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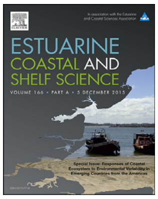

Net ecosystem production, calcification and CO_2 fluxes on a reef flat in Northeastern Brazil

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ABSTRACT

The carbon cycle in coral reefs is usually dominated by the organic carbon metabolism and precipitation-dissolution of $CaCO_3$, processes that control the CO_2 partial pressure (pCO_2) in seawater and the CO_2 fluxes through the air–sea interface. In order to characterize these processes and the carbonate system, four sampling surveys were conducted at the reef flat of Coroa Vermelha during low tide (exposed flat). Net ecosystem production (NEP), net precipitation-dissolution of $CaCO_3$ (G) and CO_2 fluxes across the air–water interface were calculated. The reef presented net autotrophy and calcification at daytime low tide. The NEP ranged from −8.7 to 31.6 mmol C m^{-2} h^{-1} and calcification from −13.1 to 26.0 mmol C m^{-2} h^{-1}. The highest calcification rates occurred in August 2007, coinciding with the greater NEP rates. The daytime CO_2 fluxes varied from −9.7 to 22.6 μmol CO_2 m^{-2} h^{-1}, but reached up to 13,900 μmol CO_2 m^{-2} h^{-1} during nighttime. Carbon dioxide influx to seawater was predominant in the reef flat during low tide. The regions adjacent to the reef showed a supersaturation of CO_2, acting as a source of CO_2 to the atmosphere (from −22.8 to −2.6 mol CO_2 m^{-2} h^{-1}) in the reef flat during ebbing tide. Nighttime gas release to the atmosphere indicates a net CO_2 release from the Coroa Vermelha reef flat within 24 h, and that these fluxes can be important to carbon budget in coral reefs.

1. Introduction

Coral reef environments exert a great influence on seawater carbon chemistry. Benthic metabolism, hydrodynamic circulation, reef zonation and geomorphology affect the carbonate chemistry in these environments (Falter et al., 2013). Photosynthesis (P), respiration (R), calcification and dissolution of carbonate have long been recognized as processes driving the changes in carbonate system observed in these ecosystems (Smith, 1973; Smith and Key, 1975; Gattuso et al., 1993, 1999). The metabolism of organic matter in aquatic systems can be expressed as the balance of photosynthesis and respiration (Net ecosystem production, NEP = P − R). NEP represents the sum of these two processes within the entire community in a coral reef, but usually the coral/zooxanthelae symbiosis and macroalgae are the main contributors. The relative importance of these primary producers will vary according environmental characteristics, such as nutrient concentrations and turbidity. Communities of epilithic and endolithic photoautotrophs may also be major primary producers in some reefs (Tribollet et al., 2006). Spatial and temporal changes in carbonate chemistry are also influenced by the physical attributes of a reef system. These changes depend on onshore wave energy flux, length and depth of the reef flat (Falter et al., 2013).

In net autotrophic ecosystems, where the rate of P is greater than R, the uptake of CO_2 in excess of that produced by remineralization increases the pH, carbonate ions concentration and saturation state, decreases dissolved inorganic carbon (DIC) and pCO_2, while total alkalinity remains (TA) unchanged except by minor changes due to nutrient uptake. In net heterotrophic ecosystems ($P < R$) the reverse alterations occurs.

The net balance between the rates of carbonate precipitation and dissolution (G) is also important to the fluxes of inorganic carbon. In coral reefs most of carbonate precipitation occurs within calcifying benthic organisms, mainly scleractinian coral. Carbonate dissolution in overlying marine waters with saturation state higher than 1 is due to macro and microborers. The unconsolidated

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sediment retained within pools of the reef flat and adjacent areas is also important to carbonate dynamics, where dissolution prevails and act as a net source of alkalinity to the reef environment (Cyronak et al., 2013a) Calcification in coral reef release about 0.6 mol of CO_2 to the surrounding environment per mole of $CaCO_3$ precipitated (Frankignoulle et al., 1994). In systems with calcification rates exceeding dissolution (net calcification) there is a decrease of 2 mol of TA and 1 mol of DIC, and release of CO_2 increasing pCO_2. The reverse occurs in systems with net dissolution.

The fluxes of carbon dioxide across the atmosphere–water interface also alter the carbonate system in coral reefs. The evasion to atmosphere will lower the concentration of dissolved inorganic carbon (DIC) and increase pH. Conversely, the influx to the water will increase DIC concentration, resulting in a lowered pH, with no change in TA. These fluxes are dependent of the stability of the aqueous diffusive sub-layer, and a slow process when wind and turbulence are low. Under these conditions, the metabolism of organic and inorganic carbon control the carbon chemistry of seawater in short time scales. Strong winds and breaking waves intensify these fluxes, and can reset the carbonate chemistry in shallow environments. Furthermore, the gradient between partial pressure of CO_2 in water and atmosphere, that define the direction of these fluxes through the air–sea interface in coral reefs is controlled by the organic carbon metabolism (primary production-respiration) and calcification–dissolution processes (Smith, 1974, 1981; Ware et al., 1991; Frankignoulle and Gattuso, 1993; Frankignoulle et al., 1994; Falter et al., 2013). The magnitude of these fluxes is controlled by winds and turbulence.

The combustion of fossil fuels has increased the atmospheric carbon dioxide concentration exponentially since 1800 (IPCC, 2013). The ocean has been absorbing about one-third of all CO_2 released into the atmosphere (Sabine et al., 2004), which causes a drop of seawater pH and the ocean acidification (Kleypas et al., 1999; Orr et al., 2005). Ocean acidification will change the carbonate equilibrium causing the decrease of the concentration of carbonate ion (CO_3^{2-}), the saturation state (Ω) of aragonite and ultimately the calcification rates (Gattuso et al., 1998; Leclercq et al., 2000; Reynaud et al., 2003).

Other factors that can influence seawater pH, carbonate speciation and calcification are of regional or local origin. Continental inputs with a high amount of organic matter lead most of the coastal waters to net heterotrophy (Smith and Mackenzie, 1987). Fringing reefs are especially affected by the loading of organic carbon and nutrients by untreated sewage outflow and terrestrial runoff. The effects in these reefs include increased NEP and lower net calcification (Silverman et al., 2007), higher rates of bioerosion by microborers (Chazottes et al., 2002), a shift in reef community from dominance of coral and coralline algae to macroalgae and subsequently filter feeders (Done, 1999), and so from photoautotrophs to heterotrophs (Smith, 1981).

The characterization of biogeochemical processes involving carbon in coral reefs in Brazil is rare in the literature – not only for the northeast coast (Costa et al., 2000, 2006), but all Brazilian reefs. There are a great number of studies concerning carbon biogeochemical processes, but geographically concentrated in relatively few Pacific and Caribbean reefs. The same holds true for all South American coral reefs, since except for the works of Manzello et al. (2008) and Manzello (2010) in Galapagos Islands, no study concerning carbonate system, net metabolism and carbonate precipitation-dissolution was found in the literature. Coral reefs of Brazil are distributed throughout 3000 km of the northeastern coast, from Southern Bahia State (17° 25′S; 39°05′W; Fig. 1) to the Northeastern Maranhão State (00°53′S; 044°16′W) (Castro and Pires, 2001) and they differ from those of Pacific and Caribbean by their lower biodiversity and high degree of endemism (Leão, 1994). There is still a need to extend these studies to reefs in less covered regions, since it could not simply be assumed that they behave exactly the same.

This paper presents the first description of carbonate system in a South American Atlantic coral reef, assessing the direction and magnitude of CO_2 fluxes across the air–sea interface and the relative importance of Net ecosystem production and calcification.

2. Materials and methods

2.1. Study area

Coroa Vermelha is a fringing reef situated in Santa Cruz de Cabrália, in the southern region of Bahia State, Northeastern Brazil (Fig. 1). The climate is tropical humid with average annual temperature of about 24 °C, while the annual rainfall is greater than 1600 mm (Aouad, 1998). The Brazilian continental shelf has a semidiurnal tidal regime. According to the classification of tidal variations proposed by Hayes (1979), the northeastern coast is upper mesotidal.

The reef system of Coroa Vermelha is part of discontinuous structures parallel to the coast. The reef is connected to the shore by a sand spit that separates the coast into two small bights, north and south. These adjacent regions, especially the north inlet, receive substantial input of nutrients and organic matter from terrestrial sources such as runoff, discharge via groundwater and untreated sewage (Fig. 1). A submerged sand bar also restricts water flow through the southward backreef of Mutá reef, forming a lagoon. When exposed in low tide, the reef flat forms shallow pools with sandy or rocky bottoms. These pools act as *in situ* incubation sites, allowing studies on the metabolic processes of benthic organisms and their interactions with the seawater.

The only published work describing the benthic community in Coroa Vermelha (Costa et al., 2005) report data from 1999 to 2000 in which macroalgae covers more than 50% of the reef flat (up to 60%), about 35% turf algae. Coral cover was less than 5%, and crustose algae less than 2%. A more recent work (Santana, 2006) describes a fleshy macroalgae cover of less than 25%, higher in the mid portion of the reef flat. Crustose cover was up to 40% near the forereef crest, but about 5% along most part of the reef flat. This work also describe that *Siderastrea stellata* and *Favia gravida* were the only coral species present in the tidepools, with a mean cover of 30%. In the larger intercommunicated pools near the sand spit (not sampled in the present work) coral cover reached 50%. *S. stellate* comprised about 70% of coral cover. The contrast between these works can be caused by methodology and or temporal changes, but by the occasion of our sampling the reef flat was dominated by turf algae, but coral cover was also conspicuous. In the shallow bights there was a sparse seagrass meadow of *Halodule wrightii*, with a mean total biomass of 26.4 g DW m^{-2} in the south bight (Personal communication Vila Nova DLD). It was also observed meadows of the same phanerogam in the north bight, apparently with higher aerial biomass but patchy distribution due to sediment erosion.

2.2. Sampling design

Four sampling surveys were performed at the Coroa Vermelha reef and adjacent regions (small bight north, small bight south and fore reef slope), in July 2006, June and August 2007 and January 2008. Field sampling was conducted during the morning low tide at the Coroa Vermelha reef flat, in the north and south bights on the forereef slope. The seawater was collected in tide pools formed during the low tide period. These pools were randomly selected on average every 10 m across a transect from the sand spit to the fore reef slope (Fig. 1; n = 6 in July 2006 and January 2008; n = 8 in June