



# Diurnal effects of *Holothuria atra* on seawater carbonate chemistry in a sedimentary environment



Francisco Vidal-Ramirez<sup>a,b,\*</sup>, Sophie Dove<sup>a,b,c</sup>

<sup>a</sup> School of Biological Sciences, The University of Queensland, St. Lucia, QLD 4072, Australia

<sup>b</sup> ARC Centre of Excellence for Coral Reef Studies, The University of Queensland, St. Lucia, QLD 4072, Australia

<sup>c</sup> Global Change Institute, The University of Queensland, St. Lucia, QLD 4072, Australia

## ARTICLE INFO

### Article history:

Received 10 March 2015

Received in revised form 18 September 2015

Accepted 15 October 2015

Available online 30 October 2015

### Keywords:

*Holothuria atra*

Sediments

Dissolution

Calcium carbonate

Diurnal

## ABSTRACT

Sea cucumbers are important to coral reef ecosystems due to their roles in the recycling of nutrients and their potential ability to elevate  $A_T/DIC$  by the dissolution of sediments in their gut. The contribution of the sea cucumber *Holothuria atra* to the dissolution of sediment  $CaCO_3$  was assessed at mid-day and midnight. The results showed that the presence of *H. atra* significantly increases sediment dissolution rates and Total Ammonia Nitrogen ( $TAN = NH_3 + NH_4^+$ ) concentrations. While there was a trend for the effect of *H. atra* on sediment dissolution to be greater during the day than at night, this trend was not significant. Significantly different day versus night responses – irrespective of sea cucumber presence – were observed for all carbonate parameters over the 1–2 h incubation periods, reflecting an impact of sediment-associated micro-organisms in closed recirculating as opposed to open water systems over a period of three days (cumulative effect). Over three days, the significantly higher daytime DIC concentrations in the presence of *H. atra* were driven by elevated bicarbonate ( $HCO_3^-$ ). During the incubation periods, the effects of the animals on DIC concentration were lost by a significant increase in  $CO_2$  concentrations arguably by microbial processes within the sediments. The ocean acidification (OA) buffering capacity of the animals, estimated by changes in  $A_T/DIC$  ratios, was greater during nighttime but equivalent to that observed in the sediments over the incubation periods and in the open water system. The results suggest that *H. atra* not only will not assist daytime calcification, given by a decrease in buffering capacity at daytime, but also may exacerbate the impacts of OA due to the dissolution of  $CaCO_3$  resulting from their turnover of sediments. Finally, in areas with seawater with prolonged residence over sediments, such as ponding lagoons, the local environment is likely to rapidly deplete any pH buffering potential offered by *H. atra*.

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## 1. Introduction

Coral reefs are able to rebuild and amass calcium carbonate following destructive storm events because the rate of calcification exceeds the rate of erosion (Eyre et al., 2014; Perry et al., 2008, 2013; Scoffin et al., 1980) over the long term. Increases in atmospheric  $CO_2$  leading to both ocean warming and ocean acidification have the potential to increase rates of erosion above those of calcification (Dove et al., 2013). The potential shift to a negative carbonate balance on reefs threatens the 3D frameworks that provide habitat for the large diversity of organisms found on reefs today (Bellwood et al., 2004; Connell and Kingsford, 1998), and may reduce coastal protection offered by reefs through a reduction in wave energy attenuation (Ferrario et al., 2014; Hoegh-

Guldborg et al., 2007). Over millennium timescales, calcium carbonate dissolution in the presence of water and  $CO_2$  will take up much of the  $CO_2$  that is currently being vented to the atmosphere as burnt fossil fuels (Archer et al., 1997). In this reaction, solid carbonates will convert to aqueous bicarbonates increasing total ocean alkalinity. The reaction time is predicted to occur over millennia, because it is limited by the dynamics of the ocean carbon cycle (Archer et al., 1997). In these global models, the contribution of coral reefs to fossil fuel neutralization is considered to be insignificant in comparison to the role played by abyssal sediments (Archer et al., 1997).

At the local reef scale, however, it has been proposed that the activities of high density Holothurians (sea cucumbers) may increase the ability of ponding lagoons to buffer pH as a result of gut sediment dissolution and ammonia production (Schneider et al., 2011, 2013). It is argued that as a result of dissolution of  $CaCO_3$  due to sea cucumber activity, the rate of increase in local seawater alkalinity is much greater than that associated with either bioeroding endolithic communities or

\* Corresponding author at: School of Biological Sciences, The University of Queensland, Level 7, Gehrman Laboratories, Building #60, St. Lucia, QLD 4072, Australia.  
E-mail address: [f.vidalramirez@uq.edu.au](mailto:f.vidalramirez@uq.edu.au) (F. Vidal-Ramirez).

microbial dissolution of sediments (Schneider et al., 2011). However, despite the efforts made to understand the role of sea cucumbers on these processes, information about how these processes may be modified by these animals in the presence of other organisms, such as microalgae and bacteria, as well as by daily fluctuations in seawater chemistry is presently lacking. Schneider et al. (2011) and Schneider et al. (2013) determined changes to seawater chemistry as the result of the introduction of fecal casts into otherwise empty aquaria (isolated from all other components of the ecosystem) over 4 h daytime incubations with the rate of change in alkalinity measured in filtered reef water. Large increases in alkalinity observed in their experiment were then used to support the case that sea cucumbers may be more effective at buffering localized anthropogenic derived acidification, than the demonstrated negligible ability associated with  $\text{CaCO}_3$  dissolution by either endolithic organisms (Tribollet et al., 2009) or sediment microbial communities (Andersson and Gledhill, 2013; Andersson et al., 2007; Reyes-Nivia et al., 2013).

The ratio between total alkalinity ( $A_T$ ) and dissolved inorganic carbon (DIC),  $A_T/\text{DIC}$ , can be used to estimate the buffering capacity of seawater (Wang et al., 2013). The relationships between buffering capacities and  $A_T/\text{DIC}$  describe 3<sup>rd</sup> polynomial functions. For  $A_T/\text{DIC} \geq 1$ , the present ocean  $A_T/\text{DIC}$  range (1.05–1.19) provides slightly less than maximal buffering capacity, and any reduction in  $A_T/\text{DIC}$  results in a decrease in buffering capacity. The buffering capacity, or the ability of seawater to counteract ocean acidification (OA), reaches a minimum when  $A_T/\text{DIC} = 1$  (Eggleston et al., 2010). The effect of OA on each component (or buffer factors) will depend ultimately on the complexity of acid–base chemistry dictated by changes in DIC and  $A_T$  (Eggleston et al., 2010; Wang et al., 2013). Therefore, these changes in DIC and  $A_T$  can be translated into six buffering factors (or capacities): buffer of  $\text{CO}_2$  due to changes in DIC, buffer of  $\text{H}^+$  (or pH) due to changes in DIC, and buffer of  $\text{CaCO}_3$  saturation state ( $\Omega$ ) due to changes in DIC. The other 3 are represented as buffers of  $\text{CO}_2$ ,  $\text{H}^+$  and  $\Omega$  due to changes in alkalinity (Eggleston et al., 2010). As a result, an increase in  $A_T$  does not necessarily mean that seawater will be less sensitive to changes in  $\text{CO}_2$ , pH or  $\Omega$ .

In reef sediments, sea cucumbers and sediment-associated microorganisms are able to modify the concentration of nutrients and carbonate parameters (Andersson and Gledhill, 2013; Andersson et al., 2007; Capone et al., 1992; Uthicke, 2001). This complex environment will interact with stressors, such as ocean acidification (OA), changes to nutrient loads and warming, to affect  $A_T/\text{DIC}$  ratios by modifying organism metabolism and/or organism community structure. As a first step to understanding the potential for sea cucumbers to buffer OA, it is fundamentally important to gain an understanding of their role on the seawater carbonate chemistry in an interacting environment where other organisms found within the system contribute to dissolution and alkalinity. The capacity of sea cucumbers, if any, to buffer OA will depend not just on their impact on the water column, but also on the ability of co-located microbes to alter  $A_T/\text{DIC}$ . The facilitation of reef calcification by sea cucumber OA buffering is unlikely in reef locations subjected to high rates of water flow. Most reefs (unlike micro-atolls such as those within the lagoon at One Tree Island) are well flushed and would dilute the potential effect of sea cucumbers on buffering the pH (Andersson et al., 2007; Kleypas and Langdon, 2006; Kleypas and Yates, 2009). But likewise, in closed systems, micro-organisms may rapidly negate the impacts of sea cucumbers on water-column dynamics.

Schneider et al. (2013) found that sediment gut dissolution by *Holothuria atra* accounted for roughly 75% of the increase in alkalinity with the remaining quotient attributed to the production of ammonia and its protonation to ammonium. By day, however, proton uptake following rapid oxidation of Total Ammonia Nitrogen ( $\text{TAN} = \text{NH}_3 + \text{NH}_4^+$ ) by nitrifying photo-autotrophic bacteria in the sea cucumber aerated sediments, as well as rapid ammonia uptake by benthic micro-algae living on the surface of the sediments, ought to rapidly counter and/or inhibit TAN induced alkalinity changes within reef lagoons. Likewise, daytime increase in alkalinity by gut

sediment digestion would have to be significantly greater than net daytime DIC production by either sea cucumbers or benthic organisms associated with the sediments to prevent high  $p\text{CO}_2$  build up in the ponding water column (Sabine et al., 2004; Revelle and Suess, 1957). Clearly by day,  $A_T/\text{DIC}$  may be elevated by photosynthetic  $\text{CO}_2$  fixation by local photoautotrophs, combined with sediment dissolution, leading to a greater proportion of  $\text{CO}_3^{2-}$  ions for the immediate uptake by adjacent calcareous organisms such as corals or, more likely, green calcareous algae of genus *Halimeda* (Borowitzka and Larkum, 1976; De Beer and Larkum, 2001) that prosper in lagoons where sea cucumbers are present at higher densities (Chao et al., 1993; Conand, 1996; Lee et al., 2008). However, by night, DIC production may significantly increase, reducing  $A_T/\text{DIC}$  ratios. Furthermore at night, sea cucumbers may be active, but not feeding (e.g. species such as *Stichopus chloronotus* do not feed during nighttime, see Uthicke, 1994), although this is not the case for the species *H. atra* that feeds constantly (feeding rates are not significantly different for daytime or nighttime, see Uthicke, 1994). The feeding behavior of *H. atra* implies that the production of  $\text{CO}_3^{2-}$  due to dissolution might be mitigated by the uptake and production of  $\text{CO}_2$  from different organisms in the sediments at these different time points. Under these different conditions, the impact of sea cucumbers on the capacity to buffer pH may be much less than that suggested by previous observations of their ability to increase seawater alkalinity, as buffering is determined by the  $A_T/\text{DIC}$ , and sea cucumbers may stimulate other processes in the system to produce DIC.

This study investigates the influence of tropical deposit feeding sea cucumbers on the dissolution of  $\text{CaCO}_3$  and local water chemistry, including their pH buffering potential, using *H. atra* as model species. The animals were placed in similar conditions to those they might experience on the reef in terms of daily changes in production (modulated by fluctuations in natural light, temperature,  $p\text{CO}_2$ , among others). The potential effect of this species on the sediment grain size, as a direct measure of dissolution of  $\text{CaCO}_3$ , was also investigated.

## 2. Material and methods

### 2.1. Experimental setup

Six individuals of the species *H. atra* (weight  $237.9 \pm 35.71$  g and length of  $21.22 \pm 1.65$  cm), along with sediments from Heron Island reef ( $23^\circ 27' \text{ S}$ ,  $151^\circ 55' \text{ E}$ ) were collected in January (2013) from the Reef flat (in front of the HIRS, within the Scientific Research Zone) and the Lagoon ( $23^\circ 26' 550'' \text{ S}$ ,  $151^\circ 56' 629'' \text{ E}$ ), over a tidally variable depth range of 0.5–5 m. Samples were placed in plastic buckets and immediately transported to the nearby Heron Island Research Station. Each animal was placed into a separate outdoor flow through aquaria and left for 48 h to allow for the expulsion of fecal pellets (which were removed periodically to avoid re-ingestion). Meanwhile, the sediments were mixed and evenly distributed to create a sediment depth of 3 cm across 12 glass aquaria ( $58.3 \text{ cm} \times 18 \text{ cm} \times 37.2 \text{ cm}$ ) lined with Marine Blue light filters (#131; Lee Filters). A pump (Hydor Koralia Nano 900) with a capacity to recirculate 900 L of seawater per hour was placed into each aquarium and the flow rate within each tank was set at  $1 \text{ L min}^{-1}$ . Animals with empty guts were randomly assigned to these glass aquaria resulting in a final design of 6 aquaria with sediments and sea cucumbers (Condition +SC, or +SC tanks), and 6 aquaria with sediments and no sea cucumbers (Condition –SC, or –SC tanks). Animals were allowed to stay for 1 day in aquaria with sediments before the measurements started. Seawater was pumped directly from the reef flat to these aquaria with fluctuating temperatures between  $24^\circ \text{ C}$  and  $32^\circ \text{ C}$  during incubations periods (recorded every 1 min with HOBO pendant water resistant loggers inside the aquaria). The experiment was conducted through the course of 6 days (3 days acclimation period and 3 days for incubations).

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