



Cold-water coral reefs thriving under hypoxia

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Abstract Reefs formed by scleractinian cold-water corals represent unique biodiversity hot spots in the deep sea, preferring aphotic water depths of 200–1000 m. The distribution of the most prominent reef-building species *Lophelia pertusa* is controlled by various environmental factors including dissolved oxygen concentrations and temperature. Consequently, the expected ocean deoxygenation and warming triggered by human-induced global change are considered as a serious threat to cold-water coral reefs. Here, we present results on recently discovered reefs in the SE Atlantic, where *L. pertusa* thrives in hypoxic and rather warm waters. This sheds new light on its capability to adapt to extreme conditions, which is facilitated by high surface ocean productivity, resulting in

extensive food supply. Putting our data in an Atlantic-wide perspective clearly demonstrates *L. pertusa*'s ability to develop population-specific adaptations, which are up to now hardly considered in assessing its present and future distributions.

Keywords Cold-water corals · *Lophelia pertusa* · Hypoxia · Adaptation · Global change

Introduction

Being ecosystem engineers, framework-forming scleractinian cold-water corals (CWCs) provide habitat for thousands of deep-sea species, revealing equally remarkable levels of biodiversity as found in tropical coral reefs (Henry and Roberts 2017). *Lophelia pertusa* is the dominant reef-forming CWC in the Atlantic, and based on its distribution correlated with ocean conditions, upper and lower tolerable limits for basic oceanographic parameters were proposed for this species (e.g., Davies and Guinotte 2011). Among them, dissolved oxygen concentrations (DO_{conc}) can exert control on its biogeographic distribution (e.g., Tittensor et al. 2009). However, lowest DO_{conc} inhabited by this species apparently differs between NE Atlantic ($\sim 3.7 \text{ mL L}^{-1}$; Dullo et al. 2008) and NW Atlantic ($\sim 2 \text{ mL L}^{-1}$; e.g., Brooke and Ross 2014) reef sites. These observations are corroborated by laboratory experiments, revealing that *L. pertusa* individuals collected from DO_{conc} of 6 mL L^{-1} at the Scottish margin, NE Atlantic, were unable to maintain normal aerobic functions at $DO_{conc} < 3.2 \text{ mL L}^{-1}$ (Dodds et al. 2007). Moreover, for *L. pertusa* specimens collected from DO_{conc} of $\sim 2.8 \text{ mL L}^{-1}$ in the Gulf of Mexico, 7-day exposure to DO_{conc} of $\sim 1.5 \text{ mL L}^{-1}$ proved fatal (Lunden et al.

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2014). Furthermore, discoveries of *L. pertusa* in the oxygen minimum zones (OMZ) of the subtropical eastern Atlantic (Colman et al. 2005; Le Guilloux et al. 2009) hinted to an even wider tolerance of *L. pertusa* to low DO_{conc} . Nevertheless, the limited capability of *L. pertusa* to thrive under DO_{conc} (artificially) reduced below those of their natural environment (Dodds et al. 2007; Lunden et al. 2014), questions its ability to cope with the global change-induced ocean deoxygenation expected for the coming century (e.g., Sweetman et al. 2017).

Although hitherto hypoxic settings were regarded as unsuitable habitats for CWC (e.g., Tittensor et al. 2009), here, we present the discovery of *L. pertusa*-dominated CWC reefs thriving in the hypoxic OMZ off Angola in the SE Atlantic. The regional adaptation of the Angolan CWC to such extreme conditions sheds new light on their potential capability to cope with expected future environmental changes in the ocean.

Methods

During RV Meteor expedition M122 in January 2016 (Hebbeln et al. 2017), in situ oceanographic parameters such as DO_{conc} and temperature were recorded off Angola (Fig. 1). Data were collected during eight dives with the remotely operated vehicle (ROV) MARUM SQUID (Online Resource 1), three benthic lander deployments (2.5–6.8 days; Online Resource 2) and 17 conventional CTD casts (Online Resource 3). The conventional CTD was additionally equipped with a non-calibrated fluorescence sensor only providing relative values shown as means per water depth averaged from all CTD casts.

Results and discussion

Discovery of cold-water coral reefs in the oxygen minimum zone off Angola

ROV video observations revealed the presence of CWC reefs dominated by *L. pertusa*, which colonize the slopes and summits of up to 100-m-high coral mounds (Fig. 1; Hebbeln et al. 2017). While dispersed CWC colonies were found in a depth range of 250–500 m, large aggregates of

healthy colonies were restricted to 330–470 m water depth (Fig. 2). The observation of > 50-cm-high colonies (Fig. 2) clearly evidenced the continuous proliferation of CWC off Angola for many years.

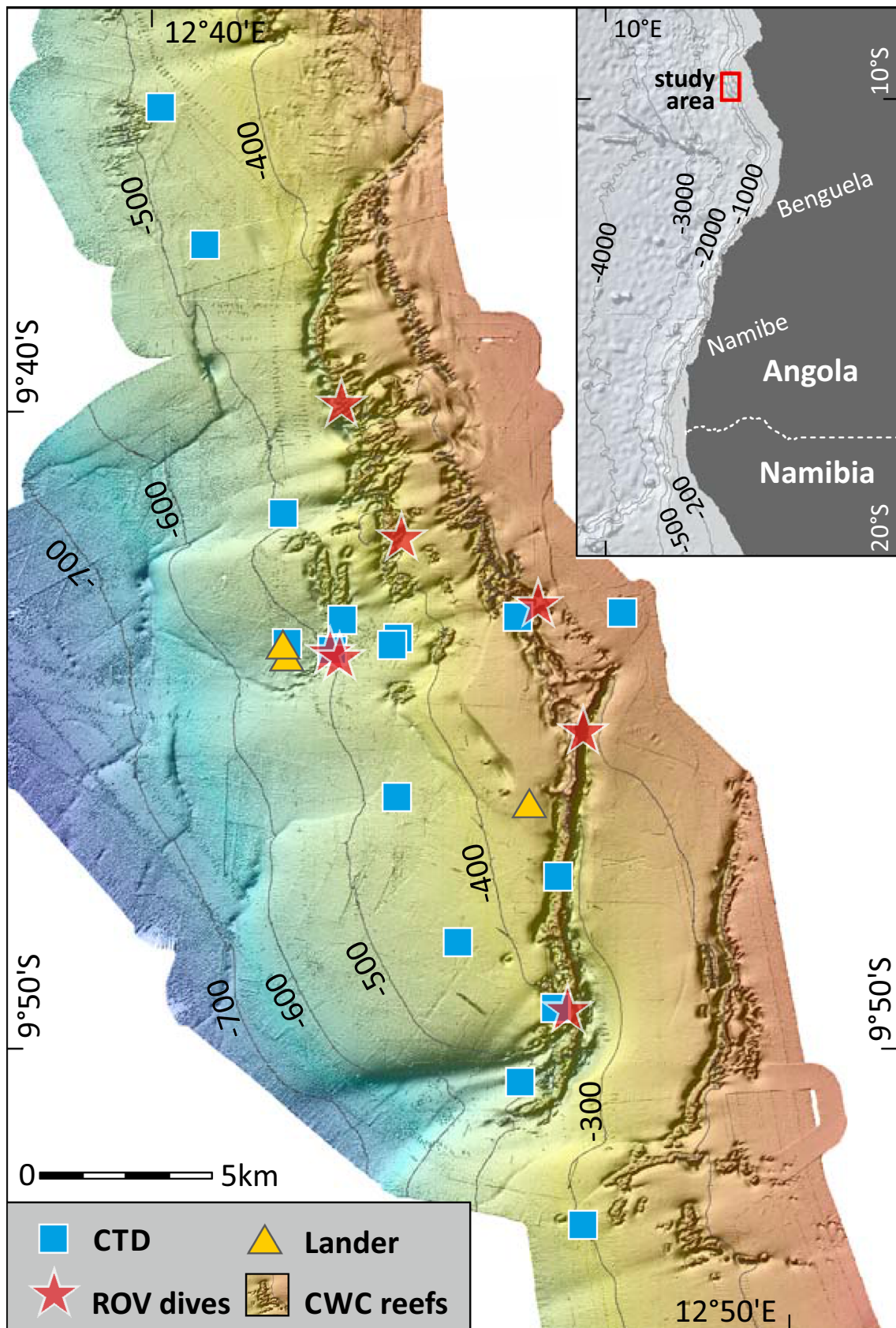
The available oceanographic data revealed water temperatures of 6.8–14.2 °C around the CWC (250–500 m; Fig. 3). The corresponding DO_{conc} of 0.6–1.5 mL L^{-1} are the lowest ever obtained from waters bathing flourishing *L. pertusa* colonies (Fig. 3). The ROV–CTD DO_{conc} measurements show the smallest variations. The slightly larger ranges of the lander and conventional CTD data (Fig. 3) likely reflect the impacts of internal waves (Hanz et al. 2019) and the larger geographical coverage, respectively.

To gain insight into the seasonal variability of DO_{conc} off Angola, as the M122 data only represent an 8.5-day snapshot from January 2016, we included further 21 CTD casts obtained within the mapped area off Angola (Fig. 1) between 1995 and 2013 (Tchikalanga et al. 2018; Online Resource 4). These data, spanning from March to September, almost completely correspond to the M122 data or reveal even lower DO_{conc} (Fig. 3). Interestingly, even in this hypoxic environment, most prolific CWC reefs are bound to the center of the Angolan OMZ where lowest DO_{conc} prevail (Fig. 3), which coincide with enhanced water-column fluorescence pointing to an increased availability of relatively fresh organic matter (Fig. 3).

Oxygen sensitivity of *Lophelia pertusa* in the Atlantic Ocean

Based on field observations in the NW and NE Atlantic (Dullo et al. 2008; Freiwald et al. 2009; Brooke and Ross 2014; Georgian et al. 2016), the assumed lower limit of *L. pertusa*'s oxygen tolerance ranges around DO_{conc} of 2–3.7 mL L^{-1} . This has recently been challenged by very low DO_{conc} of 1.1–1.4 mL L^{-1} reported from CWC sites off Mauritania (Ramos et al. 2017), which, however, are associated with only sporadic occurrences of small *L. pertusa* colonies (Wienberg et al. 2018). The new Angolan data documented for the first time *L. pertusa*'s ability to develop thriving reefs even under DO_{conc} of < 1 mL L^{-1} (Fig. 3).

In addition, off Angola *L. pertusa* lives at temperatures of up to 14.2 °C (Fig. 3), which are among the highest temperatures ever observed for this species (13.9–15.2 °C;



◀ **Fig. 1** Multibeam bathymetry map showing the distribution of cold-water coral reefs off Angola. Locations of CTD casts, benthic lander deployments, and ROV dives are indicated

e.g., Freiwald et al. 2009; Mienis et al. 2014). Thus, off Angola, the partly high temperatures could act as a second stressor since respiration rates of *L. pertusa* increase with increasing temperature (Dodds et al. 2007).

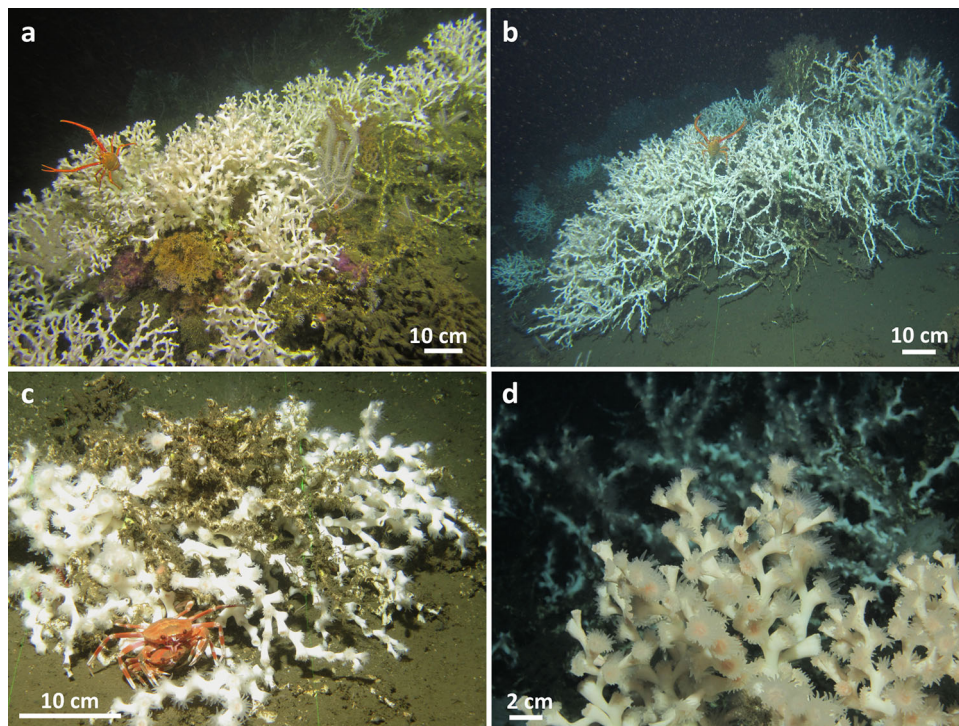
Stress induced by low DO_{conc} and relatively high temperatures is energetically a challenge for the metabolism of most marine species, but can be compensated by the availability of large quantities of high-quality organic matter (Diaz and Rosenberg 1995). The Angolan and Mauritanian margins belong to highly productive upwelling systems triggering extensive OMZs. Also at many other Atlantic reef sites, *L. pertusa* is most abundant at depth intervals with highest oxygen depletion (Freiwald 2002; Georgian et al. 2016), most likely linked to highest concentrations of suspended food particles in this layer (e.g., Freiwald 2002) which also applies to Angola (Fig. 3). Comparing ambient DO_{conc} and temperature with site-specific net primary productivity, used as a food supply indicator, for several Atlantic CWC sites, it appears plausible that the negative effects of hypoxia and high temperatures on *L. pertusa* seemingly could be compensated by significantly enhanced food supply (Fig. 4).

With respect to *L. pertusa* preferring regional oxygen minima, ambient DO_{conc} cannot provide any information about its capability to also cope with lower DO_{conc} . However, some information is provided by the aforementioned laboratory experiments. *Lophelia pertusa* collected in the NE Atlantic and the Gulf of Mexico could not withstand DO_{conc} of less than 40–50% of the ambient values (see above, Dodds et al. 2007; Lunden et al. 2014). Consequently, the range of low DO_{conc} tolerable by *L. pertusa*—also beyond its natural environment—might depend on the conditions the corals are acclimated to, thus pointing to a possible genotypic adaptive capacity of *L. pertusa*. Thus, although on a global scale the tolerable DO_{conc} limits for *L. pertusa* range from <1 to $>6 \text{ mL L}^{-1}$, smaller ranges define these limits on regional scales.

The future of *Lophelia pertusa* in a changing ocean

Cold-water coral reefs are vulnerable marine ecosystems that are partly protected within marine protected areas. These can safeguard CWC from destructive human impact (e.g., bottom trawling, hydrocarbon exploration), but offer no sustainable protection against global change-induced threats. In concert with ocean acidification (e.g., Turley et al. 2007) and warming of intermediate waters (e.g., Lunden et al. 2014), also deoxygenation is expected to become a major stressor for CWC (e.g., Sweetman et al.

Fig. 2 Thriving cold-water corals observed in the oxygen minimum zone (OMZ) off Angola. **a, b** *Lophelia pertusa* reefs in the center of the OMZ (350 m water depth). **c** Transported but alive *L. pertusa* colony in the lower OMZ (500 m depth). **d** *Lophelia pertusa* colony with many living polyps (439 m depth) (ROV images ©MARUM)



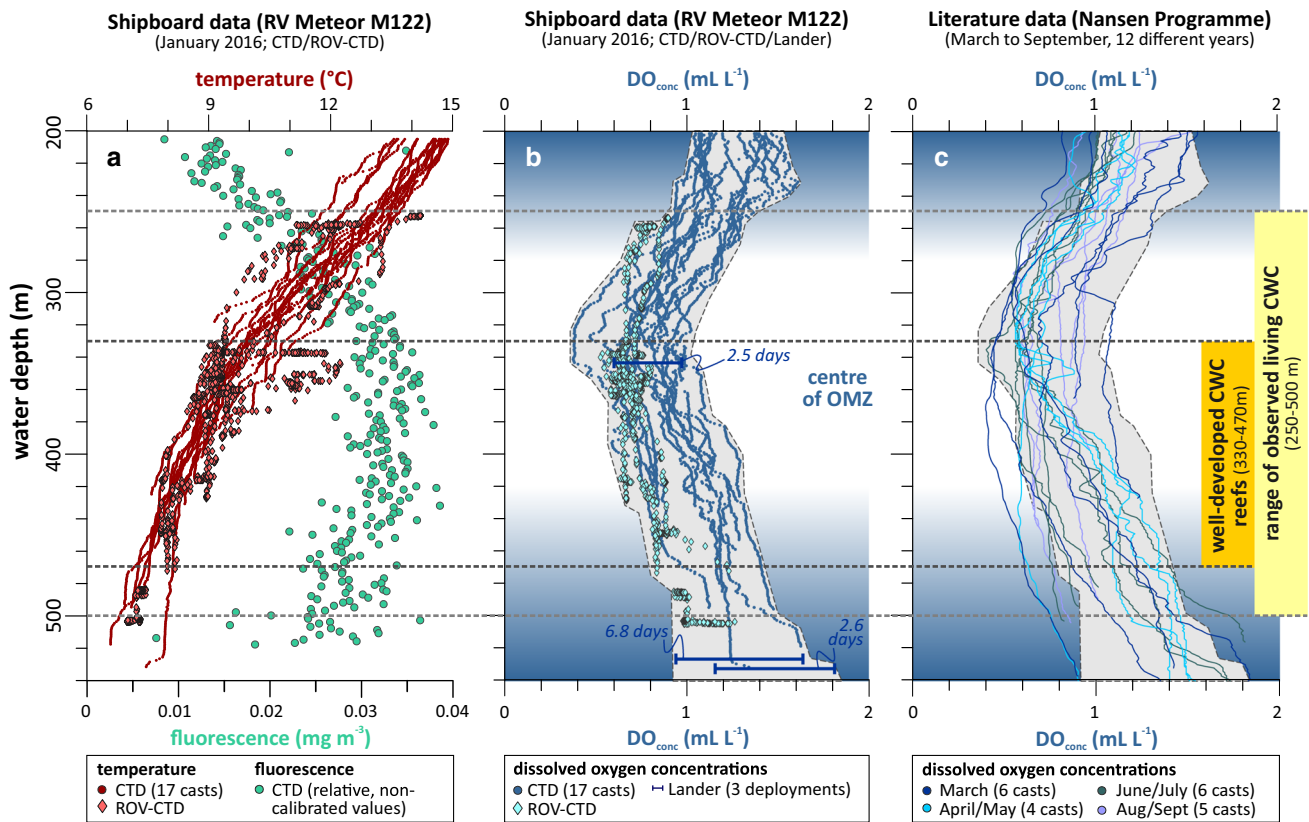


Fig. 3 Hydrographic setting at the Angolan cold-water coral (CWC) reef site recorded in January 2016. **a** Water-column temperature (red symbols) and mean relative fluorescence data (green symbols) obtained by conventional CTD and ROV-mounted CTD (temperature only). **b** Dissolved oxygen concentrations (DO_{conc}) obtained by conventional CTD, ROV-mounted CTD and benthic lander systems (light gray shading indicates entire spread of DO_{conc} data obtained

during RV Meteor expedition M122; same in c). **c** Literature DO_{conc} data spanning from March to September collected between 1995 and 2013 in the same area (Tchikalanga et al. 2018). For all graphs, the depth intervals of either well-developed CWC reefs and/or single living CWC colonies are marked in dark and light yellow, respectively

2017). However, *L. pertusa*'s general capacity to thrive under well-oxygenated as well as hypoxic bottom waters reveals a rather high oxygen tolerance, although individual *L. pertusa* populations appear to have limited adaptive capabilities to cope with reductions of 40–50% of ambient DO_{conc} values (Dodds et al. 2007; Lunden et al. 2014). Consequently, the expected decrease in oxygenation of ~ 2% along the Atlantic continental margins until 2100 (Sweetman et al. 2017) by itself might not exert a serious threat to *L. pertusa*, except for already hypoxic settings like the Angolan margin. However, paleo studies revealed that during the last ~ 20,000 years regional changes in water column structure caused the collapse of *L. pertusa*-

dominated ecosystems due to decreasing DO_{conc} (Wienberg et al. 2018; Tamborrino et al. 2019). Thus, unlike a small overall decrease in DO_{conc} , major regional reductions in DO_{conc} driven by global change-induced changes in ocean circulation have the potential to eradicate regional *L. pertusa* populations.

Even if smaller decreases in DO_{conc} alone might not pose a serious threat to *L. pertusa* reefs, these have to be considered in concert with other changing environmental parameters that might form additional stressors (e.g., temperature and pH) with largely unknown consequences for the coral's biological functions. Moreover, the flux of particulate organic carbon from the surface ocean might

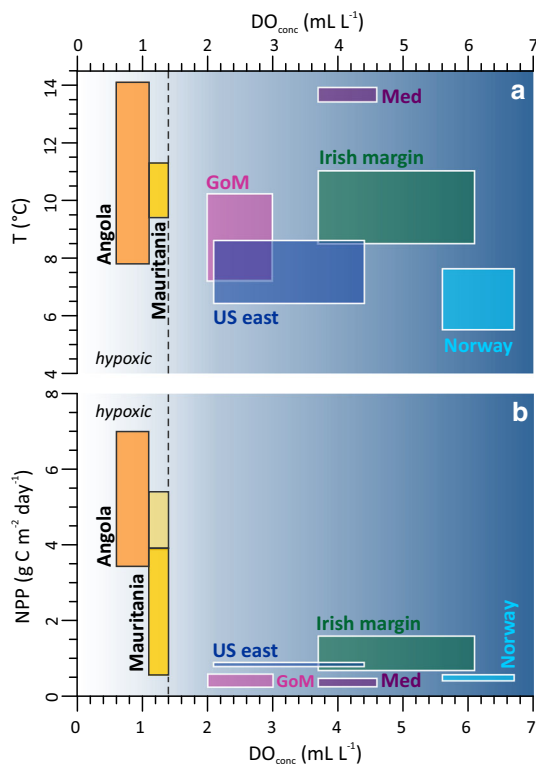


Fig. 4 Comparison of environmental parameters (dissolved oxygen concentrations: DO_{conc}; temperature: T; net primary productivity: NPP) obtained for various cold-water coral reef sites in the Atlantic: Gulf of Mexico (GoM; Georgian et al. 2016), Mediterranean Sea (Med; Freiwald et al. 2009), continental margins off Ireland (Dodds et al. 2007; Dullo et al. 2008), Mauritania (Ramos et al. 2017; light yellow: ~ 10 nm east of the CWC reefs highlighting the upwelling impacts), Norway (Dullo et al. 2008), the US east coast (US east; Brooke and Ross 2014) and Angola (this study). Relationship between **a** DO_{conc} and T and **b** DO_{conc} and NPP (Behrenfeld and Falkowski 1997)

decline by ~ 30% until 2100 along the Atlantic margins (Sweetman et al. 2017), resulting in a lower food supply to the CWC and deep-sea organisms in general, thus reducing their capacity to cope with increasing stress.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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