Reef Water CO₂ System and Carbon Production of Coral Reefs: Topographic Control of System-Level Performance

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Abstract. The variations of seawater CO₂ system and organic and inorganic carbon production of coral reefs were investigated with respect to topographic types and oceanographic settings. Because of dominant carbonate production in coral reef ecosystems, most coral reefs are likely to act as a net or at least a potential CO₂ source to the atmosphere. The comparison of the seawater CO₂ system parameters (pH, total alkalinity, dissolved inorganic carbon and partial pressure of CO₂; pCO₂) between a reef lagoon and the surrounding ocean allowed us to evaluate the system-level performance of the carbon cycle in the particular reef system. Surface pCO₂ in the lagoons of some atolls and barrier reefs in the western Pacific were consistently higher than those of their offshore waters. The alkalinity decrease in the lagoon water was attributed to calcification of reef organisms. Reef topography, especially residence time of lagoon water, affects the carbon budget of coral reefs to some extent. The offshore-lagoon differences in pCO₂ from several reefs showed a tendency to increase with the longer residence time of reef water. Another important factor controlling carbon turnover in coral reefs is proximity to land: terrestrial carbon and nutrient inputs were clearly observed in the northern Great Barrier Reef lagoon as well as a fringing reef of the Ryukyus. These coastal reefs serve as an active CO₂-releasing area due not only to calcification but also to degradation of land-derived carbon.

Keywords: coral reefs, carbon dioxide, carbon cycle, photosynthesis, calcification, metabolism, lagoon

1. INTRODUCTION
Coral reefs are recognized as major geological features of the earth’s surface, although they occupy only about 0.2% of the world’s ocean area (Smith, 1978). There are two important biogeochemical processes in a coral reef system: photosynthesis and calcification:

\[ \text{photosynthesis: } CO_2 + H_2O \rightarrow CH_2O + O_2 \]  \hspace{1cm} (1)

\[ \text{calcification: } Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + H_2O + CO_2. \]  \hspace{1cm} (2)
The rapid calcification, which leads to reef growth and sediment formation, can be attributed to a strong linkage to photosynthesis (Barnes and Chalker, 1990).

In recent decades, the role of coral reefs in the global biogeochemical cycle has attracted much attention (Smith, 1978, 1981; Crossland et al., 1991; Gattuso and Buddemeier, 2000). According to the latest estimate of the global CaCO₃ budget, coral reefs contribute 32–43% of neritic CaCO₃ production and 7–15% of global CaCO₃ production (Table 1). The global contribution of coral reefs becomes larger if we look at CaCO₃ accumulation, because of the stability of reef carbonates in the shallow marine environment. Sedimentary carbonates represent the largest reservoir of carbon on the earth and the fluctuation in global CaCO₃ budget influences atmospheric CO₂ concentration. Carbonate shells of marine calcifiers are expected to play a role of “primary neutralizers” of anthropogenic CO₂.

In the early 1990s, there appeared to be some confusion in our understanding of the function of marine calcifying organisms, particularly in coral reef science communities (e.g. Kinsey and Hopley, 1991). Dissolution of carbonate (the reverse of the reaction in Eq. (2)), not precipitation, enhances the ocean’s capacity to absorb CO₂ from the atmosphere. Ware et al. (1992) clearly stated that coral reefs generally work as sources of atmospheric CO₂, based on the “0.6 rule”. Frankignoulle et al. (1994) reinforced the “0.6 rule” with examinations using a seawater CO₂ system model and proposed a new index, Ψ (the released CO₂/precipitated carbonate ratio).

Despite the comments of Ware et al. (1992), Kayanne et al. (1995) reported the diurnal change of pCO₂ in Shiraho reef water of Ishigaki Island, the Ryukyus, together with an estimate of high net community production (110 mmol⁻¹d⁻¹) which can mask the CO₂ released from carbonate production (110 mmol⁻¹d⁻¹), and suggested the reef acts as a CO₂ sink. While their result was criticized for the great uncertainty in their estimation of the reef-offshore difference of partial pressure of CO₂ (pCO₂), based on the light—pCO₂ relationship.

Table 1. Calcium carbonate flux estimates for different oceanic regions (after Iglesias-Rodriquez et al., 2002, with partial modification). Production was calculated from flux multiplied by area. Unit for flux was converted from gC m⁻²y⁻¹ in the original table to mmol m⁻²d⁻¹.

<table>
<thead>
<tr>
<th>Area (10¹² m²)</th>
<th>Flux (mmol m⁻²d⁻¹)</th>
<th>Production (PgC y⁻¹)</th>
<th>Accumulation (PgC y⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neritic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coral reefs</td>
<td>0.6</td>
<td>41.1</td>
<td>0.108</td>
</tr>
<tr>
<td>Carbonate shelves</td>
<td>10</td>
<td>0.5–2.7</td>
<td>0.024–0.120</td>
</tr>
<tr>
<td>Halimeda bioherms</td>
<td>?</td>
<td>82</td>
<td>0.02</td>
</tr>
<tr>
<td>Bank/Bays</td>
<td>0.8</td>
<td>14</td>
<td>0.048</td>
</tr>
<tr>
<td>Non-carbonate shelves</td>
<td>15</td>
<td>0.7</td>
<td>0.05</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>0.25–0.34</td>
</tr>
<tr>
<td>Slope</td>
<td>32</td>
<td>0.4</td>
<td>0.060</td>
</tr>
<tr>
<td>Pelagic</td>
<td>283–300</td>
<td>0.3–0.6</td>
<td>0.41–1.1</td>
</tr>
</tbody>
</table>
obtained from relatively short-term observation (Gattuso et al., 1996a), their findings stimulated the subsequent debate on the sink/source problem of coral reefs (Kayanne, 1996). Suzuki et al. (1995) reported a relatively high P/R ratio for a reef-flat community, on Shiraho reef again, supporting the conclusion of Kayanne et al. (1995). Kraines et al. (1996, 1997) also reported sink-type behavior of a coral reef in Bora Bay, Miyako Island, which is adjacent to Ishigaki Island. In contrast to these results from the Ryukyu Islands of Japan, studies in Moorea, French Polynesia, and Yonge Reef of the northern Great Barrier Reef (GBR), showed that reef-flat communities are net sources of atmospheric CO2 (Gattuso et al., 1993, 1995; Frankignoulle et al., 1996; Gattuso et al., 1996b). More recently, observations from mid-oceanic reefs (Majuro Atoll, Palau barrier reef and South Male Atoll), as well as the GBR, showed high pCO2 in reef lagoons compared to that in the offshore area, confirming our current understanding that most coral reefs operate as sources of atmospheric CO2 (Kawahata et al., 1997, 2000b; Suzuki et al., 1997; Suzuki and Kawahata, 1999). While measurements of community metabolism are considered significant in the coral reef CO2 source-sink debate (Gattuso et al., 1999), the problem has been recently examined from some different points of view, including a long-term geochemical perspective and the prediction of future response to global warming (Kleypas et al., 1999, 2001).

Our knowledge of the carbon budget and cycling in coral reefs is still limited and there remain many problems other than the CO2 sink/source issue. As the number of observations increases, differences in the mode of carbon cycling among coral reefs have become evident. The variations may be related to topographic types and oceanographic settings of individual reefs as well as the influence of human disturbance (Suzuki and Kawahata, 1999, 2003).

Here we re-examine published results on reef metabolisms obtained from mid-oceanic reefs in the Indo-Pacific regions, including our own studies, in order to survey the latest progress on the CO2 sink/source issue and evaluate how and how much the topography and oceanographic settings influence the carbon turnover of coral reefs. Special attention is paid to terrestrial influences on coastal reefs.

2. DATA SETS

2.1 Observations on marine CO2 system of coral reef waters

Coral reefs, which we re-examine in this study, include Shiraho Reef of the Ryukyu Islands (Suzuki et al., 1995), Palau barrier reef (Kawahata et al., 1997), Majuro Atoll (Suzuki et al., 1997), South Male Atoll (Suzuki and Kawahata, 1999), as well as the GBR (Kawahata et al., 2000b; Suzuki et al., 2001) (Fig. 1). In order to evaluate the CO2 system in reef water and to estimate organic and carbonate carbon productions, temperature, salinity, pH, total alkalinity (AT) and dissolved inorganic carbon (DIC) were measured in discrete water samples. Details of measurements and calculations of pCO2 based on chemical equilibrium of CO2 system are described in the original papers mentioned above. In Palau reef, Majuro Atoll and the GBR, direct measurements of pCO2 were conducted...
Table 2. Summary of topographic features, carbon metabolisms and air-sea CO$_2$ flux for coral reefs in the Indo-Pacific region. After Suzuki and Kawahata (2003). Net community carbon production ("Net C Production" in the table) is expressed in units of mmol m$^{-2}$day$^{-1}$ both for organic carbon (Org-C) and inorganic carbon (CaCO$_3$) productions. Symbols $P/R$ and $R_{net}$ represent the ratio of gross community production to respiration and the ratio of net organic production to net inorganic carbon production, respectively. Symbol $\delta$CO$_2$ represent the difference in seawater pCO$_2$ between lagoon water and the offshore water and definition is given by Eq. (3) in the text. Influence on $\delta$CO$_2$ values caused by the offshore-lagoon difference in temperature and salinity were negligible for most cases. Asterisk (*) denotes that the production rates were estimated at system level including active reef flat community in a lagoon. Production estimates for Bora Bay was area-weighed average based on the values for reef flat and lagoon communities.

<table>
<thead>
<tr>
<th>Reef</th>
<th>Scale (km)</th>
<th>Area (km$^2$)</th>
<th>Mean depth (m)</th>
<th>Residence time</th>
<th>Net C production (µmol m$^{-2}$ day$^{-1}$)</th>
<th>P/R</th>
<th>R$_{net}$ (µmol m$^{-2}$ day$^{-1}$)</th>
<th>pCO$_2$ (µatm)</th>
<th>δCO$_2$ (µatm)</th>
<th>Flux</th>
<th>Reference of CO$_2$ values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atoll</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fanning Atoll*</td>
<td>15 × 15</td>
<td>125</td>
<td>5</td>
<td>32 d</td>
<td>-0.4</td>
<td>27</td>
<td>1</td>
<td>-0.01</td>
<td>400</td>
<td>370</td>
<td>+30 source Smith and Pesret (1974)</td>
</tr>
<tr>
<td>Canton Atoll*</td>
<td>11 × 11</td>
<td>110</td>
<td>6.2</td>
<td>50 d</td>
<td>3</td>
<td>14</td>
<td>—</td>
<td>0.01</td>
<td>290–400</td>
<td>330</td>
<td>+15 source Smith and Jokiel (1978)</td>
</tr>
<tr>
<td>Christmas Is.*</td>
<td>15 × 20</td>
<td>180</td>
<td>3</td>
<td>10–15 d</td>
<td>6</td>
<td>2.5</td>
<td>&gt;1</td>
<td>2.4</td>
<td>220</td>
<td>310</td>
<td>-80 sink Smith et al. (1984)</td>
</tr>
<tr>
<td>Majuro Atoll*</td>
<td>39 × 10</td>
<td>329</td>
<td>39</td>
<td>15 d</td>
<td>8</td>
<td>27</td>
<td>—</td>
<td>0.29</td>
<td>368</td>
<td>345</td>
<td>+23 source Suzuki et al. (1997)</td>
</tr>
<tr>
<td>Rukan-sho*</td>
<td>1.7 × 1</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>72</td>
<td>108</td>
<td>1.5</td>
<td>0.67</td>
<td>—</td>
<td>—</td>
<td>neutral Ohde and van Woensik (1999)</td>
</tr>
<tr>
<td>Barrier reef</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Tiahura Barrier R.</td>
<td>∼1 km wide</td>
<td>—</td>
<td>—</td>
<td>6 h</td>
<td>75</td>
<td>186</td>
<td>1.2</td>
<td>0.4</td>
<td>—</td>
<td>—</td>
<td>source Gattuso et al. (1993)</td>
</tr>
<tr>
<td>Yonge Reef</td>
<td>∼2 km wide</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>33</td>
<td>253</td>
<td>1.1</td>
<td>0.1</td>
<td>—</td>
<td>—</td>
<td>source Gattuso et al. (1996b)</td>
</tr>
<tr>
<td>Palau Barrier Reef</td>
<td>13 km wide</td>
<td>—</td>
<td>19</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>414</td>
<td>366</td>
<td>+46 source Kawahata et al. (1997)</td>
</tr>
<tr>
<td>Northern GBR</td>
<td>∼80 km wide</td>
<td>—</td>
<td>—</td>
<td>∼40</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>339</td>
<td>311</td>
<td>+29 source Suzuki et al. (2001)</td>
</tr>
<tr>
<td>Southern GBR</td>
<td>&gt;100 km wide</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>326</td>
<td>314</td>
<td>+12 source Suzuki et al. (2001)</td>
</tr>
<tr>
<td>Fringing reef (Ryukyu Islands, Japan)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shiraho Reef</td>
<td>∼1 km wide</td>
<td>—</td>
<td>1.1</td>
<td>4 h</td>
<td>110</td>
<td>100</td>
<td>1.3</td>
<td>1.1</td>
<td>157–521</td>
<td>322</td>
<td>-7 sink Kayanne et al. (1995)</td>
</tr>
<tr>
<td>Shiraho Reef</td>
<td>4–8 h</td>
<td>36</td>
<td>127</td>
<td>1.1</td>
<td>0.3</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>source Hata et al. (2002)</td>
</tr>
<tr>
<td>Bora Bay*</td>
<td>1 × 0.6</td>
<td>0.35</td>
<td>∼3</td>
<td>2–4 h</td>
<td>164</td>
<td>132</td>
<td>1.4</td>
<td>1.2</td>
<td>—</td>
<td>—</td>
<td>&lt;0 sink Kraines et al. (1997)</td>
</tr>
</tbody>
</table>
using a shipboard nondispersive infrared (NDIR) gas analyzer system with a
shower-type air-sea equilibrator onboard R/V Hakurai-Maru (Kawahata et al.,
1997; Kawahata et al., 2000b; Suzuki et al., 2001).

Other than the results described above, information on reef metabolism at the
community and/or system level and pCO₂ values from some coral reefs in the
Indo-Pacific regions was cited from published reports (Table 2). Additional
geomorphological data on each coral reef are also shown in Table 2. Coral reefs
in the table can be divided into three categories with respect to reef morphology:
(1) atolls, (2) barrier reefs, and (3) fringing reefs (Fig. 2).

2.2 Topographic characteristics of coral reefs examined

2.2.1 Atolls

Majuro Atoll (7°N, 171°E; Fig. 3A) in the Marshall Islands, central Pacific, has a semi-enclosed lagoon with a maximum depth of 67 m. The lagoon has only
one deep passage with a maximum depth of 46 m. The topography effectively
isolates the wide interior lagoon from the outside ocean. South Male Atoll (4°00′
N, 73°25′ E; Fig. 3B) of the Maldive Islands, northern Indian Ocean, is an oval-
shaped atoll. The lagoon water is connected with the offshore water through many
deep channels between shallow reef flats.

Fanning Atoll (Smith and Pesret, 1974) and Canton Atoll (Smith and Jokiel,
1978) are also oceanic atolls in the central Pacific. The coral reef of Christmas
Island, central Pacific, has a land-locked shallow lagoon (2–4 m deep) and Smith
et al. (1984) conducted the survey of this lagoon. Rukan-sho (Rukan reef) is a
small-scale atoll off Okinawa Island of the Ryukyus (Ohde and van Woesik, 1999).

2.2.2 Barrier reefs

In the Palau (Belau) Archipelago of the Caroline Islands (7°N, 134°E; Fig.
3C), a wide lagoon (Southern Lagoon; Maragos and Cook, 1995) with a maximum
depth of 55 m exists between the islands and a barrier reef platform (hereafter
Palau barrier reef lagoon). A narrow channel at the northern end of the lagoon is
the only deep passage (maximum depth 65 m) along the reef platform extending for approximately 86 km.

The GBR extends approximately 2600 km along the eastern coast of Australia, covering a wide range in latitude (15 degrees; Fig. 1). The major portion of total shelf area lies between 30 m and 40 m isobaths. Despite the name of “barrier”, the outer reefs are not continuous and the continuity of outer reefs is defined as “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%. In the northern GBR region, the wet-tropical catchments supply a large proportion of total runoff to the GBR throughout the year (Mitchell and Furnas, 1996). On the other hand, two large dry-catchment rivers (Fitzroy and Burdekin Rivers) show clear seasonality in discharge volumes. During the research cruise conducted in the dry season of 1996, freshwater input was recognized as a salinity decrease in the inshore area of the northern GBR lagoon, while no influence of freshwater input was detected in the southern GBR region (Suzuki et al., 2001). In this study we examine the data from the northern and southern parts of the GBR separately.

2.2.3 Fringing reef

Shirahobo Reef, located on the east coast of Ishigaki Island, southern Ryukyu Islands, Japan, is a well-developed fringing-type reef without a deep lagoon. The reef flat is about 800 m in width and is composed of four topographic sub-units including outer reef slope, reef crest, inner reef flat, and moat (Nakamori et al., 1992). The moat is a trough-like depression (shallow lagoon) along the coast with a depth that never exceeds 3 m (Fig. 2). Suzuki et al. (1995) measured community metabolism on the inner reef flat while Kayanne et al. (1995) reported diurnal
pCO₂ variations at a deeper station near the boundary between the moat and the inner reef flat. More recently, Hata et al. (2002) conducted a comprehensive study of carbon fluxes at Shiraho Reef in Ishigaki Island in September 1998.

3. RESULTS AND DISCUSSION

3.1 A definition of the coral reef sink-source problem

We need to start by clarifying the definition of the problem. Our concern for the CO₂ performance of coral reefs has several components. The mode change of coral reef metabolisms due to anthropogenic CO₂ increase in the atmosphere will be answered by the comparison of reef performance between pre- and post-
The role of coral reefs over a geological time scale has also been discussed elsewhere (Kleypas, 1997; Gattuso et al., 1999). Although these topics are certainly interesting, here we focus on the contribution of the coral reef ecosystem to the global carbon cycle in a current/natural state within a relatively short time scale. Some previously published reports employed a similar definition of the problem to that adopted here (Kinsey and Hopley, 1991; Ware et al., 1992; Gattuso et al., 1999).

Among studies focusing on the influence of coral reef performance on the global carbon cycle in a present state within a relatively short time scale, two different approaches have been employed. Ware et al. (1992), as well as Kinsey and Hopley (1991), focused on carbonate production of coral reefs, ignoring organic carbon production because net organic carbon production is generally believed to be small and the P/R ratio at community level is almost 1 (Crossland et al., 1991). On the other hand, Gattuso et al. (1999) stressed the significance of community metabolism measurements in the coral reef CO₂ source-sink debate. We also consider the importance of organic carbon metabolisms, as well as carbonate production, based on the following two viewpoints. First, the organic carbon production process in reef systems is somewhat different from the offshore processes, especially with respect to nutrient budgets. The high C:N:P ratio of benthic plants in coral reefs (550:30:1; Atkinson and Smith, 1983) relative to plankton (106:16:1; Redfield et al., 1963) allows reefs to produce more organic matter per unit delivery of nutrients than can be produced by adjacent plankton communities (Crossland et al., 1991). The high biomass/production ratio of coral reefs compared to the offshore ecosystems is another important characteristic of coral reef systems with respect to carbon storage (Smith, 1981). Second, our knowledge of the fate of organic carbon produced in coral reefs is still limited in terms both of the export to the surrounding ocean and sedimentary burial in a lagoon bottom (see Hata et al., 1998, 2002), which may not allow us to neglect the contribution of organic carbon production as trivial. According to the viewpoints described above, we start the examination by taking organic carbon production into account.

3.2 \( R_{OF} \): an index for sink/source behavior

The sink/source behavior of coral reefs is primarily controlled by the balance between photosynthesis and calcification, which shift the chemical equilibrium of oceanic CO₂ system in opposite directions (Eqs. (1) and (2)). Photosynthesis decreases pCO₂ while calcium carbonate production raises pCO₂. Suzuki (1998) examined seawater pCO₂ change caused by photosynthesis and calcification and proposed the molar ratio of organic to inorganic production \( (R_{OI}) \) as a criterion of the CO₂ sink/source behavior of marine metabolism. In this study, we apply the index \( R_{OI} \) to evaluate the sink/source performance of each coral reef in the data sets.
Fig. 4. Metabolic effects on sink/source potential of seawater with respect to the atmospheric CO$_2$. (A) Changes in pCO$_2$ (δpCO$_2$) caused by the various rates of photosynthesis and calcification. Calculations are conducted for salinity 35 and 25°C supposing initial condition of seawater is 2346 µmol kg$^{-1}$ in total alkalinity, 2000 µmol kg$^{-1}$ in DIC, and 345 µatm in pCO$_2$. Shaded area indicates the region where pCO$_2$ increased by metabolism. (B) Diurnal metabolism cycles and the criteria for sink/source behavior. (C) Sediment composition as an index for sink/source behavior of overlying water with respect to CO$_2$ exchange between the seawater and the atmosphere. Shaded area indicates sediment compositions where pCO$_2$ is expected to increase by sedimentary particle formation.
Figure 4A displays changes in pCO$_2$ (δpCO$_2$) caused by various combinations of net organic production (=photosynthesis – respiration) and net inorganic production (=calcification – dissolution) in seawater with a salinity of 35 at 25°C. This figure indicates that pCO$_2$ decreases (δpCO$_2$ < 0, therefore, sink-type behavior) when net organic production is larger than approximately 0.6 times net inorganic carbon production ($R_{OI} > 0.6$). In the present study, the symbol $R_{OI}^0$ denotes the critical ratio for δpCO$_2$ = 0.

The critical value of approximately 0.6 for $R_{OI}^0$ is almost identical to the Ψ value (molar ratios of released CO$_2$ to precipitated CaCO$_3$) proposed by Frankignoulle et al. (1994). Therefore, $R_{OI}$ can be recognized as a different expression of Ψ, suggesting that the degassing and absorption processes of CO$_2$ in the air-sea interface are identical to photosynthetic CO$_2$ uptake from seawater and respiratory CO$_2$ release of aquatic organisms, respectively, with respect to the effects on the chemical equilibrium in seawater.

A similar analogy can be applied to the chemical compositions of reef sediments, if the sediments store the products of past reef metabolism. According to Buddemeier (1996), a reef that is an atmospheric CO$_2$ sink has to deposit more than 12 weight % organic matter (6 weight % organic carbon) in reef sediments. This criterion can be extended to a three-component system shown in Fig. 4C.

3.3 Temporal and spatial scale of the problem

In order to apply the index $R_{OI}$ to coral reef metabolism, we need to examine the scales of discussion in time and space. Usually we discuss the sink/source behavior of coral reef organisms and/or communities on the daily or yearly basis. The concept and terminology of daily metabolism are shown in Fig. 4B, which indicates the importance of estimating net organic and inorganic production for a certain period in order to determine the CO$_2$ sink/source behavior of organisms and/or communities.

The sink/source debate in the early 1990s mostly focused on the “coral reef flat”. There are two methods for measuring metabolisms of reef communities: flow respirometry and the slack-water method. Flow respirometry has been employed on a reef flat community under unidirectional flow by many researchers, including the pioneering work by Odum and Odum (1955). The slack-water method was proposed by Kinsey (1978) and has been widely used in enclosed conditions on reef flats or moats during low tide.

Gattuso et al. (1993, 1995) reported that the reef flat community of the barrier reef of Moorea is a net source of atmospheric CO$_2$, based on daily net organic and inorganic production measurements using flow respirometry. By contrast, Kayanne et al. (1995) and Suzuki et al. (1995) employed the slack-water method to measure reef-flat metabolism in Shiraho Reef, concluding that the reef flat community showed a sink-like behavior.

Contradictory results are, at least partly, a reflection of the large errors in measuring the community metabolism rate of coral reefs. Difficulties in production estimates are caused by the relatively short residence time of water in fringing and
As an example, the diurnal pattern of pH in seawater on a fringing reef is shown in Fig. 5A. Dual modulation on variations of pH and other CO₂ parameters due to tide and light cycles makes the measurements of community metabolism difficult. The daily budget estimate cannot escape a large uncertainty caused by the integration of short-term metabolism rates.

On the other hand, deep lagoons of oceanic atolls and barrier reefs have a relatively long residence time of several weeks to months (Table 2). Consequently, the diurnal changes of pH in both the lagoon and the offshore waters are usually small (Fig. 5B). In this case, a more reliable approach to examining the CO₂ sink/source behavior of coral reefs can be successfully applied to atolls and barrier reefs (Kawahata et al., 1997; Suzuki et al., 1997). These studies compared the pCO₂ differences ($\delta$pCO₂) between the lagoon water (pCO₂,L) and the offshore waters (pCO₂,O) of mid-oceanic reefs, such as Majuro Atoll and Palau barrier reef.
δpCO₂ = pCO₂,L - pCO₂,O. \hspace{1cm} (3)

Since water and dissolved materials typically enter atolls across the reef flat from the ocean, the composition of lagoon water reflects metabolic activity, not only in the lagoon but also on the reef flats and knolls. This condition favors the evaluation of the net effect of reef metabolisms on reef water-atmosphere CO₂ exchange. Smith (1988) demonstrated the ability of a similar approach to examine nutrient budgets of confined aquatic ecosystems. This strategy can also be applied to marine CO₂ systems to examine the sink/source behavior of coral reefs at system level.

3.4 Sink/source behavior of coral reefs

In this section we test the suitability of the index \( R_{OI} \) for evaluating the sink/source performance using the data sets (Table 2). Can sink/source behavior of the particular coral reef be predicted based on a system-level \( R_{OI} \) value?

The first example is Majuro Atoll (Suzuki et al., 1997), the net organic and inorganic carbon production of which was re-calculated as 8 mmol m⁻²d⁻¹ and 27 mmol m⁻²d⁻¹, respectively (Fig. 6), supposing a residence time of 15 days reported by Kraines et al. (1999). Because the \( R_{OI} \) value is 0.29, which is less than the critical value of 0.6, it is predicted that the atoll shows positive \( \delta pCO₂ \) (CO₂ source). The average \( \delta pCO₂ \) values observed in Majuro Atoll was around +48 \( \mu \)atm and the prediction agrees with the result of pCO₂ observations (Fig. 3A).

Net organic and inorganic carbon production reported at community- and system-levels, together with observed \( \delta pCO₂ \) values, are plotted in Fig. 7. Other than Majuro Atoll, Fanning Atoll and Canton Atoll in the category of atolls in Table 2 showed considerably smaller \( R_{OI} \) values than the critical ratio. High \( \delta pCO₂ \) was evident for those atolls, indicating consistency with \( R_{OI} \)-based prediction.
While most community- and system-level estimates are plotted in the “source” region (ROI < 0.6), some exceptions are found. Christmas Island lagoon indicated higher ROI values than the critical ratio and a negative δpCO2 value was indeed observed (CO2 sink). The phosphorus input from guano deposits was expected to stimulate active organic production in the lagoon, while low salinity due to fresh water input may have partly contributed to the extremely low pCO2 in lagoon water (Smith et al., 1984). A metabolic study of Rukan reef reported 0.7 for ROI, which is close to the critical value (Ohde and van Woesik, 1999). Therefore, the community metabolism is predicted to be almost neutral with respect to air-sea CO2 flux. This prediction does not contradict the conclusion of the original authors.

Two fringing reefs, Shiraho Reef (Kayanne et al., 1995) and Bora Bay (Kraines et al., 1997) in the Ryukyu Islands, indicate higher ROI values than the critical ratio (ROI > 0.6) and a negative δpCO2 value was indeed reported from Shiraho Reef (CO2 sink) by the authors. The relationship between ROI and observed δpCO2 of these reefs is consistent with the hypothesis, even when those reefs showed a CO2-sink behavior. Is CO2-sink-like performance common for the fringing type of reefs? We cannot exclude the possibility that some fringing reefs have higher ROI values than the critical ratio due to large contribution from an active reef flat community, where high ROI values can be expected. On the other hand, the influence on reef metabolism of fertilizer used on farmland has been...
pointed out as a possible cause of the relatively high organic production in the reef flat community of Bora Bay as well as Shiraho Reef (Kraines et al., 1997).

More recently, Hata et al. (2002) conducted a comprehensive study of carbon fluxes, including community metabolism and carbon export in the form of dissolved and particulate matter at Shiraho Reef in September 1998. According to their estimates, $R_{OI}$ can be calculated to take a relatively small value of 0.3 for the reef flat community, suggesting a CO$_2$-source-like behavior. Because Shiraho Reef is the site where negative δ$pCO_2$ observation was reported previously (Kayanne et al., 1995), the implication of the results for the CO$_2$ sink/source debate is important. The study, however, was done during the recovery stage from the 1998 mass bleaching event in the region. Special caution may thus be needed when discussing this event.

In conclusion, the observations of δ$pCO_2$ listed in Table 2 agree well with the theoretical prediction that $R_{OI}$ can be used as an index of sink/source behavior (Fig. 7). Most community- and system-level estimates appeared to support a CO$_2$-source ($R_{OI} < 0.6$). Although some coral reefs showed sink-like metabolisms ($R_{OI} > 0.6$), some regional effects, which enhance organic carbon production, have been pointed out as a likely cause of their CO$_2$-sink type behavior.

3.5 Topographic control on CO$_2$ system in coral reefs

The observed δ$pCO_2$ values varied from reef to reef (Fig. 3). Although the ratio $R_{OI}$ is a primary factor determining the sink-source behavior of a particular reef system, there must be another factor controlling the magnitude of δ$pCO_2$ values. In addition, there appears to be a slightly increasing trend in δ$pCO_2$ with longer reef water residence time (Table 2). Open atolls and fringing reefs with short water residence times tend to show small or even negative δ$pCO_2$ values. In other words, the slower the renewal of the water is, the higher is pCO$_2$ in reef water.

Difference of carbon turnover in coral reefs due to residence time variation can be seen in $A_T$–DIC diagrams for South Male Atoll and Palau Barrier Reef (Fig. 8). The graphic approach to carbon cycle study of coral reefs using an $A_T$–DIC diagram was illustrated by Suzuki and Kawahata (2003). Most of the lagoon samples of both reefs are plotted around a “calcification line” in the $A_T$–DIC diagrams, suggesting predominant carbonate production in these reefs with negligible excess organic carbon production. In detail, the distance between the offshore and lagoon clusters in the diagram along the calcification line is much larger for Palau barrier reef than South Male Atoll, reflecting the larger compositional change of Palau lagoon water from the surrounding ocean.

The lagoon of South Male Atoll has an open nature, being connected to the surrounding ocean by numerous deep channels (30–70 m deep), which are much deeper than typical Pacific atoll channels. In contrast to scanty reef development in typical Pacific atoll lagoons, the flourishing of branching corals on knolls in the lagoon of Maldivian atolls (Kohn, 1964) is probably related to the large flow of oceanic water through the broad, deep channels. Thus, the small changes in CO$_2$ system parameters including $A_T$, DIC and pCO$_2$ values between the offshore
and the lagoon can be attributed to dilution due to the high flushing rate of the lagoon. On the other hand, Palau barrier reef lagoon shows a higher degree of closure than South Male Atoll, having only one deep entrance channel. As the residence time increases, more time becomes available for calcification. The observed decreases in $A_T$ and DIC in the lagoon compared to the offshore water were greater in Palau lagoon than in South Male Atoll lagoon. This evidence is consistent with the observed difference of $\delta pCO_2$ between the two reefs.

### 3.6 Terrestrial influence on coastal coral reefs

While oceanic reefs, such as South Male and Majuro atolls, have no 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 significant differences between the $A_T$-DIC diagrams of the northern and southern GBR lagoons (Fig. 9), with a remarkable difference between them in terms of water, sediment and nutrient input from land.

In the $A_T$-DIC diagram for the southern GBR lagoon (Fig. 9A), most of the lagoon samples of both reefs are plotted around a “calcification line”, suggesting predominant carbonate production with negligible excess organic carbon production. By contrast, overall displacement of the lagoon-water calcification line from the offshore compositions can be seen along the increasing DIC trend (Fig. 9B). As described in Suzuki et al. (2001), 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 oxidation of organic
matter and \( \text{DIC} \) supply from external sources such as atmospheric input, rainfall and river discharge. Suzuki et al. (2001) concluded that the possible external source of carbon into the GBR lagoon is terrestrial input, including direct discharge of \( \text{DIC} \) in freshwater and oxidation of land-derived organic matter. Calcification, together with \( \text{DIC} \) inputs from terrestrial sources, serves a major role in the net carbon cycle of the northern GBR lagoon system. No features of excess organic carbon production can be seen.

Do nutrient inputs from land stimulate organic carbon production in a reef area? Suzuki et al. (2001) estimated the riverine C:N:P molar ratio in the GBR region as 1120:30:1, based on their carbon budget calculation and annual riverine nitrogen and phosphorous 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 \( \text{DIC} \). Although nutrient inputs may stimulate organic carbon production in a reef area, net oxidation of organic matter rather than net organic carbon fixation would be expected in the GBR lagoon.

A similar influence was also recognized in the Shiraho fringing reef of the Ryukyu Islands (Kawahata et al., 2000a). Land derived freshwaters, including river water and groundwater, make a relatively large contribution to the reef’s circulation system. These terrestrial waters exhibit extremely high \( \text{pCO}_2 \), up to 6,400 \( \mu \text{atm} \), reflecting enrichments in \( A_T \) and \( \text{DIC} \) due to dissolution of carbonate rocks and decomposition of organic matter in the soil of subtropical island. These terrestrial influences may enhance \( \text{CO}_2 \) degassing from the coastal zone. While
sink-type behavior has been reported for reef flats of fringing reefs, the influence of terrestrial inputs on carbon turnover of the entire fringing reef system remains a subject for future discussion.

The future change of coral reef calcification is currently a subject of discussion with respect to global warming and the accompanying changes of carbonate saturation state in seawater (Kleypas et al., 1999, 2001). The recent degradation of coastal reef ecosystems due to anthropogenic impacts is also very severe. In addition, recurrent mass bleaching events, which can be at least partly attributed to the global warming, may result in a decrease in organic production and fishery yield in coral reefs (Hughes et al., 2003). A further understanding of carbon dynamics in coral reefs is required not only for analyzing the role of coral reefs in the global carbon cycle but also for predicting the future change of coral reefs under rapidly changing environment.

4. SUMMARY

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 CO2. Due to dominant carbonate production with negligible excess organic carbon production in coral reef ecosystems, most coral reefs act as a net, or at least CO2 source to the atmosphere. This rule is supported by observations from atolls and barrier reefs in the western Pacific: higher pCO2 and lower total alkalinity in the lagoon waters were evident compared to their offshore waters. Reef topography, especially residence time of lagoon water, affects the carbon budget of coral reefs to some extent. There is a relatively weak, but still recognizable positive relationship between the lagoon-offshore difference in pCO2 and residence time of reef water. Another important factor controlling carbon turnover in coral reefs is proximity to land: terrestrial carbon and nutrient inputs were recognized in most fringing and barrier types of reefs. Terrestrial inputs of carbon and nutrient may enhance the CO2 release from coral reefs to the atmosphere.

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