Chapter 4

Effect of light and feeding on coral calcification

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Calcification is one of the major processes in the physiology of scleractinian corals. It involves at least two different components, i) the supply of calcium and dissolved inorganic carbon (DIC) to the site of calcification and ii) the supply of an organic matrix, considered as an essential prerequisite in the formation of a biomineral structure (Allemand _et al._, 1998). High rates of calcification in corals are both dependent on auto- and heterotrophy.

Concerning autotrophy, hermatypic (symbiotic) corals display higher rates of calcification than ahermatypic corals even if in some ahermatypic species, these rates are within the range of values measured for hermatypic corals (see Tentori and Allemand, 2006 for review). It has been suggested that the higher rates of calcification in hermatypic corals are due to the involvement of autotrophic symbionts. Hermatypic scleractinian corals have indeed developed an endosymbiotic relationship with photosynthetic unicellular dinoflagellates, _Symbiodinium sp.,_ commonly referred to as zooxanthellae. The first observations of an intimate relationship between light/zooxanthellae and calcification date from the 1930's (Yonge, 1931) during the field expeditions on the Great Barrier Reef. Later field experiments confirmed that rates of calcification are higher in the light than in the dark in zooxanthellate corals (Kawaguti and Sakumoto, 1948). Since then, many hypotheses have been proposed to explain the role of zooxanthellae in the enhancement of calcification, also called Light Enhanced Calcification (LEC). Recently it has been shown that the lag-phase necessary to switch between light to dark or dark to light conditions has a value of about 25 min (Moya _et al.,_ 2006).

Several hypotheses have been proposed to explain the relationship between zooxanthellae and calcification (for a review see Allemand _et al._, 2004):

1. symbionts synthesize molecules that are essential to the calcification process (Muscatine and Cernichiari, 1969),
2. symbionts affect the DIC equilibrium within coral tissues by taking up CO_2 for photosynthesis (Goreau, 1959; McConnaughey and Whelan, 1997) or by secreting hydroxyl ions that are the product of Carbon Concentrating Mechanisms (Furla _et al._, 2000),
3. symbionts produce energy and O_2 that can accelerate the calcification process (Chalker and Taylor, 1975; Rinkevich and Loya, 1984) and
4. symbionts play a role in the removal of substances that would otherwise inhibit calcification (Simkiss, 1964).

Each hypothesis has its merits and none can be completely excluded, but each model needs to be evaluated against the most recent histological and physiological observations. Perhaps the most important observation in this regard is the general observation that the tissues which calcify at the highest rates, or which initiate calcification, do not possess zooxanthellae (Pearse and Muscatine, 1978 and for a review see Tambutté _et al._, 2007). So what role, if any, do zooxanthellae play for coral skeleton calcification? In light of the new physiological and histological data, LEC should be considered differently depending on the scale of observation: macro-scale, at the level of the organism or microscale, at the level of the cells (Tambutté _et al._, 2007). At the macro-scale level, zooxanthellae might globally enhance calcification during the day by providing in high-quantity some essential precursors for organic matrix synthesis (Cuif _et al.,_ 1999; Muscatine

et al., 2005). Other important parameters, such as ATP supply and coelenteric pH regulation are also important parameters to take into account during a diurnal cycle (Gattuso *et al.,* 1999, Allemand *et al.,* 2004). At the microscale level, the organization of the cell tissue and the presence or absence of zooxanthellae therein, must be taken into account and related to the organization and composition of the skeletal ultra-structure components.

Enhanced calcification can also be obtained through heterotrophy and plankton feeding. Corals are indeed good heterotrophs, able to catch large amounts of zooplankton (Sebens *et al.*, 1996; Yahel *et al.*, 2005), as well as dissolved and particulate organic matter (Anthony and Fabricius, 2000; Grover *et al,*. 2006). Heterotrophy was proven to significantly enhance zooxanthellae density, chlorophyll content, rates of photosynthesis and calcification (Anthony and Fabricius, 2000; Ferrier-Pagès *et al.*, 2003; Houlbrèque *et al.*, 2003; 2004), as well as lipid concentration in the tissue (Al-Moghrabi *et al.*, 1995). Wellington (1982) was one of the first to use field manipulations of light and zooplankton and to show that reduced feeding decreased the growth of *Pavona clavus*. Later many laboratory experiments demonstrated up to 30% enhancement of coral growth rate under feeding (Anthony and Fabricius, 2000; Ferrier-Pagès *et al*., 2003; Houlbrèque *et al*., 2003, 2004). Rates of dark and light calcification are both enhanced by two to three times following feeding (Houlbrèque *et al.,* 2003). Several explanations can be considered to explain this skeletal enhancement, such as:
1. a larger supply of metabolic carbon to the site of calcification. Indeed, Erez (1978) as well as Furla *et al.* (2000) demonstrated that 70 % of the DIC for calcification comes from metabolic CO_2 (respiration). Since heterotrophic feeding clearly results in a large increase in tissue growth and tissue thickening, respiration rates are also increased. Heterotrophy can therefore stimulate calcification through tissue growth and supply of metabolic inorganic carbon, as already suggested by Barnes and Lough (1993), and
2. an enhancement of the organic matrix synthesis. Allemand *et al.* (1998) suggested that heterotrophy was a source of the amino acid aspartic acid, one of the major components of the coral matrix. This was confirmed by a latter study, which observed a higher incorporation of this amino acid into the organic matrix of fed corals (Houlbrèque *et al*., 2004). Therefore, heterotrophic feeding can enhance the construction of the organic matrix by supplying additional energy, especially for the dark processes such as the calcium/proton pump, (McConnaughey and Whelan, 1997; Anthony *et al*., 2002), by providing some external amino acids necessary to the construction of the organic matrix or providing higher amounts of autotrophic amino acids by increasing photosynthesis.

In conclusion, many studies remain to be carried out, both on the LEC and heterotrophy, especially for understanding the mechanisms underlying the enhancement of calcification by these two processes. Indeed, on a fundamental point of view, it remains to be understood:

1. What are the precursors of the organic matrix, provided by the zooxanthellae?
2. What is the pH at the calcification site? and
3. What is the importance of ATP and other sources of energy supplied either by auto-and heterotrophy for calcification?

All these fundamental informations will provide a better understanding of the calcification process and its enhancement. However it must be kept in mind that both *in-situ* and in aquaria, many parameters affect calcification. Among these parameters, light intensity, light quality as well as light regime play an important role. The best irradiance under *in vitro* conditions would be the one which would closely match the natural sunshine irradiance, both in terms of spectral quality (high colour temperature), and light regime (increasing-decreasing light, following a Gaussian curve versus constant). These light parameters have to be adapted to each coral species and to *in vitro* constraints. Also being an important parameter is the flow regime, since it has been proven that relatively high flows improve diffusion of nutrients from seawater to the coral colony and decreases the diffusion-barrier created by the mucus layer (Lesser *et al.,* 1994). Many studies are still needed to fully understand the relationship between calcification, colony health and environmental parameters.

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