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Seasonal variability of the effect of coral reefs on seawater CO_2 and air–sea CO_2 exchange

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Abstract

There are complex physical and biological processes controlling the exchange of carbon dioxide (CO_2) between the ocean and atmosphere. In coral reef ecosystems, the balance of biological processes such as calcium carbonate ($CaCO_3$) formation and organic carbon production can either lead to CO_2 being retained in the oceanic environment (i.e., oceanic sink of CO_2) or returned to the atmosphere through gas exchange (oceanic source of CO_2). What remains uncertain is the fate of CO_2 in reefs subject to seasonal change and the annual balance of air–sea CO_2 flux in such systems. Here it is shown that the Bermuda coral reef acts as a source of CO_2 to seawater overlying the reef. The magnitude of this source of CO_2 varies seasonally in response to changes in the reef community between coral- and macroalga-dominated states, reflecting changes in the net balance between calcification and organic carbon production. With knowledge of the calcification rate ($\sim$5.6 to 10.6 g $CaCO_3$ m^{-2} d^{-1}) and observed modification in seawater fCO_2 by reef metabolism, rates (-0.6 to 3.3 g C m^{-2} d^{-1}) and seasonal patterns of macroalgal productivity were estimated. Whether the Bermuda coral reef system acts as an oceanic sink or source of CO_2 to the atmosphere not only depends on this seasonal variation, but, more importantly, depends on the pre-existing air–sea CO_2 disequilibrium of open ocean waters surrounding the reef system. The Bermuda coral reef system serves as a useful model for understanding the fate of CO_2 in other reefs, particularly those reefs changing because of environmental stress.

Coral reefs are biologically diverse ecosystems built upon the accumulation of calcium carbonate ($CaCO_3$) produced by frame-building scleractinian corals and calcareous algae. Within the reef system, biological processes such as photosynthesis (i.e., $CO_2 + H_2O \rightleftarrows CH_2O + O_2$) and calcification (i.e., $Ca^{2+} + CO_3^{2-} = CaCO_3$) have demonstrable effects on seawater CO_2 chemistry (e.g., Langdon et al. 2000). For example, photosynthetic fixation of CO_2 into organic carbon acts to decrease the fugacity of CO_2 (fCO_2) and total carbon dioxide (TCO_2, where $TCO_2 = HCO_3^- + CO_3^{2-} + CO_2$), respectively, whereas total alkalinity (TA, where $TA = HCO_3^- + 2CO_3^{2-} + B(OH)_4^- + OH^- + H^+ +$ minor species) remains largely unaffected. Calcification ($Ca + 2HCO_3^- \rightleftarrows CaCO_3 + CO_2 + H_2O$) acts to decrease TCO_2 and total alkalinity in the ratio of 1 : 2. The fate of CO_2 produced by calcification depends on many factors, including the ratio of organic carbon production to $CaCO_3$ production (Buddemeier 1996), irradiance levels (Gattuso et al. 1997), and the dominant type of calcifying organism (Gattuso et al. 1999*a*).

Several studies have demonstrated that coral-dominated reef ecosystems are sources of CO_2 to the surrounding waters (e.g., Ware et al. 1992; Gattuso et al. 1993*a*, 1995, 1996*a*, 1999*b*). Other studies have suggested that macroalga-dominated reef systems are sinks for CO_2 (e.g., Yamamuro et al. 1995; Kayanne et al. 1996; Gattuso et al. 1997; Kraines et al. 1997). In a recent review, Gattuso et al. (1999*b*) find that ''average'' coral reef flats are sources of CO_2 to the atmosphere. Whether coral reef ecosystems act as sources of CO_2 to the atmosphere or sinks of CO_2 appears to depend on the balance of two processes: organic carbon production by macroalgae and $CaCO_3$ production by corals. This balance is critical for carbon cycling on reefs because many reefs are shifting from coral-dominated to macroalga-dominated states in response to environmental change (e.g., Kinsey 1985; Smith and Buddemeier 1992; Hughes 1994), thereby potentially shifting reef metabolism from CO_2 release through reef calcification to CO_2 invasion driven by organic carbon production. Furthermore, it is postulated that coral reef calcification rates may decline in the future because of the increasing levels of atmospheric CO_2 change and the reduction of inorganic carbon species available for calcification (e.g., Gattuso et al. 1999*a*; Kleypas et al. 1999; Langdon et al. 2000).

The fate of CO_2 in coral reef ecosystems subject to seasonal changes and the annual balance of CO_2 in such systems remain uncertain. Previous studies have typically been restricted to observations of seawater CO_2 and associated variables over a few days only (e.g., Gattuso et al. 1993*b*; Kayanne et al. 1995; Frankignoulle et al. 1996; Kawahata et al. 1997; Ohde and Woesik 1999) to approximately 1 month (Bates et al. 2001). In the latter study, Bates et al. (2001) found that the Bermuda coral reef was a source of CO_2 to the water overlying the reef during a short period of observation. In this paper, the seasonal and interannual variability of CO_2 and air–sea CO_2 fluxes on the Bermuda coral reef over a 4-yr period (1994–1998) are investigated. The Bermuda reef CO_2 data are compared to contemporaneous sea-

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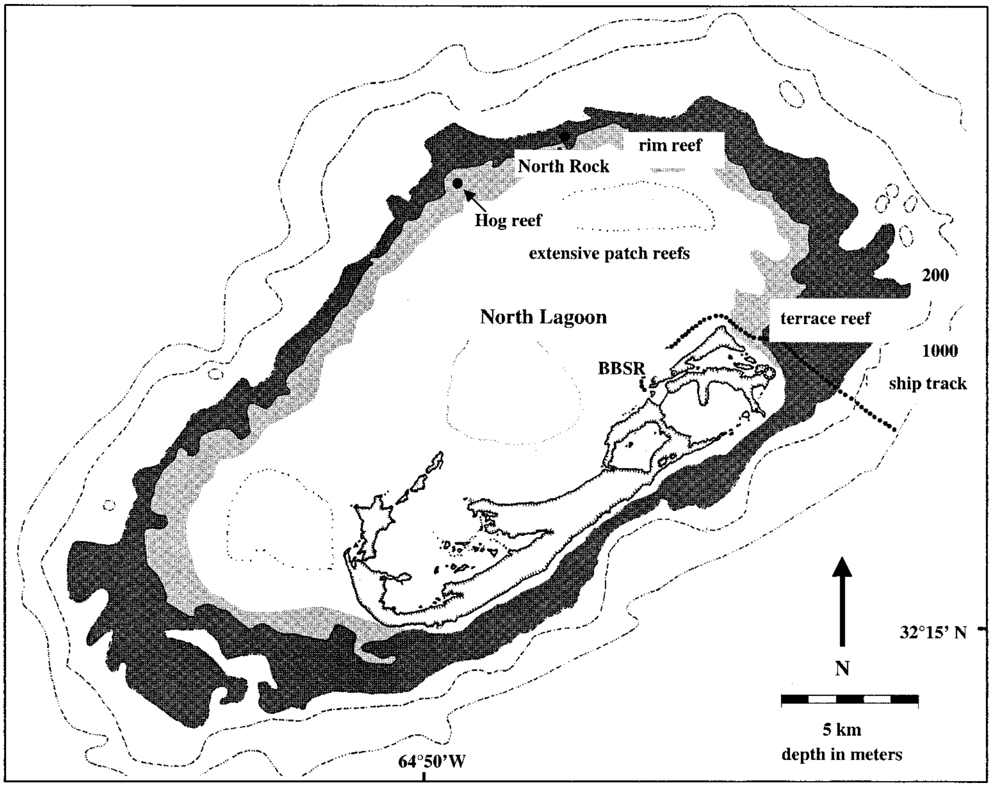

Fig. 1. Location map of the Bermuda coral reef. The route of the R/V *Weatherbird II* between the dock at BBSR and the open ocean through the eastern rim and ledge-flat reefs of Bermuda is noted on the map. The oceanographic time series site, Bermuda Atlantic Time-series Study (BATS), is located ~85 km southeast of Bermuda in a water depth of 4,500 m at 31°50′N, 64°10′W.

water CO_2 data collected from the surrounding offshore Sargasso Sea at the U.S. Joint Global Ocean Flux Study (JGOFS) Bermuda Atlantic Time-series Study (BATS) site (31°50′N, 64°10′W). Bermuda reef waters have short residence times and are continuously renewed from offshore water impinging on the reef system. Comparison of both CO_2 time series thus reveals the seasonal biogeochemical modification of Sargasso Sea water after entrainment onto the Bermuda reef. The magnitude of the Bermuda coral reef system as a source of CO_2 changes in response to seasonal changes in the community structure of the reef (i.e., coral-dominated vs. macroalga-dominated ecosystem) and the balance of organic carbon production to $CaCO_3$ production.

Materials and methods

The Bermuda coral reef system—The shallow platform waters of Bermuda are surrounded with a flank of outer terrace and rim reefs that define the North Lagoon (Fig. 1). The North Lagoon contains inshore and nearshore patch reefs and extensive sand areas, with an average depth of 8.5 m (Morris et al. 1977). The mean percent cover of hard corals and macroalgae in Bermuda waters is 20% and 11%, respectively (CARICOMP 1997). The percent cover of hard corals in the rim and terrace reefs is higher than the mean (~20–30%), whereas percent cover on the outer slope, in depths of 15–30 m, is ~60% (S. R. Smith unpubl. data).

Waters of the Bermuda platform are continuously exchanging with offshore waters of the surrounding Sargasso Sea. In the North Lagoon, residence times of water vary between 1 and 20 tidal cycles (Morris et al. 1977; R. J. Johnson unpubl. data); the variability of residence time relates to patterns of tidal and wind circulation and distance from offshore waters. On the southeastern flank of the Bermuda coral reef, through which the ship was routed, the residence time of water in the area is typically 1–3 tidal cycles (R. J. Johnson unpubl. data). There is no significant freshwater discharge from the Bermuda landmass into the shallow waters of the Bermuda platform; thus, the source waters of the Bermuda coral reef are the surrounding offshore waters of the Sargasso Sea.

Seawater and atmospheric CO_2 sampling—Two contemporaneous time series of CO_2 and associated variables were collected during a 4-yr period on the Bermuda coral reef and at an offshore open ocean site in the surrounding Sargasso Sea (i.e., at the BATS site, located ~85 km southeast of Bermuda at 32°50′N, 64°10′W), which is part of the North Atlantic subtropical gyre. Surface seawater data (i.e., fCO_2 and temperature) were collected aboard the R/V *Weatherbird II* during approximately 150 cruises between 1994 and 1998. The ship transits between the dock at the Bermuda Biological Station For Research (BBSR) and the open ocean BATS site. The ship track is routed over ~6 km of the southeastern outer rim and terrace reefs of Bermuda (Fig. 1). Coral framework builders, such as *Montastrea annularis* and *Diploria labyrinthiformis* dominate the reef, with a hard coral cover of approximately 30%. The last few kilometers of the ship route close to BBSR passes the nearshore patch reefs and sandy biotope containing occasional beds of sea grasses (e.g., *Thalassia*) and macroalgae.

Seawater and atmospheric fCO_2 measurements were collected across the Bermuda coral reef and the BATS site using a nondispersive infrared analyzer and showerhead equilibrator. Data were collected every ~2 min during the ship transits. Bermuda reef fCO_2 data used in this paper were taken from samples collected over the terrace reef. The fCO_2 measurements had an accuracy of ~1 μatm (see Bates et al. 1998*a* for details). fCO_2 is the fugacity of CO_2 in equilibrium with seawater or atmosphere, which takes account of the nonideal nature of the gas phase. Originally, partial pressure of CO_2 (pCO_2) data was collected and subsequently converted to fCO_2 values. The difference between fCO_2 and pCO_2 is very small (typically $<0.2\%$). For more details on these definitions, see Dickson and Goyet (1994).

The seasonal and interannual variability of CO_2 and the processes controlling the ocean carbon cycle and the air–sea exchange of CO_2 in the Sargasso Sea are well documented (Michaels et al. 1994; Bates et al. 1996*a,b*, 1998*a,b*, 2000; Michaels and Knap 1996; Bates 2001; Steinberg et al. 2001). CO_2, hydrographic, and biogeochemical data have been collected at the BATS site and across the Sargasso Sea since 1988 (http://www.bbsr.edu). For this analysis, fCO_2 data collected at BATS can be considered representative of the Sargasso Sea and thus can be used to constrain our knowledge of how Sargasso Sea waters contacted by the Bermuda coral reef ecosystem are modified.

Other parameters of the carbonate system—Supplemental TCO_2 and alkalinity data are also used in the analysis here. TCO_2 was determined by coulometry with a precision of 0.025% ($\sigma = 0.4$ μmol kg^{-1}) based on duplicate and triplicate analyses of $>1{,}500$ samples at BBSR from 1991 to 1998 (Bates et al. 1996*a*). Total alkalinity was determined by potentiometric titration using a modified Gran plot with a precision of 0.2% (~4 μmol kg^{-1}) (see Bates et al. 1996*a* for details).

Air–sea CO_2 fluxes—The exchange of CO_2 between ocean and atmosphere is driven by differences in fCO_2 at the air–sea interface. The net air–sea flux of CO_2 (F) is expressed as

$$F = ks(\Delta fCO_2) \tag{1}$$

where k is the transfer velocity, s is the solubility of CO_2, and ΔfCO_2 is the difference between atmosphere and ocean. The variable k is commonly parameterized as a function of wind speed (e.g., Liss and Merlivat 1986; Wanninkhof 1992; Wanninkhof and McGillis 1999), and CO_2 fluxes can vary by up to a factor of two depending on the k–wind speed relationship used. For the comparison of CO_2 fluxes on the Bermuda reef and surrounding Sargasso Sea, the quadratic k–wind speed relationship of Wanninkhof (1992) is used.

$$\mathrm{k} = 0.31u^2(660/\mathrm{Sc})^{1/2} \tag{2}$$

u is wind speed at 10 m above mean sea level, and Sc is the Schmidt number for CO_2. Sc was calculated using the equations of Wanninkhof (1992), and s (solubility of CO_2 per unit volume of seawater) was calculated from the observed temperature and salinity using the equations of Weiss (1974). Wind speed data for the period 1994–1996, collected at approximately 10.5 m above the former Naval Air Station on Bermuda, were corrected to 10 m using the equations of Smith (1988).

Results and discussion

Seasonal variability of f*CO_2 and temperature*—The Bermuda reef system undergoes considerable seasonal forcing. The seasonal patterns of surface temperature were similar for both the Bermuda reef and the Sargasso Sea (Fig. 2a), although the temperature ranges were different. The seasonal temperature range for the Bermuda reef was ~12°C compared to ~8°C at the BATS site. The shallow waters of Bermuda were cooler in winter (~17–19°C) than the Sargasso Sea (~19–21°C). Similar summertime temperature ranges occurred (~26–29°C) at both sites, with Bermuda waters marginally warmer.

Seawater pCO_2 conditions varied seasonally at both sites (Fig. 2b). The seasonal range on the Bermuda reef was ~120–150 μatm, compared to ~70–90 μatm in the Sargasso Sea. Winter pCO_2 minima at both sites were similar (~310–330 μatm), but summer maxima were markedly higher on the platform (~400–460 μatm) compared to the Sargasso Sea (~380–410 μatm).

Modification of seawater f*CO_2 on the Bermuda coral reef*—The Sargasso Sea surrounding Bermuda is the primary source of water mixed by wind and tide onto the Bermuda platform and coral reef system. Any difference in the CO_2 properties between the Bermuda platform and the Sargasso Sea thus reflects the modification of the original source waters by a combination of physical (e.g., temperature) and biological processes (e.g., coral reef $CaCO_3$ production). Seawater fCO_2 on the Bermuda reef was typically ~0–50 μatm higher than in the Sargasso Sea (Fig. 2b). Such differences in seawater fCO_2 were not, however, related to temperature gradients between offshore waters of the Sargasso Sea and reef waters of Bermuda. The effect of warming or cooling on seawater fCO_2 can be accounted for by correcting fCO_2 data to a constant temperature using an empirical thermodynamic correction of 4.23% change in fCO_2 per 1°C change (Takahashi et al. 1993). This analysis indicates that temperature-corrected seawater fCO_2 from the Bermuda reef was typically higher than in the Sargasso Sea (Fig. 2c) by as much as 50 μatm (Fig. 2d). Minor day-to-day variability in the modification of fCO_2 (up to ~10–20 μatm) on the Bermuda reef was evident (Fig. 2d), which presumably relates to variability in the mixing and modification history of water resident on the reef system during shipboard sampling.

The residence time of water on the eastern part of the Bermuda reef system (i.e., the area sampled in this study) is typically 1–3 tidal cycles (R. J. Johnson unpubl. data). Reef

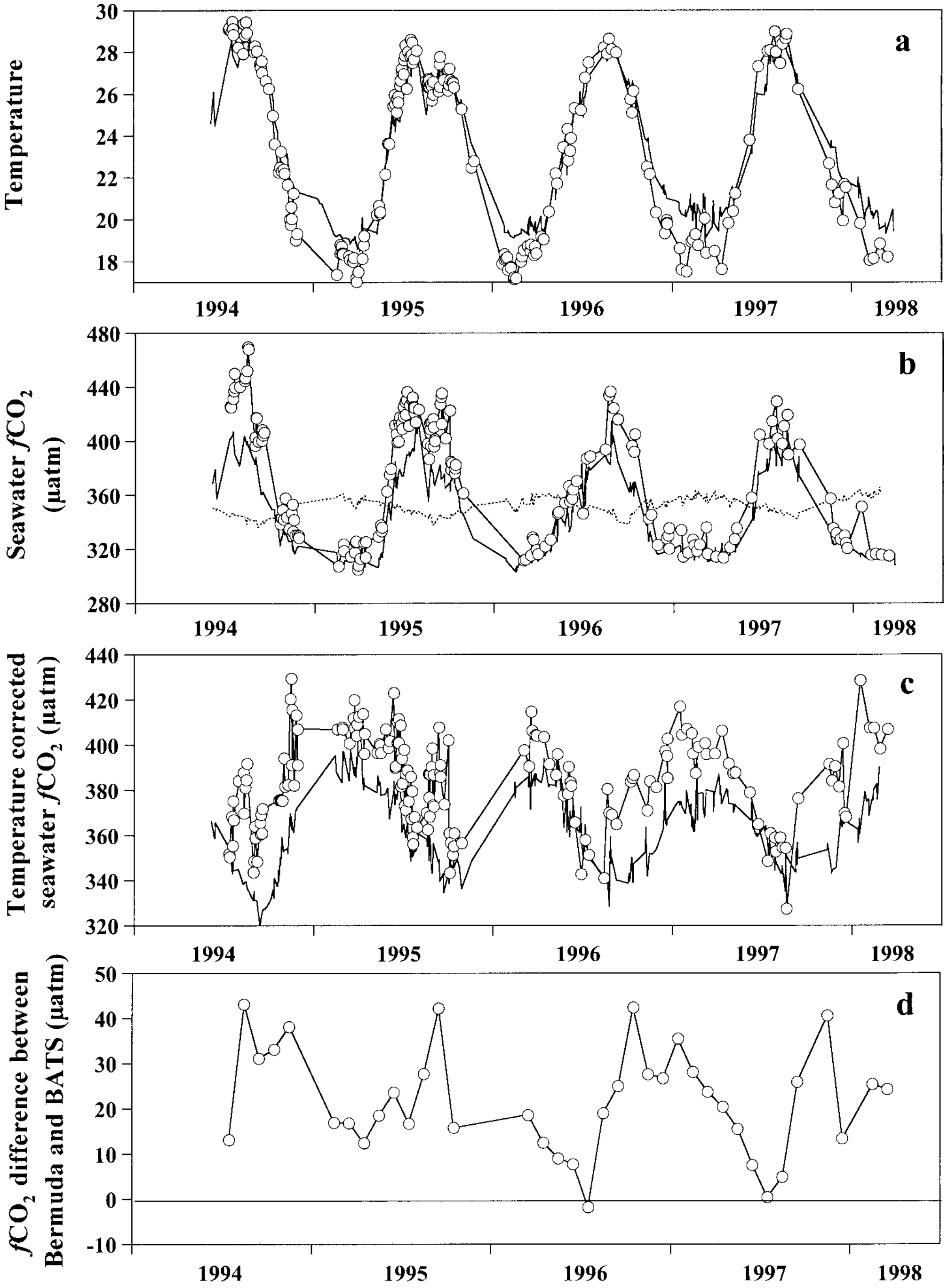

Fig. 2. Time series of temperature and CO_2 properties in the Bermuda coral reef and Sargasso Sea (i.e., BATS site). (a) Time series of temperature (°C) data from the Bermuda coral reef (open circle) and BATS (solid line). (b) Seawater fCO_2 (μatm) data from the Bermuda coral reef (open circle) and BATS (solid line). Atmospheric fCO_2 data is plotted as dotted line. (c) Seawater fCO_2 (μatm) data from the Bermuda coral reef (open circle) and BATS (solid line) corrected to a constant temperature of 25°C using the thermodynamic equation of 4.23% change in pCO_2 per °C change (Takahashi et al. 1993). Each data point for the BATS data is the mean daily temperature and fCO_2 in the vicinity of BATS and Hydrostation S. Each data point for the Bermuda Platform represents the mean temperature and fCO_2 of data collected while the R/V *Weatherbird II* was on the Platform. (d) Difference between BATS and Bermuda Platform seawater fCO_2 corrected to a constant temperature of 25°C. Each data point represents the mean difference calculated for each month over the 4 yr of observation. Seawater was pumped from a bow intake located approximately 1 m deep. Temperature and conductivity were measured continuously using a SeaBird thermosalinograph system with probes placed at the bow intake and just before the pumping system. Seawater and atmospheric pCO_2 data was measured 12 and 2 times per hour, respectively. Seawater pCO_2 data was calibrated every 30 min with four CO_2-in-dry-air standards referenced against World Meteorological Organization (WMO) standards. A slight warming (~0.05°C) was observed between bow intake and equilibrator. The warming correction for pCO_2 was within the analytical uncertainty of the pCO_2 measurement (~1 μatm; Bates et al. 1998a)

waters in this location are thus continually renewed from offshore sources within a couple of days, requiring that the observed modification of seawater fCO_2 on the reef occur quickly (i.e., within a few days). In the North Lagoon (see Fig. 1), offshore waters can reside onshore for longer periods (~5–10 d), and the enhancement of reef seawater fCO_2 relative to the Sargasso Sea can exceed 100 μatm (Bates et al. 2001).

The increase in seawater fCO_2 on the Bermuda reef system reflects the net balance of several different processes, including (1) air–sea gas exchange of CO_2, (2) water column net primary production, (3) vertical mixing processes, (4) benthic organic carbon production, and (5) $CaCO_3$ production. Analysis of the potential contribution of these five processes to changes in seawater fCO_2 on the reef system indicates that the first three terms (i.e., gas exchange, water column productivity, and vertical mixing) have a negligible effect on CO_2 dynamics. For example, air–sea fluxes of CO_2 in the Sargasso Sea generally range between +5 and −5 mmol CO_2 m^2 d^{-1}, depending on the seasonal variability of wind and ΔfCO_2 (e.g., Bates et al. 1998*a*). Considering that the residence of water on this part of the reef is short (<2 d), such rates of CO_2 flux will change seawater fCO_2 by only a small amount (<~1–2 μatm d^{-1}). The rates of water column primary production on the Bermuda coral reef are low (Morris et al. 1977), slightly higher than rates in the surrounding Sargasso Sea (Michaels and Knap 1996; Steinberg et al. 2001). Although rates of ^{14}C primary production were not measured on the reef during the period of CO_2 sampling, chlorophyll *a* (Chl *a*) biomass, an indirect proxy for production, was measured in North Lagoon from 1996 to 1998 (Connelly 1997; D. P. Connelly unpubl.). Surface Chl *a* biomass seasonally ranged from 0.1 to 0.4 mg C m^{-3} in North Lagoon compared to chlorophyll biomass of 0.02–0.4 mg C m^{-3} observed at BATS (Steinberg et al. 2001). In the Sargasso Sea, diurnal variability of seawater TCO_2 and fCO_2 due to plankton production and respiration at BATS is minor (~0.3 μmol kg^{-1} TCO_2 and <1 μatm fCO_2; Bates et al. 1996, 1998; N. R. Bates unpubl. data). Similarly, diurnal variability of seawater fCO_2 on the Bermuda reef system should also be minor (~1–2 μatm) given the low rates of water column production on the Bermuda reef system. In addition, the contribution of water column $CaCO_3$-producing phytoplankton, such as *Emiliania huxleyi,* to seawater CO_2 dynamics should be negligible considering the minor contribution of calcifying plankton to pelagic plankton found on the Bermuda reef system (Morris et al. 1977). Finally, vertical mixing processes will not contribute significantly to the observed seawater CO_2 changes because the reef waters are shallow (<8.5 m) and there is a lack of vertical thermohaline or CO_2 gradient onshore.

The modification of seawater fCO_2 (i.e., up to 50 μatm) on the Bermuda coral reef largely reflects the net balance between organic carbon production (decreasing fCO_2) and $CaCO_3$ production (increasing fCO_2). Calcification in the daylight has been measured at a rate of 12.3 ± 3.6 mmol m^{-2} h^{-1} in October 1998 (Bates et al. 2001) at Hog Reef Flat, which is approximately 10–12 km northwest of the R/V *Weatherbird II* sampling route on the Bermuda reef. This rate of calcification is comparable to rates measured (~6–16 mmol m^{-2} h^{-1}) for *Diploria* from rim reef sites by Dodge and coworkers using buoyant weight techniques (Dodge et al. 1984, 1985). Their calcification rates (g d^{-1}) were converted (mmol m^{-2} h^{-1}) assuming a hard coral coverage of 20–30%. Calcification rates measured on other reef systems have similar ranges (e.g., Kinsey 1985; Gattuso et al. 1993*b*; 1997).

Seawater changes in TCO_2 and TA concentrations are also useful as qualitative indicators of calcification because $\Delta TCO_2:\Delta TA$ ratios (normalized to a constant salinity) should theoretically range between 1 : 1 and 1 : 2 (variable depending on the balance of organic carbon to $CaCO_3$ production). In this analysis, it is assumed that the low rates of water column production and respiration do not contribute to ΔTCO_2 changes (see above discussion). A $\Delta TCO_2:\Delta TA$ change of ~1 : 1.13 was observed during a diurnal time series at Hog Reef Flat, part of the northwest rim reef (Bates et al. 2001). Seawater fCO_2 and temperature-corrected fCO_2 data measured using an autonomous fCO_2 buoy system were also higher by 20–60 μatm at this site compared to the Sargasso Sea (Bates et al. 2001). Along the ship track, a decrease in TCO_2 and TA of 5 and 12 μmol kg^{-1}, respectively, between offshore and onshore was observed in March 1996. The $\Delta TCO_2:\Delta TA$ ratio of ~1 : 2 suggests that the influence of $CaCO_3$ production on the CO_2 system was greater than organic carbon production at this time.

Analyses of organic and $CaCO_2$ composition of reef sediments can also provide long-term evidence about the dynamics of CO_2 on coral reefs. Reef systems with sediments having a weight percentage of organic carbon greater than 6% should theoretically be net sinks for CO_2, whereas reefs with sediments having a low organic carbon content (<6%) should be net sources of CO_2 to the atmosphere (Buddemeier 1996). Sediments from a variety of reef settings on Bermuda have a variable but low organic carbon content of ~3–7% (Jickells and Knap 1984), indicating that balance of processes on the Bermuda reef system releases CO_2 to the waters overlying the reef.

Seasonal patterns of CO_2 dynamics, calcification, and productivity on the Bermuda coral reef—The Bermuda reef is subject to seasonal change (i.e., temperature, irradiance, and community structure), and there are seasonal changes in the release of CO_2 from the reef to overlying waters (Fig. 3a). These changes reflect changes in the balance of organic carbon and $CaCO_3$ production that reflect seasonal changes in the reef community structure (i.e., balance of calcifying hard corals and organic carbon–producing macroalga). The modification of CO_2 on Bermuda reef waters reaches a broad maximum during the fall–winter period when Bermuda reef seawater fCO_2 was +30–+50 μatm higher than offshore conditions. The smallest or zero net modification of Bermuda reef fCO_2 occurs in the May–July period (see Fig. 3a), coincident with the period (i.e., June) of maximum solar input to the sea surface. During this period, the processes of organic carbon and $CaCO_3$ production compensate each other with almost no uptake or release of CO_2 to the water. Occasionally, the reef community becomes a sink for CO_2 (i.e., July 1996 and 1997; see Fig. 3a).

Rates of calcification and growth by extension for several

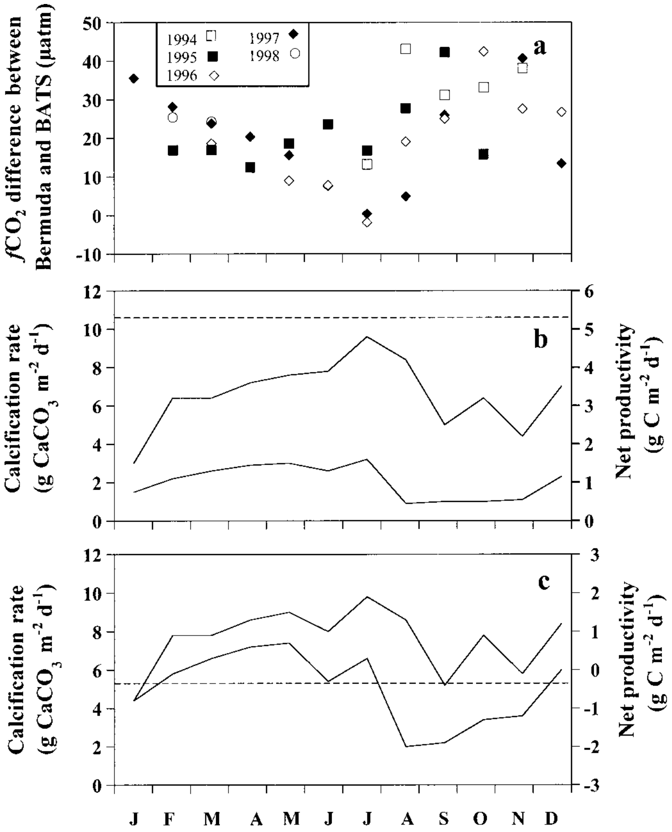

Fig. 3. Seasonal patterns of CO_2 differences, calcification, and net productivity. (a) Mean monthly difference between BATS and Bermuda Platform seawater fCO_2 (µatm) plotted against decimal year. The seawater fCO_2 data is corrected to a constant temperature of 25°C. Positive numbers indicate that Bermuda Platform seawater fCO_2 was higher than source waters at BATS. (b) High and low rates of net productivity (solid lines, g C m^{-2} d^{-1}) computed from range of mean monthly seawater fCO_2 for the period 1994–1998, and a constant *high* calcification rate of 10.6 g $CaCO_3$ m^{-2} d^{-1} (dashed line). (c) High and low rates of net productivity (solid lines, g C m^{-2} d^{-1}) computed from range of mean monthly seawater fCO_2 for the period 1994–1998, and a constant *low* calcification rate of 5.3 g $CaCO_3$ m^{-2} d^{-1} (dashed line).

hard coral species on Bermuda have been measured directly (e.g., Dodge et al. 1984, 1985; Logan and Tomascik 1991; Logan et al. 1994), whereas rates of macroalgal productivity (as an index for rate of organic carbon production) have not. Given knowledge of calcification and the seasonal dynamics of CO_2, rates of macroalgal productivity and the seasonal patterns of productivity on the reef can be quantified using carbon mass balance considerations (shown below).

Coral growth and extension rates on the Bermuda reef show distinct spatial variability and seasonality. Several studies have observed that annual coral extension rates were higher in the inshore and nearshore patch reefs of North Lagoon, compared to rim reef at the outer edge of the Bermuda Platform (Dodge and Vaisnys 1977; Logan and Tomascik 1991; Logan et al. 1994). Seasonally, two of the major framework-building coral species, *D. labyrinthiformis* and *Porites astreoides*, located in the outer rim reef, accrete narrow, high-density bands during the summer and wider low-density bands during the fall to spring (Logan and Tomascik 1991; A. L. Cohen et al. pers. comm.).

Calcification has been determined for Bermuda corals such as *D. labyrinthiformis* at a rate of 0.2–0.4 g $CaCO_3$ d^{-1} for 12-cm-diameter (size-normalized) specimens (Dodge et al. 1984, 1985). In these studies, no statistical difference between winter and summer calcification was discerned. Furthermore, although extension rates differ seasonally (Logan and Tomascik 1991; Logan et al. 1994), the mass of $CaCO_3$ accreted per unit time appears similar in both the winter wide, low-density band and summer narrow, high-density band (A. L. Cohen et al. pers. comm.). Consistent with the above studies, it is assumed that the calcification rate of hard corals in Bermuda remains fairly constant during the year. The rates of calcification measured by Dodge and coworkers can be extrapolated to an areal basis. In the southeastern outer rim, hard corals have ~30% cover (S. R. Smith unpubl. data), slightly higher than the mean hard coral cover on Bermuda (CARICOMP 1997). The rates of calcification are estimated at 5.6 and 10.6 g $CaCO_3$ m^{-2} d^{-1}, values consistent with the measured range of $CaCO_3$ production (Dodge et al. 1984, 1985). Calcification rates on other reefs tend to be higher (5–40 g $CaCO_3$ m^{-2} d^{-1} (e.g., Barnes and Lazar 1993; Gattuso et al. 1993*b*, 1996*b*, 1999*b*), but the extension rates of Bermuda corals are lower (~3 mm yr^{-1}; Logan and Tomascik 1991; Logan et al. 1994) compared to corals at low-latitude reefs (~5–15 mm yr^{-1}).

As discussed earlier, organic carbon and $CaCO_3$ production are the two primary determinants of CO_2 dynamics on the Bermuda reef. In a mass balance sense, if there is no net gain or loss of CO_2 in waters resident on the reef, the effect of organic carbon production and $CaCO_3$ production on seawater fCO_2 is in balance and equal. That is,

$$\text{if } \Delta fCO_{2\text{calc}} = \Delta fCO_{2\text{prod}}, \quad \text{then } \Delta fCO_{2\text{obs}} = 0 \qquad (3)$$

where $\Delta fCO_{2\text{obs}}$ is the observed change in seawater fCO_2 and $\Delta fCO_{2\text{calc}}$ and $\Delta fCO_{2\text{prod}}$ are the effect of calcification and organic carbon production, respectively, on seawater fCO_2. Given this condition, net productivity can be estimated at 2.3 and 4.6 g C m^{-2} d^{-1} (estimated from the two rates on calcification). Here, net productivity is primarily attributable to macroalgal production. Because of the short residence time (less than 2 d) of water in this part of the Bermuda reef, the contribution of other factors, such as water column productivity and air–sea CO_2 gas exchange, were minor contributors to the productivity estimates (<5%).

For most of the year, the effect of organic carbon production and $CaCO_3$ production on CO_2 thermodynamics is not in balance, and reef metabolism causes a considerable gain of CO_2 compared to the Sargasso Sea (Fig. 3a).

$$\text{If } \Delta fCO_{2\text{calc}} > \Delta fCO_{2\text{prod}}, \quad \text{then } \Delta fCO_{2\text{obs}} > 0 \qquad (4)$$

$$\Delta fCO_{2\text{prod}} = \Delta fCO_{2\text{calc}} - \Delta fCO_{2\text{obs}} \qquad (5)$$

Rates of net productivity can thus be determined from $\Delta fCO_{2\text{calc}}$ and $\Delta fCO_{2\text{obs}}$ with the prerequisite that carbon mass balance is maintained. Given the two bounding rates of calcification (5.6 and 10.6 g $CaCO_3$ m^{-2} d^{-1}), seasonal rates of net productivity can be determined from monthly $\Delta fCO_{2\text{obs}}$ data and knowledge of CO_2 thermodynamics (Fig.

3b,c). The lowest and highest seawater $f\mathrm{CO}_2$ changes (Fig. 3a) each month (for the 1994–1998 period) are used to bound the range of $\Delta f\mathrm{CO}_{2\mathrm{obs}}$ and rates of net productivity. It is also assumed that water on the reef is renewed every 2 d. These two simplifications smooth out the day-to-day variability in net productivity (due to changing light conditions, residence times, etc.), as evidenced in variability of $\Delta f\mathrm{CO}_{2\mathrm{obs}}$ (Fig. 2c).

This carbon mass balance analysis reveals seasonal patterns of macroalgal net productivity (Fig. 3b,c). During summertime, macroalgal net productivity reaches a maximum rate ($\sim$1–4.6 g C m^{-2} d^{-1}) and the system is net autotrophic. This seasonal maximum is coincident with the June solstice period of highest potential irradiance and a maximum in macroalgal biomass (S. R. Smith unpubl. data). Other studies have similarly shown that macroalgal productivity increases in relation to solar irradiance and seawater temperature (e.g., Gattuso et al. 1997). In the macroalga-dominated reef communities of Moorea, organic carbon production exceeded $CaCO_3$ production (and the reef acted as a sink for CO_2) during periods of highest irradiance (Gattuso et al. 1997). On the Bermuda reef, organic carbon production occasionally exceeded (in June 1995 and 1996) $CaCO_3$ production (or $\Delta f\mathrm{CO}_{2\mathrm{prod}} \geq \Delta f\mathrm{CO}_{2\mathrm{calc}}$) and the reef briefly switched to a sink for CO_2.

After summer each year, macroalgal biomass on the Bermuda reef declines (as solar input decreases and percent cloud cover increases) (S. V. Smith unpubl. data). A seasonal minimum in net productivity occurs during winter and spring (Fig. 3b,c), coincident with the seasonal minimum of macroalgal biomass (S. R. Smith unpubl. data). After summer, reef metabolism releases CO_2, with a maximum difference in seawater $f\mathrm{CO}_2$ reached by October (Fig. 3a). Although most CO_2 is released because of calcification, negative rates of net productivity during the fall–spring period (Fig. 3b,c) suggest (if the low rates of calcification are correct) that the system becomes heterotrophic, with organic carbon respiration contributing CO_2 to reef waters.

The seasonal variability of CO_2 processing on the Bermuda reef is due to changes in the balance of organic carbon and $CaCO_3$ production, which in turn appears to reflect seasonal variability in the balance of the reef ecosystem (i.e., between hard corals and macroalgae). On an annual basis, reef calcification overwhelms organic carbon production, and CO_2 is released to the water column. The dynamics of CO_2 and carbon mass balance considerations thus provide an overall, integrated, seasonal view of reef metabolism on Bermuda.

Because of assumptions and uncertainties of mass balance, the absolute rates of net macroalgal productivity remain uncertain and require comparison to direct measurements. The net productivity rate estimates for the Bermuda reef system were similar to rates on other reefs. Given the two bounding rates of calcification (5.6 and 10.6 g $CaCO_3$ m^{-2} d^{-1}) and the monthly differences in $\Delta f\mathrm{CO}_{2\mathrm{obs}}$, mean net productivity ranges from -0.6 to 3.3 g C m^{-2} d^{-1} (Table 1). The reef system appears to seasonally shift between autotrophy and heterotrophy, with a overall tendency toward annual net autotrophy. Net and gross productivity measurements on other reefs range from 0.0 to 1.5 g C m^{-2} d^{-1} (e.g., Kinsey 1985; Chisholm et al. 1990; Crossland et al. 1991) and 2.3 to $>$10 g C m^{-2} d^{-1} (Kinsey 1985; Crossland et al. 1991; Barnes and Lazar 1993; Gattuso et al. 1993*b*, 1996*b*, 1999*b*, 2000), respectively. If summertime calcification rates of Bermuda coral are lower during accretion of the narrow but higher density band, net productivity rates will be closer to 0 (-0.6 to 2.5 g C m^{-2} d^{-1}; Table 1).

Table 1. Mean calcification (g $CaCO_3$ m^{-2} d^{-1}) and net productivity (g C m^{-2} d^{-1}) rates averaged on an annual basis.

	High calcification	Low calcification
Calcification rate (g $CaCO_3$ m^{-2} d^{-1})	10.6	5.3
Net productivity* (g C m^{-2} d^{-1})	2.0–3.3	-0.5–1.0
Net productivity† (g C m^{-2} d^{-1})	1.3–2.5	-0.6–0.6

* Net productivity is calculated assuming that the rate of calcification is constant throughout the year.

† Net productivity is calculated assuming that the rate of calcification is lower during the summer months. The calcification rate for October to May is assumed as above (i.e., 10.6 and 5.3 g $CaCO_3$ m^{-2} d^{-1}, respectively). For the period June–September, the calcification rate is halved (i.e., 5.3 and 2.6 g $CaCO_3$ m^{-2} d^{-1}, respectively).

What remains uncertain are the seasonal rates and spatial variability (e.g., outer rim reef to inshore/nearshore patch reef) of productivity and calcification (i.e., organic carbon and $CaCO_3$ production) for individual hard coral and macroalgal species components of the collective ecosystem. However, the ‘‘integrated view’’ of seasonal CO_2 dynamics in response to Bermuda reef metabolism may be useful for understanding carbon cycling in other reefs, particularly those that appear to be in transition from coral-dominated communities to macroalga-dominated communities (e.g., Kinsey 1985; Smith and Buddemeier 1992; Hughes 1994),

There is some evidence that Bermuda reef metabolism may also be responding to interannual variability. In June 1996 and 1997 (compared to 1994 and 1995), reef metabolism shifted to a slight uptake of CO_2, indicative of a shift in the balance of organic carbon and $CaCO_3$ production (Fig. 2d). Such changes may be related to interannual changes in the subtropical gyre surrounding the island of Bermuda and in the supply of nutrients to the reef system. Interannual variability in temperature, salinity, primary production, mixed-layer depths, and vertical nitrate supply has been demonstrated (Bates 2001), and much of the interannual variability relates to modes of climate variability such as El Niño–Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO). For example, in 1996, in response to a shift in NAO phase to a negative state in the North Atlantic, the Sargasso Sea was cooler (by $\sim$0.5°C), mixed layers were deeper (up to 30–40 m), vertical mixing of nitrate was greater, and rates of primary production were higher (up to 200 mg C m^2 d^{-1}) compared to the mean state (Bates 2001). During this period, the oceanic uptake of CO_2 in the Sargasso Sea appears to have increased (N. Gruber et al. pers. comm.). Contemporaneous and consistent with this temporal variation of air–sea CO_2 exchange, the loss of CO_2 from the Bermuda reef system also seems to have been reduced. With longer-term reef records, mechanistic relationships between

Table 2. Estimates of air–sea gas exchange of CO_2 on the Bermuda Platform and in the Sargasso Sea at BATS. Air–sea CO_2 fluxes were calculated using the wind speed–CO_2 transfer velocity relationships of Wanninkhof (1992). Wind speed data was collected at a height of 10.5 m at the former U.S. Naval Air Station, St. David's, Bermuda.

Sampling period	Location	CO_2 flux* (mmol CO_2 m^{-2} yr^{-1})	Mean ΔfCO_2† (μatm)
10 Jul 1994–31 Dec 1994‡	Platform	+0.13	+32.9
	BATS	−0.13	+6.9
1 Jan 1995–31 Dec 1995§	Platform	−0.12	+7.4
	BATS	−0.73	−8.8
1 Jan 1996–31 Dec 1996§‖	Platform	−0.11	+5.9
	BATS	−0.85	−10.1

*Negative values denote CO_2 flux from atmosphere to ocean; positive values denote flux from ocean to atmosphere.

† ΔfCO_2 is difference between ocean and atmospheric fCO_2 where negative values denote fCO_2 values higher in the atmosphere and positive values denote fCO_2 values higher in the ocean.

‡ Although ΔfCO_2 was on *average* positive in 1994 at BATS, the flux was negative and directed into the ocean because of higher CO_2 flux in the fall when ΔfCO_2 was negative but wind speeds were much greater compared to the summer.

§ In 1995 and 1996, the CO_2 flux and ΔfCO_2 values were also opposite in sign for the Bermuda platform. In both years, ΔfCO_2 was on *average* positive, but the flux was negative (again because of higher wind speeds in the winter and spring when ΔfCO_2 was negative).

‖ Wind speed data was not available after 1996.

calcification, macroalgal productivity, and climate forcing may be clearly demonstrated in the future.

The Bermuda coral reef: Source or sink of CO_2 to the atmosphere?—There has been considerable debate about whether coral reefs are sources to the atmosphere (e.g., Ware et al. 1992; Gattuso et al. 1993*a*, 1995, 1996*a*, 1999*b*) or oceanic sinks of CO_2 (e.g., Yamamuro et al. 1995; Kayanne et al. 1996; Gattuso et al. 1997; Kraines et al. 1997). Most studies, with notable exceptions (Gattuso et al. 1995, 1996*b*, 1999*b*; Frankignoulle et al. 1996), have assumed that reef metabolism (through release or uptake of CO_2) is the only factor influencing air–sea CO_2 flux and the sink or source status of reefs. A contributing factor to the source or sink status of reefs, however, is the pre-existing air–sea CO_2 disequilibrium of offshore waters impinging on the reef system.

The Bermuda reef ecosystem, particularly the outer rim and terrace reefs, is predominantly a source of CO_2 to the water overlying the reef, but not necessarily to the atmosphere. Because of the short residence time of water on the outer rim and terrace reef, reef metabolism modifies the pre-existing air–sea CO_2 disequilibrium of waters impinging the reef. The surrounding Sargasso Sea undergoes regular seasonal changes in seawater fCO_2 and the direction of air–sea CO_2 exchange (Bates et al. 1998*a*; Bates 2001). In winter, Sargasso Sea seawater fCO_2 is lower by ~40–60 μatm than the atmosphere, and CO_2 exchange is directed from atmosphere to ocean (i.e., a net oceanic sink of CO_2). The release of CO_2 from Bermuda reef calcification elevates seawater fCO_2 on waters impinging the reef, reducing the rate of atmosphere to ocean CO_2 flux (Table 2), but not reversing the direction of gas exchange. In summer, the air–sea CO_2 disequilibrium of offshore water is reversed (i.e., seawater fCO_2 is higher than atmosphere fCO_2 by 40–60 μatm), and the release of CO_2 from reef metabolism augments the rate of sea to air CO_2 flux from the waters of Bermuda (Table 2).

The influence of the pre-existing air–sea CO_2 disequilibrium of offshore water masses impinging on the reef has also been demonstrated on the Moorea Reef in the Pacific Ocean (Gattuso et al. 1995, 1996*b*; Frankignoulle et al. 1996). Two visits in winter and summer to this reef system showed considerable differences in offshore fCO_2 conditions presumably reflecting seasonal changes in air–sea CO_2 disequilibrium. Regional maps of the air–sea CO_2 disequilibrium in the tropical/subtropical Pacific (Takahashi et al. 1997) also reveal large seasonal variation (up to 60–80 μatm) of seawater pCO_2 in offshore waters surrounding Pacific Ocean coral reef sites. Thus, factors such as seasonal offshore air–sea CO_2 disequilibrium, mixing between coral reef and offshore waters and the seasonality of biological processes (i.e., net balance of calcification and organic carbon production) must be taken into account when evaluating the regional and global significance of coral reefs to the transfer of CO_2 between the ocean and atmosphere.

CO_2 data from the Bermuda reef provide broad hints about the complexity of the processes that affect CO_2 on coral reef ecosystems. Although the geographic extent of Bermuda coral reefs are small and its coral diversity arguably is limited, the Bermuda reef (and other reefs) are subject to seasonal forcing and changes in community structure that determine the fate and dynamics of CO_2. The Bermuda reef system serves as a useful model for understanding changes in carbon cycling in other reefs that are in transition from coral-dominated to macroalga-dominated communities in response to environmental stress. A detailed understanding of the complex physical and biological interactions affecting CO_2 occurring on different types of reef ecosystems is warranted.

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