Tellus (2003), 55B, 428–444
Printed in UK. All rights reserved

TELLUS
ISSN 0280–6509

Carbon budget of coral reef systems: an overview of observations in fringing reefs, barrier reefs and atolls in the Indo-Pacific regions

By ATSUSHI SUZUKI[1,*] and HODAKA KAWAHATA[1,2], [1]*Institute for Marine Resources and Environment, National Institute of Advanced Industrial Science and Technology, Higashi 1-1-1, Tsukuba, Ibaraki 305-8567, Japan;* [2]*Graduate School of Science, Tohoku University, Aoba, Sendai, 908-8578, Japan*

(Manuscript received 7 January 2002; in final form 15 August 2002)

ABSTRACT

The seawater CO_2 system and carbon budget were examined in coral reefs of wide variety with respect to topographic types and oceanographic settings in the Indo-Pacific oceans. A system-level net organic-to-inorganic carbon production ratio (R_{OI}) is a master parameter for controlling the carbon cycle in coral reef systems, including their sink/source behavior for atmospheric CO_2. A reef system with R_{OI} less than approximately 0.6 has a potential for releasing CO_2. The production ratio, however, is not easy to estimate on a particular reef. Instead, observations planned to detect the offshore–lagoon difference in partial pressure of CO_2 ($p\mathrm{CO}_2$) and a graphic approach based on a total alkalinity–dissolved inorganic carbon diagram can reveal system-level performance of the carbon cycle in coral reefs. Surface $p\mathrm{CO}_2$ values in the lagoons of atolls and barrier reefs were consistently higher than those in their offshore waters, showing differences between 6 and 46 μatm, together with a depletion in total alkalinity up to 100 μmol kg^{-1}, indicating predominant carbonate production relative to net organic carbon production. Reef topography, especially residence time of lagoon water, has a secondary effect on the magnitude of the offshore–lagoon $p\mathrm{CO}_2$ difference. Terrestrial influence was recognized in costal reefs, including the GBR lagoon and a fringing reef of the Ryukyu Islands. High carbon input appears to enhance CO_2 efflux to the atmosphere because of their high dissolved C:P ratios. Coral reefs, in general, act as an alkalinity sink and a potentially CO_2-releasing site due to carbonate precipitation and land-derived carbon.

1. Introduction

Coral reefs occur widely, and produce a large amount of $CaCO_3$ in tropical and subtropical shallow regions. The role of coral reef systems in the global carbon cycle has attracted much attention in the last few decades (Smith, 1978; 1981; Crossland et al., 1991). In particular, the sink/source behavior of coral reefs with respect to the atmospheric CO_2 has been the subject of considerable discussion (Kayanne et al., 1995; Gattuso et al., 1996a).

The most important biogeochemical processes in the coral reef system are photosynthesis and calcification. The sink/source behavior of coral reefs is also controlled by the balance between these two processes. They shift the chemical equilibrium of the oceanic CO_2 system in opposite directions. Photosynthesis decreases the partial pressure of CO_2 ($p\mathrm{CO}_2$), while calcium carbonate production raises $p\mathrm{CO}_2$ as follows:

$$\text{photosynthesis: } CO_2 + H_2O \longrightarrow CH_2O + O_2 \qquad (1)$$

$$\text{calcification: } Ca^{2+} + 2HCO_3^- \longrightarrow CaCO_3 + H_2O + CO_2. \qquad (2)$$

---

[*] Corresponding author.
e-mail: a.suzuki@aist.go.jp

The released CO_2/precipitated carbonate ratio (Ψ) was estimated to be 0.6 in seawater by modeling the CO_2 system (Ware et al., 1992; Frankignoulle et al., 1994). Effects of photosynthesis on pCO_2 should also be taken into account, because photosynthesis occurs simultaneously with calcification. From this point of view, the criteria of the CO_2 sink/source problem were discussed by Suzuki (1998) using the ratio of net organic carbon production to inorganic carbon production (R_{OI}). When the ratio R_{OI} exceeds approximately 0.6, pCO_2 in seawater decreases and the atmospheric CO_2 is absorbed into reef water. Examinations using the parameter R_{OI} are applicable to the level of individual coral reef systems.

Kayanne et al. (1995) reported the diurnal change of pCO_2 in reef water of Ishighaki Island, the Ryukyus, together with an estimation of $R_{OI} \approx 1.1$, and suggested the reef acts as a CO_2 sink. One of the criticisms of Kayanne et al. (1995) is that the results come from a fringing reef with terrestrial and probably human disturbances and should not be applied to other types of coral reef (Gattuso et al., 1996a; 1999).

In contrast to Kayanne et al. (1995), studies in Moorea, the French Polynesia, and Yonge Reef of the northern Great Barrier Reef (GBR) showed that reef flat communities are net sources of atmospheric CO_2 (Gattuso et al., 1993; 1995; 1996b; Frankignoulle et al., 1996). Although their conclusion that most coral reefs are sources of CO_2 to the atmosphere was recently challenged by Chisholm and Barnes (1998) from the technical viewpoint for metabolism measurements, the conclusion still appears to stand (Gattuso et al., 1999).

While the sink/source debate mostly focused on "coral reef flat", interesting observations emerged from mid-oceanic reefs, such as the Majuro Atoll and Palau barrier reef, which showed high pCO_2 in reef lagoons compared to that in the offshore area: i.e. reef lagoons act as a source for the atmospheric CO_2 (Kawahata et al., 1997; Suzuki et al., 1997). Observations in the GBR lagoon, the largest reef system in the world, also showed the similar results (Kawahata et al., 2000b; Suzuki et al., 2001).

In addition to the results from coral reef flats, observations from reef lagoons confirm the current understanding that most coral reefs work as sources of the atmospheric CO_2. On the other hand, the differences in the mode of carbon cycle among coral reefs have become evident, as the number of observations increases. Although the variations may be related to topographic types and oceanographic settings of individual reefs as well as the influence of human disturbance, factors controlling the carbon cycle in coral reef systems have not yet been fully examined.

Here we re-examine our results from individual reefs in the Indo-Pacific oceans and summarize them together with published information, in order to investigate parameters controlling the carbon budget of coral reefs as well as sink/source performance with respect to the atmospheric CO_2. Special attention is paid to topographic features and water circulations in those reefs, together with terrestrial influences on costal reefs. In addition, we propose a graphic approach based the on total alkalinity (A_T)–dissolved inorganic carbon (*DIC*) diagram as a useful tool for examining the functioning of the carbon cycle in coral reef systems.

2. Research sites and methods

2.1. Observations on marine CO_2 system

The seawater CO_2 system parameters were observed on coral reefs in the Indo-Pacific region (Fig. 1). Reefs investigated include Shiraho Reef, a fringing reef of the Ryukyu Islands (Suzuki et al., 1995; Kawahata et al., 2000a), the Palau barrier reef (Kawahata et al., 1997) and Majuro Atoll (Suzuki et al., 1997) in the north equatorial Pacific and South Male Atoll of the Maldives in the Indian Ocean as well as the Great Barrier Reef (GBR, Kawahata et al., 2000b; Suzuki et al., 2001).

On all reefs investigated, discrete water samples were collected and temperature, salinity, pH, A_T and *DIC* were measured. While the simple pH method originally proposed by Culberson et al. (1970) was employed during expeditions to Ishigaki Island in September 1990 (Suzuki et al., 1995) and South Male Atoll in October 1995, the potentiometric titration method was used in later expeditions. The *DIC* was measured by a modification of the gas chromatographic method (Weiss and Craig, 1973). Details of measurements and calculations of pCO_2 based on chemical equilibrium of the CO_2 system are described in the original papers mentioned above. Direct measurements on pCO_2 were conducted using a shipboard nondispersive infrared (NDIR) gas analyzer system with a shower-type air–sea equilibrator onboard R/V Hakurai-Maru in Palau reef, Majuro Atoll and the GBR.

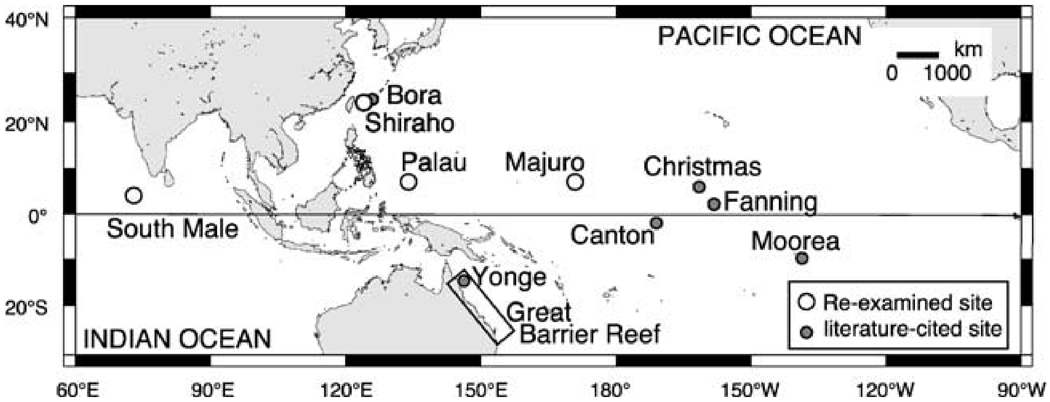

Fig. 1. Locality map of coral reefs investigated and referred in this study.

2.2. *Topographic features of coral reefs investigated*

2.2.1. Palau barrier reef (Southern Lagoon). The Ngerdiluches Barrier Reef (Maragos and Cook, 1995) is located on the southern side of the Palau (Belau) Archipelago, Caroline Islands (7°30′N, 134°330′E; Fig. 2A). A wide lagoon (Southern Lagoon) with a maximum depth of 55 m exists between the islands and a barrier reef platform. The narrow 'Toachel Mlengui' channel at the northern end of the lagoon is the only

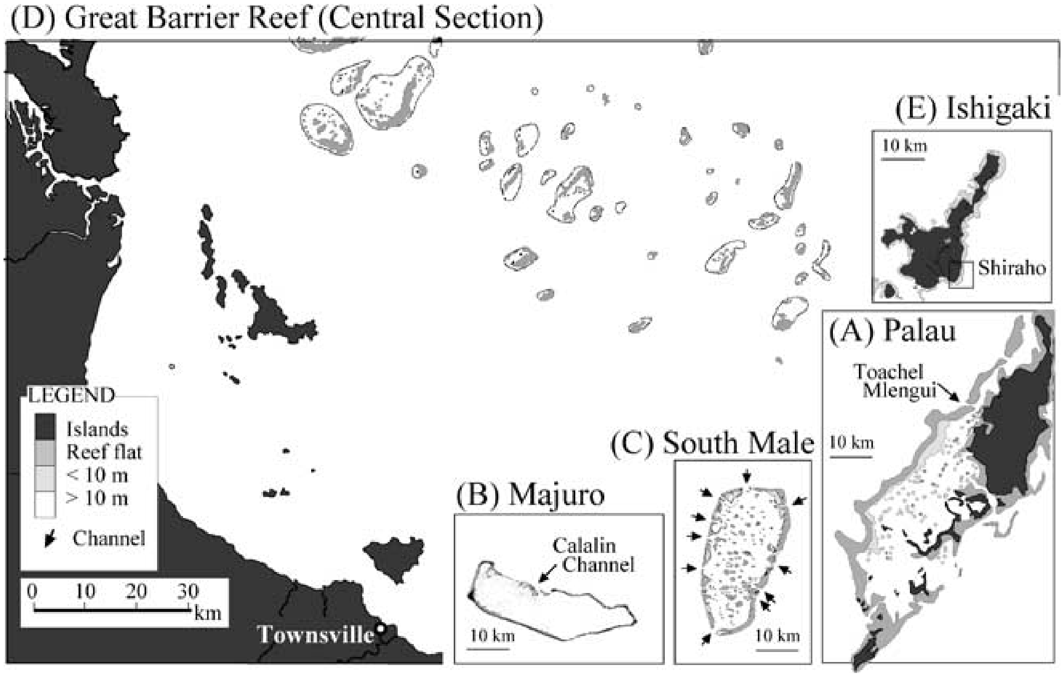

Fig. 2. Topography of the Palau barrier reef (A), Majuro Atoll (B), South Male Atoll (C), and Ishigaki Island (E), superimposed on the map of the central section of the Great Barrier Reef (GBR) near Townsville (D). All maps are shown at the same scale for comparison. Three mid-oceanic atolls investigated in this study (A, B and C) have lagoons of similar size, but those are different in the degree of closure to the surrounding sea. A contiguous north–south body of open water between the reefs and the Australian continent is referred as the "GBR lagoon" (D). As reefs occupy only a small portion of continental shelf area, the GBR may be considered a shallow coastal sea, bounded by a porous matrix of coral reefs.

deep passage with a maximum depth of 65 m. There is no other passage in the northwestern side of Southern Lagoon along the reef platform extending for approximately 86 km.

2.2.2. Majuro Atoll. Majuro Atoll (7°06′N, 171°10′E; Fig. 2B) in the Marshall Islands, the central Pacific, has a semi-enclosed lagoon with a maximum depth of 67 m. The southern side is almost entirely surrounded by an island. On the other hand, the northern side is surrounded by very shallow (0–2 m deep) reefs with a chain of sand cays. Calalin Channel, situated at the northern end of the atoll, is the only deep passage, with a maximum depth of 46 m. The topography effectively isolates the wide interior lagoon from the outside ocean. Recently, Kraines et al. (1999) succeeded in estimating the residence time of the Majuro lagoon using a three-dimensional diagnostic residual current model. Their estimate is a relatively short value of 15 days. Forcing due to radiation stress on the windward reef flat was found to be the dominant mechanism for the rapid exchange of lagoon water.

2.2.3. South Male Atoll. South Male Atoll (4°00′N, 73°25′E; Fig. 2C) in the Maldive Islands, northern Indian Ocean, is an oval-shaped atoll with maximum dimensions of 12 × 32 km. The lagoon water is connected with the offshore water through many deep channels between shallow reef flats. The channels are 30–70 m deep, i.e. much deeper than typical Pacific atoll channels. Due to its open topography, water exchange between the lagoon and offshore appears to be relatively good. In contrast to scanty reef development in typical Pacific atoll lagoons, flourishing of branching corals on the island slope in the lagoon was reported from Maldivian atolls (Kohn, 1964). This was explained in terms of the unusual large flow of oceanic water through the broad deep channels.

2.2.4. The Great Barrier Reef. The GBR extends approximately 2600 km along the eastern coast of Australia (Fig. 1), from north of Fraser Island in the south (24°20′S) to the Torres Strait in the north (9°20′S). It covers the wide range in latitude (15°) and is composed of more than 2900 individual reefs. There is a contiguous north–south body of open water, which is referred to as the "GBR lagoon", between the reefs and the continent (Fig. 2). As reefs occupy <9% of total continental shelf area (224 000 km^2; Hopley et al., 1989) the GBR may be considered a shallow coastal sea, bounded by a porous matrix of coral reefs (Furnas and Mitchell, 1996). The major portion of total shelf area and water volume lies between 30 and 40 m isobaths (Wolanski, 1994).

Despite the term "barrier", the outer reefs are not continuous, and the continuity of the outer reefs is defined as the 'linear density' of reefs along the shelf break (Pickard et al., 1977). There is a striking contrast between the northern and southern GBR. The northern GBR (9–16°S) is a continuous stretch, with the linear density reaching 90%, while the southern GBR (>16°S) exhibits apparently low values around 10%. The Capricorn Channel is open to the south and provides a wide and deep entrance to the southern end of the lagoon.

A total of 33 river basins with an aggregate catchment area of 411 000 km^2 drain eastward into the GBR. Mitchell and Furnas (1996) estimated that the average annual terrestrial freshwater input to the GBR is close to 42 km^3. In terms of water, sediment and nutrient exports, again there is a remarkable difference between the northern and southern GBR regions. In the northern GBR region, the wet-tropical catchments between the Daintree and Herbert Rivers supply a large proportion of total runoff to the GBR throughout year (ca. 40%; Mitchell and Furnas, 1996). On the other hand, two large dry-catchment rivers (Fitzroy and Burdekin Rivers) show clear seasonality in discharge volumes. Our expedition was conducted in the dry season of 1996 (Suzuki et al., 2001). Although episodic large floods during summer exert a significant impact on salinity and nutrient dynamics over large areas, riverine input to the southern GBR shelf appears to be limited during the dry season (austral winter).

2.2.5. Shiraho fringing reef, Ishigaki Island. Ishigaki Island is situated in the southern Ryukyu Islands, Japan. It lies in the path of the warm nutrient-depleted Kuroshio current (Fig. 1). Unlike other coral reefs described above, Shiraho Reef, located on the east coast of Ishigaki Island, is a well-developed fringing-type reef without a deep lagoon. The reef flat is about 800 m in width and composed of four topographic sub-units including outer reef slope, reef crest, inner reef flat, and moat. The moat is a trough-like depression (shallow lagoon) along the coast but its depth never exceeds 3 m (Nakamori et al., 1992). Suzuki et al. (1995) measured community metabolism on the inner reef flat, while Kayanne et al. (1995) reported diurnal $p\text{CO}_2$ variations at a deeper station near the boundary between the moat and the inner reef flat. Estimated water residence time of the reef flat by volume transport calculation based on our measurements is relatively short, approximately 4 h, probably due to the wave-generated through-flow circulation system, which effectively accelerates water exchange on the fringing reef. Salinity of the reef water decreases occasionally during low tide due to fresh groundwater seepage through the reef basement, which is composed of Pleistocene limestone. Kawahata et al. (2000a) reported dissolved phosphate and silica concentrations in terrestrial waters as well as CO_2 system parameters.

2.3. *Other coral reefs in the literature*

Other than the results mentioned above, information on reef metabolism at the system level and $\delta p\mathrm{CO}_2$ values are available for some coral reefs in the Indo-Pacific regions (Table 1). Additional geomorphological data of each coral reef are also shown in Table 1. Coral reefs in the table can be divided into three categories with respect to reef morphology: (1) reef flats and shallow lagoons, (2) reefs with a deep lagoon and (3) large-scale reef systems.

3. Results and discussion

3.1. *Offshore–lagoon difference in* pCO_2

In order to detect the net effect of reef systems on the air–sea CO_2 exchange, we need to compare seawater $p\mathrm{CO}_2$ between the inside and the outside of the lagoon (Gattuso et al., 1993). Here, we define the difference in $p\mathrm{CO}_2$ ($\delta p\mathrm{CO}_2$) between the lagoon ($p\mathrm{CO}_{2,\mathrm{L}}$) and the offshore ($p\mathrm{CO}_{2,\mathrm{O}}$) as follows:

$$\delta p\mathrm{CO}_2 = p\mathrm{CO}_{2,\mathrm{L}} - p\mathrm{CO}_{2,\mathrm{O}}. \qquad (3)$$

If the mean $p\mathrm{CO}_2$ value of lagoon water is higher than that in the oceanic water (i.e. $\delta p\mathrm{CO}_2 > 0$), a coral reef has the potential to work as a source of atmospheric CO_2 as a whole. By contrast, if $\delta p\mathrm{CO}_2 < 0$ it could work as a sink of CO_2.

The $p\mathrm{CO}_2$ values in reef lagoon were consistently lower than the offshore values in all coral reefs investigated except for the Shiraho reef (Fig. 3 and Table 1). Average $\delta p\mathrm{CO}_2$ values observed in the Palau barrier reef and Majuro Atoll were around 48 and 25 μatm, respectively. In the case of the South Male Atoll, $\delta p\mathrm{CO}_2$ has a small value of 6 μatm, but again, the lagoon water has a higher $p\mathrm{CO}_2$ than the offshore water. The northern and southern GBR lagoons also showed positive $\delta p\mathrm{CO}_2$ values.

Local decreases in $p\mathrm{CO}_2$ were observed on reef flats or shallow banks during the daytime in the Majuro Atoll, South Male Atoll and Shiraho fringing reef, where comprehensive spatial surveys were conducted. These areas showing negative $\delta p\mathrm{CO}_2$ may act as a temporary sink for atmospheric CO_2. However, these effects seem to be limited to the small areas of the reef flats, because the lagoons dominate these reef systems in terms of both area and volume of water. The observed $\delta p\mathrm{CO}_2$ must represent the system-level metabolic performance of coral reefs.

According to theoretical examination of Suzuki (1998), the $p\mathrm{CO}_2$ change in seawater can be predicted by R_{OI} values of the system (Fig. 4A). The first problem is whether observed $\delta p\mathrm{CO}_2$ value in a coral reef can be predictable using a system-level R_{OI} value for the reef or not. Among four coral reefs with a deep lagoon examined in this study, reliable carbon production estimations are available only for a shallow area of the Majuro Atoll (Suzuki et al., 1997). It is predicted that the atoll shows positive $\delta p\mathrm{CO}_2$ based on the estimated R_{OI} value of 0.29 (Suzuki et al., 1997), which is smaller than the critical value of 0.6. The prediction agrees with the results from $p\mathrm{CO}_2$ observations.

Production ratios at system level are available in literature for several reefs in the Indo-Pacific regions (Table 1). Two reefs in the first category, Shiraho fringing reef (Kayanne et al., 1995) and Christmas Island lagoon (Smith et al., 1984), indicate higher R_{OI} values than the critical ratio, and indeed their $\delta p\mathrm{CO}_2$ values were observed to be negative (CO_2 sink). On the contrary, Tiahura Barrier Reef and Yonge Reefs (Frankignoulle et al., 1996; Gattuso et al., 1996a,b) showed low R_{OI} values compared to the critical value of 0.6. Although they reported no values on the $\delta p\mathrm{CO}_2$, their conclusion that these two reefs act as atmospheric CO_2 source agrees with the prediction based on their low R_{OI} values. Two reefs in the second category, Fanning Atoll (Smith and Pesret, 1974) and Canton Atoll (Smith and Jokiel, 1978), showed considerably smaller R_{OI} values than the critical ratio and high $p\mathrm{CO}_2$ in lagoon waters were evident. In conclusion, the observations of $\delta p\mathrm{CO}_2$ listed in Table 1 agree well with the theoretical prediction based upon R_{OI}, including a controversial report from Shiraho Reef (Fig. 4B). This also means that R_{OI} of the system is the dominant factor for determining the CO_2 performance of reef systems.

While the ratio R_{OI} is a primary factor determining the sink–source behavior of a particular reef system, there seems to be another factor controlling the magnitude of $\delta p\mathrm{CO}_2$ values. The observed $\delta p\mathrm{CO}_2$ values

Table 1. *Summary of geomorphological dimensions, water residence time, carbon metabolisms and CO_2 flux between reef water and atmosphere for investigated coral reefs*

Reef	Scale (km)	Area (km^2)	Mean depth (m)	Residence time (day)	Net C production		P/R	R_{OI}	pCO$_2$ (μatm)		δpCO$_2$ (μatm)	Flux	Reference for pCO$_2$ values
					Org-C	CaCO$_3$			Inside	Outside			
Reefs with flat and shallow lagoon													
Tiahura barrier reef	~1 km wide	–	–	0.25	75	186	1.2	0.4	–	–	–	Source	Gattuso et al. (1996b)
Yonge reef	~2 km wide	–	–	–	33	253	1.1	0.1	–	–	–	Source	Gattuso et al. (1996b)
Christmas Is.	15 × 20	180	3	10–15	6	2.5	>1	2.4	220	310	−80	Sink	Smith et al. (1984)
Shiraho fringing reef	~1 km wide	–	1.1	0.2	110	100	1.3	1.1	157–521	322	−7	Sink	Kayanne et al. (1995)
Reefs with deep lagoon													
Fanning Atoll	15 × 15	125	5	32	−0.4	27	1	−0.01	400	370	+30	Source	Smith and Pesret (1974)
Canton Atoll	11 × 11	110	6.2	50	3	14	–	0.01	290–400	330	+15	Source	Smith and Jokiel (1978)
Palau barrier reef	13 km wide	–	19	–	–	–	–	–	414	366	+46	Source	Kawahata et al. (1997)
Majuro Atoll	39 × 10	344	39	15	46	141	–	0.29	368	345	+23	Source	Suzuki et al. (1997)
South Male Atoll	32 × 18	–	68	–	–	–	–	–	368	362	+6	Source	
Large-scale reef systems													
Northern GBR	~80 km wide	–	~40	8	–	–	–	–	339	311	+29	Source	Suzuki et al. (2001)
Southern GBR	>100 km wide	–	~40		–	–	–	–	326	314	+12	Source	Suzuki et al. (2001)

Figures on reef morphological features are quoted from Nugent (1946). Most estimates of residence time are derived from same references as pCO$_2$ values, while residence time of Majuro Atoll is after Kraines et al. (1999). Residence time for the GRB is the estimate for the entire lagoon (Suzuki et al., 2001). Net community carbon production ('Net C production' in the table) is expressed in the unit of mmol m^{-2} d^{-1} both for organic carbon (Org-C) and inorganic carbon (CaCO$_3$) productions. The symbols P/R and R_{OI} represent the ratio of gross community production to respiration and the ratio of net organic production to net inorganic carbon production, respectively. The symbol δpCO$_2$ represents the difference in seawater pCO$_2$ between lagoon water and the offshore water, and defined by eq. (3) in the text. Influences on δpCO$_2$ due to temperature difference between the offshore and lagoon are corrected by normalization of lagoonal δpCO$_2$ values at offshore temperature. Normalized δpCO$_2$ values at 25 °C and salinity 35 are shown for the GBR because of large offshore–lagoon differences in water temperature and salinity.

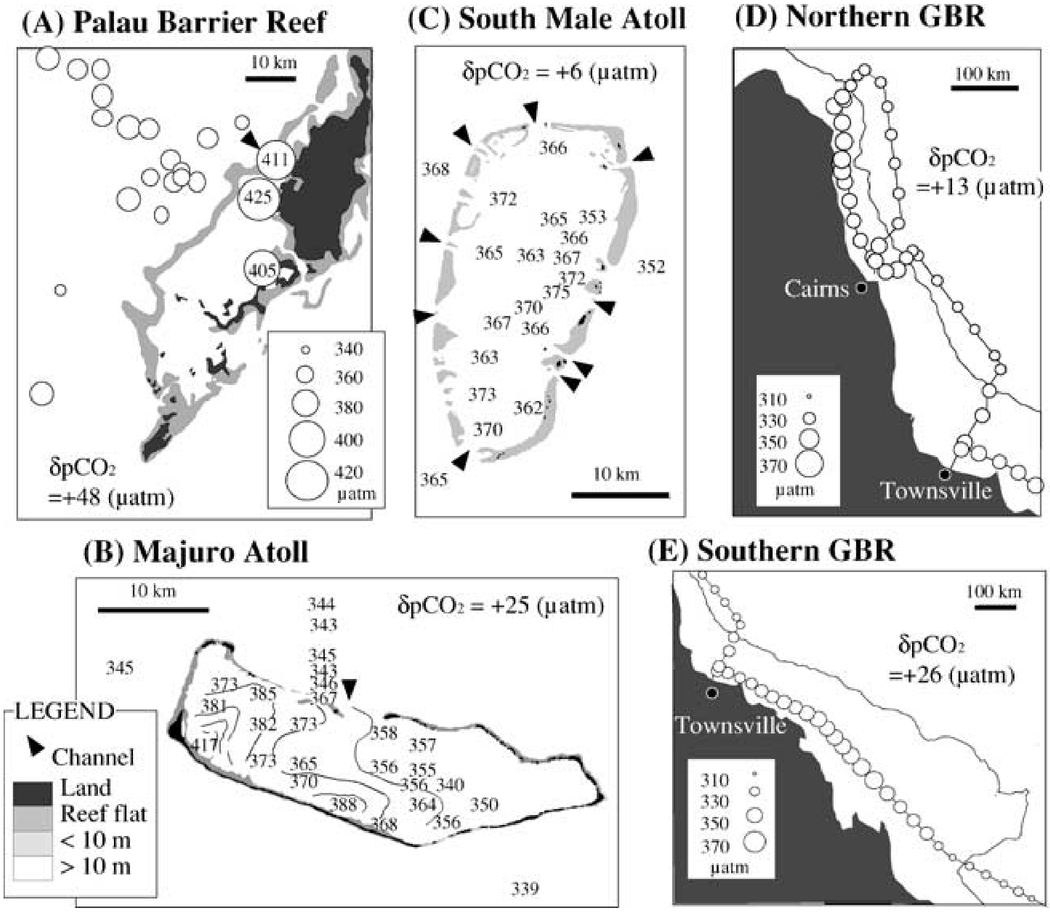

Fig. 3. Spatial distributions of pCO_2 in surface waters around the Palau barrier reef (A), Majuro Atoll (B) and South Male (C), and the northern and southern GBR lagoons (D and E). The average value of the offshore–lagoon difference in pCO_2 (δpCO_2) at in-situ temperature and salinity observed in each reef is shown in each panel.

varied from reef to reef (Fig. 3). In addition, the data listed in Table 1 suggest that there are relatively weak positive relationships between δpCO_2 and the residence time of reef water, including studies of reef flats and shallow lagoons: the slower the renewal of the water is, the higher is pCO_2 in the reef water. Therefore, the most likely factor controlling the magnitude of δpCO_2 is water circulation in the lagoon.

The lagoon of South Male Atoll has an open nature, being connected to the open ocean by numerous deep channels. Shallow reef flats also contribute to water exchange between the lagoon and the offshore water. According to our understanding of the circulation in the atoll lagoon (e.g. Kench, 1994), South Male Atoll seems to be the most well flushed among the three oceanic reefs examined. Therefore, the small δpCO_2 value can be attributed to the well flushed nature of the lagoon. On the other hand, Majuro Atoll shows a higher degree of closure than South Male Atoll, having only one deep entrance channel. Majuro Atoll exhibited higher δpCO_2 values than those of South Male Atoll. This can be explained by its high continuity of the reef platform and the relatively long residence time of the lagoon water. Palau barrier reef lagoon appears to be of intermediate degree of closure among three oceanic reefs examined. Palau lagoon must be less flushed than South Male Atoll lagoon, but we have no information for a detailed comparison between the Palau and Majuro Atoll lagoons.

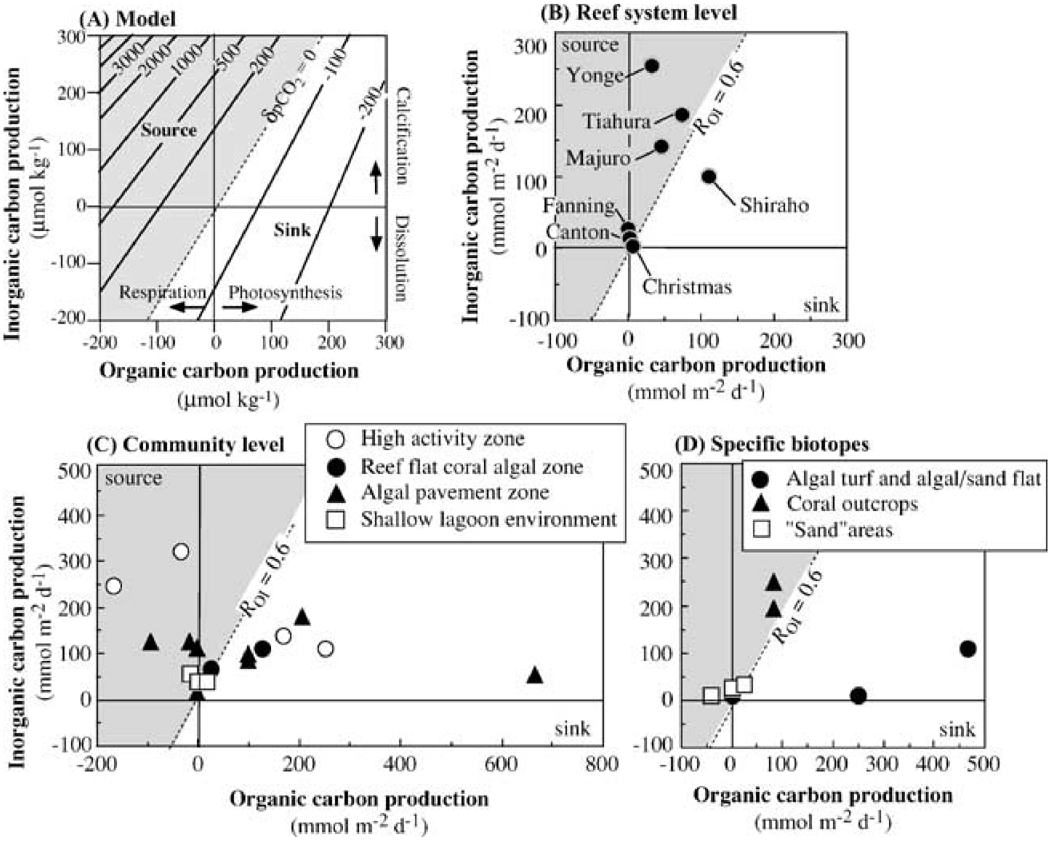

Fig. 4. Metabolism and its effect on sink/source behavior with respect to the atmospheric CO_2. (A) Changes in pCO_2 (δpCO_2) caused by the various rates of photosynthesis and calcification. Negative values of carbon production rates indicate their reverse reactions. Calculations are conducted for salinity 35 and and 25 °C supposing the initial condition of seawater is 2346 μmol kg^{-1} in total alkalinity, 2000 μmol kg^{-1} in *DIC* and 345 μatm in pCO_2. The shaded area indicates the range of increased pCO_2. (B) System-level estimates of net organic and inorganic carbon production rates listed in Table 1. Note that estimates for the Shiraho reef and Christmas Island are plotted in the 'sink' area of the diagram. (C and D) Rates of net organic and inorganic carbon production of community-level measurements (C) and specific biotopes (D) reviewed by Kinsey (1985). A line, which shows that the ratio of organic production to inorganic production (R_{OI}) equals 0.6, is given in each diagram. The line is a critical boundary for constant pCO_2 for normal surface seawater with salinity of 35 at 25 °C (Suzuki, 1998). The shaded area indicates the region where pCO_2 increased by metabolism.

An interesting finding is that δpCO_2 values in the northern and southern GBR lagoons are relatively high despite their open nature (Figs. 2D, 3D and 3E). When pCO_2 values at in-situ temperature and salinity are compared, the southern GBR lagoon shows a higher δpCO_2 value than the northern lagoon (Fig. 3). However, normalized pCO_2 values at 25 °C and salinity 35 give the opposite result: δpCO_2 of the northern lagoon (+29 μatm) is larger than the southern lagoon (+12 μatm; Table 1). This contrast appears to correspond to the high linear density of the outer reef in the northern GBR lagoon compared to the southern lagoon.

While reliable R_{OI} values are reported for some reef communities (see review by Kinsey, 1985), the number of system-level R_{OI} estimates is still low. The production ratio is not always easy to estimate on a particular reef. Entire reef production estimates, using the piecewise summation of metabolic studies at the scale of community or smaller ecological units on the reef, are subject to a large potential error (Atkinson and Grigg, 1984; Nakamori et al., 1992). On the other hand, the reef lagoon systems in enclosed atolls are suitable for large-scale budget studies (Smith, 1988). Smith and colleagues employed a salt/water budget calculation for evaluating water residence time, coupled with non-conservative deviations of C, N and P from salinity as measures of net system biogeochemical fluxes (Smith and Pesret, 1974; Smith and Jokiel, 1978; Smith et al., 1984). The disadvantage of this approach is that their net ecosystem metabolism estimate may be biased by hydrographical constraints and that it gives little information about internal behavior and outer reef slope communities. Despite these disadvantages, we emphasize the merit of using chemical properties in the reef lagoon, including $p\mathrm{CO}_2$, which provide information at a much more integrated scale in space and time. Once discrimination based on the R_{OI} value is demonstrated to be a reliable indicator for determining whether a certain reef system acts as a sink or source of atmospheric CO_2, evaluation of $\delta p\mathrm{CO}_2$ itself can be considered as a new ecosystem parameter for discussing the mode of carbon cycling in a coral reef system.

3.2. *Total system analysis based on an* A_T–DIC *diagram*

Several biogeochemical processes, including photosynthesis, respiration, carbonate precipitation and dissolution, and gas exchange always accompany changes in A_T and *DIC* in a predictable manner. Deffeyes (1965) introduced a "graphic approach" by using a diagram of *DIC* versus A_T for solving a wide variety of problems in CO_2 equilibrium system. Contours of corresponding pH and $p\mathrm{CO}_2$ values in seawater can be drawn on the A_T–*DIC* plane using thermodynamic relationships. We propose this graphic approach based on A_T–*DIC* diagram as a novel tool for examining the performance of carbon cycle in coral reef systems. Biogeochemical processes have vector properties in 2-space of the A_T–*DIC* plane (Fig. 5A).

Photosynthesis lowers *DIC*, while calcification decreases A_T 2 mole per mol of CaCO_3 precipitated (Smith and Key, 1975). If calcification occurs without photosynthesis, the calcification path is represented on the diagram by a line whose slope is 2 ('calcification line' in Figs. 5A and 6). On the other hand, organic carbon production, oxidation and CO_2 gas exchange do not alter A_T, and thus these processes can be represented by horizontal displacements on the diagram. Strictly speaking, consumption and release of nutrients (NO_3^- and PO_4^{3-}) accompanied by photosynthesis and respiration also affect A_T. In the open

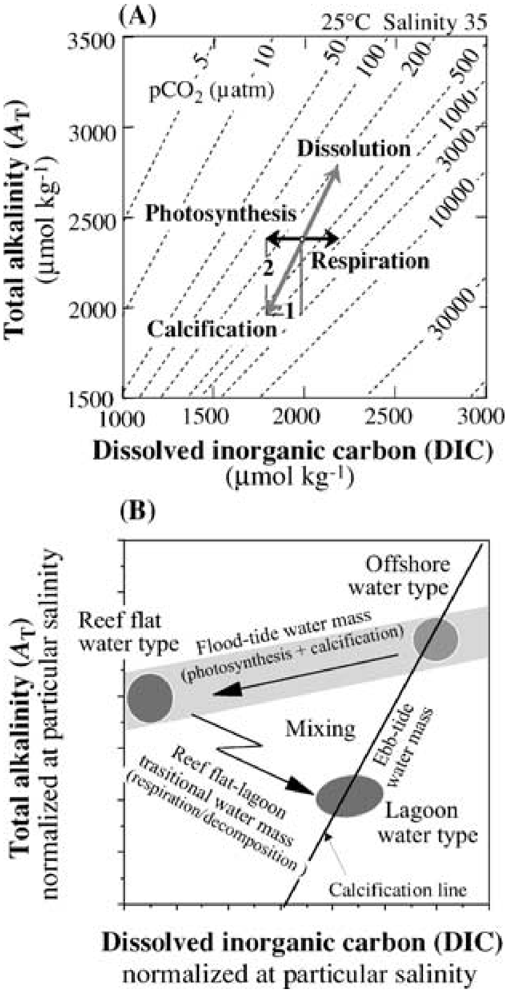

Fig. 5. (A) Total alkalinity vs. *DIC* diagram illustrating the effects of photosynthesis, calcification and their reverse reactions. Contours of $p\mathrm{CO}_2$ correspond to 25 °C and salinity 35. Organic and inorganic processes have vector properties on the A_T–*DIC* diagram. Each vector diagram denotes the direction of compositional changes accompanying 200 μmol kg^{-1} of the indicated process. On the A_T–*DIC* diagram, photosynthesis and respiration can be represented by vectors slightly tilting downward and upward, respectively, instead of horizontal vectors, because organic processes accompany alkalinity changes due to nutrient uptake. However, the correction is not employed because the effect seems to be small in coral reefs compared to the open ocean (see the text). (B) Schematic diagram showing alteration paths of reef-water chemistry in a reef system with a deep lagoon. The terms 'water type' and 'water mass' follow the terminology of the *T*–*S* diagram of oceanography. A water type is an end-member of a water mass's properties, and a water mass results from the mixing of two or more water types.

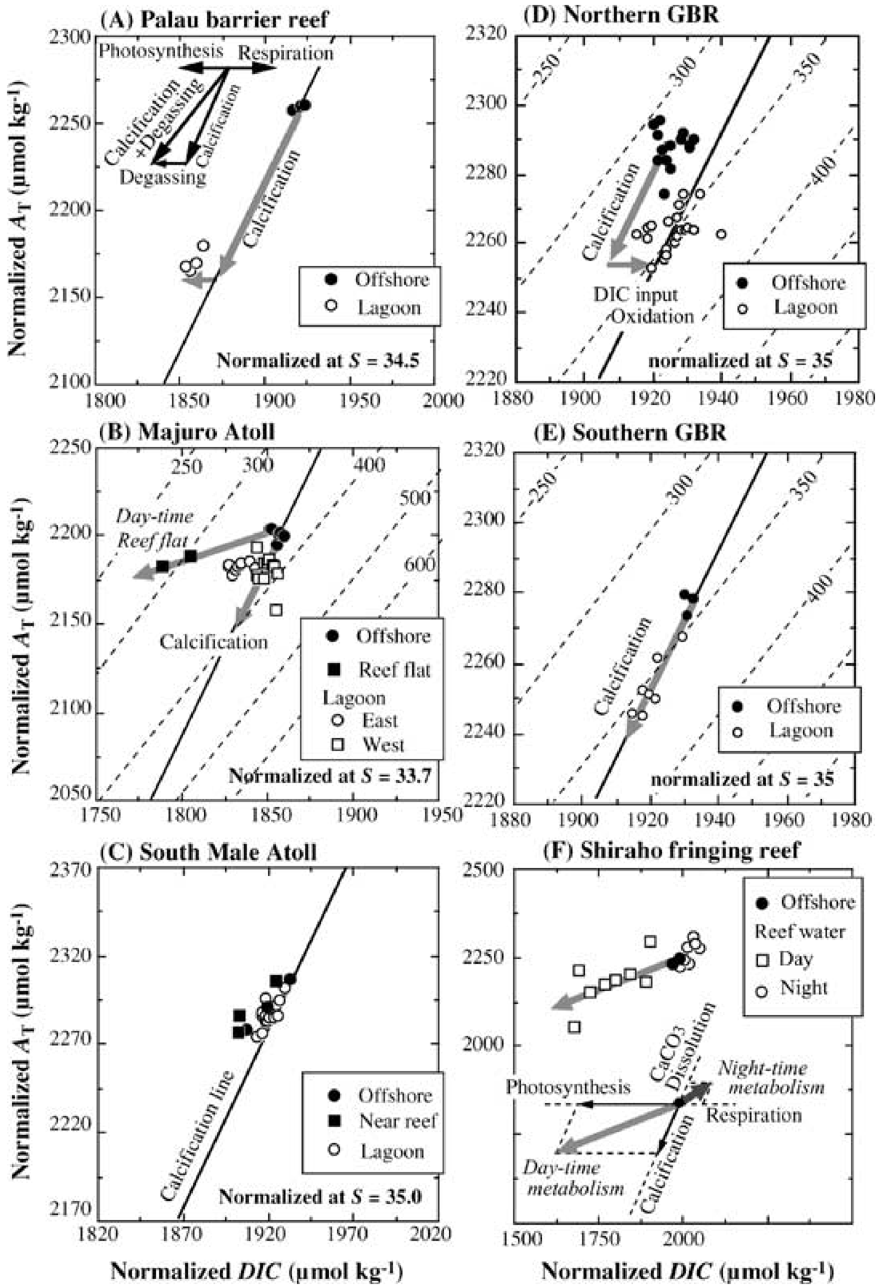

Fig. 6. Total alkalinity vs. *DIC* plots with corresponding $p\mathrm{CO}_2$ (μatm) contours for reef systems investigated in this study: the Palau barrier reef (A), Majuro Atoll (B) and South Male (C), the northern and southern GBR lagoons (D and E) and Shiraho fringing reef (F). Normalized values at constant salinities are plotted in order to remove the influences from rainwater input and evaporation. Major metabolic and biogeochemical processes are shown in each panel. The dominant process in coral reefs is calcification, and a calcification path is represented on the A_T–*DIC* diagram by a line whose slope is 2. An illustration in panel (F) explains the application of the concept of vector decomposition: daytime metabolism observed in the Shiraho fringing reef can be attributed to co-occurrence of photosynthesis and calcification, with a photosynthesis/calcification molar ratio of approximately 6.

ocean, the alkalinity change is estimated to be relatively large value of 17 mol for 106 mol of organic carbon production (Chen et al., 1982) based on the C:N:P ratio of primary production for phytoplankton (106:16:1; Redfield et al., 1963). In this case, photosynthesis can be represented by a vector slightly tilting downward rather than a horizontal vector on the A_T–*DIC* diagram. However, C:N:P ratio of benthic marine macroalgae and seagrass in coral reefs is reported to be about 550:30:1 (Atkinson and Smith, 1983) and different from the Redfield ratio for phytoplankton. Since alkalinity changes per mol of organic carbon are $17/106$ and $31/550$ for phytoplankton and coral reef algae, respectively, the effect of nutrient uptake on alkalinity seems much less important in coral reefs compared to the open ocean. Therefore, we assume that alkalinity change due to organic carbon metabolism is negligible in the following discussion.

Results from Majuro Atoll (Suzuki et al., 1997) provide an example of the application of the graphic approach (Fig. 6B). All measured A_T and *DIC* values were plotted after normalization to a constant salinity (the offshore salinity in this case) in order to correct the effects of freshwater dilution. Offshore water samples have the largest values among all samples, both for A_T and *DIC*. The reef flat community on the atoll margin is significant as the site of both organic and inorganic carbon production. The two points representing reef flat water and the average for the points of the offshore water make a straight line. The slope of this line corresponds to the photosynthesis (p_n)/calcification (g) molar ratio of the reef flat community during the day. The ratio (p_n/g) can be obtained by solving the following equations simultaneously:

$$\Delta A_\mathrm{T} = 2g, \quad \Delta DIC = p_\mathrm{n} + g \tag{4}$$

and

$$p_\mathrm{n}/g = 2\Delta DIC/\Delta A_\mathrm{T} - 1 \tag{5}$$

where ΔA_T and ΔDIC represent changes in A_T and *DIC* between the offshore mean and reef water sample, respectively. The slope of the line ($\Delta A_\mathrm{T}/\Delta DIC = \sim 0.27$) corresponds to a p_n/g value of approximately 6. We call this line the "production line" of the active periphery of Majuro Atoll, although the production line may have a large zone of uncertainty due to the limited data set. Repetition of water sampling would yield a more accurate estimate. Estimation of the p_n/g ratio is also available using the concept of vector decomposition, as illustrated in Fig. 6F. In the initial approximation, most of the lagoon samples of Majuro Aoll, especially samples from the western part of the lagoon, are located around the calcification line, suggesting predominant carbonate production in this reef. Further investigations on the difference between the eastern and western lagoons are discussed in Suzuki et al. (1997).

The alteration paths of reef-water chemistry can be summarized in a schematic diagram (Fig. 5B). The terms used for temperature–salinity diagrams (*T–S* diagrams) in descriptive physical oceanography are also useful to interpret the A_T–*DIC* diagram. When discussing the *T–S* diagram, a water body whose properties are represented by a point is called a 'water type', while one represented by a line is called a 'water mass' (Pickard and Emery, 1990). In other words, a water type is an end-member of water mass properties, and a water mass results from the mixing of two or more water types.

On the A_T–*DIC* diagram, three water types can be identified: 'offshore water type', 'reef flat water type' and 'lagoon water type' (Fig. 5B). Offshore water type is the source of incoming water to the reef system. Reef flat water type is introduced as an end-member which is subjected to active organic and inorganic production on the reef flat community and whose A_T and *DIC* were largely consumed. Furthermore, there are three water masses on the diagram, namely 'flood-tide water mass', 'ebb-tide water mass' and 'reef flat-lagoon transitional water mass'. Because the offshore water enters the reef system through the reef flat and stays in the lagoon for a while before being drained to the offshore, the general alteration pathway of reef water chemistry is from flood-tide water mass to ebb-tide water mass via reef flat-lagoon transitional water mass with partial mixing of each water mass. In other words, variation of the CO_2 property of reef water can be represented by a three end-member system of the offshore, reef flat and lagoon waters.

The position of a lagoon water type on the A_T–*DIC* diagram is critical to the total system performance of a coral reef. When organic matter is all decomposed, lagoon water type is plotted on the "calcification line" which intersects the position of offshore water type. In this case, the reef system has no net (excess) organic production, while some amounts of calcium carbonate remain on the reef. If lagoon water type is plotted on the left side of the calcification line, it indicates that some portions of organic matter escaped from oxidation and this system as a whole has net organic carbon production.

The A_T–*DIC* plots for Majuro Atoll (western lagoon), South Male Atoll and the southern GBR (Figs. 6B, C and E) showed that their lagoon water types are plotted close to the calcification line, although the position of the calcification line has some uncertainty due to indefinite offshore water type position. This indicates that a considerable part of organic production transported to the lagoon was decomposed, and organic matter deposited in the lagoon bottom is quite small. The higher $p\mathrm{CO}_2$ in the lagoon water can be attributed to the calcification process, as shown by the $p\mathrm{CO}_2$ contours in the A_T–*DIC* plot. In the case of the Palau barrier reef (Fig. 6A), lagoon water samples are plotted on the left side of the calcification line. Kawahata et al. (1997) interpreted this shift as the result of CO_2 degassing due to high $p\mathrm{CO}_2$ in the lagoon compared to the air, rather than the sign of net organic production of the system. A disadvantage of the graphic approach using an A_T–*DIC* plot is that it cannot distinguish net organic production from CO_2 degassing. However, air–sea CO_2 exchange is usually small compared to the metabolic flux of the benthic community in a shorter time-scale (Frankignoulle et al., 1996). In addition, taking the contribution of A_T change due to photosynthetic nutrient uptake into account, discrimination between these two processes becomes possible.

In contrast to the the A_T–*DIC* plots for reefs with a deep lagoon (Figs. 6A–E), the plot for the Shiraho fringing reef (Fig. 6F) represents mostly diurnal variation of the reef water CO_2 system without any sign of long-term net flux. Water residence time in the moat is estimated to be around 4 h. Due to the lack of a water body of longer residence time, only short-term metabolic performance was captured in this diagram. Reef water is drained to the offshore, probably with organic matter in the form of DOC and POC. This interpretation of the diagram is consistent with the relatively high R_{OI} ratio reported for this reef (Kayanne et al., 1995). The Shiraho reef corresponds to the reef flat of Majuro Atoll, as indicated by the similarity of their A_T–*DIC* plots (Figs. 6B and F). As organic matter produced on the reef flat of Majuro Atoll is decomposed in the lagoon, exported organic matter from the Shiraho reef is also expected to be decomposed on a relatively short time scale. The CO_2 sink-like behavior of a fringing type reef needs special care when estimating net carbon flux.

As discussed in the previous section, the high $\delta p\mathrm{CO}_2$ values found in the Palau barrier reef compared to South Male Atoll are related to the difference in degree of closure between the two reefs. As the residence time increases, more time becomes available for calcification. The observed decrease in A_T in the lagoon compared to the offshore water was greater in the Palau lagoon than the South Male Atoll lagoon. This evidence is consistent with the difference in $\delta p\mathrm{CO}_2$ between the two reefs.

3.3. *Terrestrial influences on coral reef systems*

While the Palau barrier reef, Majuro Atoll and South Male Atoll are oceanic reefs without terrestrial influence from land, the GBR and Shiraho reef are closely located along the coast. Alteration of the mode of carbon cycling can be expected in these coastal reef systems. Indeed, we found unexpected results in the A_T–*DIC* diagram for the northern GBR lagoon (Fig. 6D). The lagoon water samples were plotted on the right side of the calcification line from the offshore composition.

In Fig. 6D, the offshore water is located at points concentrated at 2290 and 1922 μmol kg^{-1} in normalized A_T and *DIC*, respectively. The offshore samples have larger A_T values than the lagoon samples. In contrast to A_T, there is no distinct difference in the range of *DIC* variations between the offshore and the lagoon samples. However, most of the lagoon samples are plotted in the diagonal strip whose slope is approximately 2 on the A_T–*DIC* plane, suggesting that calcification dominates the lagoon. The calcification pathway of lagoon samples should intercept the cluster of the offshore samples, if all A_T and *DIC* are from the surface offshore water. However, overall displacement of the calcification line from the offshore compositions along the *DIC* increasing trend can be seen. This indicates the presence of net external carbon inputs to the lagoon other than surface oceanic exchange. Possible processes which increase *DIC* of the system are intrusion of deep water from the outside of the lagoon, oxidation of organic matter and *DIC* supply from external sources such as atmospheric input, rainfall and river discharge. However, deep water intrusion cannot explain the displacement, because deep water is rich in A_T as well as *DIC*. Therefore, deep water intrusion would shift the calcification line toward the increasing A_T direction on the diagram. In the case of organic matter oxidation, the source of such organic matter must not come from the offshore water, because there is no signal of net *DIC* fixation on the diagram. Therefore, atmospheric CO_2 invasion, rainfall input and river discharge remain possible process for supplying *DIC* from external sources. In our initial approximation, calcification, together with *DIC* inputs from external sources, serves a major role in the net carbon cycle of the northern GBR lagoon system. There no features can be seen indicating a *DIC* decrease due to photosynthesis and/or outgassing on the A_T–*DIC* diagram. Suzuki et al. (2001) recently concluded that the possible external source of carbon entering the GBR lagoon is river water discharge, because atmospheric input and rainfall are small sources of DIC. River waters may carry considerable amounts of dissolved and particulate organic carbon (DOC and POC) as well as DIC.

A similar influence was also recognized in Shiraho fringing reef of the Ryukyu Islands (Kawahata et al., 2000a). Land-derived freshwaters, including river water and groundwater, have a relatively large contribution to the circulation system of the reef. These terrestrial waters exhibit extremely high $p\mathrm{CO}_2$ up to 6400 μatm, reflecting enrichments in A_T and *DIC* due to dissolution of carbonate rocks and decomposition of organic matter in the soil of subtropical islands.

When we look at nutrient dynamics in the Shiraho reef and the northern GBR lagoon, again we find these two reef systems to be similar. According to the report of Kawahata et al. (2000a), terrestrial waters have high DIC/DIP ratios (molar ratios of dissolved inorganic carbon to phosphate) ranging from 3600 to 35 000. Suzuki et al. (2001) estimated the riverine C:N:P molar ratio in the GBR region to be 1120:30:1, based on their carbon budget calculation and annual riverine nitrogen and phosphorus input estimated by Furnas et al. (1995). These ratios are much higher than the Redfield ratio for plankton (106:16:1; Redfield et al., 1963), and the ratio of benthic plants in coral reefs (550:30:1; Atkinson and Smith, 1983). Therefore, even if all discharged nutrients are utilized by biological processes of both planktonic organisms and benthic communities, surplus carbon must remain in the reef water as oxidized DIC. Although nutrient inputs may stimulate organic carbon production in the reef area, net oxidation of organic matter rather than net organic carbon fixation would be expected in both the northern GBR lagoon and Shiraho fringing reef. It is worth emphasizing that there exists a similarity in nutrient dynamics between these two reef systems despite the difference on a spatial scale (Fig. 2). As suggested by many researchers (e.g. Hatcher, 1997), proximity of land, together with residence time of water and degree of system closure, appear to be important factors for controlling the carbon cycle in coral reef systems.

Kayanne et al. (1995) estimated negative $\delta p\mathrm{CO}_2$ value for the Shiraho reef based of the monitoring of diurnal change of $p\mathrm{CO}_2$ in reef water, together with an estimation of $R_{\mathrm{OI}} \approx 1.1$. The CO_2-sink type behavior of the Shiraho reef has been attributed to its high algal biomass (Gattuso et al., 1996; 1999). Their argument is based on the understanding that reef communities and biotopes rich in algal components tend to have high R_{OI} values compared to coral-dominant communities, as shown in Figs. 4C and D. However, Kawahata et al. (2000a) suggested the possibility of CO_2 efflux to the air along the coast of the Shiraho reef due to terrestrial carbon input. One must reconsider the system-level R_{OI} estimate and net CO_2 budget of the Shiraho reef as a whole.

Besides the Shiraho reef, the result from Christmas Island lagoon goes against the current view of CO_2 performance of coral reefs (Table 1). In addition, Kraines et al. (1996) reported a relatively high P/R ratio for

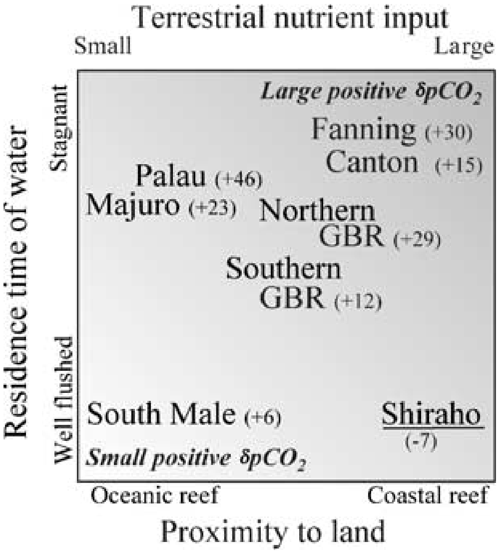

Fig. 7. Schematic representation of the relationship between the offshore–lagoon difference in $p\mathrm{CO}_2$ ($\delta p\mathrm{CO}_2$) and morphological characteristics of coral reefs. The $\delta p\mathrm{CO}_2$ values are shown in parentheses following reef names. Each reef is located along a gradient of two factors: proximity to land and residence time of reef water. An underlined reef denotes that observations were conducted on a "coral reef flat", while others are results from reef lagoons. In general, $\delta p\mathrm{CO}_2$ increases as degree of reef system closure increases. Two exceptions are Shiraho Reef and Christmas Island (not shown), showing negative $\delta p\mathrm{CO}_2$ values probably due to high nutrient input from land. See text for discussion.

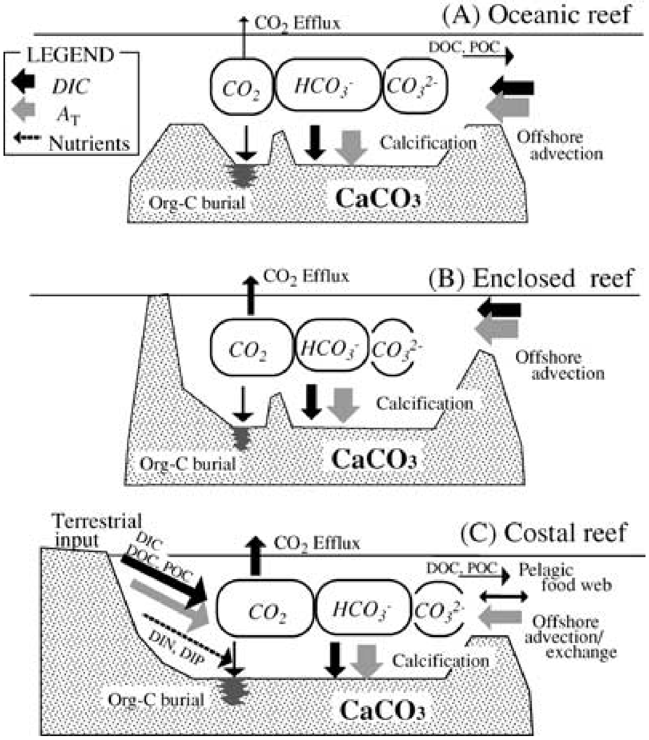

Fig. 8. Schematics of the mode of carbon cycle corresponding to three characteristic reef morphologies, including a well flushed oceanic reef (A), an enclosed reef (B), and a costal reef (C). A graphic approach base on the A_T–*DIC* diagram can reveal the size of DIC pool in the lagoon as well as the relative abundance of CO_2 species.

the reef community in Bora Bay of the Miyako Islands, next to Ishigaki Island. Some regional effects, which enhance organic carbon production, have been pointed out as a likely cause of their CO_2-sink type behavior. In the case of Christmas Island lagoon, phosphorus input from guano deposits in the island was also expected to stimulate active organic production in the lagoon, while low salinity due to freshwater input may have partly contributed to the extremely low pCO_2 in lagoon water (Smith et al., 1984). On the other hand, the influence of fertilizer used in farming land on reef metabolism has been pointed out as the cause of the relatively high organic production rate in the reef community of Bora Bay.

In summary, we present two schematic diagrams: one explains the variation of δpCO_2 values among reefs (Fig. 7) and the other is an illustration of the variation of the mode of carbon cycle in accordance with the topographic setting of the reef systems (Fig. 8). While the system-level R_{OI} determines the sense (positive/negative) of δpCO_2 of the reef, residence time of reef water and, probably, proximity of land are important factors for controlling the magnitude of δpCO_2 values of the reef system (Fig. 7). The graphic approach can be used for estimating the relative abundance of CO_2 species in the DIC pool of reef water (Fig. 8). More quantitative examination of major factors controlling the carbon cycle in reef systems is required for a better understanding of the consequences of global climatic change, including the increase of sea-surface temperature and sea-level rise, on organic and inorganic carbon production of coral reef ecosystems (Gattuso and Buddemeier, 2000; Kleypas et al., 2001).

4. Conclusions

A system-level net organic-to-inorganic carbon production ratio is a master parameter for controlling sink/source behavior of coral reefs with respect to atmospheric CO_2. The production ratio, however, is not always easy to estimate on a particular reef. Instead, we propose a graphic approach based on an A_T–DIC plot, together with observations on the offshore–lagoon difference in pCO$_2$. We examined the data of reef-water CO_2 systems reported from coral reefs of a wide variety with respect to topography and oceanographic settings in the Indo-Pacific oceans. Reefs examined include three oceanic reefs (Palau barrier reef, Majuro Atoll, South Male Atoll) and two coastal reefs (Shiraho reef and the GBR) as well as several coral reefs in the literature. Surface pCO$_2$ in the lagoons of atolls and barrier reefs were consistently higher than those of their offshore waters. The A_T–DIC plots for individual reef systems indicate that high pCO$_2$ in the lagoons is caused by predominant carbonate production relative to net organic carbon production. Reef topography, especially residence time of lagoon water, appears to have a secondary effect on the magnitude of the offshore–lagoon pCO$_2$ difference. In addition to the recent demonstrations from coral reef flats (Gattuso et al., 1993; Gattuso et al., 1995; Frankignoulle et al., 1996; Gattuso et al., 1996a,b), our results from reef lagoons also confirm the current understanding that most coral reefs work as sources of atmospheric CO_2. Terrestrial influence on the reef water CO_2 system was recognized in coastal reefs. High carbon input appears to enhance CO_2 efflux to the atmosphere. Coral reefs, both of oceanic and coastal origin, act as an alkalinity sink and a potentially CO_2-releasing site due to carbonate precipitation and land-derived carbon.

5. Acknowledgements

We express our appreciation to T. Ayukai of the Australian Institute of Marine Science and F. Nishibori and K. Goto of the Kansai Environmental Engineering Center Co. Ltd. (KANSO). We also thank L. P. Gupta for valuable comments on our manuscript. This study was supported by the "Northwest Pacific Carbon Cycle Study" consigned to KANSO by NEDO. Additional support was from GCMAPS funded by the Ministry of Education, Culture, Sport, Science and Technology and "Study on the disturbance and restoration of the coral reef" funded by the Ministry of the Environment of Japan.

REFERENCES

Atkinson, M. J. and Grigg, R. W. 1984. Model of a coral reef ecosystem II. Gross and net benthic primary production at French Frigate Shoals, Hawaii. *Coral Reefs* **3**, 13–22.

Atkinson, M. J. and Smith, S. V. 1983. C:N:P ratios of benthic marine plants, *Limnol. Oceanogr.* **28**, 568–574.

Chen, C.-T. A., Pytkowicz, M. and Olson, E. J. 1982. Evaluation of the calcium problem in the South Pacific. *Geochem. J.* **16**, 1–10.

Chisholm, J. R. M. and Barnes, D. J. 1998. Anomalies in coral reef community metabolism and their potential importance in the reef CO_2 source–sink debate. *Proc. Natl. Acad. Sci. USA* **95**, 6566–6569.

Crossland, C. J., Hatcher, B. J. and Smith, S. V. 1991. Role of coral reefs in global ocean production. *Coral Reefs* **10**, 55–64.

Culberson, C. H., Pytkowicz, R. M. and Hawley, J. E. 1970. Seawater alkalinity determination by the pH method. *J. Mar. Res.* **28**, 15–21.

Deffeyes, K. S. 1965. Carbonate equilibria: a graphic and algebraic approach. *Limnol. Oceanogr.* **10**, 412–426.

Frankignoulle, M., Canon, C. and Gattuso, J. P. 1994. Marine calcification as a source of carbon dioxide: Positive feedback of increasing atmospheric CO_2. *Limnol. Oceanogr.* **39**, 458–462.

Frankignoulle, M., Gattuso, J.-P., Biondo, R., Bourge, I., Copin-Montegut, G. and Pichon, M. 1996. Carbon fluxes in coral reefs. II. Eulerian study of inorganic carbon dynamics and measurements of air–sea CO_2 exchange. *Mar. Ecol. Prog. Ser.* **145**, 123–132.

Furnas, M. J. and Mitchell, A. W. 1996. Biological oceanography of the Great Barrier Reef. In: *Proceedings of the Great Barrier Reef Science, Use and Management; a national conference*, Great Barrier Reef Marine Park Authority, Townsville, 75–87.

Furnas, M. J., Mitchell, A. W. and Skuza, M. 1995. *Nitrogen and phosphorous budgets for the central Great Barrier Reef Shelf,* Great Barrier Reef Marine Park Authority Research Report No. 36, Great Barrier Reef Marine Park Authority, Townsville, 194 pp.

Gattuso, J.-P. and Buddemeier, R. W. 2000. Ocean biogeochemistry: calcification and CO_2. *Nature* **407**, 311–313.

Gattuso, J.-P., Frankignoulle, M. and Smith, S. V. 1999. Measurement of community metabolism and significance in the coral reef CO_2 source-sink debate. *Proc. Natl. Acad. Sci. USA* **96**, 13017–13022

Gattuso, J.-P., Pichon, M. and Frankignoulle, M. 1995. Biological controle of air-sea CO_2 flux: effect of photosynthetic and calcifying marine organisms and ecosystem. *Mar. Ecol. Prog. Ser.* **129**, 307–312.

Gattuso, J.-P., Pichon, M., Delesalle, B. and 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.

Gattuso, J.-P., Frankignoulle, M., Smith, S. V., Ware, J. R. and Wollast, R. 1996a. Coral reefs and carbon dioxide. *Science* **271**, 1298.

Gattuso, J.-P., Pichon, M. R., Delesalle, B., Canon, C., Copin-Montegut, G., Pichon, M. and Frankignoulle, M. 1996b. Carbon fluxes in coral reefs. I. Lagrangian measurements of community metabolism and resulting air–sea CO_2 disequilibrium. *Mar. Ecol. Prog. Ser.* **145**, 109–121.

Hatcher, B. G. 1997. Coral rre ecosystems: how much greater is the whole than the sum of parts? *Coral Reefs* **16**, suppl. S77–S91.

Hopley, D., Parnell, K. E. and Isdale, P. J. 1989. The Great Barrier Reef Marine Park: Dimensions and regional patterns. *Austr. Geogr. J.* **27**, 47–66.

Kawahata, H., Suzuki, A. and Goto, K. 1997. Coral reef ecosystems as a source of atmospheric CO_2: evidence from pCO$_2$ measurements of surface waters. *Coral Reefs*, **16** 261–266.

Kawahata, H., Yukino, I. and Suzki, A. 2000a. Terrestrial influence on the Shiraho fringing reef, Ishigaki Island, Japan: high carbon input relative to phosphate. *Coral reefs* **19**, 172–178.

Kawahata, H., Suzuki, A., Ayukai, T. and Goto, K. 2000b. Distribution of the fugacity of carbon dioxide in the surface seawater of the Great Barrier Reef. *Mar. Chem.* **72**, 257–272.

Kayanne, H., Suzuki, A. and Saito, H. 1995. Diurnal changes in the partial pressure of carbon dioxide in coral reef water. *Science* **269**, 214–216.

Kench, P. 1994. Hydrodynamic observations of the Cocos (Keeling) Islands lagoon. *Atoll Res. Bull.* **408**, 1–21.

Kinsey, D. W. 1985. Metabolism, calcification and carbon production. I Systems level studies. *Proc. 5th Int. Coral Reef Congr.* **4**, 505–526.

Kleypas, J. A., Buddemeier, R. W. and Gattuso, J.-P. 2001. The future of coral reefs in an age of global change. *Int. J. Earch Sci.* **90**, 426-437.

Kohn, A. J. 1964. Notes on reef habitats and gastropod molluscs of a lagoon island at North Male Atoll, Maldives. *Atoll Res. Bull.* **102**, 1–5.

Kraines, S., Suzuki, Y., Yamada, K. and Komiyama, H. 1996. Separating biological and physical changes in dissolved oxygen concentration in a coral reef. *Limnol. Oceanogr.* **41**, 1790–1799.

Kraines, S. B., Suzuki, A., Yanagi, T., Isobe, M., Guo, X. and Komiyama, H. 1999. Rapid water exchange between the lagoon and open ocean at Majuro Atoll due to wind, waves and tide. *J. Geophys. Res.* **104**, 15635–15653.

Maragos, J. E. and Cook, C. W. Jr. 1995. The 1991–1992 rapid ecological assessment of Palau's coral reefs. *Coral Reefs* **14**, 237–252.

Mitchell, A. W. and Furnas, M. J. 1996. Terrestrial inputs of nutrients and suspended sediments to the GBR lagoon. In: *Proceedings of the Great Barrier Reef Science, Use and Management; a national conference,* Great Barrier Reef Marine Park Authority, Townsville, 59–71.

Nakamori, T., Suzuki, A. and Iryu, Y. 1992. Water circulation and carbon flux on Shiraho coral reef of the Ryukyu Islands, Japan. *Continent. Shelf Res.* **12**, 951–970.

Nugent, L. E., Jr. 1946. Coral reefs in the Gilbert, Marshall, and Caroline Islands. *Bull. Geol. Soc. Am.* **57**, 735–780.

Pickard, G. L., Donguy, J. R., Henin, C. and Rougerie, F. 1977. A review of the physical oceanography of the Great Barrier Reef and western Coral Sea. *Aust. Inst. Mar. Sci., Monogr. Ser.* 2, 134 pp.

Pickard, G. L. and Emery, W. L. 1990. *Descriptive physical oceanography: an introduction*. 5th edition, Pergamon Press, Oxford, 654 pp.

Redfield, A. C., Ketchum, B. H. and Richards, F. A. 1963. The influence of organisms on the composition of sea-water. In: *The sea* (ed. M. N. Hill), vol. 2, Wiley, New York, 26–77.

Smith, S. V. 1978. Coral-reef area and the contributions of reefs to processes and resources of the world's oceans. *Nature* **273**, 225–226.

Smith, S. V. 1981. Marine macrophytes as a global carbon sink. *Science* **211**, 838–840.

Smith, S. V. 1988. Mass balance in coral reef-dominated area. In: *Coastal–offshore ecosystem interactions* (ed. B.-O. Jansson), Lecture Notes on Coastal and Estuarine Studies, vol. 22, Springer, Berlin, 209–226.

Smith, S. V. and Jokiel, P. L. 1978. Water composition and biogeochemical gradients in the Canton Atoll lagoon. *Atoll Res. Bull.* **221**, 15–53.

Smith, S. V. and Key, G. S. 1975. Carbon dioxide and metabolism in marine environments. *Limnol. Oceanogr.* **20**, 493–495.

Smith, S. V. and Pesret, F. 1974. Processes of carbon dioxide flux in the Fanning Island lagoon *Pacific Sci.* **28**, 225–245.

Smith, S. V., Chandra, S., Kwitko, L., Schneider, R. C., Schoonmaker, J., Seeto, J., Tebano, T. and Tribble, G. W. 1984. Chemical stoichiometry of lagoonal metabolism. *U. Hawaii/U. South Pacific Int. Sea Grant Prog. Tech. Rep. UNIHI-SEAGRANT-CR-84-02.*

Suzuki, A. 1998. Combined effects of photosynthesis and calcification on the partial pressure of carbon dioxide in seawater. *J. Oceanogr.* **54**, 1–7.

Suzuki, A., Kawahata, H. and Goto, K. 1997. Reef water CO_2 system and carbon cycle in Majuro Atoll, the Marshall Islands in the central Pacific. *Proc. 8th Int. Coral Reef Symp.* **1**, 971–976.

Suzuki, A., Nakamori, T. and Kayanne, H. 1995. The mechanism of production enhancement in coral reef carbonate systems: model and empirical results. *Sediment. Geol.* **99**, 259–280.

Suzuki, A., Kawahata, H., Ayukai, T. and Goto, K. 2001. The oceanic CO_2 system and carbon budget in the Great Barrier Reef, Australia. *Geophys. Res. Lett.* **28**, 1243–1246.

Ware, J. R., Smith, S. V. and Reaka-Kudla, M. L. 1992. Coral reefs: sources or sinks of atmospheric CO_2? *Coral Reefs* **11**, 127–130.

Weiss, R. F. and Craig, H. 1973. Precise shipboard determination of dissolved nitrogen, oxygen, argon, and total inorganic carbon by gas chromatography. *Deep-Sea Res.* **20**, 291–303.

Wolanski, E. 1994. *Physical occeanographic process of the Great Barrier Reef.* CRC Press, Boca Raton, 194 pp.