Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

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Photosynthesis and calcification in zooxanthellate scleractinian corals and coral reefs are reviewed at several scales: cellular (pathways and transport mechanisms of inorganic carbon and calcium), organismal (interaction between photosynthesis and calcification, effect of light) and ecosystemic (community primary production and calcification, and air-sea [CO.sub.2] exchanges).

The coral host plays a major role in supplying carbon for the photosynthesis by the algal symbionts through a system similar to the carbon-concentrating mechanism described in free living algal cells. The details of carbon supply to the calcification process are almost unknown, but metabolic [CO.sub.2] seems to be a significant source. Calcium supply for calcification is diffusional through oral layers, and active membrane transport only occurs between the calicoblastic cells and the site of calcification. Photosynthesis and calcification are tightly coupled in zooxanthellate scleractinian corals and coral reef communities. Calcification is, on average, three times higher in light than in darkness. The recent suggestion that calcification is dark-repressed rather than light-enhanced is not supported by the literature. There is a very strong correlation between photosynthesis and calcification at both the organism and community levels, but the ratios of calcification to gross photosynthesis (0.6 in corals and 0.2 in reef communities) differ from unity, and from each other as a function of level.

The potential effect of global climatic changes (p[CO.sub.2] and temperature) on the rate of calcification is also reviewed. In various calcifying photosynthetic organisms and communities, the rate of calcification decreases as a function of increasing p[CO.sub.2] and decreasing calcium carbonate saturation state. The calculated decrease in Ca[CO.sub.3] production, estimated using the scenarios considered by the International Panel on Climate Change (IPCC), is 10% between 1880 and 1990, and 9-30% (mid estimate: 22%) from 1990 to 2100. Inadequate understanding of the mechanism of calcification and its interaction with photosynthesis severely limits the ability to provide an accurate prediction of future changes in the rate of calcification.

INTRODUCTION

Coral reefs are the most striking example of benthic, photosynthetic and calcifying ecosystems. They display the greatest abundance and diversity of Ca[CO.sub.3]-depositing organisms that carry out photosynthesis (calcareous algae) or harbor photosynthetic symbionts (scleractinian corals, foraminiferans and mollusks). The photosynthetic fixation of carbon dioxide ([CO.sub.2]) and precipitation of Ca[CO.sub.3] are intimately linked both at spatial (cell to ecosystem) and temporal (day-night) scales. Large fluxes of carbon and calcium carbonate occur at the cell and community levels on reefs. Transepithelial calcium transport in scleractinian corals can reach 1,700 nmol [cm.sup.-2] [h.sup.-1] (Wilbur and Simkiss, 1979), which would be equivalent to 149 mol Ca [m.sup.-2] [yr.sup.-1], while the rates of community gross primary production and respiration of coral reef fiats range, respectively, from 79 to 584 and from 76 to 538 mol C [m.sup.2] [yr.sup.-1], the rate of net calcification ranges from 5 to 126 mol C [m.sup.2] [yr.sup.-1] (Gattuso et al., 1998b).

The modern study of coral calcification began more than 40 years ago with the pioneering works of Goreau and collaborators (Goreau and Bowen, 1955; Goreau, 1959; Goreau and Goreau, 1959; Goreau, 1963) but many aspects, such as the transport mechanisms of calcium and inorganic carbon from the surrounding seawater to the sites of photosynthesis and skeletogenesis, and their environmental controls, remain poorly known. Likewise, the concentrations and transport of secondary products ([OH.sup.-] and [H.sup.+]), as well as the interaction between photosynthesis and calcification, are poorly understood; the latter is a matter of recent controversy (Carlon, 1996; Goreau et al., 1996; Marshall, 1996a, b).

Photosynthetic [CO.sub.2] fixation and [CO.sub.2] release by calcification are relatively minor components of the present

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

global carbon cycle (Ware et al., 1992; Smith, 1995) but may have contributed to the control of atmospheric p[CO.sub.2] during glacial-interglacial cycles (Opdyke and Walker, 1992). Global climatic changes, such as the predicted increases in temperature and p[CO.sub.2] (Houghton et al., 1996), and changes in related parameters, such as pH and aragonite saturation state, are likely to have significant effects on the cycling of carbon and carbonate in coral reefs. These effects are discussed using the limited information available about scleractinian corals and coral communities, as well as some data for temperate coralline algae.

The aim of our paper is to review the cycles of carbon and carbonate in zooxanthellate scleractinian corals and coral reefs. We first provide background information on processes (photosynthesis, respiration and calcification) and carbonate chemistry. We then consider several scales: molecular and cellular (pathways and transport mechanisms of inorganic carbon and calcium), organismal (interaction between photosynthesis and calcification, effect of light), and ecosystemic (community production and calcification, and air-sea [CO.sub.2] fluxes). We also review the effect of changes in the seawater carbonate chemistry and provide a tentative prediction of the effect of increased p[CO.sub.2] and temperature on the rate of calcification.

BACKGROUND INFORMATION ON CHEMISTRY AND PROCESSES

Calcium and inorganic carbon are the two major substrates of photosynthesis and calcification. Calcium chemistry is relatively simple because there is only one primary ionic species of this element, although various neutral and charged complexes of the divalent ion are known to exist in seawater (Kennish, 1994). In contrast, carbonate chemistry is much more complex because it involves a gaseous form and both ionic and neutral species as well as complexed forms in seawater.

Carbonate chemistry

Dissolved inorganic carbon (DIC) comprises 3 species: dissolved [CO.sub.2] ([CO.sub.2] + [H.sub.2][CO.sub.3]) as well as bicarbonate ([MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]) and carbonate ions ([MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]):

(1) [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]

The distribution of these species is set by the two equilibrium constants that describe the acid/base reactions of inorganic carbon in seawater:

(2a) [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]

(2b) [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]

Where [X] is the total (free + complexed) concentration of component X in seawater, and [K.sub.1] and [K.sub.2] are the equilibrium constants which depend on temperature, salinity and pressure (Dickson and Millero, 1987; Roy et al., 1993). These two equations have several implications for chemical dynamics. First, any change in temperature induces a change in K1 and K2 and therefore modifies the chemical speciation. Second, the speciation strongly depends on pH (pH = -[log.sub.10] [[H.sup.+]]). For `standard' surface seawater pH condition (ca. 8 to 8.25), the respective contributions of [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] and [CO.sub.2] are approximately 90%, 10%, and [is less than] 1%. Third, any biological or chemical process that consumes or releases one of the three inorganic carbon species changes the speciation as a result of ultimate control by these thermodynamic equilibrium constants.

In addition to its dynamics in solution, inorganic carbon also interacts with both the gaseous and solid phases according to the following thermodynamic constants:

(3) [K.sub.0] = p[CO.sub.2]/[[CO.sub.2]] and

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

(4) [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]

Where [K.sub.0] is the solubility constant of dissolved [CO.sub.2], [K.sub.s] is the solubility constant of the carbonate mineral considered, and [M.sub.2+] is the metal involved (e.g., [Ca.sup.2+] or [Mg.sup.2+]). These constants also depend on temperature, salinity and pressure. In contrast with the dynamics in solution, equilibrium with the gas and solid phases is seldom achieved in seawater. Surface seawater is often under- or super-saturated with respect to atmospheric [CO.sub.2] on short time scales (e.g., diel) and local spatial scales, because processes that modify the dissolved [CO.sub.2] concentration are faster than the time required to restore equilibrium through air-sea [CO.sub.2] exchange. However, at larger scales of both space and time, the surface mixed layer remains close to equilibrium with the atmospheric [CO.sub.2] concentration; this equilibrium permits estimation of the overall effects of atmospheric concentration change on marine biomineralization. Also, surface seawater is super-saturated with respect to both calcite and aragonite, the two major forms of calcium carbonate, down to a depth of a few thousand meters (reviewed in Morse and Mackenzie [1990]). Each solid carbonate is characterized by a saturation state ([Omega]) defined as:

(5) [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]

where a value of unity means saturation equilibrium (100% saturation). Values greater than 1 indicate supersaturation. The typical present-day oceanic aragonite and calcite saturation states are ca. 4 and 6.1 for `standard' surface seawater at 25 [degrees] C (salinity = 35, p[CO.sub.2] = 360 [micro]atm, and total alkalinity = 2,350 [micro]eq [kg.sup.-1]).

Increased atmospheric p[CO.sub.2] and temperature, both of which are expected as global climatic changes, have opposite effects on the saturation state (Fig. 1). Increased concentration of dissolved [CO.sub.2] results in a decreased carbonate concentration and, therefore, a decreased saturation state. Increased temperature results in a decreased Ks, and an increase in [Omega]. The chemical forcing (p[CO.sub.2] change) is far more important than the physical forcing (temperature change). According to the mid-range estimates of the International Panel on Climate Change (Houghton et al., 1996), the aragonite and calcite saturation states of tropical surface seawater will decrease by 39% from 1880 to 2100 (Table 1).

[Figure 1 ILLUSTRATION OMITTED]

TABLE 1. Carbonate chemistry of tropical surface seawater in glacial and interglacial periods.(*)

	Glacial	Pre-industrial	Present
Temperature ([degrees] C)	25	27	27
Salinity	35	35	35
pH (SWS)	8.29	8.16	8.08
TA ([micro] eq [kg.sup.1])	2,457	2,350	2,350
p[CO.sub.2] ([micro] atm)	200	280	360
[HCO.sub.3] ([micro] mol [kg.sup.1])	1,566	1,613	1,708
[MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]	370	305	266
DIC ([micro] mol [kg.sup.1])	1,942	1,925	1,983
[Omega] aragonite	5.87	4.88	4.26
[Omega] calcite	8.91	7.36	6.42

	Year 2065	Year 2100
Temperature ([degrees] C)	28.2	29
Salinity	35	35
pH (SWS)	7.92	7.83
TA ([micro] eq [kg.sup.1])	2,350	2,350
p[CO.sub.2] ([micro] atm)	560	706
[HCO.sub.3] ([micro] mol [kg.sup.1])	1,845	1,908

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

[MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]	210	184
DIC ([micro] mol [kg.sup.1])	2,070	2,110
[Omega] aragonite	3.38	2.98
[Omega] calcite	5.08	4.46

(*) The parameters shown in bold were used to compute the parameters shown in standard fonts. TA during the glacial time is from Broecker and Peng (1982). Values for p[CO.sub.2] was well as future increase of temperature in 2065 and 2100 are the mid-range estimates (IS95a) of the International Panel for Climate Change (Houghton et al., 1996). We assumed that surface seawater is fully equilibrated with atmospheric [CO.sub.2] and that the increase in temperature will be identical in air and seawater. TA was held constant at its pre-industrial value from the late 1800s onward. The [CO.sub.2] speciation and pH, on the seawater pH scale, were computed using the constants of Roy et al. (1993). The aragonite and calcite saturation states were calculated according to Mucci (1983).

Photosynthesis and calcification

Dissolved inorganic carbon is used by the animal host to deposit skeletal Ca[CO.sub.3] and by the endosymbiont for its photosynthesis. Photosynthesis, respiration (of the animal and algal components) and calcification can take place simultaneously according to the following simplified equations:

(6) [CO.sub.2] + [H.sub.2]0 [right arrow] [CH.sub.2]O + [O.sub.2] (photosynthesis)

(7) [CH.sub.2]O + [O.sub.2] [right arrow] [CO.sub.2] + [H.sub.2]O (respiration)

(8) [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]

Photosynthesis and calcification both consume inorganic carbon (eqs. 6 and 8) but the combined processes can also be viewed as mutually supporting because [CO.sub.2] generated by calcification can be used for photosynthetic carbon fixation.

Photosynthesis is higher than respiration during most of the daylight period; the resulting sum of eqs. 6-8 is then:

(9) [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]

Whereas at night the equations combine to:

(10) [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]

Eqs. 9 and 10 hold in freshwater only because the ratio of [CO.sub.2] released/Ca[CO.sub.3] precipitated ([Psi]), which is close to 1 in freshwater, is approximately 0.6 in standard seawater due to its buffering capacity (Frankignoulle et al., 1994). The amount of [CO.sub.2] generated by marine calcification that can potentially be used by photosynthesis is therefore lower than suggested by the stoichiometry of eq. 9.

CELLULAR PATHWAYS OF CALCIUM AND CARBON

Coral polyps are organisms whose anatomy can be simply compared to a "bag" enclosing a coelenteric (=gastrovascular) cavity open to the surrounding seawater by the mouth. The coelenteric cavities of neighboring polyps are connected. In actual fact, the "bag" is far from simple; its shape conforms to the complex skeletal structure of the calyx, it is partially compartmentalized by mesenteries, and tentacles, and it contains cilia that are capable of inducing water movement. The walls of the polyp are made of two single-cell-thick epithelial layers, the ectoderm (epidermis) and the endoderm (gastrodermis), separated by a thin connective layer, the mesoglea. The oral ectoderm (which includes the body wall at the oral, as opposed to basal, end of the organism as well as the tissues of the mouth itself) is in contact with the external

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

seawater and the aboral ectoderm is in contact with the calcium carbonate skeleton. Both the oral and the aboral endoderm are in contact with the fluid in the coelenteric cavity. These relationships are illustrated for the coenosarc, the region located between the polyps, in Figure 2.

[Figure 2 ILLUSTRATION OMITTED]

The processes of calcification and photosynthesis are spatially separated (Vandermeulen and Muscatine, 1974). Skeletogenesis is performed by the ectodermal cells of the aboral layers, the calicoblastic epithelium, whereas photosynthesis is carried out by zooxanthellae which are mainly located in the endodermal cells of the oral layers. The distance separating the sites of photosynthesis and calcification is at least 25 [micro]m. The calicoblastic cells are long (10 to 100 [micro]m) in the direction parallel to the skeletal surface, thin (0.5 to 3 [micro]m) in the dimension normal to that surface, highly digitate (Johnston, 1980; E. Tambutte and D. A., unpublished data), and attached to the skeleton by desmocytes (Muscatine et al., 1997).

The composition of the coelenteric fluid is influenced by photosynthesis, by calcification, by advective exchange of seawater through the mouth and/or by transepithelial transport mechanisms (Fig. 3). Wright and Marshall (1991) have argued that water exchange through the mouth is probably too small to supply the amounts of calcium and bicarbonate ions required for coral calcification and photosynthesis, but there are no data to confirm this hypothesis, and the results of Tambutte et al. (1996) indicate rapid coelenteron equilibration with the external seawater that would be consistent with both passive transport through oral layers and advective exchange. The fact that such equilibration is not dependent on cellular energy (cyanide insensitive) argues in favor of a passive pathway. Whether or not such exchange occurs with the coelenteron, transepithelial ion fluxes through transcellular and/or paracellular pathways, are required to provide material fluxes to and from the sites of photosynthesis and calcification. The transcellular pathway involves membrane protein (carriers) and at least one energy-dependent step, either uptake by or efflux from the cell, depending on the electrochemical potential of the transported molecule. The paracellular pathway is driven by molecular diffusion through the lateral cell junctions that enable attachment of cells among themselves, although there is some evidence that suggests the possibility of advective transport (discussed below). Different septate desmosomes (Green and Flower, 1980; Holley, 1985) and tight junctions (Vandermeulen, 1975; Kinchington, 1980) have been described for the two layers of actinians, suggesting that they exhibit different permeability characteristics.

[Figure 3 ILLUSTRATION OMITTED]

Benazet-Tambutte et al. (1996b) demonstrated that the oral epithelial layers of the coral Heliofungia actiniformis and the sea anemone Anemonia viridis are "leaky," i.e., transepithelial transport is essentially achieved by a diffusional paracellular pathway. High permeability is restricted to small ions such as [Na.sup.+], [Cl.sup.-] and [Ca.sup.2+]. Larger molecules such as amino-acids do not cross the oral epithelial layers. Low water permeability (Benazet-Tambutte and Allemand, 1997) is probably an adaptation to maintain a positive intracoelenteric hydrostatic pressure (Batham and Pantin, 1950).

The pathways of calcium and inorganic carbon molecules are reviewed in the next two sub-sections. There are relatively few studies of ion transport in zooxanthellate scleractinian corals. We will use additional data collected in taxonomically-related groups such as octocorals and actinians, bearing in mind that these groups have different evolutionary lineages and environmental preferences. The calcium pathways, which are better known and simpler in many ways than the carbon pathways, are reviewed first. Because of the limited number of relevant studies, the findings reviewed relate to a variety of organisms--different taxa, both calcifying and non-calcifying, with a wide range of phyologenetic relationships. The assumption inherent in this approach is that the mechanisms and structures involved are the same or very similar across the wide range of organisms considered. This review process is thus a mechanism for hypothesis development; to the extent that contradictions among studies appear, the assumption is questionable and new hypotheses are needed.

A specific example of this hypothesis-oriented approach is the fact that the review of laboratory experiments suggests that the concentration of calcium, and possibly of other ions as well, in the extracytoplasmic calcifying fluid (ECF) is controlled

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

by the calicoblastic epithelium, and depends on active, transcellular transport mechanisms. Such control is not in agreement with the fact that corals from a wide variety of taxa and locations have been shown to produce skeletal records of factors affecting seawater Sr, Cd, Pb, Mn, Ba, and U, suggesting relatively free passage of elements between seawater and the ECF (reviewed by Dunbar and Cole, 1993).

Strontium is the minor skeletal component that has been most studied but conflicting results were obtained. Chalker (1981) concluded that Sr is transported via a transcellular, carrier-mediated pathway, in Aeropora cervicornis. He also showed that a competition for the transport exists between [Sr.sup.2+] and [Ca.sup.2+], suggesting that skeletal Sr and Ca are not in equilibrium with seawater. Ip and Krishnaveni (1991) found opposite results in Galaxea fascicularis and suggested a paracellular transport pathway for [Sr.sup.2+]. This differs from the transport mechanisms of [Ca.sup.2+] discussed below, which might help to explain the discrepancies observed between skeletal Sr/Ca and [[Delta].sup.18]O, two proxies of temperature (Boiseau et al., 1997). More information on the transport of trace elements and stable isotopes is therefore required in order to reconcile the laboratory experiments with the field observations.

Calcium pathways

The mechanisms of calcium transport for calcification in corals are poorly known, as is the case in other invertebrates (Simkiss and Wilbur, 1989). Potential pathways of calcium from the surrounding seawater to the coelenteron and to the site of skeletogenesis are shown in Figure 3A. Calcium ions can reach the ECF by transcellular transport (energy-dependent), by paracellular diffusion and possibly by advection (both are energy-independent), or a combination of all processes.

An active process is involved in the incorporation of calcium into the coral skeleton (Chalker and Taylor, 1975; Chalker, 1976; Tambutte et al., 1996). It follows a saturable kinetics with respect to external calcium concentration, implying an enzyme-mediated step (Chalker, 1976; Krishnaveni et al., 1989; Tambutte et al., 1996). At ambient seawater [Ca.sup.2+] concentration (ca. 10 mM), the rate of calcification is saturated in some species (Chalker, 1976; Tambutte et al., 1996) but not in others (Chalker, 1976; Krishnaveni et al., 1989). Calcium limitation of skeletogenesis, as was proposed by Chapman (1974), can therefore occur.

The [Ca.sup.2+] transepithelial pathway involves at least one transcellular mechanism (e.g., Marshall, 1996a; Tambutte et al., 1996) but there are conflicting results on the location of the active calcium transport. Wright and Marshall (1991) suggested it occurs across both the oral and aboral epithelia. Active transport across oral layers is not consistent with the results of [sup.45][Ca.sup.2+] efflux experiments which showed that equilibrium of the coelenteron of Stylophora pistillata with external seawater results from passive transport (Tambutte et al., 1995a). Also, oral epithelia of the coral Heliofungia actiniformis are leaky with respect to divalent ions (Benazet-Tambutte et al., 1996b) and fluxes into the coelenteron does not appear to limit the incorporation [sup.45][Ca.sup.2+] in the skeleton (Benazet-Tambutte et al., 1996b; Tambutte et al., 1996). Tambutte et al. (1996) showed, using a compartmental approach, that [sup.45][Ca.sup.2+]is incorporated into the skeleton of the coral Stylophora pistillata after a lag of less than 2 min from which they infered a very fast equilibration with seawater calcium and the absence of a large calcium pool for calcification. Uptake and efflux experiments indicate that there is only one transcellular, energy-dependent step of calcium transport, located in the calicoblastic epithelium. The other steps result from rapid paracellular pathways (Tambutte et al., 1996).

Although the concentration of free calcium is at least 100,000 times lower in cells than in seawater (10-100 nM vs. 10 mM), calcium does not diffuse freely into the cell, and specialized transport proteins, [Ca.sup.2+] channel and/or cation antiporter, are required to mediate [Ca.sup.2+] entry across the lipid bilayer of the aboral ectoderm. The pharmacological properties of the coral [Ca.sup.2+] channel are typical of an L-type of voltage-dependent [Ca.sup.2+] channel (Tambutte et al., 1996). The [Alpha]l subunit of this protein was cloned and immunolocalized on the calicoblastic epithelium (Zoccola and Allemand, 1996; Zoccola et al., in press). This subunit cannot be assigned to one of the known L-type subfamilies but it has an 86% similarity in the amino-acid sequence with the rabbit [Alpha]1C subunit.

Once inside the calicoblastic cells, [Ca.sup.2+] ions must be sequestered in vesicles or organelles and/or bound to [Ca.sup.2+]-binding proteins in order to maintain a low free intracellular concentration (Bronner, 1990).

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

[Ca.sup.2+]-binding substances have been isolated from the skeletal organic matrix (Isa, 1986; Isa and Okazaki, 1987) but the role of such compounds remains to be investigated in calicoblastic cells. Vesicles within the calicoblastic cells do not contain calcium (Kinchington, 1980), in spite of previous reports of vesicles containing electron dense material (Kawaguti and Sato, 1968), "crystals" (Hayes and Goreau, 1977; Goreau and Hayes, 1977) or of [Ca.sup.2+]-rich cytoplasm (Vandermeulen, 1975). Transcellular [Ca.sup.2+] transport through vesicles is suggested by the sensitivity of calcification to inhibitors of cytoskeleton polymerization (Kinchington, 1980; Tambutte et al., 1996). However, it has been shown recently that the cytoskeletal-dependent step of calcification is the exocytosis of organic matrix-containing vesicles rather than the intracellular [Ca.sup.2+] transport (Allemand et al., 1998b).

Calcium exit from the calicoblastic cells may occur by two mechanisms: [Na.sup.+]/[Ca.sup.2+] exchanger (Marshall, 1996a) and [Ca.sup.2+]ATPase (Isa et al., 1980). The [Ca.sup.2+] affinity of the [Ca.sup.2+]-ATPase investigated by Isa et al. (1980; 700 [micro]M) is too high to account for a plasma-membrane [Ca.sup.2+]-ATPase, whose affinity is generally well below 1 [micro]M (Carafoli, 1987). More recently, Ip et al. (1991) isolated two components of a [Ca.sup.2+]-sensitive ATPase in the coral Galaxea fascicularis. These two components have distinct affinities (150 and 2.1 [micro]M). The low affinity component is likely a plasma-membrane [Ca.sup.2+]-ATPase but it is unknown whether it is the one that accounts for the exit of [Ca.sup.2+] from the calicoblastic cells. One intriguing point, which has never been explored, is the coupling mechanism between [Ca.sup.2+] uptake and [Ca.sup.2+] efflux that is required to maintain a low [Ca.sup.2+] concentration in calicoblastic cells despite large transepithelial [Ca.sup.2+] fluxes.

McConnaughey (1991, 1995; see also McConnaughey and Whelan, 1997) suggested that the [H.sup.+] generated by Ca[CO.sub.3] precipitation was removed by a [Ca.sup.2+]-ATPasemediated 1[Ca.sup.2+]/2[H.sup.+] exchanger. A constant pumping of [H.sup.+] from the site of skeletogenesis to the coelenteron must occur but how such a large flux is achieved in the cytoplasm of the aboral epithelial cells without disrupting the intracellular pH remains unknown.

Carbon pathways

The preferred DIC substrate for coral photosynthesis is external [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] (Land et al., 1975; Goreau, 1977; Al-Moghrabi et al., 1996; Goiran et al., 1996), although it has been suggested that [CO.sub.2] is a major source (Taylor, 1983). DIC transport for photosynthesis of zooxanthellate Anthozoa is reviewed by Allemand et al. (1998a). The DIC reservoir used by free-living algae is seawater, while the immediate source used by zooxanthellae is that in the coral host cell, which is derived to a significant extent from the external seawater. Possible transepithelial pathways are shown in Figure 3B. Carbon supply is saturated at ambient DIC concentrations in corals (ca. 2.2 mM; Burris et al., 1983; Goiran et al., 1996). The relatively high affinity (i. e., concentration at which half-saturation is achieved) of photosynthetic 02 release for inorganic carbon (Burris et al., 1983; Goiran et al., 1996) strongly suggests that a carbon concentrating mechanism (CCM)-like system, which actively absorbs [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] to sustain photosynthesis, operates in the animal host, as previously hypothesized by Raven (1992). Ribulose biphosphate carboxylase-oxygenase (Rubisco) is an enzyme that catalizes net photosynthetic carbon fixation that also exhibits a high affinity for oxygen, which decreases its photosynthetic efficiency. Rubisco is a form II enzyme in dinoflagellates (Morse et al., 1995; Whitney et al., 1995). This form, usually restricted to anaerobic proteobacteria, has a high affinity for [0.sub.2] that prevents net fixation of carbon in an aerobic environment. The presumably high [CO.sub.2] concentration near Rubisco due to a CCM-like activity could favor the carboxylase function of the enzyme at the expense of its oxygenase function (Rowan et al., 1996).

Al-Moghrabi et al. (1996) and Goiran et al. (1996) demonstrated that the uptake of [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] by the host cell involves two anion carriers that are sensitive to DIDS, an inhibitor of anion transport. One of them is either a [Na.sup.+]-dependent Cl-/[MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] exchanger or a [Na.sup.+]/[MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] cotransporter. The nature of the second carrier is not clear. DIC is supplied to zooxanthellae by a transepithelial active mechanism present in both endodermal and ectodermal cells of the oral layers of the temperate zooxanthellate sea anemone Anemonia viridis (Benazet-Tambutte et al., 1996a; Furla et al., 1998a, b). Within the endodermal cell, [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] is dehydrated into [CO.sub.2] the substrate of Rubisco. The transepithelial transport of [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] generates, under light conditions, a net efflux of OH

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

(or net [H.sup.+] uptake) into (or from) the coelenteric cavity resulting in a pH gradient of about 0.8 unit across the tentacle of the anemone (Furla et al., 1998a, b). If this process occurs in corals, it could represent a portion of the mechanism by which [H.sup.+] ions produced by Ca[CO.sub.3] precipitation are buffered, maintaining the high levels of aragonite saturation state that are needed to sustain calcification.

There are very limited data on the source and transport mechanisms of the inorganic carbon used for coral calcification. Radioisotopic tracer experiments demonstrate that DIC from seawater can be incorporated into the skeleton (Goreau 1961, 1963; Taylor, 1983). However, the observation that the skeletal [[Delta].sup.13]C isotopic ratio is different from the one in seawater (e.g., Keith and Weber, 1965) suggests that a DIC source other than external seawater can also be used. Feeding with [sup.14]C-labelled food provided direct evidence that some [CO.sub.2] generated by host respiration is deposited in the skeleton as carbonate (Pearse, 1970, 1971). Goreau (1977) estimated, from stable isotope data, that approximately 40% of the carbon supply is from seawater DIC and 60% from recycled metabolic [CO.sub.2]. Erez (1978) showed, using double labelling experiments ([sup.14]C and [sup.45]Ca), that the skeletal ratio of [sup.14]C/[sup.45]Ca ranges from 0.1 to 0.5 in the light suggesting that the major part (50 to 90%) of the skeletal carbon originates from metabolic [CO.sub.2] in the species (S. pistillata and A. variabilis) and under the conditions studied. Lucas and Knapp (1997) obtained similar results with the spicules of the non-zooxanthellate octocoral Leptogorgia virgulata. Goreau (1961) suggested that DIC supply may be rate-limiting in calcification. Such limitation has been observed in the temperate non-symbiotic octocoral, Corallium rubrum (Allemand and Grillo, 1992) but there are no data available for scleractinian corals. However, the discussion of saturation state effects (above) indicates that carbonate ion concentration can be limiting; if pH is held constant, this translates into a DIC limitation.

More than one [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] transport mechanism is probably involved in calcification. Tambutte et al. (1996) showed that DIDS inhibits the rate of calcification in the scleractinian coral, Stylophora pistillata by up to 95%, both in the light and in the dark. This indicates that the anion-carrier mechanism is the rate-controlling process, but does not prove the absence of other pathways. Lucas and Knapp (1997) found that DIDS does not completely inhibit calcification in the non-zooxanthellate octocoral L. virgulata, suggesting that [CO.sub.2] can reach the site of skeletogenesis by a passive transport pathway and be used as a substrate for calcification. Carbonic anhydrase, an enzyme located in the calicoblastic epithelium (Isa and Yamazato, 1984), catalyzes the conversion of respiratory [CO.sub.2] into [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII], as demonstrated by inhibition experiments (Goreau, 1959; Tambutte et al., 1996).

INTERACTIONS BETWEEN PHOTOSYNTHESIS AND CALCIFICATION

The first indication of a possible link between zooxanthellar photosynthesis and coral calcification is probably the finding by Kawaguti and Sakumoto (1948) that calcification is higher in the light than in darkness. The analysis of 108 data compiled from 26 publications provides overwhelming evidence that calcification in the light is significantly higher than calcification in the dark. The ratio of light:dark calcification ranges from negative values (Ca[CO.sub.3] dissolution has been observed in 4% of the observations) to 127 (Fig. 4). Skeletal dissolution, which is not related to calcification, has not been found in corals since the early measurements of the 1940s. Only 9% of the observations are in the range 0-1 (calcification higher in the dark than in the light), 71% are in the range 1-5, and 15% of the ratios are higher than 5. The median ratio is 3.0. These data were collected using various techniques (e.g., [sup.14]C and [sup.45]Ca fixation, buoyant weight and alkalinity anomaly techniques), under a wide range of environmental (e.g., light, temperature, pH, [pO.sub.2] and p[CO.sub.2]) and biological (e.g., feeding) conditions, both in situ and in the field, which probably accounts for the wide range of variation. The site of Ca[CO.sub.3] deposition is also different between light and dark periods (Marshall and Wright, 1998), but it is likely that the same transport mechanisms are used (Marshall, 1996a; Marshall and Wright, 1998).

[Figure 4 ILLUSTRATION OMITTED]

Mechanisms invoked to explain the higher rate of calcification in light than in darkness include the uptake by zooxanthellae of animal metabolic wastes (Yonge, 1968; Crossland and Barnes, 1974) or of substances interfering with Ca[CO.sub.3] precipitation (Simkiss, 1964); the translocation of photosynthate to fuel active transport mechanisms (Chalker and Taylor, 1975) or to synthesize the organic matrix (Wainwright, 1963); the increase of Ca[CO.sub.3]

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

saturation by photosynthetic [CO.sub.2] uptake (Goreau, 1959); and the maintenance of an oxic environment (Rinkevich and Loya, 1984; Rands et al., 1992). It remains unclear as to which of these mechanisms (or set of thereof) is involved. It was nevertheless generally accepted, until recently, that calcification was light-enhanced during the day (see Barnes and Chalker, 1990). However, Marshall (1996a) measured similar rates of calcification in a non-zooxanthellate coral and in a zooxanthellate coral incubated in the light and argued that calcification is not light enhanced in zooxanthellate corals but, rather, that it is dark-repressed. This view has been subsequently challenged by several authors who pointed out some limitations in Marshall's results, especially with regard to the normalization of the data (Carlon, 1996; Goreau et al., 1996). There is, additionally, valuable information on the rate of calcification of colonies of the same species harboring a normal or a reduced density of zooxanthellate, whether naturally occurring or artificially obtained (for convenience the latter colonies will be referred to as nonzooxanthellate hereafter). Calcification in light is higher in zooxanthellate than in non-zooxanthellate specimens (Goreau, 1959; Goreau and Goreau, 1959; Jacques et al., 1977; Jacques and Pilson, 1980; Jacques et al., 1983; Kajiwara et al., 1995), with a ratio from 1.1 to 19 (median = 1.9), observations that cannot be explained by a dark-repression mechanism. Rates of dark Ca[CO.sub.3] precipitation are more equivocal as the zooxanthellate:non-zooxanthellate calcification ratio ranges from 0.9 to 3.1. Therefore, at least in some species and/or under some experimental conditions, the presence of zooxanthellae slightly enhances, not repress, calcification in darkness.

Interaction at the cellular level

There are two major hypothesis regarding the interactions between photosynthesis and calcification at the cellular level. In the first one, photosynthetic [CO.sub.2] uptake lowers the extracellular [CO.sub.2] partial pressure in the coral tissue, which increases carbonate saturation and favors precipitation of Ca[CO.sub.3] (Goreau, 1959, 1961). In the second model (trans calcification; McConnaughey, 1991, 1995; McConnaughey and Whelan, 1997), [Ca.sup.2+]-ATPase supplies [Ca.sup.2+] to and removes [H.sup.+] from the site of calcification (stoichiometry: 1[Ca.sup.2+]/2[H.sup.+]). In the coelenteron, protons may generate [CO.sub.2] by dehydrating [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]. This mechanism favors (1) Ca[CO.sub.3] precipitation by maintaining an elevated pH of the extracytoplasmic calcifying fluid and (2) photosynthesis by increasing the coelentric [CO.sub.2] reservoir. These two models imply a high concentration of bicarbonate in the coelenteron to buffer calcification-induced [H.sup.+]. The coelenteric [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] pool has never been measured in corals but it becomes quickly depleted during the day in the sea anemone A. viridis (Benazet-Tambutte et al., 1996a; Furla et al., 1998a, b).

The validity of the trans calcification mechanism was tested using various approaches. Decreased calcium seawater concentration inhibits photosynthesis in corals (McConnaughey, 1994 and personal communication; Al-Moghrabi et al., 1996), foraminiferan (Kuile et al., 1989a), coccolithophorids (Brownlee et al., 1994), and calcareous macroalgae (McConnaughey 1991; McConnaughey and Falk, 1991). A similar result was obtained in the coral Galaxea fascicularis using a calcium-channel inhibitor (Al-Moghrabi et al., 1996). In contrast, an inhibitor of mineral deposition (HEBP) inhibits coral calcification by 99% without any effect on the rate of photosynthesis (Yamashiro, 1995). Similarly, protein-synthesis inhibitors decrease coral calcification by 60 to 85% without disturbing photosynthesis (Allemand et al., 1998b). In coccolithophorids, the decrease of photosynthesis in low-calcium seawater could result from a direct inhibition of [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] transport rather than from an effect mediated by the inhibition of calcification (Brownlee et al., 1994). The inhibition of coral photosynthesis by verapamil increases linearly for concentrations ranging from 0 to 250 [micro]M (Al-Moghrabi et al., 1996), whereas calcification is almost totally inhibited at a concentration of 100 [micro]M (Tambutte et al., 1996). This suggests that photosynthesis does not depend on calcification for carbon supply.

Photosynthesis and calcification could also compete for a single DIC pool as shown in a symbiont-bearing foraminiferan (Kuile et al., 1989b). The inhibition of calcification should make more inorganic carbon available for photosynthesis and stimulate photosynthesis. As mentioned above, such response as not been observed (Yamashiro, 1995; Al-Moghrabi et al., 1996). This supports the concept of complementarity rather than competition for carbon between photosynthesis and calcification (Taylor, 1983).

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

The endodermal cell layer of Anemonia viridis secretes [OH.sup.-] in the light and generates a pH gradient of about 0.8 units across the epithelial layers, with the endodermal side (i.e., the coelenteric cavity) being alkaline (Furla et al., 1998b; Allemand et al., 1998a). Such secretion of OH- could neutralize the [H.sup.+] generated by coral calcification, providing an alternative explanation to Goreau's hypothesis that photosynthesis stimulates calcification by removing by-products.

Interactions at the organism level

It has been suggested, on the basis of eq. 9, that photosynthetic and calcifying plants, symbiotic animals and ecosystem often display ratios of calcification to photosynthesis (G/P) close to 1 (e.g., McConnaughey and Whelan, 1997). In the literature, it is not always reported whether [P.sub.g], [P.sub.n], or an undefined production value (when photosynthesis is measured using the [sup.14]C fixation technique) is considered. Furthermore, these production estimates are sometimes examined together (e.g., McConnaughey, 1994; McConnaughey and Whelan, 1997). G/[P.sub.n], relates to the amount of [CO.sub.2] that can potentially be supplied by calcification to the [CO.sub.2] required by net photosynthesis (i.e., taking into account the [CO.sub.2] supplied by respiratory processes). The G/[P.sub.g] ratio is difficult to analyze because [P.sub.g] is not known accurately for either corals or reef communities, as it is derived from [P.sub.n], and R, the night-time respiration. Such a procedure underestimates Ps, and overestimates G/[P.sub.g] because respiration has been shown, at least in corals, to be significantly higher during the day than at night (e.g., Kuhl et al., 1995).

Yamashiro (1995) measured the rates of photosynthesis ([sup.14]C fixation) and calcification at three irradiances and showed that the G/P ratio decreases as a function of increasing irradiance. There are, however, very few data available on the relationship between photosynthesis and calcification over a diel cycle in zooxanthellate corals. Data obtained on a colony of Stylophora pistillata (S. Romaine-Lioud and J.-P.G., unpublished data) can be used to study the relationship between G and P during the course of 24-hr. These data are limited to one species under certain conditions, but they provide insight into the interaction between P and G at the organism level. Peak net photosynthetic [CO.sub.2] fixation and net Ca[CO.sub.3] precipitation are, respectively, 160 and 176 [micro]mol [CO.sub.2] [(mg Chl-a).sup.-1] [hr.sup.-1] [CO.sub.2] uptake by net photosynthesis under saturating irradiance is significantly higher than the concurrent [CO.sub.2] release by calcification (ca. 160 vs. 106 [micro]mol [CO.sub.2] [(mg Chl-a).sup.-1] [hr.sup.1]; Fig. 5). An additional source of inorganic carbon (from external seawater) is therefore required to sustain photosynthetic [CO.sub.2] fixation.

[Figure 5 ILLUSTRATION OMITTED]

An analysis of data from the literature confirms the wide range of variation of the molar G/[P.sub.g] (0.2 to 1.5; median = 0.6) and G/[P.sub.n] (-8 to 17; median = 1.3) ratios (Fig. 6). The median G/[P.sub.n], ratio of 1.3 indicates that [CO.sub.2] generated by Ca[CO.sub.3] deposition (0.6 times net calcification) could potentially supply 78% of the inorganic carbon required for zooxanthellar photosynthesis. As discussed earlier, the actual significance of this DIC source remains unclear.

[Figure 6 ILLUSTRATION OMITTED]

Interactions at the community level

Reef metabolic data have recently been reviewed by Gattuso et al. (1998b). Coral/ algal reef flats exhibit wide ranges of community gross primary production ([P.sub.g],: 79584 mol C [m.sup.-2] [yr .sup.-1]), respiration (R: 76538 mol C [m.sup.-2] [yr.sup.-1]), and net calcification (G: 5-126 mol Ca[CO.sub.3] [m.sup.-2] [yr.sup.-1]). Such variability is mostly due to differences in the community structure of the sites investigated (e.g., Pichon, 1997). For example, it is well established that community primary production increases and community calcification decreases with increasing surface cover of fleshy algae (e.g., Smith, 1973). Community metabolism data have been compiled from the literature and distributed in the categories defined by Kinsey (1985). Overall, G and [P.sub.g] are significantly correlated and the G/[P.sub.g] estimated as the slope of the geometric regression, is 0.2 (Fig. 7 and Table 2). However, no significant correlation is found when the various categories are examined separately, except for algal-dominated areas. An opposite trend (i.e., decrease in G with increasing [P.sub.g]) is observed in three of the systems examined (lagoons, algal pavements, and whole reefs). Nevertheless, most daily G/[P.sub.g] ratios are distributed in the range 0.1-0.4 in the

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

various communities and ecosystems, and they rarely exceed 0.5 (data not shown). The suggestion that G/[P.sub.g] = 1 in photosynthetic and calcifying communities (e.g., McConnaughey, 1994) is therefore not supported by the relevant literature.

[Figure 7 ILLUSTRATION OMITTED]

TABLE 2. Correlation between the rates of community gross primary production and calcification of coral reef ecosystems and communities, and median value of the G/[P.sub.g] ratio.(*)

Community	Correlation coefficient	N	P	Median of G/[P.sub.g]
Overall	0.49	52	0.000	0.2
Algal-dominated zones	0.98	4	0.02	0.0
Whole reefs	0.67	5	0.09	0.2
Lagoons	0.82	4	0.18	0.1
Sediments	0.63	4	0.21	0.1
High activity areas	0.43	4	0.18	0.2
Reef flats	0.10	29	0.61	0.1
Algal pavements	-	2	-	0.4

(*) Categories of communities defined by Kinsey (1985). N = sample number; P = probability. The data set is available from JPG.

Daily calcification and net community production at various sites are not significantly correlated, but short-term data obtained at the same site are strongly correlated. For example, G and [P.sub.n] have recently been estimated on two Pacific reef fiats using a Lagrangian technique (Gattuso et al., 1996b). Both processes are significantly correlated, with a G/[P.sub.n], ratio of about 0.1 at both sites (Fig. 8). The ratios estimated at the same sites using an Eulerian technique are higher (0.37 and 0.24; Frankignoulle et al., 1996). Both estimates clearly show that the [CO.sub.2] generated by community calcification is not the major source of inorganic carbon sustaining net community production when the water residence time is short. The large decrease in p[CO.sub.2] measured in such systems during the day (down to ca. 250 [micro]atm; Frankignoulle et al., 1996) demonstrates that DIC is drawn from the seawater reservoir and, to a much lesser extent, from the invasion of atmospheric [CO.sub.2]. It has been proposed, based on both theoretical considerations (Smith, 1985) and data from non-reefal systems (e.g., Smith and Veeh, 1989), that organic production tightly controls calcification when the residence time is longer (ca. 1 year), pH and Ca[CO.sub.3] saturation rise when the net community production exceeds the invasion of atmospheric [CO.sub.2]. Calcification is therefore stimulated, increases p[CO.sub.2] and reduces the [CO.sub.2] invasion induced by the net organic carbon metabolism. The net air-sea [CO.sub.2] flux is close to zero in such systems as a result of this tight interaction between the organic and inorganic carbon metabolism.

[Figure 8 ILLUSTRATION OMITTED]

Despite the drawdown of [CO.sub.2] during the day, most reef flats are sources of [CO.sub.2] to the atmosphere, on a 24-hr basis, due to their low net fixation of [CO.sub.2] via photosynthetic processes (excess [=net] production close to 0) and rather large release of [CO.sub.2] by precipitation of calcium carbonate (Ware et al., 1992; Gattuso et al., 1993; Gattuso et al., 1995; Smith, 1995; Frankignoulle et al., 1996; Gattuso et al., 1996b). There is one notable exception: algal-dominated reef communities, which exhibit a larger community excess production and/or a lower community calcification, are sinks for atmospheric [CO.sub.2] (e.g., Kayanne et al., 1995; Gattuso et al., 1996a; Gattuso et al., 1997).

EFFECT OF GLOBAL ENVIRONMENTAL CHANGE: CARBONATE CHEMISTRY

The signs and magnitudes of many environmental changes that are expected in the next decades (Pittock, 1999) are similar to the current range of climatic variation within which reefs exist (Done, 1999; Kleypas et al., 1999), and are considerably less extreme than those experienced by reefs during geological history (Buddemeier and Smith, 1999;

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

Benzie, 1999 issue; Pandolfi, 1999). This suggests that existence of efficient adaptative mechanisms in reef organisms and the potential for the persistence of reef ecosystems. Reef ecosystems may respond to environmental change through alteration in their physical and ecological structure and through changes in rate constants of accretion and biogeochemical cycling (Gates and Edmunds, 1999; B. G. Hatcher, personal communication). However, the potential for adaptation of reef organisms may be overwhelmed, as present and predicted rates of change of some global climatic parameters and local non-climatic variables (e.g., nutrients) are unprecedented in the geological record.

Smith and Buddemeier (1992) identified the following major parameters that may affect the structure and function of coral reefs: sea level, temperature, p[CO.sub.2], ultraviolet (UV) radiation, hydrodynamics, sedimentation, salinity and nutrients. They also pointed out that some of these variables will change at a global scale (sea level rise and p[CO.sub.2]), some at a regional scale (temperature), and some at a local scale (nutrients). This section is deliberately focused on the response of the carbon and carbonate metabolism to changes in the carbonate chemistry driven by increasing p[CO.sub.2] and temperature. Reef response to other environmental variables have recently been reviewed by Smith and Buddemeier (1992), whereas the acclimation of scleractinian corals to environmental changes has been addressed by Brown (1997a, b) and Gates and Edmunds (1999). Additionally, a recent special issue of Global Change Biology (1996, 2(6)) is dedicated to global change issues in coral reefs, other specific information is available on UV (Dunlap and Shick, 1998) as well as on temperature and coral bleaching (Glynn, 1993, 1996; Brown, 1997c)

Response at the organism and community levels

Photosynthesis of marine phototrophs is generally not considered as carbon-limited due to the large pool of total inorganic carbon in the form of bicarbonate (Raven, 1997). This is only valid for phototrophs able to use bicarbonate effectively, i.e., species having a carbon-concentrating mechanism (CCM). Photosynthesis can be stimulated by [CO.sub.2] enrichment in species lacking a CCM or when the CCM is not operating. For example, short-term or long-term exposure of seagrasses to elevated [CO.sub.2] leads to a 3-fold increase of photosynthesis (Zimmerman et al., 1997). Similarly, some diatoms (Riebesell et al., 1993), macroalgae (Borowitzka and Larkum, 1976; Gao et al., 1993b), and microalgae (Nimer and Merrett, 1993) exhibit higher rates of photosynthesis under [CO.sub.2] enrichment. A decrease of pH at constant DIC concentration stimulates the rate of photosynthesis of [CO.sub.2]-users, whereas it inhibits that of [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]-users (Munoz and Merrett, 1989). Consequently, [CO.sub.2] enrichment should enable [CO.sub.2]-users to compete more effectively with [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]-users.

The available evidence indicates that coral symbiotic units as well as isolated zooxanthellae are [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] -users (Burris et al., 1983; Al-Moghrabi et al., 1996; Goiran et al., 1996). During short-term experiments, the rate of photosynthesis of the coral Galaxea fascicularis is not significantly different at pH 7.5 and 8.0. It is inhibited when pH is lower than 7.5, even when DIC is maintained at a constant concentration (Goiran et al., 1996); this is presumably due to pH effects on physiological and biological processes (Madshus, 1988) rather than on the DIC system. There is no information on the response of coral photosynthesis to long-term increase in DIC and p[CO.sub.2].

Until recently, carbonate chemistry was generally not considered to be an important parameter controlling calcification (see Smith and Buddemeier, 1992; Buddemeier, 1994) and there are limited data on the effect of the calcium carbonate saturation state ([Omega]) on Ca[CO.sub.3] deposition of photosynthetic and calcifying marine organisms and communities. There are four data sets on temperate and tropical coralline algae (Smith and Roth, 1979; Borowitzka, 1981; Agegian, 1985; MacKenzie and Agegian, 1989; Gao et al., 1993a), two data sets on scleractinian corals (Gattuso et al., 1998a; E Marubini and M. J. Atkinson, personal communication) and one on a coral reef community (Langdon et al., submitted). Techniques used to manipulate [Omega] were: changes in pH, p[CO.sub.2], DIC and calcium concentrations. Six out of 7 data sets clearly show a linear or curvilinear decrease in the rate of calcification as a function of decreasing [Omega] (over the range 0 to 6.2; Table 3). These data confirm that carbonate chemistry has a significant role in the control of calcification (see Gattuso et al., 1998a and references therein).

TABLE 3. Relationship between the relative rate of calcification (Y, % of the maximum rate measured) as a function of the

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

aragonite saturation state ([Omega]) of photosynthetic and calcifying marine organisms and communities.(*)

System	a	b	c	N
Bossiela orbigniana (temperate coralline alga)	77.2	0.24	16.8	6
Amphiroa foliacea (tropical coralline alga)	17.0	-0.99	-	5
Porolithon gardineri (tropical coralline alga)	14.5	28.5	-	15
Corallina pilulifera (temperate coralline alga)	44.5	-37.1	-	2
Stylophora pistillata (scleractinian coral)	226.5	0.69	127	5
Biosphere 2 reef mesocosm	21	-41.1	-	26
Porites compressa (scleractinian coral)	29.1	41.9	-	2

System	[r.sup.2]	Source
Bossiela orbigniana (temperate coralline alga)	0.95	Smith and Roth (1979)
Amphiroa foliacea (tropical coralline alga)	0.99	Borowitzka (1981)
Porolithon gardineri (tropical coralline alga)	0.87	Agegian (1985) and Mackenzie and Agegian 1989
Corallina pilulifera (temperate coralline alga)	1	Gao et al. (1993b) and K. Gao (personal communication)
Stylophora pistillata (scleractinian coral)	0.99	Gattuso et al. (1998a)
Biosphere 2 reef mesocosm	0.81 1	Langdon et al. (submitted)
Porites compressa (scleractinian coral)	1	F. Marubini and M. J. Atkinson (personal communication)

(*) In some instances the data were visually interpolated from figures. [Omega] was calculated according to Mucci (1983) using two parameters among the following: pH, TA, DIC and p [CO.sub.2]. The data were fitted, depending on the distribution of the data points, to a linear (Y = b + a [Omega]) or an exponential (Y = a (1 - exp(-[Omega]/b) + c) function using [Omega] values ranging from 0 to 6.2. N, number of data; [r.sup.2], coefficient of determination.

The curves described by the equations in Table 3 were used to predict the response of calcification to expected changes in (Fig. 9) calculated from the updated IPCC estimates of temperature and p[CO.sub.2] increases (Houghton et al., 1996; Pittock, 1999). The decrease of calcification in response to the predicted change of [Omega] was estimated for each individual relationship and averaged. [CO.sub.2] emission scenarios considered were: high (IS92e), mid (IS92a), and low (IS92c). It was assumed that the surface seawater and the atmosphere are in equilibrium with respect to [CO.sub.2] and that the increase in seawater temperature will be identical to the predicted increase in atmospheric temperature. According to these calculations, the rate of Ca[CO.sub.3] deposition of photosynthetic and calcifying marine organisms and communities may have been 10% higher in 1880 than in 1990, and may decrease by 9 to 30% (mid estimate: 22%) between 1990 and 2100 (Fig. 9). The rate of calcification can be expected to decrease by 15% by 2065, the year during which p[CO.sub.2] would be twice its pre-industrial value under the IS92a scenario.

[Figure 9 ILLUSTRATION OMITTED]

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

These estimates must be considered with caution. First, the database used in small (N = 5) and comprises a very limited number of taxa and communities. Second, although the effect of increased temperature on fl has been considered, its effect on metabolic processes has not and the synergistic effect of both changes remains to be investigated. Third, most studies were carried out in the short term (typically hours to weeks), and very little is known on the acclimation processes that may enable these organisms and communities to overcome the adverse effect of decreased [Omega]. Of special interest is the response of photosynthesis to [CO.sub.2] fertilization as it may partly offset the inhibition due to the decreased Ca[CO.sub.3] saturation state. Even though corals are bicarbonate users, a CCM-like system is costly in terms of energy; it might be possible that [CO.sub.2] use will increase, at it becomes more available, at the expense of [HCO.sub.3] use (Beardall et al., 1998). Increased p[CO.sub.2] could have other adverse effects such as to cause bleaching of corals and other symbiont-bearing reef invertebrates (Pecheux, 1993).

Corals are being increasingly used as sources of environmental information (Barnes and Lough, 1996), and data obtained from coral cores might be used to check whether calcification has decreased over the past century. Unfortunately, only one paper provides information on past coral calcification. Lough and Barnes (1997) reported that the annual rate of calcification of 35 cores of the massive coral Porites declined significantly over the period 1934-1982 but other, sometimes larger, declines occurred prior to that period in a subset of 10 cores. The calcification record is strongly correlated with temperature and no information is available on the contribution of other environmental factors to the observed changes in calcification.

What is the implication of changes in coral calcification in terms of the global carbon cycle? Calcification is known to be a source of dissolved [CO.sub.2] in the surrounding water due to chemical equilibria involved in the precipitation process (Wollast et al., 1980; Ware et al.,1992; Frankignoulle et al., 1995). The ratio of released [CO.sub.2] to precipitated carbonate ([Psi]) displays a positive feedback response to increasing p[CO.sub.2] (Frankignoulle et al., 1994). It will increase from its present value of 0.57 (for p[CO.sub.2] = 360 [micro]atm) to 0.69 for a p[CO.sub.2] of 706 [micro]atm (Tables 1 and 4). The increase of p[CO.sub.2] in surface seawater resulting from anthropogenic carbon release in the atmosphere has therefore two antagonistic effects on air-sea [CO.sub.2] fluxes. The p[CO.sub.2] of coral reef waters will generally be equilibrated with the higher atmospheric [CO.sub.2] levels, but non-atmospheric inputs will (1) diminish as a consequence of the decreased rate of calcification, and (2) increase as a result of the increased [Psi] value. Present available evidence suggest that calcification may be 30% lower in 2100 than it was in 1880 but changes in the carbonate equilibrium during the same period will increase the amount of [CO.sub.2] generated per mole Ca[CO.sub.3] precipitated by 33% (Table 4). It is therefore predicted that the release of [CO.sub.2] to the atmosphere due to calcification may not change significantly in the future.

TABLE 4. Calcification, ratio of [CO.sub.2] released to Ca [C0.sub.3] precipitated ([Psi]), and predicted estimate of [CO.sub.2] release in seawater by Ca [CO.sub.3] precipitation.(*)

	Pre-industrial	Present	Year 2065	Year 2100
Calcification	1	0.90	0.76	1
[Psi]	0.52	0.57	0.65	0.69
[CO.sub.2] release	0.52	0.51	0.49	0.48

(*) The rate of calcification is arbitrarily set at 1 in 1880 and decreases as predicted in Figure 9 using the revised IPCC IS92a [CO.sub.2] emission estimate. [Psi] was calculated as described by Frankignoulle et al. (1994) using the parameters shown in Table 1.

Cellular mechanisms

The cellular and molecular mechanisms involved in the response of calcification to increased p[CO.sub.2] observed at the organism and community levels are difficult to estimate due to the paucity of data. It is also difficult to predict the long-term response from short term experimental data.

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

It is predicted that seawater pH may decrease by 0.25 unit by 2100 (Table 1). There is no information available on the value of intracellular pH (p[H.sub.i] in coral cells and its control by seawater pH but it is well established that changes of external pH alter p[H.sub.i] and regulate numerous cellular process (e.g., Busa and Nucitelli, 1984). For example, a decrease of external pH as small as 0.07 unit induces a decrease of p[H.sub.i] of 0.06 unit, which can trigger tyrosine phosphorylation and gene activation in renal epithelial cells (Yamaji et al., 1994, 1997). It is also well established that the activity of a large number of intracellular enzymes is pH-sensitive and displays a pH optimum around the physiological range (Madshus, 1988). For example, the activity of phosphofructokinase, a key enzyme of the glycolytic pathway, exhibits a 10- to 20-fold reduction when pH decreases by as little as 0.1 unit below the physiological pH optimum (Trivedi and Danforth, 1966). Membrane permeability and conductance can also change greatly over a small pH interval. A decrease in external pH increase anionic permeability (reviewed by Madshus, 1988). Cell acidification can also increase the intracellular calcium concentration (e.g., Neglescu and Machen, 1990), which can, in turn, trigger numerous events such as exocytosis, kinase activation, and stimulation of cell membrane transport (Carafoli and Penniston, 1985).

Despite the significant effect of p[H.sub.i] on cellular processes, the questions are whether (1) the expected decrease of seawater pH is large enough to trigger a cellular response, and (2) the cellular machinery will be able to compensate for those changes in the long term. Bown (1985) calculated that p[H.sub.i] would decrease by only 0.008 units in plant cells in response to an increase of p[CO.sub.2] of 330 Ixatm. Additionally, coral cells undergo daily changes in external pH larger than those expected in the next century: the pH of the coral surface can change within 5 min from 7.5 in the dark to 8.5 in the light (Kuhl et al., 1995). Changes measured in the coelenteric cavity of sea anemones are even more dramatic, with pH ranging from ca. 7 to 9 (Furla et al., 1998b).

The increase in p[CO.sub.2] will not only affect phi but will also increase the total DIC concentration and change the proportion of its various species (Table 1). Zooxanthellae display considerable ability to change their mechanism of carbon supply depending on their environment. In hospite, the species of inorganic carbon transported across the algal membrane is [CO.sub.2] (produced by dehydration of bicarbonate in the host cell) whereas it is [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] in cultured zooxanthellae (Al-Moghrabi et al., 1996; Allemand et al., 1998a). As mentioned earlier, coral photosynthesis is saturated at ambient DIC concentration, so the predicted increase in [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] may have no effect on photosynthesis. However, the increased concentration of dissolved [CO.sub.2] together with the increase in uncatalyzed rate of [CO.sub.2] generation by [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] dehydration, may favor the diffusional carbon supply at the expense of the CCM-like carbon supply (Beardall et al., 1998).

The effect of the predicted decrease of [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] is more difficult to analyze. It can be transported by the [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] exchanger (Boron, 1985). Its role as a carbon source for photosynthesis is poorly documented but seems minor (Smith, 1988). Goiran et al. (1996) found no evidence for [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] transport in the coral Galaxea fascicularis.

The physico-chemical characteristics of the extracytoplasmic calcifying fluid are unknown but if the carbonate saturation state is largely biologically-controlled, it is difficult to determine the cellular processes involved in the decrease of calcification as a function of decreasing Ca[CO.sub.3] saturation state. When the Ca[CO.sub.3] saturation state is altered by manipulating the seawater calcium concentration, the decrease in calcification can be due to [Ca.sup.2+] limitation. The interpretation is less straightforward when the carbonate concentration is manipulated because seawater DIC may not dominate the carbon supply for the skeletal carbonate (see above) and there is likely no [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII] carrier in the membrane of ectodermal cells (Goiran et al., 1996). This, in combination with the near-equilibrium of many coral skeletons with seawater isotopes and chemistry may suggest that at least some taxa have a significant component of advective or rapid diffusional control over the composition of the ECF.

We suggest that the different calcification mechanisms used by corals and coralline algae could explain the higher sensitivity to changes in [Omega] of an algal-dominated coral reef community .(Langdon et al., submitted) and coralline algae (Smith and Roth, 1979; Borowitzka, 1981; Agegian, 1985; Mackenzie and Agegian, 1989) compared to zooxanthellate scleractinian corals (Gattuso et al., 1998a). The site of skeletogenesis is external in calcareous algae

Photosynthesis and Calcification at Cellular, Organismal and Community Levels in Coral Reefs: A Review on Interactions and Control by Carbonate Chemistry(1).

(Borowitzka, 1984), which are therefore extremely sensitive to changes in seawater [Omega]. Conversely, Ca[CO.sub.3] deposition occurs between the calicoblastic epithelium and the skeleton in corals, a much more isolated site.

CONCLUSION

Short-term experiments show that the rate of calcification of photosynthetic and calcifying organisms and communities decreases, sometimes dramatically, in response to increased p[CO.sub.2]. However, inadequate understanding of the mechanisms of coral calcification and its interactions with photosynthesis, as well as the response of both processes to environmental variables severely limits our ability to provide an accurate prediction of future changes.

The responses of scleractinian corals to short-term changes in a single environmental parameter are reasonably well known through experimental and ecological observations, but synergistic effects are extremely difficult to predict. Furthermore, responses in experimental tanks, over periods of days to months, have been studied, but there has been no attempt to investigate the long-term (several years) response of reef communities to large-scale changes in environmental variables. FACE (Free Air [CO.sub.2] Enrichment; Hendrey, 1993) and FATI (Free Air Temperature Increase; Nijs et al., 1996) have been used successfully to investigate the effect of elevated p[CO.sub.2] and temperature on terrestrial communities in open field conditions. The use of such approach in marine communities would be technically difficult, although not impossible, but probably too expensive to implement. The use of experimental mesocosms would certainly be easier due to recent advances in their design and maintenance (Adey, 1983; Jaubert, 1989).

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