A geochemical model for coral reef formation

T. Nakamura · T. Nakamori

Received: 9 February 2007 / Accepted: 21 May 2007 / Published online: 10 July 2007
© Springer-Verlag 2007

Abstract The conspicuous growth of a reef crest and the resulting differentiation of reef topography into a moat (shallow lagoon), crest and slope have long attracted the interest of scientists studying coral reefs. A geochemical model is here proposed for reef formation, taking into account diffusion-limited and light-enhanced calcification. First, to obtain data on net photosynthesis and calcification rates in the field, a typical coral community was cultured in situ on a reef flat. Using these data, equations including parameters for calcification were then developed and applied in computer simulations to model the development over time of reef profiles and the diffusion of carbon species. The reef topography simulated by the model was in general agreement with reef topography observed in nature. The process of reef growth as shown by the modeling was as follows. Increases in the shore-to-offshore gradients of the concentrations of carbonate species result from calcification by reef biota, giving a lower rate of growth on near-shore parts of the reef than on those further offshore. As a result, original topography is diversified into moat and reef crest for the first time. Reef growth on the reef crest is more rapid than in the inshore moat area, because more light is available at the crest. Reef growth on the near-shore side of the reef is further inhibited by damming of carbon-rich seawater on the seaward side of the reef by

the reef crest. Over time, the topographic expression of the reef crest and moat becomes progressively more clearly defined by these geochemical processes.

Keywords Calcification · Photosynthesis · Reef formation · Simulation

Introduction

The upper parts of well-developed coral reefs have a unique topography that differs markedly from those of other marine coastal environments. Most of the fringing reefs of the Ryukyu Islands, for example, are characterized by both a convex “reef crest” and a concave “moat” (shallow lagoon). These structures are common, differing only in scale, not only on fringing reefs but also on barrier reefs and atolls. Understanding why such topography is regularly formed is one of the most important unresolved problems in coral reef geology.

Growth histories of coral reefs in the Ryukyu Islands from the Holocene to the present have been reconstructed based on core samples from both raised coral reefs in uplifted areas, and on recent reef flats in more stable regions (Konishi et al. 1983; Takahashi et al. 1988; Kan and Hori 1993; Yonekura et al. 1994; Kan et al. 1995, 1997; Yamano et al. 2001b). Like coral reefs in the tropics, those in the Ryukyu Islands grew remarkably during the postglacial sea-level rise and the ensuing stillstand. Most Japanese Holocene reefs began to develop from around 10,000 years before present (BP), which is later than the time of initiation of typical reefs in the tropics. Catch-up reef growth dominated from 10,000 to 6,000 years BP because of rapid sea-level rise. The reef crest structures grew quickly after this stage and caught up with the rate of sea-level change

Communicated by Geology Editor B. Riegl.

T. Nakamura (✉) · T. Nakamori
Institute of Geology and Paleontology,
Graduate School of Science, Tohoku University,
Aobayama, Sendai 980-8578, Japan
e-mail: takachi@dgsc.tohoku.ac.jp

during the period from 6,000 to 4,000 years BP (Takahashi et al. 1988; Yamano et al. 2001a). Construction of a shallow reef crest diversified the reef environment by the development of a wave-affected fore-reef, and a calm back-reef with a depressed topography in the form of a moat (Takahashi et al. 1988; Yamano et al. 2001a). This growth history suggests that reef crests grow rapidly during periods of sea-level rise. Montaggioni (2005) reported this peculiar pattern not only from the Ryukyu Islands but also from the other parts of coral reef areas, e.g., Pointe-au-Sable reef, Mauritius, Indian Ocean (Montaggioni and Faure 1997), Koror barrier reef, Palau, Western Pacific (Kayanne et al. 2002), One Tree Reef, Central Great Barrier Reef (Marshall and Davies 1982), Central area, Lord Howe Island, Tasman Sea, Western Pacific (Kennedy and Woodroffe 2000), and Punta Islotes fringing reef, Costa Rica, Eastern Pacific (Cortés et al. 1994).

The growth rate of reef crests and the development of other morphological characteristics of the reef systems would have been affected by calcification of coral reef biota, because the reef framework is made of carbonate skeletons precipitated by them. Recent scientific work has shown that calcification can be defined by a simple function relating to environmental parameters, such as light intensity (Chalker 1981), and available chemical components (Gattuso et al. 1998a; Marubini and Thake 1999; Odhe and van Woesik 1999; Leclercq et al. 2000, 2002; Langdon et al. 2000). This study builds on that work, and proposes a model for coral reef growth that is based on calcification and other chemical and physical processes in the reef environment.

It is important that the effect of “light-enhanced calcification” by hermatypic corals (Goreau and Goreau 1959; Barnes and Chalker 1990) is included in the model. This phenomenon has been reported on the basis of observations carried out at different spatial scales; for example, a coral colony (Goreau 1959), a coral community (Suzuki et al. 1995), and a complete reef (Barnes and Devereux 1984). Hermatypic corals are well known for their symbiosis with the dinoflagellate algae zooxanthellae. Incubation experiments suggest that photosynthesis by zooxanthellae enhances coral calcification (Goreau 1959; Gattuso et al. 1999), although the calcification does not have such effect on the photosynthesis under inhibited calcification (Yamashiro 1995; Gattuso et al. 2000). The photosynthesis of marine organisms is expressed by the following two equations:

and the calcification process can be expressed as follows:

The production of OH^- during photosynthesis, as shown in Eq. (1), and of H^+ during calcification, as shown in Eq. (3), is significant, as discussed subsequently.

Gattuso et al. (1999) reviewed investigations into photosynthesis-enhanced calcification by hermatypic corals and pointed out that the endodermal cell layer secretes OH^- during photosynthesis and generates a pH gradient across the epithelial layer, with the endodermal side being alkaline. This OH^- can neutralize the H^+ produced during coral calcification and accelerate the calcification. Although the interaction between calcification and endosymbiont photosynthesis remains unclear (Gattuso et al. 2000), it is generally accepted that photosynthesis and light availability are the main factors controlling the rate of calcification.

Another factor controlling the calcification rate is the degree of aragonite saturation, Ω_{arag} ($= [\text{Ca}^{2+}][\text{CO}_3^{2-}]/K_{\text{arag}}$, where K_{arag} is the solubility product for aragonite), or $[\text{CO}_3^{2-}]$, which is the dominant variable in the expression of Ω_{arag} . The dependency of the calcification rate on Ω_{arag} or $[\text{CO}_3^{2-}]$ has been elucidated in laboratory experiments using the hermatypic corals *Stylophora pistillata* (Gattuso et al. 1998a), *Porites compressa* (Marubini and Atkinson 1999), and *Porites porites* (Marubini and Thake 1999). This phenomenon has also been observed in coral reef communities (Suzuki et al. 1995; Langdon et al. 2000; Leclercq et al. 2000, 2002). Langdon et al. (2000) concluded that the Ω_{arag} of the seawater can be correlated to the calcification rate of coral reef community in the Biosphere 2 ocean during short term (days) and long term (months to years). This result also supported that coral reef calcification is controlled by Ω_{arag} (or $[\text{CO}_3^{2-}]$).

Metabolism within active coral reef communities changes the composition of seawater carbonate species. The calcification reduces both the total amount of carbon and the alkalinity, resulting in a decrease of $[\text{CO}_3^{2-}]$ and an increase in the fugacity of CO_2 ($f\text{CO}_2$) in seawater owing to a fall of pH. Gradients of pH, total carbon, total alkalinity, and $f\text{CO}_2$ were observed along transects across lagoons of the Palau Barrier Reef, Majuro Atoll, South Male Atoll (Suzuki et al. 1997; Suzuki and Kawahata 1999), Great Barrier Reef (Kawahata et al. 2000), and Palau barrier reef (Watanabe et al. 2006). It is therefore possible that the rate of calcification is limited by the supply of CO_3^{2-} from the open ocean, because the $[\text{CO}_3^{2-}]$ in seawater is reduced by calcification, and the calcification is reduced by the decrease of $[\text{CO}_3^{2-}]$.

The above review shows that the primary factors controlling reef growth might be geochemical processes, such as diffusion of carbonate species and light-enhanced

calcification. Previous authors, however, have not verified their ideas by using field data or computer simulations. Reconstruction of the growth history of reef topography and the distribution of carbonate species in seawater by using finite difference modeling methods are therefore an important advance.

The aims of this study were to test the hypothesis that basic Holocene reef morphological development can be explained by a limited set of linked fundamental process: light-enhanced calcification, eddy diffusion on chemical constituents in seawater, carbonate equilibrium, etc. To this end, this paper (1) proposes equations for photosynthesis and calcification rates of a coral community using data from in situ incubation on a coral reef, (2) constructs a geochemical model for coral reef formation incorporating reef growth and diffusion of inorganic carbon species, and (3) executes computer simulations of that model.

Materials and methods

Study area

The Shiraho coral reef, which is south of Ishigaki Island (24°22'N, 124°15'E) in the southwestern part of the Ryukyu Islands, Japan (Fig. 1), was selected for this study. The climate of Ishigaki Island is subtropical. Most of the coast of Ishigaki Island is surrounded by fringing reefs that have well-developed reef-crest and moat topography. These features are also evident off the Shiraho area, where topographic zones are arranged parallel to the coastline. The width of the reef within the study area is about 700 m in the north and 1,000 m in the south, which is about the average width of Japanese coral reefs. Nakamori (1986)

reported a zonation of coral communities concordant with topographic trends at this site.

Topography and coral communities

The characteristic reef flat (near shore) and reef slope (off shore) at the study site has been described in detail in a previous study (Nakamura and Nakamori 2006). The reef flat is a horizontal plane with patches of coral and depressions shallower than 3 m depth. The reef slope is a steeply inclined plane extending from sea level to a depth of 30 m off Ishigaki Island. The reef flat can be divided into four subunits: a moat (shallow lagoon), an inner reef flat, a reef crest, and an outer reef flat (Fig. 2a).

Nakamura and Nakamori (2006) reported six coral communities in the study area (Fig. 2b–d), and, on the basis of cluster analysis, named them the “massive *Porites* - *Goniastrea aspera* community”, “*Montipora stellata* community”, “branching *Acropora* community”, “*Montipora digitata* community”, “encrusting *Acropora* community”, and “*Pocillopora verrucosa* - tabular *Acropora* community”.

Experimental design

For in situ incubation, a sealed aquarium (Fig. 3) was settled on the floor of the moat at a distance of 400 m from the shore (2.43 m deep) on the transect (Fig. 1). The acrylic aquarium was a cuboid shape of 0.6 m length, 0.6 m width, and 0.3 m height. The seawater inside the aquarium could be exchanged by releasing the upper part of the aquarium from its base, to which it was attached by eight locks. Two rubber gloves were included in the design of the aquarium to allow access to enclosed equipment (Fig. 3).

Fig. 1 Site of the aquarium used for in situ incubation on the cross-reef transect of Nakamura and Nakamori (2006) at Shiraho, Ishigaki Island. Aerial photograph (95 ISHIGAKI C15-34) acquired from the Geographical Survey Institute, Ministry of Construction, Japan

Fig. 2 Cross sections along the cross-reef transect of the fringing reef at Shiraho (modified from Nakamura and Nakamori 2006). **a** Depth profile and topographic zonation, **b** coverage of corals, **c** relative abundance of coral species, and **d** zonation of coral communities

The coverage of the hermatypic corals inside the aquarium was estimated from a sketch and some underwater photographs. Total alkalinity (A_T) and pH were measured to determine net photosynthesis and calcification rates (P_n and G) of the coral community. Photon flux density (F_p) and the practical salinity of the seawater were measured simultaneously during the experiment. In some cases, the original author's symbols have been modified to be consistent with notation adopted. All symbols are listed in Table 1.

The pH was reconstructed from voltage by using a pHC2001 electrode and PHM240 pH meter (Radiometer Analytical, France). The electrode was calibrated with NBS-scale buffer solutions. Seawater A_T was obtained using the pH method of Culbertson et al. (1970). Fifteen milliliters of 0.01 mol l^{-1} HCl solution was added to 50-ml filtered seawater samples, and the A_T of the samples was then estimated from the pH values of the acidified sample. Sample temperature was kept constant at 25.0°C (≈ 298.15 K) during pH and A_T measurements by using a

water bath. The standard deviation (1σ) of the A_T values obtained by this method by the previous authors was 4 $\mu\text{mol kg}^{-1}$ (Suzuki and Kawahata 1999). F_p was measured with an MDS MkV/L photon sensor (Alec Electronics Co Ltd, Japan) at the observation site. The salinity of the seawater was obtained using an electrode conductivity salinometer MODEL 601 MK-IV (Yeo-Kal Electronics Pty Ltd, Australia).

Experiments to measure P_n and G in the coral community during summer were carried out over 24 h from 0900 hours on 26 August to 0900 hours on 27 August 2004. Seawater samples (500 ml) were collected immediately before and after the experiment to determine the long-term salinity trend. The net photosynthesis and calcification rates (P_n and G) of the communities in the aquarium were determined in this study by using the following procedure every 3 h over 24 h: (1) sampling of seawater in the aquarium in a cylindrical bottle, (2) isolation of the seawater in the aquarium from surrounding waters, (3) measurement of pH and A_T of samples, (4) resampling of the

Fig. 3 Aquarium used for in situ incubation in this study. **a** Schematic diagram of aquarium and other equipment, **b** photograph of closed aquarium on site

seawater in the aquarium after 3 h, and (5) exchange of water in the aquarium with surrounding water. These steps were repeated every 3 h over 1 day (24 h). The interval of 3 h was chosen to minimize damage to the coral community during sealing of the aquarium, and to obtain adequate temporal sampling of the seawater chemistry. The pH and A_T values of samples were measured within 1 h of sampling in a laboratory at Shiraho Village. The photon flux sensor was placed inside the aquarium (Fig. 3) to measure natural F_P at 1-min intervals during the experiment.

Determination of P_n and G

Values of P_n and G were determined using the alkalinity anomaly method of Smith and Key (1975) and Smith and Kinsey (1978). Chisholm and Gattuso (1991) compared G measured by this method with values obtained by complexometric titration of Ca with EGTA and concluded that

Table 1 Definitions of symbols

Symbol	Parameter
A_T	Total alkalinity
C_T	Total carbon dioxide
A_{T0}	Initial total alkalinity
C_{T0}	Initial total carbon dioxide
B_T	Total boron
K_1'	First dissociation constant of carbonic acid
K_2'	Second dissociation constant of carbonic acid
K_B'	Dissociation constant of boric acid
ρ_W	Density of seawater
ρ_R	Density of reef rock
P_n	Net photosynthesis rate
P_g	Gross photosynthesis rate
R	Respiration rate
G	Calcification rate
G'	Generalized calcification rate
k_P	Constant, defined in Eq. (9)
k_G	Constant, defined in Eq. (12)
k	$= k_P \cdot k_G$, constant, defined in Eq. (14)
k'	$= k/20.7$, constant, defined in Eq. (15)
Cov	Coverage of corals
F_P	Photon flux density
F_{P0}	Photon flux density on sea surface
h	Water depth
α	Albedo of sea surface
a	Constant, defined in Eq. (19)
b	Constant, defined in Eq. (19)
c	Constant, defined in Eq. (19)
λ	Extinction coefficient of seawater
V_R	Growth rate of the reefs
V_S	Rate of sea-level rise
D	Diffusion coefficient in Eq. (21)
M	Molecular mass of CaCO_3
x	Coordinates on horizontal axes
y	Coordinates on vertical axes
K_x	Horizontal eddy diffusion coefficient
K_v	Vertical eddy diffusion coefficient

the alkalinity anomaly method is valid, especially for measuring G . In this method, P_n and G values are obtained by solving simultaneous equations relating to a conservation law of A_T and total carbon dioxide (C_T). C_T is defined as the sum of concentrations of three carbonate species ($C_T = [\text{CO}_2(\text{aq})^*] + [\text{HCO}_3^-] + [\text{CO}_3^{2-}]$, where $\text{CO}_2(\text{aq})^*$ is dissolved carbon dioxide). These concentrations and C_T were calculated from equilibrium equations for pH and A_T proposed by Suzuki et al. (1995). The thermodynamic parameters of the first and second dissociation constants of carbonic acid (K_1' and K_2') (Mehrbach et al. 1973), the

Fig. 4 Makeup of the coral community in the aquarium. **a** Underwater photograph, **b** sketch

dissociation constant of boric acid (K_B') (Lyman 1957), total borate concentration (B_T) (Culkin 1965), and the dissociation constant for water (K_W) and activity coefficient of hydrogen ions (f_H) of Culberson and Pytkowicz (1973) were adopted in this study. These constants were converted to the appropriate values considering the sample temperature ($T = 298.15$ K) and measured salinity. The G and P_n values ($\mu\text{mol m}^{-2}$ per unit time) for the community are given by:

$$G = -\frac{1}{2} \rho_W H \Delta A_T / \Delta t, \quad (5)$$

and

$$P_n = -\rho_W H \Delta C_T / \Delta t - G, \quad (6)$$

where ρ_W is density of seawater, H is height of the aquarium ($H = 0.3$ m), $\Delta A_T / \Delta t$ is the change in A_T in $\mu\text{mol kg}^{-1}$ per unit time, and $\Delta C_T / \Delta t$ is the change in C_T in $\mu\text{mol kg}^{-1}$ per unit time.

Table 2 Coverage of coral species in the aquarium

Species	Coverage (%)
<i>Montipora stellata</i>	1.9
<i>Montipora cactus</i>	1.1
<i>Acropora microphthalma</i>	16.6
<i>Porites cylindrica</i>	1.2
Total	20.7

Results

Coverage and species composition

Total coverage of the hermatypic coral community in the aquarium was 20.7%. *A. microphthalma* (16.6%) was the species with the highest coverage. *Montipora cactus* (1.9%), *Porites cylindrica* (1.2%), and *Montipora stellata* (1.1%) were also present (Fig. 4, Table 2). This combination of coral species is representative of a typical branching *Acropora* community on the inner reef flat (Fig. 2).

Results of incubation experiments

Changes in pH, A_T , and C_T inside the aquarium before and after sealing at 3-h intervals are shown in Fig. 5 and Table 3. Three-hour averages of F_P , G , P_n , and concentrations of carbon species ($[\text{CO}_2(\text{aq})^*]$ and $[\text{CO}_3^{2-}]$) are shown in Fig. 6 and Table 3. The F_P values obtained over the period

Fig. 5 Time series of **a** pH, **b** total alkalinity (A_T), and computed total carbon (C_T), assuming equilibrium of seawater. Arrows indicate seawater-sampling times

Table 3 Variations in pH, total alkalinity (A_T), and total carbon (C_T) every 3 h, and average rates of photon flux density (F_P), calcification rate (G), net photosynthesis rate (P_n), $[CO_2(aq)^*]$, and $[CO_3^{2-}]$

	pH (NBS)	A_T ($\mu\text{mol kg}^{-1}$)	C_T ($\mu\text{mol kg}^{-1}$)	F_P ($\text{mol m}^{-2} \text{h}^{-1}$)	G ($\mu\text{mol m}^{-2} \text{h}^{-1}$)	P_n ($\mu\text{mol m}^{-2} \text{h}^{-1}$)	$[CO_2(aq)^*]$ ($\mu\text{mol kg}^{-1}$)	$[CO_3^{2-}]$ ($\mu\text{mol kg}^{-1}$)
2004/8/26								
9:00 ^a	8.243	2149	1827	4.11	4169	9910	7.852	228.91
12:00 ^b	8.348	2068	1690					
12:00 ^a	8.403	2122	1700	4.17	2863	5071	5.225	278.64
15:00 ^b	8.446	2066	1623					
15:00 ^a	8.339	2148	1765	1.69	1124	−400	7.105	245.41
18:00 ^b	8.320	2126	1758					
18:00 ^a	8.262	2155	1820	0.06	0	−1546	9.072	216.68
21:00 ^b	8.237	2155	1836					
2004/8/27								
21:00 ^a	8.225	2165	1852	0.00	0	−1258	10.083	205.02
0:00 ^b	8.204	2165	1865					
0:00 ^a	8.193	2164	1869	0.00	−270	−221	10.720	197.48
3:00 ^b	8.193	2169	1874					
3:00 ^a	8.187	2167	1876	0.00	−358	174	10.804	197.20
6:00 ^b	8.195	2174	1878					
6:00 ^a	8.198	2179	1881	0.95	1815	3144	10.143	203.72
9:00 ^b	8.226	2144	1832					

^a Start time^b End time **Fig. 6** Time series of **a** photon flux density (F_P), calcification rate (G), and net photosynthesis rate (P_n), and **b** calculated concentrations of carbonic species

from 0900 to 1500 hours on 26 August were high (about $4 \text{ mol m}^{-2} \text{h}^{-1}$) and remained relatively high during the day. F_P decreased during the evening, and was almost $0 \text{ mol m}^{-2} \text{h}^{-1}$ through the night. It increased again at sunrise, indicating a typical diurnal variation. The P_n value was highest ($9,910 \mu\text{mol m}^{-2} \text{h}^{-1}$) between 0900 and 1200 hours on 26 August, and then gradually decreased.

It was negative during the night, reaching a minimum ($-1,546 \mu\text{mol m}^{-2} \text{h}^{-1}$) between 1800 and 2100 hours. It returned to a positive value around sunrise, when F_P also increased. The variation of G was similar to that of P_n . Maximum G ($4,169 \mu\text{mol m}^{-2} \text{h}^{-1}$) was observed between 0900 and 1200 hours, but it was low at almost $0 \mu\text{mol m}^{-2} \text{h}^{-1}$ during the night. $[CO_2(aq)^*]$ decreased from 0900 to 1500 hours, and rose slowly during the afternoon and night. A small decrease was observed early in the morning of 27 August. The temporal change of $[CO_3^{2-}]$ showed an inverse relationship with that of $[CO_2(aq)^*]$.

Discussion

Models of photosynthesis and calcification

P_n model

The trend of the temporal change of P_n was very similar to that of F_P (coefficient of determination $r^2 = 0.75$) (Fig. 6). P_n is the difference between respiration rate (R) and gross photosynthesis (P_g):

$$P_n = P_g - R. \quad (7)$$

Therefore, P_n (or P_g) is clearly dependent on F_P . This relationship has been well documented in studies of the production of coral colonies (Chalker 1981), reefs (Barnes

and Devereux 1984), and other photosynthetic organisms (Zimmerman et al. 1997; Martin et al. 2006).

Acceleration of coral growth and photosynthesis rates because of increased levels of $[\text{CO}_2(\text{aq})^*]$ have been reported from experiments on diatoms (Riebesell et al. 1993), green algae *Halimeda* (Borowitzka and Larkum 1976), giant algal coenocytes (Lucas 1975), red algae (Borowitzka 1981), red calcareous algae (Gao et al. 1993), and sea grasses (Zimmerman et al. 1997). The P_n value recorded between 1200 and 1500 hours on 26 August was much lower than that recorded between 0900 and 1200 hours on the same day, although F_P values over the two periods were almost the same. It is interesting that a decrease in $[\text{CO}_2(\text{aq})^*]$ was observed over that time. The P_n value between 1500 and 1800 hours on 26 August was also lower than that between 0600 and 0900 hours on 27 August, whereas F_P during the former period was higher than that during the latter period. $[\text{CO}_2(\text{aq})^*]$ between 1500 and 1800 hours on 26 August was less than that between 0600 and 0900 hours on 27 August. These results strongly suggest that the P_g rate is dependent on $[\text{CO}_2(\text{aq})^*]$.

It is here assumed that P_g is proportional to both F_P and $[\text{CO}_2(\text{aq})^*]$, because, as discussed above, it depends on both:

$$P_g = k_P \cdot F_P \cdot [\text{CO}_2(\text{aq})^*], \quad (8)$$

where k_P is a constant. The P_g – F_P curve is usually composed of two phases: a linear phase at low F_P ; and a constant phase, owing to saturation, at higher F_P . In previous studies, P_g was commonly fitted to the non-linear part of the function (Chalker 1981; Barnes and Devereux 1984; Zimmerman et al. 1997). The P_g in this study was, however, assumed to be a linear function of F_P , because the saturation levels were not observed in this study. Here, P_n is derived by substituting P_g from Eq. (8) in Eq. (7) on the assumption that R is constant. Thus,

$$P_n = k_P \cdot F_P \cdot [\text{CO}_2(\text{aq})^*] - R. \quad (9)$$

Using the least-squares method (Fig. 7), the two unknowns, k_P and R , were determined as follows:

$$k_P = 3.054 \times 10^{-4} \quad (10)$$

and

$$R = 1,058 \mu\text{mol m}^{-2} \text{h}^{-1} (= 25,392 \mu\text{mol m}^{-2} \text{d}^{-1}). \quad (11)$$

Units used for P_n , F_P , and $[\text{CO}_2(\text{aq})^*]$ in this model were $\mu\text{mol m}^{-2} \text{h}^{-1}$, $\text{mol m}^{-2} \text{h}^{-1}$, and $\mu\text{mol kg}^{-1}$, respectively. The coefficient of determination for the data of this study

Fig. 7 Regression of net photosynthesis rate (P_n) with product of photon flux density (F_P) and $[\text{CO}_2(\text{aq})^*]$

as described by Eq. (9) ($r^2 = 0.87$) (Fig. 7) suggests that this model for P_n is valid.

G model

Because the temporal behavior patterns of G are similar to those of P_n ($= P_g - R$) (Fig. 6), G and P_g should be expressed by similar equations. There is good correlation between G and P_g ($r^2 = 0.89$). A similar positive correlation between G and P_n (or P_g) for hermatypic corals has been reported by Suzuki et al. (1995), Gattuso et al. (1999), and Barnes and Devereux (1984), and termed “light enhanced calcification” (Goreau 1959; Goreau and Goreau 1959; Barnes and Chalker 1990; Gattuso et al. 1999, 2000). A model where G is a function of P_g is therefore adopted in this study.

The G is a function of Ω_{arag} on the basis of coral incubation experiments. Values of G have previously been fitted to a non-linear Ω_{arag} function of the saturation curve for the hermatypic coral *Stylophora pistillata* (Gattuso et al. 1998a), to linear functions of Ω_{arag} for both the hermatypic coral *Porites porites* (Marubini and Thake 1999) and a coral reef community (Odhe and van Woesik 1999; Leclercq et al. 2000, 2002). Langdon et al. (2000) found a similar linear relationship between G and Ω_{arag} for a coral reef community during short-term (days) and long-term (months to years) experiments carried out in the Biosphere 2 ocean.

Although Ω_{arag} is proportional to the product of $[\text{Ca}^{2+}]$ and $[\text{CO}_3^{2-}]$, it is here expressed as a function only of $[\text{CO}_3^{2-}]$, because the concentration of Ca^{2+} in the seawater was so high ($\sim 10^4 \mu\text{mol kg}^{-1}$) that small changes in its

Fig. 8 Regression of calcification rate (G) with product of gross photosynthesis rate (P_g) and $[\text{CO}_3^{2-}]$

concentration had negligible effect on Ω_{arag} . Thus, it was assumed that G is proportional to the product of P_g and $[\text{CO}_3^{2-}]$:

$$G = k_G \cdot P_g \cdot [\text{CO}_3^{2-}], \quad (12)$$

where k_G is a constant. The value of the coefficient k_G was determined by using the least-squares method:

$$k_G = 1.683 \times 10^{-3}. \quad (13)$$

The units for G , P_g , and $[\text{CO}_3^{2-}]$ are $\mu\text{mol m}^{-2} \text{h}^{-1}$, $\mu\text{mol m}^{-2} \text{h}^{-1}$, and $\mu\text{mol kg}^{-1}$, respectively. The regression line (Fig. 8) derived from Eq. (12) suggests that the relationship expressed by Eq. (12) is valid ($r^2 = 0.91$).

The Eq. (12) model for G includes the metabolic parameter P_g , which can be removed by substitution of Eq. (8) in Eq. (12). Thus:

$$G = k \cdot F_P \cdot [\text{CO}_2(\text{aq})^*] \cdot [\text{CO}_3^{2-}], \quad (14)$$

where $k = k_P \cdot k_G$, and G is now expressed only in terms of physical and chemical parameters.

Model for coral reef formation

Calcification rate

The values of G given by Eq. (14) can be applied only to the calcification rate of the coral community in the aquarium, because the biomass within the community varies from place to place. Another equation must be developed that can be applied more generally. The calcification rate of coral communities may depend on the

biomass per unit area, i.e., map view coverage. Therefore, the simple model that the calcification rate is proportional to coverage (Cov, %) is here proposed. The revised calcification rate (G') is a product of G and Cov:

$$G' = G \cdot \text{Cov} / 20.7 \quad (15)$$

$$= k' \cdot F_P \cdot [\text{CO}_2(\text{aq})^*] \cdot [\text{CO}_3^{2-}] \cdot \text{Cov},$$

where $k' = k/20.7$. The value of 20.7 in Eq. (15) is the actual coverage (%) obtained for the community in this study.

The F_P received by corals (Eq. 15) can be calculated only as a function of water depth (h). It decreases exponentially with increasing depth as follows:

$$F_P = F_{P0} (1 - \alpha) \exp[-\lambda h], \quad (16)$$

where F_{P0} is the photon flux density at the sea surface, α is the albedo of seawater, and λ is the absorption coefficient of seawater.

The $[\text{CO}_2(\text{aq})^*]$ and $[\text{CO}_3^{2-}]$ in Eq. (15) can be computed from C_T , if some assumptions are made. Most decreases in C_T are derived from calcification, because heterotrophic organisms living around the corals consume most of the organic matter, and because the P_g/R ratio of the coral community is close to 1 (Odum and Odum 1955; Kinsey 1977; Crossland et al. 1991; Nakamori et al. 1992; Gattuso et al. 1998b). So, it is assumed that all of the C_T change is the result of calcification. The value of A_T is given by the following equation:

$$A_T = A_{T0} - 2(C_{T0} - C_T), \quad (17)$$

where A_{T0} and C_{T0} are initial values of A_T and C_T , respectively. Using C_T and A_T computed from Eq. (17), $[\text{CO}_2(\text{aq})^*]$ and $[\text{CO}_3^{2-}]$ can be computed by solving the equations in equilibrium (Suzuki et al. 1995).

Modeling of Cov in Eq. (15) is difficult, because Cov is affected by damage from various sources, e.g., by bottom sedimentation, turbidity, and nutrients. However, coral coverage was observed to be lower in depressions than in other parts of the study area. A simple assumption that the coverage is 0% where the reef surface is depressed and 100% in other areas was introduced. This concept is expressed by the following conditions of depth (h):

$$\text{Cov} \rightarrow \begin{cases} 0 \%, & \text{if } \nabla h \approx 0 \cap \nabla^2 h < 0 \\ 100 \%, & \text{otherwise} \end{cases}, \quad (18)$$

where ∇h is the gradient of h , and $\nabla^2 h$ is curvature of h . The surface is flat when ∇h equals 0; it is depressed if $\nabla^2 h < 0$. A simple function to describe coverage was defined as follows:

$$\text{Cov} = 50 \{ 1 + \tanh[a\nabla^2 h + b(\nabla h)^2 - c] \}, \quad (19)$$

where a , b , and c are constants. Furthermore, corals tend not to inhabit an environment shallower than the low-tide level, so the following condition was applied:

$$\text{Cov} = 0\%, \quad \text{if } h < 0.6 \text{ m}. \quad (20)$$

Thus, Cov is a function of h in this model.

In conclusion, G' as given by Eq. (15) can be written as a simple function of two variables, i.e., h and C_T .

Reef profile

Depth (h) is considered to influence various phenomena in a reef environment; for example, reef growth, sea-level change, and mass movement by erosion or deposition. Changes in h can be expressed by the following equation:

$$\frac{\partial h}{\partial t} = -V_R + V_S + D \frac{\partial^2 h}{\partial x^2}, \quad (21)$$

where x is a coordinate on the horizontal axis, V_R is the growth rate of the reef, V_S is the rate of sea-level rise, and D is a constant. The first term of right-hand side represents a decrease in h as a result of upward reef growth. The second term represents an increase in h as a result of sea-level rise. The last term has the effect of surface smoothing, and represents transportation of carbonate mass by erosion and secondary deposition. This term was proposed by Scheidegger (1970) by drawing an analogy between geomorphology and thermodynamics. The V_R of Eq. (21) can be derived from the variable G' by using the following equation:

$$V_R = \frac{M}{\rho_R} G', \quad (22)$$

where M is molecular mass of CaCO_3 and ρ_R is the density of the reef rock. Buddemeier and Smith (1988) concluded that the average value of ρ_R within reef systems is 1.4 g cm^{-3} .

Distribution of C_T

The distribution of C_T in seawater in a reef environment may exhibit a complicated pattern, caused mainly by tidal

effects. Total fluxes due to ebb and flow are the same. It implies that the averaged advection should be zero. If considered over long periods (years), and at large scale (meters to kilometers), the tidal effects can be represented by a simple eddy, and approximated by eddy diffusion. The C_T distribution can then be determined using the following two-dimensional diffusion equation:

$$\frac{\partial C_T}{\partial t} = K_x \frac{\partial^2 C_T}{\partial x^2} + K_y \frac{\partial^2 C_T}{\partial y^2}, \quad (23)$$

where x and y are coordinates on horizontal and vertical axes, and K_x and K_y are the horizontal and vertical eddy diffusion coefficients of seawater, respectively. The boundary condition between seawater and coral reef ($y = h$) is given by Fick's law of diffusion:

$$G' = -\rho_w K_y \frac{\partial C_T}{\partial y} \bigg|_{y=h}, \quad (24)$$

where G' is the C_T flux as a result of calcification.

Simulations of coral reef formation

Computer simulations were carried out by applying the finite difference method on variables indicating space and time to the geochemical model for coral reef formation described above. Depth profiles given by Eq. (21) were calculated every 20 m along the x -axis ($0 \leq x \leq 2,560 \text{ m}$). The initial profile of h is represented by an inclined flat plane (Fig. 9a). The boundary conditions at $x = 0$ and $x = 2,560$ were chosen to satisfy $\partial h / \partial t = V_S$. The rate of sea-level rise, V_S in Eq. (21) and in boundary conditions, was constant at $0.002 \text{ m year}^{-1}$. The calculations of C_T distribution from Eq. (23) were carried out in two-dimensional space ($2,560 \times 16 \text{ m}$). Grid dimensions of 20 m horizontal (x) and 0.5 m vertical (y) were chosen to provide adequate resolution of a vertical cross-section of reef topography. The reef–seawater boundary was mapped onto the lattice shown in Fig. 10 and was updated for every output of topography in the simulation. The initial condition for C_T of seawater was set at a homogeneous concentration of $2,000 \mu\text{mol kg}^{-1}$ (Fig. 9b). Zero flux boundary conditions were applied at the atmosphere–seawater and reef–seawater interfaces in the horizontal

Fig. 9 Initial conditions of **a** water depth profile and **b** concentration of total carbon dioxide

Fig. 10 Modeled reef–seawater boundary and boundary conditions

Table 4 Parameters used for computer simulations

Symbol	Value	Unit
A_{T0}	2400	$\mu\text{mol kg}^{-1}$
C_{T0}	2000	$\mu\text{mol kg}^{-1}$
B_T	430	$\mu\text{mol kg}^{-1}$
K_1'	9.95×10^{-7}	
K_2'	7.61×10^{-10}	
K_B'	2.03×10^{-9}	
F_{P0}	2.50×10^{10}	$\mu\text{mol m}^{-2} \text{ year}^{-1}$
α	0.07	
a	5.0	
b	50	
c	0.2	
λ	0.44	
D	1.0	$\text{m}^2 \text{ year}^{-1}$
K_x	$10^7 \sim 10^8$	$\text{m}^2 \text{ year}^{-1}$
K_v	1.0×10^4	$\text{m}^2 \text{ year}^{-1}$

direction. The vertical component of the flux at the reef–seawater boundary was determined from Eq. (24). The Dirichlet condition ($C_T = 2,000 \mu\text{mol kg}^{-1}$) was employed at the boundary 2,560 m distant from the shore, because C_T in the offshore environment was assumed to be constant at around $2,000 \mu\text{mol kg}^{-1}$ (Fig. 9). The period of the simulation step was set to 1.0×10^{-6} years for the past 5,000 years. The values of other parameters used in the simulation are provided in Table 4.

First, the effects of changing the eddy diffusion coefficient, K_x , were examined. The topography at $t = 5,000$ years for the four cases of $K_x = 1.0 \times 10^7$, 2.5×10^7 , 5.0×10^7 , and $1.0 \times 10^8 \text{ m}^2 \text{ year}^{-1}$ were calculated (Fig. 11). The crest-like structure emerged for each of these simulations. The rate of reef deposition was higher when K_x was higher. The gradient of the simulated C_T at high K_x was gentler than at low K_x .

Oceanward gradients of pH, C_T , A_T and $f\text{CO}_2$ across lagoons as a result of calcification were observed at Palau Barrier Reef, Majuro Atoll, South Male Atoll (Suzuki

et al. 1997; Suzuki and Kawahata 1999), and the Great Barrier Reef (Kawahata et al. 2000). In most cases, the values of C_T in lagoons were lower than those in the adjacent open oceans. Watanabe et al. (2006) observed the two-dimensional vertical profiles of C_T through the Palau barrier reef, and reported decreases from offshore to shore, and also from deep to shallow areas. In the model simulations of this study, C_T also consistently decreased from offshore to shore, and from deep to shallow areas (Fig. 11b, d, f, h).

In conclusion, the results of the modeling described here are supported by some of the reef system phenomena that have been observed in nature. For example, growth rates of coral reefs are generally faster on the windward side than on the leeward side (Hopley and Barnes 1985; Kan et al. 1997; Yamano et al. 2001a). One of the most conspicuous difference between the windward and leeward environments is the level of hydrodynamics. In fact, wind-driven water circulation in coral reefs has been reported by Atkinson et al. (1981) and Yamano et al. (1998). The circulation rate on the windward side, for example, is faster than that on the leeward side, and is considered to be the result of horizontal eddy diffusion. In the computer simulations of this study, reef development was greater when high K_x values were used (Fig. 11e–h) because of the greater availability of carbon (high C_T). The difference in the degree of reef development from the windward to the leeward side of the reef may result from corresponding differences in diffusion rate and carbon supply.

Figure 12 shows the evolution of the reef for the case where $K_x = 2.5 \times 10^7 \text{ m}^2 \text{ year}^{-1}$. Snapshots of the topography and C_T distribution at 1,000-year intervals between $t = 1,000$ and $t = 5,000$ years are shown. The following process is evident in the series of simulations. The horizontal surface of the carbonate platform is constructed as sea-level rises over the first 2,000 years (Fig. 12a, c). The C_T gradient from offshore to shore becomes steeper over the first 3,000 years (Fig. 12b, d, f). As a result, the near-shore growth rate of the reef falls (Fig. 12e), and crest-like

Fig. 11 Morphological changes in coral reef topography (a, c, e, and g) and concentration of total carbon dioxide (b, d, f, and h) obtained from simulations varying horizontal diffusion coefficients. Intervals between simulations were 5,000 years

convex structures develop at around 3,000 years and persist in the ensuing years (Fig. 12g). The seaward crest inhibits carbon supply to the moat and the C_T gradient becomes progressively steeper from 4,000 to 5,000 years (Fig. 12h, j). The growth rate of the seaward crest remains high during this period, because this area receives enough light and carbon to maintain rapid growth. At the same time, the growth rate of the moat decreases because of a lower supply of light and carbon. Finally, after 5,000 years, both the seaward crest and the moat are clearly defined as a result of these geochemical processes (Fig. 12i).

Takahashi et al. (1988) reconstructed reef growth during the Holocene sea-level change at Kume Island, in the Ryukyu Islands, on the basis of radiometric ages obtained from core samples. They proposed five phases: (1) the initial reef phase (7,400–7,000 years BP), (2) the juvenile phase (7,000–6,000 years BP), (3) the crest growth phase (6,000–5,500 years BP), (4) the back-reef growth phase (5,500–5,000 years BP), and (5) the fore-reef growth phase (5,000–2,000 years BP). In their study, reef growth

in most areas kept up with the rise in sea level, resulting in a lack of differentiation between the moat and the crest during the phase (1) to the phase (2). A distinct crest developed rapidly during the phase (3), when the moat was also constructed. The sea-level rise has finally stopped, and back-reef and fore-reef were developed during the phase (4) to the phase (5). The results of the simulations are almost identical to the phases (1), (2) and (3), when setting of the simulation for sea-level and actual pattern are almost the same. It is also worthy of note that the patterns of reef growth shown in the simulations of this study (Fig. 12) during sea-level rise are very similar to those observed in nature.

This model accurately reconstructed the growth history of the Holocene reef system in Ryukyu Islands. The model, therefore, has potential applications within a range of reef studies in many different geographical contexts. For example, it is considered that the model could be used to reconstruct the Holocene histories of many reef systems worldwide, and the timing of their effects on coastal

Fig. 12 Evolution of water depth profile and concentration of total carbon dioxide from 1,000 to 5,000 years. The horizontal eddy diffusion coefficient $K_x = 2.5 \times 10^7$ ($\text{m}^2 \text{year}^{-1}$) was used for the simulations

hydrodynamics. Or, the geochemical model, together with reef framework and topography, could be used to constrain reconstructions of sea-level history.

References

- Atkinson M, Smith SV, Stroup ED (1981) Circulation in Enewetak Atoll lagoon. *Limnol Oceanogr* 26:1074–1083
- Barnes DJ, Chalker BE (1990) Calcification and photosynthesis in reef-building corals and algae. In: Dubinsky (ed) *Coral reefs*. Elsevier, Amsterdam, pp 109–131
- 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
- Borowitzka MA (1981) Photosynthesis and calcification in the articulated coralline algae *Amphiroa anceps* and *A. foliaceae*. *Mar Biol* 62:17–23
- Borowitzka MA, Larkum WD (1976) Calcification in the green algae *Halimeda*. III. The source of inorganic carbon for photosynthesis and a model of the mechanism of calcification. *J Exp Bot* 27:879–893
- Buddemeier RW, Smith SV (1988) Coral reef growth in an era of rapidly rising sea level: predictions and suggestions for long-term research. *Coral Reefs* 7:51–56
- Chalker BE (1981) Simulating light-saturation curves for photosynthesis and calcification by reef-building corals. *Mar Biol* 63:135–141
- Chisholm JRM, Gattuso JP (1991) Validation of alkalinity anomaly technique for investigating calcification and photosynthesis in coral reef communities. *Limnol Oceanogr* 36:1232–1239
- Cortés J, Macintyre IG, Glynn PW (1994) Holocene growth history of an Eastern Pacific fringing reef, Punta Isletes, Costa Rica. *Coral Reefs* 13:65–73
- Crossland CJ, Hatcher BJ, Smith SV (1991) Role of coral reefs in global ocean production. *Coral Reefs* 10:55–64

- Culberson CH, Pytkowicz RM (1973) Ionization of water in seawater. *Mar Chem* 1:309–316
- Culberson CH, Pytkowicz RM, Hawley JE (1970) Seawater alkalinity determination by the pH method. *J Mar Res* 28:15–21
- Culkin F (1965) The major constituents of seawater. In: Riley JP, Skirrow G (eds) *Chemical oceanography*. Academic Press, New York, pp 121–161
- Gao K, Aruga Y, Asada K, Ishihara T, Akano T, Kiyohara M (1993) Calcification in the articulated coralline alga *Corallina pilulifera*, with special reference to effect of elevated CO₂ concentration. *Mar Biol* 117:129–132
- Gattuso JP, Frankignoulle M, Bourge I, Romaine S, Buddemeier RW (1998a) Effect of calcium carbonate saturation of seawater on coral calcification. *Global Planet Change* 18:37–46
- Gattuso JP, Frankignoulle M, Wollast R (1998b) Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annu Rev Ecol Syst* 29:405–433
- Gattuso JP, Allemand D, Frankignoulle M (1999) Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: a review on interaction and control by carbonate chemistry. *Am Zool* 39:160–183
- Gattuso JP, Reynaud-Vaganay S, Furla P, Romaine-Lioud S, Jaubert J, Bourge I, Frankignoulle M (2000) Calcification does not stimulate photosynthesis in the zooxanthellate scleractinian coral *Stylophora pistillata*. *Limnol Oceanogr* 45:246–250
- Goreau TF (1959) The physiology of skeleton formation in corals. I. A method for measuring the rate of calcium deposition by corals under different conditions. *Biol Bull* 116:59–75
- Goreau TF, Goreau NI (1959) The physiology of skeleton formation in corals. II. Calcium deposition by hermatypic corals under various conditions in the reef. *Biol Bull* 117:239–250
- Hopley D, Barnes R (1985) Structure and development of a windward fringing reef, Orpheus Island, Palm Group, Great Barrier Reef. *Proc 5th Int Coral Reef Symp* 3:141–146
- Kan H, Hori N (1993) Formation of topographic zonation on the well-developed fringing reef-flat, Minna Island, the Central Ryukyus. *Transactions Japanese Geomorphological Union* 14:1–16
- Kan H, Hori N, Nakashima Y, Ichikawa K (1995) The evolution of narrow reef flats at high-latitude in the Ryukyu Islands. *Coral Reefs* 14:123–130
- Kan H, Hori N, Kawana T, Kaigara T, Ichikawa K (1997) The evolution of a Holocene fringing reef and island: Reefal environmental sequence and sea level change in Tonaki Island, the Central Ryukyus. *Atoll Res Bull* 443:1–20
- Kawahata H, Suzuki A, Ayukai T, Goto T (2000) Distribution of the fugacity of carbon dioxide in the surface seawater of the Great Barrier Reef. *Mar Chem* 72:257–272
- Kayanne H, Yamano H, Randall RH (2002) Holocene sea-level changes and barrier reef formation on an oceanic island, Palau Islands, western Pacific. *Sediment Geol* 150:47–60
- Kennedy DM, Woodroffe CD (2000) Holocene lagoonal sedimentation at the latitudinal limits of reef growth, Lord Howe Island, Tasman Sea. *Mar Geol* 169:287–304
- Kinsey DW (1977) Seasonality and zonation in coral reef productivity and calcification. *Proc 3rd Int Coral Reef Symp* 2:382–388
- Konishi K, Tsuji Y, Goto T, Tanaka T, Futakuchi K (1983) Multi-hole shallow drilling of coral reefs—a case history of the Holocene in Kikai Island, central Ryukyus. *Monthly Marine Science* 15:154–164
- Langdon C, Takahashi T, Sweeney C, Chipman D, Goddard J (2000) Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Global Biogeochem Cycles* 14:639–654
- Leclercq N, Gattuso JP, Jaubert J (2000) CO₂ partial pressure controls the calcification rate of a coral community. *Global Change Biol* 6:329–334
- Leclercq N, Gattuso JP, Jaubert J (2002) Primary production, respiration, and calcification of a coral reef mesocosm under increased CO₂ partial pressure. *Limnol Oceanogr* 47:558–564
- Lucas WJ (1975) Photosynthetic fixation of ¹⁴Carbon by internodal cells of *Chara corallina*. *J Exp Biol* 26:331–346
- Lyman J (1957) Buffer mechanism of sea water. PhD Thesis, University of California, Los Angeles, p 198
- Marshall JF, Davies PJ (1982) Internal structure and Holocene evolution of One Tree Reef, Southern Great Barrier Reef. *Coral Reefs* 1:21–28
- Martin S, Castets MJ, Clavier J (2006) Primary production, respiration and calcification of the temperate free-living coralline algae *Lithothamnion corallioides*. *Aquat Bot* 85:121–128
- Marubini F, Atkinson M (1999) Effects of lowered pH and elevated nitrate on coral calcification. *Mar Ecol Prog Ser* 188:117–121
- Marubini F, Thake B (1999) Bicarbonate addition promotes coral growth. *Limnol Oceanogr* 44:716–720
- Mehrbach C, Culberson H, Hawley E, Pytkowicz M (1973) Measurement of the apparent dissociation constants of carbonic acid in seawater at atmospheric pressure. *Limnol Oceanogr* 18:897–907
- Montaggioni LF (2005) History of Indo-Pacific coral reef systems since the last glaciation: development patterns and controlling factors. *Earth-Sci Rev* 71:1–75
- Montaggioni LF, Faure G (1997) Response of reef coral communities to sea-level rise: a Holocene model from Mauritius (western Indian Ocean). *Sedimentology* 44:1053–1070
- Nakamori T (1986) Community structures of recent and Pleistocene hermatypic corals in the Ryukyu Islands, Japan. *Tohoku University Science Report, 2nd series (Geology)* 56:71–133
- Nakamori T, Suzuki A, Iryu Y (1992) Water circulation and carbon flux on Shiraho coral reef of the Ryukyu Islands, Japan. *Cont Shelf Res* 12:951–970
- Nakamura T, Nakamori T (2006) Population dynamics of hermatypic coral communities on reef slope vs. reef flat at Shiraho, Ishigaki Island, southwest Japan. *Proc 10th Int Coral Reef Symp* 460–477
- Odhe S, van Woesik R (1999) Carbon dioxide flux and metabolic processes of a coral reef, Okinawa. *Bull Mar Sci* 65:559–576
- Odum HT, Odum EP (1955) Trophic structure and productivity of windward coral reef community on Enewetok Atoll. *Ecol Monogr* 25:292–320
- Riebesell U, Wolf-Gladrow DA, Smetacek V (1993) Carbon dioxide limitation of marine phytoplankton growth rate. *Nature* 361:249–251
- Scheidegger AE (1970) *Theoretical geomorphology*. 2nd edn. Springer, New York
- Smith SV, Key GS (1975) Carbon dioxide and metabolism in marine environments. *Limnol Oceanogr* 20:493–495
- Smith SV, Kinsey DW (1978) Calcification and organic carbon metabolism as indicated by carbon dioxide. In: Stoddart DR, Johannes RE (eds) *Coral reefs: research methods*. UNESCO, pp 469–484
- Suzuki A, Kawahata H (1999) Partial pressure of carbon dioxide in coral reef lagoon waters: comparative study of atolls and barrier reefs in the Indo-Pacific Oceans. *J Oceanogr* 55:731–745
- Suzuki A, Nakamori T, Kayanne H (1995) The mechanism of production enhancement in coral reef carbonate system: model and empirical results. *Sediment Geol* 99:259–280
- Suzuki A, Kawahata H, Goto K (1997) Reef water CO₂ system and carbon cycle in Majuro Atoll, the Marshall Islands in the central Pacific. *Proc 8th Int Coral Reef Symp* 1:971–976
- Takahashi T, Koba M, Kan H (1988) Relationship between reef growth and sea level on the Northwest coast of Kume Island, the Ryukyus: data from drill holes on the Holocene coral reef. *Proc 6th Int Coral Reef Symp* 3:194–196

- Watanabe A, Kayanne H, Hata H, Kudo S, Nozaki K, Kato K, Negishi A, Ikeda Y, Yamano H (2006) Analysis of the seawater CO₂ system in the barrier reef-lagoon system of Palau using total alkalinity-dissolved inorganic carbon diagram. *Limnol Oceanogr* 51:1614–1628
- Yamano H, Kayanne H, Yonekura N, Nakamura H (1998) Water circulation in a fringing reef located in a monsoon area: Kabira Reef, Ishigaki Island, southwest Japan. *Coral Reefs* 17:89–99
- Yamano H, Abe O, Kitagawa H, Niu E, Nakamura T (2001a) Coral reef evolution at the leeward side of Ishigaki Island, southwest Japan. *Radiocarbon* 43:899–908
- Yamano H, Kayanne H, Yonekura N (2001b) Anatomy of a modern coral reef flat: a recorder of storms and uplift in the late Holocene. *J Sediment Res* 71:295–304
- Yamashiro H (1995) The effects of HEBP, an inhibitor of mineral deposition, upon photosynthesis and calcification in the scleractinian coral, *Stylophora pistillata*. *J Exp Mar Biol Ecol* 191:57–63
- Yonekura N, Kayanne H, Matumoto E, Ishii T, Matushima Y, Hori N, Nakai T (1994) Geomorphic development of modern fringing reef of Yoron Island, Ryukyu Arc, Japan. *Quat Res (Tokyo)* 33:67–79
- Zimmerman RC, Kohrs DG, Steller DL, Alberte RS (1997) Impacts of CO₂ enrichment on productivity and light requirements of eelgrass. *Plant Physiol* 115:599–601