Long-term growth rates of four Mediterranean cold-water coral species maintained in aquaria

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ABSTRACT: Growth rates of the cold-water corals (CWC) *Madrepora oculata*, *Lophelia pertusa*, *Desmophyllum dianthus* and *Dendrophyllia cornigera* were measured over 8 mo under controlled conditions (12°C in the dark, fed 5 times a week) by means of the buoyant weight technique. Additionally, linear growth rates were measured in *M. oculata* and *L. pertusa* for 2 and 1 yr, respectively. The weight measurements revealed growth rates, expressed as percent growth per day (mean ± SD), of 0.11 ± 0.04 for *M. oculata*, 0.02 ± 0.01 for *L. pertusa*, 0.06 ± 0.03 for *D. dianthus* and 0.04 ± 0.02 % d^{-1} for *D. cornigera*. Growth in *M. oculata* was significantly higher (p < 0.0001) than in the other 3 CWC species. For *M. oculata* and *L. pertusa*, also linear growth was recorded. These values (mean ± SD) were 0.014 ± 0.007 and 0.024 ± 0.018 mm d^{-1} for *M. oculata* and *L. pertusa*, respectively. This is the first study that compares the growth rates of 4 different CWC species under the same experimental conditions of water flow, temperature, salinity and food supply. These corals have different growth rates, both in terms of total weight increase and linear increase, and these growth rates can be related to interspecific physiological differences. Data on growth rates are essential to understand the population dynamics of CWC as well as the recovery capacity of these communities after disturbance.

KEY WORDS: *Madrepora oculata* · *Lophelia pertusa* · *Desmophyllum dianthus* · *Dendrophyllia cornigera* · Buoyant weight · Linear growth · Branching patterns · Mediterranean Sea

INTRODUCTION

Growth rates of tropical coral species have been widely studied both *in situ* (e.g. Bongiorni et al. 2003, De'ath et al. 2009) and under controlled laboratory conditions, which has allowed single environmental variables on skeletal growth to be assessed (Buddemeier & Kinzie 1976, Tambutté et al. 1995, Reynaud et al. 2002, Houlbrèque et al. 2009). In contrast to their tropical congeners, growth rates of cold-water corals (CWC) and the factors influencing their growth have been much less studied owing to the difficulty in accessing their habitats. The abundance, distribution and growth of CWC may be strongly influenced by several biotic and abiotic factors such as food supply,

turbidity, temperature, hydrography and ocean chemistry (Cairns & Parker 1992, Guinotte et al. 2006, Thiem et al. 2006, White et al. 2007, Roberts et al. 2009). In the last 15 yr, technological advances facilitated access to deep-water ecosystems that harbour CWC communities. Remotely operated vehicles (ROVs) and manned submersibles equipped with manipulators assist in the photography and recording of these communities, as well as in sample collection. Several recent studies, such as those performed on *Gerardia* sp. and bamboo corals, have assessed the growth of CWC from the Atlantic and Pacific oceans, as well as the Caribbean Sea (Matsumoto 2007, Andrews et al. 2009, Parrish & Roark 2009, Thresher 2009) and found very slow growth rates of a few micrometres in radial growth per

year. However, a higher axial growth rate of 0.5 to 1 cm yr^{-1} was estimated for large and old bamboo coral colonies. Other studies on CWC were dedicated to the growth of scleractinian species sampled in the Atlantic and Pacific oceans and the North Sea. The main species studied was *Lophelia pertusa*, owing to its wide distribution and abundance in the CWC communities of these regions (Teichert 1958, Wilson 1979, Freiwald et al. 1997, Mortensen & Rapp 1998, Gass & Roberts 2006, Orejas et al. 2008, Brooke & Young 2009). The linear extension rate of this species was estimated to range from 5 to 34 mm yr^{-1} (reviewed in Roberts et al. 2009). Some other scleractinian species, such as *Desmophyllum dianthus*, *Oculina varicosa* and *Enallopsammia rostrata* were also studied (Boerboom et al. 1998, Cheng et al. 2000, Risk et al. 2002, 2005, Adkins et al. 2004, Houlbrèque et al. 2010). Similar to the octocorals cited above, these scleractinians present very low radial growth rates of a few micrometres per year. A summary of growth rates from different species (including scleractinians, octocorals and antipatharians) measured with different methods has also recently been published (Roberts et al. 2009). These results generally show that growth rate estimates are extremely variable in conjunction with habitat diversity (including depth) of collection sites; this suggests that more data are needed to accurately predict CWC growth.

In contrast to the CWC of the Atlantic and Pacific oceans and the North Sea, Mediterranean cold-water scleractinian corals have received much less attention. They are, however, very abundant in locations of the central and northwestern Mediterranean Sea (e.g. Taviani et al. 2005, Freiwald et al. 2009, Orejas et al. 2009), as reported during the first quantitative surveys (Orejas et al. 2009). Although it remains to be confirmed, these CWC are most likely living at the upper limits of their thermal tolerance (12 to 14°C) because the Mediterranean Sea is warmer than all other studied sites where CWC have been recorded (e.g. Norwegian margin and northern, eastern and western Atlantic Ocean). To date, only 2 studies that used different methodologies, including linear growth measurements and calcification rates, have assessed the growth rates of *Lophelia pertusa* and *Madrepora oculata* under laboratory conditions (Orejas et al. 2008, Maier et al. 2009). In this study, we compare the growth of 4 Mediterranean scleractinian CWC species (*M. oculata*, *L. pertusa*, *Desmophyllum dianthus* and *Dendrophyllia cornigera*) maintained in aquaria under the same controlled conditions. Growth rates were measured by means of (1) the buoyant weight technique (Jokiel et al. 1978, Davies 1989) for the 4 species and (2) the linear extension rate for *M. oculata* and *L. pertusa*. To better understand CWC biology and

ecology, we consider the various factors that influence the growth of CWC species in comparison with their tropical relatives. Considering the major role of CWC as ecosystem engineers in vulnerable marine ecosystems (VME) (Freiwald et al. 2004), this study presents crucial results that can be used to assess their growth rates, which is important to better understand the dynamics of these populations. Additionally, we may learn more about the recovery time of CWC communities after disturbances of natural or anthropogenic origin.

MATERIALS AND METHODS

Study species. *Madrepora oculata* forms fragile fan-shaped colonies 30 to 50 cm in height and small polyps 3 to 5 mm in diameter (Fig. 1a). *M. oculata* can be found in water as shallow as 55 m off the coast of Brazil and as deep as 1950 m off the coast of Iceland (Zibrowius 1980). *Lophelia pertusa* is also a branched coral that grows to a size of more than 130 cm (Gass & Roberts 2006) and forms reefs as high as 33 m (Mortensen et al. 2001). *L. pertusa* polyps measure ~5 to 15 mm in height and ~1 cm in diameter (Fig. 1b). This species dwells mostly between 100 and 400 m depth but has also been found at depths of 40 to 3000 m (Zibrowius 1980, Cairns 1994, Freiwald 1998, Fosså et al. 2002). *Desmophyllum dianthus* (Esper 1794) (known in the Mediterranean as *D. cristagalli* Milne Edwards & Haime 1848) forms solitary polyps of 5 to 10 cm height and 1.5 to 3 cm in diameter (Fig. 1c) and lives between 100 and 4000 m depth (Risk et al. 2002). *Dendrophyllia cornigera* forms colonies 15 cm high with large polyps 2 to 4 cm in diameter (Fig. 1d) and can be found between 200 to 800 m deep but locally as shallow as 30 m (Castric-Fey 1996).

Species collection. *Madrepora oculata* and *Dendrophyllia cornigera* colonies were collected in the Cap de Creus canyon (NW Mediterranean Sea) from 250 m depth and placed on board the RV 'García del Cid' during the cruises 'Deep Coral I_Coral4' and 'HERMES IV_Coral8' in July 2006 and September 2007, respectively. *Lophelia pertusa* and *Desmophyllum dianthus* were collected off the Island of Malta at 300 m depth in September 2007 and placed on board the RV 'Urania' during the cruise 'MARCOS'. Samples were collected and returned to the 'García del Cid' by means of the ROV PHANTOM HD2 + 2 and the manned submersible JAGO (IFM-GEOMAR, Kiel, Germany), whereas samples returned to the 'Urania' were collected by means of an epibenthic sledge.

Growth rate measurements using the buoyant weight technique. Ten colonies of *Madrepora oculata*, 8 of *Lophelia pertusa*, 8 of *Desmophyllum dianthus* and
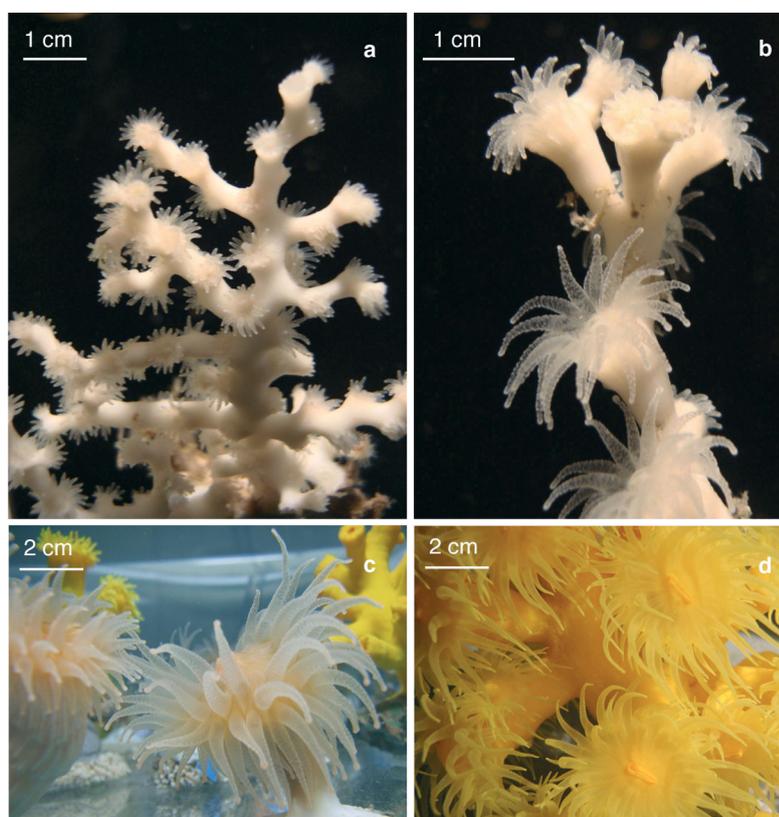
Fig. 1. (a) *Madrepora oculata*, (b) *Lophelia pertusa*, (c) *Desmophyllum dianthus* and (d) *Dendrophyllia cornigera*. Photos of studied specimens

al. 1978, Davies 1989) and an analytical balance (Mettler, model AT 261; precision 0.1 mg). This technique has been widely used with tropical and temperate corals (e.g. Coles & Jokiel 1978, Rodolfo-Metalpa et al. 1999) and consists of determining the dry weight of the skeleton from its weight in seawater based on Archimede's Principle, which accounts for the density of the coral skeleton and the density of seawater (Davies 1989). We also estimated, with the method of Davies (1989), that the buoyant weight of the tissue accounted for 3 to 4% of the skeletal buoyant weight, which was used to produce a correction factor.

After 3 wk of acclimation 9 measurements were taken: for *Madrepora oculata* at Times 0, 1 (+27 d), 2 (+62 d), 3 (+86 d), 4 (+107 d), 5 (+146 d), 6 (+174 d), 7 (+209 d) and 8 (+244 d), and for the other 3 CWC species (*Lophelia pertusa*, *Desmophyllum dianthus* and *Dendrophyllia cornigera*) at Times 0, 1 (+21 d), 2 (+56 d), 3 (+80 d), 4 (+101 d), 5 (+140 d), 6 (+168 d), 7 (+203 d) and 8 (+238 d).

Growth (G_t) was expressed in percentages of daily weight increase as follows:

$$G_t \ = \ 100 \times \frac{M_{t+1} - M_t}{M_t \, (T_{t+1} - T_t)}$$

where M_t and M_{t+1} are the coral weights (mg) at the beginning (T_t) and the end (T_{t+1}) of each growth interval. Growth is expressed as percent increase per day (% d^{-1}). To detect possible differences in growth among the 4 species with optimal precision, a linear regression of the natural logarithm of coral nubbin biomass (mg) versus the experimental time (d) was calculated. The slopes of the regression lines represent the growth rates and were compared with 1-way ANOVA. Owing to the unequal number of specimens for each coral species, the harmonic mean was used to estimate 'n' in the Student-Newman-Keuls post hoc test.

Growth rate measurement using the linear growth. Seventeen colonies of *Madrepora oculata* and 10 of *Lophelia pertusa* were maintained in a 40 l tank with a continuous flow of Mediterranean seawater pumped from 15 m depth at a rate of 5 l h^{-1} and filtered by a 50 μm sand filter. Two submersible pumps (MAREA 3200) provided continuous water movement in each tank with a flow rate of 3200 l h^{-1}. The water was maintained under the same temperature (12°C) as mentioned above (Olariaga et al. 2009). Corals were fed 5 times a week as above, with frozen cyclops (to

3 of *Dendrophyllia cornigera* were maintained in a 50 l tank with a continuous flow of oligotrophic Mediterranean seawater pumped from 50 m depth at a rate of 5 l h^{-1}. Two submersible pumps (Minijet MN 606, RENA) created a continuous current in the tank. The seawater contained low amounts of organic and inorganic nutrients (Ferrier-Pagès et al. 1998). Water was maintained at a constant temperature of 12°C, which corresponds to the temperature of the corals' natural habitat. Heaters in combination with 2 refrigeration systems were connected to an open flow batch tank in which the water temperature was controlled to within ±0.1°C. To minimize shock to the corals that could affect their growth rate, we regulated the temperature very precisely. Corals were maintained in the dark and fed 5 times a week with Mysidacea, frozen *Cyclops* and *Artemia salina* nauplii. Corals were observed under a binocular microscope to confirm they actually ingested food by transferring the captured prey to their gastrovascular cavity.

From October 2008 to June 2009, the 4 coral species were maintained for 250 d under the above controlled conditions and the skeletal growth rate was assessed by means of the buoyant weight technique (Jokiel et

M. oculata) and mysidacea *Artemia salina* adults (to *L. pertusa*). The solitary polyps of *Desmophyllum dianthus*, as well as the large size and growth structure of *Dendrophyllia cornigera* colonies, did not permit us to determine their linear growth. From December 2006 to December 2008, linear growth measurements were made with the colonies of *M. oculata* over 729 d, and of *L. pertusa* over 391 d. For each *M. oculata* colony, 8 photographs were taken at Times 0, 1 (+88 d), 2 (+162 d), 3 (+338 d), 4 (+437 d), 5 (+528 d), 6 (+631 d) and 7 (+729 d), whereas for *L. pertusa,* measurements started at Time 3. Photos were always taken at the same distance and with the same angle. A photoseries for an *M. oculata* colony is presented in Fig. 2. Linear growth (mm d^{-1}) was measured on branches located in the same plane of the photograph with CARNOY 2.1 software (Schols & Smets 2001). To calibrate the images we used a ruler (shown in Fig. 2).

Linear specific growth rates were calculated as the slopes of the regression lines relating the coral nubbins' linear extensions (mm) versus the experimental time (d). Results were expressed as linear specific growth rates per day (mm d^{-1}). Slopes of the regression lines were compared to look for statistically significant differences between linear growth rates of the different species via an unpaired *t*-test. Moreover, as a further parameter describing the linear extension of the coral nubbins, the increase in the number of polyps for each nubbin was recorded over the same time period; the mean increase in polyp number per day was calculated for each species following the same method described above.

RESULTS

Buoyant weight

The growth rates obtained for the 4 species were (mean ± SD): 0.11 ± 0.04 % d^{-1} for *Madrepora oculata*, 0.02 ± 0.01 % d^{-1} for *Lophelia pertusa*, 0.06 ± 0.03 % d^{-1} for *Desmophyllum dianthus* and 0.04 ± 0.02 % d^{-1} for *Dendrophyllia cornigera*, with a higher growth rate for *M. oculata* compared with the growth rates of the 3 other CWC species (Fig. 3). The ANOVA of the slopes of the linear regression (growth rates) revealed significant differences (p < 0.0001) between *M. oculata* and the other 3 species (Table 1).
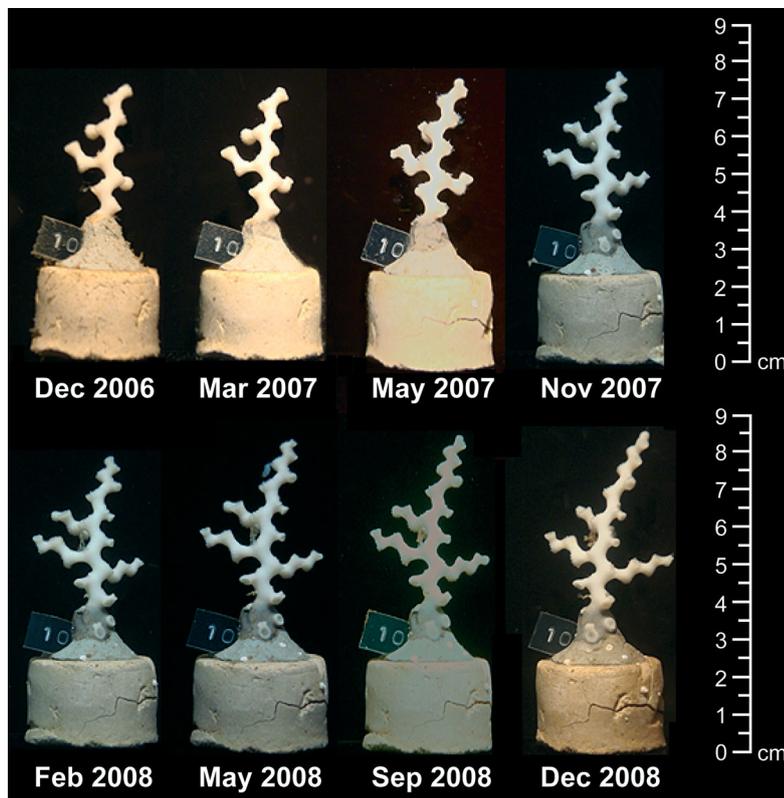
Linear growth

The linear growth rates (mean ± SD; mm d^{-1}) of *Madrepora oculata* and *Lophelia pertusa* were 0.014 ± 0.007 and 0.024 ± 0.018 mm d^{-1}, respectively (Fig. 3). The variability between the different nubbins was very high for both species; *M. oculata* presented minimum and maximum growth rates of 0.003 and 0.026 mm d^{-1}, respectively, whereas *L. pertusa* presented minimum values of 0.008 mm d^{-1} and maxima of 0.058 mm d^{-1}. The unpaired *t*-test revealed no significant difference (p > 0.05) between the linear growth rates of *M. oculata* and *L. pertusa*.

Polyp number (always means ± SD) for *Madrepora oculata* presented a high variability between the different nubbins (6.2 ± 4.2 polyps per nubbin) and was associated with the different sizes of the nubbins. Polyp number increased from 6.2 ± 4.2 polyps per nubbin at the beginning to 10.9 ± 4.8 at the end of the experiment. The mean rate of polyp addition was 0.0075 ± 0.0038 polyps d^{-1}, which corresponds to a mean of one new

Fig. 2. *Madrepora oculata*. Photographic series of the linear growth of one of the measured nubbins
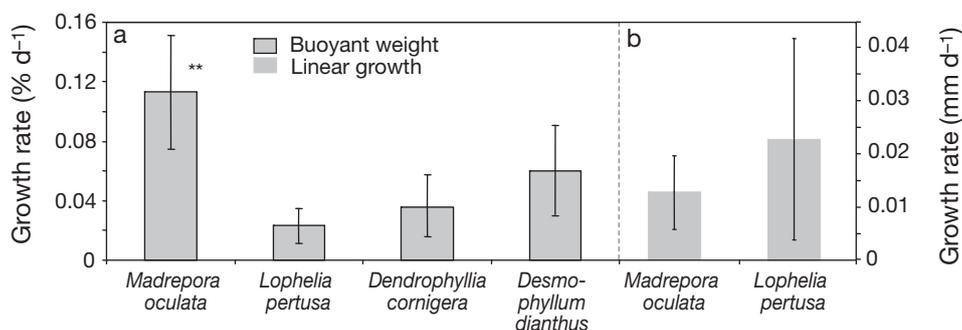
Fig. 3. (a) *Madrepora oculata*, *Lophelia pertusa*, *Desmophyllum dianthus* and *Dendrophyllia cornigera*. Growth rates (% d^{-1}, mean ± SD) for each CWC species after the buoyant weight measurements. (b) *Madrepora oculata* and *Lophelia pertusa*. Growth rates (mm d^{-1}, mean ± SD) for each CWC species after the linear growth measurements. **p < 0.0001

Table 1. *Madrepora oculata*, *Lophelia pertusa*, *Desmophyllum dianthus* and *Dendrophyllia cornigera*. (a) ANOVA for growth rate for the 4 CWC species. (b) Student-Newman-Keuls post hoc tests comparing species growth rates. *p < 0.0001

(a) Species	df	Sum of squares	F	p
Residual	3	4.341×10^{-6}	19.541	<0.0001
	25	1.851×10^{-6}		

(b) Species	Mean difference	Critical difference
D. cornigera, *D. dianthus*	-4.583×10^{-5}	3.278×10^{-4}
D. cornigera, *L. pertusa*	1.354×10^{-4}	3.278×10^{-4}
D. cornigera, *M. oculata*	-0.001	3.963×10^{-4}*
D. dianthus, *L. pertusa*	1.813×10^{-4}	3.963×10^{-4}
D. dianthus, *M. oculata*	-0.001	3.278×10^{-4}*
L. pertusa, *M. oculata*	-0.001	4.375×10^{-4}*

budded polyp every 4 mo. Polyp number for *Lophelia pertusa* was also variable among nubbins for the same reason. The number increased from 2.9 ± 1.1 polyps per nubbin at the beginning to 4.2 ± 2.4 at the end of the experiment. The mean rate of polyp addition was 0.0037 ± 0.0043 polyps d^{-1}, which corresponds to 1 new polyp budded after ~7 mo.

DISCUSSION

Results obtained from the buoyant weight measurements show a high variability in growth rates between and within the CWC species. This variability has been recorded by Brooke & Young (2009) in an *in situ* experiment with *Lophelia pertusa*, which presented a high variability between the different nubbins used for that experiment. Additionally, the great plasticity of

colony morphology observed in *L. pertusa* (Cairns 1979, Brooke & Schroeder 2007, Roberts et al. 2009) suggests that growth of this species is naturally highly variable, which could also be the case for the other CWC species in this study.

Because all species have been maintained in aquaria under exactly the same conditions, the significant differences observed between the growth rate of *Madrepora oculata* and the other 3 species are not due to differences in environmental factors, but rather due to interspecific differences in their physiology. High growth rates might be due to the branched form of *M. oculata*, which is more ramified than the other CWC. It is known that calcification rates in tropical corals are higher in branched than in massive species (Goreau & Goreau 1959), as different skeletal structures and shapes of colonies lead to different rates of carbonate deposition (Goreau & Goreau 1959, Schlöder & D'Croz 2004). *Acropora*, one of the most ramified genus among tropical corals, also grows faster than other branched corals (Sorokin 1995). Additionally, the 4 CWC species differ in the number of polyps per skeletal surface area owing to the different size of the polyps. *M. oculata* colonies have the highest polyp density (Fig. 1) and a higher rate of polyp budding than do *Lophelia pertusa* colonies. These differences may increase the efficiency of prey capture and energy input in the coral tissue as shown in tropical corals (Anthony 2000, Anthony & Fabricius 2000, Ferrier-Pagès et al. 2003, Palardy et al. 2005, 2008); therefore, they have a positive effect on the growth rates. Factors that influence growth rates include food availability and quality. Because energy allocation in corals is divided into tissue and skeletal growth (Anthony et al. 2002), the small size of the *M. oculata* polyps compared with the other 3 CWC species suggests that more energy is allocated to the growth of the skeleton. Conversely, *L. pertusa*, *Desmophyllum dianthus* and *Dendrophyllia cornigera* have larger

polyps, so they build more soft tissue and may in turn allocate less energy to skeletal growth (Anthony et al. 2002). In the case of *L. pertusa*, Mortensen (2000) suggested that linear growth is correlated with seasonal temperature variations, but also noted that temperature may covary with other factors such as food supply. Thus, aquarium studies of this species in Norway and Scotland (Mortensen 2001, Roberts & Anderson 2002) indicated that increased food supply was followed by high extension rates. Therefore, seasonal changes in food supply, rather than temperature, may control growth rates of *L. pertusa* in the field.

Furthermore, different skeletal microstructures highly influence coral growth rates (Nothdurft & Webb 2007), which could explain the distinct growth rates observed among species considering the different results were obtained through 2 different measuring methods. Even if there is some information on the skeletal microstructure of CWC species, this has been studied in order to explore its use as palaeoarchives (e.g. Blamart et al. 2007, Montagna et al. 2008) and not as a tool to interpret ecological or ecophysiological studies. To our knowledge, no studies have been conducted to investigate the possible relationships between growth and corallite microstructure. These data would greatly improve our understanding of CWC growth rates and corals in general.

Temperature is known to be an important factor affecting the growth rate of tropical, temperate (e.g. Buddemeier & Kinzie 1976, Lough & Barnes 1997, 2000, Bessat & Buigues 2001, Howe & Marshall 2002, McNeil et al. 2004, Allemand et al. 2010) and cold-water corals (Matsumoto 2007) with a thermal adaptation of the different coral species (Clausen 1971, Clausen & Roth 1975, Rodolfo-Metalpa et al. 2008). Consequently, it is highly likely that CWC have adapted to lower temperatures, even though the optimum and critical temperatures for CWC species still need to be determined. Nevertheless, analyses of fossilized coral (Wienberg et al. 2009) as well as recent studies (Keller & Os'kina 2008) have shown that *Madrepora oculata* appears to be more tolerant to a wide range of changing environmental conditions than other species. The higher temperature tolerance of *M. oculata* may explain the observed 'faster' growth, possibly owing to better adaptation to the current 'warm' Mediterranean conditions (in relation to its geological history, especially before the Holocene sea level rise) when *Lophelia pertusa* and *Dendrophyllia cornigera* were better adapted to the cooler temperatures (Wienberg et al. 2009). Furthermore, previous experiments comparing growth rates of tropical coral versus a CWC species reported similar rates for the zooxanthellate coral *Galaxea fascicularis* and the CWC *M. oculata* despite a 15°C temperature difference

(Orejas et al. in press). This could confirm a considerably faster relative growth rate of *M. oculata* if it is located within warmer waters. Studies on CWC growth rates are vital to increase our knowledge of population dynamics of these organisms, as well as to predict the recovery time of CWC communities after disturbances. Indeed, the gaps in our knowledge of growth rates also limit our understanding of palaeo records when confronted with current and future threats, such as bottom trawling and global climate change (Roberts et al. 2009).

Further research is clearly needed to improve our knowledge on the factors that drive CWC growth patterns, especially in future scenarios where seawater acidification plays an important role in coral growth. This role has been shown experimentally by several authors at the organism level (Marubini & Atkinson 1999, Marubini et al. 2001, 2003, 2008, Schneider & Erez 2006) and the community level (Langdon 2000, Leclercq et al. 2000, Langdon et al. 2003).

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