



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)

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ABSTRACT

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 ($0.6\text{--}1.5\text{ mL L}^{-1}$). This study assessed the respiration rates of this coral in a short-term (10 days) aquarium experiment under naturally low oxygen concentrations ($1.4 \pm 0.5\text{ mL L}^{-1}$) as well as under saturated oxygen concentrations ($6.1 \pm 0.6\text{ mL L}^{-1}$). 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 $2\text{--}3.7\text{ mL L}^{-1}$ (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

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(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 ($1.1\text{--}1.3\text{ mL L}^{-1}$) 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 ($0.6\text{--}1.5\text{ mL L}^{-1}$) (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 ($09^{\circ} 43.700' \text{ S} - 012^{\circ} 42.876' \text{ E}$) 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 ($1.8 \pm 0.3\text{ mL L}^{-1}$) in hermetically sealed plastic chambers ($\sim 400\text{ mL}$ 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

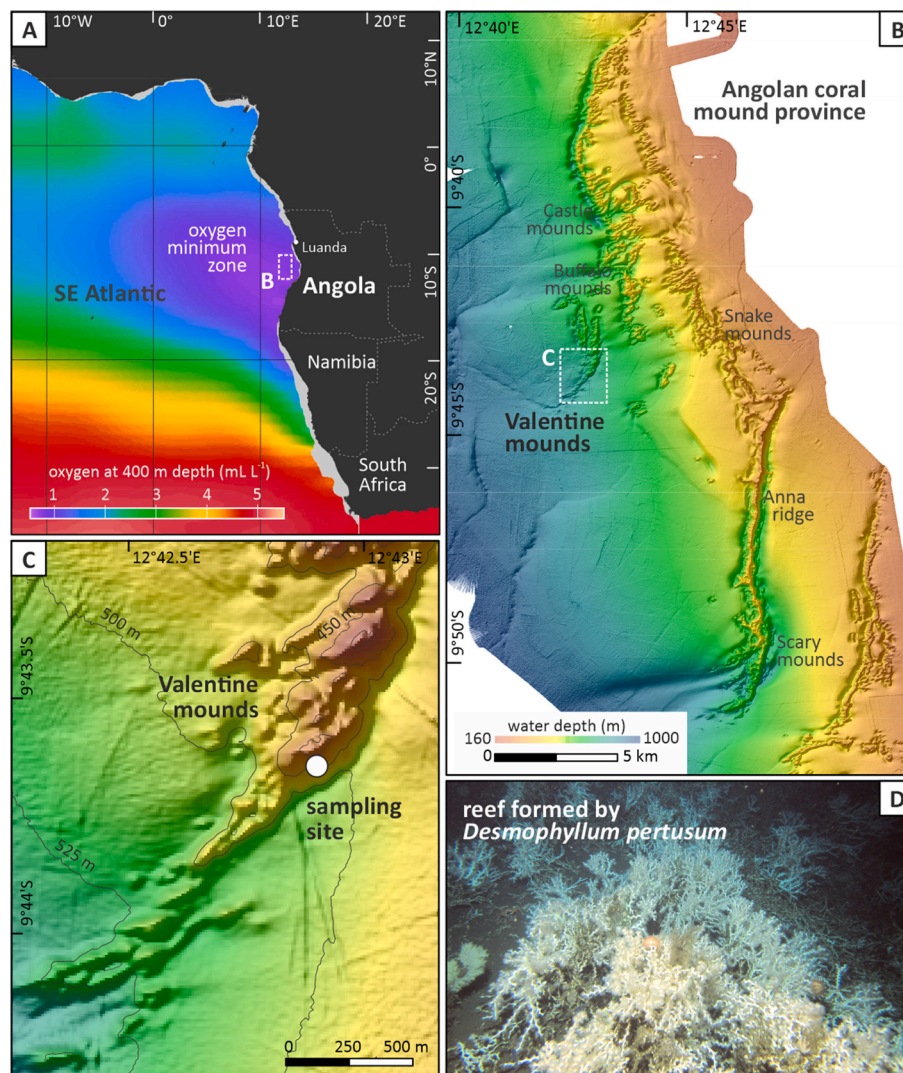


Fig. 1. (A) Overview map showing the location of the Angolan coral mound province in the SE Atlantic Ocean. Dissolved oxygen concentrations at 400 m water depth are displayed. (B) Bathymetric map showing the Angolan coral mound province. (C) Detailed map showing the sampling site on the Valentine mounds. (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).

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 L⁻¹ h⁻¹) was always higher than oxygen variation in control beakers (<0.01 mL L⁻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

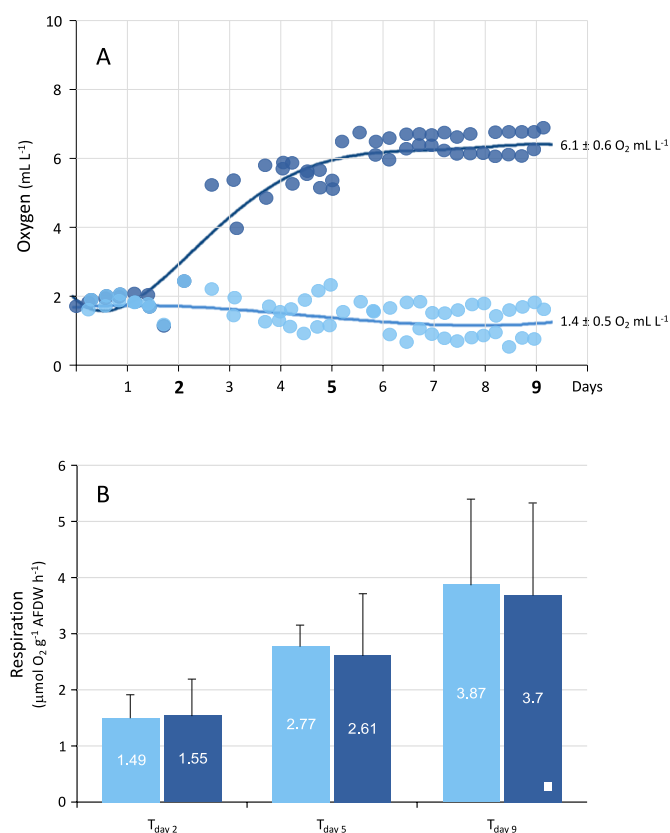


Fig. 2. (A) Oxygen concentration (mL L⁻¹) during the experiment in the naturally low oxygen concentration (light blue) and the increased oxygen concentration (dark blue) treatments. Days of experimental incubations are highlighted in bold. Variability in the oxygen concentration was due to the water 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.

Table 2

Respiration rates of *Desmophyllum pertusum* under the two experimental treatments (natural low O₂ and increased O₂) 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	
		($\mu\text{molO}_2 \text{ DW g}^{-1} \text{ h}^{-1}$)	($\mu\text{molO}_2 \text{ AFDW g}^{-1} \text{ h}^{-1}$)
		mean $\pm$ SD	mean $\pm$ SD
Natural low O ₂ ($1.4 \pm 0.5 \text{ mL L}^{-1}$)	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 ($6.1 \pm 0.6 \text{ mL L}^{-1}$)	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} ($2.60\text{--}6.08 \mu\text{mol O}_2 \text{ AFDW g}^{-1} \text{ h}^{-1}$, equivalent to $0.131\text{--}0.281 \mu\text{mol O}_2 \text{ DW g}^{-1} \text{ h}^{-1}$) were in the same order of magnitude as rates previously recorded for the species in the Northeast Atlantic under normoxic conditions and similar temperatures ($8\text{--}9^\circ\text{C}$) (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 $0.85 \pm 0.10 \text{ mL L}^{-1}$ at T_{day 2}, $0.71 \pm 0.22 \text{ mL L}^{-1}$ at T_{day 5}, and $0.42 \pm 0.25 \text{ mL L}^{-1}$ 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 ($0.6\text{--}1.5 \text{ mL L}^{-1}$, 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 ($6\text{--}12^\circ\text{C}$, Naumann et al., 2014), and respiration values in the warmer Mediterranean deep sea ($12\text{--}13^\circ\text{C}$, 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 ($6\text{--}9^\circ\text{C}$, Dodds et al., 2007; Larsson et al., 2013; Khrpounoff 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 ($12\text{--}13^\circ\text{C}$, 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 mortality when experimentally exposed to hypoxic conditions ($1.57 \pm 0.28 \text{ mL L}^{-1}$, 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 O₂ 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 supplying 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)	<i>ex situ</i> 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)	<i>ex situ</i> 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)	<i>ex situ</i> 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)	<i>ex situ</i> 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)	<i>in situ</i> measurement	–	10.0	4.5–5.6	–	0.321	–	Khripounoff et al. (2014)
Western Mediterranean (Cap de Creus Canyon)	<i>ex situ</i> experiment	fed	12.0	–	–	0.118 ± 0.052	–	Gori et al. (2014) ^a
Western Mediterranean (Cap de Creus Canyon)	<i>ex situ</i> experiment	fed	12.0–9.0–6.0	–	–	1046	–	Naumann et al. (2014)
Northeast Atlantic (Mingulay Reef)	<i>ex situ</i> 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)	<i>ex situ</i> 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)	<i>ex situ</i> 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)	<i>ex situ</i> 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, Høla and Steinavaer Reefs)	ex situ experiment	-	5.0 15.0	- -	- -	- -	10 ± 11 30 ± 11	Dorey et al. (2020)
Northeast Atlantic (Nakken Reef)	in situ experiment	-	7.7 6.8 6.8 7.5	- - - -	- - - -	0.20 ± 0.07 0.11 ± 0.05 0.27 ± 0.04 0.52 ± 0.05	- - - -	Mäler et al. (2020) ^a
Southeast Atlantic (Valentin Mounds)	ex situ experiment	natural food in seawater	8.2 ± 0.4 8.2 ± 0.4	1.4 ± 0.5 6.1 ± 0.6	- -	0.175 ± 0.071 0.195 ± 0.085	3.87 ± 1.54 3.70 ± 1.64	this study

^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.

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Appendix A. Supplementary data

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