

Biogeochemical and physical factors influencing seawater $f\text{CO}_2$ and air-sea CO_2 exchange on the Bermuda coral reef

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Abstract

It is uncertain whether coral reef ecosystems are oceanic sources or sinks of carbon dioxide (CO_2). Understanding the complex interactions between biogeochemical and physical processes within reef ecosystems is important for determining the contribution of coral reefs to the global carbon cycle and the air-sea flux of CO_2 . The influence of biogeochemical and physical processes on CO_2 cycling was examined for 1 month at Hog Reef Flat, part of the rim reef of Bermuda. The fugacity of seawater CO_2 ($f\text{CO}_2$) was measured hourly by use of a Carbon Interface Ocean Atmosphere buoy, providing the longest time series of seawater CO_2 data on a coral reef ecosystem. Seawater $f\text{CO}_2$ ranged from ~ 340 to $470 \mu\text{atm}$, with a diurnal variability ranging from ~ 20 – $60 \mu\text{atm}$. Air-sea CO_2 was directed from ocean to atmosphere with a mean flux of $3.3 \pm 4.6 \text{ mmoles CO}_2 \text{ m}^{-2} \text{ d}^{-1}$. The reef data are compared with a seawater CO_2 time series collected at the U.S. Joint Global Ocean Flux Study Bermuda Atlantic Time-series Study (BATS) site ($31^\circ 50' \text{N}$, $64^\circ 10' \text{W}$) in the Sargasso Sea surrounding Bermuda. Sargasso Sea waters are the original source for Bermuda platform water, providing a context for understanding the biogeochemical modification of reef water at Hog Reef Flat. Seawater $f\text{CO}_2$ at Hog Reef Flat was elevated relative to the Sargasso Sea by ~ 0 to $\sim 120 \mu\text{atm}$, primarily as a result of calcium carbonate production. However, the ability of the reef to act either as a source or sink of CO_2 to/from the atmosphere largely depended on the air-sea CO_2 disequilibrium of offshore Sargasso Sea waters impinging on the reef site. This study also revealed that an assessment of the fate of CO_2 on coral reefs is dependent on understanding the reef's physical regime and forcing. The dynamics of wind, tide, platform circulation, and fluxes of offshore or onshore waters are necessary context for all coral reef sites.

Coral reefs contribute to the ocean carbon cycle through the processes of photosynthesis, respiration, calcium carbonate (CaCO_3) production, and dissolution. These processes control the distribution of the different CO_2 carbon species in seawater and determine the fate and transformations of CO_2 and, ultimately, the exchange of CO_2 between the ocean and atmosphere.

Organic carbon production (photosynthetic CO_2 fixation) and consumption (respiratory release of CO_2) influences the oceanic CO_2 system by decreasing or increasing the fugacity of CO_2 ($f\text{CO}_2$) and dissolved inorganic carbon (DIC) content of seawater, respectively. In the open ocean, for example, biological processes causes considerable depletion of surface nutrients, DIC, and $f\text{CO}_2$ (e.g., Takahashi et al. 1993; Bates et al. 1996a). Photosynthesis and respiration have minor impact on the alkalinity (TA) of seawater, except through liberation or uptake of H^+ associated with the assimilation or dissimilation of ammonium (NH_4^+), nitrate (NO_3^-), and phosphate (HPO_4^{2-}) (Brewer and Goldman 1976).

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CaCO_3 production by marine calcifying organisms, such as frame-building scleractinian corals, calcareous algae, and coccolithophorids, should theoretically release CO_2 , according to the following equations:



Although there is a debate about which inorganic carbon substrate is used in calcification (e.g., Langdon et al. 2000), both reactions generate CO_2 . If CO_3^{2-} is used, for each mole of CaCO_3 precipitated, DIC and alkalinity decrease by 1 and 2 moles, respectively, thereby increasing seawater $f\text{CO}_2$. If HCO_3^- is used, the CO_2 produced by calcification may be internally used for photosynthesis or released to the external marine environment. Calcifying marine phytoplankton, such as coccolithophorids, for example, may internally use CO_2 generated from calcification for photosynthesis (e.g., Nimer et al. 1994). The impact on coccolithophorid calcification on seawater $f\text{CO}_2$ can range from neutral (e.g. Robertson et al. 1994) to a source of CO_2 to seawater (e.g., Bates et al. 1996b). Internal use of CO_2 generated by calcification has not been demonstrated for scleractinian corals (Gattuso et al. 2000a). For coral reefs, several studies have demonstrated that coral-dominated reef ecosystems are sources of CO_2 to the marine environment (e.g., Ware et al. 1992; Gattuso et al. 1993, 1996a, 2000b; N. R. Bates unpubl.), whereas other studies have suggested that some reef ecosystems are sinks for CO_2 (Kayanne et al. 1995; Yamamuro et al. 1995; Kraines et al. 1997). The fate of CO_2 in coral reefs is dependent

on many factors, including the ratio of organic carbon production to CaCO_3 production (e.g., Buddemeier 1996; Gattuso et al. 2000b), irradiance levels (e.g., Gattuso et al. 1997), and the dominant type of calcifying organism. The balance of these processes ultimately determines whether coral reefs are sources or sinks of CO_2 .

Investigations of the processes controlling seawater $f\text{CO}_2$ and the air-sea exchange of CO_2 in coral reef ecosystems have generally been based on measurements of pH, TA, and dissolved oxygen (e.g., Smith 1973; Suzuki et al. 1995; Kraines et al. 1997; Chisholm and Barnes 1999). Direct measurements of seawater $f\text{CO}_2$ have only been made on a few coral reefs ecosystems, either in a survey mode (Kawahata et al. 1997) or as time series of a few days, by use of an air-sea CO_2 flux chamber (Gattuso et al. 1993, 1997; Frankignoulle et al. 1996) or in situ systems (Kayanne et al. 1995). The aim of this study was to examine the potential factors that influence CO_2 variability on a coral reef ecosystem and the air-sea exchange of CO_2 . For nearly 1 month, we deployed an autonomous CARIOCA (CARbon Interface Ocean Atmosphere) buoy at Hog Reef Flat on the Bermuda platform. The CARIOCA buoy collected a range of atmospheric and oceanic variables each hour. These data constitute one of the longest time series of CO_2 for a reef site and reveals the influence of diurnal processes as well as longer term oceanic and atmospheric forcing.

The source of Bermuda platform waters is the surrounding Sargasso Sea. An oceanic time series of biogeochemistry and hydrography data has been collected at the U.S. Joint Global Ocean Flux Study (JGOFS) Bermuda Atlantic Time-series Study (BATS) site ($31^\circ 50' \text{N}$, $64^\circ 10' \text{W}$) since 1988 (Michaels and Knap 1996; Bates in press). The BATS data can thus be used to examine the modification of seawater once on the Bermuda platform by processes such as calcification and organic carbon production. On seasonal to interannual timescales, the Bermuda coral reef ecosystem acts as a source of CO_2 , increasing seawater $f\text{CO}_2$ of the platform, compared with the Sargasso Sea (Bates unpubl.). Herein, the biological and physical processes affecting CO_2 over shorter timescales (i.e., diurnal to 1 month) on the Bermuda reef system were examined. This study reveals the importance of understanding the physical regime (e.g., tidal and wind dynamics platform circulation and residence times, and air-sea CO_2 disequilibrium of offshore waters) of the reef system when investigating whether coral reefs are sources or sinks of CO_2 .

Materials and methods

Carbonate chemistry—Coral reef ecosystems are characterized by both photosynthetic and calcifying organisms. Photosynthesis, respiration, precipitation, and dissolution of CaCO_3 are therefore important processes controlling seawater carbonate system. This system is bivariant and fully described by two variables that are chosen from among the four measurable parameters: pH, $f\text{CO}_2$, DIC, and TA. DIC is defined as

$$\text{DIC} = [\text{CO}_2^*] + [\text{HCO}_3^-] + [\text{CO}_3^{2-}] \quad (3)$$

where $[\text{CO}_2^*]$ represents the concentration of all unionized

carbon dioxide, whether present as H_2CO_3 or as CO_2 . The TA is defined as

$$\begin{aligned} \text{TA} = & [\text{HCO}_3^-] + 2[\text{CO}_3^{2-}] + [\text{B}(\text{OH})_4^-] + [\text{OH}^-] \\ & + [\text{HPO}_4^{2-}] + 2[\text{PO}_4^{3-}] + [\text{SiO}(\text{OH})_3^-] + [\text{HS}^-] \\ & + [\text{NH}_3] + \dots - [\text{H}^+] - [\text{HSO}_4^-] - [\text{HF}] \\ & - [\text{H}_3\text{PO}_4] - \dots \end{aligned} \quad (4)$$

where $\text{HCO}_3^- + 2\text{CO}_3^{2-} + \text{B}(\text{OH})_4^-$ are the major components of seawater alkalinity and other species are minor components having negligible impact on alkalinity. DIC and TA are expressed as $\mu\text{moles kg}^{-1}$.

$f\text{CO}_2$ is the fugacity of CO_2 in equilibrium with seawater. It takes account of the non-ideal nature of the gas phase. The difference between $f\text{CO}_2$ and $p\text{CO}_2$ is very small, typically $<0.2\%$. For more details on these definitions, see, e.g., Dickson and Goyet (1994).

The reef site at Hog Reef Flat—The coral reefs and platform waters of Bermuda are located on a thin layer (~ 50 – 100 m) of Pleistocene and Holocene carbonate sediments overlying a volcanic seamount. The Bermuda platform occupies a total area of 775 km^2 . The island of Bermuda (area of $\sim 55 \text{ km}^2$) and several inshore seawater basins ($\sim 54 \text{ km}^2$ area) are located on the southeastern edge of the Bermuda platform. The Bermuda platform ($\sim 665 \text{ km}^2$) comprises a broad rim reef and the North Lagoon, which contains patch coral reefs and extensive sand areas (Fig. 1). Reef and lagoonal waters are continuously exchanging with surface waters of the surrounding Sargasso Sea. The average depth of water on the Bermuda platform is ~ 8.5 m, and the residence time of water is ~ 4 d (Morris et al. 1977). There is no significant freshwater discharge from the island of Bermuda into the reef, lagoonal, or inshore seawater basins.

The reef platform of Bermuda undergoes large seasonal changes in temperature and seawater $f\text{CO}_2$ (Bates unpubl.). The temperature range is $\sim 12^\circ\text{C}$ with summer maxima of 26 – 30°C and winter minima of ~ 17 – 19°C . The range of seawater $f\text{CO}_2$ is $\sim 150 \mu\text{atm}$ with summer maxima of 400 – $460 \mu\text{atm}$ and winter minima of ~ 310 – $330 \mu\text{atm}$. Similar seasonal temperature and seawater $f\text{CO}_2$ variability is observed in the surrounding Sargasso Sea, with notable exception. Winter temperatures on the Bermuda platform are typically 1 – 2°C cooler than the Sargasso Sea, whereas summertime $f\text{CO}_2$ on the platform tends to be 30 – $50 \mu\text{atm}$ higher (Bates et al. 1998b; Bates unpubl.).

The CARIOCA buoy was deployed on Hog Reef Flat on 12 October 1998 (day 285 of the year) until 4 November 1998 (day 308 of the year). Hog Reef Flat is a rim reef, located in the northwestern part of the Bermuda platform (Fig. 1), regularly monitored by the Bermuda Biological Station For Research (BBSR) as part of a coral reef health program. The average depth of the reef is ~ 6 m. The dominant reef-building species are *Diploria strigosa* and *D. labyrinthiformis*, with other common genera present, including *Montastrea annularis* and *Porites astreoides*. Hard coral and macroalgal cover were $\sim 22\%$ and 52% , respectively (Smith unpubl. data).

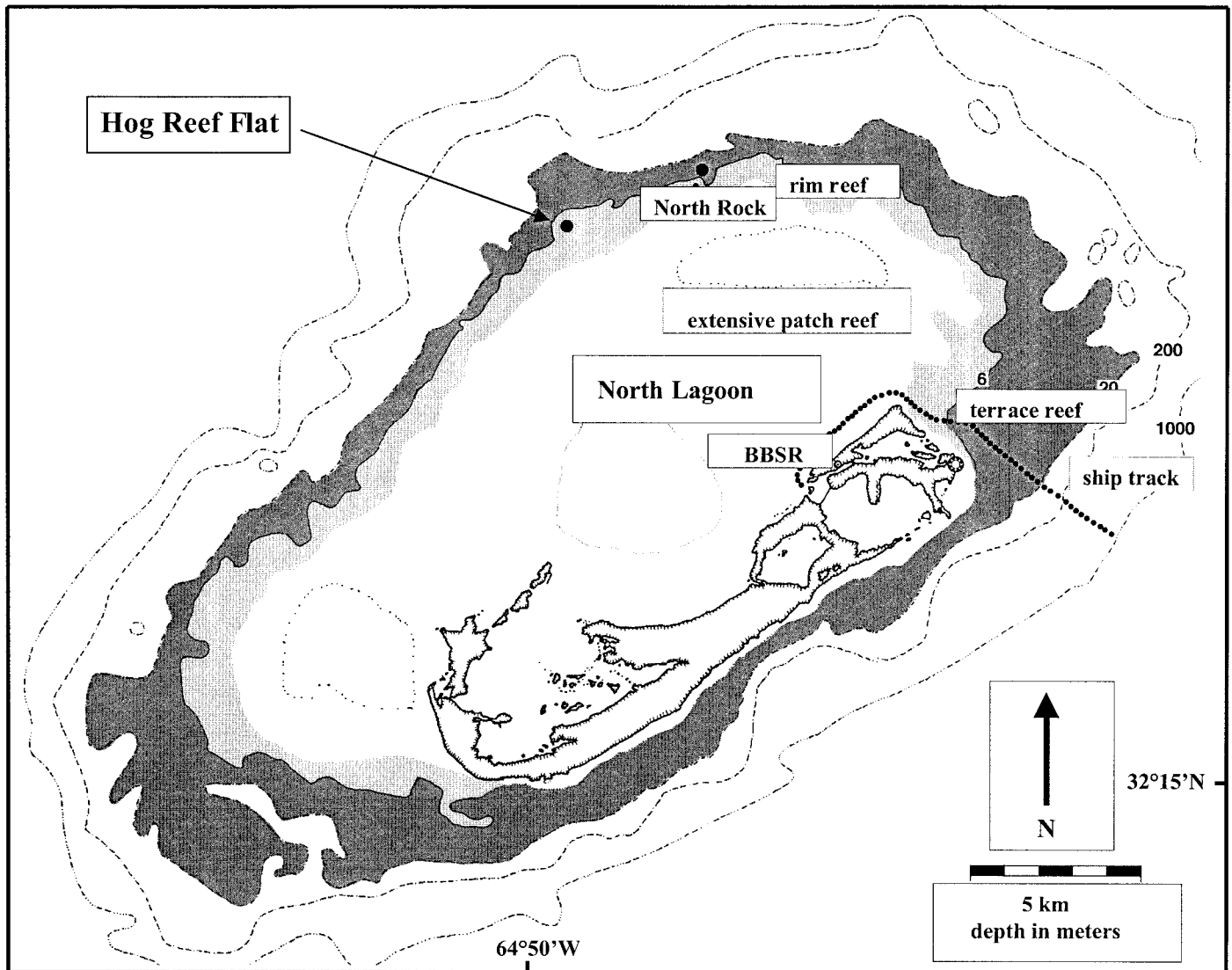


Fig. 1. Location map of the Hog Reef Flat on the Bermuda platform.

CARIOCA buoy measurements—The CARIOCA buoy made autonomous hourly measurements of atmospheric and oceanic variables. Atmospheric pressure, temperature, and wind speed were collected from a mast at a height of 2 m. Wind speed was measured by use of an RM Young Wind Monitor Jr. propeller anemometer, which has an accuracy of 0.3 m s^{-1} when compared with contemporaneous shipboard measurements. Oceanic parameters such as seawater temperature, $f\text{CO}_2$, and fluorescence were sampled from an intake at 2 m depth. Seawater temperature data was measured by use of two Betatherm thermistors with an accuracy of 0.05°C . Tri-butyl tin tubing was used internally, and a copper plate was mounted at the seawater intake of the CARIOCA buoy; both were used to reduce the possibility of biofouling affecting the $f\text{CO}_2$ sensor.

Seawater $f\text{CO}_2$ measurements were conducted by use of an automated spectrophotometric technique (Hood et al. 1999; <http://www.lodyc.jussieu.fr/carioca/>). The two major components of the CARIOCA buoy $f\text{CO}_2$ system are the

exchanger cell and optical detector. In the exchanger cell, a CO_2 -permeable silicon membrane separates seawater from a color indicator. Diffusion of CO_2 across the membrane maintains equilibrium between CO_2 concentrations in seawater and the color indicator, which consists of a 1.10^{-4} thymol blue solution diluted in artificial seawater. The time constant of CO_2 equilibrium in the exchanger cell is 30 min. Seawater $f\text{CO}_2$ values were determined from spectrophotometric absorbance data and internal temperature data. Other theoretical considerations used for the calculation included the dissociation constant of the dye, dissociation constants of carbonic acid in seawater, solubility coefficient of CO_2 , and the alkalinity and concentration of the indicator solution.

The CARIOCA buoy $f\text{CO}_2$ measurements were calibrated in the laboratory prior to deployment by use of a Licor infrared CO_2 analyzer (Model 6262) and CO_2 -in-air gas standards. Seawater was pumped in parallel through an equilibrator-Licor analyzer system and the CARIOCA exchanger cell. Linear regression curves of the spectrophotometric and

Licor $f\text{CO}_2$ data were calculated and subsequently used to determine $f\text{CO}_2$ from spectrophotometric absorbance and temperature data. The accuracy of the CARIOCA buoy $f\text{CO}_2$ measurements is $\sim 3 \mu\text{atm}$ (Bates et al. 2000).

Other inorganic carbon measurements—A short time series of inorganic carbon parameters was collected at Hog Reef Flat on 29 October 1998 (day 302 of the year) once per hour from 0800 to 1600 h. Sampling was undertaken within 10 m of the CARIOCA buoy. Deteriorating weather conditions prevented sampling during a complete diurnal cycle. Surface samples (~ 2 m deep) of DIC and TA were drawn from Niskin samplers into individually numbered, clean 0.5 dm^3 size Pyrex glass reagent bottles, by use of established gas sampling protocols (Bates et al. 1996a). A head space of $<1\%$ of the bottle volume was left to allow for water expansion, and all samples were poisoned with 100 or 200 μl of saturated HgCl_2 solution to prevent biological alteration. Bottles were sealed with ground-glass stoppers and Apiezon silicon vacuum grease. Rubber bands were placed around the lip of the bottle and stopper to provide positive closure. Samples were returned to BBSR for analysis.

DIC was measured by a gas extraction/coulometric technique (see Bates et al. 1996a,b for details), using a Single-Operator Multi-Metabolic Analyzer to control the pipetting and extraction of seawater samples and a UIC CO_2 coulometer detector. The precision of DIC analysis was better than 0.025% ($\sim 0.4 \mu\text{moles kg}^{-1}$), on the basis of duplicate and triplicate analyses of >2000 seawater samples analyzed at BBSR from 1992 to 1999. Seawater certified reference materials (CRMs; prepared by A. G. Dickson, Scripps Institution of Oceanography) were analyzed to ensure that the accuracy of DIC was within 0.03% ($\sim 0.5 \mu\text{moles kg}^{-1}$). TA was determined by potentiometric titration with HCl (see Bates et al. 1996a,b for details). CRM samples were also analyzed for TA. These values were within 0.15% ($\sim 2\text{--}3 \mu\text{moles kg}^{-1}$) of certified TA values reported by A. G. Dickson (<http://www.dickson.ucsd.edu>).

Rates of net primary production and calcification—Net primary production and calcification were calculated from the short time-series data of DIC and TA collected on 29 October 1998, as follows (Gattuso et al. 2000b):

$$p_{\text{net}} = \frac{\Delta\text{DIC}\rho z}{\Delta t} - g + F \quad (5)$$

$$g = \frac{\Delta\text{TA}\rho z}{2\Delta t} \quad (6)$$

where p_{net} is the rate of net primary production ($\text{mmoles m}^{-2} \text{ h}^{-1}$); ρ is the density of seawater (kg m^{-3}); z is the depth (m) of water; g is the rate of calcification ($\text{mmoles CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$); Δt is the duration of the time series (hours); and F is the air-sea flux of CO_2 ($\text{mmoles CO}_2 \text{ m}^{-2} \text{ h}^{-1}$). Daytime hourly fluxes *only* were determined for this experiment, since nighttime measurements were not collected.

Air-sea CO_2 gas exchange—The exchange of CO_2 between ocean and atmosphere is driven by differences in $f\text{CO}_2$

at the air-sea interface. The net air-sea flux of CO_2 (F) is expressed as

$$F = ks(\Delta f\text{CO}_2) \quad (7)$$

where k is the transfer velocity, s is the solubility of CO_2 , and $\Delta f\text{CO}_2$ is the difference between atmosphere and ocean. The transfer velocity k is a function of wind speed and transfer velocity-wind speed relationships. Herein, we use the transfer velocity-wind speed relationships of Wanninkhof (1992), which are based on a quadratic dependency between wind speed and transfer velocity:

$$k = 0.31u^2 \left(\frac{660}{Sc} \right)^{1/2} \quad (8)$$

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

Other data sets—The physical and biogeochemical variability of the oligotrophic subtropical gyre of the western North Atlantic (i.e., the Sargasso Sea) has been well characterized (e.g., Michaels and Knapp 1996). The BATS site is located ~ 85 km southeast of Bermuda. Since the original source of Bermuda platform waters is the Sargasso Sea, we use DIC, TA, seawater, and atmospheric $f\text{CO}_2$ data collected at BATS (Bates et al. 1996a,b; 1998a,b; Bates in press, pers. comm.; <http://www.bbsr.edu>) for comparative purposes. Although there are meridional and zonal biogeochemical gradients across the subtropical gyre, BATS biogeochemical data are representative of the oligotrophic waters surrounding Bermuda (Bates and Hansell 1999).

Statistical analyses—Seawater $f\text{CO}_2$ data were corrected to a constant temperature of 25°C by use of the thermodynamic equation [i.e., $(\delta f\text{CO}_2/\delta T)/f\text{CO}_2 = 0.0423^\circ\text{C}^{-1}$] of Takahashi et al. (1993). This correction allows the effect of temperature on $f\text{CO}_2$ to be removed, thereby allowing an evaluation of the underlying trends affecting seawater $f\text{CO}_2$.

Cross-correlation and auto-correlation coefficient analysis and spectral analyses were performed on all of the data, to evaluate statistical relationships between parameters. In order to perform the spectral analysis, longer term seasonal trends in the data were removed, allowing us to assume stationarity of the data for the power spectra calculation. A Fast Fourier Transform algorithm was used to construct a periodogram of the data, since the CARIOCA buoy data were discrete rather than continuous. A filter (or lag window) was then applied to the discrete periodogram, to estimate continuous power spectra (Priestley 1981). The smallest resolvable sampling frequency (the Nyquist frequency) was 2 h.

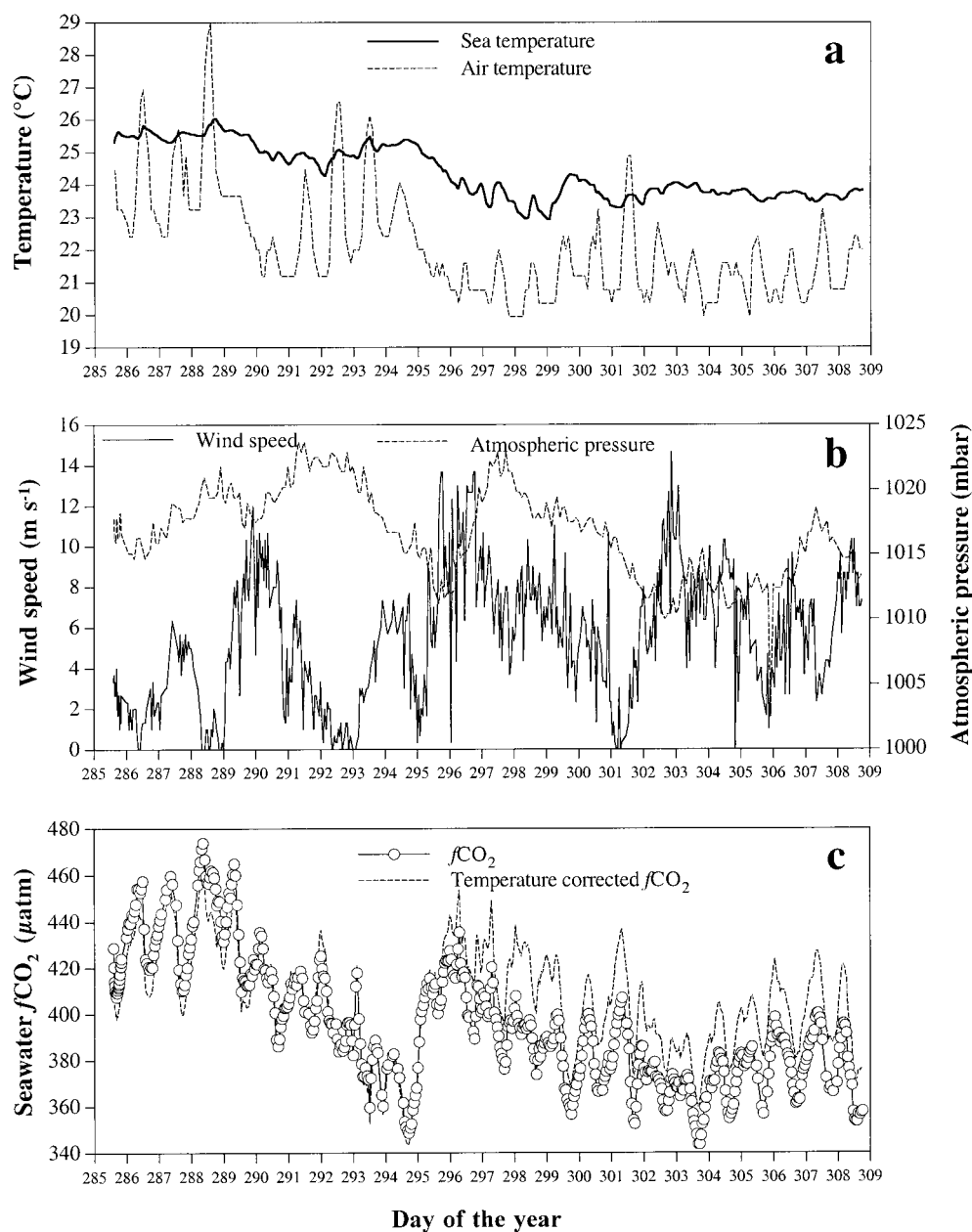


Fig. 2. Time series of CARIOCA buoy data collected from 12 October to 4 November 1998 (days of the year 285–308). (a) Air and surface seawater temperature (°C). (b) Wind speed corrected to 10-m height (m s^{-1}) and atmospheric pressure (mbar). (c) Seawater $f\text{CO}_2$ and $f\text{CO}_2$ corrected to a constant temperature of 25°C.

Results

Time series of CARIOCA buoy measurements—During the CARIOCA buoy deployment, the range of air temperatures (20–28°C) was greater than that of sea temperatures (23–26°C). Both air and sea temperatures decreased over the 24-d deployment period (Fig. 2a), reflecting the typical seasonal cooling occurring at this time of year. Diurnal warming and cooling were evident in both temperature records, and the mean diurnal ranges for air and surface seawater were 2.5°C and 0.5°C, respectively. Wind speeds ranged from 0–15 m s^{-1} ,

the highest winds generally occurring as atmospheric low pressure systems passed over the island (low pressure generally coincides with stronger winds; days of the year 290, 295–296, and 302–303; Fig. 2b). Seawater $f\text{CO}_2$ ranged from ~340 to 470 μatm during the 24-d deployment (Fig. 2c). The $f\text{CO}_2$ maxima and minima were observed on days of the year 288 and 294, respectively. Diurnal changes of $f\text{CO}_2$ ranged from ~20 to 60 μatm , with a mean of 41 μatm . Temperature-corrected seawater $f\text{CO}_2$ data showed variability similar to uncorrected $f\text{CO}_2$ (Fig. 3c), indicating that factors other than temperature influenced $f\text{CO}_2$ on the reef site.

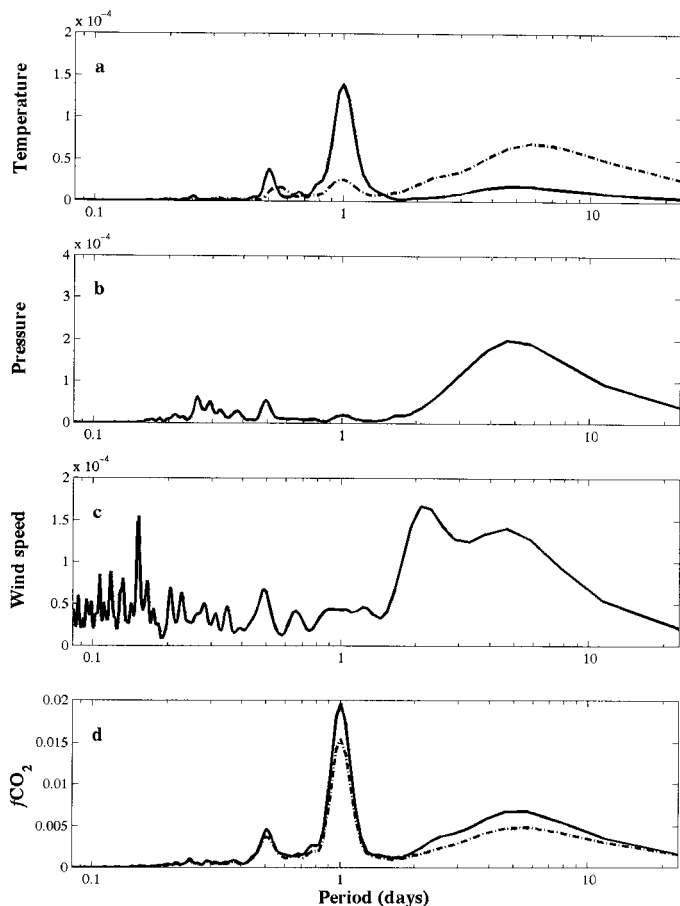


Fig. 3. Power spectrum of CARIOCA buoy data collected from 12 October to 4 November 1998 (days of the year 285–308). (a) Air (solid line) and surface seawater (dashed line) temperature ($^{\circ}\text{C}$). Seawater temperature is exaggerated in the vertical axis by 20 times. (b) Atmospheric pressure (mbar). (c) Wind speed (m s^{-1}). (d) Seawater $f\text{CO}_2$ (solid line) and $f\text{CO}_2$ corrected (dashed line) to a constant temperature of 25°C .

Power spectra of atmospheric and oceanic parameters (Fig. 3) revealed variability (some obvious, others less so) over different timescales, with periodicities of ~ 12 h, 1 d, and 2–8 d. Atmospheric variables such as pressure and wind speed had a broad spectral peak at a period of 2–8 days (Fig. 3b,c). This reflects the timescale of atmospheric fronts passing through the region. Diurnal processes, however, primarily influenced air temperature, as shown by the distinct spectral peak at 1 d (see Fig. 3a). Oceanic parameters had a broader range of variability. Most of the variance of seawater temperature occurred between 3 and 8 d. This may reflect changes in the physical exchange of waters between the platform and the surrounding Sargasso Sea, which in turn are related to atmospheric forcing and tidal dynamics. Most of the variance of seawater $f\text{CO}_2$ and temperature-corrected $f\text{CO}_2$ occurred at a period of 1 d, with a broader secondary band between 4 and 8 d (Fig. 3d). Because the spectral peak of 1 d remains dominant for the temperature-corrected $f\text{CO}_2$, most of the diurnal variability of $f\text{CO}_2$ results from factors such as calcification, production, and respiration, rather than temperature. This contrasts to the Sargasso Sea, where di-

urnal variability of $f\text{CO}_2$ is due primarily to temperature forcing (Bates et al. 1998b, 2000b). Both seawater temperature and $f\text{CO}_2$ also have tertiary spectral peaks at ~ 12 h. This probably reflects the influence of tidal ebb and flow at the reef site.

Air-sea CO_2 gas exchange—As shown in Eq. 7, the air-sea flux of CO_2 is a function of wind speed and the air-sea difference in $f\text{CO}_2$. Wind speeds, corrected to 10 m, were variable, with higher wind events occurring on days of the year 290–291, 296–300, and 302–305, respectively (Fig. 2b). The difference between atmospheric (estimated from the atmospheric $f\text{CO}_2$ record at BATS; Bates et al. 1998b) and seawater $f\text{CO}_2$ values (i.e., $\Delta f\text{CO}_2$) was variable, ranging from $+120 \mu\text{atm}$ (i.e., oceanic $f\text{CO}_2$ greater than atmosphere) to $-15 \mu\text{atm}$, with a mean $\Delta f\text{CO}_2$ of $41.8 \pm 28.2 \mu\text{atm}$ (Fig. 4a). For most of the deployment, $\Delta f\text{CO}_2$ values were positive, indicating that air-sea fluxes were primarily directed from ocean to atmosphere (Fig. 4b). Instantaneous CO_2 fluxes, based on the equations of Wanninkhof (1992; herein Eq. 8), ranged from -0.6 to $+29 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$, with a mean flux of $3.3 \pm 4.6 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$.

Rates of net community production and calcification—Daytime rates of net community production (NCP; equivalent to p_{net}) and calcification were determined from the short time series of data collected at Hog Reef Flat on 29 October 1998. During this experiment, temperature and salinity showed little variability (Fig. 5a). From 0800 h, DIC and alkalinity decreased by 33 and $28 \mu\text{moles kg}^{-1}$, respectively (Fig. 5b), whereas seawater $f\text{CO}_2$, measured from the CARIOCA buoy, decreased from 378 to $358 \mu\text{atm}$ (Fig. 5c).

The DIC and TA properties of Hog Reef Flat water (and Bermuda platform water) were modified from the original source (i.e., the Sargasso Sea). In the Sargasso Sea, alkalinity is a conservative function of salinity (Bates et al. 1996b; Fig. 5d), whereas DIC has a predictable range in concentration depending on the time of year (Bates et al. 1996a; Fig. 5e). Compared with Sargasso Sea waters, TA and DIC at Hog Reef Flat decreased by up to ~ 45 and $\sim 30 \mu\text{moles kg}^{-1}$, respectively (Fig. 5d,e). Daytime changes in DIC and TA were significantly correlated (Fig. 5f), the ratio of $\Delta\text{DIC} : \Delta\text{TA}$ being 1.13 : 1.

Rates of NCP and calcification at Hog Reef Flat were estimated, by use of Eqs. 4 and 5, to be $16.8 \pm 9.9 \text{ mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ and $12.3 \pm 3.6 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ (under the assumption of a mean depth of 6 m), respectively, during the daytime. The air-sea CO_2 flux, F , used in the calculation of NCP, was a minor contributor to DIC changes (i.e., $0.07 \pm 0.05 \text{ mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$). Rates of respiration could not be estimated because of the lack of nighttime observations.

The rate of calcification measured on Hog Reef Flat was comparable to that of other coral reef ecosystems. Kinsey (1985) reported calcification rates ranging $8\text{--}14 \text{ g CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ ($\sim 3\text{--}6 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ hr}^{-1}$) for “standard” reef flats. The rate of calcification determined at Hog Reef Flat was slightly higher ($12.3 \pm 3.6 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ hr}^{-1}$) than that in other studies reporting rates of calcification ($\sim 8\text{--}10 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ hr}^{-1}$) from diel experiments (e.g., Gattuso et al. 1993, 1997; Ohde and van Woesik 1999). It was

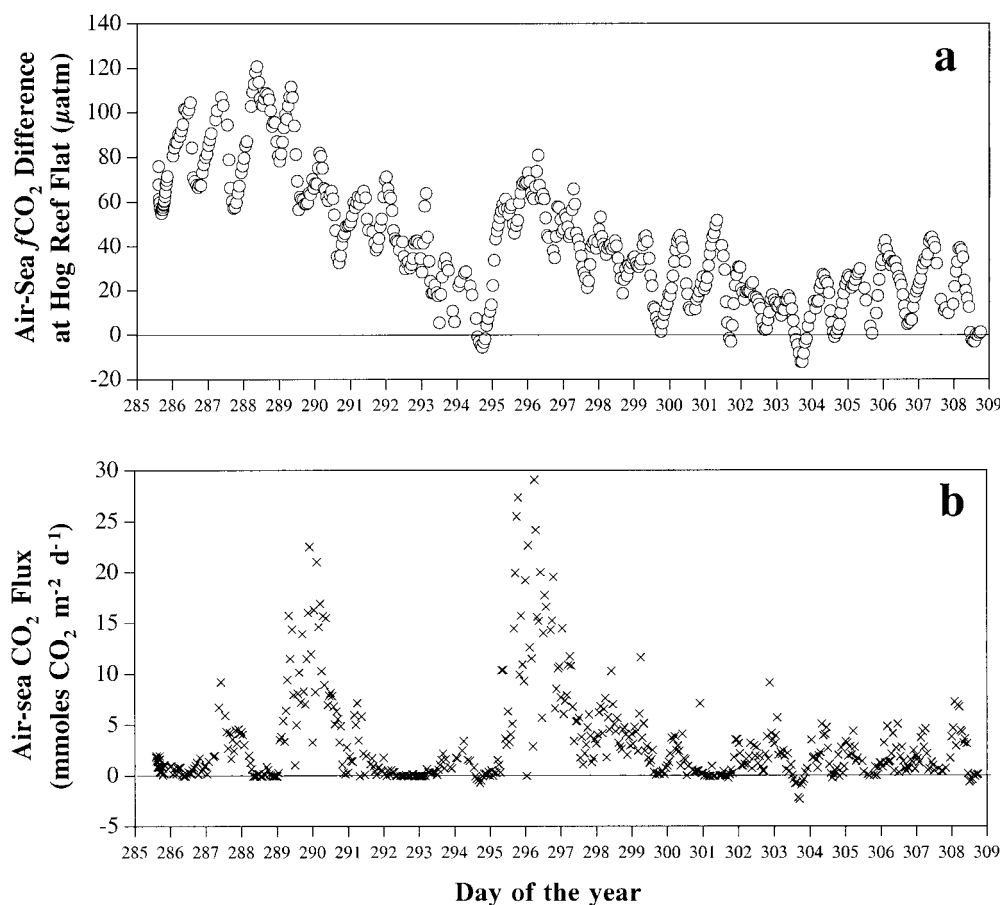


Fig. 4. Time series of atmospheric and oceanic variables from 12 October to 4 November 1998 (days of the year 285–308). (a) Air-sea difference in $f\text{CO}_2$ ($\Delta f\text{CO}_2$). Positive value indicate that ocean $f\text{CO}_2$ is greater than that in the atmosphere. Units are μatm . (b) Air-sea flux of CO_2 ($\text{mmoles CO}_2 \text{ m}^{-2} \text{ d}^{-1}$). Positive values represent flux from ocean to atmosphere. Negative values represent flux from atmosphere to ocean.

not possible to determine the daily rate of calcification at Hog Reef Flat, since only a daytime rate was measured. Calcification rates, however, tend to be lower at night, and it is likely that the daily rate at Hog Reef Flat falls within the range of other studies. Even so, this daytime rate cannot be extrapolated to annual rates of calcification because of several uncertainties, including: whether Hog Reef Flat is representative of the Bermuda coral reef ecosystem; what the day-to-day variability of calcification is due to changing light conditions, nutrient inputs, wave energy, and the balance of onshore/offshore water at the reef site; and whether rates of calcification change seasonally. A time series of seawater $f\text{CO}_2$ measurements collected from the southeastern part of the Bermuda rim reef suggests that rates of calcification change seasonally (Bates unpubl.). Logan and Tomascik (1991) have reported that several species of corals from Bermuda have higher growth rates (the authors equate “extension rate” with “growth rate”) during the fall and winter period.

Discussion

Diurnal variability of seawater $f\text{CO}_2$ on coral reef ecosystems—Recent studies have shown a wide range of diurnal

seawater $f\text{CO}_2$ variability at different reef sites (Table 1; Gattuso et al. 1993, 1997; Frankignoulle et al. 1996; Kawahata et al. 1997; Ohde and Woesik 1999). Diurnal amplitudes of seawater $f\text{CO}_2$ ranged from $\sim 120 \mu\text{atm}$ on a Moorea (French Polynesia) reef (Gattuso et al. 1993) to $\sim 700\text{--}850 \mu\text{atm}$ on an Okinawa reef (Ohde and Woesik 1999). In comparison, the diurnal variability of seawater $f\text{CO}_2$ at Hog Reef Flat was much smaller (i.e., $41 \mu\text{atm} \pm 20 \mu\text{atm}$).

The wide divergence of diurnal seawater $f\text{CO}_2$ ($\sim 40\text{--}850 \mu\text{atm}$; Table 1) probably reflects differences in the rates and balance of calcification and organic carbon production at each coral reef site. It probably also reflects the variable depths of water found at each site and the release of the CO_2 produced by calcification into the overlying water column. The large seawater $f\text{CO}_2$ amplitude ($\sim 700\text{--}850 \mu\text{atm}$), observed by Ohde and Woesik (1999) at the Okinawa reef, occurred in very shallow water ($\sim 0.18 \text{ m}$). A “dampened” diurnal seawater $f\text{CO}_2$ variability ($\sim 41 \mu\text{atm}$) at Hog Reef Flat occurred in waters with a depth of $\sim 6 \text{ m}$. Although there is uncertainty in the true depths and variability of depth at each reef site, adjusting the diurnal variability of seawater $f\text{CO}_2$ to a mean depth of 1 m brings a convergence of diurnal amplitudes to $\sim 80\text{--}240 \mu\text{atm}$ (Table 1).

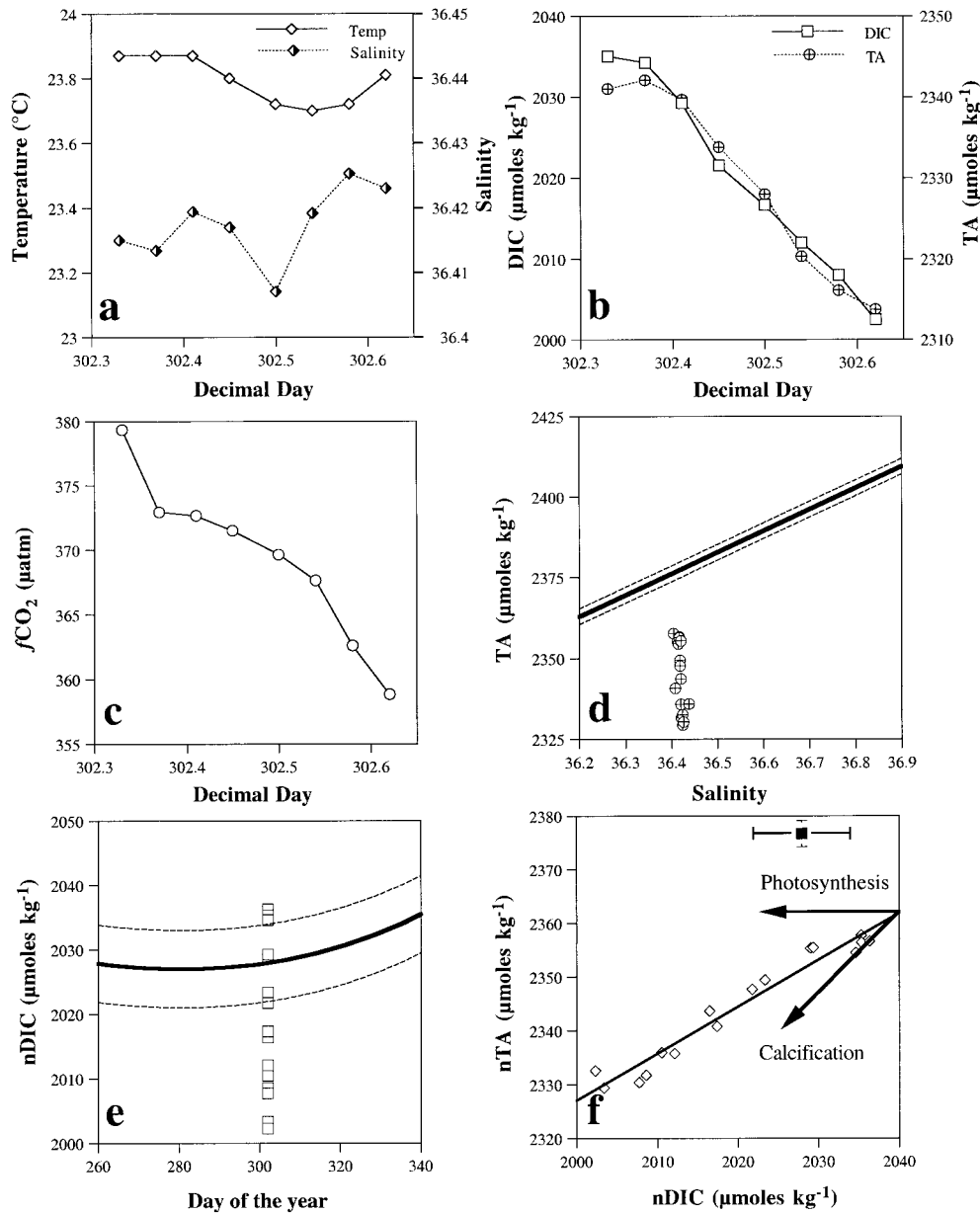


Fig. 5. Hydrographic and biogeochemical variability from the short time series on 29 October 1998 at Hog Reef Flat. (a) Time series of temperature and salinity. (b) Time series of DIC and TA. (c) Time series of $f\text{CO}_2$ from the CARIOCA buoy. (d) Deviation of Hog Reef Flat alkalinity (circles), compared with alkalinity-salinity relationships observed in the Sargasso Sea. The solid line represents the alkalinity-salinity regression for data observed at the BATS site in the Sargasso Sea from 1990 to 1998 (Bates et al. 1996b, in press). Alkalinity at BATS is a conservative function of salinity (solid line) with a RMS error of $2.45 \mu\text{moles kg}^{-1}$ (dashed lines). (e) Deviation of Hog Reef Flat DIC (open squares), compared with DIC from the sources water of the Sargasso Sea. The curves plotted for Sargasso Sea DIC were determined from data collected at BATS from 1988 to 1998 (Bates et al. 1996a, in press). The mean Sargasso Sea DIC (bold solid line) for the fall period is plotted as a polynomial function of all BATS DIC data. The RMS error of DIC is $6.7 \mu\text{moles kg}^{-1}$ (plotted as dashed lines). (f) Changes in DIC and TA at Hog Reef Flat. Both DIC and TA were normalized to a salinity of 36.41 . The arrows denote theoretical changes due to photosynthesis and calcification. The DIC and TA properties of Sargasso Sea source waters are denoted by the closed square symbol. Error bars denote the RMS error associated with DIC-time and TA-salinity relationships in the Sargasso Sea.

Table 1. Comparison of seawater *f*CO₂ diurnal variability for Hog Reef Flat, Bermuda, and other coral reef ecosystems.

| Reef site | Range of seawater <i>f</i> CO ₂ (μatm) | Diurnal <i>f</i> CO ₂ amplitude (μatm) | Mean depth (m) | Diurnal <i>f</i> CO ₂ amplitude adjusted to a depth of 1 m (μatm) | Reference |
|---------------------------|---|---|----------------|--|---------------------------|
| Okinawa, site 1 (Japan) | 73–1069 | ~700–850 | 0.18 | ~125–150 | Ohde and van Woessik 1999 |
| Younge Reef (Australia) | ~250–680 | ~110–130 | ? | NA | Frankignoulle et al 1996 |
| Moorea (French Polynesia) | ~270–580 | ~300 | <1 | ~200 | Gattuso et al 1997 |
| Mourea (French Polynesia) | ~240–420 | ~150–180 | 1.4 | ~105–130 | Frankignoulle et al 1996 |
| Okinawa, site 2 (Japan) | 134–448 | ~160 | 2 | ~80 | Ohde and van Woessik 1999 |
| Moorea (French Polynesia) | NA | ~120 | 1.4 | ~85 | Gattuso et al 1993b |
| Hog Reef Flat (Bermuda) | ~340–470 | 41 ± 20 | 4–6 | ~160–240 | This study |
| Palau (French Polynesia) | NA | 48† | 55‡ | NA | Kawahata et al 1997 |
| Majuro Atoll (Polynesia) | NA | 4† | 67‡ | NA | Kawahata et al 1997 |

* NA, not applicable.

† Onshore-offshore gradient in seawater *f*CO₂.

‡ Maximum depth reported, but no mean depth given.

Comparison of Hog Reef Flat and Sargasso Sea CO₂ variability—Sargasso Sea waters surrounding Bermuda are the original source of waters mixed onto the Bermuda platform through tidal and wind dynamics. Any difference in the CO₂ properties observed at Hog Reef Flat and the Sargasso Sea reflects the modification of the source waters through temperature changes, air-sea gas exchange of CO₂, and biological processes occurring on the platform. This modification occurs within a few days of water being mixed onshore, since the residence time of water on the platform is short (~4 d; Morris et al. 1977). The half-life of water resident on the rim reef at Hog Reef Flat ranges from 2 to 6 tidal cycles, according to a physical model of tidal dynamics on the Bermuda platform (Johnson unpubl. data). The half-life of water resident within the North Lagoon ranges from 8 to 16 tidal cycles.

Hog Reef Flat seawater *f*CO₂, measured by the CARIOCA buoy, ranged from ~340 to 470 μatm (Fig. 6a). As a comparison, seawater in the Sargasso Sea had minor variability, ranging from ~340 to 360 μatm over the sampling period (Fig. 6a). The mean Sargasso Sea *f*CO₂ value, illustrated by the curve fit in Fig. 6, was generated from *f*CO₂ data collected at BATS from 1994 to 1998 and had a root-mean square (RMS) error of 8.8 μatm. Hog Reef Flat seawater *f*CO₂ was typically higher than Sargasso Sea seawater by 0 to ~120 μatm, with a mean difference of 52 ± 23 μatm. Similar positive modification of platform seawater *f*CO₂ has been observed in the southeastern part of the reef system near Bermuda for the month of October in previous years (+15–40 μatm; 1994–1997; Bates unpubl.). Enhanced seawater *f*CO₂ has also been observed in lagoonal waters of Palau Barrier Reef and Majuro atoll, compared with offshore waters (Kawahata et al. 1997).

The enhancement of Hog Reef Flat seawater *f*CO₂ from the original Sargasso Sea source reflects the net balance of different biological and physical processes, including coral reef CaCO₃ production and dissolution; net community production, including organic carbon production decomposition and bacterial remineralization of organic matter; water column net primary production and respiration; air-sea CO₂ gas

exchange; temperature changes; and the physical evolution of platform waters, which is influenced by various factors such as impingement and dilution by Sargasso Sea waters, tidal and wind mixing, and residence time. We argue that the increase in seawater *f*CO₂ largely results from balance of CaCO₃ production and organic carbon production. This biogeochemical signal is subsequently modulated by the physical evolution of waters on the Bermuda platform.

Several of the above processes are minor contributors to changes in CO₂ chemistry on the Bermuda platform. Water column net primary production and respiration do not contribute significantly to seawater *f*CO₂ changes. Phytoplankton biomass reaches a maximum in July, and rates of primary production on the North Lagoon (Morris et al. 1977) are slightly higher than the rates observed in the oligotrophic Sargasso Sea (~4–20 mg C m³ d⁻¹; Michaels and Knap 1996). Diurnal variability of seawater *f*CO₂ due to phytoplankton production and respiration is therefore small (~1–2 μatm). Calcifying phytoplankton such as coccolithophorids are minor components of the pelagic community on the Bermuda platform (Morris et al. 1977) and in the Sargasso Sea (Hulbert 1990). Air-sea CO₂ exchange contributes to a minor loss of CO₂ from the Bermuda platform. The average flux of 3.3 ± 4.6 mmoles CO₂ m⁻² d⁻¹ from ocean to atmosphere represents a small daily decrease in seawater *f*CO₂ (~0.5 μatm d⁻¹, under the assumption of a mean depth of 8.5 m on the platform).

Decomposition of organic matter represents a minor contribution to seawater CO₂ changes on the Bermuda platform. Bacterial biomass is low in Bermuda platform and Sargasso Sea waters, compared with that in other marine environments (Carlson and Ducklow 1996). Rates of bacterial remineralization of dissolved organic carbon are low (~0.5 μmoles kg⁻¹ d⁻¹; Carlson and Ducklow 1996; Countway 1999), contributing to a potentially small gain in seawater *f*CO₂ of ~0.6 μatm d⁻¹. It is unlikely that there is a significant respiratory CO₂ flux out of the reef sediments, which have low organic carbon contents (~3%–7%; Morris et al. 1977; Jickells and Knap 1984), compared with other reef settings.

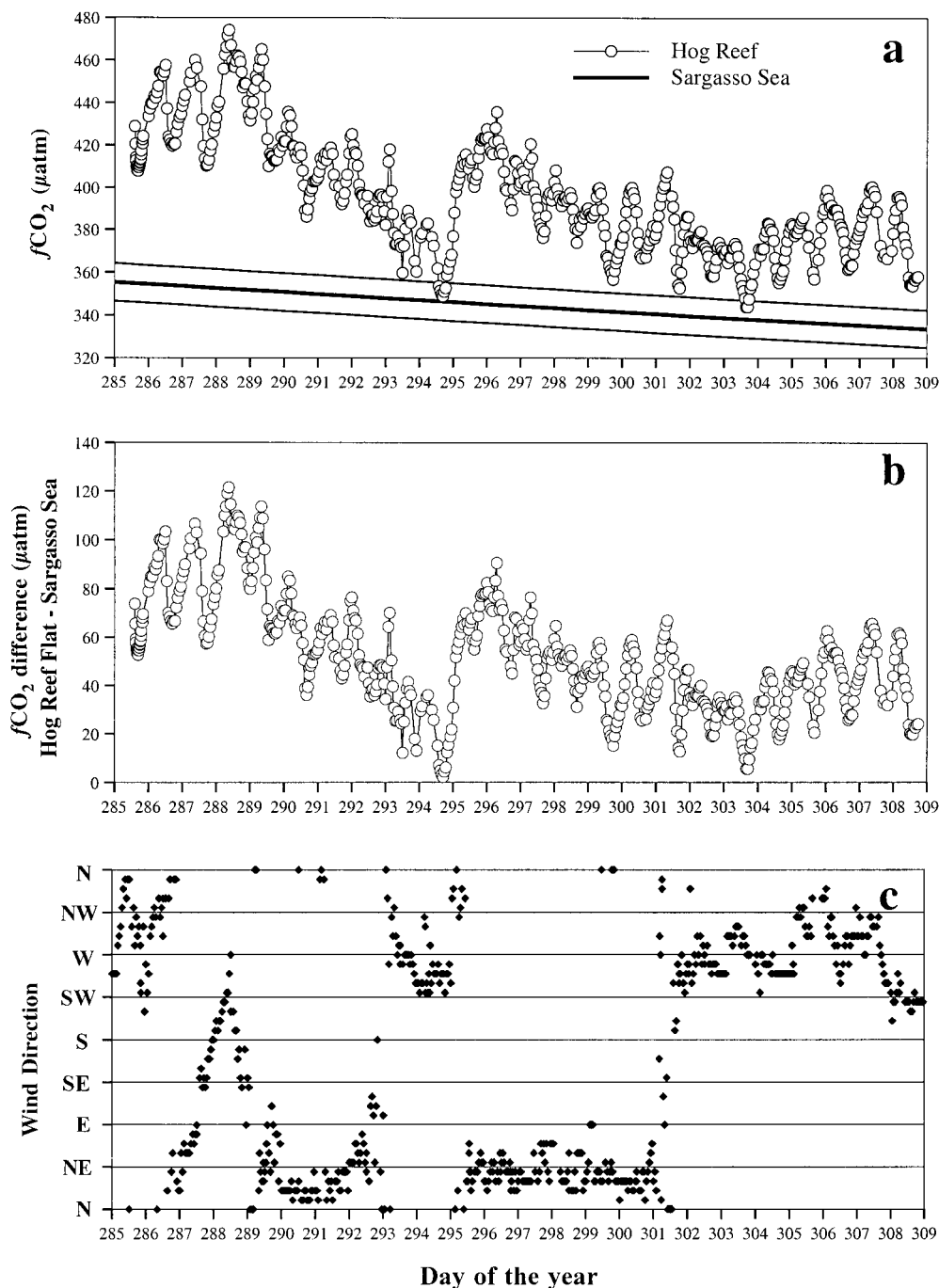


Fig. 6. Time series of atmospheric and oceanic variables from 12 October to 4 November 1998 (days of the year 285–308). (a) Seawater $f\text{CO}_2$ from Hog Reef Flat and the Sargasso Sea. The curve for the Sargasso Sea reflects the mean seawater $f\text{CO}_2$ observed in the Sargasso Sea over a 4-yr period (1994–1998). (b) Difference in seawater $f\text{CO}_2$ between Hog Reef Flat and the surrounding Sargasso Sea. (c) Wind direction.

Contribution of coral reefs to the ocean carbon cycle—There is debate about whether coral reef ecosystems are oceanic sinks or sources of CO_2 . Several studies have suggested that coral-dominated reef ecosystems are sources of CO_2 to atmosphere (e.g., Ware et al. 1992; Gattuso et al. 1993, 1996a,b, 1999, 2000; Frankignoulle et al. 1994; Buddemeier 1996; Kawahata et al. 1997; Bates unpubl.). Other studies

have suggested that some reef ecosystems are neutral (Ohde and van Woesik 1999) or are oceanic sinks for atmospheric CO_2 (Kinsey and Hopley 1991; Kayanne et al. 1995, 1996; Yamamuro et al. 1995; Gattuso et al. 1996a; Kraines et al. 1997; Chisholm and Barnes 1999). The causes of such differences between reef sites seem to result from a wide variety of inter-related factors, including: (1) differences in reef

Table 2. Comparison of mean wind direction and speed and seawater $f\text{CO}_2$ difference between Hog Reef Flat and Sargasso Sea (μatm); positive values denote that Hog Reef Flat has higher seawater $f\text{CO}_2$, 1 SD of the mean values are also given.

| Days of year | Mean wind direction | Seawater $f\text{CO}_2$ difference between Hog Reef Flat and Sargasso Sea (μatm) | Mean wind speed (m s^{-1}) |
|--------------|---------------------|--|--|
| 285.0–286.5 | 285 ± 38 NW | 69 ± 15 | 2.4 ± 1.4 |
| 287.0–287.5 | 84 ± 37 E | 84 ± 18 | 3.0 ± 1.7 |
| 288.7–289.0 | 141 ± 26 SE | 93 ± 10 | 2.1 ± 1.0 |
| 289.0–290.0 | 57 ± 26 NE | 76 ± 19 | 5.4 ± 1.3 |
| 290.0–292.0 | 20 ± 12 ENE | 60 ± 12 | 6.4 ± 2.1 |
| 292.0–293.0 | 72 ± 35 E | 50 ± 12 | 2.2 ± 0.7 |
| 293.5–295.0 | 254 ± 18 W | 22 ± 13 | 5.6 ± 1.7 |
| 295.0–295.50 | 351 ± 27 N | 61 ± 8 | 2.2 ± 1.5 |
| 295.5–301.0 | 41 ± 346 NE | 51 ± 16 | 6.8 ± 2.1 |
| 301.5–305.0 | 261 ± 21 W | 30 ± 10 | 7.3 ± 3.1 |
| 305.0–306.2 | 309 ± 19 NW | 46 ± 11 | 4.2 ± 1.8 |
| 306.4–306.9 | 271 ± 17 W | 37 ± 9 | 6.2 ± 1.7 |
| 307.0–307.5 | 296 ± 13 NW | 55 ± 9 | 5.9 ± 1.0 |
| 307.7–308.7 | 227 ± 13 SW | 38 ± 15 | 7.7 ± 4.7 |

community structure; (2) decomposition of organic matter and nitrification; (3) widely variable seawater $f\text{CO}_2$ of offshore water with $f\text{CO}_2$ out of equilibrium with the atmosphere; and (4) the residence time of water on the reef affects the biogeochemical evolution of seawater $f\text{CO}_2$.

Differences in community structure, which influences the net balance of CaCO_3 production and organic carbon production, have a major role in determining the fate of CO_2 in reef settings (Kleypas et al. 1999; Gattuso et al. 1999, 2000b). Reefs dominated by hard corals appear to be sources of CO_2 to the atmosphere, whereas reefs dominated by macroalgae appear to be oceanic sinks of CO_2 . This has relevance to the global carbon cycle, because many coral reefs appear to be transitioning from hard coral-dominated states to macroalgal-dominated states (Smith and Buddemeier 1992; Hughes 1994). A detailed evaluation of the status and changes in community structure was not undertaken during the Hog Reef Flat study. However, Bates (unpubl.) observed seasonal changes in the enhancement of Bermuda platform seawater $f\text{CO}_2$ relative to the Sargasso Sea. The enhancement of Bermuda platform seawater $f\text{CO}_2$ reaches its maximum ($\sim 60 \mu\text{atm}$) in the fall, when hard coral growth rates are at their maximum (e.g., *D. strigosa* and *D. labyrinthiformis*; Logan and Tomascik 1991). In June and July, the biomass of turf forming and coralline algae reach their maximum (Smith unpubl. data), coinciding with minimal ($0\text{--}20 \mu\text{atm}$) enhancement of Bermuda platform seawater $f\text{CO}_2$ (Bates unpubl.).

The decomposition of organic matter and nitrification could influence seawater alkalinity and $f\text{CO}_2$, but its significance is uncertain (Chisholm and Barnes 1999; Gattuso et al. 2000b). Recently, Chisholm and Barnes (1999) suggested that nitrification of organic matter in coral reef sediments might influence seawater $f\text{CO}_2$ by affecting alkalinity. For example, $1 \mu\text{moles kg}^{-1}$ of nitrification (i.e., ammonium to nitrate oxidation) decreases alkalinity by $2 \mu\text{moles kg}^{-1}$ (Brewer and Goldman 1976), thereby increasing seawater $f\text{CO}_2$ by $\sim 3.2 \mu\text{atm}$. Gattuso et al. (2000b) argue that rates

of nitrification in reef settings are insufficient to explain the increase in reef seawater $f\text{CO}_2$. It seems unlikely that nitrification caused the increase in seawater $f\text{CO}_2$ at Hog Reef Flat, for several reasons. Nitrate and ammonium concentrations on the Bermuda platform are low (about <0.2 and $0.03 \mu\text{moles kg}^{-1}$, respectively; Morris et al. 1977; Lipshultz unpubl. data), rates of nitrification and ammonium uptake on the Bermuda platform are low (Lipshultz unpubl. data), and rates of primary production are low and are only slightly higher than those in the oligotrophic Sargasso Sea. These processes do not appear to be important at Hog Reef Flat or in reefs of Bermuda in general.

The variability of offshore seawater $f\text{CO}_2$ and the disequilibrium of CO_2 relative to the atmosphere are important determinants of whether coral reefs are oceanic sources or sinks of CO_2 . Coral reef CaCO_3 production at Hog Reef Flat (this study) and on the Bermuda platform (Bates unpubl.) increases seawater $f\text{CO}_2$ relative to the Sargasso Sea. The air-sea flux of CO_2 , however, is dependent on the seawater $f\text{CO}_2$ of offshore waters and on other factors that affect the biogeochemical evolution of waters on the platform (e.g., short-term physical processes, seasonal changes, etc.). Air-sea fluxes of CO_2 at Hog Reef Flat are mainly directed from ocean to atmosphere (i.e., oceanic source of CO_2 to the atmosphere), but there are occasional reversals of this direction (see Fig. 5c; days of year 294 and 303). Indeed, during the winter, the air-sea flux of CO_2 on the Bermuda platform is directed from atmosphere to ocean (i.e., oceanic sink of CO_2 from the atmosphere). This occurs because Sargasso Sea waters impinging onto the platform have lower seawater $f\text{CO}_2$ than the atmosphere (Bates et al. 1996a, 1998a,b), and reef CaCO_3 production does not increase $f\text{CO}_2$ sufficiently for the platform to become a source of CO_2 to the atmosphere (Bates unpubl.). Coral reef supplies CO_2 to the water column, but, because of preexisting air-sea CO_2 disequilibrium, this does not necessarily translate into the coral reef ecosystem behaving as a source of CO_2 to the atmosphere.

In determining whether other reefs systems are sources or

sinks of CO_2 , it is critically important to determine the CO_2 properties of the original offshore water and the air-sea CO_2 disequilibrium of the original offshore water. The reef sites at which CO_2 dynamics have been studied are all located in the Pacific Ocean (e.g., Moorea, Yonge Reef, Okinawa, Palau Barrier Reef, and Majuro Atoll), and all have considerable seasonal variation in temperature. Time-series records of seawater $f\text{CO}_2$ at the Hawaii Ocean Time-series (Winn et al. 1994) and regional maps of the air-sea disequilibrium of seawater $f\text{CO}_2$ in the tropical/subtropical Pacific Ocean (Takahashi et al. 1997, 1999) reveal large seasonal variability (up to 60–80 μatm) of seawater $f\text{CO}_2$ in the offshore vicinity of these reef sites. Thus previous assessments about whether Pacific Ocean reefs are sources or sinks of CO_2 could change if a reevaluation of reef CO_2 data were made in light of recent improvements in our knowledge of Pacific Ocean CO_2 variability.

The biogeochemical evolution of reef water, which is influenced by the rates of advection of offshore water onto the reef site, residence time of water, and wind and tidal dynamics, should also be evaluated. The difference between seawater $f\text{CO}_2$ at Hog Reef Flat and the Sargasso Sea varied from ~ 0 –120 μatm over the short deployment period of the CARIOCA buoy (Fig. 6b). Since the CARIOCA buoy sampled waters at a fixed location, this range of modification reflects the biogeochemical variability of waters passing through Hog Reef Flat. As stated earlier, the residence time of water at Hog Reef Flat (2–6 tidal cycles) is shorter than that in waters of the North Lagoon (8–16 tidal cycles). The enhancement of seawater $f\text{CO}_2$ (relative to Sargasso Sea) in the North Lagoon should be greater than that at Hog Reef Flat, since these waters have undergone longer periods of modification due to CaCO_3 production. Indeed, continuous sampling of surface water during transects across the platform (Bates unpubl. data) indicates that there is an increasing gradient of seawater $f\text{CO}_2$ of ~ 25 μatm from close to Hog Reef Flat across the North Lagoon to the island of Bermuda. The seawater CO_2 variability, therefore, likely reflect changes in the advection of offshore (i.e., Sargasso Sea) and onshore waters (i.e., North Lagoon) and their relative proportions at the sampling site. Such changes in CO_2 are mediated by tidal and wind dynamics on the Bermuda platform, but there is a lack of surface current information and direct tracer evidence of the contribution of each water mass. However, the qualitative influence of tidal and wind dynamics can be evaluated indirectly.

Hog Reef Flat is located on the northwestern rim of the Bermuda platform. During the deployment of the CARIOCA buoy at Hog Reef Flat, wind directions frequently changed between a west-northwest and east-northeast orientation (Fig. 6c). These wind directions were maintained for periods of up to 5 d. The mean differences in seawater $f\text{CO}_2$ between Hog Reef Flat and Sargasso Sea were lowest (~ 20 –40 μatm) during periods of predominantly westerly winds (see Fig. 7; Table 2). The difference in seawater $f\text{CO}_2$ increased to a maximum (~ 60 –100 μatm) during periods of predominantly easterly winds. Although quantitative estimates cannot be made, these changes probably result from changes in the relative proportion of offshore and onshore water at Hog Reef Flat. Surface currents associated with west-northwest

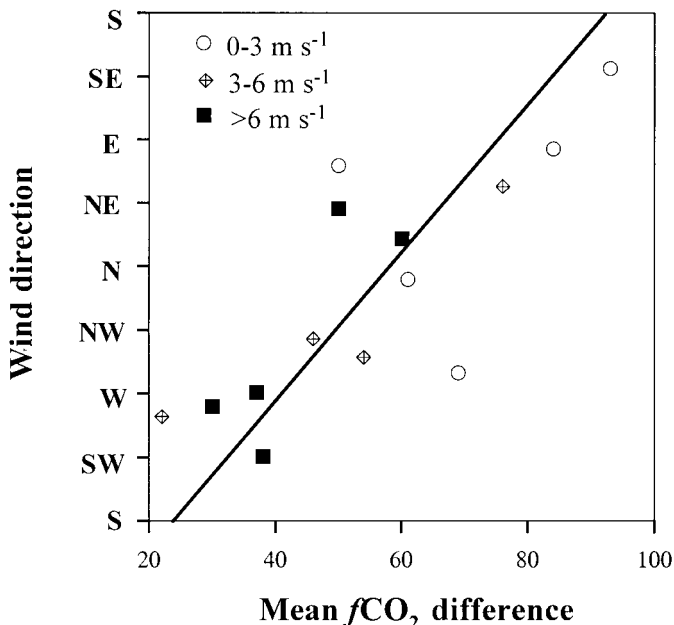


Fig. 7. Plot of wind direction against mean difference in seawater $f\text{CO}_2$ between Hog Reef Flat and the surrounding Sargasso Sea for periods given in Table 2. Different symbols represent average winds for the time periods in Table 2.

winds should bring offshore waters onto the platform. This should increase the proportion of offshore water and decrease the residence time at Hog Reef Flat, resulting in the reduced seawater $f\text{CO}_2$ difference (Fig. 7). In contrast, surface currents associated with east-northeast winds should preferentially bring lagoonal waters to Hog Reef Flat. Considering that lagoonal waters have a higher load of CO_2 because of CaCO_3 production and longer residence time on the platform, it is not surprising that the largest difference in seawater $f\text{CO}_2$ was observed at Hog Reef Flat during east-northeast winds.

The influence of tidal and wind dynamics on coral reef platforms provides another complication in the evaluation of reefs as sources or sinks of CO_2 . Short-term variability in the physical forcing of the Bermuda platform contributes to a large range in the estimates of the enhancement of CO_2 resulting from coral reef calcification. Other reef sites will be similarly influenced by variability in the physical forcing. Future assessments of the influence of coral reefs on CO_2 requires longer term biogeochemical studies in the context of a detailed knowledge of the physical regime and forcing.

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