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Temporal changes in the growth of two Mediterranean cold-water coral species, *in situ* and in aquaria



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ABSTRACT

In situ growth patterns of two-species of reef-building cold-water corals were investigated for the first time at different temporal scales, based on the redeployment of coral nubbins in their natural environment. *Lophelia pertusa* and *Madrepora oculata* were collected in November 2010 and May 2011 from the Lacaze-Duthiers canyon in the northwestern Mediterranean Sea (520 m depth). Three *in situ* growth experiments were performed from November 2010 to May 2011, May to September 2011 and November 2010 to September 2011. For comparison, aquaria experiments over comparable lengths of time were conducted with coral colonies collected in November 2010. In the canyon, new polyps from *M. oculata* and *L. pertusa* displayed similar growth rates in summer (5.8 ± 3.8 and 7.3 ± 1.7 mm yr⁻¹ respectively), but *M. oculata* grew significantly slower during winter/spring than *L. pertusa* (4.1 ± 1.8 and 8.4 ± 2.7 mm yr⁻¹ respectively). Budding rates however (the rate of new polyp addition per mother polyp per year) were similar between both species in winter/spring ($45 \pm 40\%$ for *M. oculata* and $48 \pm 72\%$ for *L. pertusa*), but were significantly lower in summer for *M. oculata* ($14 \pm 19\%$) compared to *L. pertusa* ($58 \pm 94\%$). This seasonal difference in the growth between *L. pertusa* and *M. oculata* might reflect differences in species-specific physiology (such as reproduction) or feeding strategy, or a higher sensitivity of *M. oculata* to the variability of food supply in the Lacaze-Duthiers canyon resulting from periodic cascading events. The comparison of *in situ* and aquaria growth experiments showed no significant differences for budding and new polyp growth rates, which supports the validity of aquaria experiments for these kinds of investigations. However the budding rates observed were consistently lower in coral maintained in aquaria than those in *in situ* conditions, a finding which is to be considered when extrapolating laboratory based investigation results to the naturally occurring coral ecosystem.

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1. Introduction

Cold-water corals (CWCs) play a key role in deep-sea ecosystems, forming reefs and structures that provide niches and nursery grounds for a variety of species, including commercial fish and decapod species (Freiwald et al., 2004). The two dominant reef-building species of white corals, *Lophelia pertusa* and *Madrepora oculata*, are considered as major ecosystem engineers in the deep waters of the northeast Atlantic and the Mediterranean Sea (Roberts et al., 2006; Freiwald et al., 2009). These species exhibit a slower rate of growth than the majority of shallow-water

zooxanthellate species, rendering them sensitive to disturbance and making CWC reefs particularly vulnerable to anthropogenic activities such as deep sea fishing, waste discharge or ocean acidification (Hall-Spencer et al., 2002; Clark and Tittensor, 2010; Form and Riebesell, 2012). A better knowledge of the growth rates of these deep-sea reef builder species is required to assess potential recovery times for the associated ecosystems after physical disturbance (e.g., as may result from bottom trawling), and to determine the influence of environmental factors on reef regeneration capacity (Roberts et al., 2009).

Over the last two decades, significant research efforts have been dedicated to the characterization of CWC growth patterns and for prediction of reef resilience to environmental perturbation (see review in Roberts et al., 2009). A range of methodologies have been utilized to gauge growth rates, including aquaria

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experiments (Mortensen, 2001; Orejas et al., 2008, 2011a; Maier et al., 2009), direct observations of colonies grown on man-made structures (Bell and Smith, 1999; Gass and Roberts, 2006, 2011), and geochemical proxies using stable (Mikkelsen et al., 1982; Mortensen and Rapp, 1998; Risk et al., 2002; Adkins et al., 2004) or radiogenic isotopes (Cheng et al., 2000; Sabatier et al., 2012). These varying approaches have reported a diverse range of growth rates (i.e., 5–27 mm yr⁻¹ for *L. pertusa* and 3–18 mm yr⁻¹ for *M. oculata*), which suggests that the growth of deep-water corals may be strongly influenced by a variety of biotic and abiotic factors such as food supply, turbidity, temperature, hydrography and seawater chemistry (Cairns and Parker, 1992; Guinotte et al., 2006; Thiem et al., 2006; White et al., 2007; Roberts et al., 2009). *In situ* experiments have to date been limited in number due to the technological constraints on deep-sea operation. The factors that control growth rates under *in situ* conditions are therefore poorly known. Based on the deployment and recovery (after 13.5 months) of stained *L. pertusa* fragments in the Gulf of Mexico Brooke and Young (2009) provided the first direct measurements of *in situ* growth rates for this species. Furthermore, since no temporal investigation of the *in situ* growth rate (e.g., intra-annual and longer term fluctuations) was performed, the degree to which changes in environmental factors (such as annual temperature variation) could affect CWC growth at different temporal scales remains unknown.

The aim of the present study was to document temporal variations in the growth patterns of CWCs in a submarine canyon of the Catalan shelf at intra-annual scales. This region of the western Mediterranean Sea is characterized by large scale, meteorologically-driven hydrological events during winter, resulting from severe coastal storms or from the formation and sinking of dense water masses (i.e., ‘cascading’) that have profound effects on deep-sea ecosystems (Canals et al., 2006; Palanques et al., 2006; Company et al., 2008; Danovaro et al., 2008; Sanchez-Vidal et al., 2012).

The experimental approach was based on the deployment and recovery of small fragments of *L. pertusa* and *M. oculata* in an area of the Lacaze-Duthiers canyon (LDC) where colonies of both species are naturally abundant (Petit and Laubier, 1962; Reyss and Soyer, 1965; Orejas et al., 2009; Fiala-Medioni et al., 2012). Growth rate measurements are commonly inferred from the buoyant weight technique, the linear extension of the branches, and the size of the new polyp formed, completed with the rate of new polyp addition (Mortensen, 2001; Orejas et al., 2008, 2011a; Strömberg et al., 2010; Gass and Roberts, 2011). Because growth of the colonies of these two species is primarily driven by the addition of new polyps (Gass and Roberts, 2011; Lartaud et al., 2013), budding and new polyp growth rates were considered relevant to provide spatially-explicit information of growth. In this study, growth rate measurements were inferred from the rate of new polyp addition and the size of the new polyp formed. A comparative growth study was also carried out with fragments of both species in the laboratory.

2. Material and methods

2.1. Experimentation site

The LDC is located in the southwestern region of the Gulf of Lions. The canyon runs northwest-southeast direction over a distance of 23 km from 150 m at its shallowest (NW) in a southeasterly direction to a depth of 1000 m. Recent explorations (May–July 2008, November 2008, and June 2009) highlighted the abundance of *L. pertusa* and *M. oculata* from 300 m to 600 m depth within the canyon (Fiala-Medioni et al., 2012; Fournier et al., 2012).

Continuous hydrological monitoring conducted since 1993 in the deeper extremity of the LDC has revealed an annual recurrence of cold shelf water overflow, a pulsed phenomenon lasting several weeks, with strong inter-annual variation in intensity (Durrieu de Madron et al., 2005; Heussner et al., 2006; Palanques et al., 2006). Dense water formation occurs as a result of wind-induced cooling and evaporation of surface waters during winter (Durrieu de Madron et al., 2005; Canals et al., 2006, 2009). The dense water plume, which overflows the shelf edge, is associated with significant fluctuations in temperature, with a maximum drop to 3 °C below the normally stable 13 °C commonly observed throughout the year. Maximum current speeds peak at up to 60–80 cm s⁻¹ during these events (far above the average 1.9 cm s⁻¹ observed when no overflow event present), and transport large amounts of coarse sediment and organic matter (Heussner et al., 2006; Palanques et al., 2006; Sanchez-Vidal et al., 2008).

The experiment was conducted at 520 m depth (42°32.72'N, 03°25.26'W), in an area (Fig. 1A–D) characterized by numerous coral patches including large colonies (> 1 m) of *L. pertusa* and smaller (< 50 cm) colonies of *M. oculata*, together with solitary corals *Desmophyllum dianthus* and two living species of oysters, *Neopycnodonte cochlear* (< 10 cm) and larger specimens (> 20 cm) likely *Neopycnodonte zibrowii*, a species previously described from the Azores Archipelago deep-waters (Wissihak et al., 2009).

2.2. Sampling

Operations were conducted during three cruises in November 2010, May 2011 and September 2011 using a Remotely Operated Vehicle (ROV Super Achille on R/V Minibex from the COMEX Company). Coral collections were made in a small area (< 50 m²) and thus species are expected to belong to the same genetic population. The samples were collected in November 2010 from four distinct colonies (three *L. pertusa* colonies, one *M. oculata* colony). They were recovered in thermally insulated polypropylene boxes maintaining the ambient bottom water temperature (~13 °C) during transport to the surface. On board, the collected coral branches were transferred to aerated seawater tanks maintained at 13 °C using a chiller. The apical part of the colonies was cut into small fragments, each nubbin containing 3 ± 2 intact polyps of *L. pertusa* and 8 ± 4 polyps of *M. oculata*. Nubbins were the pasted onto 10 cm² cement blocks using an aquatic epoxy resin and fixed on cobblestones for deployment *in situ*. These cobbles were then placed into transplant units, containing five nubbins of *L. pertusa* and five of *M. oculata* oriented vertically and horizontally to mimic different orientations in a 3-dimensional structure (Fig. 1E–G). Three different photographs of the nubbins were acquired pre- and post-deployment for comparison in order to identify branch extension and addition of new polyps. Four transplant units were deployed in November 2010 close to a CWC patch. Two of these were recovered in May 2011, corresponding to 6 months of growth *in situ* and referred to as the ‘winter/spring’ branches in the result section. The remaining two transplant units were recovered in September 2011, corresponding to 10 months of growth *in situ*. In May 2011 fragments from a further colony of *L. pertusa* and of *M. oculata* were collected. These nubbins were similarly prepared and deployed from May to September 2011, corresponding to 4 months of growth *in situ* and referred to as the ‘summer’ branches in the result section (Table 1).

To compare coral fragment growth rates *in situ* and in the aquaria, 25 coral nubbins from one colony of *L. pertusa* and 12 nubbins from one colony of *M. oculata* (collected in November 2010) were maintained in 80 L tanks, continuously supplied (with a flowthrough rate of 18.5 mL min⁻¹) with coastal seawater piped from a depth of 4 m and refrigerated using chillers to achieve equilibrium with the ambient temperature of the thermo-regulated (13 ± 1 °C) cold room. Corals were maintained in the dark and fed three times a week with

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