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NOTE

Physiological performance of the cold-water coral *Dendrophyllia cornigera* reveals its preference for temperate environments

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Abstract Cold-water corals (CWCs) are key ecosystem engineers in deep-sea benthic communities around the world. Their distribution patterns are related to several abiotic and biotic factors, of which seawater temperature is arguably one of the most important due to its role in coral physiological processes. The CWC *Dendrophyllia cornigera* has the particular ability to thrive in several locations in which temperatures range from 11 to 17 °C, but to be apparently absent from most CWC reefs at temperatures constantly below 11 °C. This study thus aimed to assess the thermal tolerance of this CWC species, collected in the Mediterranean Sea at 12 °C, and grown at the three relevant temperatures of 8, 12, and 16 °C. This species displayed thermal tolerance to the large range of seawater temperatures investigated, but growth, calcification, respiration, and total organic carbon (TOC) fluxes severely decreased at 8 °C compared to the in situ temperature of 12 °C. Conversely, no significant differences in calcification, respiration, and TOC fluxes were observed between corals maintained at 12 and 16 °C, suggesting that the fitness of this CWC is higher in temperate rather than cold environments. The capacity to maintain physiological functions between 12 and 16 °C allows *D. cornigera* to be the most abundant CWC species in deep-sea ecosystems where temperatures are too warm for other CWC species (e.g., Canary Islands). This study also shows that not all CWC species occurring in the Mediterranean Sea (at deep-water temperatures of 12–14 °C) are currently living at their upper thermal tolerance limit.

Keywords Physiological ecology · Thermal tolerance · Coral calcification · Coral growth · Coral respiration · Organic carbon fluxes

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Introduction

Cold-water corals (CWCs) are among the main engineering species (sensu Jones et al. 1994) in deep-sea ecosystems all over the world (Freiwald et al. 2004; Roberts et al. 2006, 2009a), where they play a crucial structural and functional role (Wildish and Kristmanson 1997; Gili and Coma 1998). From a structural point of view, many CWC species generate spatial heterogeneity by forming complex three-dimensional reef frameworks that provide suitable habitat for hundreds of associated species (Krieger and Wing 2002; Roberts et al. 2009a; Buhl-Mortensen et al. 2010). The main environmental features, such as current flow, food availability, and sediment re-suspension, vary widely within these complex structures, and this heterogeneity increases the abundance and functional diversity of the associated fauna (Fosså et al. 2002; Henry and Roberts

2007), particularly fish species (Baillon et al. 2012; Miller et al. 2012). From a functional point of view, CWCs determine a significant flow of matter and energy from the pelagic to the benthic system (Gili and Coma 1998; Van Oevelen et al. 2009), by capturing plankton and particulate organic matter suspended in the water (Duineveld et al. 2004, 2007, 2012; Carlier et al. 2009; Dodds et al. 2009). Dissolved and particulate organic mucoid compounds synthesized by CWCs and released into the water as an end product of catabolism can act as a vector for energy and a matter carrier in benthic–pelagic coupling, stimulating bacterioplankton growth and enhancing nutrient recycling via the microbial loop (Ferrier-Pages et al. 2000; Wild et al. 2004, 2008, 2009; Naumann et al. 2010).

The distribution of CWC species has been related to several abiotic and biotic factors such as seawater temperature and density, water flow regimes, aragonite saturation state, oxygen concentration, presence of suitable substrate, and food supply (Roberts et al. 2006; Davies et al. 2008; Dullo et al. 2008). Seawater temperature is considered one of the most important ecological factors driving CWC distribution (Freiwald et al. 2009; Roberts et al. 2009a) because it strongly controls coral physiological processes such as respiration (Buddemeier and Kinzie 1976; Coles and Jokiel 1977; Dodds et al. 2007; Naumann et al. 2014) and calcification (Clausen and Roth 1975; Howe and Marshall 2002; Naumann et al. 2014). Above or below their optimum thermal range, corals reduce their polyp activity (i.e., polyp expansion) and metabolism (Howe and Marshall 2001; Previati et al. 2010; Ferrier-Pagès et al. 2012), before the appearance of lethal effects (Jokiel and Coles 1977; Coles and Fadlallah 1991; Rodolfo-Metalpa et al. 2006).

Among cold-water scleractinians, some species such as *Lophelia pertusa*, *Madrepora oculata*, *Solenosmilia variabilis*, and *Desmophyllum dianthus* show a widespread distribution throughout the world's oceans. Conversely, other CWC species like *Dendrophyllia cornigera* (Fig. 1) are restricted to particular geographical areas (Zibrowius 1980; Cairns 1994; Roberts et al. 2009a). The currently known distribution of *D. cornigera* (Fig. 2; Electronic Supplementary Material, ESM Table 1) includes the Mediterranean Sea at temperatures ~12 to 14 °C (Pérès and Picard 1964; Zibrowius 1980; Freiwald et al. 2009; Orejas et al. 2009; Salomidi et al. 2010; Bo et al. 2011; Gori et al. 2013), and the Eastern Atlantic from the south of Ireland to the Cape Verde Islands (Le Danois 1948; Zibrowius 1980; Álvarez-Claudio 1994; Brito and Ocaña 2004; Sánchez et al. 2009; Braga-Henriques et al. 2013), at temperatures ranging from 11 to 17 °C (Le Danois 1948; Barton et al. 1998; Castaing et al. 1999; Valencia et al. 2004). In the Bay of Biscay, *D. cornigera* locally forms dense mono-specific aggregations between 50 and 620 m

Fig. 1 The cold-water coral *Dendrophyllia cornigera*. Photo by PJ López-González

Fig. 2 Known distribution of *Dendrophyllia cornigera* based on a literature review of the confirmed identifications of live specimens (quoted in the text)

depth (Le Danois 1948; Álvarez-Claudio 1994; Reveillaud et al. 2008; Sánchez et al. 2009), and occurs at shallower depths of 30 m in areas characterized by upwelling of sea water at 11–14 °C (Castric-Fey 1996). Around the Canary Islands, *D. cornigera* is the dominant CWC species between 200 and 400 m depth (Brito and Ocaña 2004), at temperatures ranging from 13 to 16 °C (Barton et al. 1998). However, *D. cornigera* is absent from the north-eastern Atlantic, where temperatures range from 5 to 10 °C and reefs are dominated by *L. pertusa* (Dullo et al. 2008; Roberts et al. 2009b; Huvenne et al. 2011; Purser et al. 2013). All these observations suggest that, unlike other

CWC species, the fitness of *D. cornigera* may be higher in temperate rather than cold environments.

To assess the potential effects of seawater temperature on the physiology of *D. cornigera,* rates of growth, calcification, respiration, and organic carbon (C) fluxes were measured at two temperatures (12 and 16 °C) near the extremes of its current thermal range, and at a lower temperature (8 °C) that is characteristic of the north-eastern Atlantic CWC reefs (Dullo et al. 2008; Roberts et al. 2009b) where *D. cornigera* is absent. The aim of this study was to increase our knowledge on the thermal tolerance of *D. cornigera*, as temperature may be a key driver of its distribution.

Materials and methods

Coral collection and maintenance

Specimens of *D. cornigera* (Lamarck, 1816) (Fig. 1) were collected in the Menorca Channel (Balearic Archipelago, western Mediterranean Sea, 40°00′00″N; 003°32′20″E, at 180–330 m depth) by means of the manned submersible JAGO (IFM-GEOMAR, Kiel, Germany), and maintained alive on board the RV 'García del Cid' during the cruise INDEMARES 3 (April 2010). Corals were transported to the Institut de Ciències del Mar (CSIC; Barcelona, Spain) and maintained there in a 140-L tank with a continuous flow of Mediterranean sea water pumped from 15 m depth at a rate of 60 L h^{-1} and filtered by a 50-µm sand filter (Olariaga et al. 2009). Water temperature was maintained close to in situ conditions (12 ± 1.0 °C), and two submersible pumps provided continuous water movement in the tank with a flow rate of 3,200 L h^{-1}. Corals were fed five times a week with frozen *Mysis* (Crustacea, Eumalacostraca) and *Artemia salina* (Crustacea, Sarsostraca) adults. For the development of the experimental work, 15 specimens of *D. cornigera* were transferred to the Centre Scientifique de Monaco (CSM; Monaco, Principality of Monaco) and maintained during a month at the same temperature as in Barcelona (12 ± 1.0 °C) in order to allow the specimens to acclimate. Corals were then placed into three different 25-L darkened tanks (five nubbins per tank) with a continuous flow of Mediterranean sea water freshly pumped from 50 m depth at a rate of 20 L h^{-1}. Water temperature was maintained in each tank at 12 ± 0.5 °C by means of chillers (Teco TR 20, Ravenna, Italy) and 300-W heaters (Aquarium Systems Visi-therm, Sarrebourg, France) connected to independent temperature controllers (West 6100, Kassel, Germany). A submersible pump provided continuous water movement in each tank with a flow rate of 320 L h^{-1}. Nubbins were distributed in order to have approximately the same skeletal mass and polyp number in each tank (Table 1) to ensure comparable magnitudes of growth and calcification rates. After one week under the above-controlled conditions, seawater temperature in two of the three tanks was changed stepwise (0.5 °C d^{-1}) to reach the three experimental temperatures of 8 ± 0.5, 12 ± 0.5, and 16 ± 0.5 °C. Corals were fed five times a week with a controlled daily supply of four *Mysis* per polyp and were maintained for 150 d under these conditions. *Mysis* were pipetted two to three times a day onto protruded polyps, and subsequent capture and ingestion were visually monitored to ensure food intake. To determine daily organic C supply, 12 *Mysis* were freeze-dried (Christ Alpha 2-4 LD, Osterode am Harz, Germany), acidified with H_3PO_4 (1 mol L^{-1}, 100 µL), and subsequently analysed using an elemental analyzer (Perkin Elmer, Waltham, MA, USA). Mean daily food-derived organic C input (184 ± 16 µmol C $polyp^{-1}$ d^{-1}) was calculated using certified glycine standards (K-factor 32.0 % C; Naumann et al. 2011).

Physiological measurements

After 10-d incubation at the right temperatures, the weight of each coral nubbin was assessed by means of the buoyant weight technique (Jokiel et al. 1978; Davies 1989) using an analytical balance (Mettler AT 261, L'Hospitalet de Llobregat, Spain, precision 0.1 mg). During the following

Table 1 Weight, surface, and number of polyps of the *Dendrophyllia cornigera* nubbins incubated under the three experimental temperatures

Treatment (°C)	Weight (g)	Surface area (cm^2)	Number of polyps
8	15.8	34.4	2
	12.4	31.9	1
	9.4	23.7	2
	6.6	19.0	2
	2.1	8.7	1
	9.3 ± 5.3	23.5 ± 10.4	
12	20.5	34.6	1
	10.6	22.2	2
	10.2	18.4	1
	8.6	21.3	2
	2.0	8.2	1
	10.4 ± 6.6	20.9 ± 9.4	
16	15.3	28.2	2
	15.0	32.3	2
	9.8	32.4	2
	6.2	18.2	1
	3.3	12.9	1
	9.9 ± 5.3	24.8 ± 8.8	

150 d, the weight of each nubbin was measured eight times (approximately every 20 d). Feeding was suspended 48 h before weight measurements to rule out excretion of undigested particulate food items. The bulk growth rate (i.e., skeletal + tissue) of each nubbin was calculated as the slope of the linear regression between the natural logarithm of the nubbin biomass (mg) *versus* the experimental time (d). Bulk growth rates were expressed as percentages of daily weight increase (% d^{-1}) (Orejas et al. 2011a). The known percentage contribution of organic tissue biomass to bulk dry mass (14 ± 4 %; Movilla et al. 2014) allowed estimation of organic C flux into tissue growth (Naumann et al. 2011), assuming a comparable tissue ash-free dry weight organic C content, as previously reported for scleractinian corals and marine benthic macrofauna (41 and 40 %, respectively; Kang 1999; Schutter et al. 2010).

After 150 d under the three temperature conditions, three sets of incubations were performed to assess the rates of calcification, respiration, and organic C fluxes. Five nubbins per treatment were incubated for 6 h in individual beakers (370 mL), completely filled (without any air space) with 50 µm pre-filtered sea water, hermetically closed with a plastic membrane impermeable to air, and maintained at the corresponding temperature in a water bath. One beaker, filled with pre-filtered sea water without any coral, was used as a control. Constant water movement inside the beakers was ensured by a Teflon-coated magnetic stirrer. The coral calcification rate was assessed by the total alkalinity (TA) anomaly technique (Smith and Key 1975; Langdon et al. 2010), assuming a consumption of two moles of alkalinity for every mole of calcium carbonate produced (Langdon et al. 2010). Seawater samples (120 mL) were drawn, before and after incubation, from each beaker, sterile-filtered (0.2 µm), and kept refrigerated (4 °C) pending analysis (performed within less than 48 h). TA was determined on six subsamples of 20 mL from each beaker using a titration system composed of a 20-mL open thermostated titration cell, a pH electrode calibrated on the National Bureau of Standards scale, and a computer-driven titrator (Metrohm 888 Titrando, Riverview, FL, USA). Seawater samples were kept at a constant temperature (25.0 ± 0.2 °C) and weighed (Mettler AT 261, L'Hospitalet de Llobregat, Spain, precision 0.1 mg) before the titration to determine their exact volume from temperature and salinity. TA was calculated from the Gran function applied to pH variations from 4.2 to 3.0 as the function of added volume of HCl (0.1 mol L^{-1}), and TA values were corrected for changes in ammonium concentration (resulting from metabolic waste products) in experimental and control beakers (Jacques and Pilson 1980; Naumann et al. 2011). Samples for ammonium analysis (20 mL) were sterile-filtered (0.2 µm) and kept frozen (−20 °C) until ammonium concentration was determined in four replicates per sample by means of the spectrofluorometric method of Holmes et al. (1999). Variation in the TA measured from the control beaker was subtracted from those measured in the beakers with corals, and calcification rates were derived from the recorded depletion of TA over the 6-h incubation. Respiration rates were assessed by determining oxygen concentration in each beaker, at the beginning and end of the incubation, using an optode sensor (Hach-Lange HQ 40b, Loveland, CO, USA, precision 0.2 mg L^{-1}). Variation in the oxygen concentration measured from the control beaker was subtracted from those measured in the coral beakers, and respiration rates were derived from the recorded depletion of dissolved oxygen over the incubation. Oxygen consumption rates were converted to C equivalents (µmol) according to the equation $C\ respired = O_2\ consumed \cdot RQ$, where RQ is a coral-specific respiratory quotient equal to 0.8 mol C mol^{-1} O_2 (Anthony and Fabricius 2000; Ribes et al. 2003; Naumann et al. 2011). Organic C fluxes were assessed by calculating the difference in the seawater total organic carbon (TOC) concentration between the beginning and end of the incubation (Naumann et al. 2011). Seawater samples (60 mL) were drawn, before and after incubation, from each beaker, transferred into pre-combusted (450 °C, 5 h) glass vials, acidified with phosphoric acid (20 %, 250 µL) to pH < 2, and kept frozen (−20 °C) until analysis by high-temperature catalytic oxidation (Shimadzu TOC-VCPH, Kyoto, Japan). Variation in the TOC measured from the control beaker was subtracted from those measured in the coral beakers, and TOC net fluxes were derived from the recorded variation of TOC over the 6-h incubation. Results from calcification, respiration, and organic C flux measurements were normalized to the coral skeletal surface area (fully covered by coral tissue), in order to allow for comparison with other coral species. The skeletal surface area (S) of each coral nubbin was determined by means of advanced geometry (Naumann et al. 2009) according to the equation $S = \pi \cdot (r + R) \cdot a + \pi \cdot R^2$, where r and R represent the basal and apical radius of each polyp, respectively, and a is the apothem measured with calipers (Rodolfo-Metalpa et al. 2006).

Statistical analyses

All results are expressed as mean ± standard deviation. Normal distribution of the data was tested by means of Kolmogorov–Smirnov test performed with the R-language function ks.test of the R software platform (R Development Core Team 2012). Homogeneity of variances was tested by means of the Bartlett test performed with the R-language function bartlett.test. Differences among the three experimental temperatures in bulk growth rate, calcification, respiration, and organic C fluxes were tested by one-way

ANOVA and subsequent post hoc analysis performed with the R-language function aov and tukeyHSD, respectively.

Results

Significant differences in bulk growth rate assessed by means of the buoyant weight technique (Fig. 3) were observed among the three temperatures (ANOVA, $F = 21.69$, p value <0.001; Table 2). Corals maintained at 8 °C grew significantly slower (0.019 ± 0.012 % d^{-1}) than those maintained at 12 °C (0.061 ± 0.020 % d^{-1}), which also grew significantly slower than those maintained at 16 °C (0.116 ± 0.040 % d^{-1}). Changes in TA in the incubation chambers (1.9–18.6 μEq L^{-1} h^{-1}) were always distinguishable from changes measured in the control chambers (<1.7 μEq L^{-1} h^{-1}), and calcification rates assessed by the TA anomaly technique (Fig. 4a) were significantly different among the experimental temperatures (ANOVA, $F = 12.11$, p value $= 0.001$; Table 2). Corals maintained at 8 °C calcified slower (0.4 ± 0.2 μmol $CaCO_3$ cm^{-2} d^{-1}) than those maintained at 12 °C (1.5 ± 0.6 μmol $CaCO_3$ - cm^{-2} d^{-1}) or 16 °C (1.9 ± 0.6 μmol $CaCO_3$ cm^{-2} d^{-1}). Oxygen depletion attributable to coral respiration in the incubation chambers (2.5–11.6 μmol L^{-1} h^{-1}) was always higher than oxygen depletion in control chambers due to microbial respiration (<1.2 μmol L^{-1} h^{-1}), and respiration rates (Fig. 4b) were significantly different among the tested temperatures (ANOVA, $F = 10.47$, p value $= 0.002$; Table 2). Corals maintained at 8 °C respired significantly less (1.4 ± 0.3 μmol C cm^{-2} d^{-1}) than those maintained at 12 °C (2.0 ± 0.3 μmol C cm^{-2} d^{-1}) or 16 °C (2.4 ± 0.5 μmol C cm^{-2} d^{-1}). TOC fluxes (Fig. 4c) were significantly different among the three temperatures treatments (ANOVA, $F = 20.92$, p value <0.001; Table 2), with a net uptake of TOC observed in corals maintained at 8 °C (-0.56 ± 0.15 μmol TOC cm^{-2} d^{-1}), which contrasted with the substantial release of TOC observed in corals maintained both at 12 °C (0.88 ± 0.34 μmol TOC cm^{-2} d^{-1}) and 16 °C (0.87 ± 0.59 μmol TOC cm^{-2} d^{-1}).

Concerning the C budget of *D. cornigera* at the three temperatures, feeding accounted for a mean organic C input of 184 ± 16 μmol C $polyp^{-1}$ d^{-1} corresponding to 13 ± 4 μmol C cm^{-2} d^{-1}. Respiration accounted for the main consumption of this organic C input and increased with temperature (11, 17, and 20 % at 8, 12, and 16 °C, respectively). Tissue growth also increased with temperature and accounted for 4, 12, and 16 % at 8, 12, and 16 °C, respectively. It has to be noticed that at 8 °C, seawater TOC contributed to the input of organic C, in addition to the particulate feeding (4 % of the total organic C input), whereas at 12 and 16 °C, the release of TOC (9 and 7 % of the organic C input at 12 and 16 °C, respectively) represented an additional loss of C from the coral.

Table 2 Pairwise test for comparison of the growth rate, calcification, respiration, and organic carbon fluxes, among the three experimental temperatures

	8/12 °C (p value)	8/16 °C (p value)	12/16 °C (p value)
Growth	0.037*	<0.001***	0.007**
Calcification	<0.001***	0.001**	0.505
Respiration	0.048*	0.002**	0.192
Organic carbon fluxes	<0.001***	<0.001***	0.999

* p value <0.05, ** p value <0.01, *** p value <0.001

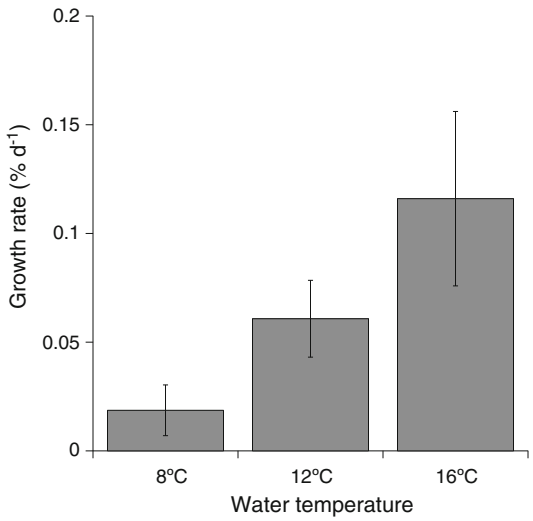

Fig. 3 Growth rate of *Dendrophyllia cornigera* under the three experimental temperatures, as a result of eight weight measurements carried out during 150 d (approximately every 20 d). Values are presented as mean ± SD

Discussion

Dendrophyllia cornigera exhibited, in laboratory conditions, a pronounced tolerance to a wide thermal range (from 8 to 16 °C). It has been previously demonstrated that lethal effects appear in corals at temperatures outside the species thermal range (Coles and Fadlallah 1991; Colella et al. 2012), with polyp contraction followed by massive loss of tissue (Jokiel and Coles 1977; Rodolfo-Metalpa et al. 2006). Such mortality was observed in *L. pertusa* when maintained for a week at 15 °C or at higher temperatures (Brooke et al. 2013). Conversely, no damage or coral mortality was observed in *D. cornigera* during our experiment (5 months) and until the present day (after 24 months), confirming that the upper thermal threshold of

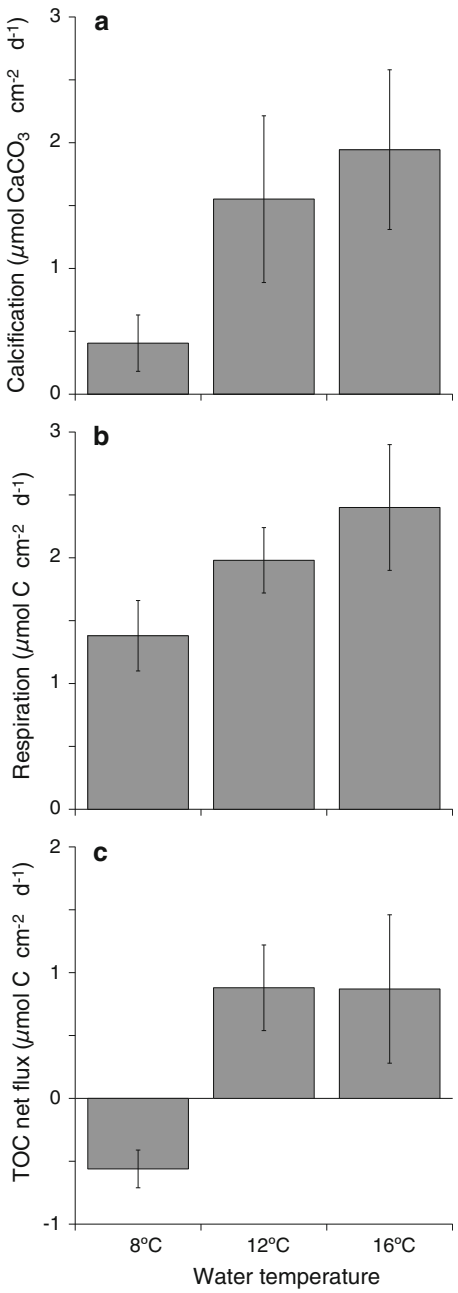

Fig. 4 Calcification rate (**a**), respiration rate (**b**), and total organic carbon (TOC) net flux (**c**) of *Dendrophyllia cornigera* under the three experimental temperatures, as the result of coral nubbins incubation in individual beakers for 6 h. Values are presented as mean ± SD normalised to coral skeletal surface area

some CWC species may be higher than previously assumed (Naumann et al. 2013).

Dendrophyllia cornigera demonstrated no thermal acclimation to low temperatures, suggesting that the fitness of this CWC is higher in temperate rather than cold-water environments. Indeed, its metabolism was severely decreased at 8 °C compared to the in situ temperature of 12 °C, with a significant reduction in growth rate by 300 %, calcification rate by 70 %, and respiration rate by 30 %. The observed shift from release to uptake of TOC at 8 °C also supports this substantial reduction in coral metabolism at this low temperature, since organic matter release by corals in ambient sea water depends on their metabolic activity (Ferrier-Pagès et al. 1998; Wild et al. 2008; Naumann et al. 2011). Such a reduction in metabolism was previously observed in tropical coral species when seawater temperature fell below their natural thermal range (Coles and Fadlallah 1991; Kemp et al. 2011). Calcification rates of tropical (e.g., Jokiel and Coles 1977; Coles and Jokiel 1978; Lough and Barnes 2000; Abramovitch-Gottlib et al. 2002) and temperate corals (e.g., Jacques et al. 1983; Howe and Marshall 2002; Rodolfo-Metalpa et al. 2008a) are strongly influenced by temperature, and a growth response to temperature has been previously observed also in the CWC *Oculina varicosa* (Reed 1981). Low growth rates could be directly induced by the effect of temperature on the activity of the enzymes involved in calcification (such as the carbonic anhydrases; Ip et al. 1991; Al-Horani et al. 2003; Allemand et al. 2004), since enzyme activity is maximal within the thermal range of the organism and decreases otherwise (Jacques et al. 1983; Marshall and Clode 2004; Al-Horani 2005). Moreover, a possible reduced digestion and/or assimilation efficiency at low temperature (Glynn and Stewart 1973) could also have resulted in a lower organic C availability for corals maintained at 8 °C, even if the amount of ingested organic C was the same for all corals (see Materials and Methods). This is also suggested by the observed decrease in the amount of C employed for tissue growth, respiration, and organic C fluxes at 8 °C (~19 % of the ingested organic C), compared to 12 °C (~38 %) and 16 °C (~43 %). No significant differences in the rates of calcification, respiration, and TOC release were observed between corals maintained at 12 and 16 °C, suggesting that *D. cornigera* can tightly control its metabolic activity within its natural thermal range (Sassaman and Mangum 1970; Jacques et al. 1983; Howe and Marshall 2001). Such a thermal acclimation was previously observed in *L. pertusa* colonies from the Mediterranean Sea, which kept respiration rates constant between 6 and 12 °C, and calcification rates constant between 9 and 12 °C (Naumann et al. 2014), as well as in the temperate coral *Leptosammia pruvoti*, whose calcification rate was not correlated with seawater temperature (Caroselli et al. 2012). Although the calcification rate assessed by the TA anomaly technique was not significantly different between 12 and 16 °C, the enhanced growth rates at 16 °C shown by the buoyant weight measures is in agreement with the observed higher tissue growth at 16 °C and highlights that *D. cornigera* metabolism is more efficient at the higher temperature within its thermal range.

Growth, calcification, and respiration rates of *D. cornigera* at the in situ Mediterranean temperature of 12 °C are consistent with previous data obtained from the same species (Orejas et al. 2011a; Naumann et al. 2013) and are in the same order of magnitude as those reported for other Mediterranean CWCs *L. pertusa*, *M. oculata* (e.g., Maier et al. 2009, 2012; Orejas et al. 2011a, 2011b; Naumann et al. 2014), and *D. dianthus* (Naumann et al. 2011, 2013). Overall, Mediterranean CWCs have a reduced metabolic activity (Naumann et al. 2011) and lower calcification rates compared to most tropical corals (13.9–194.0 μmol $CaCO_3$ cm^{-2} d^{-1}; Lough and Barnes 2000; Carricart-Garnivet 2004; Colombo-Pallotta et al. 2010), but have comparable rates to most temperate coral species (1.5–3.12 μmol $CaCO_3$ cm^{-2} d^{-1}; Kevin and Hudson 1979; Jacques et al. 1983; Howe and Marshall 2002; Rodolfo-Metalpa et al. 2008b). Organic C release at the in situ temperature of 12 °C was higher in *Dendrophyllia cornigera* (0.88 ± 0.34 μmol C cm^{-2} d^{-1}) than in *Desmophyllum dianthus* (~0.4 μmol C cm^{-2} d^{-1}, Naumann et al. 2011), which highlights its functional role as a source of particulate and/or dissolved organic matter that can stimulate bacterioplankton growth and enhance nutrient recycling via the microbial loop (Ferrier-Pagès et al. 1998; Wild et al. 2008, 2009). However, both species release much less organic matter than *L. pertusa* (~9.6 μmol C cm^{-2} d^{-1}; Wild et al. 2008). The bulk of organic matter released by corals mainly originates from coral mucus (Crossland 1987; Wild et al. 2004; Naumann et al. 2010), which may play an important role in the entanglement and capture of small food particles (Lewis and Price 1975). This may suggest a possible low importance of mucus production in the trophic strategy of *Dendrophyllia cornigera* and *Desmophyllum dianthus*, possibly due to a preference of these species for large prey captured by means of tentacle activity (Lewis and Price 1975) of their large polyps.

The severe reduction observed in the rates of the main physiological processes at 8 °C may explain why *D. cornigera* is currently absent from areas dominated by other CWC species and characterized by temperatures constantly below 12 °C (e.g., Norwegian reefs, Tisler reef, Mingulay reef; Dullo et al. 2008; Roberts et al. 2009b; Huvenne et al. 2011). However, its capacity to maintain efficient physiological function between 12 and 16 °C enables *D. cornigera* to be the most abundant CWC species in deep-sea ecosystems where temperature conditions are currently not suitable for the otherwise more widespread CWCs *L. pertusa* and *M. oculata* (e.g., Canary Islands; Brito and Ocaña 2004). The thermal tolerance of *D. cornigera* also highlights that not all CWC species dwelling on the continental shelf and slope of the Mediterranean Sea (at temperatures of 12–14 °C) are currently living at their upper thermal limit (Freiwald et al. 2009; Brooke et al. 2013). Large-scale warming of the Mediterranean Sea (Walther et al. 2002) and its deep waters (~0.12 °C in 30 yr in the Western basin; Bethoux et al. 1990) may therefore contribute to a future shift in the Mediterranean CWC community composition, with a potential reduction in *L. pertusa* abundance (whose upper limit of thermal tolerance is near 15 °C; Brooke et al. 2013), and an increase in *D. cornigera* abundance.

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