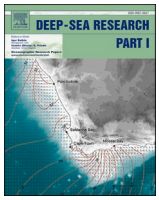
Deep–Sea Research I 197 (2023) 104052

Contents lists available at ScienceDirect

Deep-Sea Research Part I

journal homepage: www.elsevier.com/locate/dsri



Natural hypoxic conditions do not affect the respiration rates of the cold-water coral *Desmophyllum pertusum* (*Lophelia pertusa*) living in the Angola margin (Southeastern Atlantic Ocean)

Andrea Gori [a,b,c,d,*], Covadonga Orejas [e,f], Furu Mienis [g], Christine Ferrier-Pagès [h], Meri Bilan [d], Sebastian Flöter [i,j], Stephanie Reynaud [h], Andrew K. Sweetman [k], J Murray Roberts [l], Claudia Wienberg [m,1], Dierk Hebbeln [m,1]

[a] Universitat de Barcelona (UB), Department de Biologia Evolutiva, Ecologia i Ciències Ambientals, Av. Diagonal 643, 08028, Barcelona, Spain
[b] Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), Barcelona, Spain
[c] Institut de Ciències del Mar, Consejo Superior de Investigaciones Científicas (ICM-CSIC), Pg. Marítim de la Barceloneta 37-49, 08003, Barcelona, Spain
[d] Università del Salento, Dipartimento di Scienze e Tecnologie Biologiche e Ambientali, Campus Ecotekne, 73100, Lecce, Italy
[e] Centro Oceanográfico de Gijón, Instituto Español de Oceanografía, Consejo Superior de Investigaciones Científicas (IEO-CSIC), Av. Príncipe de Asturias 70 bis, 33212, Gijón, Spain
[f] Hanse-Wissenschaftskolleg Institute for Advanced Study (HWK), Lehmkuhlenbusch 4, 27753, Delmenhorst, Germany
[g] NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 53, 1790 AB, Den Burg, the Netherlands
[h] Centre Scientifique de Monaco (CSM), 8 Quai Antoine Ier, 98000, Principality of Monaco
[i] GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Wischhofstr. 1-3, 24148, Kiel, Germany
[j] Department of Earth Sciences, University of Geneva, Geneva, Switzerland
[k] Scottish Association for Marine Science, Oban, Argyll, UK
[l] School of GeoSciences, University of Edinburgh, Edinburgh, UK
[m] Center for Marine Environmental Sciences (MARUM), University of Bremen, Leobenerstraße, 8, 28359, Bremen, Germany

A B S T R A C T

Large, well-developed and flourishing reefs dominated by the cold-water coral *Desmophyllum pertusum* have recently been discovered along the Angola margin in the southeastern Atlantic Ocean living under very low oxygen concentrations (0.6–1.5 mL L^{-1}). This study assessed the respiration rates of this coral in a short-term (10 days) aquarium experiment under naturally low oxygen concentrations (1.4 ± 0.5 mL L^{-1}) as well as under saturated oxygen concentrations (6.1 ± 0.6 mL L^{-1}). We found no significant difference in respiration rates between the two oxygen concentrations. Furthermore, the respiration rates of *D. pertusum* were in the same order of magnitude as those of the same species living under normoxic conditions in other areas. This work expands the current knowledge on the metabolic activity of cold-water corals under hypoxic conditions, evidencing that low oxygen conditions are not a general limiting factor for the overall distribution of *D. pertusum*.

1. Introduction

The framework-forming cold-water coral (CWC) *Desmophyllum pertusum* (formerly *Lophelia pertusa*, Addamo et al., 2016), is a cosmopolitan species with a wide bathymetric distribution range (50–3000 m depth) (Roberts et al., 2006, 2009). Sufficiently high dissolved oxygen concentrations were suggested to be an important factor in controlling its distribution (Tittensor et al., 2009), with *D. pertusum* growing in food-rich, well-oxygenated waters under strong bottom currents (Davies et al., 2008). Although *D. pertusum* is able to regulate its oxygen consumption across a range of oxygen levels, laboratory studies showed that it is unable to maintain normal aerobic metabolic activity below approximately 3 mL L^{-1} (Dodds et al., 2007). These results, and the known distribution of the species in the North Atlantic Ocean, suggest that *D. pertusum* should not be found in low-oxygen environments, with a lower limit of dissolved oxygen tolerance of 2–3.7 mL L^{-1} (Dullo et al., 2008; Davies et al., 2008; Freiwald et al., 2009; Brooke and Ross 2014; Georgian et al., 2016). Indeed, experimental exposure of *D. pertusum* from the Gulf of Mexico to lower dissolved oxygen concentrations (1.5 mL L^{-1}) resulted in complete coral mortality after only a few days

* Corresponding author. Universitat de Barcelona (UB), Department de Biologia Evolutiva, Ecologia i Ciències Ambientals, Av. Diagonal 643, 08028 Barcelona, Spain.
E-mail address: gori@ub.edu (A. Gori).
[1] These authors share last authorship.

https://doi.org/10.1016/j.dsr.2023.104052
Received 26 November 2022; Received in revised form 21 March 2023; Accepted 21 April 2023
Available online 22 April 2023

(Lunden et al., 2014).

However, recent studies report the occurrence of live *D. pertusum* under hypoxic conditions. Occurrences of *D. pertusum* at low dissolved oxygen concentrations (1.1–1.3 mL L^{-1}) were observed off Mauritania (Ramos et al., 2017; Wienberg et al., 2018), and well-developed reefs dominated by *D. pertusum* have been recently reported along the Angolan margin at even lower dissolved oxygen concentrations (0.6–1.5 mL L^{-1}) (Hanz et al., 2019; Hebbeln et al., 2020), in a low-oxygen zone resulting from the bacterial respiration of the flux of particulate organic carbon generated by the high surface primary production in this upwelling zone (Chavez and Messié 2009). Despite these low oxygen conditions, Angolan CWC reefs have a dense living coral cover with a diverse associated fauna (Hanz et al., 2019; Hebbeln et al., 2020; Orejas et al., 2021).

To better understand the physiological performance of *D. pertusum* in the hypoxic waters off Angola, an experiment was performed to assess coral respiration rates under naturally low oxygen concentrations and after short-term (7 days) exposure to increased oxygen conditions. The aim was to explore the potentially limiting effect of low oxygen concentrations on coral metabolism, since hypoxia typically limits respiration, resulting in reduced metabolic rates, up to death (Rabalais et al., 2002; Vaquer-Sunyer and Duarte 2008). Two experimental hypotheses were tested: (1) *D. pertusum* respiration at naturally hypoxic conditions is limited by oxygen availability and will therefore increase under increased oxygen concentration; (2) *D. pertusum* respiration at naturally hypoxic conditions will be lower than previous records for the species at normoxic conditions.

2. Materials and methods

2.1. Coral collection and experimental setup

Specimens of *D. pertusum* were collected at 480–500 m depth on the Valentine Mounds (09° 43.700′ S - 012° 42.876’ E) at the Angolan margin (Fig. 1), using the Remotely Operated Vehicle (ROV) MARUM SQUID onboard the RV *Meteor* during expedition M122 in January 2016 (Hebbeln et al., 2017). Corals were collected with the ROV manipulator arm, stored in bioboxes during the ascent to the surface, and immediately transferred to aquaria after the ROV was recovered on deck. Eight coral nubbins (4–7 polyps, Table 1) were maintained under naturally low oxygen concentrations (1.8 ± 0.3 mL L^{-1}) in hermetically sealed plastic chambers (~400 mL volume, one nubbin per chamber) filled with sea water collected from 5 m above the seafloor with Niskin bottles arranged in a Rosette. Constant water movement inside the chambers

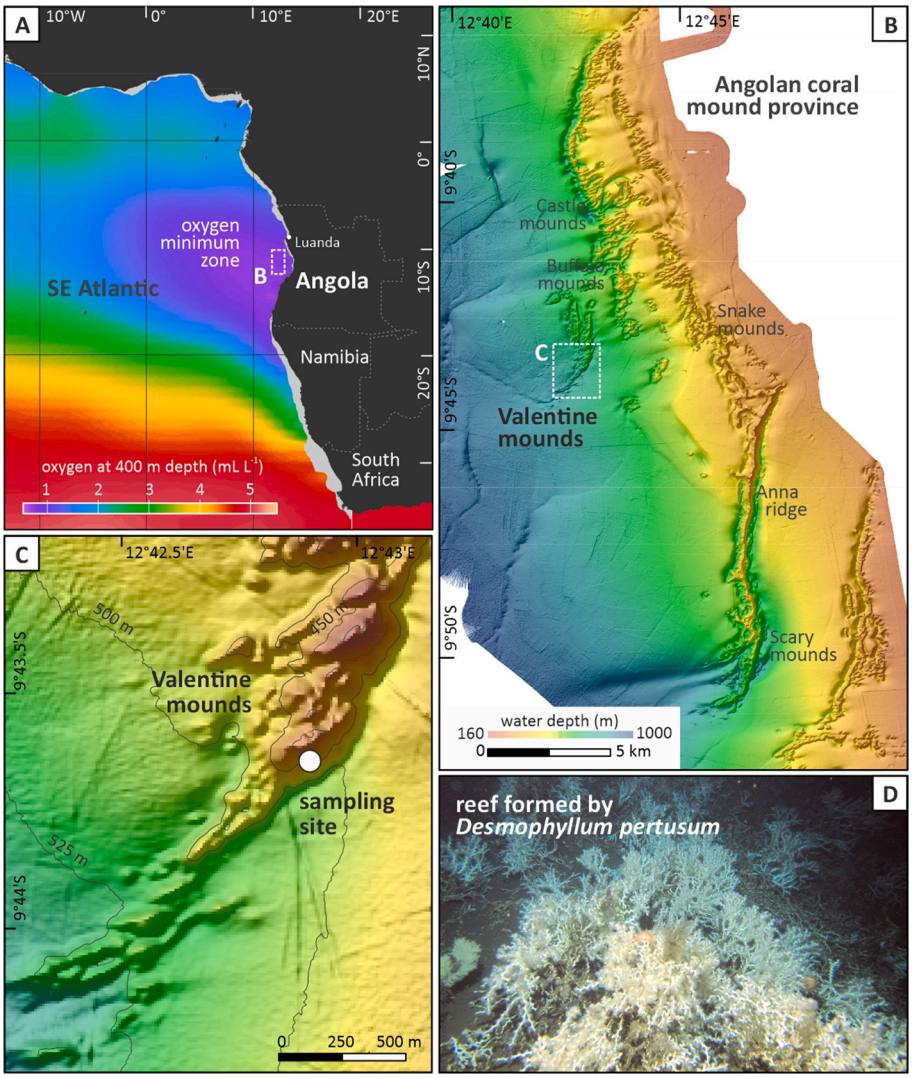


Fig. 1. (A) Overview map showing the location of the Angolan coral mound province in the SE Atlantic Ocean. Dissolved oxygen concentrations at 400 m water depth are displayed. (B) Bathymetric map showing the Angolan coral mound province. (C) Detailed map showing the sampling site on the Valentine mounds. (D) ROV image of the reef formed by *Desmophyllum pertusum* on the Valentine mounds (480–500 m depth). Image: MARUM ROV SQUID, Bremen, Germany.

Table 1
Number of polyps, dry weight (DW) and ash free dry weight (AFDW) of the *Desmophyllum pertusum* nubbins used in the experiment.

Treatment	Nubbin	Number of polyps	DW (g)	AFDW (g)
Naturally low O_2 (1.4 ± 0.5 mL L^{-1})	1	5	9.9	0.46
	2	6	21.9	0.84
	3	4	15.0	0.70
	4	7	17.6	0.88
Increased O_2 (6.1 ± 0.6 mL L^{-1})	5	5	22.1	1.16
	6	4	9.6	0.53
	7	6	20.5	1.05
	8	4	7.4	0.38

was created using Teflon-coated magnetic stirrers, and temperature was maintained at 8.0 ± 0.3 °C (mean ± SD) (natural *in situ* temperature, Hebbeln et al., 2020) in a water bath with a chiller (Hailea HC 150A, Raoping, China). The seawater was completely renewed in each chamber every 6–8 h with water freshly collected from the seafloor (also providing corals with natural food). After 2 days under these conditions, four of the eight chambers were opened, to allow oxygen concentration increase to saturation (Fig. 2A). Corals were maintained for 7 days under two contrasting treatments: (1) naturally low oxygen concentration (1.4 ± 0.5 mL L^{-1}, mean ± SD), (2) increased oxygen concentration (6.1 ± 0.6 mL L^{-1}, mean ± SD). Again, seawater was renewed every 6–8 h with fresh seawater from the seafloor and adjusted to the appropriate oxygen concentration. Temperature and oxygen concentrations were monitored in each chamber 3–4 times a day (before and after each water renewal).

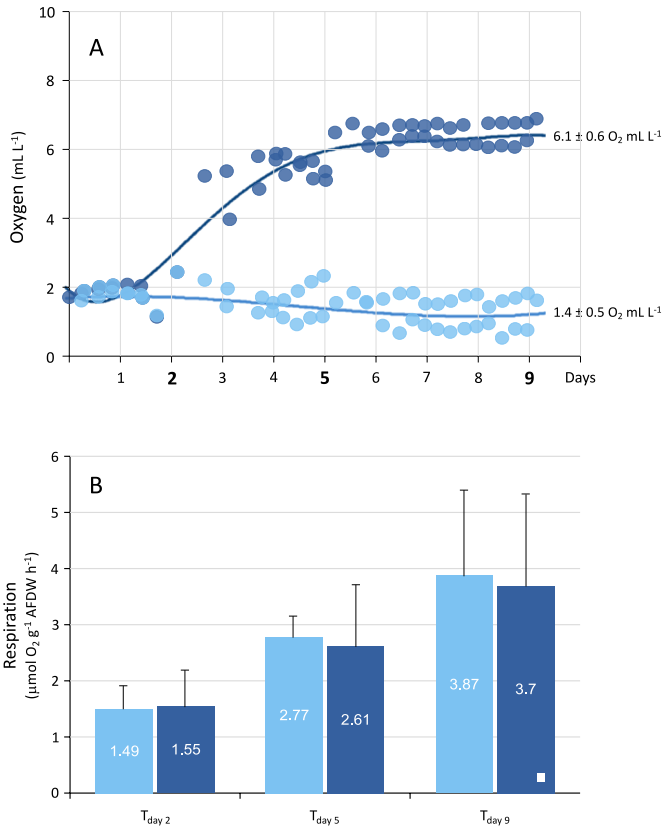


Fig. 2. (A) Oxygen concentration (mL L^{-1}) during the experiment in the naturally low oxygen concentration (light blue) and the increased oxygen concentration (dark blue) treatments. Days of experimental incubations are highlighted in bold. Variability in the oxygen concentration was due to the water changes performed every 6–8 h (see text for details). (B) Respiration of *Desmophyllum pertusum* under natural low oxygen concentration (1.2 ± 0.1 mL L^{-1}), as well as after 3 and 7 days under contrasted natural (1.4 ± 0.5 mL L^{-1}) and increased (6.1 ± 0.6 mL L^{-1}) oxygen concentration.

2.2. Respiration measurements

Coral respiration was assessed under the natural low oxygen concentration ($T_{day\ 2}$), and after three ($T_{day\ 5}$) and seven days ($T_{day\ 9}$) under the two oxygen concentration treatments (Fig. 2A). Incubations (8 h) were performed in glass beakers (328 mL), filled with 50 µm pre-filtered seawater (without any air space), hermetically sealed with an air-impermeable plastic membrane, and maintained at 8.2 ± 0.4 °C (mean ± SD) in a water bath. Four beakers, without any coral and filled with pre-filtered seawater, were incubated under the same conditions and used as controls. Constant water movement inside the beakers was ensured by a Teflon-coated magnetic stirrer. Respiration rates were assessed by measuring oxygen concentrations in each beaker, at the beginning and end of the incubation, using an optode sensor (YSI ProODO Optical Dissolved Oxygen meter, accuracy 0.14 mL L^{-1}). Mean variation in oxygen concentrations measured in the control beakers was subtracted from those measured in the coral beakers, and respiration rates were derived from the recorded changes in dissolved oxygen during the incubation. Results were normalized to the dry weight (DW) and the ash free dry weight (AFDW) of the coral nubbins. For this purpose, after the experiment coral nubbins were first heated to 60 °C for 48 h in a laboratory oven, and weighed using an analytical balance (Mettler AT 261, L'Hospitalet de Llobregat, Spain, accuracy 0.1 mg) to determine the DW. Subsequently, they were burnt at 500 °C for 4 h in a laboratory furnace and the ash weight (AW) measured and used to calculate the AFDW (AFDW = DW - AW).

2.3. Statistical analyses

Results are expressed as mean ± standard deviation. All statistical analyses were performed with the R software platform (R Core Team 2022). Normality was tested using a *Kolmogorov–Smirnov* test performed with the function *ks.test*. Homogeneity of variances was tested using a Bartlett test performed with the function *bartlett.test*. Differences in respiration rates among the two oxygen concentration treatments (natural 1.4 ± 0.5 mL L^{-1} *versus* increased 6.1 ± 0.6 mL L^{-1}) and the three measurement times ($T_{day\ 2}$ - $T_{day\ 5}$ - $T_{day\ 9}$) were tested by two-way within subject ANOVA with repeated measures on time factor. The analysis was performed with the function *anova* from the *car* package, applied to a linear model built with the function *lm*, confirming the assumption of sphericity of variances (Mauchly's test statistic = 0.409, p-value = 0.107). When significant differences were observed, a posteriori multiple comparisons were performed with paired t-tests conducted with the *t.test* function, with Holm (1979) correction for multiple comparisons.

3. Results and discussion

Oxygen depletion attributable to coral respiration in the incubation beakers (0.02–0.21 $mL^{-1}\ h^{-1}$) was always higher than oxygen variation in control beakers (<0.01 $mL^{-1}\ h^{-1}$), and there was no difference in respiration rates between corals maintained under hypoxic and normoxic conditions in our 8 h incubations (ANOVA, F = 0.02, df = 1, p-value = 0.893) (Fig. 2B and Table 2), allowing us to reject our first hypothesis (*D. pertusum* respiration under naturally hypoxic conditions is limited by oxygen availability). Respiration rates increased significantly with time (ANOVA, F = 28.86, df = 2, p-value <0.001) under both conditions (Fig. 2B and Table 2), without any significant interaction between the two factors (ANOVA, F = 0.09, df = 2, p-value = 0.912). The increase was significant from $T_{day\ 2}$ to $T_{day\ 5}$ (t = −8.63, df = 7, p < 0.001) as well as from $T_{day\ 5}$ to $T_{day\ 9}$ (t = −3.62, df = 7, p-value = 0.008). Respiration rates of *D. pertusum* in the hypoxic waters of Angola

Table 2
Respiration rates of *Desmophyllum pertusum* under the two experimental treatments (natural low O_2 and increased O_2) at the three sampling times ($T_{day\ 2}$, $T_{day\ 5}$ and $T_{day\ 9}$), normalized by coral dry weight (DW) and ash free dry weight (AFDW).

Treatment	Time	Respiration	
		($\mu molO_2$ DW g^{-1} h^{-1})	($\mu molO_2$ AFDW g^{-1} h^{-1})
		mean ± SD	mean ± SD
Natural low O_2 (1.4 ± 0.5 mL L^{-1})	$T_{day\ 2}$	0.067 ± 0.020	1.49 ± 0.43
	$T_{day\ 5}$	0.125 ± 0.018	2.77 ± 0.39
	$T_{day\ 9}$	0.175 ± 0.071	3.87 ± 1.54
Increased O_2 (6.1 ± 0.6 mL L^{-1})	$T_{day\ 2}$	0.081 ± 0.033	1.55 ± 0.66
	$T_{day\ 5}$	0.138 ± 0.059	2.61 ± 1.12
	$T_{day\ 9}$	0.195 ± 0.085	3.70 ± 1.64

at $T_{day\ 9}$ (2.60–6.08 μmol O_2 AFDW g^{-1} h^{-1}, equivalent to 0.131–0.281 μmol O_2 DW g^{-1} h^{-1}) were in the same order of magnitude as rates previously recorded for the species in the Northeast Atlantic under normoxic conditions and similar temperatures (8–9 °C) (Larsson et al., 2013; Hennige et al., 2015; Maier et al., 2019) (Table 3). Thus, our second hypothesis is also rejected (*D. pertusum* respiration under naturally hypoxic conditions is lower than previous records under normoxic conditions). However, how the respiration behaved during the incubations could not be addressed in our experiment. Consequently, we cannot exclude a possible reduction of *D. pertusum* respiration with oxygen concentration decreasing to 0.85 ± 0.10 mL L^{-1} at $T_{day\ 2}$, 0.71 ± 0.22 mL L^{-1} at $T_{day\ 5}$, and 0.42 ± 0.25 mL L^{-1} at $T_{day\ 9}$ in the beakers at the end of the 8 h incubation in the low-oxygen treatment (SEM 1). Even so, such low values are still within or close to the oxygen concentrations observed in the *D. pertusum* reefs off Angola (0.6–1.5 mL L^{-1}, Hanz et al., 2019; Hebbeln et al., 2020), thus being the measured respiration rates representative for the species in its natural environment.

Respiration rates in *D. pertusum* have generally shown to increase with temperature and to decrease when corals are starved (Dodds et al., 2007; Larsson et al., 2013; Maier et al., 2019; Dorey et al., 2020). However, under prolonged incubations, *D. pertusum* also showed a regulatory capacity for respiration in its natural thermal range (6–12 °C, Naumann et al., 2014), and respiration values in the warmer Mediterranean deep sea (12–13 °C, Maier et al., 2013; Gori et al., 2014) were generally in the same order of magnitude as those measured for the species in the colder Northeast Atlantic (6–9 °C, Dodds et al., 2007; Larsson et al., 2013; Khripounoff et al., 2014; Maier et al., 2019, 2020) and Gulf of Mexico (8 °C, Georgian et al., 2016) (Table 3). Compared to these values, respiration rates for *D. pertusum* in Angolan hypoxic waters at 8 °C were even higher than some of the values recorded in the warmer Mediterranean deep sea (12–13 °C, Maier et al., 2013; Gori et al., 2014) (Table 3), and suggest that some cold-water coral reefs may be capable of surviving local declines in oxygen caused by global change in the deep sea (Levin and Le Bris 2015; Sweetman et al., 2017). *D. pertusum* respiration can be extremely variable, showing up to one order of magnitude higher respiration rates in some studies in the Northeast Atlantic and the Mediterranean Sea (Hennige et al., 2014; Naumann et al., 2014; Dorey et al., 2020) (Table 3), possibly due to the experimental design and acclimation time after sampling (Hennige et al., 2015). In our experiment, corals showed a significant increase in respiration in the days following sampling, likely due to acclimation and recovery from the stress induced by the collection. Similarly, increased respiration over time has been observed in corals from the Mediterranean Sea exposed to different pH levels (Maier et al., 2013). Interestingly, *D. pertusum* from the Northeast Atlantic living under normoxic conditions, has shown to significantly reduce its respiration when experimentally exposed to low oxygen concentrations (below 3.26 mL L^{-1}, Dodds et al., 2007), and the same species from the Gulf of Mexico showed complete morality when experimentally exposed to hypoxic conditions (1.57 ± 0.28 mL L^{-1}, Lunden et al., 2014). This contrasts with *D. pertusum* thriving in coral mounds in the hypoxic Angolan waters, where the observed high respiration rates thus suggest an acclimation or local adaptation to hypoxic conditions. Similar local acclimation or adaptation may explain the divergent changes in *D. pertusum* respiration under ocean acidification observed in the Northeast Atlantic and the Gulf of Mexico (Hennige et al., 2014; 2015; Georgian et al., 2016).

Acclimation or adaptation mechanisms allow several marine species to survive when exposed to reduced oxygen levels (Gray et al., 2002; Cheung et al., 2008; Vaquer-Sunyer and Duarte 2008). Reduced activity, metabolic depression and anaerobic respiration are the main mechanisms to survive periodic short to medium-term exposures to low oxygen levels (Nilsson and Renshaw 2004; Semenza 2007; Murphy and Richmond 2016; Huo et al., 2018; Nelson and Altieri 2019, and references therein). A metabolic shift from aerobic to anaerobic glycolysis metabolism (Meng et al., 2018) has been indeed observed in the tropical coral *Acropora tenuis* and *Montipora capitata* facing short-term exposures to low oxygen conditions (Murphy and Richmond 2016; Alderdice et al., 2020) but, if hypoxia stress persists, mortality can ultimately occur due to insufficient energy production or lactic acid accumulation to lethal levels (Hughes et al., 2020). However, other two physiological mechanisms may allow maintaining activity and aerobic metabolism in species living under lifelong hypoxia, as observed in invertebrates living at high-altitudes or in marine oxygen minimum zones (Childress 1971, 1975; Rostgaard and Jacobsen 2005; Ding et al., 2018; Storz and Scott 2019). Since, aerobic respiration in mitochondria is based on the use of oxygen as a substrate for cytochrome C oxidase in the respiratory chain (Semenza 2007), transcription of alternative isoforms of C oxidase with increased affinity for O_2 has been shown to provide a mechanism for maintaining efficient cellular aerobic respiration under reduced oxygen availability (Semenza 2007). Such a functional variation in cytochrome C oxidase may be a physiological mechanism for organisms to live under lifelong hypoxia (Scott et al., 2011; Zhang et al., 2013). Additionally, microbiome associated to *D. pertusum* have been shown to fix inorganic carbon through nitrification (Middelburg et al., 2015), and recent research has shown that nitrifying microbes can produce oxygen under hypoxia (Kraft et al., 2022), thus possibly suppling additional oxygen to the coral (but it has to be considered that the measured rates of inorganic carbon fixed through nitrification were very low, Middelburg et al., 2015). Such physiological mechanisms, possibly together with the previously observed enhanced polyp expansion and movements of epidermal cilia to increase oxygen exchanges (Shapiro et al., 2014; Yum et al., 2017; Pacherres et al., 2020; Tambutté et al., 2021), could explain the respiration rates observed in *D. pertusum* under hypoxia in our study, and the species distribution even in hypoxic zones (Lunden et al., 2014; Hebbeln et al., 2020). Additional focussed research is needed to explore these potential physiological mechanisms allowing coral respiration in hypoxic waters.

Overall, the capability of *D. pertusum* to respire at its usual rate and to grow under hypoxic conditions (Georgian et al., 2014; Wienberg et al., 2018; Hanz et al., 2019; Hebbeln et al., 2020) further extend the potential suitable habitat for this species. In this sense, in the frame of the increasing deoxygenation forecast because of the ongoing global change (Vaquer-Sunyer and Duarte 2008), our results suggest a geographically heterogeneous vulnerability of *D. pertusum*, with possible physiological acclimation or adaptation to regional conditions appearing as important aspects to be considered in the development of models to predict species distribution in space and time (Hällfors et al., 2016; DeMarche et al., 2019).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

Table 3
Respiration rates of *Desmophyllum pertusum* measured in previous studies.

Location	Method	Feeding	Temperature	O_2	pCO_2	Respiration		Reference
			(°C)	(mL L^{-1})	(µatm)	(µmolO_2 DW g^{-1} h^{-1})	(µmolO_2 AFDW g^{-1} h^{-1})	
Northeast Atlantic (Mingulay Reef)	*ex situ* experiment	fed	6.5	6.6–8.7	–	0.12–0.16	–	Dodds et al. (2007) [a]
			9.0	6.2–8.2	–	0.18–0.23	–	
			11.0	6.0–7.8	–	0.29–0.31	–	
Northeast Atlantic (Tisler Reef)	*ex situ* experiment	fed	7.0	–	–	0.27 ± 0.05	4.4 ± 0.8	Larsson et al., 2013
		fed	8.0	–	–	0.22 ± 0.05	4.2 ± 1.0	
		unfed	7.0	–	–	0.165	2.7	
Western Mediterranean (Lacaze-Duthiers Canyon)	*ex situ* experiment	fed	13.0	–	368	0.146 ± 0.073	–	Maier et al. (2013)
		fed	13.0	–	534	0.216 ± 0.092	–	
		fed	13.0	–	883	0.117 ± 0.030	–	
		fed	13.0	–	1215	0.162 ± 0.096	–	
Northeast Atlantic (Mingulay Reef)	*ex situ* experiment	fed	9.5	–	380	–	28.6 ± 7.3	Hennige et al. (2014)
		fed	9.5	–	750	–	11.4 ± 1.4	
Northeast Atlantic (Bay of Biscay)	*in situ* measurement	–	10.0	4.5–5.6	–	0.321	–	Khripounoff et al. (2014)
Western Mediterranean (Cap de Creus Canyon)	*ex situ* experiment	fed	12.0	–	–	0.118 ± 0.052	–	Gori et al. (2014) [a]
Western Mediterranean (Cap de Creus Canyon)	*ex situ* experiment	fed	12.0–9.0–6.0	–	–	1046	–	Naumann et al. (2014)
Northeast Atlantic (Mingulay Reef)	*ex situ* experiment	fed	9.0	–	380	–	4.2–5.9	Hennige et al. (2015) [a]
			9.0	–	750	–	2.8–3.5	
			9.0	–	1000	–	3.7–7.2	
			12.0	–	380	–	1.3–4.8	
			12.0	–	750	–	2.3–6.0	
Gulf of Mexico (Viosca Knoll)	*ex situ* experiment	fed	8.1	6.4	552	–	6.9 ± 1.8	Georgian et al. (2016)
			8.1	6.4	831	–	4.4 ± 1.1	
			8.1	6.4	1164	–	2.6 ± 0.5	
Northeast Atlantic (Tisler Reef)	*ex situ* experiment	fed	7.9	5.7	579	–	5.5 ± 1.8	Georgian et al. (2016)
			7.9	5.7	845	–	7.4 ± 1.6	
			7.9	5.7	1208	–	8.9 ± 1.7	
Northeast Atlantic (Nakken Reef)	*ex situ* experiment	fed	8.1	–	–	0.16 ± 0.03	–	Maier et al. (2019)[a]

(*continued on next page*)

Table 3 (*continued*)

Location	Method	Feeding	Temperature (°C)	O_2 (mL L^{-1})	pCO_2 (µatm)	Respiration (µmolO_2 DW g^{-1} h^{-1})	(µmolO_2 AFDW g^{-1} h^{-1})	Reference
Northeast Atlantic (Sula, Nord-Leska, Hola and Steinavaer Reefs)	*ex situ* experiment	–	5.0	–	–	–	10 ± 11	Dorey et al. (2020)
			15.0	–	–	–	30 ± 11	
Northeast Atlantic (Nakken Reef)	*in situ* experiment	-	7.7	–	–	0.20 ± 0.07	–	Maier et al. (2020)[a]
			6.8	–	–	0.11 ± 0.05	–	
			6.8	–	–	0.27 ± 0.04	–	
			7.5	–	–	0.52 ± 0.05	–	
Southeast Atlantic (Valentin Mounds)	*ex situ* experiment	natural food in seawater	8.2 ± 0.4	1.4 ± 0.5	–	0.175 ± 0.071	3.87 ± 1.54	this study
			8.2 ± 0.4	6.1 ± 0.6	–	0.195 ± 0.085	3.70 ± 1.64	

[a] Respiration values normalized by coral DW or AFDW were supplied by the authors.

the work reported in this paper.

Data availability

Raw data are shared as Supplementary Material.

Acknowledgements

We wish to express our sincere gratitude to the nautical and scientific crews for on-board assistance during the RV Meteor cruise M122 (ANNA). We especially feel indebted to N Nowald, C Seiter, V Vittori and T Leymann from the ROV SQUID team at MARUM (University of Bremen), as well as to WC Dullo and D Saturov from GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, and R Abed from Sultan Qaboos University. We like to thank the German Science Foundation (DFG) for enabling the RV Meteor cruise M122 and for funding the application of the MARUM ROV SQUID. This research received further support from the Cluster of Excellence "The Ocean Floor - Earth's Uncharted Interface" (Germany's Excellence Strategy - EXC-2077-390741603 of the DFG) (DH, CW). The research leading to the results in this manuscript received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 818123 (iAtlantic) and the United Kingdom Research and Innovation (UKRI) Global Challenges Research Fund (GCRF) One Ocean Hub (Grant Ref: NE/S008950/1). This manuscript reflects the authors' view alone, and the European Union cannot be held responsible for any use that may be made of the information contained herein. A Gori received funding from a Beatriu de Pinos 2013 research grant (BP–B00074) from the Generalitat de Catalunya and the Marie Curie Fellowship from the EU-funded project Ithaca, as well as from a Juan de la Cierva 2015 research grant (IJCI-2015- 23962) from the Spanish government. C Orejas has been supported by the German Academic Exchange Service (DAAD), as well as by the Hanse-Wissenschaftskolleg Institute for Advanced Study for a fellowship obtained from October 2021 to July 2022. F Mienis was supported by the Innovational Research Incentives Scheme of the Netherlands Organisation for Scientific Research (NWO-VIDI grant no. 0.16.161.360 and NWO-VENI grant 863.11.012). M Bilan received funding from Dipartimenti di Eccellenza 2018–2022, Ministero dell'Istruzione e del Merito (MIUR) from the Italian Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2023.104052.

References

Addamo, A.M., Vertino, A., Stolarski, J., García-Jiménez, R., Taviani, M., Machordom, A., 2016. Merging scleractinian genera: the overwhelming genetic similarity between solitary *Desmophyllum* and colonial *Lophelia*. BMC Evol. Biol. 16, 108.

Alderdice, R., Suggett, D.J., Cárdenas, A., Hughes, D.J., Kühl, M., Pernice, M., Voolstra, C.R., 2020. Divergent expression of hypoxia response systems under deoxygenation in reef-forming corals aligns with bleaching susceptibility. Global Change Biol. 27, 312–326.

Brooke, S., Ross, S.W., 2014. First observations of the cold-water coral *Lophelia pertusa* in mid-Atlantic canyons of the USA. Deep Sea Res. II 104, 245–251.

Chavez, F.P., Messié, M., 2009. A comparison of eastern boundary upwelling ecosystems. Prog. Oceanogr. 83, 80–96.

Cheung, S.G., Chan, H.Y., Liu, C.C., Shin, P.K.S., 2008. Effect of prolonged hypoxia on food consumption, respiration, growth and reproduction in marine scavenging gastropod *Nassarius festivus*. Mar. Pollut. Bull. 57, 280–286.

Childress, J.J., 1971. Respiratory adaptations to the oxygen minimum layer in the bathypelagic mysid *Gnathophausia ingens*. Biol. Bull. 141, 109–121.

Childress, J.J., 1975. The respiratory rates of midwater crustaceans as a function of depth of occurrence and relation to the oxygen minimum layer off southern California. Comp. Biochem. Physiol. 50A, 781–199.

Davies, A.J., Wisshak, M., Orr, J.C., Roberts, J.M., 2008. Predicting suitable habitat for the cold-water coral *Lophelia pertusa* (Scleractinia). Deep Sea Res. 55, 1048–1062.

DeMarche, M.L., Doak, D.F., Morris, W.F., 2019. Incorporating local adaptation into forecasts of species' distribution and abundance under climate change. Global Change Biol. 25, 775–793.

Ding, D., Liu, G., Hou, L., Gui, W., Chen, B., Kang, L., 2018. Genetic variation in PTPN1 contributes to metabolic adaptation to high-altitude hypoxia in Tibetan migratory locusts. Nat. Commun. 9, 4991.
Dodds, L.A., Roberts, J.M., Taylor, A.C., Marubini, F., 2007. The cold-water coral *Lophelia pertusa* (Scleractinia) reveals metabolic tolerance to temperature and dissolved oxygen change. J. Exp. Mar. Biol. Ecol. 349, 205–214.
Dorey, N., Gjelsvik, Ø., Kutti, T., Büscher, J.V., 2020. Broad thermal tolerance in the cold-water coral *Lophelia pertusa* from Arctic and Boreal reefs. Front. Physiol. 10, 1636.
Dullo, W.C., Flögel, S., Rüggeberg, A., 2008. Cold-water coral growth in relation to the hydrography of the Celtic and Nordic European continental margin. Mar. Ecol. Prog. Ser. 371, 165–176.
Freiwald, A., Beuck, L., Rüggeberg, A., Taviani, M., Hebbeln, D., 2009. The white coral community in the central Mediterranean Sea revealed by ROV surveys. Oceanography 22, 58–74.
Georgian, S.E., Shedd, W., Cordes, E.E., 2014. High-resolution ecological niche modelling of the cold-water coral *Lophelia pertusa* in the Gulf of Mexico. Mar. Ecol. Prog. Ser. 506, 145–161.
Georgian, S.E., Dupont, S., Kurman, M., Butler, A., Strömberg, S.M., Larsson, A.I., Cordes, E.E., 2016. Biogeographic variability in the physiological response of the cold-water coral *Lophelia pertusa* to ocean acidification. Mar. Ecol. 37, 1345–1359.
Gori, A., Grover, R., Orejas, C., Sikorski, S., Ferrier-Pagès, C., 2014. Uptake of dissolved free amino acids by four cold-water coral species from the Mediterranean Sea. Deep Sea Res. II 99, 42–50.
Gray, J.S., Wu, R.S., Or, Y.Y., 2002. Effects of hypoxia and organic enrichment on the coastal marine environment. Mar. Ecol. Prog. Ser. 238, 249–279.
Hällfors, M.H., Liao, J., Dzurisin, J., Grundel, R., Hyvärinen, M., Towle, K., Wu, G.C., Hellmann, J.J., 2016. Addressing potential local adaptation in species distribution models: implications for conservation under climate change. Ecol. Appl. 26, 1154–1169.
Hanz, U., Wienberg, C., Hebbeln, D., Duineveld, G., Lavaleye, M., Juva, K., Dullo, W.C., Freiwald, A., Tamborrino, L., Reichart, G.J., Flögel, S., Mienis, F., 2019. Environmental factors influencing benthic communities in the oxygen minimum zones on the Angolan and Namibian margins. Biogeosciences 16, 4337–4356.
Hebbeln, D., Wienberg, C., Bender, M., Bergmann, F., Dehning, K., Dullo, W.C., Eichstädter, R., Flöter, S., Freiwald, A., Gori, A., Haberkern, J., Hoffmann, L., Mendes João, F., Lavaleye, M., Leymann, T., Matsuyama, K., Meyer-Schack, B., Mienis, F., Bernardo Moçambique, I., Nowald, N., Orejas, C., Ramos Cordova, C., Saturov, D., Seiter, C., Titschack, J., Vittori, V., Wefing, A.M., Wilsenack, M., Wintersteller, P., 2017. ANNA Cold-Water Coral Ecosystems off Angola and Namibia. Cruise No. M122, December 30, 2015 – January 31, 2016, Walvis Bay (Namibia) - Walvis Bay (Namibia). METEOR-Berichte, M122, 74. DFG-Senatskommission Ozeanographie.
Hebbeln, D., Wienberg, C., Dullo, W.C., Freiwald, A., Mienis, F., Orejas, C., Titschack, J., 2020. Cold-water coral reefs thriving under hypoxia. Coral Reefs 39, 853–859.
Hennige, S.J., Wicks, L.C., Kamenos, N.A., Bakker, D.C.E., Findlay, H.S., Dumousseaud, C., Roberts, J.M., 2014. Short-term metabolic and growth response of the cold-water coral *Lophelia pertusa* to ocean acidification. Deep Sea Res. II 99, 27–35.
Hennige, S.J., Wicks, L.C., Kamenos, N.A., Findlay, H.S., Roberts, J.M., 2015. Hidden impacts of coral acclimation to ocean acidification. Proc. Biol. Sci. 282, 20150990.
Holm, S., 1979. A simple sequentially rejective multiple test procedure. Scand. J. Stat. 6, 65–70.
Hughes, D.J., Alderdice, R., Cooney, C., Kühl, M., Pernice, M., Voolstra, C.R., Suggett, D. J., 2020. Coral reef survival under accelerating ocean deoxygenation. Nat. Clim. Change 10, 296–307.
Huo, D., Sun, L., Ru, X., Zhang, L., Lin, C., Liu, S., Xin, X., Yang, H., 2018. Impact of hypoxia stress on the physiological responses of sea cucumber *Apostichopus japonicus*: respiration, digestion, immunity and oxidative damage. PeerJ 6, e4651.
Khripounoff, A., Caprais, J.C., Le Bruchec, J., Rodier, P., Noel, P., Cathalot, C., 2014. Deep cold-water coral ecosystems in the Brittany submarine canyons (Northeast Atlantic): hydrodynamics, particle supply, respiration, and carbon cycling. Limnol. Oceanogr. 59, 87–98.
Kraft, B., Jehmlich, N., Larsen, M., Bristow, L.A., Könneke, M., Thamdrup, B., Canfield, D.E., 2022. Oxygen and nitrogen production by an ammonia-oxidizing archaeon. Science 375, 97–100.
Larsson, A.I., Lundälv, T., van Oevelen, D., 2013. Skeletal growth, respiration rate and fatty acid composition in the cold-water coral *Lophelia pertusa* under varying food conditions. Mar. Ecol. Prog. Ser. 483, 169–184.
Levin, L.A., Le Bris, N., 2015. The deep ocean under climate change. Science 350, 766–768.
Lunden, J.J., McNicholl, C.G., Sears, C.R., Morrison, C.L., Cordes, E.E., 2014. Acute survivorship of the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico under acidification, warming, and deoxygenation. Front. Mar. Sci. 1, 78.
Maier, C., Bils, F., Weinbauer, M.G., Watremez, P., Peck, M.A., Gattuso, J.P., 2013. Respiration of Mediterranean cold-water corals is not affected by ocean acidification as projected for the end of the century. Biogeosciences 10, 5671–5680.
Maier, S.R., Kutti, T., Bannister, R.J., van Breugel, P., van Rijswijk, P., van Oevelen, D., 2019. Survival under conditions of variable food availability: resource utilization and storage in the cold-water coral *Lophelia pertusa*. Limnol. Oceanogr. 64, 1651–1671.
Maier, S.R., Bannister, R.Y., van Oevelen, D., Kutti, T., 2020. Seasonal controls on the diet, metabolic activity, tissue reserves and growth of the cold-water coral Lophelia pertusa. Coral Reefs 39, 173–187.
Meng, J., Wang, T., Li, L., Zhang, G., 2018. Inducible variation in anaerobic energy metabolism reflects hypoxia tolerance across the intertidal and subtidal distribution of the Pacific oyster (*Crassostrea gigas*). Mar. Environ. Res. 138, 135–143.
Middelburg, J.J., Mueller, C.E., Veuger, B., Larsson, A.I., Form, A., van Oevelen, D., 2015. Discovery of symbiotic nitrogen fixation and chemoautotrophy in cold-water corals. Sci. Rep. 5, 17962.
Murphy, J.W.A., Richmond, R.H., 2016. Changes to coral health and metabolic activity under oxygen deprivation. PeerJ 4, e1956.
Naumann, M.S., Orejas, C., Ferrier-Pagès, C., 2014. Species-specific physiological response by the cold-water corals *Lophelia pertusa* and *Madrepora oculata* to variations within their natural temperature range. Deep Sea Res. II 99, 36–41.
Nelson, H.R., Altieri, A.H., 2019. Oxygen: the universal currency on coral reefs. Coral Reefs 38, 177–198.
Nilsson, G.E., Renshaw, G.M.C., 2004. Hypoxic survival strategies in two fishes: extreme anoxia tolerance in the North European crucian carp and natural hypoxic preconditioning in a coral-reef shark. J. Exp. Biol. 207, 3131–3139.
Orejas, C., Wienberg, C., Titschack, J., Tamborrino, L., Freiwald, A., Hebbeln, D., 2021. *Madrepora oculata* forms large frameworks in hypoxic waters off Angola (SE Atlantic). Sci. Rep. 11, 15170.
Pacherres, C.O., Ahmerkamp, S., Schmidt-Grieb, G.M., Holtappels, M., Richter, C., 2020. Ciliary vortex flows and oxygen dynamics in the coral boundary layer. Sci. Rep. 10, 7541.
R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org.
Rabalais, N.N., Turner, R.E., Wiseman, W.J., 2002. Gulf of Mexico hypoxia, a.k.a "The dead zone. Annu. Rev. Ecol. Systemat. 33, 235–263.
Ramos, A., Sanz, J.L., Ramil, F., Agudo, L.M., Presas-Navarro, C., 2017. The giant cold-water coral mounds barrier off Mauritania. In: Ramos, A., Ramil, F., Sanz, J.L. (Eds.), Deep-sea Ecosystems off Mauritania: Research of Marine Biodiversity and Habitats in the Northwest African Margin. Springer Netherlands, Dordrecht.
Roberts, J.M., Wheeler, A.J., Freiwald, A., 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 213, 543–547.
Roberts, J.M., Wheeler, A.J., Freiwald, A., Cairns, S., 2009. Cold-water Corals: the Biology and Geology of Deep-Sea Coral Habitats. Cambridge University Press, Cambridge.
Rostgaard, S., Jacobsen, D., 2005. Respiration rate of stream insects measured in situ along a large altitude range. Hydrobiologia 549, 79–98.
Scott, G.R., Schulte, P.M., Egginton, S., Scott, A.L., Richards, J.G., Milsom, W.K., 2011. Molecular evolution of cytochrome c oxidase underlies high-altitude adaptation in the bar-headed goose. Mol. Biol. Evol. 28, 351–363.
Semenza, G.L., 2007. Oxygen-dependent regulation of mitochondrial respiration by hypoxia-inducible factor 1. Biochem. J. 405, 1–9.
Shapiro, O.H., Fernandez, V.I., Garren, M., Guasto, J.S., Debaillon-Vesque, F.P., Kramarsky-Winter, E., Vardi, A., Stocker, R., 2014. Vortical ciliary flows actively enhance mass transport in reef corals. Proc. Natl. Acad. Sci. USA 111, 13391–13396.
Storz, J.F., Scott, G.R., 2019. Life ascending: mechanism and process in physiological adaptation to high-altitude hypoxia. Annu. Rev. Ecol. Evol. Syst. 50, 22, 1–22.24.
Sweetman, A.K., Thurber, A.R., Smith, C.R., Levin, L.A., Mora, C., Wei, C.L., Gooday, A. J., Jones, D.O.B., Rex, M., Yasuhara, M., Ingels, J., Ruhl, H.A., Frieder, C.A., Danovaro, R., Würzberg, L., Baco, A., Grupe, B.M., Pasulka, A., Meyer, K.S., Dunlop, K.M., Henry, L.A., Roberts, J.M., 2017. Major impacts of climate change on deep-sea benthic ecosystems. Element. Sci. Anthropocene 5, 4.
Tambutté, E., Ganot, P., Venn, A.A., Tambutté, S., 2021. A role for primary cilia in coral calcification? Cell Tissue Res. 383, 1093–1102.
Tittensor, D.P., Baco, A.R., Brewin, P.E., Clark, M.R., Consalvey, M., Hall-Spencer, J., Rowden, A.A., Schlacher, T., Stocks, K.I., Rogers, A.D., 2009. Predicting global habitat suitability for stony corals on seamounts. J. Biogeogr. 36, 1111–1128.
Vaquer-Sunyer, R., Duarte, C.M., 2008. Thresholds of hypoxia for marine biodiversity. Proc. Natl. Acad. Sci. USA 105, 15452–15457.
Wienberg, C., Titschack, J., Freiwald, A., Frank, N., Lundälv, T., Taviani, M., Beuck, L., Schröder-Ritzrau, A., Krengel, T., Hebbeln, D., 2018. The giant Mauritanian cold-water coral mound province: oxygen control on coral mound formation. Quat. Sci. Rev. 185, 135–152.
Yum, L.K., Baumgarten, S., Röthig, T., Roder, C., Roik, A., Michell, C., Voolstra, C.R., 2017. Transcriptomes and expression profiling of deep-sea corals from the Red Sea provide insight into the biology of azooxanthellate corals. Sci. Rep. 7, 6442.
Zhang, Z.Y., Chen, B., Zhao, D.J., Kang, L., 2013. Functional modulation of mitochondrial cytochrome c oxidase underlies adaptation to high-altitude hypoxia in a Tibetan migratory locust. Proc. R. Soc. B 280, 20122758.