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The response of a natural phytoplankton community from the Godavari River Estuary to increasing CO_2 concentration during the pre-monsoon period

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ABSTRACT

This paper reports for the first time upon the effects of increasing CO_2 concentrations on a natural phytoplankton assemblage in a tropical estuary (the Godavari River Estuary in India). Two short-term (5-day) bottle experiments were conducted (with and without nutrient addition) during the pre-monsoon season when the partial pressure of CO_2 in the surface water is quite low. The results reveal that the concentrations of total chlorophyll, the phytoplankton growth rate, the concentrations of particulate organic matter, the photosynthetic oxygen evolution rates, and the total bacterial count were higher under elevated CO_2 treatments, as compared to ambient conditions (control). $\delta^{13}C$ of particulate organic matter (POM) varied inversely with respect to CO_2, indicating a clear signature of higher CO_2 influx under the elevated CO_2 levels. Whereas, $\delta^{13}C_{POM}$ in the controls indicated the existence of an active bicarbonate transport system under limited CO_2 supply. A considerable change in phytoplankton community structure was noticed, with marker pigment analysis by HPLC revealing that cyanobacteria were dominant over diatoms as CO_2 concentrations increased. A mass balance calculation indicated that insufficient nutrients (N, P and Si) might have inhibited diatom growth compared to cyanobacteria, regardless of increased CO_2 supply. The present study suggests that CO_2 concentration and nutrient supply could have significant effects on phytoplankton physiology and community composition for natural phytoplankton communities in this region. However, this work was conducted during a non-discharge period (nutrient-limited conditions) and the responses of phytoplankton to increasing CO_2 might not necessarily be the same during other seasons with high physicochemical variability. Further investigation is therefore needed.

1. Introduction

The projected rise in atmospheric CO_2 has the potential to affect the marine ecosystem in various ways and at different magnitudes (Wolf-Gladrow et al., 1999; Doney et al., 2009). The global ocean is a significant sink for atmospheric CO_2, currently absorbing almost one-third of it (Sabine et al., 2007). As a consequence, surface ocean carbonate chemistry is considerably affected (direct impact), resulting in redistribution of inorganic carbon species (Brewer, 1997; Raven et al., 2005). On the other hand, increasing mean global temperature is likely to cause enhanced sea surface temperature (SST), resulting in warmer surface seawater mass, redistribution of isotherms, reduced upwelling, and greater light penetration (indirect impact) (Raven et al., 2005). Thus, either directly or indirectly, there is a strong possibility that the projected changes will affect marine phytoplankton physiology (primary production, nitrogen fixation, calcification etc.), taxonomic composition (floristic change) and geographic distribution (Boyd and Doney, 2002; Bopp et al., 2001; Raven et al., 2005; Boyd et al., 2010).

The responses of marine phytoplankton to increasing CO_2 are not yet fully understood. The marine phytoplankton community comprises diverse groups from different geographic locations, each possessing its own unique ecophysiology and biogeography. During the last decade, numerous discrete studies have been conducted on marine phytoplankton (laboratory pure cultures, shipboard and field experiments) to test the effects of increasing CO_2 and a wide range of responses have been observed (Doney et al., 2009; Riebesell, 2004; Riebesell et al., 2008). While increased primary production under high CO_2 conditions has been observed in marine phytoplankton assemblages from many different regions of the world's oceans (Chen and Gao, 2003; Hein and Sand-Jensen, 1997; Hare et al., 2007; Feng et al.,

Abbreviations: DIC, Dissolved inorganic carbon; DIN, Dissolved inorganic nitrogen; DIP, Dissolved inorganic phosphate; CCM, Carbon concentrating mechanism; POM, Particulate organic matter; POC, Particulate organic carbon; PON, Particulate organic nitrogen.

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2009; Leonardos and Geider, 2005; Tortell et al., 2008), numerous other studies have shown no such enhancement (Delille et al., 2005; Yoshimura et al., 2009). The non-heterocystous marine nitrogen-fixer *Trichodesmium* has been found to show considerably higher carbon and nitrogen fixation rates when incubated under elevated pCO_2 levels (Barcelos et al., 2007; Hutchins et al., 2007; Levitan et al., 2007). In contrast, the heterocystous nitrogen-fixing cyanobacteria *Nodularia spumigena* (from the Baltic Sea) has shown reduced cell division and nitrogen fixation rates when supplied with higher DIC (Czerny et al., 2009). Reduced calcification in marine calcifying phytoplankton is a well-established response to reduced pH (Riebesell et al., 2009).

Shifts in phytoplankton community composition in response to rising CO_2 have been shown to be significant but highly varied across a diverse range of geographical regions (Kim et al., 2006; Tortell et al., 2002; Tortell et al., 2008; Yoshimura et al., 2009). Additionally, in combination with changing carbonate chemistry, presence of the major nutrients also plays a vital role in determining the taxonomic composition of marine phytoplankton, depending on their nutritional preference, demand and uptake efficiency (Riebesell, 2004). However, the key reasons for the observed differences in behavioral response of marine phytoplankton to increasing CO_2 are still not clear. They are assumed to be related to carbon metabolism pathways and cellular energy distribution (Giordano et al., 2005; Rost et al., 2008).

It has been proposed in the past that, in the marine environment, phytoplankton photosynthesis is limited by CO_2 supply, and that open ocean pCO_2 ranges cannot satisfy even half the saturation level of the carbon-fixing enzyme RuBisCO (Riebesell et al., 1993). Moreover, RuBisCO in general has a very low affinity for CO_2 (Badger et al., 1998), and so to enhance the DIC supply at the carboxylation site of the cell, most marine phytoplankton have developed an active carbon concentration mechanism (CCM), which involves the active uptake of CO_2 and HCO_3^-, or only HCO_3^-, (Giordano et al., 2005) at the cost of energy (Raven and Johnston, 1991). In parallel, there is also continuous diffusive loss of CO_2 from the cell. The uptake of CO_2 in groups of phytoplankton without active CCM occurs mainly by diffusive transport across the cell membrane. Under the scenario of increasing CO_2, the enhanced external CO_2 concentration may lead to a simultaneous enhancement in diffusive CO_2 supply inside the cell and decreased diffusive loss of CO_2 from the cell. This may slow down CCM activity, resulting in the saving and reallocation of cellular energy (Fridlyand et al., 1996; Giordano et al., 2005; Rost et al., 2008), and hence faster growth (Tortell et al., 2008). Previous studies have shown that some groups of phytoplankton possess highly efficient CCMs and might not show any alteration in growth and primary production under elevated CO_2 (Cassar et al., 2004; Rost et al., 2003).

In contrast to open-ocean phytoplankton, estuarine phytoplankton production is not limited by nutrients or CO_2, but mainly by light penetration due to heavy suspended sediment load in the estuarine water. Tropical estuaries and coastal regions are places of huge material flux, with high turnover rates of the major elements (C, N, P), mainly because of extensive biological activity (both autotrophic and heterotrophic). Therefore, these areas exert great control over the global carbon cycle. Summer-monsoon-induced heavy precipitation and river discharge are largely responsible for controlling the biogeochemistry of tropical estuaries. Huge amounts of organic matter, suspended sediment and nutrients from agricultural and anthropogenic sources are delivered into estuarine systems, leading to partial or complete heterotrophic conditions (characterized by high pCO_2 values in the water column) (Biswas et al., 2004; Mukhopadhyay et al., 2002; Sarma et al., 2009, Bouillon et al., 2003). In contrast, non-discharge (pre-monsoon) periods (April–June) are mostly characterized by low levels of nutrients and low pCO_2 (created by enhanced autotrophy due to increased light penetration), which can limit phytoplankton production. Under the scenario of increasing atmospheric CO_2 levels, it is possible that tropical estuarine phytoplankton communities may not show any alteration in growth and primary production when CO_2 is not the limiting factor, i.e. mainly during monsoon and post-monsoon months. In contrast, during the non-discharge pre-monsoon period, when CO_2 can be limiting, phytoplankton communities may show a response to increased CO_2 availability, and this response could potentially have an influence on the biological carbon pump in the estuary.

There is virtually no literature available regarding the above notion, and there is a particular lack of research focusing on the Indian subcontinent, which of course harbors one of the largest river systems in the world. To address this gap, the present study, which was conducted in the Godavari River Estuary in India, aimed to fulfill the following objectives: 1) to investigate whether CO_2 and nutrient supply can limit growth and primary production of the natural phytoplankton community during the pre-monsoon period; and 2) to study the impact of increasing CO_2 on the phytoplankton community.

2. Study site

The sampling site was chosen in the mixing zone of the Godavari River Estuary, almost 30 km upstream from the Bay of Bengal (Fig. 1). The Godavari River is one of the major rivers in the east coast region of India and supplies a huge amount of nutrients and organic load to the Bay of Bengal (Gupta et al., 1997). Monsoonal run-off and river discharge coupled with turbidity, light penetration and nutrient availability, are the key factors controlling the biogeochemistry of this estuary (Sarma et al., 2009). Most tropical estuaries are eutrophic, acting as a source of atmospheric CO_2. However, as mentioned above, during the non-discharge pre-monsoon period, major nutrients (N, P, Si) and low pCO_2 might limit phytoplankton primary production. Usually, during May–June (pre-monsoon), discharge in the Godavari River ceases. Coupled with no precipitation, the estuary thus becomes an area of negative water balance (evaporation exceeds precipitation), leading to the occurrence of low-nutrient, high-saline water. Restricted river discharge also limits the supply of organic carbon loads (particulate and dissolved) to the estuary, resulting in bacterial respiration being lower than autotrophic production. Consequently, the rate of dissolved inorganic carbon removal from the surface water by photosynthetic activity exceeds the production of CO_2 by heterotrophic activity, resulting in comparatively low pCO_2 conditions (Bouillon et al., 2003; Sarma et al., 2009). At the same time, high levels of salinity decrease the carbon dioxide solubility in the water. On an annual scale, diatoms are the dominant group of phytoplankton, along with some nitrogen-fixing cyanobacteria, dianoflagellates, and green algae.

3. Materials and methods

3.1. Sample collection and experimental setup

As described above, the pre-monsoon season was chosen for this investigation because of the occurrence of high salinity, low nutrients, and low pCO_2 in the water column, which could all limit phytoplankton primary production. During May and June, 2009 (when river discharge had ceased completely), estuarine surface water was collected in 20 L polycarbonate carboys (Nalgene) from Yanam, the mixing zone of the Godavari River (Fig. 1) and taken immediately back to the laboratory. 5.6 L borosilicate screw-capped bottles were used for further incubation. CO_2 levels were manipulated by adding base and acid following the methodology of Riebesell et al. (2010). Among the processes available for manipulating CO_2 levels in seawater, this method has been recommended as the best for small-volume bottle experiments. After adjusting the pCO_2, the bottles were incubated in triplicates for each CO_2 level in a water bath under ambient light conditions for 5 days. A set of controls was also kept in triplicates without changing the carbon chemistry. Each bottle was mixed very gently every day to avoid any sedimentation of the