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Primary production and respiration of hypersaline microbial mats as a response for high and low CO₂ availability

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BGD

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**Hypersaline
microbial mats
response for CO₂
availability**

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Abstract

Here we report a time series of experiments performed in a microcosm to test the response of hypersaline microbial mats to diverse atmospheric CO₂ conditions. Different from most part of the literature, our study used a sample chamber where carbon dioxide concentration was controlled. Our aim was to test the effect of different atmospheric CO₂ conditions in benthic gross and net primary production, and respiration. This study showed for the first time to our knowledge absolute carbon limitation in a microbial mat. Oxygen concentration profile varied from a flattened shape to almost linear when atmospheric CO₂ at the chamber reached 0 ppm, with NPP reaching 0 nmol cm⁻³ s⁻¹ throughout most part of the profile. In this conditions sediment community respiration represented 100 % of GPP. Extreme close coupling between primary production and respiration in microbial mats can be even self-sustainable in environments with temporarily no atmospheric CO₂ available. When submitted to even high CO₂ concentrations (550 ppm), our sample showed a characteristic shape that indicate limitation composed by a more rectilinear oxygen profile, and NPP peaks mainly restricted to deeper layers. Therefore, we suggest that phototrophic communities in aquatic shallow ecosystems can be carbon limited. This limitation could be common especially in ecosystems submitted to variable water depth conditions, like coastal lagoons and intertidal sediments.

1 Introduction

Carbon is normally not considered a limiting factor for photosynthesis in aquatic environment (Tortell et al., 2000; Raven and Jhonston, 1991). This is mostly due to the prevalence of heterotrophy and carbon dioxide supersaturation in aquatic ecosystems (Duarte and Prairie, 2005; Marotta et al., 2009) and the ability of microautotrophs, especially cyanobacteria, to use both bicarbonate (HCO₃⁻) and carbon dioxide (CO₂) as carbon source (Raven, 1997). A wide variety of cyanobacteria taxa also uses the well known carbon concentration mechanism to create a CO₂ supersaturated environment

BGD

9, 12735–12755, 2012

Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

around RUBISCO, enhancing the efficiency of the photosynthetic process (Giordano et al., 2005).

Photoautotrophs submitted to extreme conditions like hypersaline lakes, frequently exposed to high pH and oxygen supersaturation can experience carbon limitation (Rasmussen et al., 1983; Hein, 1997), but this limitation is poorly tested in literature. Most part of the studies that test CO₂ limitation and supersaturation influence in the benthic compartment use different pH values to simulate different concentrations of free CO₂ in the water (Jensen and Revsbech, 1989; Glud et al., 1992; Rothschild, 1994; Grotzschel et al., 2002; Cook and Roy, 2006), altering field conditions remarkably. CO₂-enriched air atmosphere impact on primary production was already tested in marine phytoplankton communities (Hein and Sand-Jensen, 1997; Riebesell, 2004; Riebesell et al., 2007; Gao et al., 2012; Low-Decarie et al., 2011; Kremp et al., 2012; Delille et al., 2005; Engel et al., 2005) and in stream ecosystems (Hargrave et al., 2009).

Microbial mats are communities of microorganisms that colonize surfaces, ranging from single layers to multi-layer of a wide diversity of prokaryotes and eukaryotes (Stal, 2001; Franks and Stolz, 2009). In addition to the inner physiological complexity of these communities (Stewart and Franklin, 2008), microbial mats develop under a wide range of environmental conditions (Vangemeren, 1993), including extreme environments like hypersaline coastal lagoons (Bento et al., 2007). This abiotic stress prevent grazing activities (Stal, 2002), but may also have direct effect on the biogeochemistry of the laminated community, since excess salt may affect community diversity and behavior (Oren, 2007).

Small lakes and ponds dominate the areal extent of continental waters (Downing, 2010) and processes occurring in these ecosystems may assume global significance (Downing et al., 2006). Since inland aquatic ecosystems have an important role in global carbon cycle (Tranvik et al., 2009), the study of carbon limitation in tropical shallow ecosystems is of major importance. Furthermore, one of the main stressors of climate change is elevated atmospheric CO₂ concentrations (IPCC, 2007) and this process could have important multiple levels impacts in freshwater ecosystems

BGD

9, 12735–12755, 2012

Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



(Woodward et al., 2010). Here we report the response of hypersaline microbial mats to different CO₂ atmospheric levels. Our aim was to test the effect of high and low atmospheric CO₂ conditions in benthic gross and net primary production, and respiration.

2 Material and methods

2.1 Study area

Visgueiro lagoon (22°11' S and 41°24' W) is located at the Jurubatiba National Park, in the North of Rio de Janeiro state, Brazil (Fig. 1). It is characterized as hypersaline, since its salinity is always higher than the ocean, reaching levels up to 100. Visgueiro is classified as a shallow coastal lagoon orientated parallel to the coast and the balance between ocean water exchange, evaporation and precipitation controls its depth. The studied lagoon water depth is variable, ranging from zero (no water) to 0.5 m.

2.2 Sampling and analysis

Water samples for pelagic parameters measurement were collect with pre-washed (HCl 0.5 M) plastic bottles and are described in Table 1. pH was analyzed with a pHmeter Analion PM 608 and total alkalinity was determined from Gran titration. Temperature and salinity were measured with a Termosalinometer YSI-30.

Sediment samples were collected with Plexiglas cores at Visgueiro Lagoon on January 2005. They were taken right after sampling to a field lab and stabilized with lagoon water before the measurements. The main groups of phototrophs in the samples were identified as diatoms (pennate) and filamentous cyanobacteria (Microcoleus).

2.3 Oxygen profiles and primary production

Sediment oxygen profiles were measured with an oxygen microsensor (OX 25 – 2744, UNISENSE, response time < 100 ms) positioned by a motor-driven micromanipulator

BGD

9, 12735–12755, 2012

Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



and a controller (Encoder Mike Controller 18011, UNISENSE). The microsensor current was measured by a picoammeter (PA 2000, UNISENSE) connected to an A/D converter that transferred the signal to a notebook.

Microbial mat net primary production (NPP) was calculated using the software PRO-FILE (Berg et al., 1998). Gross primary production (GPP) was measured using the oxygen microprofiles technique (Revsbech and Jorgensen, 1983). This method was primarily described by Revsbech et al. (1981) and is based on the determination of oxygen concentrations in several sediment depths during light-dark shifts with an oxygen microsensor. The main premise of this method is that oxygen concentration in the algal biofilm is constant during illumination time and after light shut off, oxygen concentrations decay linearly (Glud et al., 1992). Therefore, photosynthetic rates are measured from the rates of oxygen decrease after 1 or 2 s of dark period that the sample is submitted after light turning off at each depth of the oxygen profile (Revsbech et al., 1986). Sediment integrated respiration rates was calculated as the difference between gross and net photosynthesis depth integrated rates (Jensen and Revsbech, 1989).

2.4 Experimental design

The sample chamber consisted in a 20 ml plastic vial cut diagonally (to avoid condensation and water dripping at the sample), covered by a thin plastic film, so that the atmospheric concentration of CO₂ could be controlled. This plastic film contained a small hole for moving the microsensor that was only pulled out of the plastic vial at the end of each experiment. The CO₂ atmosphere was regulated by a peristaltic pump (IPC Ismatec, IPC-24 V2.03), which controlled the flow of CO₂ and synthetic air (purged with 70 % water and NaOH) to the atmosphere of the chamber. Therefore, the sample was submitted to regular atmospheric concentrations of nitrogen and oxygen, with only CO₂ concentration changes during the experiment.

The concentration of CO₂ at the atmosphere of the sample chamber was calculated based on the linear relationship between different peristaltic pump signals and the time

Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



taken to fill a flat-bottom flask of known volume with synthetic air. The slope was used to convert different signals of the peristaltic pump to CO₂ atmospheric concentration.

The experiments were conducted to evaluate gross and net primary production and respiration at high and low CO₂ concentrations. During the first set of experiments, only high CO₂ concentrations were applied to the mats. During the second set of experiments, a new microbial mat sample was stabilized and low concentrations of CO₂ were applied to the mats associated with different light intensities. The oxygen concentrations were measured at equal depth intervals (0.005 cm). Profiles were performed with the same sediment sample, at the same spot. Several profiles were measured before and after CO₂ or light changes, but only the steady state profiles were used in this study. There were no significant alterations of pH and temperature in the water (7–8 and 25–26 °C, respectively).

The microbial mat samples were 21.5 cm distant from the main light source, a slide projector with no front lenses (Nards Light Express, Halogen, JC 24 V 150 W Bose GY6.35). Photosynthetically active radiation (PAR) was 1.20 μW cm⁻² (planar sensor) and 550 μE (bulb sensor), both 2 mm below water surface. Light reduction was performed by changing slides with different number of black plastic net layers, being corrected for nonlinearity. At high CO₂ concentrations, light was maintained at 550 μE. Low CO₂ concentration experiments were conducted in combination with different light intensities: 550 μE, 204 μE and 157 μE.

3 Results

3.1 High CO₂ concentrations

Changes in CO₂ concentrations altered both oxygen concentration profile and NPP, and in CO₂ concentrations normally considered high (550 ppm) our sample showed a flattened oxygen profile (Fig. 2). This profile shape was maintained at atmospheric CO₂ concentrations (380 ppm) and sediment integrated NPP reached almost negligible

BGD

9, 12735–12755, 2012

Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



values (380 ppm, $0.007 \text{ nmol cm}^{-2} \text{ s}^{-1}$, Fig. 6). In this situation, respiration of the sediment community represented 97 % of GPP (380 ppm, Fig. 6).

In a vertical analysis of oxygen concentrations, NPP and GPP values showed the formation of two different layers (Figs. 2 and 3). The top layer, close to the sediment surface, had the highest oxygen concentration, NPP and GPP peaks at 5000 ppm (438 μM , $6.5 \text{ nmol cm}^{-3} \text{ s}^{-1}$ and $5.2 \text{ nmol cm}^{-3} \text{ s}^{-1}$, respectively). The photosynthetic activity of the top layer decreased with lower CO_2 concentrations at the atmosphere of the sample chamber, reaching lower values of the same parameters at 380 ppm (188 μM , $0.4 \text{ nmol cm}^{-3} \text{ s}^{-1}$ and $1.8 \text{ nmol cm}^{-3} \text{ s}^{-1}$, respectively). The bottom layer, close to the oxic-anoxic interface, had an opposite behavior since its photosynthetic activity was stimulated even with lower CO_2 concentrations at the sample chamber atmosphere. At this layer, NPP was enhanced ca. 78 % from 5000 ppm to 380 ppm (1.8 and $3.2 \text{ nmol cm}^{-3} \text{ s}^{-1}$, respectively) and GPP increased approximately 3.5 times in the same conditions (1.6 and $5.7 \text{ nmol cm}^{-3} \text{ s}^{-1}$, respectively).

3.2 Low CO_2 concentrations

At low CO_2 concentrations, especially when concentrations were changed from 380 ppm to 0 ppm an absolute carbon limitation was imposed to the sediment photoautotrophs in the new mat sample. Oxygen concentration profile switched from a flattened shape characteristic of the first set of experiments to almost linear (Fig. 4), with NPP reaching $0 \text{ nmol cm}^{-3} \text{ s}^{-1}$ throughout most part of the profile (0 ppm; Fig. 4). In this conditions sediment community respiration represented 100 % of GPP (0 ppm, 550 μE ; Fig. 6).

The decrease of incident light increased the efficiency of the photosynthetic process, decreasing respiration and enhancing NPP participation in GPP. This effect was higher at 100 ppm, when respiration decreased 2.4 times (from 0.19 to $0.08 \text{ nmol cm}^{-3} \text{ s}^{-1}$, 550–157 μE ; Fig. 6) and NPP participation in GPP increased from 15 to 26 % (550–157 μE ; Fig. 6). The bottom layer was more affected than the top layer at lower light. At

BGD

9, 12735–12755, 2012

Hypersaline microbial mats response for CO_2 availability

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

100 ppm, a light decrease from 550 to 157 μE caused a 39 and 58 % decrease in NPP and GPP, respectively (Figs. 4 and 5).

4 Discussion

This study showed for the first time to our knowledge absolute carbon limitation in a microbial mat. The linear oxygen profile was a result of a closed cycle between photosynthesis and respiration. Phototrophs were not only limited by CO_2 but also by bicarbonate, since respiration represented 100 % of gross primary production when atmospheric CO_2 was removed from the atmosphere of the sample chamber. In shallow aquatic ecosystems most part of the carbon fixed by phototrophs can be rapidly recycled within the sediment, as confirmed by ^{13}C -labeling (Oakes et al., 2010).

Directly modifications of atmospheric CO_2 concentrations changed considerably oxygen concentration and net primary production profiles at the sediment. When submitted to CO_2 concentrations normally considered high (550 ppm), our sample showed a characteristic shape that indicate limitation composed by a more rectilinear oxygen profile, and NPP peaks mainly restricted to deeper layers. NPP at the bottom layer could be maintained by carbon mineralization at the bottom of the sediment since it is a major source of CO_2 into microbial mats (Glud et al., 1992). The shift to higher CO_2 concentration conditions of our study (5000 and 2000 ppm) modified the oxygen profiles and NPP as well, showing that photosynthetic activity could be stimulated even in extremely high CO_2 concentrations. In communities influenced by sediment microalgae, the limited oxygen and carbon dioxide influx/outflux could be the most important factor controlling primary production rates (Krause-Jensen and Sand-Jensen, 1998). This complex O_2/CO_2 influences the effectiveness of RUBISCO carboxylation, were dominant CO_2 conditions prevail photosynthesis and dominant O_2 conditions prevail photorespiration (Glud et al., 1992).

Light excess can reduce photosynthetic rate (Barsanti and Gualtiere, 2006) and even cause physical damage to the photosynthetic apparatus (Latifi et al., 2009). The

BGD

9, 12735–12755, 2012

Hypersaline microbial mats response for CO_2 availability

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

increase of light penetration can also indirectly enhance sediment respiration due to higher oxygenation of deep sediment layers (Revsbech et al., 1981; Epping and Jorgensen, 1996; Kuhl et al., 1996) and by the respiration of labile compounds excreted by cyanobacteria in light stress conditions (Glud et al., 1999). In the studied ecosystem, microalgae can actively migrate vertically in the sediment (Garciapichel et al., 1994; Kruschel and Castenholz, 1998), searching for a better biogeochemical conditions and a consequently relief of the limiting factors. The downward and upward movement of cyanobacteria can be controlled by excess of light as demonstrated in microbial mats (Kruschel and Castenholz, 1998; Bebout and Garciapichel, 1995) and in intertidal microphytobenthos (Blanchard et al., 2004; Serodio et al., 2008). When submitted to elevated light intensities, deep layers of microbial mats have higher photosynthetic efficiency (Lassen et al., 1992), as confirmed by our data, influencing the migration behavior of phototrophs. Other important controlling factor of the migration behavior could be the limitation by CO₂ (Kromkamp et al., 1998), forcing cyanobacteria to go towards the main source of inorganic carbon in deeper sediment layers. This dual availability of inorganic carbon from above (water column) and below (oxic–anoxic interface) could be the main explanation of the two peaks of net and gross primary production described in our study. This explanation was already suggested by Ibelings and Maberly (1998) in dense cyanobacteria blooms, but the same condition could be also common in aquatic shallow ecosystems like the one described here.

This study indicates the extreme close coupling between primary production and respiration in microbial mats that can be even self-sustainable in environments with no atmospheric CO₂ available. Since the light intensity used in our microcosm study is common in field conditions (especially in the tropics) and the CO₂ concentrations are close to our actual and projected future atmospheric conditions (380 and 550 ppm, respectively), we suggest that phototrophic communities in aquatic shallow ecosystems can be carbon limited. Field studies in a tropical tidal salt flat revealed repeated flattened oxygen profiles during day time (Oliveira et al., 2011), corroborating our suggestion.

This limitation could be common especially in ecosystems submitted to variable water depth conditions, like coastal lagoons and intertidal sediments.

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BGD

9, 12735–12755, 2012

Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Table 1. Water column limnological parameters of Visgueiro lagoon when the microbial mat was sampled.

Visgueiro lagoon	
Salinity	57.4
Temperature (°C)	24.4
Oxygen (mg l ⁻¹ /%)	4.3/69.8
pH	8.94
Alkalinity (u Eq l ⁻¹)	2624
Dissolved organic carbon (mg l ⁻¹)	73.7
Water Chlorophyll (µg l ⁻¹)	1.9
Dissolved phosphorus (µmol l ⁻¹)	0.43
Total phosphorus (µmol l ⁻¹)	2.22
NH ₄ (µmol l ⁻¹)	0.33

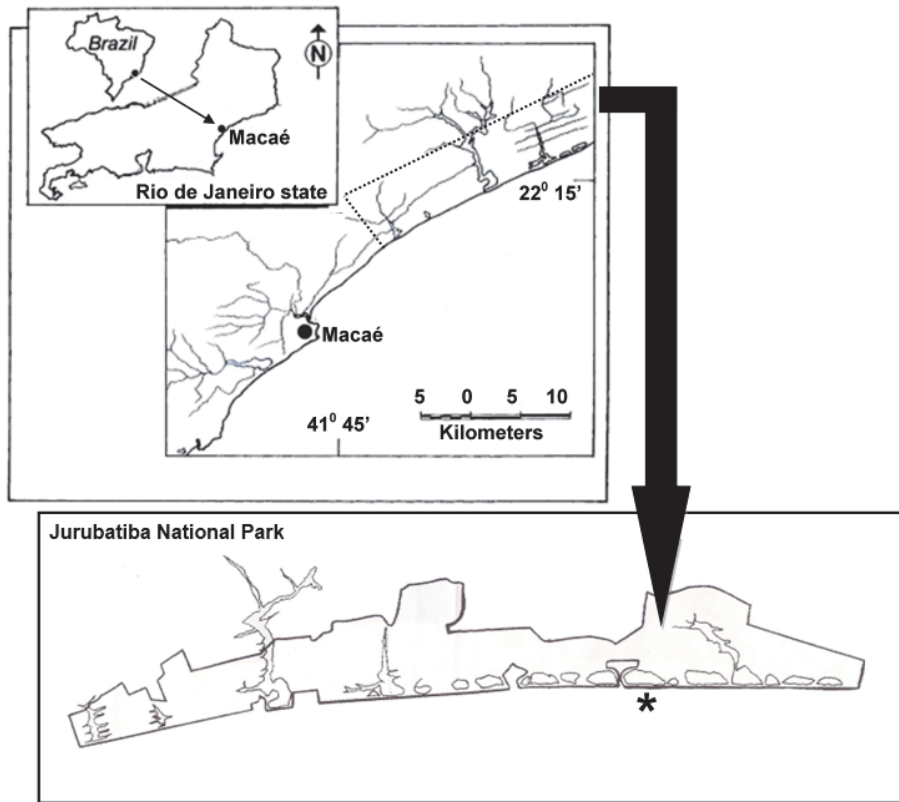


Fig. 1. Geographic localization of the studied area. Visgueiro lagoon is identified by an asterisk.

**Hypersaline
microbial mats
response for CO₂
availability**

L. Bento et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

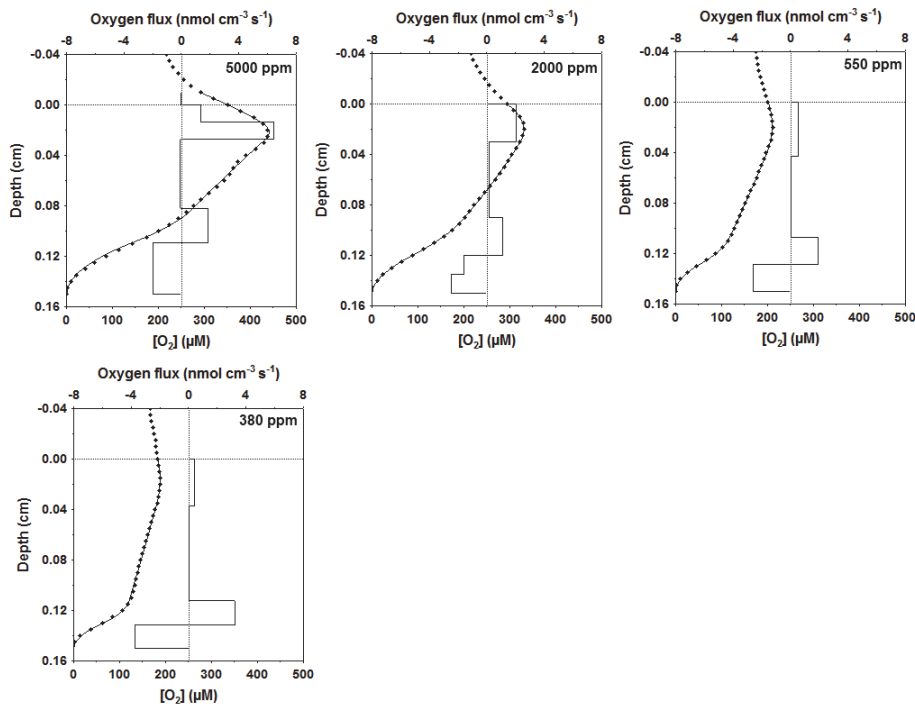


Fig. 2. Measured oxygen concentration (circles), modeled oxygen profile (line connecting circles) and modeled net primary production (NPP, square line) of the first set experiments. All graphs represent steady-state profiles of each treatment. Light is 550 μE for all treatments.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

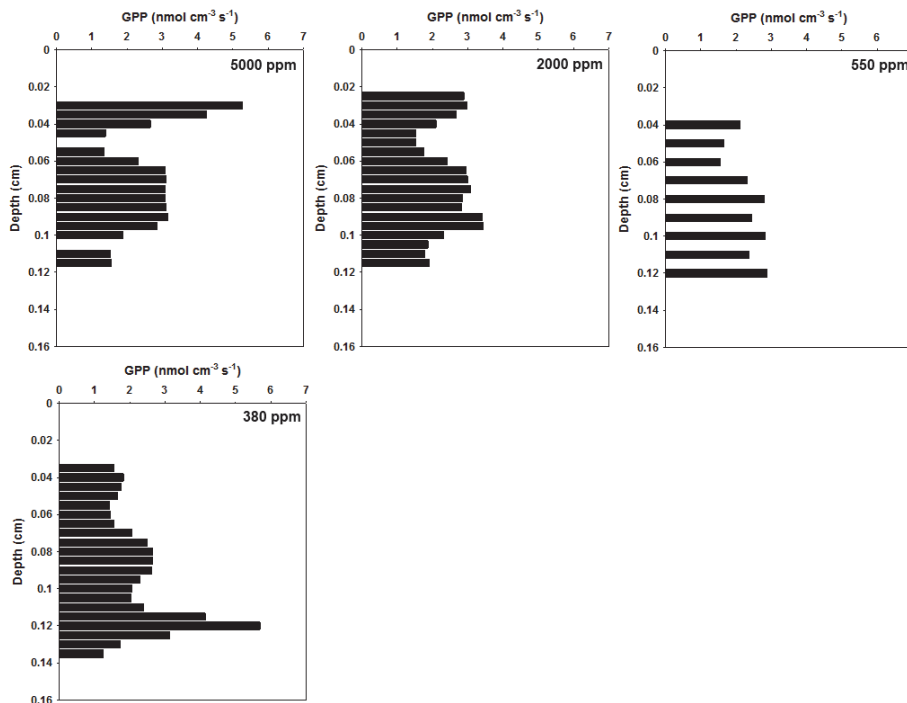


Fig. 3. Steady-state profiles of the microbial mat gross primary production (GPP) submitted to different atmospheric CO₂ concentrations of the first set of experiments. Light is 550 μ E for all treatments.

Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

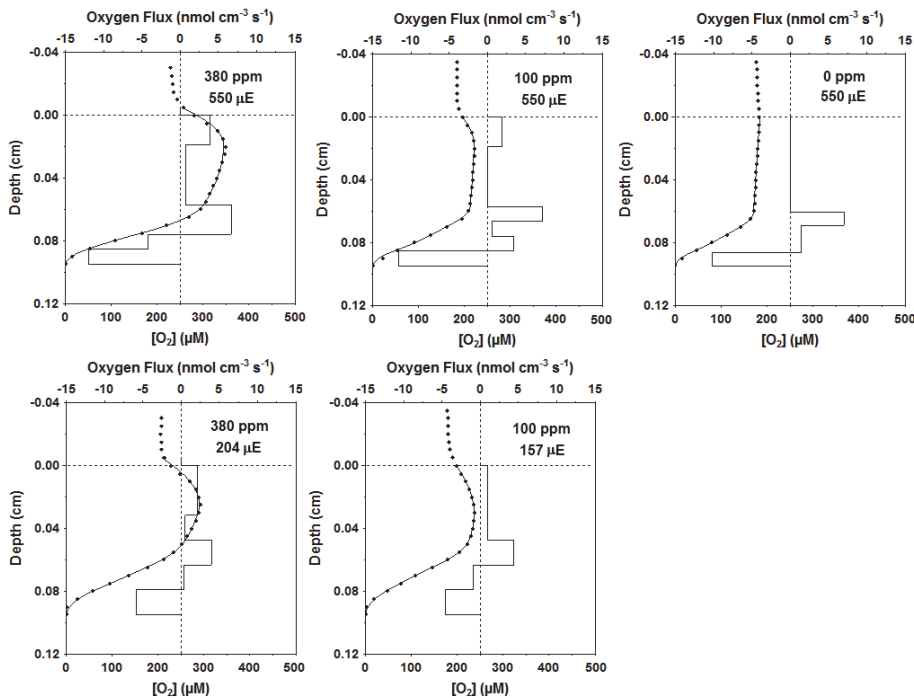


Fig. 4. Measured oxygen concentration (circles), modeled oxygen profile (line connecting circles) and modeled net primary production (NPP, square line) of the second set experiments. All graphs represent steady-state profiles of each treatment.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

⏪ ⏩

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

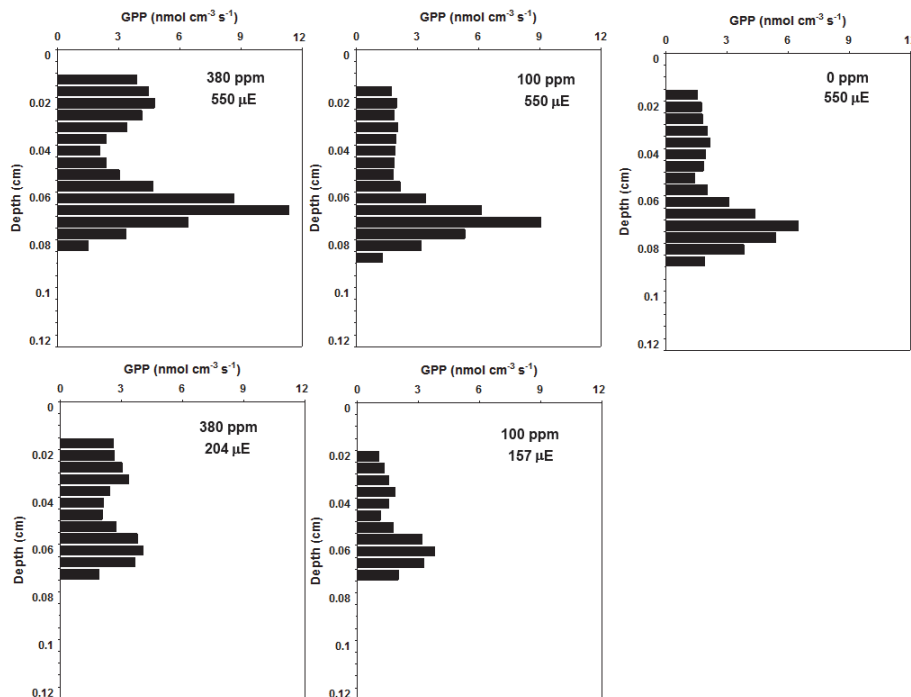


Fig. 5. Steady-state profiles of the microbial mat gross primary production (GPP) submitted to different atmospheric CO₂ concentrations and light of the second set of experiments.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Hypersaline microbial mats response for CO₂ availability

L. Bento et al.

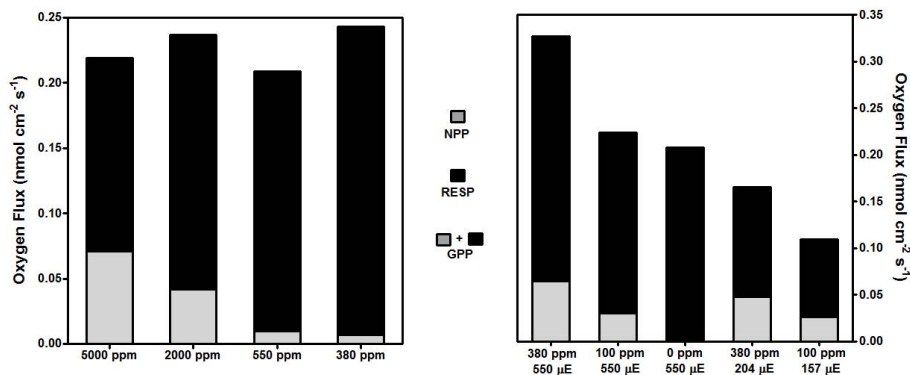


Fig. 6. Depth integrated net primary production (NPP), respiration (R) and gross primary production (GPP) of the microbial mat samples of the two sets of experiments. Each graph represents different mat samples from the same studied area.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion