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Carbonate sediment production in the equatorial continental shelf of South America: Quantifying *Halimeda incrassata* (Chlorophyta) contributions

Pedro Bastos de Macêdo Carneiro [a, *], Jader Onofre de Morais [b]

[a] Universidade Federal do Ceará/LABOMAR, Av. Abolição, 3207, CEP 60165-081, Fortaleza, Ceará, Brazil
[b] Universidade Estadual do Ceará/LGCO, Av. Dr. Silas Munguba, 1700, CEP 60714-903, Fortaleza, Ceará, Brazil

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ABSTRACT

The middle and outer continental shelves of eastern equatorial South America (ESA) are characterized by intense production of carbonate sediments. Qualitative analyses of sediment deposits suggest that the calcareous green alga *Halimeda incrassata* is among the top $CaCO_3$ producers. Nevertheless, no study so far has quantified its real contributions. To better understand the sediment dynamic in this area, we measured biomass, growth rates and calcium carbonate production by this alga. The species exhibited high growth rates (3.38 segments.individual^{-1}.day^{-1}), coverage (174 individuals.m^{-2}) and biomass (214.02 g.m^{-2}). Substitution of segments may allow a sedimentation rate of 1.53 mm.yr^{-1} and a complete turnover of the population every 60.2 days. The rapid growth indicates that this alga can produce as much $CaCO_3$ (1.19 kg $CaCO_3$.m^{-2}.year^{-1}) as other tropical organisms, such as corals and rhodoliths. In a conservative estimate, 773.500 tonnes of $CaCO_3$ are produced per year in a 5000 km^2 area off the northern coast of Brazil. Sedimentation rate seems to be higher than that promoted by continental inputs in middle and outer continental shelf. On the other hand, population turnover is twice as slow as in other *H. incrassata* assemblages, suggesting that South American populations are sensible to physical disturbances. New studies are necessary to accurately estimate *H. incrassata* coverage along the Brazilian coast and to integrate data on other $CaCO_3$ producers, such as foraminifera and coralline algae. This would allow a better understanding of the role of South American continental shelf on the global carbon budget. Furthermore, analysis on the health of these organisms is urgent, since a decline in their populations could negatively affect ecosystems functioning and services.

1. Introduction

The continental margin of eastern equatorial South America (ESA) is a high-energy mixed carbonate-siliclastic platform (Testa and Bosence, 1998; Vital et al., 2008). Along middle and outer continental shelves, relict siliclastic sediments are mixed with locally produced $CaCO_3$-rich sands under the influence of oceanic and tidal currents (Milliman, 1977; Vital et al., 2010; Gomes et al., 2015). Due to a semi-arid climate, continental inputs are mostly restricted to the inner continental shelf. For example, the influence of one of the largest rivers on this coast is mostly limited to the first 6 km from the shore, or 10% of the entire shelf width (Dias et al., 2013). Outside this influence zone, local carbonate sediment production helped to shape major underwater bedforms, significantly affecting the submerged landscape (Testa and Bosence, 1999).

This local carbonate production occurred throughout the Holocene, sustained by a rich biota of foraminifera, coralline and calcareous algae (Gomes et al., 2015). However, despite the relevance of these $CaCO_3$ inputs (Milliman, 1977; Testa and Bosence, 1999), no study has adopted quantitative approaches to measure modern carbonate production on the ESA continental shelf. Available data from the eastern Brazilian coast suggest high production rates, but are restricted to rhodolith-forming coralline red algae at much higher latitudes (e.g. Gherardi, 2004; Amado-Filho et al., 2012). The obvious ecological importance of calcium carbonate producers indicates an urgent need of additional studies to better assess ecosystem health and the sedimentary dynamics in the ESA (Gomes et al., 2015).

* Corresponding author.
E-mail address: pedrocarneiro@ufc.br (P.B.M. Carneiro).

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Among modern calcium carbonate producers, calcareous green algae of the genus *Halimeda* are one of the most prominent worldwide (Milliman, 1977; Freile et al., 1995; Rees et al., 2006). These seaweeds grow fast, often attaining high biomasses and substrate coverage (Hillis-Colinvaux, 1980; Drew, 1983; Garrigue, 1991; van Tussenbroek and van Dijk, 2007). Their highly carbonated thalli are segmented and subject to breakage, resulting in coarse grained calcareous sediments (Drew, 1983; Hudson, 1985; Drew and Abel, 1985; Multer, 1988; Payri, 1988; Freile et al., 1995). Extensive *Halimeda* meadows, which are normally associated with large accumulations of algal debris, are found in many oceans, with potential to influence the global carbon budget (Drew and Abel, 1985; Rees et al., 2006).

On the ESA continental shelf, *Halimeda* dead fragments are frequent in sediment deposits (Milliman, 1977; Testa and Bosence, 1999; Knoppers et al., 1999; Vital et al., 2010). Living meadows of *Halimeda* are also found growing on sand banks along this platform, the most common species being *Halimeda incrassata* (J. Ellis) J.V. Lamouroux (Kempf, 1970; Cocentino et al., 2010). These meadows are usually found on the middle continental shelf (between 20 m and 40 m) (Kempf, 1970), growing on troughs amid submerged sand dunes and sand ribbons that are mostly composed of carbonate sediments (Testa and Bosence, 1999; Monteiro, 2011). No estimates of the area occupied by these meadows are available, but they are observable among these bedforms even in medium spatial resolution satellite images (i.e., LANDSAT TM) (Testa and Bosence, 1999). This indicates that this species may play an important structural role and has relevant ecological influence on the semi-arid coast of the ESA. Nevertheless, no published study measured $CaCO_3$ production by *Halimeda* in the entire South American continental shelf. Most ecological research is limited to surveys on species distribution (e.g. Bandeira-Pedrosa et al., 2004; Cocentino et al., 2010).

The present study aims to analyze current biogenic production of sediments in the ESA middle continental shelf. This will be accomplished by measuring growth rate and $CaCO_3$ production by *Halimeda incrassata*, one of the most common species found on soft-bottom ecosystems along this coast. These data will provide a better understanding of the processes acting on the sediment budget in this area. They'll also allow a better comprehension of one of the forces that shaped the Brazilian northeastern continental shelf through the Holocene (Testa and Bosence, 1999; Gomes et al., 2015). Finally, we aim to provide baseline data on the production of offshore *Halimeda* beds, located in open waters at relatively large depths, which remains poorly studied worldwide.

2. Materials and methods

The study was conducted on algal meadows located on the eastern province of the Brazilian equatorial margin, 22.2 km offshore (03°59′S, 037°59′W), at depths of 25 m (Fig. 1).

The region has a semi-arid to sub-humid climate (BSh to Aw in Köppen classification), with rains concentrated between February and June. *Halimeda incrassata* annual growth rate and calcium carbonate production were estimated in two field campaigns, one in May and another in August 2013, covering both rainy and dry seasons. The distance to the coast and unpredictable adverse sea conditions prevented additional campaigns. However, climatic conditions are sufficiently homogeneous in the whole ESA. The climate's intra-annual variability is basically restricted to seasonal changes in rainfall and wind speed (Hastenrath and Heller, 1977; Philander and Pacanowski, 1986; Werner and Gerstengarbe, 2003; Polzin and Hastenrath, 2014). Furthermore, the main distribution area of *H. incrassata* is between 20 and 40 m deep (Kempf, 1970). This depth range tends to have relatively stable conditions of temperature and salinity, being situated outside the influence of both fluvial and oceanic water masses (Dias et al., 2013). Accordingly, environmental conditions known to affect *Halimeda* development - temperature, light, nutrients and water movement (Hudson, 1985; Littler et al., 1988; Wolanski et al., 1988; Vroom et al., 2003; Yñiguez et al., 2008) - seem to be relatively stable within each season in this area. Therefore, we consider that the replicate sampling effort can produce sufficiently accurate annual estimates of growth and $CaCO_3$ production.

Halimeda incrassata growth rate was measured by staining algae with Alizarin Red S, following a methodology adapted from Vroom et al. (2003). In each campaign, by means of SCUBA diving, at least 30 healthy mature individuals - defined as all branches arising from a single holdfast - were covered with 5L transparent plastic bags containing 1 mL of Alizarin Red S 1% solution. Each alga remained 24 h in contact with dye before the bags were removed. The algae were harvested 17 and 12 days after the staining, respectively in the first and second campaign.

The harvested algae were cleaned to remove epiphytes and sand, and submerged in sodium hypochlorite (NaOCl) solution to accentuate color contrast. Due to the bleaching effect of NaOCl, old segments remained pink while new ones became white. The number of segments was counted, and growth rate was measured by dividing the number of new segments by the number of days between staining and harvesting.

Mean algal mass was measured after drying the algae at 60 °C until constant weight was reached (approximately 48 h). Segment mass was calculated by dividing algal mass by the number of segments. Calcium carbonate percentage was calculated as the difference between the dry weight of fresh and decalcified individuals with HCl solution (0.1 M). The absolute density of the segments was calculated as the ratio between mass and volume, which was measured as the amount of water displaced by a given alga dry mass in a graduated cylinder.

The number of individuals per square meter (i.e. algal coverage) was measured in 50×50 cm quadrats distributed haphazardly over the algal meadow, but outside the area used for the growth experiment. At least 15 quadrats were used per campaign. In each sample all visible individuals were counted to estimate the number of algae per square meter.

Finally, from these measurements, biomass, population turnover time, $CaCO_3$ production, and potential sedimentation rate were estimated. Population descriptors and estimates were annualized by pooling together the values from both months.

3. Results

Discontinuous algal meadows were found growing on deposits of $CaCO_3$-rich sediments, covering large areas of the substrate, particularly bellow 20 m deep. With the exception of epibionts (mostly brown algae and hydrozoa), these meadows were composed exclusively of *Halimeda incrassata*. This alga grew attached by large bulbous holdfasts and often formed dense aggregations, stabilizing the substrate. Visually, *H. incrassata* debris are ubiquitous on the area, at least in the upper layers of the substrate. Measured descriptors of this population are summarized in Table 1 and the parameters estimated from these descriptors in Table 2.

Individual growth rate ranged from 0 to 15.17 (Fig. 2) new segments produced per day, and was usually higher in the rainy season (Fig. 3a). On the other hand, the number individuals varied from 4 to 724 individuals.m^{-2}, being higher in the dry season (Fig. 3b).

Multiplying average algal coverage by the mean algal mass, it was calculated an algal biomass of 214.02 g.m^{-2}. Additionally, multiplying algal coverage by growth rate, it was estimated that