NOTE

Biological control of air-sea CO_2 fluxes: effect of photosynthetic and calcifying marine organisms and ecosystems

J.-P. Gattuso[1,*], M. Pichon[2,**], M. Frankignoulle[3]

[1]Observatoire Océanologique Européen, Centre Scientifique de Monaco, Avenue Saint-Martin, MC-98000 Monaco, Principality of Monaco
[2]Australian Institute of Marine Science, PMB No 3, Townsville M.C., Queensland 4810, Australia
[3]Université de Liège, Laboratoire d'Océanologie, Institut de Chimie B6, B-4000 Sart Tilman par Liège 1, Belgium

ABSTRACT: A simple expression enables prediction of the effect of photosynthetic and calcifying systems on air-sea CO_2 exchange at all spatial scales (from organism to ecosystem). Input data are: gross primary production (P_g), respiration (R), net calcification (G) and the ratio of CO_2 released to $CaCO_3$ precipitated (ψ); the output is the amount of dissolved inorganic carbon (F_{CO_2}) which needs to be exchanged with the atmosphere to balance biologically mediated changes in the concentration of dissolved inorganic carbon in an open sea water system: $F_{CO_2} = -P_g + R + \psi G$. Coral reef data were used in the model to illustrate the relative influence of organic and inorganic carbon metabolism on ocean-atmosphere CO_2 cycling. A coral reef comprised of calcareous and non-calcareous organisms can be shown to act as a sink for atmospheric CO_2 when excess (= net) production is high and $CaCO_3$ precipitation is low. These characteristics are not typical of actively developing reef systems which typically exhibit a nearly balanced organic carbon metabolism ($P_g/R \approx 1$) and relatively high rates of calcification. In these circumstances, reef communities can be expected to cause CO_2 evasion to the atmosphere. This prediction is confirmed by the only existing measurement of air-sea CO_2 flux in a coral reef system.

KEY WORDS: Community metabolism · Primary production · Respiration · Calcification · Air-sea CO_2 flux · Coral reefs

Carbon dioxide uptake by photosynthesis and its release by respiration are major processes by which marine organisms and ecosystems can alter the concentration of carbon dioxide in seawater. Another set of reactions, precipitation and dissolution of calcium carbonate, has drawn a lot of attention recently. It is well established that calcification induces shifts in the seawater carbonate equilibrium which generates dissolved CO_2 and is therefore a source of CO_2 to seawater (Chamberlain 1898, Wollast et al. 1980). The deposition of 1 mol of calcium carbonate releases nearly 1 mol of CO_2 in freshwater (Frankignoulle et al. in press) but releases approximately 0.6 mol of CO_2 in seawater (Ware et al. 1992, Frankignoulle et al. 1994). It was suggested that changes in the magnitude and relative importance of precipitation and dissolution of $CaCO_3$ have played a significant role in glacial-interglacial regulation of atmospheric CO_2 concentration (the so-called 'coral reef' hypothesis; Berger 1982, Opdyke & Walker 1992, Broecker 1993).

High rates of calcium carbonate precipitation are often associated with high rates of photosynthesis, both at the organism (e.g. zooxanthellate scleractinian corals, calcareous algae, coccolithophorids) and the ecosystem (coral reefs) scales. Photosynthesis, respiration and calcification are tightly coupled in certain marine systems. For example, CO_2 released by calcification may be used as a substrate for photosynthesis. Such coupling has hampered elucidation of the effects of marine systems on air-sea CO_2 fluxes (Sikes & Fabry 1994, Sikes et al. in press). As pointed out by Holligan et al. (1993): 'the interacting effects of photosynthesis, calcification and regenerative oxidation of organic matter are difficult to unravel'. These metabolic processes must, therefore, be investigated simultaneously in order to assess the biological control exerted by marine systems on air-sea CO_2 exchange. The aim of this paper is to establish a relationship between surface layer metabolic processes of photosynthetic and calcifying organisms and ecosystems (photosynthesis, respiration, calcification) and air-sea CO_2 fluxes. We derived a simple model and used published data in

*E-mail: gattuso@naxos.unice.fr
**Present address: URA 1453 CNRS, Laboratoire EPHE/Biologie Marine, Université, F-66860 Perpignan Cedex, France

order to provide some indication of the role of these systems on the inorganic carbon system and air-sea CO_2 fluxes.

Background. Carbon dioxide is the major form of inorganic carbon in the gas phase. The inorganic carbon system is much more complicated in solution and comprises 4 different species: dissolved carbon dioxide, carbonic acid (H_2CO_3), bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}). Their concentrations depend upon pH according to the following equilibrium:

$$CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO_3^- \leftrightarrow 2H^+ + CO_3^{2-} \tag{1}$$
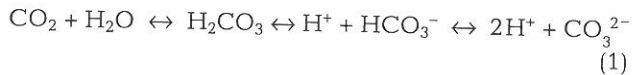
Dissolved inorganic carbon (DIC) or total carbon dioxide (TCO_2 or ΣCO_2) refers to the sum of the 4 inorganic carbon species:

$$DIC = [CO_2] + [H_2CO_3] + [HCO_3^-] + [CO_3^{2-}] \tag{2}$$

It is important to point out that dissolved CO_2 is the only species which can be exchanged with the atmosphere.

Total alkalinity (TA) is another important parameter related to the CO_2 system which can be defined as the excess of bases (proton acceptors) over acids (proton donors) (see Dickson 1981 for a more detailed definition):

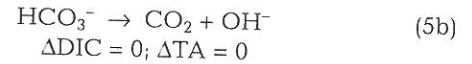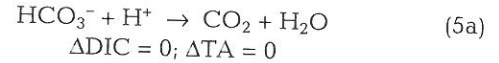$$TA = [HCO_3^-] + 2[CO_3^{2-}] + [B(OH)_4^-] + [OH^-] - [H^+] \tag{3}$$

The model. Two sets of biological processes are taken into consideration: metabolism of organic and inorganic carbon. Their influence on the seawater inorganic carbon system and, thereby, on air-sea CO_2 fluxes operates via changes in DIC and TA.

Production and degradation of 1 mol of organic matter by photosynthesis (P) and respiration (R, considered as positive throughout the paper) respectively decreases and increases dissolved inorganic carbon (DIC) by 1 mol:

$$CO_2 + H_2O \leftrightarrow CH_2O + O_2 \tag{4}$$
$$\Delta DIC = +1 \ (R) \text{ or } -1 \ (P); \Delta TA = 0$$
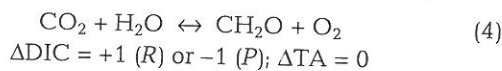
Photosynthesis and respiration occur simultaneously in any biological system. The net change in CO_2 is defined as the 'net primary production' (P_n) while the sum of P_n and R is termed 'gross primary production' (P_g). Carbon fixation during photosynthesis per se does not affect total alkalinity since its substrates do not contribute to TA. The concentration of free CO_2 is similar in seawater and air (10 vs 16 µM) but the diffusion coefficient is 10^4 times lower in seawater than in air, which makes the supply of CO_2 to the photosynthetic apparatus more difficult in marine than in terrestrial plants. Some marine plants overcome this problem by transporting bicarbonate ions which represent approximately 90% of DIC. The uptake of HCO_3^- does not

result in any alkalinity change since it must be transformed into CO_2 prior to its use by photosynthesis according to one of the following 2 reactions:

$$HCO_3^- + H^+ \rightarrow CO_2 + H_2O \tag{5a}$$
$$\Delta DIC = 0; \Delta TA = 0$$

$$HCO_3^- \rightarrow CO_2 + OH^- \tag{5b}$$
$$\Delta DIC = 0; \Delta TA = 0$$

Small changes in total alkalinity are associated with production and degradation of organic carbon through assimilation and excretion of nutrients. Ammonium uptake by organic production lowers TA and uptake of nitrate and phosphorus raises TA (Brewer & Goldman 1976). The reverse changes take place during oxidation of organic matter. The nutrient contribution to TA changes is negligible in corals (Chisholm & Gattuso 1991) and coral reefs (Kinsey 1978) and is not taken into account in the model presented here (see also Sundquist 1993). This contribution can easily be taken into consideration using the Redfield ratio as described by Goyet & Brewer (1993) in systems where nutrient assimilation and excretion are not negligible. Production and assimilation of other compounds contributing to TA, such as dimethylsulphonium propionate (DMSP), may also have to be taken into account in some instances (Raven 1993).

Calcification decreases DIC by 1 mol and total alkalinity by 2 equivalents for each mole of calcium carbonate precipitated; dissolution of $CaCO_3$ has the opposite effect:

$$Ca^{2+} + 2 HCO_3^- \leftrightarrow CaCO_3 + CO_2 + H_2O \tag{6}$$

$$\Delta DIC = +1 \text{ (dissolution) or } -1 \text{ (calcification)}$$
$$\Delta TA = +2 \text{ (dissolution) or } -2 \text{ (calcification)}$$

The calcification rate measured in calcifying systems is usually the net calcification rate (G) which represents the balance between gross calcification and dissolution.

The total change in DIC and TA when incubating a photosynthetic and calcifying system in a sealed volume of seawater (temperature being held constant) can be calculated by combining changes in DIC and TA resulting from the metabolism of organic (ΔDIC^o and ΔTA^o) and inorganic carbon (ΔDIC^i and ΔTA^i):

$$\Delta DIC = \Delta DIC^o + \Delta DIC^i \tag{7a}$$
$$\Delta TA = \Delta TA^o + \Delta TA^i \tag{7b}$$

Since:

$$\Delta DIC^o = -P_g + R = -P_n, \tag{8a}$$
$$\Delta DIC^i = -G, \tag{8b}$$
$$\Delta TA^o = 0 \tag{8c}$$
and $$\Delta TA^i = -2G, \tag{8d}$$

then:

$$\Delta DIC = -P_g + R - G \tag{9a}$$
$$\Delta TA = -2G \tag{9b}$$

Upon opening the system to the atmosphere, a flux of CO_2 will occur across the air-sea interface until the partial pressure of CO_2 on both sides of the interface is equal:

$$F_{CO_2} = F^o_{CO_2} + F^i_{CO_2} \qquad (10)$$

where $F^o_{CO_2}$ and $F^i_{CO_2}$ refer, respectively, to the CO_2 flux generated by the metabolism of organic and inorganic carbon. Since the aim of the present paper is to predict the net effect of metabolic processes on air-sea CO_2 flux, we only refer to the magnitude of air-sea CO_2 flux and not to the rate of gas transfer which depends on a number of factors, including water motion.

Since we assumed that $\Delta TA^o = 0$, $F^o_{CO_2}$ can be estimated from the relationship:

$$F^o_{CO_2} = \Delta DIC^o = -P_g + R \qquad (11)$$

The 1:1 relationship between $CaCO_3$ and CO_2 shown in Eq. (6) is nearly true in freshwater but is not so in seawater due to its buffering capacity (Ware et al. 1992, Frankignoulle et al. in press). Numerical analysis of the inorganic carbon system has shown that 0.6 mol of CO_2 are liberated (consumed) per mole of $CaCO_3$ precipitated (dissolved; Ware et al. 1992). This ratio was defined as Ψ and an analytical expression enabling its computation has been developed (Frankignoulle et al. 1994). We then have:

$$F^i_{CO2} = \Psi G \qquad (12)$$

where:

$$\Psi = \frac{CO_2 \text{ released}}{CaCO_3 \text{ precipitated}} \qquad (13)$$

Frankignoulle et al. (1994) have shown that $\Psi = 0.6$ for seawater displaying the following characteristics: $pCO_2 = 356$ µatm, $TA = 2.37$ mEq kg^{-1}, temperature = 25°C and salinity = 35 psu. The amount of CO_2 which needs to be exchanged at the air-sea interface in order to bring seawater back to its pre-metabolic pCO_2 can thus be computed from:

$$F_{CO_2} = -P_g + R + 0.6G \qquad (14a)$$

or,

$$F_{CO_2} = -P_n + 0.6G \qquad (14b)$$

with P, R and G expressed in molar units per day.

F_{CO_2} can be normalized to the respiration rate (R) in order to enable the comparison of systems displaying a wide range of metabolic activity:

$$F_{CO_2}/R = 1 - P_g/R \, (1 - \psi G/P_g) \qquad (15)$$

Results and discussion. Eq. (14a) can be illustrated by a numerical example similar to the one presented by Ware et al. (1992). Parameters of the seawater inorganic carbon system were calculated using the following combinations of variable: {pCO_2, TA} and {DIC, TA}; all computations were carried out with the freeware program 'CO$_2$' (available from M. Frankignoulle).

Sikes et al. (in press) made distinctions between systems open and closed to the atmosphere, and photosynthetic systems. They demonstrated that the ratio of CO_2 released to precipitated calcium carbonate is 0.06 in a closed system and suggested that it varies 'between zero for the photosynthetic system to about 0.6 for the open system with complete CO_2 efflux to the atmosphere'.

A closed-system model is one in which there is no exchange of any chemical species with the surrounding environment, including the atmosphere. Such systems have been used repeatedly in ecophysiological studies of marine organisms, both in the laboratory and *in situ*, but do not apply to any species or ecosystems in their natural environment and give no insight on processes occurring at the air-sea interface. Open-system models or experiments take into account fluxes and reactions at interfaces and are the method of choice to assess the effect of metabolic activities on air-sea CO_2 fluxes. Such a system is used in the following calculations.

Seawater with the characteristics shown in Table 1 is equilibrated with the atmosphere ($pCO_2 = 356$ µatm). A photosynthetic and calcifying biological system is incubated in this medium at constant temperature. P_g/R and G/P_g are 1.5 and 0.33, respectively (Table 1). At the completion of the incubation, with the volume still sealed from the atmosphere, TA and DIC have fallen to 2.320 mEq kg^{-1} (= initial TA – 2G) and 1.971 (= initial DIC – P_g + R – G), respectively. pCO_2 is down to 341 µatm. Upon opening of the incubation chamber, seawater reequilibrates with the atmosphere by absorbing CO_2 (until pCO_2 is back to 356 µatm) without altering TA. DIC increases to 1.982 mmol kg^{-1}, the CO_2 invasion is then –0.010 mmol kg^{-1} (we adopt the

Table 1. Effect of primary production, respiration and calcification on the inorganic carbon system. Derived chemical data (in italics) were obtained from the fixed parameters (in bold) with the freeware program 'CO$_2$'. pH is on the seawater scale (sws) and the CO_2 constant set is from Goyet & Poisson (1989)

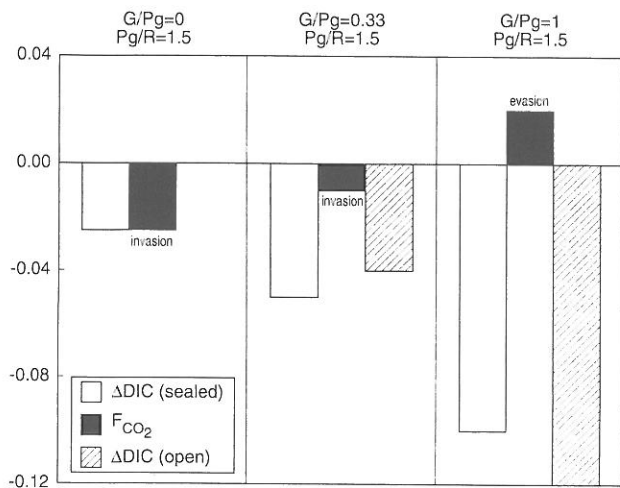|	Initial	Final (sealed)	Final (open)
Chemical and physical parameters			
TA (mmol kg^{-1})	**2.370**	**2.320**	**2.320**
pCO_2 (µatm)	**356**	*341*	**356**
Temperature (°C)	25	25	25
Salinity (psu)	35	35	35
pH (sws)	*8.090*	*8.104*	*8.082*
DIC (mmol kg^{-1})	*2.021*	**1.971**	*1.982*
Metabolic parameters			
P_g (mmol DIC)		0.075	
R (mmol DIC)		0.050	
G (mmol CaCO$_3$)		0.025	
P_g/R		1.50	
G/P_g		0.33	

Fig. 1. Numerical example of the effect of organic and inorganic carbon metabolism on seawater inorganic carbon after incubation in a closed volume ('sealed') and upon opening of the incubation chamber to the atmosphere ('open'). P_g: gross primary production; R: respiration, G: net calcification

convention of assigning a negative sign to CO_2 invasion and a positive sign to CO_2 evasion). This value equals F_{CO_2} computed according to Eq. (14a):

$$F_{CO_2} = -0.075 + 0.050 + (0.6 \times 0.025)$$
$$= -0.010 \text{ mmol kg}^{-1}$$

The result of this computation for $P_g/R = 1.5$ and $G/P_g = 0.33$ is shown in Fig. 1 together with F_{CO_2} calculated for systems displaying the same P_g/R ratio but different G/P_g ratios (0 and 1). If the system does not calcify ($G/P_g = 0$), CO_2 is absorbed by seawater after opening the incubation chamber in order to exactly balance the decrease in DIC. CO_2 invasion also occurs when net precipitation of $CaCO_3$ is moderate compared to gross primary production ($G/P_g = 0.33$) but CO_2 generated by calcification becomes higher than CO_2 uptake when $G/P_g = 1$ and CO_2 evasion takes place.

F_{CO_2}/R is plotted as a function of the P_g/R and G/P_g ratios in Fig. 2. F_{CO_2}/R increases directly with G/P_g and inversely with P_g/R. The role of photosynthetic and calcifying systems on the direction of air-sea CO_2 exchange depends on the relative magnitude of primary production and calcification rather than on the absolute rate of each. For example, organic carbon metabolism by corals and coralline algae results in net removal of CO_2 when their P_g/R ratio is higher than 1, but these calcareous organisms generate CO_2 when G/P_g exceeds a threshold set by P_g/R: e.g. when $P_g/R = 1.5$, the threshold is $G/P_g = 0.56$.

Coral reefs are major photosynthetic and calcifying ecosystems and can be used as a case study. They exhibit a number of physiographic zones that signifi-

cantly differ in rates of primary production and calcification (Done 1983). The metabolic performances of reef flats are, by far, the best known of the reef zones. This stems from the fact that community metabolism of the other reefal areas (outer reef slope, algal pavement and lagoons) is technically much more difficult to investigate. Kinsey (1983) observed that reef flats exhibit rather uniform metabolic rates and suggested the following performances for a 'standard' reef flat:

$$P_g = R = 583 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$$
and $$G = 110 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$$

F_{CO_2}/R computed from these estimates is $+0.11$ (Fig. 2) suggesting that coral reef flats are sources of CO_2 to the atmosphere. It is worth noting that when community production and respiration are nearly balanced ($P_g/R \approx 1$, e.g. most coral reef flats; Kinsey 1985), biologically induced air-sea CO_2 fluxes are dominated by the increase in seawater pCO_2 that results from calcification. Gattuso et al. (1993) investigated the community metabolism of a barrier reef flat at Moorea (French Polynesia) and the associated air-sea CO_2 flux. They reported the following rates (P_g and R expressed in terms of O_2 were converted to CO_2 units by setting the photosynthetic and respiratory quotients to 1):

$$P_g \text{ and } R = 640.2 \text{ and } 642 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1};$$
and $$G = 243 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$$

The only measurement of air-sea CO_2 flux driven by coral reef metabolism made so far showed that the reef flat released CO_2 to the atmosphere (Gattuso et al.
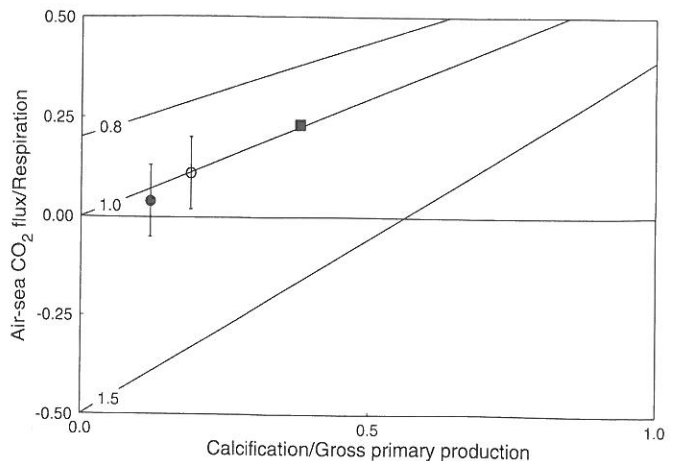

Fig. 2. Model estimate of air-sea CO_2 budget as a function of P_g/R and G/P_g. Model output is shown for the following P_g/R ratios: 0.8, 1.0 and 1.5. P_g, R and G in mmol m^{-2} d^{-1}. (■) Moorea barrier reef flat (Gattuso et al. 1993); (○) average coral-algal reef flat (Kinsey 1983); (●) average coral reef ecosystem (Smith 1983, Crossland et al. 1991)

1993), in concordance with the output of the model presented here ($F_{CO_2}/R = +0.23$; Fig. 2).

There are few estimates of metabolic performances of 'entire' reef systems, i.e. which integrate the effect of the various physiographic zones of the reef. Crossland et al. (1991) proposed that P_g and R of such systems are, respectively, 250 and 242 mmol CO$_2$ m^{-2} d^{-1}. Smith (1983) suggested that whole coral reefs produce an average of about 30 mmol CaCO$_3$ m^{-2} d^{-1}. Our model predicts that the average 'entire' reef ecosystem also causes an efflux of CO$_2$ to the atmosphere ($F_{CO_2}/R = +0.04$; Fig. 2).

The estimated amount of dissolved inorganic carbon (F_{CO_2}) which needs to be exchanged with the atmosphere is quite sensitive to the uncertainty associated with the P_g/R ratio. P_g and R are often calculated by numerically integrating photosynthesis-irradiance curves (e.g. Barnes & Devereux 1984). There is presently no statistical procedure enabling the computation of the standard error of such metabolic parameters. Kinsey (1983) claimed that the P_g/R ratio of an average reef flat that he reported was known to ± 0.1 but this refers to a range rather than to a statistical parameter (D. W. Kinsey pers. comm. 1995). The error bars around F_{CO_2}/R for coral reef flats and whole coral reef systems were calculated using this uncertainty. The error bars do not include $F_{CO_2}/R = 0$ for coral reef flats but F_{CO_2}/R derived for whole coral reef systems may not differ statistically from 0 (Fig. 2). This suggests that the prediction that an average coral reef flat is a source of CO$_2$ is robust but that the influence of whole reef systems on atmospheric CO$_2$ remains uncertain.

The proposed expression predicts the net effect of primary production and calcification on air-sea CO$_2$ exchange of isolated marine organisms and stable open marine systems (e.g. coral reefs). It is however sensitive to uncertainties associated with the P_g/R ratio. Future work should be carried out to derive a statistical procedure enabling estimation of the standard error of metabolic parameters. When sufficient data become available, the model will allow examination of important dynamic systems, most notably coccolithophorid blooms, which appear to exhibit significant changes in the ratio of inorganic to organic carbon production during the course of population growth and decline (Holligan et al. 1993).

LITERATURE CITED

Barnes DJ, Devereux MJ (1984) Productivity and calcification on a coral reef: a survey using pH and oxygen electrode techniques. J exp mar Biol Ecol 79:213–231

Berger WH (1982) Increase of carbon dioxide in the atmosphere during deglaciation: the coral reef hypothesis. Naturwissenschaften 69:87–88

Brewer PG, Goldman JC (1976) Alkalinity changes generated by phytoplankton growth. Limnol Oceanogr 21:108–117

Broecker WS, Peng TH (1993) What caused the glacial to interglacial CO$_2$ change? In: Heimann M (ed) The global carbon cycle. Springer-Verlag, Berlin, p 95–115

Chamberlain TC (1898) The influence of great epochs of limestone formation upon the constitution of the atmosphere. J Geol 6:609–621

Chisholm JRM, Gattuso JP (1991) Validation of the alkalinity anomaly technique for investigating calcification and photosynthesis in coral reef communities. Limnol Oceanogr 36:1232–1239

Crossland CJ, Hatcher BG, Smith SV (1991) Role of coral reefs in global ocean production. Coral Reefs 10:55–64

Dickson A (1981) An exact definition of total alkalinity and a procedure for the estimation of alkalinity and total inorganic carbon from titration data. Deep Sea Res 28:609–623

Done TJ (1983) Coral zonation: its nature and significance. In: Barnes DJ (ed) Perspectives on coral reefs. Australian Institute of Marine Science, Townsville, p 107–147

Frankignoulle M, Canon C, Gattuso JP (1994) Marine calcification as a source of carbon dioxide: positive feedback of increasing atmospheric CO$_2$. Limnol Oceanogr 39: 458–462

Frankignoulle M, Pichon M, Gattuso JP (in press) Aquatic calcification as a source of carbon dioxide. In: Carbon sequestration in the biosphere. Springer-Verlag, Berlin

Gattuso JP, Pichon M, Delesalle B, Frankignoulle M (1993) Community metabolism and air-sea CO$_2$ fluxes in a coral reef ecosystem (Moorea, French Polynesia). Mar Ecol Prog Ser 96:259–267

Goyet C, Brewer PG (1993) Biochemical properties of the oceanic carbon cycle. In: Willebrand J, Anderson DLT (eds) Modelling oceanic climate interactions. Springer-Verlag, Berlin, p 271–297

Goyet C, Poisson A (1989) New determination of carbonic acid dissociation constants in seawater as a function of temperature and salinity. Deep Sea Res 36:1635–1654

Holligan PM, Fernandez E, Aiken J, Balch WM, Boyd P, Burkill PH, Finch M, Groom SB, Malin G, Muller K, Purdie DA, Robinson C, Trees CC, Turner SM, van der Wal P (1993) A biogeochemical study of the coccolithophore, *Emiliania huxleyi*, in the North Atlantic. Global biogeochem Cycles 7:879–900

Kinsey DW (1978) Alkalinity changes and coral reef calcification. Limnol Oceanogr 23:989–991

Kinsey DW (1983) Standards of performance in coral reef primary production and turnover. In: Barnes DJ (ed) Perspectives on coral reefs. Australian Institute of Marine Science, Townsville, p 209–220

Kinsey DW (1985) Metabolism, calcification and carbon production. I. System level studies. Proc 5th int Coral Reefs Congr 4:505–526

Opdyke BN, Walker JCG (1992) Return of the coral reef hypothesis: basin to shelf partitioning of $CaCO_3$ and its effect on atmospheric CO_2. Geology 20:733–736

Raven JA (1993) Carbon: a phycocentric view. In: Evans GT, Fasham MJR (eds) Towards a model of ocean biogeo-chemical processes. Springer-Verlag, Berlin, p 123–152

Sikes CS, Fabry VJ (1994) Photosynthesis, $CaCO_3$ deposition, coccolithophorids, and the global carbon cycle. In: Tolbert E, Preiss J (eds) Photosynthetic carbon metabolism and regulation of atmospheric CO_2 and O_2. Oxford University Press, Oxford, p 217–233

Sikes CS, Wierzbicki A, Fabry VJ (in press) From atomic to global scales in biomineralization. Bull Inst océanogr Monaco

Smith SV (1983) Coral reef calcification. In: Barnes DJ (ed) Perspectives on coral reefs. Australian Institute of Marine Science, Townsville, p 240–247

Sundquist ET (1993) The global carbon dioxide budget. Science 259:934–941

Ware JR, Smith SV, Reaka-Kudla ML (1992) Coral reefs: sources or sinks of atmospheric CO_2? Coral Reefs 11: 127–130

Wollast R, Garrels RM, Mackenzie FT (1980) Calcite-seawater reactions in ocean surface waters. Am J Sci 280:831–848

This note was submitted to the editor