Growth Patterns of Mediterranean Calcifying Cold-Water Corals

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Abstract

Skeletal growth is a key physiological function, which in the case of calcifying organisms, provides support for the general colony structure together, whilst simultaneously providing protection for internal soft tissues. Given this fundamental importance, growth patterns can therefore reflect the health status of organisms. Additionally, engineer species forming 3D structures, such as scleractinian cold-water corals, enhance local biodiversity through the provision of new structural and hydrodynamic habitats. Furthermore, cold-water corals may be used as paleoclimate indicators, and act as sources for novel pharmaceutical compounds as well as represent significant sinks for CO_2 sequestration. At time of writing, cold-water coral reefs are facing several serious threats, particularly in the Mediterranean Sea, where the combined effects of climate change and other anthropogenic environmental disturbances are interacting in regions of coral colonisation. The characterisation of the Mediterranean cold-water coral growth patterns is thus a crucial step for accurate forecasting of reef resilience under environmental change and for the establishment of adequate conservation strategies. From the organisation of soft tissues to the resulting mineralogical structures formed from the polyp to the reef scale, this chapter gives an overview of the state of the art of the current understanding of scleractinian cold-water coral growth patterns. The main environmental parameters that control calcification and their influence on cold-water corals in the context of ongoing global environmental change are illustrated with examples from studies conducted with different calcifying species from the Mediterranean Sea, utilising both aquaria and *in situ* experimental studies.

Keywords

Scleractinia · Skeleton · Calcification · Environmental factors · Forecast of reef growth · Cold-water corals · Mediterranean

36.1 Introduction

The appearance of hard structure calcifying fauna during the Cambrian was a major step in the evolution of the animal kingdom tightly linked with the global CO_3^{2-} and CO_2 budgets. The skeleton secreted by these fauna both supports the general shape of the organism as well as protects soft tissues against biotic (e.g., predation) or abiotic threats. Though a range of substances may be secreted to form hard structure skeletons, calcium carbonate based skeletal structure are the most abundant and diversified in terms of mineralogy and structure. Shells and skeletons may be made from a range of calcium carbonate compounds (e.g. aragonite, low or high-magnesium calcite, amorphous calcium carbonate), and dozens of microstructures have been identified among which the most widespread are prismatic, fibro-prismatic, nacreous and crossed-lamellar (Carter 1980).

Calcifying species build their skeletons by the periodic addition of carbonate. Both environmental conditions and metabolic activity control the rhythm and growth rates of the biomineralising fauna and deposition rate of the carbon-

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C. Orejas, C. Jiménez (eds.), *Mediterranean Cold-Water Corals: Past, Present and Future*, Coral Reefs of the World 9,
https://doi.org/10.1007/978-3-319-91608-8_36

ate material. Together with respiration, reproduction and energy storage, calcification is one of the key physiological indicators of organism fitness in calcifying fauna. Biomineralisation studies offer the capacity to address research questions on both short-term (i.e., hourly to daily) and long-term (i.e., annual or multi-annual) scales, with a dual perspective: (1) to address the rapid response of organisms to biotic and/or abiotic changes in the ecosystem, and (2) to assess the resilience of calcifying species to ongoing and persistant environmental change. Additionally, calcifying organisms may be used as oceanographic and paleoceanographic environmental archives, by the analysis of geochemical proxies locked within their carbonate skeletons at the time of deposition. In particular, changes in deep-water mass dynamics can be inferred from trace metal and isotope analyses of cold-water coral (CWC) skeletons (Montero-Serrano et al. 2013).

As it is the case for their shallow water counterparts, CWCs act as ecosystem engineers, forming reefs in cold and deep waters. Indeed, scleractinian corals form three-dimensional structures, potentially accumulating over millennia following death, that provide various ecological niches for associated fauna, including feeding, spawning and nursery habitats for a variety of species (Rueda et al., this volume; D'Onghia, this volume). As a result, corals are key species that partially support the biodiversity of marine ecosystems. Hence, reef-building scleractinian corals are species of great ecological value. In the Mediterranean Sea there are several locations where well developed CWC ecosystems have been described, such as the Santa Maria di Leuca coral province in the Ionian Sea (Vertino et al. 2010; D'Onghia et al. 2011; Chimienti et al., this volume) and the submarine canyons of the Gulf of Lion (Orejas et al. 2009; Fiala-Medioni et al. 2012; Gori et al. 2013; Fourt et al., this volume; Puig and Gili, this volume) and Catalan Margin (Lastras et al. 2016, this volume; Aymà et al., this volume).

The biology of CWCs is much less understood than that of tropical corals, but during the last few decades significant research efforts have been dedicated to the characterisation of CWC physiology and ecology (Roberts et al. 2009). The analysis of CWC growth patterns to date has been based on both aquaria and *in situ* studies. Many studies have been conducted in the North-East Atlantic and in the Gulf of Mexico, though in recent years a substantial number of works focusing on CWCs within the world ocean have been published, including the Mediterranean. Many CWC studies conducted in the Mediterranean have been focused in the influence of temperature and acidification in these communities, being thus particularly relevant to the forecasting of CWC reef resilience to global change (see Maier et al., this volume; Movilla, this volume).

36.2 Living Tissues and Calcified Material

36.2.1 Anatomy of Corals

Corals are characterised by stinging cells (cnidocytes) that are used for prey capture and as a defence mechanism against predators. Each polyp is made of two cell layers: ectodermal and endodermal layers, separated by the mesoglea which is a collagen network (Allemand et al. 2004). The polyps are linked together by the coenosarc made by an oral (facing seawater) and aboral (facing skeleton) epithelium. Polyps and coenosarc thus cover the skeleton much like a glove (Fig. 36.1), leading to an endogenous biomineralisation.

Biomineralisation occurs in a submicrometric interface between the cells and the skeleton known as the extracellular calcifying medium, from an organic matrix composed of a mixture of proteins, glycoproteins, and polysaccharides that precisely self-assemble and control the $CaCO_3$ crystal formation (Allemand et al. 2011). Different functions have been attributed to this organic matrix, including control of the concentration of precursor ions, constitution of a tridimensional framework, template for crystal nucleation, for determination of the calcium carbonate polymorph, control of crystal elongation, inhibition of crystal growth, determination of spatial arrangement of crystal units, and involvement with enzymatic functions and cell signalling (Marin et al. 2008).

During the calcification process, carbonic anhydrase is involved in hydration/dehydration reactions by supplying dissolved inorganic carbon to the calcification site and removing carbonic acid from the calcification site. This process is performed by the metabolic conversion of CO_2 into HCO_3^- and HCO_3^- into CO_3^{2-} (Bertucci et al. 2013). Finally, the nucleation – the pathfinder for crystal formation in the extracellular calcifying medium – allows the formation of an initial thermodynamically unstable mineral form, the amorphous calcium carbonate, prior to its transformation into aragonite. As an example, for the shallow-water coral *Stylophora pistillata* from the Gulf of Aqaba, this transient skeletal compartment has a short half-life (12.9 min) compared to the bulk of the skeleton (167 h) (Tambutté et al. 1996). The resulting structure is thus composed of self-assembled aragonite minerals with an inter- and intracrystalline organic matrix.

36.2.2 Anatomical Particularities of Scleractinian Cold-Water Corals and Their Implications for Skeletal Growth

Although reef-building CWCs exhibit many similar growth traits to other calcifying cnidarians, they also form some distinct patterns in morphology which have to be taken into

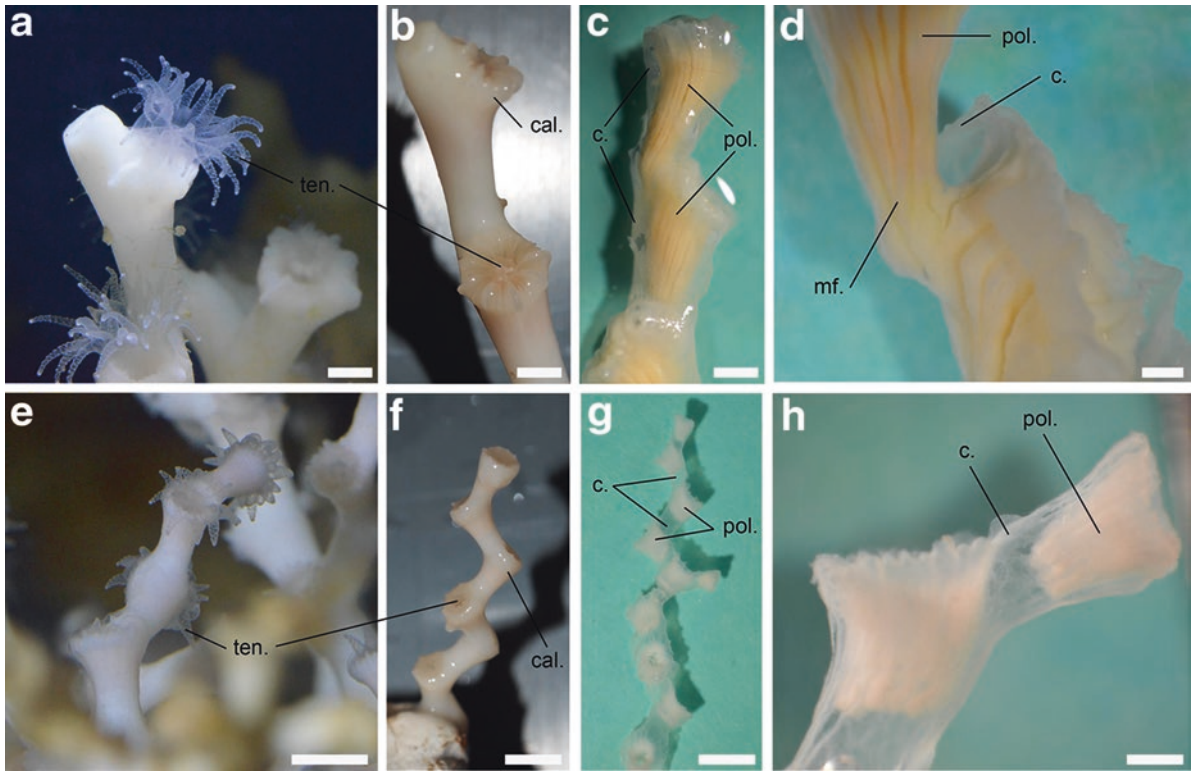

Fig. 36.1 Anatomy of two cold-water coral species from the Gulf of Lion, northwestern Mediterranean Sea. (**a**) *Lophelia pertusa* fragment showing polyp distribution along the skeleton with open polyps displaying the tentacles, (**b**) *Lophelia* polyps retracted inside the calices, (**c**, **d**) Coral tissues after decalcification showing polyp junction by both mesenterial filaments and the ceonosarc cover, (**e–h**) Same sequence of images as from (**a**) to (**d**) but corresponding in this case to a *Madrepora oculata* nubbin; note that in *M oculata* the coenosarc only connects the polyps. *Ten* tentacles, *cal* calix, *c* coenosarc, *pol* polyp, *mf* mesenterial filaments. Scale is 5 mm in (**a–c**) and (**e–g**) and 1 mm in (**d**) and (**h**). (Photographs © A.L. Meistertzheim (CNRS) and F. Lartaud (Sorbonne University))

account in growth studies (Lartaud et al. 2017a). This is particularly true for colonial species that form tree-like structures, such as *Lophelia pertusa* (recently synonymised to *Desmophyllum pertusum*) (Addamo et al. 2016), *Madrepora oculata, Solenosmilia variabilis* and *Dendrophyllia cornigera*.

Even though CWC colonies display the same general anatomy as many shallow-tropical corals, with polyps linked externally together by the coenosarc tissues, CWCs tend to exhibit larger polyps that extend linearly (Gass and Roberts 2011; Lartaud et al. 2017a). A branch of colonial CWC is formed by the successive addition of large calices, growing directly on tip of previous generations of polyps, which can lead to a considerable separation between polyps (Fig. 36.1a, b, e, f), in contrast to the closely packed, tiny polyps often forming the colonial structure of most tropical corals (Lartaud et al. 2017a).

The distance between polyps could also have consequences for energy distribution within a colony. Decalcification of coral skeletons shows that different species do not display the same patterns in soft tissue connection (Fig. 36.1c, d, g, h). *Lophelia pertusa* polyps are connected by both the coenosarc and mesenterial filaments, located within the calix. This provides different pathways for molecule transfer within the tissues. On the opposite, *M. oculata* grows with a clear separation between polyps, only connected by the thin coenosarc. This leads to a single route (i.e. the coenosarc) for molecule transfer inside the colony.

Coral calcification also occurs extracellularly. This is particularly prevalent for azooxanthellate colonial corals such as *L. pertusa*, which produce large amounts of extracellular mucus (EMS), which can contribute to the calcification of the parchment-like tube of the symbiotic worm *Eunice norvegica* (Roberts 2005) (Fig. 36.2). This mucus has various functions, such as acting as an antifouling agent, protecting the coral skeleton from attacks from endolithic and boring organisms, and also as an aid in removing sediment particles. The occurrence of identical protein patterns within EMS and the newly formed aragonite suggests that EMS plays a central role in the calcification process of the skeletal parts (Reitner 2005). Mucus could also be involved in facilitating coral attachment to the substrate (e.g., rock, dead or still living corals), as it is frequently observed *in situ*, as well as in association with corals maintained in aquaria (Fig. 36.3).

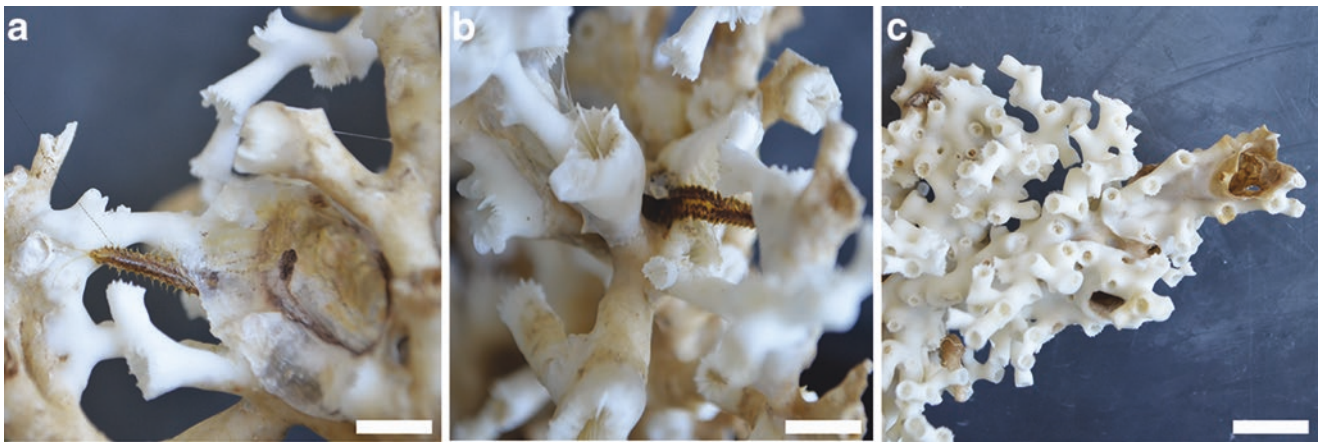

Fig. 36.2 Coral fragments where the calcification over the tube produced by the symbiotic worm *Eunice norvegica* can be seen. (**a**) *E. norvegica* coming out from its tube (behind the oyster shell). (**b**) Opposite view of the same worm showing the tube covered by *Lophelia pertusa* polyps. (**c**) Calcified tube of *E. norvegica* by *Madrepora oculata*. Those specimens were collected in the Lacaze-Duthiers canyon, northwestern Mediterranean Sea. Scale bar is 1 cm. (Photographs © F. Lartaud (Sorbonne University))

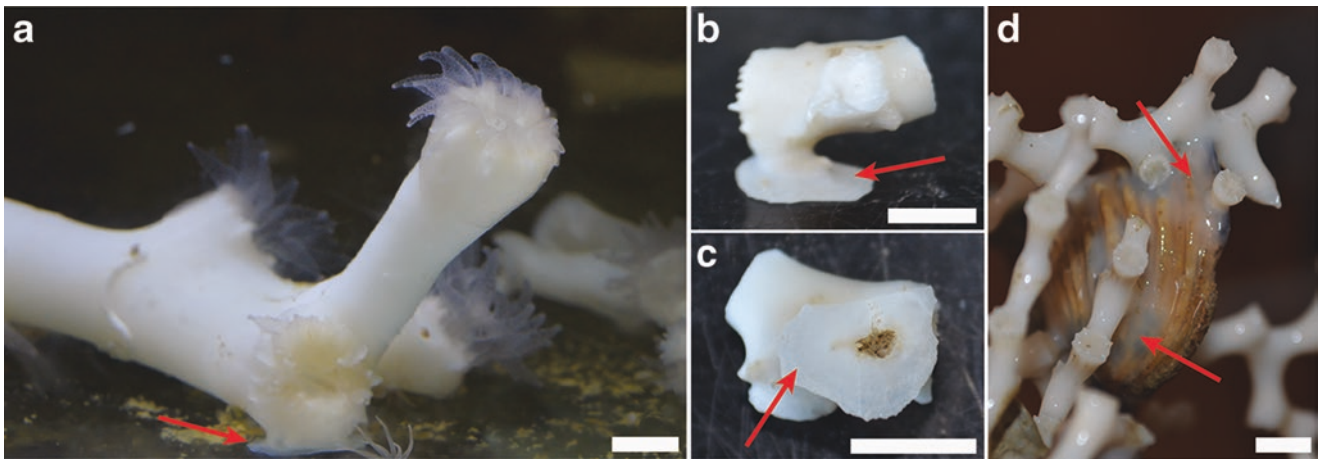

Fig. 36.3 (**a**) Coral extra-skeleton calcification at the base of *Lophelia pertusa* polyp when deployed lengthened in aquaria (highlighted by a red arrow). The specimen was collected in the Lacaze-Duthiers canyon, northwestern Mediterranean Sea (**b**) lateral view of the polyp showing the extra-polyp cementation, (**c**) view from the polyp basis of extra-skeleton calcification, (**d**) *Madrepora oculata* colony from the Lacaze-Duthiers canyon covering a bivalve shell with extra-skeleton mineralisation (© UPMC-Fondation TOTAL). Scale bars are 5 mm. (Photographs © F. Lartaud (Sorbonne University))

36.3 Skeleton Microstructure and Crystallography

36.3.1 Initiation of Calcification and Growth Models

The observation of scleractinian CWC skeletal features reveals two types of microstructures. Aragonite fibres are the main skeletal components, representing the vast majority of the calcified volume. Spatially-restricted areas of micrometric scale are also present, traditionally called centers of calcification (COC) and also referred to as early mineralisation zones (EMZ) or rapid accretion deposits (RAD). These zones are characterised by granular crystals arranged in clusters (Constantz 1989). The distribution of these structures differs according to the species, with arrangements varying from discrete clusters to continuous chains (Cohen and McConnaughey 2003). In *Lophelia pertusa*, they are organised in a continuous line from the base of the corallite up to the calix, near the inner edge of the wall, as shown in the scanning electron microscope (SEM) image after treating the samples with an acid etching solution (Fig. 36.4a). These regions are located close to the starting point of diverting fibres and are considered to be nucleation sites for calcification (Bryan and Hill 1941). Indeed, contrary to the meaning of the traditional name (centers of calcification), these structures are not formed by a unique crystal (Fig. 36.4b), nor are they located at the physical middle of the coral wall. The

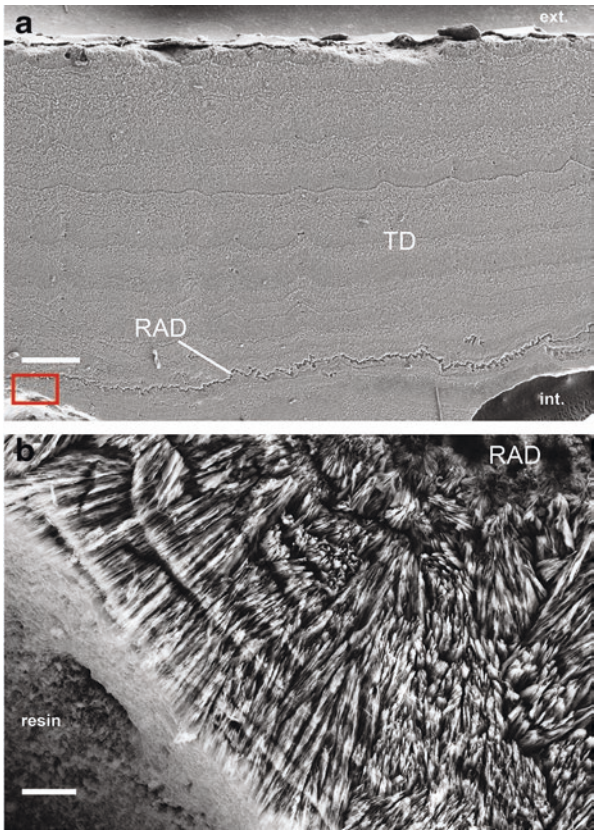

Fig. 36.4 (**a**) Microstructures in the wall of *Lophelia pertusa* skeleton from the Whittard canyon (NE Atlantic) under SEM, showing the Rapid Accretion Deposit (RAD) arranged in a continuous line and the Thickening Deposits (TD) layers made of aragonite fibres. Longitudinal growth direction is from left to right. Scale bar: 200 µm. *ext.* external part of the skeleton, *int.* internal part, located in the calix, (**b**) Detail of the bottom left part of (**a**) included in the red rectangle. SEM view of layers in aragonite fibres near the RAD on the internal edge of the skeleton. Scale bar: 10 µm

COCs (or RADs) are the first biomineralised structures to appear in the wall formation (Rollion-Bard and Blamart 2014), and this term is generally used in regards to their initial support role in further crystallisation events.

Since the granular crystals have a sub-micron size, it is likely that part of the calcification process is intracellular (Constantz 1989). Vesicles have been observed in the apical membrane of the epithelium which are probably responsible for providing some material to the calcifying space (Johnston 1980), as they can be a pathway for seawater. Though no mineralised structures have been observed in these vesicles, they may act as stabilisation sites for amorphous calcium carbonate (Cohen and McConnaughey 2003; Rollion-Bard et al. 2010).

It is widely agreed that the calicoblastic layer plays a role in calcification (Tambutté et al. 2011); however different models grant it a more or less important function in this process: a direct control of the calicoblastic layer (Barnes 1970; Johnston 1980), a two-steps model (Cuif and Dauphin 1998; Cuif et al. 2011), and a layered model (Stolarski 2003). In the later, COCs are called Centres of Rapid Accretion (CRA) and they are arranged into a Rapid Accretion Front (RAF). CRA and RAF form deposits composing of a mineral phase as well as an organic phase (dCRA and dRAF, respectively), themselves recovered by successive layers of mainly mineral Thickening Deposits (TD).

In the calcifying space, the supersaturation state allows spontaneous formation of nucleation clusters comprised of hydrated ions (Cölfen and Antonietti 2005). As these clusters grow, they eventually become critical crystal nuclei, putatively composed of amorphous calcium carbonate (ACC), which is thought to act as a precursor of mineralised calcium carbonate (Addadi et al. 2003). ACC is known to be present in numerous biominerals (Weiner et al. 2003), but its presence in coral skeletons is debated (Cuif and Dauphin 1998; Falini et al. 2013). Proteins and polysaccharides present in the matrix fix themselves around these nanoparticles and induce a stabilisation of the particles that can orientate themselves for association with other similar nuclei. By forming clusters and welding, they are able to form single crystals (Cartwright et al. 2012).

After putative ACC turned into nanometric crystals, aragonite fibres (located in the TD region) grow from these RADs to form sclerodermites, shaped in fans towards the external side of the skeleton and polyp to increase skeleton thickness.

36.3.2 Growth Structures in the Thickening Deposits Region

The skeleton resulting from sclerodermite formation is not homogenous. Density layers, such as the annual bands formed in tropical corals have not been observed in CWCs, but growth structures defined by opaque and translucent bands in the coral wall have been seen under transmitted light of *L. pertusa* from Sweden (Wainwright 1964) and *Desmophyllum dianthus* collected from the NW Atlantic (Lazier et al. 1999). These optically visible bands were originally interpreted as annual patterns (Risk et al. 2005). The bands were thought to have been formed by successive nucleation phases during the life of the polyp, associated with advances and retreats of the outer tissue layer that covers the corallite (Lazier et al. 1999). It has been demonstrated that the opaque and translucent bands are indeed thickening phases of the wall but their temporal meaning is probably not uniform. Indeed, Gass and Roberts (2011) found the same amount of annual banding in living polyps of different ages from the same *L. pertusa* colony growing on North Sea oil platforms. As a result of this analysis, it seems that these bands are not useful to establish temporal calibrations of polyp age.

Recently, new microlayers (20–100 µm width) were observed under SEM after light etching of skeletal sections

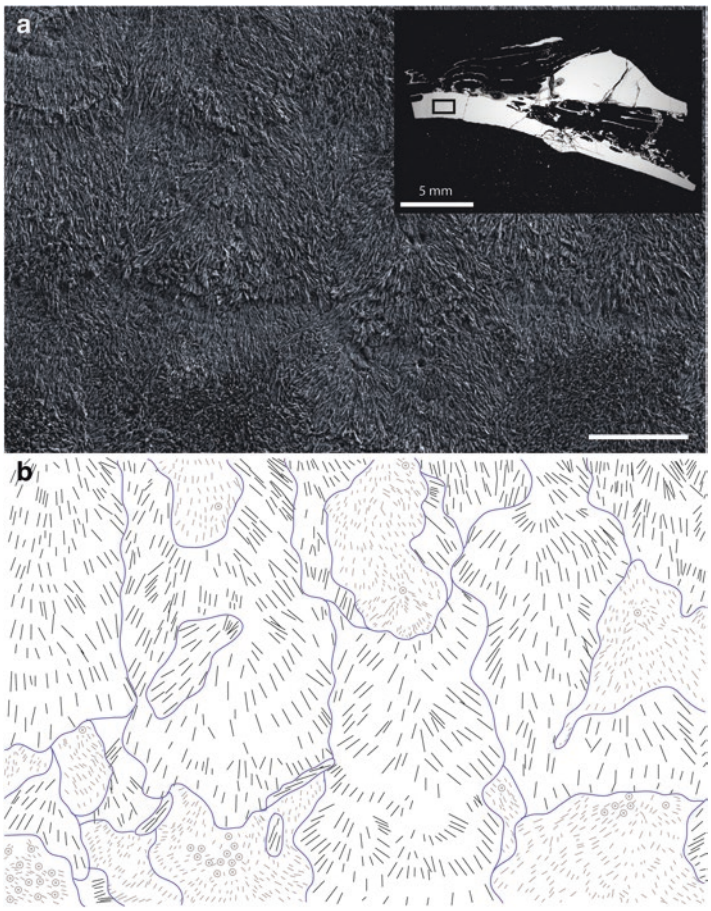

Fig. 36.5 (**a**) SEM view of Thickening Deposits (TD) in the middle of the wall of a *Lophelia pertusa* specimen from the Porcupine Seabight (NE Atlantic), showing different packets of aragonite fibre orientations. Scale bar 100 μm, (**b**) interpretation of the SEM image from (**a**): Black lines represent subhorizontal fibres, grey lines represent oblique fibers and circles represent subvertical fibers compared to the section. Longitudinal growth is from left to right and radial growth from top to bottom

from *L. pertusa* of the NE Atlantic and the Mediterranean Sea (Mouchi et al. 2014). General growth rates and strontium fluctuations across an orthogonal transect to these increments tend to indicate that each microlayer corresponds to a period of one lunar month of growth. Though temporal calibration of the skeleton from these microlayers is promising, it is often hampered by the apparent lateral discontinuity of these structures, particularly when occurring in opaque bands. From SEM observations of *L. pertusa* specimens, taken from a variety of locations in the NE Atlantic and the Mediterranean Sea, coral skeletons seem to exhibit successive growth phases in all three dimensions (Fig. 36.5) that prevents continuity of microlayers (Mouchi et al. 2014).

It is also worthwhile mentioning that no bands or layers have been observed in *L. pertusa* by Mouchi et al. (2014) which may indicate growth patterns along the longitudinal axis (i.e., in the maximum growth direction of the corallite). Still, longitudinal growth do occur as indicated by proof of crystal growth competition on solely one side of sclerodermites (i.e., the side facing the basis of the corallite with pre-existing sclerodermites), while the other side (opposite to the basis) is well ordered without disturbance (Mouchi et al. 2017). Mortensen and Rapp (1998) described white and dark lines in both the transverse and the longitudinal sections of the theca and the septa of *L. pertusa* from Norway, but without clear temporal pattern. Thin microlayers (<10 μm) have been observed in the septa of the cup coral *D. dianthus* (Lazier et al. 1999) and the authors suggested a possible relationship between these microlayers and biological clocks, such as (real or inherited) feeding cycles. Still, further chronological calibration is required to improve the understanding of skeletal growth in time and space, and facilitate the interpretations of analysed transects of geochemical proxies in terms of climatic conditions, as was the case for tropical corals and the identification of annual banding.

36.4 Synthesis of the Different Methods Used for CWC Growth Measurements

Contrary to solitary polyps such as *Desmophyllum dianthus* collected from the NW Atlantic, which form their skeleton along a unidirectional growth axis, the structural complexity inferred by the three-dimensional morphology of colonial species (both stony and soft corals) makes it more difficult to measure colony growth. Additionally, compared to their shallow-water counterparts, direct measurements of growth are constrained by the limited accessibility to deep-waters

where CWCs live. As a result, *in situ* growth studies are still scarce for CWCs compared to other biogenic carbonates.

Methods to gauge the skeletal growth patterns of colonial CWCs are mainly derived from those developed for the investigation of shallow-water scleractinians. They include both non-destructive methods and those which require the sacrifice of live coral fragments. Some methods can only be used in aquaria experiments, whereas others can be implemented under *in situ* conditions. All of these methods provide useful complementary information but with several restrictions. The selection of the method is determined by the scientific objectives of the studies and the time available to conduct the study. *In situ* direct observations are suitable for the study at colony level, but the specific role of various parameters influencing growth can be difficult to interpret. Regarding aquaria experiments, the complexity of the natural habitat is difficult to mimic, but the advantage of this kind of experiments is that the environmental conditions can be manipulated, with results of experimental studies therefore providing insight into the understanding of the potential drivers and environmental controls on CWC growth (see Orejas et al., this volume). Whenever possible, *in situ* experiments are recommended, in order to investigate the influence of environmental variability and the combination of abiotic factors in their natural habitats on coral growth processes (e.g., Brooke and Young 2009 for *Lophelia pertusa* in the Gulf of Mexico and Lartaud et al. 2014 for Mediterranean *L. pertusa* and *Madrepora oculata*).

The main methods for the study of CWC growth can be summarised into different sets of techniques, each providing different types of information.

The first group relates to techniques that measure calcification rates (generally expressed as g $CaCO_3$ g^{-1} skeleton day^{-1} or % day^{-1}). These techniques are mainly used in aquaria experiments to test the causal relationship between physicochemical changes in water chemistry and the biomineralisation response of the CWCs (e.g., Orejas et al. 2011a, b; Naumann et al. 2014; Gori et al. 2014; Rodolfo Metalpa et al. 2015 for *L. pertusa*, *M. oculata*, *Dendrophyllia cornigera* and *D. dianthus* from the Mediterranean Sea). The techniques most frequently used to measure calcification rates are: the alkalinity anomaly, the buoyant weight or the radioisotope techniques (Maier et al. 2009; Form and Riebesell 2012).

The second group of techniques quantify linear or surface growth rates (expressed in mm $year^{-1}$ or cm^2 $year^{-1}$). These methods can be used in aquaria and *in situ* (see Orejas et al. 2011a; Lartaud et al. 2017b for *L. pertusa*, *M. oculata*, *D. cornigera* and *D. dianthus*, in both cases with specimens from the Mediterranean Sea). The surface and linear growth extension of coral fragments can be measured at the colony level, or more accurately at polyp level using sclerochronological or sclerochemical tools. Radiometric dating is also used to determine the rates of extension.

The third group of methods investigates the renewal rate of the colony, by determining the budding rate (i.e. new polyp addition over a period of time) (see Mortensen 2001; Lartaud et al. 2014). Due to logistical constraints and the long life cycle of many CWC species, the modelling approach (Galli et al. 2016) is a further promising technique for the study of CWC growth patterns.

36.4.1 Alkalinity Anomaly

Alkalinity anomaly is a commonly used technique to estimate skeletal growth. Measures take place in closed chambers where coral fragments are incubated; water samples are collected from the chambers at the beginning and at the end of the experimental period. The water volume of the chambers needs to be small enough to allow an accurate measure of potential changes in the total alkalinity (A_T). Calcification rates use the 2:1 stoichiometric relationship between the decrease of A_T and $CaCO_3$ precipitation (Chisholm and Gattuso 1991). A correction must be applied for the changes of A_T due to the significant release of inorganic nutrients during incubation, as has been documented for *L. pertusa* and *M. oculata* collected from the Lacaze-Duthiers canyon in the Gulf of Lion (Maier et al. 2013). The alkalinity anomaly technique is however not always applicable for long-term experiments due to several side-effects on the water chemistry (e.g. microbial activity of biofilters, water exchanges, feeding) which are indistinguishable from the corals' calcification activity (Form and Riebesell 2012 in *L. pertusa* from the Norwegian coast).

36.4.2 Buoyant Weight

The buoyant weight technique is a common method used for CWC growth experiments in aquaria. Calcification is inferred from changes in weight of the living organism in seawater of known density. The method is based on the Archimedes' Principle and a correction factor is applied as it has been observed that tissue weight accounts for 3–4% of the skeletal buoyant weight for *M. oculata* from Cap de Creus canyon in the NW Mediterranean and *L. pertusa* from the Island of Malta (Orejas et al. 2011a) and 14 ± 4% for *D. cornigera* corals from Cap de Creus canyon and *D. dianthus* from the Island of Malta (Movilla et al. 2014b). The net buoyant weight values of corals is converted into dry weight (DW) using the density of the pure aragonite (2.94 $g.cm^{-3}$) (Rodolfo Metalpa et al. 2015 on *D. dianthus* from Malta and *D. cornigera* from the Ionian Sea). Although a negative influence of handling cannot be excluded, this method is suitable for

measuring calcification over monthly intervals or longer and it can be recommended for long-term rather than short-term experiments. Results however need to be taken with caution as potential artefacts of coral response can be associated to long-term aquaria studies.

36.4.3 Radioisotopes

The radioisotope method involves the incubation of a fresh coral fragment in a seawater volume containing radioactive elements (^{45}Ca or ^{14}C). After an incubation period of several minutes to hours, the coral pieces are rinsed in filtered seawater, the tissue removed, the skeleton dried and dissolved with a strong acid and the incorporated radioactivity measured using a scintillation counter (e.g. Hennige et al. 2014b for *L. pertusa* from the Mingulay Reef Complex, NE Atlantic). The radioisotope method is highly accurate for measurements at short timescales (periods can be minutes), but this method requires sacrificing the organism for analyses and is restricted to small volumes (e.g., 50 mL Falcon tubes).

36.4.4 Surface and Linear Growth Extension

This is a useful technique, both for *in situ* and aquaria measurements. The growth measures are performed by means of image analysis of photographs taken at different periods. The surface extension provides information on the colony size changes (in cm^2) (see Larcom et al. 2014 on *L. pertusa* from the Gulf of Mexico), and the linear growth extension highlights the growth rate (in mm year^{-1}) of coral branches along the main growth axis (Orejas et al. 2008 for *L. pertusa* and *M. oculata* from Cap de Creus canyon, northwestern Mediterranean Sea; Orejas et al. 2011a for *M. oculata* and *L. pertusa* from the Cap de Creus canyon and *L. pertusa* and *D. dianthus* from the Island of Malta; Lartaud et al. 2017b for *L. pertusa* and *M. oculata* from the Lacaze-Duthiers canyon, NW Mediterranean Sea). Key benefits of this method are the "low cost" of the approach and that the technique is non-destructive and particularly suitable for aquaria studies.

36.4.5 Sclerochronology and Sclerochemistry

The analysis of growth increments (sclerochronology) or fluctuations of geochemical signals throughout the growth (sclerochemistry) requires sacrificing the organisms under study. These analyses however provide an accurate measure of growth rates in coral stem and branches and/or time allowing a better characterisation of the temporal dynamics in CWC growth.

Sclerochronology is the "biomineral" equivalent to dendrochronology used on trees. The concept is based on the assumption that each growth increment has been formed by the organism in successive equivalent time intervals whatever their thickness (Knutson et al. 1972). The production of carbonate structures by calcifying species periodically decelerates and eventually ceases, although environmental conditions still remain favourable for skeletal growth. Growth increments (also called growth bands or growth rings) are formed according to different periodicities, from infra-daily to annual rates. The observations are made on skeletal sections (radial or longitudinal, depending on the species) under optical microscopy, scanning electron microscopy or X-ray fluorescence. The method is currently used for deep-water octocorals and antipatharians (e.g., Sherwood et al. 2005 on *Primnoa resedaeformis* collected offshore Nova Scotia, Canada) and for shallow-water stony corals (Le Tissier et al. 1994 on *Porites lutea* from Indo-Pacific and *Porites porites* from Caribbean Sea), but it is still rarely applied to scleractinian CWCs due to limited knowledge on the growth periodicity increments formation (Lartaud et al. 2017a and references in Sect. 36.3.2 of this chapter).

The use of chemical markers is very useful, as they allow a "time 0" point to be marked within the coral (i.e. the date of dye use), and the growth of the coral after this point can then be measured. The incorporation of fluorochromes into the skeleton produces an internal fluorescent mark and subsequently the growth increment can be readily estimated. Calcein (Hassenrück et al. 2013 for *D. dianthus* from Patagonia; Lartaud et al. 2013 for *L. pertusa* and *M. oculata* from the Gulf of Lion) and alizarin red (Brooke and Young 2009 for *L. pertusa* from the Gulf of Mexico; Form and Riebesell 2012 for *L. pertusa* from Norwegian coast) are classically used in mark and recapture experiments with CWCs. However, recent comparison between calcein and alizarin red stainings have shown that calcein appears more suitable than alizarin red, as the last has been shown to strongly limit growth of NW Mediterranean *L. pertusa* and *M. oculata* by delaying coral recovery following the treatment (Lartaud et al. 2017b).

Geochemical proxies (e.g., stable isotopes, minor and trace metals) can also be analysed along the growth profile to determine growth patterns. Sclerochemistry methods were developed for shallow-water species, particularly for scleractinian corals (Pätzold 1984). However, the use of the sclerochemistry is limited with CWCs due to important metabolically-induced skeleton geochemical changes (so called "vital effects"), leading to an uptake of isotopes and elements during the ion transfer between seawater and skeleton (Adkins et al. (2003) for *L. pertusa* and *D. dianthus* from the NW Atlantic; López-Correa et al. (2010) for *L. pertusa* from the Santa Maria di Leuca coral province in the Ionian Sea; Marali et al. (2013) for *D. dianthus* from the

Azores; Raddatz et al. (2013) for *L. pertusa* from various locations from the European continental margin).

36.4.6 Radiometric Dating

Radiometric or radioactive dating compares the abundance of a naturally occurring radioactive isotope within the skeleton to the abundance of its decay products, which form at a constant rate. Different techniques are used for CWC species, including ^{14}C (Roark et al. 2006 for *Corallium secundum*, *Gerardia* sp. and *Leiopathes glaberrima* off Hawaii), ^{230}Th-U (Cheng et al. 2000 for *D. dianthus* from the Pacific, Atlantic and Southern Oceans) and ^{210}Pb-^{226}Ra (Sabatier et al. 2012 for *L. pertusa* and *M. oculata* from Røst Reef, off Norway). Initially applied for ageing fossil-reef structures, radiogenic isotopes are also useful to determine the life span of long-lived species when ring counting is not possible.

36.4.7 Budding Rate

Colonial CWCs (such as *L. pertusa* and *M. oculata*) produce large polyps compared to octocorals and most tropical scleractinians. Colony growth is primarily driven by the addition of new polyps (Gass and Roberts 2011). Quantifying the new polyp additions over a period of time (budding rate) is a useful and non-destructive technique to measure colony-growth. Comparison between studies is however difficult as different works start with different polyp number. A standardised method was proposed by Lartaud et al. (2014) for *L. pertusa* and *M. oculata* from the Lacaze-Duthiers canyon, NW Mediterranean Sea, using the rate of new polyp addition per polyp initially present per year (expressed in %).

36.4.8 Growth Modelling

A complementary approach to the direct measurement of growth is CWC modelling. Numerical simulation techniques for marine fauna have been developed across different scales, ranging from small-scale physiological processes to whole ecosystem dynamics. Organism and population growth models are based on the "bioenergetics approach", calibrated with experimental observations. A bioenergetic growth model describes growth as the evolution of a quantity (energy, biomass or mass of a specific compound) over time through the balance of input and output fluxes, through the system boundary and between compartments within the system. The simplest formula considers one single compartment for biomass (or energy), one input and one output flux that depend on the system biomass/energy usage according to allometric laws (Glazier 2005). The resulting estimations typically allow forecasting of the number of polyps and colony masses over time (see more details in Lartaud et al. 2017a). Those models appear particularly relevant for the study of ecological properties and their impacts on coral growth under changing environmental conditions, such as illustrated by Galli et al. (2016) on *Corallium rubrum,* an endemic species to the Mediterranean Sea.

36.5 Growth: From the Colony to the Reef

36.5.1 Extension of the Colony

For scleractinian corals, colony-growth rate measurements refer mainly to the linear extension (increase in length), whereas growth rate estimates for soft corals (gorgonian, zoanthid and antipatharian species) mostly derive from radial thickening analysis. As they form the largest reef structures across many regions of the North and South Atlantic, as well as the Mediterranean, growth studies were principally dedicated to *Lophelia pertusa*. In contrast, little effort has thus far been dedicated at determining growth rates of other Mediterranean scleractinians such as *Madrepora oculata*, *Dendrophyllia cornigera* or *Dianthus dianthus*.

Lophelia pertusa exhibits the highest growth rates from all CWC known species thus far investigated, ranging from 0.01 to 38.1 mm year^{-1} (see Table 36.1 and Roberts et al. 2009). The reason for this large inter-individual variability is unknown. At present, no clear influence of bathymetry has been detected in CWC growth rates. However different environmental conditions can contribute to partially explain the high variability recorded in *L. pertusa* growth rates. Environmental variability can be considered at different scales (e.g. between oceans or at the habitat scale) and local topography or current flow exposition may explain the large growth fluctuations observed within the same geographic area. An example of these local variations are the growth rates recorded for corals from two different locations in the western Mediterranean: (1) 2.2–17 mm year^{-1}, for specimens collected at ~200 m in the Cap de Creus canyon (Orejas et al. 2008, 2011a) and (2) 0.01–38.1 mm year^{-1} for specimens growing at ~500 m in the Lacaze-Duthiers canyon (Lartaud et al. 2014, 2017b). This example also shows that Mediterranean CWC specimens of *L. pertusa* can reach similar maximum growth rates to those observed to date in the North Sea and in the Gulf of Mexico (maximum observed of 34 mm year^{-1} in the North Sea (Gass and Roberts 2006) and 32.3 mm year^{-1} in the Gulf of Mexico (Larcom et al. 2014)). Finally, *in situ* tag and recapture techniques have shown a decrease in colony growth rate over time (Fig. 36.6). This may reflect faster growth in younger colonies (Larcom et al. 2014) and suggest that the age of a colony could also play an important role, partially explaining differences between growth rate measurements (Table 36.1).

Table 36.1 Linear extension (in mm year^{-1}) measured for scleractinian cold-water corals from different locations

Species	Localisation	Depth (m)	Growth rates (mm.year^{-1})	Method	References
Lophelia pertusa	Central Mediterranean Sea	300	15–17	Aquaria	Orejas et al. (2008)
Lophelia pertusa	Central Mediterranean Sea	300	8.8 ± 6.6	Aquaria	Orejas et al. (2011a)
Lophelia pertusa	Western Mediterranean Sea	520	1.3 ± 1.5 (old) – 7.5 ± 1.2 (young polyps)	*In situ* mark and recapture	Lartaud et al. (2013)
Lophelia pertusa	Western Mediterranean Sea	520	0.01–12.1	*In situ* deployment and recapture	Lartaud et al. (2014)
Lophelia pertusa	Western Mediterranean Sea	480–520	2.2–38.1	*In situ* mark and recapture	Lartaud et al. (2017b)
Lophelia pertusa	Northeast Atlantic	955–1005	7.0	Observations of colonies from man-made structure	Duncan (1877)
Lophelia pertusa	Northeast Atlantic	800	6.0	Observations of colonies from man-made structure	Wilson (1979)
Lophelia pertusa	Northeast Atlantic	220	2.2–5.0	U-Th dating	Pons-Branchu et al. (2005)
Lophelia pertusa	North Sea	60–110	26.0	Observations of colonies from man-made structure	Bell and Smith (1999)
Lophelia pertusa	North Sea	100	5.0	Observations of colonies from man-made structure	Roberts (2002)
Lophelia pertusa	North Sea	90–115	19.0–34.0	Observations of colonies from man-made structure	Gass and Roberts (2006)
Lophelia pertusa	Norway	300	25.0	Sclerochemistry	Mikkelsen et al. (1982)
Lophelia pertusa	Norway	250	19.0	Sclerochemistry	Freiwald et al. (1997)
Lophelia pertusa	Norway	200–350	6.0	Sclerochemistry	Mortensen and Rapp (1998)
Lophelia pertusa	Norway	80–315	9.4	Aquaria	Mortensen (2001)
Lophelia pertusa	Norway	340	8.0	Pb-Ra dating	Sabatier et al. (2012)
Lophelia pertusa	Gulf of Mexico	460–510	2.4–3.8	*In situ* mark and recapture	Brooke and Young (2009)
Lophelia pertusa	Gulf of Mexico	200–800	3.2–32.3	Observations of colonies from man-made structure	Larcom et al. (2014)
Madrepora oculata	Western Mediterranean Sea	250	3.0–18.0	Aquaria	Orejas et al. (2008)
Madrepora oculata	Western Mediterranean Sea	250	5.1 ± 2.6	Aquaria	Orejas et al. (2011a)
Madrepora oculata	Western Mediterranean Sea	520	1.2 ± 1.2 (old) – 3.5 ± 2.1 (young polyps)	*In situ* mark and recapture	Lartaud et al. (2013)
Madrepora oculata	Western Mediterranean Sea	520	0.5–8.4	*In situ* deployment and recapture	Lartaud et al. (2014)
Madrepora oculata	Western Mediterranean Sea	480–520	0.01–18.0	*In situ* mark and recapture	Lartaud et al. (2017b)
Madrepora oculata	Norway	340	14.4 ± 1.1	Pb-Ra dating	Sabatier et al. (2012)
Oculina varicosa	Florida	80	16		Reed (2002)
Enallopsammia rostrata	North Atlantic	1410	5.0	Pb-Ra dating	Adkins et al. (2004)
Solenosmilia variabilis	Tasmania	890–1455	0.84–1.25	^{14}C dating	Fallon et al. (2014)
Desmophyllum dianthus	Atlantic, Pacific, Southern Oceans	420–2200	0.1–3.0	U-Th dating	Cheng et al. (2000)
Desmophyllum dianthus			0.5–1.0	U-Th and ^{14}C dating	Risk et al. (2002)
Desmophyllum dianthus	South Pacific		0.5–2.0	Pb-Ra dating	Adkins et al. (2004)

(continued)

Table 36.1 (continued)

Species	Localisation	Depth (m)	Growth rates (mm.year^{-1})	Method	References
Desmophyllum dianthus	Patagonia	25	2	Observations of colonies from man-made structure	Försterra and Häussermann (2003)
Desmophyllum dianthus	Patagonia	15–20	0.4–1.0	*In situ* mark and recapture	Hassenrück et al. (2013)

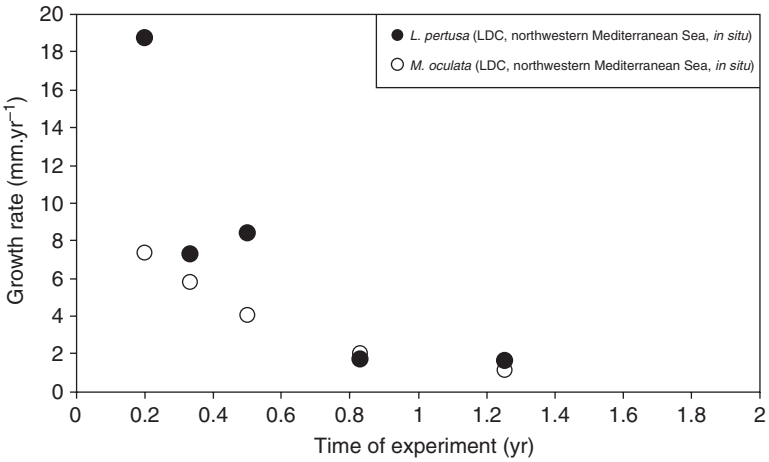

Fig. 36.6 Estimated growth rates of coral nubbins throughout the experimental time (in years: yr). *LDC* Lacaze-Duthiers Canyon. (Adapted from Lartaud et al. 2014, 2017b)

Madrepora oculata from the NW Mediterranean Sea shows mean growth rates ranging from 0.01 to 18 mm year^{-1} (Orejas et al. 2008, 2011a; Lartaud et al. 2013, 2014, 2017b). These values are within the same range as those measured in the Norwegian Sea for this species and elsewhere for other colonial species, except for *Solenosmilia variabilis* which has been observed to have very slow growth rates (~1 mm year^{-1}; Table 35.1). As for *L. pertusa*, a decrease in colony growth rate over time for *M. oculata* is observed (Fig. 36.6).

Currently, no data exist for the rates of extension of *D. cornigera* in its habitat. However, several studies have been conducted with this species in aquaria, using the buoyant weight technique. *D. cornigera* displays growth rates of 7–30% per year (Orejas et al. 2011a; Gori et al. 2014), which are similar to the calcification rates of the long-life span *D. dianthus* (>200 years, Risk et al. 2002), with calcification rates of 11–33% (Orejas et al. 2011a; Rodolfo Metalpa et al. 2015). This last species exhibits growth rates lower than 3 mm year^{-1} (Table 36.1).

36.5.2 Growth Dynamics

In addition to long-term changes, seasonal differences in growth rates have been identified. In the Lacaze-Duthiers canyon differences have been observed over the year for *M. oculata* growth patterns (budding and polyp growth rates) (Lartaud et al. 2014); these differences may be owed to the seasonal change in hydrodynamic conditions that occurs in the canyon heads of the Gulf of Lion (NW Mediterranean). For instance, the observed increase in budding rate during the winter/spring period may be promoted by organic particle supply induced by episodes of dense water shelf cascades and associated resuspension events (Canals et al. 2006; Heussner et al. 2006; Palanques et al. 2006). The response to environmental changes seems however species-specific as *L. pertusa* specimens living in the same habitat display the same growth rates throughout the year (Lartaud et al. 2014). This behaviour suggests more plasticity in the energetic requirement of this species, likely associated with different feeding strategies (Kiriakoulakis et al. 2005) and bacterial-host associations (Meistertzheim et al. 2016). This growth pattern contrasts with the seasonal reproductive cycle described for *L. pertusa* but not for *M. oculata* (Waller and Tyler 2005).

Differences in growth patterns also occur at a long term scale. *L. pertusa* from the NE Atlantic produces micro-layers according to monthly lunar cycle (28 days) and the Sr/Ca composition inside the micro-layers revealed an additional cycle related to semi-lunar oscillations (14 days) (Mouchi et al. 2014). Drivers of those growth rate changes seem to be related to the hydrological context, as in the studied region of the N Atlantic, rapid downwelling of surface waters are caused by hydraulic control of tidal flow, associated with advection onto deep bottom water reefs during peak tides, which periodically increase the availability of organic parti-

cles for coral colonies (Davies et al. 2009). As deep as 900 m water depth, tidal influence induces substantial temperature changes (1.5–2 °C) and input of organic matter in canyon ecosystems (van Haren et al. 2014). The thickness of carbonate micro-layers varies according to growth rate changes, showing two slow phases during each year: one in winter months likely caused by a decrease in food availability, with the second possibly correlated with the gametogenesis period (Mouchi et al. 2014).

Similar micro-layers have been detected but poorly revealed in Mediterranean *L. pertusa* (Mouchi et al. 2014). To date, no chronological calibration has been done and more investigations of these structures in an ecosystem free of strong tidal control would be of great interest to better determine the role of environmental or endogenous rhythms on the biomineralisation of scleractinians.

36.5.3 Main Environmental Parameters Governing CWC Growth

A large number of environmental factors (e.g. temperature, salinity, nutrient concentration, currents) and/or biotic factors (symbiosis, predation, competition) can affect coral calcification (Miller 1995). The direct impact and relative importance of these various parameters on CWC growth remains to be defined, and most probably they will be different for the different species. Laboratory studies suggest that an increase in food supply (considering quality and quantity), rather than temperature, may be more important in determining growth rates of scleractinian CWCs (as seen for *L. pertusa* from Norway by Mortensen 2001 and *M. oculata* from Cap de Creus canyon, NW Mediterranean by Orejas et al. 2011b). Growth rates observed in aquaria for NW Mediterranean *M. oculata* are higher when corals are fed five times a week with a mixed diet of *Mysidacea*, frozen Cyclops and *Artemia salina* nauplii (Orejas et al. 2011a) compared to growth rates of corals fed three times a week with *A. salina* nauplii only (Lartaud et al. 2013). Temperature and pH are also important parameters that can affect growth rates, with distinct responses depending on the species or local habitat conditions (cf. details from Sect. 36.6 of this chapter, as well as chapters by Reynaud and Ferrier-Pagès, this volume; Maier et al., this volume; and Movilla, this volume).

Sediment accumulation stress slows coral growth, as seen for *L. pertusa* from south Norway (Larsson et al. 2013). The authors suggest that lower growth is likely due to the additional energy for polyps to clean themselves which decrease the energy available for feeding, or to a lower polyp extension to reduce abrasion risk by sediment particles, limiting ion exchanges from the environment to extracellular medium (i.e., the area where mineralisation occurs). Anthropogenic pollutants such as drill cuttings can create a similar stressor to sedimentation (Larsson et al. 2013 on *L. pertusa* from south Norway).

36.5.4 Reef Formation

After settlement of a coral larva, asexual formation of new polyps drives extension of the colony in three dimensions. Self-recognition of adjacent coral colonies, as well as skeletal fusion in areas with low levels of aragonite crystal organisation and strong molecular bonding, facilitate ecosystem engineering, as described for *L. pertusa* from Norway (Hennige et al. 2014a). Morevover, coral skeleton cementation can also occur between different species, such as for *L. pertusa* and *M. oculata* from the NW Mediterranean (Fig. 36.7), inducing spatial complexity of the living area. Polyp death rates at the base of colonies increase with the colony lifespan, and hence the proportion of dead coral framework increases, leading to zonation of the habitat (Buhl-Mortensen et al. 2010). Other organisms actively promote reef aggregation as well, such as the symbiotic worm *Eunice norvegica*, which stimulates excessive calcification of Norwegian *L. pertusa* (Roberts 2005; Mueller et al. 2013). Coral calcification over the tube produced by worms living within the coral branches strengthens the framework by thickening and connecting coral branches (Fig. 36.2).

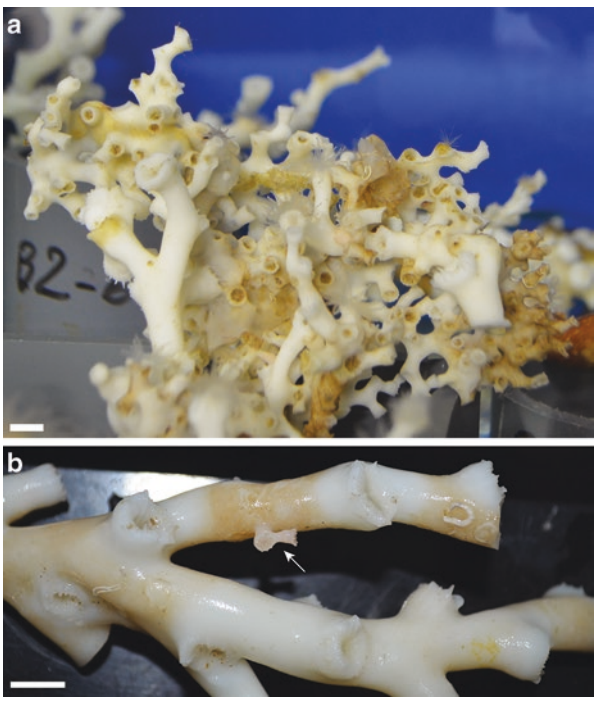

Fig. 36.7 (**a**) Skeleton cementation between *Lophelia pertusa* and *Madrepora oculata* corals from the Gulf of Lion (Lacaze-Duthiers canyon). (**b**) *M. oculata* (white arrow) growing on the wall of two living *L. pertusa* polyps. Scale bar:1 cm. (Photographs © F. Lartaud (Sorbonne University))

Sponges and fungi that attack dead coral parts at the base of the reef tend to form coral rubble by bioerosion. Rubble also contributes in reef formation by providing a substratum for new larvae settlement (Roberts et al. 2009).

Colony extension occurs over the whole lifespan of the coral, and it is supported by the long lifespan of some reef-building species. Radioisotope measurements reveal that the age of a 40 cm high *L. pertusa* colony from the NE Atlantic can be up to 250 years (Pons-Branchu et al. 2005). This means that a 2–3 m high colony needed several centuries to reach this size. However, lifespan differs depending on the species and/or the environment as a 45 cm high *M. oculata* colony from Norway has been estimated to be ~40 years old (Sabatier et al. 2012). Nevertheless if sedimentation takes place at a slower rate than coral growth, colony growth and colonisation by additional coral larvae in the dead or living part of the reef contributes to maintain reef formation over very long periods. The oldest *L. pertusa* reef found to date is estimated in 8600 years old and it is located in Norwegian waters (Hovland and Mortensen 1999).

Reef growth is divided into five stages, corresponding to: (1) reef initiation, (2) framework expansion, (3) framework collapse, (4) partial burial of the coral rubble by superficial sediments, and (5) finally possible larval recruitment on the coral rubble depending on the environmental conditions, allowing the formation of a geological structure induced by cyclic alternation of these different phases (Douarin et al. 2014). The cyclic stages are facilitated by climatic evolution (e.g., glacial/interglacial cycles) allowing formation of coral carbonate mounds over thousands of years (Roberts et al. 2006). The present-day CWC reefs in the Mediterranean Sea were initiated at the Late Pliocene/Early Pleistocene (Taviani et al. 2005, this volume). Depending on the area, reef formation may have been interrupted for long periods inducing temporary extinction of CWCs in the eastern Mediterranean Sea during the early to middle Holocene from 11.4 to 5.9 kyr BP linked to low oxygen conditions (Fink et al. 2012).

36.6 Growth in the Future Mediterranean Sea

36.6.1 Potential Influence of Climate Change on the Mediterranean CWCs

It is estimated that >80% of global warming over the last 40 years has been taken up by the oceans and penetrated to depths of at least 700 m (Barnett et al. 2005). Among other anthropogenic stressors, the imprint of climate change on deep and intermediate Mediterranean waters is expected to generate specific threats to CWC habitats, such as in canyons or seamount flanks (see Ramirez-Llodra et al. 2010; Levin and Le Bris 2015). The combination of warming and acidification of mediterranean intermediate waters combined with change in nutrient supply and deoxygenation could affect the capacity of CWCs to maintain growth rates (Cordes et al. 2016). Predictive habitat modelling approaches and global datasets of key environmental parameters (e.g. temperature, salinity, dissolved O_2 and nutrients), are suggesting changes in the distribution of suitable habitats for CWC taxa in future climate scenarios (IPCC 2014), though there are still large uncertainties in these approaches (Davies and Guinotte 2011). The spatial resolution and accuracy of these models are still largely insufficient to anticipate responses due to short-term changes in local conditions (e.g. recovery times after physical disturbance, fluctuations of environmental factors and feeding constraints). According to future predicted climate IPCC-A2 scenario (IPCC 2014), the average temperature for the deep Mediterranean Sea may increase by 1.5 °C by the end of the twenty-first century with an increase of 0.23 for salinity (Somot et al. 2006). Together with the increase of temperature, pH will decrease as a result of anthropogenic CO_2 absorbed by seawater. In the future (year 2100) Mediterranean deep waters, the pH change is estimated to be between −0.005 and −0.06 units (Palmiéri et al. 2015). The local enhancement of acidification (e.g. due to an increase in organic matter remineralisation) and associated cumulative stressors yet constitute potential threats to CWCs.

Consequences of climate change for Mediterranean CWCs and their associated communities have to be evaluated. Details on this topic are given by Maier et al. (this volume) and Movilla (this volume).

36.6.2 Impact of Temperature

Physiological behaviour of scleractinian CWCs have been monitored in aquaria under different thermal conditions. Long-term (12 months) aquaria experiments on *Lophelia pertusa* from the Atlantic Ocean do not show absolute changes in calcification rates under seawater temperatures of 9 °C and 12 °C (Hennige et al. 2015). *Lophelia pertusa* and *M. oculata* from the Mediterranean Sea however revealed species-specific growth rate responses with similar calcification rates at 9 °C and 12 °C for *L. pertusa*, but lower rates at 9 °C for *M. oculata*. At 6 °C, both species show low calcification rates (Naumann et al. 2014). Similarly, calcification of *Dendrophyllia cornigera* from the Menorca Channel decreases from 12 to 8 °C (Gori et al. 2014).

Thermal acclimation of calcification processes is well established for a number of temperate and tropical scleractinian coral species and the optimal temperatures for several species have been determined. However, for scleractinian CWCs the thermal optimum and the potential for adaptation to temperature changes are still unknown. *In situ* and aquaria experiments suggested that the upper lethal temperature for

L. pertusa from the Gulf of Mexico is near 15 °C (Brooke et al. 2013). Freiwald et al. (2004) suggested that scleractinian CWCs, which occur less frequently in the Mediterranean Sea than in Atlantic and Pacific oceans, are at the uppermost of their thermal tolerance range in the Mediterranean (14 °C). Considering this optimal range, it would be expected that growth experiments conducted at temperatures higher than 13 °C, should display a decline in the calcification rate for CWCs. However, not all CWC species follow this rule as the calcification of *D. cornigera* from the shallow part of the Menorca Channel (~200 m) increases when temperature rises from 12 to 16 °C (Gori et al. 2014). *Desmophyllum dianthus* from a deeper location in the Adriatic Sea (430 m) shows significant decreases in calcification rates when exposed for a long period (8 months) to 15 °C waters (Gori et al. 2016); this might be linked to the decline in activity of enzymes involved in calcification (e.g., carbonic anhydrase). Reef formation in the future Mediterranean may be dramatically affected by global warming or, assuming the different thermal tolerances of species (e.g. *D. cornigera* exhibits a metabolism more efficient at higher temperature, Gori et al. 2014), an increase in temperature may contribute to a shift in Mediterranean CWC community composition. Analyses of fossils (Wienberg et al. 2009) and recent corals from the Atlantic (Keller and Os'kina 2008) suggest a higher temperature tolerance of *M. oculata* compared to *L. pertusa*. Additionally, scleractinian deep-water corals (*Dendrophyllia* sp. and *Eguchipsammia fistula*) have been found in the Red Sea at temperatures exceeding 20 °C, leading to a revisiting on the main persistence and resilience concepts for CWCs (Roder et al. 2013). If the future baseline temperature changes in the deep Mediterranean provinces, questions regarding acclimation of Mediterranean corals have to be addressed. *D. cornigera* from Cap de Creus canyon, NW Mediterranean, and *D. dianthus* from south of Malta, tolerate elevated temperatures (17.5 °C) during 3 months in aquaria, showing higher growth rates for *D. cornigera* when temperature increases, which suggests that those species may be more capable of surviving in warmer environments than previously thought (Naumann et al. 2013).

36.6.3 Ocean Acidification

Acidification is known to alter growth rate of calcifying organisms as global ocean composition becomes undersaturated in calcium carbonate. However, for scleractinian CWCs, long-term aquaria studies generally suggest that calcification of *L. pertusa*, *M. oculata* and *D. cornigera* colonies and *D. dianthus* solitary corals from the Mediterranean Sea are not affected by the pCO_2 level projected at the end of the century (Maier et al. 2013; Rodolfo Metalpa et al. 2015; Gori et al. 2016), although some studies report an expected higher sensititvity of *L. pertusa* and *D. cornigera* species (Movilla et al. 2014b). McCulloch et al. (2012) estimated that the energetic cost associated with pH up-regulation was ~10% per 0.1 pH unit decreases in seawater. A recent study suggests that a small fraction (<3%) of the total energy demand is required for *M. oculata* calcification, allowing corals from the Adriatic Sea to maintain growth rates in more acidic waters even under low feeding conditions (Maier et al. 2016).

The synergic effect of temperature and ocean acidification has been recently tested and the first results suggest that crystallographic and molecular-scale bonding organisation rather than calcification rate of *L. pertusa* from NE Atlantic are affected by thermal and pCO_2 changes (Hennige et al. 2015). Nevertheless, additional studies providing information on the main sources of energy metabolised are required, as highlighted by results from Gori et al. (2016) on *D. dianthus* from the Adriatic Sea.

As this volume includes two chapters (already mentioned in this text) dealing with effects of ocean acidification in CWCs, no more details on this topic will be included in this section.

36.6.4 Impact of Oceanographic Conditions on the Growth of CWCs: The Case Study of Dense Water Shelf Cascades in the Mediterranean Sea

In the Mediterranean Sea, different areas (Aegean Sea, Adriatic Sea, Catalan Margin, Creta Island, Gulf of Lion) are influenced by episodic dense water shelf cascades driven by wind-induced conditions (Canals et al. 2006). These dense water plumes that overflow the shelf edge are associated with significant decreases in temperature, significant increases in the current speed and they may transport of large amounts of coarse sediment and organic matter (Palanques et al. 2006; Heussner et al. 2006; Canals et al. 2006). The precise effects of cascading on CWC communities are not well documented (but see Puig and Gili, this volume). As mentioned before, *in situ* experiments showed a seasonal difference in the growth patterns of *M. oculata*, which are suspected to result from differences in the food availability induced by winter cascading events in the Lacaze-Duthiers canyon (Lartaud et al. 2014). The expected scenario for the end of the twenty-first century by the IPCC suggests a stronger stratification of the water column, which would result in a decrease of cascading events of at least 60%, compared to the present climate conditions (Hermann et al. 2008). Considering these preliminary results, the effects of climate change could result in additional strong threats to the resilience of CWC reefs in the Mediterranean Sea.

36.7 Conclusion

The study of growth patterns is a basic approach to determine the age of corals and to better understand the ecological features of CWCs. The evolution of methodologies and techniques to determine growth rates of CWCs provides increasily more precise approaches to measure growth, and also improvements in the standardisation to compare results obtained from CWCs and tropical and temperate corals, as well as among juvenile and adult individuals. Unexpected results have been highlighted by recent research, for instance the observation that some CWC species can reach growth rates similar to those of some tropical species. Still, growth rates differ depending on location, age of colony or the period of the year. Differences between species, including those living in the same habitat, have also been identified, raising the possibility that specific ecological niches may be preferencially occupied by specific species. These observed differences point out that further work is needed to determine the most effective conservation strategies for the CWC fauna which display diverse ecological performance.

Further, more studies are necessary to elucidate the key environmental and physiological drivers of growth, from the integration of inter-disciplinary studies to take into consideration skeletal growth as a part of the response of the whole organism. For example, a detailed understanding of the biology of the main CWC species still lacks, including knowledge of the role of reproductive cycle, the associated microbiome or the energy invested in growth by the calcifying species. Understanding critical aspects of CWC growth will require studies with substantial multiparameter monitoring – both biotic and abiotic – focusing on several temporal scales. Within this framework, the Mediterranean Sea is a perfect fieldwork environment as numerous CWC species have been identified in the area, and the effects of global environmental changes on these could be particularly remarkable in this semi-enclosed sea. For the survival of the associated biodiversity, the growth and survival of CWC species in this small ocean is critical.

Acknowledgements FL, LC and NLB works on CWC have been supported under the chair 'Biodiversity, extreme marine environments and global change' of UPMC supported by Fondation Total. LC doctoral contract is supported by UPMC (ED129 Doctoral school of environmental sciences). VM work presented in this paper was made possible by the ENS Ph.D. programme. The Earth and Natural Sciences Doctoral Studies Programme is funded under the Programme for Research in Third-Level Institutions Cycle-5 and co-funded under the European Regional Development Fund. Autun Purser is acknowledged for his support in editing the English language of the manuscript. We also thank the guest editor for his advices and inviting us to contribute to this chapter, and two anonymous reviewers for their helpful comments.

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Cross-References

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