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Effect of light and temperature on calcification and strontium uptake in the scleractinian coral *Acropora verweyi*

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ABSTRACT: Strontium thermometry has been suggested as a powerful tool for reconstructing seawater surface temperature (SST). In corals, an inverse relationship between SST and skeletal Sr/Ca ratios has been found. However, this ratio might also vary with calcification, which in turn is dependent on light and temperature. The aim of this study was to improve our knowledge of the uptake of Sr^{2+} as a function of light and temperature in the scleractinian coral *Acropora verweyi*. Two experiments were performed in which nubbins were acclimated over 4 wk either to 3 light intensities (100, 200 and 400 µmol m^{-2} s^{-1}) or to 3 temperatures (20, 25, and 29°C) and growth rates were monitored. At the end of the 4 wk, nubbins were incubated, under the above light levels and temperatures, in individual beakers containing seawater spiked with the radiotracer ^{85}Sr. Parallel incubations were carried out in dark beakers, in order to compare rates of Sr^{2+} incorporation in light and dark. The results obtained showed that growth rates were significantly higher under high light (0.16 ± 0.01 and 0.27 ± 0.01 % d^{-1} for 100 and 400 µmol photons m^{-2} s^{-1}) and under high temperature (0.06 ± 0.01 % d^{-1} at 20°C to 0.35 ± 0.03 % d^{-1} at 29°C). Rates of Sr^{2+} incorporation into the coral skeleton were also higher under high light (32.4 ± 3.0, 72.9 ± 13.5 and 91.2 ± 9.0 nmol (g dry weight, DW)$^{-1}$ d^{-1}, for corals cultured at 100, 200 and 400 µmol m^{-2} s^{-1} respectively) and high temperature (89 ± 14, 224 ± 38 and 436 ± 58 nmol (g DW)$^{-1}$ d^{-1} for corals cultured at 20, 25 and 29°C respectively). Rates of Sr^{2+} uptake were also 2 to 3 times lower in the dark than in the light, comparable with the incorporation of calcium. Our results finally show a strong correlation between Sr^{2+} uptake and growth rates. Strontium uptake therefore follows the same pattern as calcium uptake, both ions being regulated by the calcification biochemistry.

KEY WORDS: Coral · Skeleton · Strontium · Tracer · Calcification · Light · Temperature · Culture

INTRODUCTION

The interpretation of coral skeleton chemistry is becoming increasingly popular for reconstructing past climate history. Retrieval of climatic data from geologic records is important for validating climate models in which temperature is a crucial parameter. Strontium thermometry has been suggested as a powerful tool for reconstructing sea surface temperature, SST (Beck et al. 1992); this is based on an inverse relationship between SST and Sr/Ca ratios (Weber 1973, Smith et al. 1979, Lea et al. 1999), and on the long residence time of calcium (Ca^{2+}) and strontium (Sr^{2+}) in the oceans (Broecker & Peng 1982). Scleractinian corals form aragonitic carbonate skeletons containing minor elements such as magnesium and strontium (Milliman et al. 1974). Good correlations have been observed between the Sr/Ca ratio in coral skeletons and SST (Beck et al. 1992, Alibert & McCulloch 1997, McCulloch et al. 1999). However, some studies have also

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argued that the Sr/Ca thermometer is problematic, because it has been shown to vary between or within species (Allison 1996, Rosenthal et al. 1997), or to correlate well with coral extension (de Villiers et al. 1994, 1995) and calcification rates (Alibert & McCulloch 1997, Allison et al. 2001). Ion probe microanalyses across coral daytime and nighttime growth layers have also revealed a heterogeneous strontium distribution (Hart & Cohen 1996, Allison et al. 2001, Cohen et al. 2002, Meibom et al. 2003). As noticed by deVilliers et al. (1994), this poses interesting questions related to physiological control of Sr/Ca uptake in biogenic aragonite and to the observed offset between Sr^{2+} uptake in biogenic versus inorganic aragonite (Zhong & Mucci 1989).

All these observations suggest that temperature is not the only factor controlling Sr/Ca ratio in coral skeletons, and that biological factors must also play a role (Hart & Cohen 1996, Cohen et al. 2001, 2002). No clear dependency of Sr/Ca ratios on temperature has, therefore, been established, due to the lack of understanding of the extent to which skeletal chemistry is controlled by physiological parameters (Boiseau et al. 1997). Only a few studies have investigated the kinetics of strontium uptake in scleractinian corals (Chalker 1981, Ip & Krishnaveni 1991, Ferrier-Pagès et al. 2002). Whereas Ip & Krishnaveni (1991) suggested that the transport of strontium is a diffusive process, the 2 other studies supported the view that strontium is actively transported to the calcification sites via a transepithelial pathway involving calcium channels. In this case, rates of strontium incorporation might vary with calcification rates. Since calcification itself varies with several environmental factors, such as light (Chalker 1981, Kajiwara et al. 1995), temperature (Clausen & Roth 1975, Howe & Marshall 2002) and nutrients (Atkinson et al. 1995, Marubini & Atkinson 1999), strontium uptake rates in corals should also be affected by these. In addition, Greegor et al. (1997) have shown that strontium does not solely substitute calcium in its structural sites and form strontianite crystals ($SrCO_3$). The rate of formation of these crystals depends on the rate of calcification and also on other factors such as seawater temperature, since strontianite is 5 to 10 times less soluble than aragonite (Greegor et al. 1997).

The aim of our study, therefore, was to improve our understanding of Sr^{2+} uptake by the scleractinian coral *Acropora verweyi*, especially the relationship between light, temperature, calcification rate and strontium uptake. For this purpose, 2 different experiments were set up, in which coral colonies were grown under 3 different light levels or 3 temperatures over 4 wk. Growth rates were monitored every week and strontium uptake was measured at the end of the incubation using the radiotracer ^{85}Sr.

MATERIALS AND METHODS

Experimental set-up. Experiments were performed using colonies of the branching zooxanthellate scleractinian coral *Acropora verweyi* (identified by M. Pichon), originating from New Caledonia and maintained for a few months in the aquaria of the Oceanographic Museum. 'Nubbins' were obtained by cutting terminal portions of branches from a parent colony and were then suspended with a nylon mesh in aquaria. They were all of the same size (ca. 1 cm long). After 2 wk of healing, the exposed skeleton was entirely recovered with tissue and coral fragments were ready to be used for experiments. The culture tanks were continuously supplied with Mediterranean seawater (salinity = 38.5) pumped from 50 m depth, aerated and heated using a temperature controller (EW, PC 902/T), and continuously mixed with a Rena® pump (6 l min^{-1}). The renewal rate was approximately 5 times d^{-1}. Nubbins were fed once a week for 12 wk with *Artemia salina* nauplii. Light was provided by metal halide lamps (Phillips HPIT, 400 W) on a 12 h light:12 h dark photoperiod.

For the light experiment, 27 nubbins (9 nubbins per tank) were distributed among 3 tanks (30 l), receiving 3 light intensities (100, 200 and 400 µmol photons m^{-2} s^{-1}, referred to below as low light (LL), medium light (ML) and high light (HL) respectively). Nubbins were maintained for 4 wk under these culture conditions. The light intensities correspond to 4.3, 8.6 and 17.3 mol photons m^{-2} d^{-1} respectively. As an indication, Davies (1991) measured that, at 3 m depth in turbid water, a typical sunny day generates 14.4 mol m^{-2} d^{-1}, while a cloudy day generates 6.2 mol m^{-2} d^{-1}. The temperature was kept constant at 27°C. Corals were weighed once a week, according to the buoyant weight technique (Jokiel et al. 1978).

For the temperature experiment, 15 nubbins were distributed among 3 tanks (30 l) heated to 20, 25 or 29°C. The light was kept constant (400 µmol photons m^{-2} s^{-1}). Nubbins were maintained for 4 wk under the above conditions and were weighed once a week (Jokiel et al. 1978).

Radioactive measurements. At the end of the 4 wk incubation under either light- or temperature-controlled conditions, the uptake of radioactive strontium was measured in 5 nubbins randomly taken from each tank according to the protocol described in Ferrier-Pagès et al. (2002) modified from Tambutté et al. (1996). Care was taken to maintain nubbins so that the whole skeleton was entirely covered by animal tissue, in order to avoid any direct contact of the skeleton with the external seawater containing the radiotracer.

For the light experiment, 5 nubbins from each culture condition (i.e. low, medium or high light) were

incubated for 4 h in beakers containing 50 ml of seawater spiked with 7.052 Bq ml^{-1} of the radiotracer ^{85}Sr (carrier-free, obtained from LEA, $T_{1/2}$ = 64.85 d). The beakers were placed on a multi-stirring station and were continuously stirred during the incubation. Temperature was kept constant at 27°C by incubating the beakers in a water-bath. The light level was equal to that set up in the culture conditions (400, 200, or 100 µmol photons m^{-2} s^{-1}). To compare rates of Sr^{2+} uptake in the light and dark, 5 nubbins from each light treatment were also incubated in parallel for 4 h under the above conditions, except that they were maintained in dark beakers.

For the temperature experiment, 5 nubbins from each culture condition (20, 25 or 29°C) were incubated for 24 h in beakers containing 50 ml of seawater spiked with the radiotracer ^{85}Sr. The light was set to 400 µmol photons m^{-2} s^{-1}, and the temperature was maintained at the level set up in the culture conditions (20, 25, or 29°C). The incubation time was longer in this experiment because nubbins incubated at 20°C had low growth rates and, therefore, a very low incorporation of strontium. In order to obtain a significant ^{85}Sr signal, an extended incubation time was required. However, results obtained in both experiments are comparable since it has been demonstrated that strontium uptake by coral skeleton is linear for up to 10 d (Ferrier-Pagès et al. 2002).

At the end of incubation, colonies were rinsed with normal seawater, blotted dry on absorbent paper to eliminate any adhering radioactive medium, then incubated for 30 min in beakers containing 50 ml of seawater (efflux). This step is necessary to get rid of the radio-labeled seawater contained in the coelenteric cavity of the corals (corresponding to radioactivity not incorporated into the tissue or the skeleton). The time needed to complete the efflux procedure was determined in previous experiments (Tambutté et al. 1996) where it was shown that 30 min are sufficient to totally renew the coelenteric content. Upon completion of the efflux, tissues were dissolved for 20 min in 1 ml of 1 N NaOH at 90°C. Samples were then neutralized with 1N HCl and the total soluble protein content was measured using the Bradford method (Bradford 1976) with the Coomassie protein assay reagent (Pierce). Optical density was read at 595 nm using a microplate reader (Multiskan® Bichromatic) and bovine gamma globulin (BGG) was used as a standard. Skeletons were then dried, weighed and transferred into counting vials.

The gamma emission of ^{85}Sr (506 k eV) was measured in the skeleton, tissues and seawater using 2 well-type NaI detectors (3 inch) connected to a multi-channel analyzer and a computer using a spectral analysis software. The activity of the samples was corrected for background, radioactive decay and counting efficiency, and compared with standards of appropriate geometry. Counting times were adjusted to give a relative propagated error of <5% at the 1 SD level, i.e. 5 min for the skeleton, 20 min for the tissues and the efflux seawater. Incorporation of Sr^{2+} into the tissue and skeleton is expressed as nmol l^{-1}, as obtained from ^{85}Sr activity (Bq ml^{-1}) and from ^{85}Sr-specific radioactivity of the experimental medium (for details see Tambutté et al. 1995). Uptake rates were then calculated (nmol Sr^{2+} (g DW)$^{-1}$ h^{-1}) to facilitate the interpretation of the results obtained.

Measurement of environmental variables. Temperature (accuracy: ±0.05°C) was logged at 10 min intervals using a Seamon® temperature recorder. Salinity and irradiance were measured using a conductivity meter (Meter LF196) and a 4π quantum sensor (Li-Cor, LI-193SA) respectively.

Calcification rate. Corals were weighed once a week during the experiment according to the buoyant weight technique (Jokiel et al. 1978), using a Mettler AT 261 balance (accuracy ± 0.01 mg). Calcification rates were calculated using the following formula:

$$G = (M_{t+1} - M_t)/M_t\,(T_{t+1} - T_1)$$

where M_t and M_{t+1} are the coral weight (mg) at the beginning (T_1) and the end (T_{t+1}) of each growth interval. The size and the age of a coral colony may affect its growth rate measurements (i.e. growth rate of a colony decreases when the initial size of the colony increases, Vago et al. 1997). In this experiment, we were able to normalize the growth of the nubbins to their initial skeletal weight, because these nubbins were all of the same size. Marchioretti (1999), in a large experiment using nubbins of *Stylophora pistillata* prepared according to the same technique as our *Acropora verweyi* nubbins, also showed that there was no correlation between size and growth of the nubbins.

Statistical analysis. All statistical analyses were carried out using the statistical package JMP 3.1.6 (SAS Institute). Results are reported as means ± standard error (SE), and N is the sample size.

RESULTS

Physiological parameters

The amount of soluble protein measured in tissue at the end of the exposure period was not significantly different among light treatments (ANOVA, p = 0.4, average equal to 3.3 ± 0.5 mg (g DW)$^{-1}$) or temperature treatments (ANOVA, p = 0.1, average value equal to 3.5 ± 0.5 mg (g DW)$^{-1}$).

Rates of calcification measured during the 4 wk of culture at the 3 irradiances were significantly different between treatments (ANOVA, p < 0.0001) (Fig. 1) and

equal to 0.16 ± 0.001, 0.20 ± 0.01 and 0.27 ± 0.01 % d^{-1} at low, medium and high light respectively. Temperature also had a significant effect on the calcification rates (ANOVA, $p < 0.0001$) (Fig. 1), which were equal to 0.06 ± 0.01, 0.22 ± 0.41, and 0.35 ± 0.03 % d^{-1} at 20, 25 and 29°C, respectively.

Incorporation of radioactive strontium

For both experiments, ^{85}Sr was rapidly incorporated into the coral skeleton, since the tissue fraction represented less than 3 % of the total radioactivity measured at the end of the 4h incubation (results not shown). Therefore, only the results of the skeletal incorporation of strontium will be presented in this section.

The uptake rates of strontium at the different light levels were significantly different (ANOVA, $p < 0.005$), and were equal to 1.86 ± 0.14, 4.55 ± 0.92 and 5.43 ± 0.59 nmol (g DW)$^{-1}$ h^{-1}, for corals cultured at low, medium and high light respectively (Fig. 2). This gives daily incorporation rates of 32.64, 73.08 and 91.32 nmol (g DW)$^{-1}$ d^{-1} respectively.

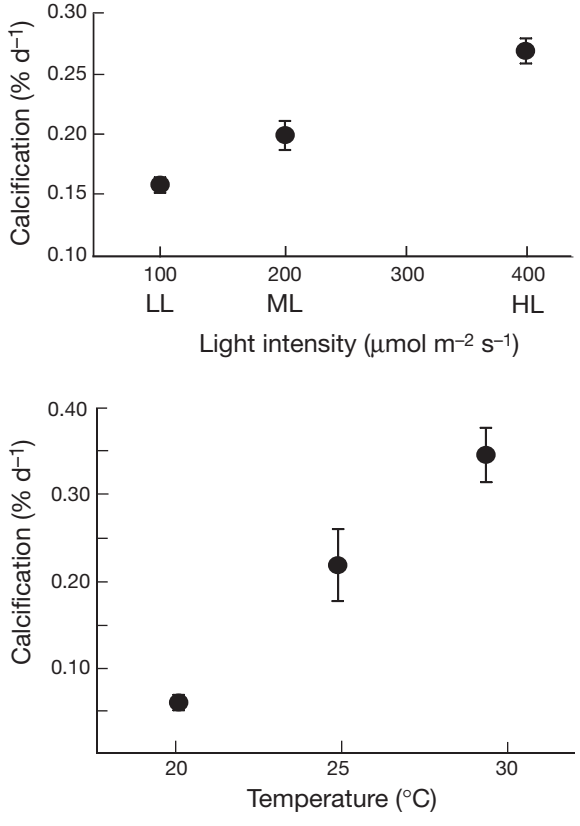

Fig. 1. *Acropora verweyi*. Variation in the calcification rate (% d^{-1}) with light level (LL: low light, 100 µmol photons m^{-2} s^{-1}; ML: medium light, 200 µmol photons m^{-2} s^{-1}; HL: high light, 400 µmol photons m^{-2} s^{-1}), and temperature. Means ± SE are shown

When normalized per protein content, these rates were equal to 0.41 ± 0.08, 1.01 ± 0.38 and 1.34 ± 0.35 nmol Sr^{2+} (mg protein)$^{-1}$ h^{-1} for corals cultured at low, medium and high light respectively.

Uptake rates measured in the light were 2.2 to 3 times higher than the rates measured in the dark. Dark incorporation of strontium was also significantly different according to the culture conditions (i.e. the amount of light received) (ANOVA, $p < 0.001$), and were equal to 0.86 ± 0.14, 1.54 ± 0.20 and 2.18 ± 0.15 nmol (g DW)$^{-1}$ h^{-1}, for corals cultured at low, medium and high light respectively. This corresponds to rates of 0.15 ± 0.05, 0.32 ± 0.09, and 0.57 ± 0.11 nmol (mg protein)$^{-1}$ h^{-1}, respectively.

Strontium uptake rates of corals maintained at different temperatures (and after 24h exposure to ^{85}Sr) were significantly different (ANOVA, $p < 0.0002$), and were equal to 89 ± 14, 224 ± 38 and 436 ± 58 nmol (g DW)$^{-1}$ d^{-1}, for corals cultured at 20, 25 and 29°C respectively (Fig. 3) or 14.22 ± 6.43, 30.51 ± 8.37 and 47.62 ± 8.75 nmol (mg protein)$^{-1}$ d^{-1}, respectively.

Relationship between strontium uptake and calcification

A significant positive relationship was found between strontium accumulation in the skeleton and calcification rates for nubbins of the scleractinian coral *Acropora verweyi* (Fig. 4) (Bartlett's test of correlation, df = 2, $\chi^2 = 42.36$, $p < 0.001$). When fitted to a linear regression, (Fig. 4), the equation of the curve is: Sr^{2+} uptake (nmol (g DW)$^{-1}$ d^{-1}) = 1003.3 × calcification (% d^{-1}) – 14.7, ($R^2 = 0.8$).

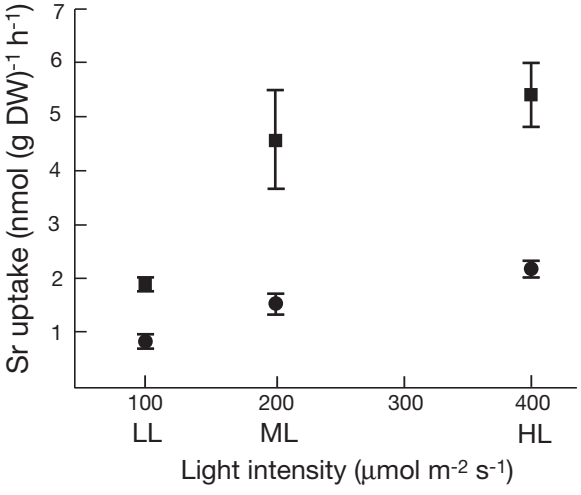

Fig. 2. *Acropora verweyi*. Strontium uptake (nmol (g DW)$^{-1}$ h^{-1}) in the light (■) and in the dark (●) by corals cultured at different light intensities (LL: low light; ML: medium light; HL: high light)

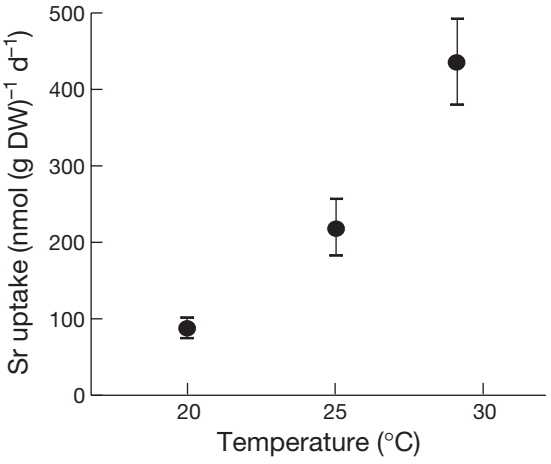

Fig. 3. *Acropora verweyi*. Strontium uptake (nmol (g DW)$^{-1}$ d^{-1}) by nubbins grown at different temperatures

DISCUSSION

Over the past 20 years, the Sr/Ca ratio of coral skeleton has been widely used to determine the temperatures of ancient seas (Swart 1981, Aharon 1991), based on the earlier work by Kinsman & Holland (1969) who published an inverse relationship between temperature and Sr/Ca in inorganic aragonite. Later, Weber (1973) also calculated an inverse relationship between SST and the Sr/Ca ratio in coral skeletons. Since then, relationships have been reported between this ratio and SST with a precision of ±0.5°C (Swart 1981, Beck et al. 1992, de Villiers et al. 1995, Hughen et al. 1999, McCulloch et al. 1999). However, de Villiers et al. (1994, 1995) were among the first to underscore problems with the strontium thermometer, because they found that the Sr/Ca ratio also correlated very well with coral extension rates. These observations were followed by several others suggesting problems with the use of Sr/Ca as a thermometer (Allison 1996, Hart & Cohen 1996, Alibert & McCulloch 1997, Greegor et al. 1997, Rosenthal et al. 1997, Cohen et al. 2001, 2002). Finally, Cohen et al. (2002) suggested that the Sr/Ca ratio measured in non-symbiotic corals could be considered to be primarily controlled by variations in SST, whereas the Sr/Ca ratio recorded in symbiotic species is largely under strong biological control.

The present study was, therefore, designed to gain a better understanding of the uptake of strontium by a symbiotic coral, *Acropora verweyi*. Until now, studies on coral calcification have mainly focused on the incorporation of calcium into the skeleton. They have shown that this incorporation is saturable and carrier-mediated (Chalker 1981, Tambutté et al. 1996), involving both passive steps through calcium channels, and energy-requiring steps via Ca-ATPases along a transcellular pathway (Marshall 1996, Tambutté et al. 1996, Zoccola et al. 2004). Few studies have investigated the incorporation of strontium into coral skeletons. Except in the work of Ip & Krishnaveni (1991), Sr^{2+} incorporation has been shown to follow the same process as calcium uptake (Goreau 1977, Chalker 1981, Wright & Marshall 1991, Ferrier-Pagès et al. 2002).

The present study shows that the uptake of strontium into coral skeleton is directly correlated with calcification, represented here by growth-rate measurements. Growth rates of *Acropora verweyi* were in the same range as those obtained previously in the laboratory with *Acropora* species maintained under the same light levels (Reynaud-Vaganay et al. 2001, Reynaud et al. 2002, 2003), i.e. an increase of between 0.2 and 0.5% d^{-1}. They were also comparable to growth rates measured for other scleractinian species, such as *Porites cylindrica*, *A. variabilis* and *Stylophora pistillata* (Steven & Broadbent 1997, Vago et al. 1997, Yap et al. 1998, Ferrier-Pagès et al. 2001). The rates of strontium uptake measured in this study are in agreement with those previously obtained using the same radioactive technique (Ferrier-Pagès et al. 2002). When compared to the rates of calcium incorporation for *Acropora* sp. maintained at 26°C and under 180 mol photons m^{-2} s^{-1} (214 nmol Ca^{2+} (mg protein)$^{-1}$ h^{-1}, Gattuso et al. 1998), the rates of strontium incorporation are ca. 100 times lower. This reflects the Sr^{2+} and Ca^{2+} concentrations in seawater (0.1 and 10 mM respectively).

By changing light and temperature over a period long enough to reduce or enhance calcification, we changed the strontium uptake rates. Hence, following calcification, strontium uptake rates increased with light and temperature. They were also repressed by 54 to 66% in the dark compared to the light. The positive correlation of calcification with light (Houck et al. 1977, Oliver et al. 1983, Marubini et al. 2001, Reynaud-

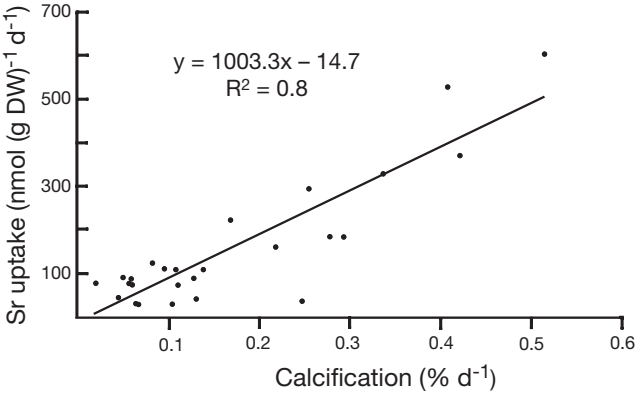

Fig. 4. *Acropora verweyi*. Relationship between strontium incorporation into the coral skeleton and calcification rates

Vaganay et al. 2001) or temperature (Lough & Barnes 1997, 2000, Howe & Marshall 2002) is well known. Several studies have also demonstrated that calcification rates measured in the light are ca. 2 to 4 times higher than those measured in the dark (Barnes & Chalker 1990, Gattuso et al. 1999, Furla et al. 2000), a process that has been described as light-enhanced calcification. Several hypotheses have been put forward to explain this enhancement, and the interactions between calcification and photosynthesis, in particular, still remain poorly understood and are a matter of controversy (Goreau et al. 1996, Marshall 1996, Gattuso et al. 1999, McConnaughey et al. 2000). Uptake rates of strontium also appeared to level off as light increased (Fig. 2), whereas they increased exponentially as temperature increased (Fig. 3). This different pattern of Sr^{2+} deposition is dependent on the calcification process, which followed the same tendency. An irradiance of 300 µmol photons m^{-2} s^{-1} is enough to obtain maximal photosynthetic rates under our culture conditions (Ferrier-Pagès et al. 2001), giving maximal calcification rates. Therefore, calcification and strontium uptake will not increase indefinitely with increasing light. The growth of *Acropora* sp. nubbins seems to be more limited by temperature than by light, as demonstrated in a previous study (Reynaud-Vaganay et al. 1999).

Our results differ from those of Ip & Krishnaveni (1991), who found that the deposition rate of radioactive Sr^{2+} in polyps of the symbiotic coral *Galaxea fascicularis* incubated under a light intensity of 200 µmol photons m^{-2} s^{-1} was not significantly different from that in polyps incubated in darkness. They concluded that Sr^{2+} deposition was not enhanced by photosynthetic activity and was independent of light intensity. This difference might be either due to different patterns of Sr^{2+} incorporation according to the coral species or, more convincingly, to different techniques used in measuring strontium uptake. Indeed, in a previous experiment (Ferrier-Pagès et al. 2002) we found that the incorporation of Sr^{2+} was carrier-mediated, as also previously suggested by Chalker (1981), while Ip & Krishnaveni (1991) found that this uptake was diffusive.

A dependency of the Sr/Ca ratio on calcification rate has been suggested for coccolithophores (Stoll & Schrag 2000, Rickaby et al. 2002) and foraminifera (Lea et al. 1999). Recently, Cohen et al. (2001), using an ion microprobe technique, also concluded that the Sr/Ca ratio in the symbiotic coral *Porites lutea* depends more on calcification rates than on seawater temperature. They observed that the Sr/Ca content of the daytime skeleton was always lower than that of the adjacent nighttime skeleton, as a potential result of the 'light-enhanced calcification' effect.

Our results also showed that there is a 'coral memory' effect on the uptake of strontium, since the rates of Sr^{2+} accumulation in the dark were less repressed in corals previously cultured under 400 than under 100 µmol m^{-2} s^{-1}. This light effect should not be attributed to the time taken for the pH to change under the calicoblastic layer after initial darkness, since Al-Horani et al. (2003) showed in their microsensor study that changes in pH beneath the calicoblastic epithelium occur within less than 10 min. Since our Sr^{2+} uptake rates were measured after 4 h incubation in the dark, pH changes during light-dark transition cannot explain our results. Conversely, Houlbrèque et al. (2003, 2004) recently showed that the calcification rate in the dark is dependent upon the nutritional status of the animal. These authors measured a higher dark calcification in corals fed for 3 wk with particulate food than in corals maintained unfed over the same period of time. We can, therefore, hypothesize that the different light regimes applied to our *Acropora verweyi* nubbins might have produced differences in nutritional status; the additional food provided by high-light levels might have been used for dark strontium uptake. However, this assumption remains to be validated.

In conclusion, results obtained in this study show that strontium uptake follows the same pattern as calcium uptake. The Sr/Ca thermometer is clearly not based on thermodynamics or on the physico-chemical principles that regulate the deposition of these ions in inorganically precipitated aragonite (Kinsman & Holland 1969). Instead, biochemical pathways regulate the delivery of Ca^{2+} and its analogue Sr^{2+} to the calcification sites. Light also regulates calcification rate and our results show that light significantly affects the incorporation of strontium, independently of temperature. Nutrients are also known to affect calcification rates in corals (Atkinson et al. 1995, Marubini & Atkinson 1999). It is therefore important to restrict Sr/Ca thermometer measurements to coral species that grow under very limited light variations and in oligotrophic waters. Since it was impossible to follow the incorporation of radioactive calcium and strontium into the coral skeletons at the same time (due to technical impossibilities), the obvious next step in this research will be to monitor the changes in the Sr/Ca ratio with temperature and/or light under laboratory-controlled conditions.

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