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# Experimental comparison of skeletal growth rates in the cold-water coral *Madrepora oculata* Linnaeus, 1758 and three tropical scleractinian corals

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## ABSTRACT

The skeletal growth rate of the cold-water coral (CWC) *Madrepora oculata* Linnaeus, 1758 was measured during 3 months under controlled conditions (at 12 °C in the dark, fed five times a week), using the buoyant weight technique. In order to interpret CWC growth in a wider context, we also measured the skeletal growth rates of three tropical scleractinian species: *Stylophora pistillata* (Esper, 1797), *Turbinaria reniformis* (Bernard, 1896) and *Galaxea fascicularis* (Linnaeus, 1767), likewise maintained under controlled conditions (at 25 °C, 250 μmol photons $m^{-2}$ $s^{-1}$, either fed five times a week or unfed). The skeletal growth rate of *M. oculata* was equal to $0.20 \pm 0.09\%$ $d^{-1}$ (mean ± SD), similar to the growth of unfed and fed nubbins of *G. fascicularis* ($0.14 \pm 0.01\%$ $d^{-1}$ and $0.36 \pm 0.11\%$ $d^{-1}$ respectively) despite the large differences in seawater temperatures. Skeletal growth rates of *S. pistillata* ($1.20 \pm 0.49\%$ $d^{-1}$ to $2.68 \pm 0.65\%$ $d^{-1}$ unfed/fed) and *T. reniformis* ($0.78 \pm 0.34\%$ $d^{-1}$ to $0.94 \pm 0.14\%$ $d^{-1}$ unfed/fed) were significantly higher. These results confirm that the CWC *M. oculata* can grow at rates that are comparable to those of some tropical corals, despite the lack of autotrophy (lacking zooxanthellae) and the low temperatures of its environment.

## 1. Introduction

Growth rates of cold-water corals (CWC) are still poorly known in comparison to the growth rates of symbiotic tropical corals, which have been well studied, both in situ (e.g., Bongiorni et al., 2003; De'ath et al., 2009) and under laboratory conditions (e.g., Atkinson et al., 1995; Buddemeier and Kinzie, 1976; Houlbrèque et al., 2009; Tambutté et al., 1995). The first studies on tropical corals showed that growth was enhanced by the presence of symbiotic dinoflagellates, called zooxanthellae, which transfer most of their photosynthates to the host for its own energetic needs (i.e., light-enhanced calcification, see Gattuso et al., 1999 for a review). More recently, heterotrophic feeding was also shown to significantly increase growth in some species (see Houlbrèque and Ferrier-Pagès, 2009 for a review).

The still scarce knowledge of growth rates of CWC is due to the inaccessibility of the environments that they inhabit, which are frequently difficult to reach (as in case of underwater canyons) and very deep. However, in the last two decades, spreading use of cost effective technology allowed scientists to better access those deep-water ecosystems that harbour CWC communities. Remotely operated vehicles (ROVs) equipped with manipulators allow us to photograph and record these communities, as well as to collect samples. This technological progress has mainly concentrated on scleractinian CWC from the deep Atlantic, Pacific, and North Sea. As a consequence, growth rates of some conspicuous and widespread CWC species of these regions, such as *Lophelia pertusa* and *Oculina varicosa*, have been assessed (e.g., Brooke and Young, 2009; Freiwald et al., 1997; Gass and Roberts, 2006; Reed, 2002) and range from 5 to 34 mm $y^{-1}$ for *L. pertusa* and from 3 to 18 mm $y^{-1}$ for *M. oculata*, albeit using different measurement methods (Roberts et al., 2009 and references herein). Conversely, Mediterranean CWC have received less attention; the growth of *L. pertusa* and *M. oculata* has been estimated in only three studies (Maier et al., 2009; Orejas et al., 2008; Orejas et al., 2011), and a very recent paper also measured the growth of *Desmophyllum dianthus* and *Dendrophyllia cornigera* (Orejas et al. 2011).

In a recent review, Roberts et al. (2009) have summarized all data on CWC growth rates, including scleractinians, octocorals and antipatharians. However, due to different methodologies in assessing growth rates, different environmental conditions, or even different units to express growth rates, comparisons between CWC species or with other coral species are difficult.

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The aim of this paper was therefore to use the same methodology to compare the growth rates of the azooxanthellate Mediterranean CWC *M. oculata* to the growth rates of three zooxanthellate tropical corals: *Stylophora pistillata*, *Turbinaria reniformis* and *Galaxea fascicularis*. For this purpose, the buoyant weight methodology was used to determine the growth rate of all the species investigated (Davies, 1989; Jokiel et al., 1978). The results are discussed in terms of the various factors that are likely to influence growth of tropical and CWC species, in order to contribute to our understanding of CWC metabolism and growth.

## 2. Materials and methods

Laboratory experiments were carried out from January to April 2008 using the azooxanthellate CWC *M. oculata*. Colonies were collected at 250 m depth in the Cap de Creus canyon (NW Mediterranean) on board the RV "García del Cid," during July 2006 and September 2007. *M. oculata* (Fig. 1) is a branched, white coloured scleractinian species, with large polyps of 5–7 mm in diameter (Cairns, 1995). The species is marked by a cosmopolitan distribution (missing only from continental Antarctica), and its bathymetric range varies from 15 to 1500 m depth (Cairns, 1995). Its skeletal growth, measured under experimental conditions, was compared with that of three zooxanthellate tropical species from the Red Sea: *Stylophora pistillata*, *Turbinaria reniformis* and *Galaxea fascicularis* (Fig. 1).

One setup contained 10 colonies of *M. oculata*, 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 $h^{-1}$. A submersible pump (Minijet MN 606, RENA) created a continuous flow. The seawater was not pre-filtered and thus contained low amounts of organic and inorganic nutrients (<1 µM inorganic nutrients, and no macrozooplankton income, Ferrier-Pagès et al., 1998). The values of salinity (around 38 psu) and pH (8.1) were comparable to those found at 500 m depth (unpublished data, and Taviani, personal communication). Water was maintained at 12.5 °C, which corresponds to the temperature of the animals' habitat in the Cap de Creus canyon (maximum temperature recorded was 14 °C, minima around 11 °C, Palanques et al., 2006). Temperature was kept constant during the 4 months experiment using two refrigerating systems connected to an open flow batch tank. Corals were maintained in the dark and fed five times a week using *Artemia salina* nauplii at repletion (Houlbrèque et al., 2003). The ingestion of *A. salina* was visually monitored under the binocular at the beginning of the experiment according to Tsounis et al. (2010). The animals were acclimated to these conditions for least 3 weeks prior to any growth measurements.

In the second setup, 12 nubbins of each tropical zooxanthellate coral species (*S. pistilla*: 11 nubbins) were divided equally into 30 l tanks, three nubbins in each tank. The tanks were continuously supplied with Mediterranean seawater under the same conditions as described for the CWC setup, but heated to 27 °C using 300 W heaters connected to temperature controllers (EW, PC 902/T). Metal halide lamps (400 W) (HPIT, Philips) provided a constant irradiance of 250 µmol photons $m^{-2}$ $s^{-1}$ (photoperiod 12:12). Tanks were cleaned twice a week in order to avoid algal growth. Two different treatments were applied to the setup using the three tropical coral species: In two tanks, coral colonies were kept unfed, (with autotrophic nutrition only), while in the two other tanks, colonies were fed five times a week with *A. salina* nauplii at repletion (auto and heterotrophic nutrition). Here again, corals were acclimated to the experimental conditions 3 weeks prior to any growth measurements (Houlbrèque et al., 2003).

After the acclimation period, tropical corals were maintained in the experimental conditions for 6 weeks, whilst *M. oculata* was maintained for 15 weeks. Growth rates were measured using the buoyant weight technique (Davies, 1989; Jokiel et al., 1978) with a Mettler AT 261 balance (precision 0.1 mg). We also used the method

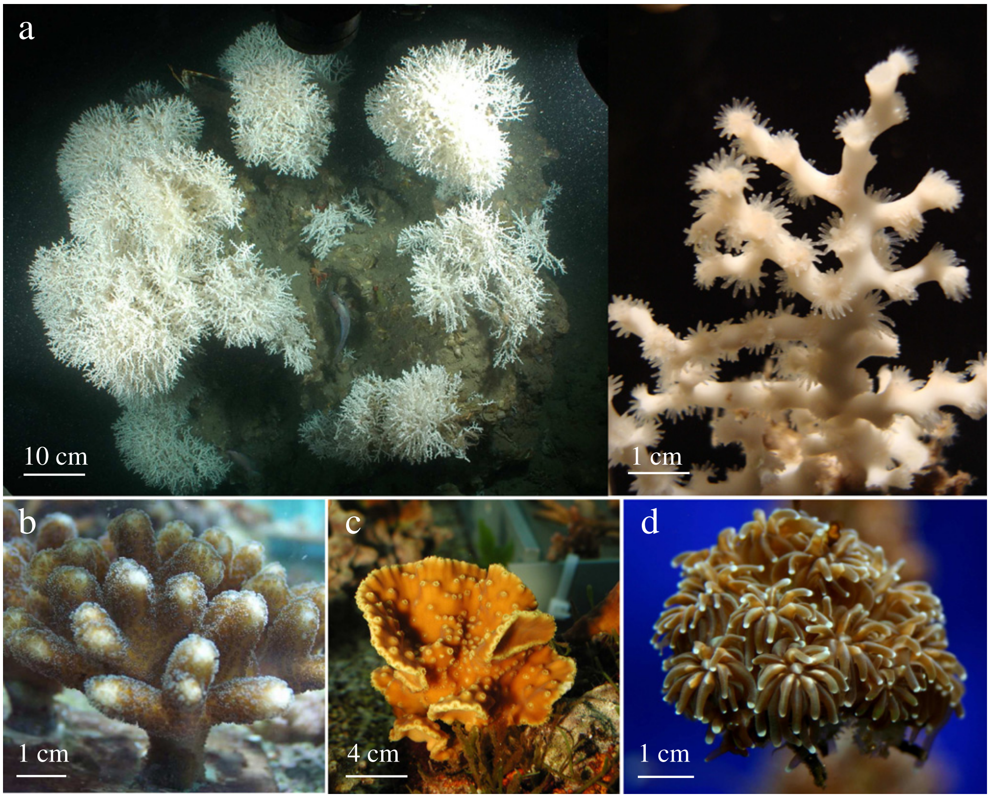

**Fig. 1.** (a) Left: patch of colonies of the cold-water coral *Madrepora oculata* in the Cap de Creus canyon (NW Mediterranean) at 250 m depth; right: colony of *Madrepora oculata* in aquaria, (b) *Stylophora pistillata*, (c) *Turbinaria reniformis*, and (d) *Galaxea fascicularis*.

of Davies (1989) to estimate the buoyant weight of the tissue of each species, which accounted for 2–4% of their skeletal buoyant weight, and allowed to produce correction factors.

Four measurements were taken for *M. oculata*: at times 0, 1 (+25 days), 2 (+46 days) and 3 (+77 days). For *S. pistillata*, *T. reniformis* and *G. fascicularis* three skeletal growth measurements were taken at time 0, time 1 (+10 days) and time 2 (+17 days) for *S. pistillata* (17 days in total), and time 0, time 1 (+10 days) and time 2 (+20 days) for *T. reniformis* and *G. fascicularis* (20 days in total).

Growth (Gt) was expressed in percentages of daily skeletal weight increase as follows (Jokiel et al., 1978):

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

where $M_t$ and $M_{t+1}$ are the coral weight (mg) at the beginning ($T_t$) and the end ($T_{t+1}$) of each growth interval. Skeletal growth will be expressed as % increase per day$^{-1}$ (% d$^{-1}$).

In order to detect possible differences in growth among the four species with optimal precision, a linear regression of the natural logarithm of coral nubbin biomass (mg) versus the experimental time (days) has been calculated, so that the growth rates represented by the slopes of the regression lines could be derived. The growth rates of the 4 species under fed conditions were then compared using one-way ANOVA. In order to test for differences in the growth rate of the three tropical corals between unfed and fed conditions, two 1-way ANOVA analyses were applied. A Scheffe's post hoc test was used to detect the origin of the differences.

## 3. Results

The following mean growth rates (± SD), expressed in % d$^{-1}$ for the three unfed coral species, were measured: *S. pistillata*: 1.20 ± 0.49% d$^{-1}$; *T. reniformis*: 0.78 ± 0.34% d$^{-1}$; *G. fascicularis*: 0.14 ± 0.01% d$^{-1}$ (Fig. 2). The mean growth rates for the fed corals were: *S. pistillata*: 2.68 ± 0.65% d$^{-1}$; *T. reniformis*: 0.94 ± 0.14% d$^{-1}$; *G. fascicularis*: 0.36 ± 0.11% d$^{-1}$ and for *M. oculata*: 0.20 ± 0.09% d$^{-1}$ (Fig. 2). Highest rates for both unfed and fed colonies were for *S. pistillata* (2.04 and 4.47% d$^{-1}$, respectively), whereas the lowest corresponded to *G. fascicularis* (unfed: 0.28, fed: 0.74% d$^{-1}$) and *M. oculata* (fed: 0.72% d$^{-1}$ respectively).

Skeletal growth rates measured for the four species maintained under fed conditions were significantly different between species (ANOVA, $F = 125.7$, $p < 0.0001$). The Scheffe post hoc test revealed significant differences in growth rates among all species, except between *G. fascicularis* and *M. oculata* ($p = 0.19$) (Table 1). Comparison of the growth rates of unfed and fed nubbins from the tropical species showed significant differences between species under both treatments (unfed: ANOVA, $F = 14.4$, $p < 0.001$, fed: ANOVA, $F = 78.6$, $p < 0.0001$) (Table 2), except for *Stylophora pistillata* and *Turbinaria reniformis* which did not present significant differences in their growth rates under the "unfed" treatment ($p = 0.98$).

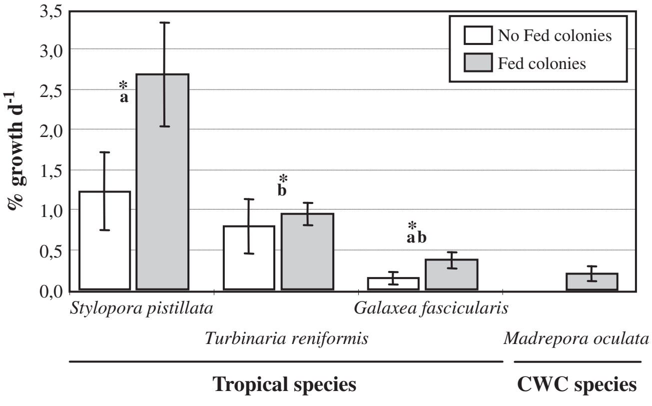

**Fig. 2.** Mean skeletal growth rates, expressed as % per day (% d$^{-1}$) (± SD) of *Madrepora oculata*, *Stylophora pistillata*, *Turbinaria reniformis* and *Galaxea fascicularis*. White bars: unfed specimens (all except *M. oculata*), grey bars: fed specimens (all species). * = Statistical significant differences ($p < 0.05$) between fed and unfed species; a = Statistical significant differences ($p < 0.001$) for both treatments between *S. pistillata* and *G. fascicularis* and b = Statistical significant differences ($p < 0.001$) also for both treatments between *T. reniformis* and *G. fascicularis*.

## 4. Discussion

The main conclusion of this work is that the azooxanthellate CWC *M. oculata* maintained under culture conditions grows at a rate that is similar to the tropical zooxanthellate species *G. fascicularis* (either fed or unfed), despite the fact that *M. oculata* was maintained at a much lower temperature (−12 °C) while being fed. The concern that optimal culture conditions (e.g., food quality and quantity) during our experiments might have lead to overestimating skeletal growth rates appears unfounded when comparing linear growth rates for *L. pertusa* obtained through laboratory (Orejas et al., 2008) and in situ studies (Gass and Roberts, 2006).

The conclusion that growth rates of some CWC are similar to rates of some tropical corals thus appears valid and is furthermore supported by the hypothesis developed by Marshall (1996), who questioned the validity of the assertion that calcification in zooxanthellate hermatypic corals always proceeds at a higher rate than in azooxanthellate corals. However, it is clear that this was the case for one of the tropical species investigated, whereas the other two grew significantly faster than *M. oculata*. Indeed, skeletal growth rates of *S. pistillata* and *T. reniformis* were approximately one order of magnitude higher than for *M. oculata* and *G. fascicularis*. Large differences in skeletal growth rates have already been observed among tropical species (see for example Goreau and Goreau, 1959, as well as Schlöder and D'Croz, 2004). These authors detected a clear difference in calcification rates between branched and massive corals (with the latter exhibiting lower growth rates); however, the reasons for these differences still remain unknown. The similar growth of the branched CWC *M. oculata* and the massive tropical *G. fascicularis* suggests that higher growth rates of branching corals also occur in CWC species. However, recent data show significantly higher growth rates for *M. oculata*, compared to three other Mediterranean CWC species, among which two were branching corals and one was a solitary coral (Orejas et al. 2011). There could be several explanations for this faster growth of *M. oculata*; however, the two aspects, which should have the most important influence are feeding and temperature (e.g.,

**Table 1**

| | df | Fed nubbins | | |
|---|---|---|---|---|
| | | Sum of squares | *F* | *P* |
| Species | 3 | 0.002 | 125.7 | < 0.0001 |
| Residual | 24 | $1.171 \times 10^{-4}$ | | |

| | Fed nubbins | | *P* | |
|---|---|---|---|---|
| | Mean diff. | Crit. diff. | | |
| *G. fascicularis*, *M. oculata* | 0.003 | 0.003 | 0.199 | |
| *G. fascicularis*, *S. pistillata* | −0.019 | 0.004 | <0.0001 | * |
| *G. fascicularis*, *T. reniformis* | −0.004 | 0.004 | 0.021 | * |
| *M. oculata*, *S. pistillata* | −0.021 | 0.003 | <0.0001 | * |
| *M. oculata*, *T. reniformis* | −0.007 | 0.003 | <0.0001 | * |
| *S. pistillata*, *T. reniformis* | 0.014 | 0.004 | <0.0001 | * |

a) ANOVA table for growth rate for the fed nubbins from *Stylophora pistillata*, *Turbinaria reniformis*, *Galaxea fascicularis* and *Madrepora oculata*; b) Results of Scheffe post hoc test. *Statistical significant difference.

**Table 2**

| df | Unfed nubbins |  |  | Fed nubbins |  |  |  |
|---|---|---|---|---|---|---|---|
|  | Sum of squares | F | P | df | Sum of squares | F | P |
| 2 | $2.841\times10^{-4}$ | 14.403 | 0.0004 | 2 | 0.001 | 78.594 | $<0.0001$ |
| 14 | $1.381\times10^{-4}$ |  |  | 15 | $1.104\times10^{-4}$ |  |  |

|  | Unfed nubbins |  |  | Fed nubbins |  |  |
|---|---|---|---|---|---|---|
|  | Mean diff. | Crit. diff. |  | Mean diff. | Crit. diff. |  |
| *Galaxea fascicularis*, *Stylophora pistillata* | −0.010 | 0.005 | * | −0.019 | 0.004 | * |
| *Galaxea fascicularis*, *Turbinaria reniformis* | −0.006 | 0.005 | * | −0.004 | 0.004 | * |
| *Stylophora pistillata*, *Turbinaria reniformis* | 0.004 | 0.005 |  | 0.014 | 0.004 | * |

a) One-way ANOVA table for growth rate for "unfed" and "fed" nubbins from *Stylophora pistillata*, *Turbinaria reniformis* and *Galaxea fascicularis*; b) Results of post hoc test Scheffe. S = statistical significant difference ($p<0.05$).

Frederiksen et al., 1992; Freiwald, 2002; White et al., 2005), whereas light does not play the determining role in CWC corals, as it does in tropical ones (Allemand et al., 2010a).

The effect of feeding enhancing growth in the tropical species studied here (Fig. 2) is in line with numerous studies on tropical (see review by Houlbrèque and Ferrier-Pagès, 2009) and temperate corals (Kevin and Hudson, 1979; Miller, 1995; Rodolfo-Metalpa et al., 2008). This effect suggests that corals allocate a high proportion of heterotrophic energy to calcification, which indeed is an energy-dependent process (Chalker and Taylor, 1975; Tambutté et al., 1996). However, since species with similar branching morphology show different growth rates, it appears that not all species have the same grazing rates and that the positive effect of heterotrophy may be species-specific (Ferrier-Pagès et al., 2010). Concerning CWCs, studies on food availability and consumption rates are still scarce (but see Roberts et al., 2003, 2006; Duineveld et al., 2004; Kiriakoulakis et al., 2005; Tsounis et al., 2010; Purser et al., 2010). However, there are some insights from field observations which suggest that CWC should be able to obtain enough energy via heterotrophy to meet metabolic needs and invest surplus energy into calcification, though perhaps at slower rates than zooxanthellate corals (Miller, 1995). This is the case for the populations of the CWC *Oculina arbuscula* (McCloskey, 1970) studied by Miller (1995) in North Carolina (USA). *O. arbuscula* occupies dark habitats (i.e., overhangs, crevices or inside wrecks), but thrives on a heterotrophic diet which allows it to grow during most of the year, despite the low winter temperatures (temperatures range seasonally from 5 to 19 ºC) (Miller, 1995). Moreover, other observations indicate that food intake does influence growth rates considerably, as asymbiotic colonies of *Oculina varicosa* found in Florida grow at higher rates at 80 m depth than symbiotic colonies at 6 m depth (Reed, 1981, 2002), showing that the nutritive potential of a heterotrophic diet may be higher than the one obtained through the zooxanthellae. Indeed it has been shown with the symbiotic anemone *Aiptasia* sp. that photosynthate molecules are mainly used for immediate energetic processes like respiration, whereas the more complex heterotrophic organic molecules are used to build cellular structures (Bachar et al., 2007). Further, other food sources, such as picoplankton, particulate and dissolve organic carbon, among others, could be part of the diet of these organisms, as already observed in suspension feeders from high latitudes (e.g., Orejas et al., 2003; Pile et al., 1996).

Temperature is also another important parameter that can affect coral growth. In tropical corals, several studies showed that a 1 °C increase in mean annual temperature increased mean annual coral calcification rate by about 3.1%, except when temperatures increased above the upper threshold for corals (Bessat and Buiges, 2001; Carricart-Garnivet, 2004; Kajiwara et al., 1995; Lough and Barnes, 1997; 2000; McNeil et al., 2004). However, other studies have found similar calcification rates for corals of high and low latitudes (Harriot, 1998; Marsh, 1992; Smith, 1981; van Woesik and Done, 1997), and more recent evidence suggests that a significant number of hermatypic species can survive at temperatures as low as 14 °C (reviewed by Veron, 1995). Since it seems that corals adapt to their thermal environment (Clausen, 1971; Clausen and Roth, 1975; Rodolfo-Metalpa et al., 2008), reef development is not limited by the low temperature tolerance of corals (Veron, 1995), but is rather linked to coral community structure (Kleypas, 1996; van Woesik and Done, 1997). This adaptation to lower temperature should be the case for the CWC species investigated, and has in fact been observed previously (Marshall, 1996; Marshall and Clode, 2004). These authors measured similar calcification rates between the temperate and azooxanthellate species *Dendrophyllia* sp and *Tubastrea faulkneri* and the tropical zooxanthellate species *G. fascicularis*. Thus, it is very likely that the effect of temperature in growth rates is species-specific (e.g., Harriot, 1998,1999; Allemand et al., 2010a,b). Furthermore, not only the present temperature but also the thermal history seems also to highly influence growth of framework corals (Van Woesik and Done, 1997).

This study shows a marked similarity in growth between coral species thriving in very different habitats, and thus underlines the fact that calcification is regulated not by one, but by several environmental factors, which interact with each other. Although their optimum and critical temperatures for CWC species are still unknown, it is possible that the observed similar skeletal growth rates of *G. fascicularis* and *M. oculata* suggest an optimisation of skeletal deposition processes to the ambient temperature at which the corals grow. Future research on CWC species would profit from studying possible changes in growth rate under different temperature regimes, considering as well the physiological characteristics of the corals and trophic conditions of the habitat.

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