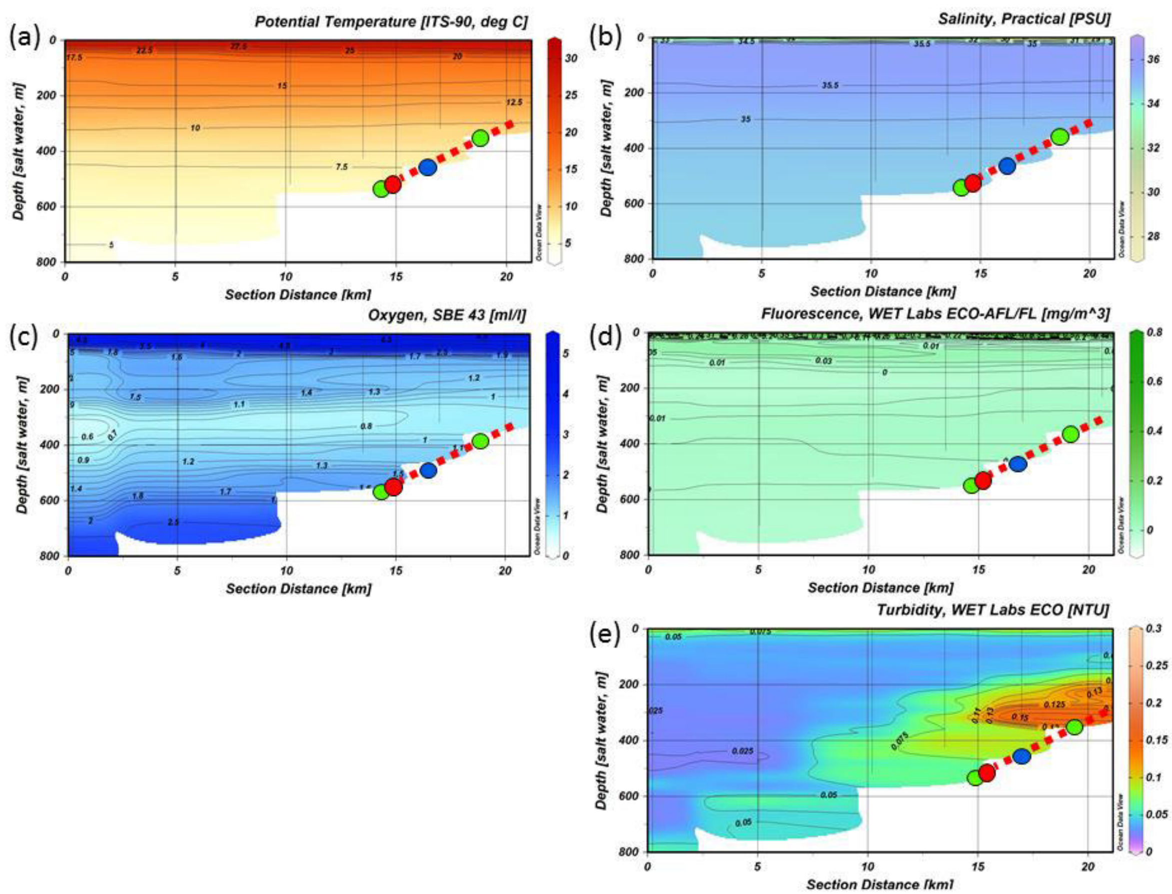

Figure 5 CTD transect across the Angolan margin. Shown are data for (a) potential temperature (°C), (b) salinity (PSU), (c) dissolved oxygen concentration (ml l^{-1}), (d) fluorescence (mg m^{-3}), (e) turbidity (NTU) (data plotted using Ocean Data View v.4.7.8; http://odv.awi.de; Schlitzer, 2011). The depth occurrence of CWC mounds is marked by a red, dashed line, the lander deployments are indicated by colored dots.

3.~~1.~~2~~2~~ Near bottom environmental data

3.2.1 Namibian margin

~~***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)~~ (Table 2, Fig. 6) showing oscillating fluctuations with a maximum semidiurnal (~~Δt~~ ΔT ~ 6h) change of ~Δ 1

°C (on 9.1.2016~~8~~). 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 DO_{conc} ~~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~~. During this period on the 6th of January~~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. The w~~W~~ind direction changed from anticlockwise cyclonic rotation towards alongshore winds. 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 on average higher DO_{conc} was present. The SLM lander recorded an average pH of 8.01.

.~~ The m~~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~~ explained >80 % of the pressure fluctuations (Table ~~2~~3), with a semidiurnal signal, M2 (principal lunar semi-diurnal), generating an amplitude of >0.35 dbar and thus being the most important constituent. Before the 6th of January the current direction oscillated between SW and SE ~~where~~ after which it changed into a dominating northern current direction~~. The current speed remained rather constant during the deployment period~~ (Fig. ~~5~~6). ~~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 estimated ~~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 (Δ up to 0.2 ml l^{-1}).

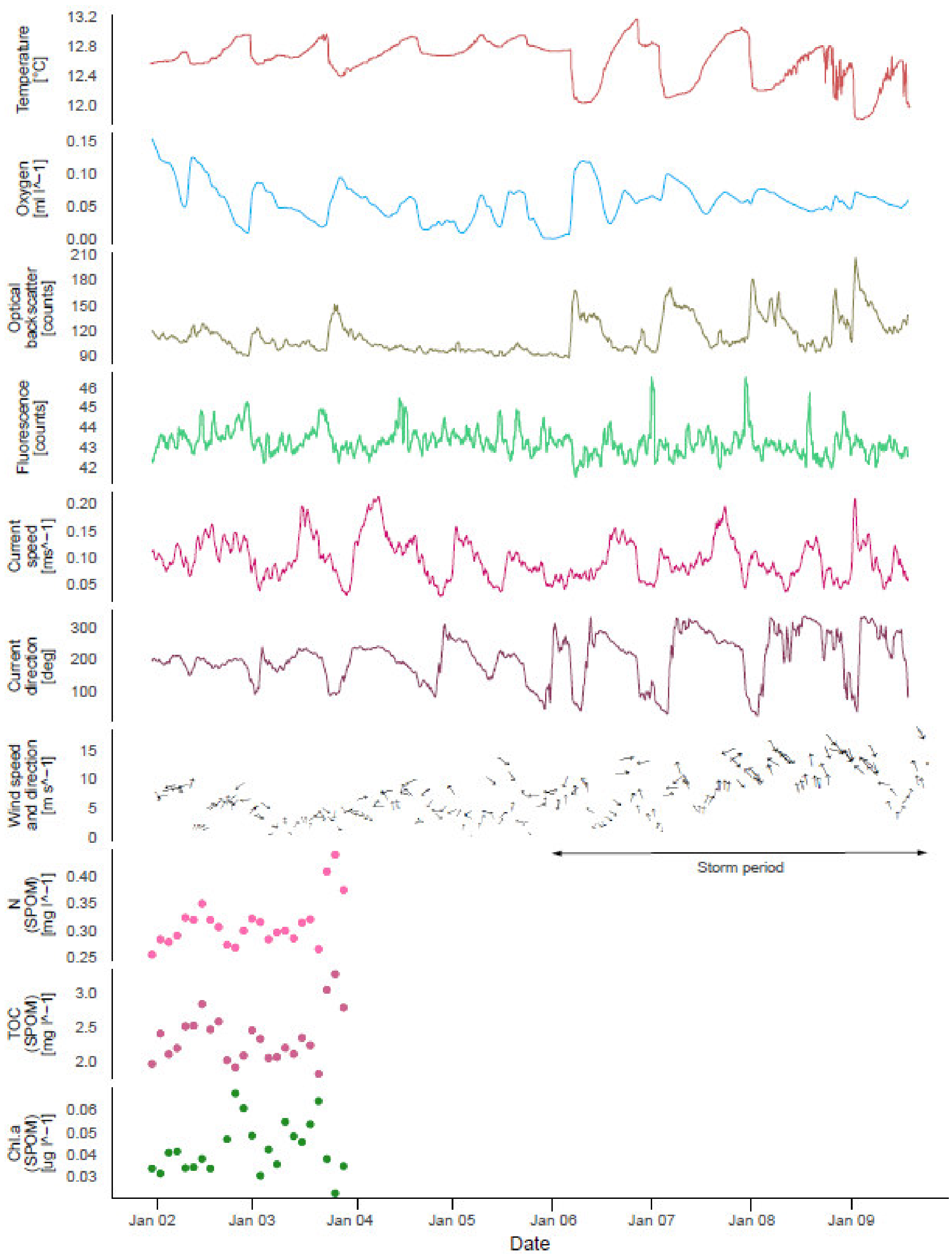

Figure 6~~5~~ Data recorded by the ALBEX lander (210 m) at the Namibian margin in January 2016. Shown are data for temperature (°C; red), dissolved oxygen concentrations (ml l^{-1}; blue), optical backscatter (turbidity; moss green), fluorescence (counts per second green), current speed (m s^{-1}; pink), 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).

3.2.2 Angolan margin

Mean bottom water temperatures was 6.73 °C at the deeper site (530 m) and 10.06 °C at the shallower site (340 m, Fig. 7, Table 2). The maximum semidiurnal (ΔT ~ 6h) temperature change was Δ 1.60 °C at the deepest site and Δ 2.4 °C at the shallow site (Fig. 7). 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), whereas the range of diurnal fluctuations was much smaller compared to the shallow site. DO_{conc} was 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, being 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 explained 29.8-54.9% of the horizontal current fluctuations. The M2 amplitude was 0.06-0.09 m s^{-1} and was the most important signal (Table 3). A decrease in turbidity was observed 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.5). 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 deployment and $r=0.50$, $p<0.01$, deep deployment). The SLM lander recorded an average pH of 8.12.

The short-term temperature fluctuations imply a vertical tidal movement of around 130 m (12.9-9.1 °C measured by lander ≙ 218-349 m depth in CTD above lander at station GeoB20966).

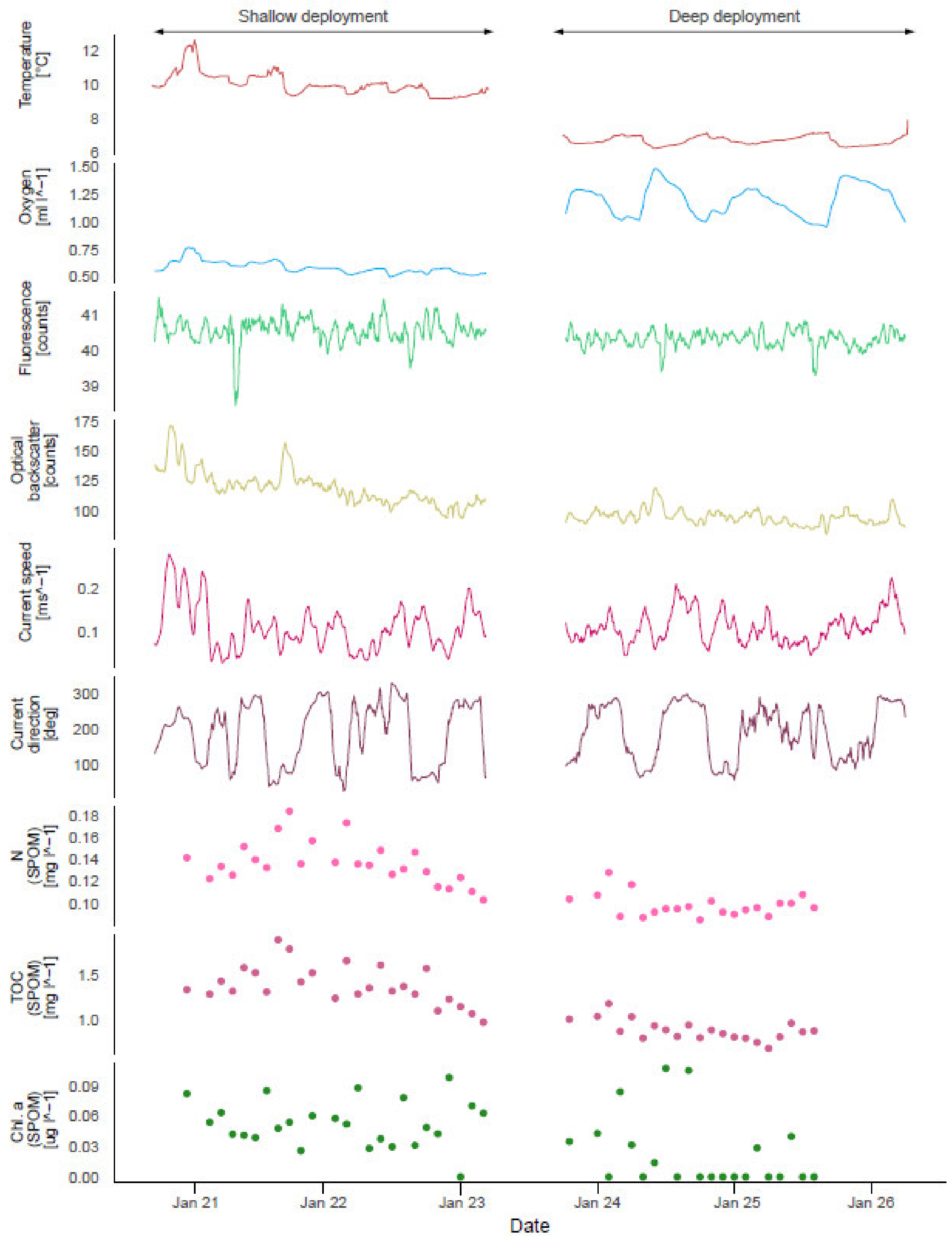

Figure 7 Lander data (ALBEX) recorded during at the shallow (~340 m water depth) and deep sites (~530 m water depth) off Angola (January 2016). Shown are temperature (°C; red), dissolved oxygen concentration (ml l^{-1}; blue), fluorescence (counts per second; green), optical backscatter (turbidity; yellow), 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.~~1.3~~3 ~~Food supply~~Suspended particulate matter

3.3.1 Namibian margin

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~~8). 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. 8a). The C/N ratio ranged from 8.5~~ to ~~-6.8 and was on average 7.4 (Fig 8b). 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~~of 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}).

3.3.2 Angolan margin

In general TOC and N concentrations of SPOM higher at the shallow compared to the deep site. Nitrogen concentrations varied around 0.14 mg l^{-1} at 340 m and around 0.1 mg l^{-1} at 530 m depth (Fig. 8b). The $\delta^{15}N$ values at the shallow site ranged from 1.6-6.2 ‰ (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 340 m and 0.9 mg l^{-1} at 530 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 chlorophyll-α concentrations of the SPOM collected by the McLane pump varied between 0.1 and 0.02 µg l^{-1}, with an average ∑Phaeopigment/ 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.

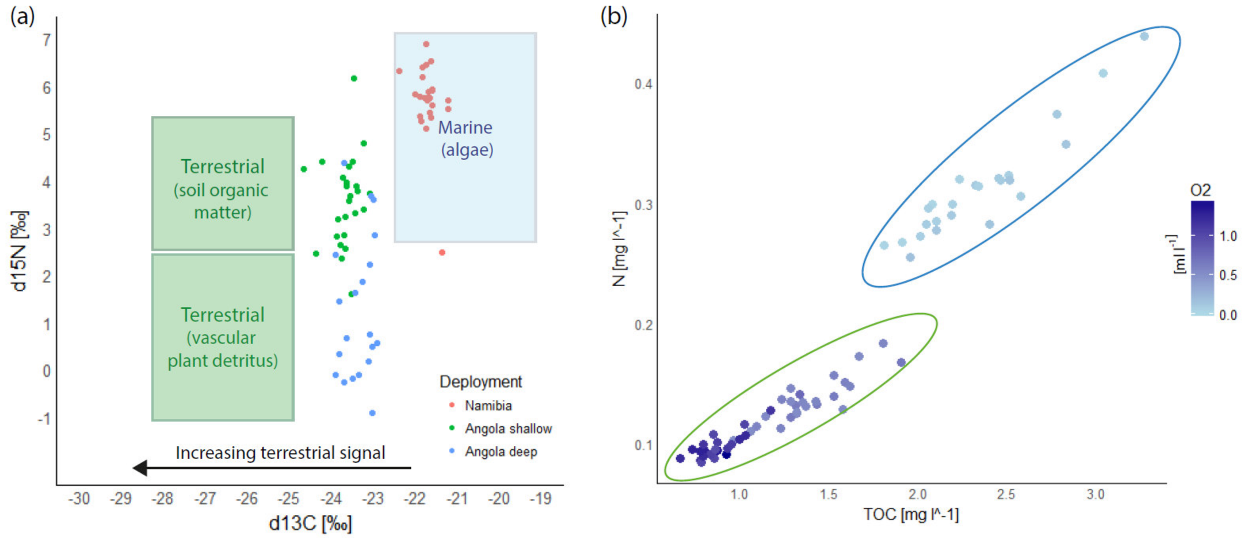

Figure ~~6~~ 8 Composite records of SPOM collected by the McLane pump of the ALBEX lander at the Namibian and Angolan margins during all three deployments. (a) $\delta^{15}N$ and $\delta^{13}C$ isotopic values at the Namibian (red dots) and Angolan (blue and green dots) margins. Indicated by the square 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 $\delta^{13}C$ 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 found down to a depth of 70 m, characterized by a higher salinity (35.8). SACW was observed between 70-600 m, featuring showing 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 showed 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 aA distinct zone of enhanced turbidity was obsderved on the continental margin between 200-350 m water depth.

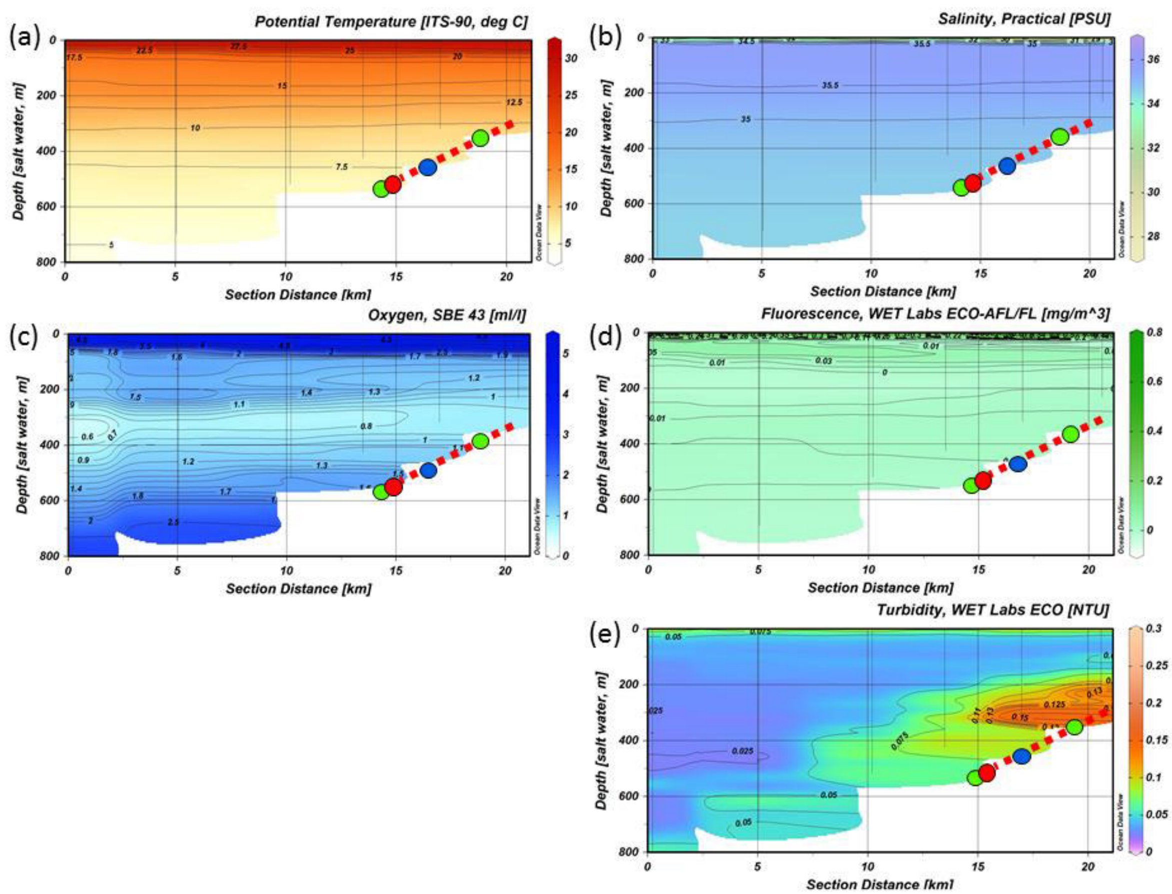

Figure 7 CTD transect across the Angolan margin. Shown are data for (a) potential temperature (°C), (b) salinity (PSU), (c) dissolved oxygen concentration (ml l^{-1}), (d) fluorescence (mg m^{-3}), (e) turbidity (NTU) (data plotted using Ocean Data View v.4.7.8; http://odv.awi.de; Schlitzer, 2011). The 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 aA decreasing decrease in turbidity was observed 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).

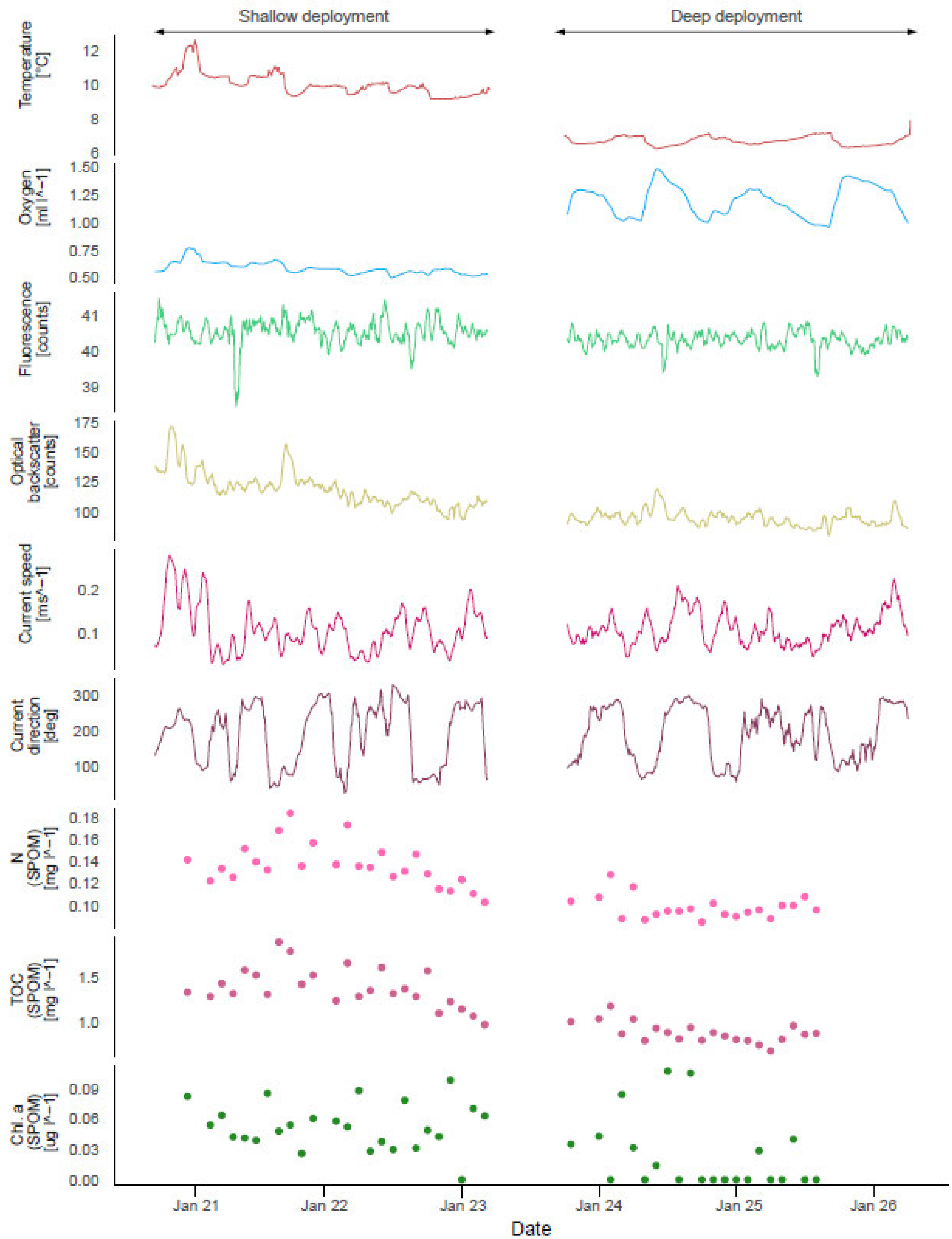

Figure 8 Lander data (ALBEX) recorded during the at the shallow (~340 m water depth) and deep deployments sites (~530 m water depth) off Angola (January 2016). Shown are temperature (°C; red), dissolved oxygen concentration (ml l^{-1}; blue), fluorescence (counts per second; green), optical backscatter (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~~ along the oxygen-limited southwestern African margin, ~~two CWC mound ecosystems~~CWC mounds with two distinct benthic ecosystems were ~~observed~~ found~~along the Namibian and Angolan margins~~. ~~The CWCs at the Angolan margin were also occurring outside of the expected density envelope of 27.35-27.65 kg m^{-3} in densities well below 27 kg m^{-3}, which was suggested by (Dullo et al., 2008).~~ 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 likely indicate that different environmental conditions ~~influencing~~ influence the 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} (Chapman and Shannon, 1987)~~(Mohrholz et al., 2008)~~. 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 ESACW ~~ESAC water~~ is smaller (Mohrholz et al., 2008). Due to this seasonal pattern, the DO_{conc} measured in this study (January; Fig~~s~~. 4) most likely do not represent minimum concentrations, which are expected to occur in the following months, but nevertheless give a valuable impression about the extent of the OMZ (February to May; ~~(~~Mohrholz et al., 2014). Interestingly, we captured a flow reversal after the 6^{th} of January from a southward to an equatorward current direction during high wind conditions on the Namibian margin (Fig. ~~5~~6), leading to an intrusion of ESACW with higher DO_{conc} (Δ ~~+~~ 0.007 ml l^{-1} on average) and lower temperatures (Δ -0.23 °C on average, Fig. 5) than the SACW ~~after the 6^{th} of January~~. This was~~,~~ leading to a~~n~~ temporal ~~relaxation of the oxygen stress~~increase in the DO_{conc}. 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 (Mohrholz et al., 2008). Such relaxations are likely important for the survival of the abundant ~~invertebrate~~ benthic fauna present on the relict coral mounds ~~under the conditions generally considered unsuited for them(Davies and Guinotte, 2011)({~~Gibson et al. , 2003 ~~#301})~~. 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~~SPOM at the mound areas (Fig. ~~6~~8, 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 DO_{conc} ~~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. In addition rivers transport terrestrial organic matter to the margin, which is reflected ~~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~~ which 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, also confirming admixing of terrestrial matter (Perdue and Koprivnjak, 2007). This terrestrial matter contains suitable food sources as well as less suitable food sources, like~~. Additional~~ carbon rich polymeric material (cellulose, hemicellulose and lignin)~~,~~ which cannot easily be taken up by marine organisms~~ and constitute a less suitable food source~~ (Hedges and Oades, 1997). 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 (Ramos et al., 2017). Age dating of the Namibian fossil coral framework ~~shows~~ showed that CWCs disappeared about 5 ka BP, which coincides with an intensification in upwelling and therefore most likely a decline of DO_{conc} (Tamborrino et al., accepted), ~~. This is~~ supporting~~ing~~ the assumption that ~~the~~ the low DO_{conc} ~~is~~ are responsible for the demise of CWCs on the Namibian margin. Although no living corals were observed on the Namibian coral mounds, we observed a dense living community dominated by sponges and bryozoans (Hebbeln et al., 2017). Several sponge species have been reported to survive at extremely low DO_{conc} within OMZs. For instance, along the lower boundary of the Peruvian OMZ sponges were found at DO_{conc} as low as 0.06-0.18 ml l^{-1} (Mosch et al., 2012). Mills et al. (2018) recently found a sponge (*Tethya wilhelma*) to be physiologically almost insensitive to oxygen stress and to respire aerobically under low DO_{conc} (0.02 ml l^{-1-}). Sponges can potentially stop their metabolic activity during unfavorable conditions and re-start their metabolism when some oxygen becomes available, for instance during diurnal irrigation of water with somewhat higher DO_{conc}. The existence of a living sponge community off Namibia might ~~hence~~ therefore be explained by the diurnal ~~baroclinic~~ tides occasionally flushing the sponges with more oxic water enabling them to metabolize, when food availability is ~~also~~ highest (~~pulse of suspended particulate matter with a higher amount of TOC and N during oxygenated conditions,~~ Figs. ~~5~~6~~, 8~~)~~)~~. Increased biomass and abundances in these temporary hypoxic-anoxic transition zones were already observed for macro- and mega-fauna in other OMZs and is referred to as the "edge effect" (Mullins et al., 1985; Levin et al., 1991; Sanders, 1969). It is very likely that this mechanism plays a role for the benthic communities on the Namibian as well as the Angolan margin.

Along the Angolan margin low oxygen concentrations apparently do not restrict the proliferation of thriving CWC reefs even though DO_{conc} are considered hypoxic (0.5-1.5 ml l^{-1}). The DO_{conc} measured off Angola are well below the lower DO_{conc} limits for *L. pertusa* based ~~either on habitat suitability modelling (Davies et al., 2008) or~~ on laboratory experiments and earlier field observations (Schroeder, 2002; Brooke and Ross, 2014). The DO_{conc} encountered at the shallow mound sites (<0.8 ml l^{-1}) are even below the so far lowest limits known for single CWC colonies from the Mauritanian margin (Ramos et al., 2017b). Since in the present study, measured DO_{conc} were even lower than the earlier established lower limits~~3~~ this could suggest ~~at~~ a much higher tolerance of *L. pertusa* to low oxygen levels as low as 0.5 ml l^{-1} ~~-~~at least in a limited time-period ~~as low as 0.5 ml l^{-1}~~ (4% O_2 saturation)~~, which was measured by the ALBEX lander as well as the CTD during the cruise in 2016. Even though concentrations at the Angolan margin showed to be relatively stable, it should be emphasized that the observation period was limited and long-term (year-long) observations 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~~with the upper limit being close to 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). The CWCs ~~at the Angolan margin~~ were also occurring outside of the expected density envelope of 27.35-27.65 kg m^{-3} in densities well below 27 kg m^{-3}~~, which was suggested by~~ (Fig. 3, Dullo et al., 2008). 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. However this creates a negative feedback, since with increased food availability and higher temperatures the oxygen concentration will decrease due to bacterial decomposition of organic substances.~~. The CWCs at the Angolan margin were also occurring outside of the expected density envelope of 27.35-27.65 kg m^{-3} in densities well below 27 kg m^{-3}, which was suggested by (Dullo et al., 2008).~~

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~~ is ~~in contrast to mounds on the Namibian margin or the deeper Angolan mound area~~. Probably here the increase of one stressor is compensated by a reduction of another stressor~~ in the shallow Angolan mound areas~~. On the Namibian margin ~~or~~ and the deeper Angolan mound sites ~~we found~~ the opposite pattern ~~were~~was found, with highest temperatures during lowest DO_{conc}. ~~The occurrence of *L. pertusa*~~However, 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~~7). 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} results 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 mechanistically linked CWC mound growth periods with enhanced surface water productivity and hence organic matter supply. Here we found evidence for high quality and quantity of SPOM~~ in the vicinity of the coral mounds on the Namibian as well as on the Angolan margin~~ in both areas indicated by ~~. Indicators for the high quality of food in the SPOM at both sites were~~ high TOC and N concentrations (Figs. ~~6~~6~~,~~ and ~~10~~7) in combination with a low C/N ratio (Fig. ~~7~~8), a low isotopic signature of $\delta^{15}N$ and only slightly degraded pigments~~ (∑phaeopigment/ chlorophyll-α ratio of on average 6.5 and 3.2 off Namibia and Angola, respectively)~~.

The Namibian margin is known for its upwelling cells, where phytoplankton growth is fueled by nutrients from deeper water layers producing high amounts of phytodetritus (Chapman and Shannon, 1985), which subsequently sinks down to the relict mounds on the slope. Benthic communities on the mounds off Namibia occur at relatively shallow depths, hence downward transport of SPOM from the surface waters is rapid and time for decomposition of the sinking particles in the water column is limited. ~~This high flux~~

and accumulation of fresh SPOM towards the reefs is evident as a slightly increased fluorescence deeper in the water column around the mound sites (Fig. 4d). Furthermore, the increased fluorescence and chlorophyll-α concentrations coincide with low DO_{conc} which both are in line with downward movement of waters with a lower DO_{conc} from the OMZ above (Fig. 5). The higher turbidity during lower current speeds provides additional evidence that the material settling from the surface is not transported away with the strong currents (Fig. 56). Mounds off Namibia occur at relatively shallow depths, hence downward transport of SPOM from the surface waters is rapid and hence time for decomposition of the sinking particles in the water column is limited. This fast delivery of SPOM over short depth intervals appears to be linked to both, high primary productivity (high surface fluorescence, Fig. 4d) and reduced decomposition due to low oxygen concentrations (Pichevin et al., 2004; Cavan et al., 2017), leads to a generous food supply for several benthic organisms thus enabling them to survive under hypoxic conditions. ,

At the Angolan coral mounds, SPOM appeared to have a signature corresponding to higher quality organic matter compared to off Namibia. The phytopigments were less degraded (i.e. higher chlorophyll-α concentration, lower ∑phaeopigment/ chlorophyll-α ratio) and the $\delta^{15}N$, TOC and N concentration of the SPOM was lower than off Namibia. However, here lower $\delta^{15}N$ and higher ∑phaeopigment/ chlorophyll-α ratio are likely connected to a mixture with terrestrial OM input, which might constitutes a less suitable food source for CWCs (Hedges and Oades, 1997). On the other hand the riverine input delivers dissolved nutrients, which can support the growth of phytoplankton, indirectly influencing food supply (Kiriakoulakis et al., 2007; Mienis et al., 2012). Moreover, the food quality at the shallow Angolan reefs was not coupled to periods of other environmental stressors and variations were relatively small during this study. At the Angolan margin we see a rather constant delivery availibilityavailability of SPOM. The slightly higher turbidity during periods of highest DO_{conc}, (Fig. 87) suggest that the SPOM on the Angolan margin originates from the bottom nepheloid layer on the margin directly above the CWC mounds (Fig. 7e5e), which may represents a constant reservoir of fresh SPOM. This reservoir is likely fueled by directly sinking as well as advected organic matter from the surface ocean.. This again indicates that CWCs can benefit from a constant source of high quality SPOM on the margin somewhat above the coral mound areas and are not exclusively depending on SPOM settling from the surface (like at the Namibian margin), since the strong stratification inhibits mixing of the different water masses. This is also supported by the fact, that's increased fluorescence off Angola was not as strongly correlated with the downward currents as off Namibia.

4.4 Tidal currents

The semidiurnal tidal currents observed ~~probably~~ likely play a major role in the survival of benthic fauna on the ~~southwestern~~ SW African margin. On the Namibian margin internal waves deliver oxygen from the surface and deeper waters ~~semi-diurnally about 70 m towards to the inside~~to the OMZ and thereby enablinge~~e~~ benthic fauna on the fossil coral framework to survive in hypoxic conditions (Fig. 9a). At the same time these currents are likely responsible for the delivery of fresh SPOM from the surface productive zone to the communities on the margin, since they promote mixing between the water masses as well as they vertically displace the different water layers.~~.~~

On the Angolan margin internal tides produce slightly faster currents and vertical excursions of up to 130 m which are twice as high as those on the Namibian margin. Similar to the Namibian margin these tidal excursions deliver oxygen from shallower and deeper waters to the mound zone and thereby deliver water with more suitable characteristics over the whole extend of the parts of the OMZ which otherwise may harbor unsuitable properties for CWCs (Fig. 9b). Internal tides are also responsible for the formation of a bottom nepheloid layer in 200-350 m depth (Fig. ~~7e~~5e). This layer is formed by trapping of organic matter as well as bottom erosion due to turbulences created by the interaction of internal waves with the margin topography, which ~~the intensification of~~intensifies near-bottom water movements. These i~~,~~nternal waves are able to move on the density gradient between water masses, ~~which~~ which are located ~~is indicated by maxima of the buoyancy frequency N^2 in~~ in 225 and 300 m depth (Fig. 3)~~(GeoB20977-1, not shown)~~. Tidal waves will be amplified due to a critical match between the characteristic slope of the internal M2 tide and the bottom slope of the Angolan margin, as is known from other continental slope regions (Dickson and McCave, 1986; Mienis et al., 2007). As argued above, this turbid layer is likely important for the nutrition of the slightly deeper situated CWC mounds, since vertical mixing is otherwise hindered by the strong stratification.

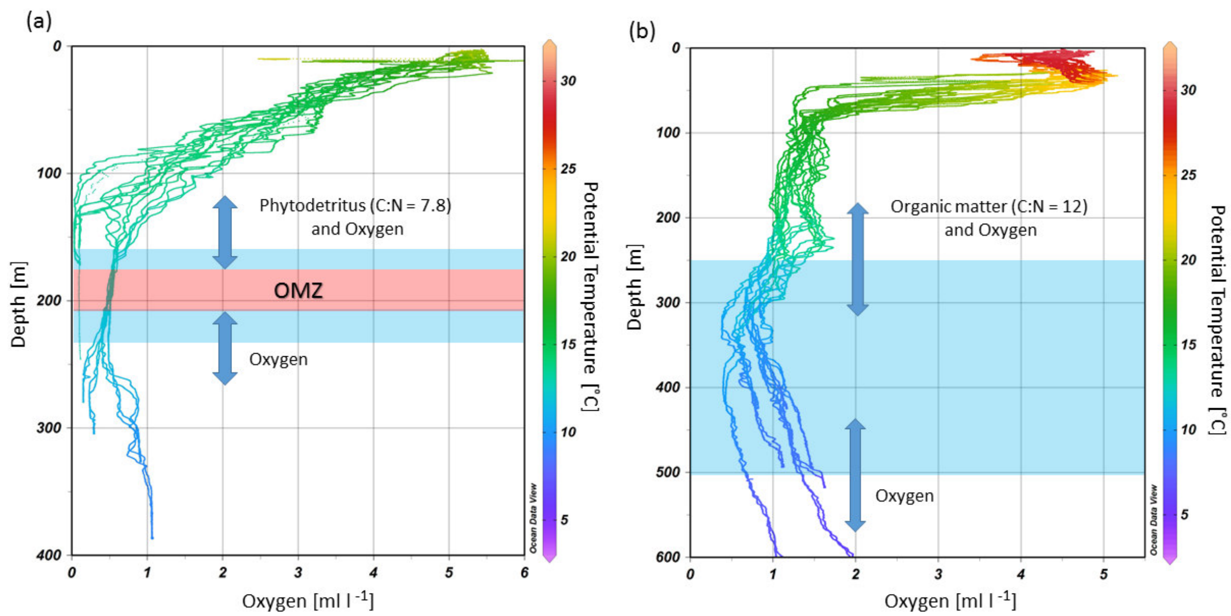

Figure 9 Depth range of cold-water coral mound occurrences (blue shaded areas) at the (a) Namibian and (b) Angolan margins in relation to the dissolved oxygen concentrations and potential temperature. Diurnal tides are delivering mainly phytodetritus (shown in (a) and organic matter from the benthic 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 the benthic communities ~~CWCs~~ on the southwestern African margin including temperature, DO_{conc}, food supply and tidal movements. The DO_{conc} likely defines the presence ~~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 benthic 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.

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~~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~~ benthic fauna ~~are~~is 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.

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*~~ *L. 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*~~ *L. pertusa* 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 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**~~ **Figure 6** 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 7 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 8 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** 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.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** 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
	20506-1	off-mound	SLM	01.-16.01.16	20°43.93'	12°49.11'	~~231~~230	12.5	
Angola	20921-1	off-mound	ALBEX	20.-23.01.16	9°46.16'	12°45.96'	~~342~~340	2.5	+ particle pump
	20940-1~~20940-1~~	off-mound~~off-mound~~	ALBEX ~~ALBEX~~	23.-26.01.16 ~~23.-26.01.16~~	9°43.84'~~9°43.84'~~	12°42.15' ~~12°42.15'~~	530~~532~~	2.6~~2.6~~	+ particle pump~~+ particle pump~~
	20915-2	off-mound	SLM	19.-26.01.16	9°43.87'	12°43.87'	430	6.8	

Table 2 Environmental properties at the Namibian and Angolan margins.

	Namibia	Angola
Temperature [°C]	11.8-13.2	6.73-12.9
DO_{conc} [ml l^{-1}]	0-0.15	0.5-1.5
Fluorescence [NTU]	42-45	38.5-41.5
Current speed max. [m s^{-1}]	0.21	0.3

Current speed average [m s^{-1}]	0.09	0.1
Tidal cycle	Semi-diurnal (0.37 dbar, 3 cm s^{-1})	Semi-diurnal (0.6 dbar, 8.2 cm s^{-1})
Average pH	8.01	8.12

Table 3~~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.

	Station no. (GeoB ID)	Depth (m)	Mean current speed (cm s^{-1})	Current direction (°)	Tides [%] (p)	Const. [dbar]	Tides [%] (u)	Const. [cm s^{-1}]
Namibia	20507-1	~~433~~430	9.34	221.6	81.8	M2: 0.37	10.5	M2: 3.1 M3: 0.8
Angola	20921-1	~~532~~340	9.96	247.9	91.6	M2: 0.59 M3: 0.04	36	M2: 7.8 M8: 0.7
	20940-1	~~228~~530	8.92	275.6	86.8	M2: 0.60 M8: 0.02	50.9	M2: 8.6 M3: 3.7