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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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Received: 16 August 2012 – Accepted: 30 August 2012 – Published: 18 September 2012

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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Abstract

Here we report a time series of experiments performed in a microcosm to test the response of hypersaline microbial mats to diverse atmospheric CO_2 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 CO_2 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 CO_2 at the chamber reached 0 ppm, with NPP reaching $0 \text{ nmol cm}^{-3} \text{ s}^{-1}$ 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 temporally no atmospheric CO_2 available. When submitted to even high CO_2 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 (HCO_3^-) and carbon dioxide (CO_2) as carbon source (Raven, 1997). A wide variety of cyanobacteria taxa also uses the well known carbon concentration mechanism to create a CO_2 supersaturated environment

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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 SandJensen, 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 (Vangemertden, 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

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(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.

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2 Material and methods

5 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 10 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 15 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 20 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

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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 PROFILE (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

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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

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values (380 ppm, 0.007 nmol cm⁻² 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 nmol cm⁻³ s⁻¹ and 5.2 nmol cm⁻³ s⁻¹, respectively). The photosynthetic activity of the top layer decreased with lower CO₂ concentrations at the atmosphere of the sample chamber, reaching lower values of the same parameters at 380 ppm (188 µM, 0.4 nmol cm⁻³ s⁻¹ and 1.8 nmol cm⁻³ 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 CO₂ 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 nmol cm⁻³ s⁻¹, respectively) and GPP increased approximately 3.5 times in the same conditions (1.6 and 5.7 nmol cm⁻³ s⁻¹, respectively).

15 3.2 Low CO₂ concentrations

At low CO₂ 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 20 reaching 0 nmol cm⁻³ 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 nmol cm⁻³ s⁻¹, 25 550–157 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

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).

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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).

Direct 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 Gualtieri, 2006) and even cause physical damage to the photosynthetic apparatus (Latifi et al., 2009). The

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

Acknowledgement. The authors are grateful to CNPq, CAPES and FAPERJ for the financial support and scholarships.

5 References

Barsanti, L. and Gualtieri, P.: Photosynthesis, in: *Algae – Anatomy, Biochemistry, and Biotechnology*, CRC Press, Boca Raton, 135–158, 2006.

Bebout, B. M. and Garciapichel, F.: UVB-induced vertical migrations of cyanobacteria in a microbial mat, *Appl. Environ. Microbiol.*, 61, 4215–4222, 1995.

Bento, L., Guimarães-Souza, B. A., Santoro, A. L., Marotta, H., Esteves, F. A., and Enrich-Prast, A.: Microphytobenthic primary production of two tropical shallow lagoons using oxygen micro-sensors, *Acta Limnol. Brasil.*, 19, 101–107, 2007.

Berg, P., Risgaard-Petersen, N., and Rysgaard, S.: Interpretation of measured concentration profiles in sediment pore water, *Limnol. Oceanogr.*, 43, 1500–1510, 1998.

Blanchard, G. F., Guarini, J., Dang, C., and Richard, P.: Characterizing and quantifying photoinhibition in intertidal microphytobenthos, *J. Phycol.*, 40, 692–696, 2004.

Cook, P. L. M. and Roy, H.: Advective relief of CO₂ limitation in microphytobenthos in highly productive sandy sediments, *Limnol. Oceanogr.*, 51, 1594–1601, 2006.

Delille, B., Harley, J., Zondervan, I., Jacquet, S., Chou, L., Wollast, R., Bellerby, R. G. J., Frankignoulle, M., Borges, A. V., Riebesell, U., and Gattuso, J. P.: Response of primary production and calcification to changes of *p*CO₂ during experimental blooms of the coccolithophorid *Emiliania huxleyi*, *Global Biogeochem. Cy.*, 19, Gb2023, doi:10.1029/2004GB002318, 2005.

Downing, J. A.: Emerging global role of small lakes and ponds: little things mean a lot, *Limnetica*, 29, 9–24, 2010.

Downing, J. A., Prairie, Y. T., Cole, J. J., Duarte, C. M., Tranvik, L. J., Striegl, R. G., McDowell, W. H., Kortelainen, P., Caraco, N. F., Melack, J. M., and Middelburg, J. J.: The global abundance and size distribution of lakes, ponds, and impoundments, *Limnol. Oceanogr.*, 51, 2388–2397, 2006.

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Duarte, C. M. and Prairie, Y. T.: Prevalence of heterotrophy and atmospheric CO₂ emissions from aquatic ecosystems, *Ecosystems*, 8, 862–870, doi:10.1007/s10021-005-0177-4, 2005.

Engel, A., Zondervan, I., Aerts, K., Beaufort, L., Benthien, A., Chou, L., Delille, B., Gattuso, J. P., Harley, J., Heemann, C., Hoffmann, L., Jacquet, S., Nejstgaard, J., Pizay, M. D., Rochelle-
5 Newall, E., Schneider, U., Terbrueggen, A., and Riebesell, U.: Testing the direct effect of CO₂ concentration on a bloom of the coccolithophorid *Emiliania huxleyi* in mesocosm experiments, *Limnol. Oceanogr.*, 50, 493–507, 2005.

Epping, E. H. G. and Jorgensen, B. B.: Light-enhanced oxygen respiration in benthic phototrophic communities, *Mar. Ecol-Prog. Ser.*, 139, 193–203, doi:10.3354/meps139193,
10 1996.

Franks, J. and Stoltz, J. F.: Flat laminated microbial mat communities, *Earth-Sci. Rev.*, 96, 163–172, doi:10.1016/j.earscirev.2008.10.004, 2009.

Gao, K., Xu, J., Gao, G., Li, Y., Hutchins, D. A., Huang, B., Wang, L., Zheng, Y., Jin, P., Cai, X.,
15 Haeder, D.-P., Li, W., Xu, K., Liu, N., and Riebesell, U.: Rising CO₂ and increased light exposure synergistically reduce marine primary productivity, *Nature Clim. Change*, 2, 519–523, doi:10.1038/nclimate1507, 2012.

Garciapichel, F., Mechling, M., and Castenholz, R. W.: Diel migrations of microorganisms within a benthic, hypersaline mat community, *Appl. Environ. Microbiol.*, 60, 1500–1511, 1994.

Giordano, M., Beardall, J., and Raven, J. A.: CO₂ concentrating mechanisms in algae: mechanisms, environmental modulation, and evolution, *Annu. Rev. Plant Biol.*, 58, 99–131, 2005.

Glud, R. N., Ramsing, N. B., and Revsbech, N. P.: Photosynthesis and photosynthesis-coupled respiration in natural biofilms quantified with oxygen microsensors, *J. Phycol.*, 28, 51–60,
20 1992.

Glud, R. N., Kuhl, M., Kohls, O., and Ramsing, N. B.: Heterogeneity of oxygen production and consumption in a photosynthetic microbial mat as studied by planar optodes, *J. Phycol.*, 35, 270–279, 1999.

Grotzschel, S., Abed, R. M. M., and de Beer, D.: Metabolic shifts in hypersaline microbial mats upon addition of organic substrates, *Environ. Microbiol.*, 4, 683–695, 2002.

Hargrave, C. W., Gary, K. P., and Rosado, S. K.: Potential effects of elevated atmospheric carbon dioxide on benthic autotrophs and consumers in stream ecosystems: a test using experimental stream mesocosms, *Global Change Biol.*, 15, 2779–2790, 2009.

Hein, M.: Inorganic carbon limitation of photosynthesis in lake phytoplankton, *Freshwat. Biol.*, 37, 545–552, 1997.

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Hein, M. and Sand-Jensen, K.: CO₂ increases oceanic primary production, *Nature*, 388, 526–527, 1997.

Ibelings, B. W. and Maberly, S. C.: Photoinhibition and the availability of inorganic carbon restrict photosynthesis by surface blooms of cyanobacteria, *Limnol. Oceanogr.*, 43, 408–419, 1998.

5 IPCC: The physical sciences basis, in: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Parry, M., Canziani, O., Palutikof, J., Van der Linden, P., and Hanson, C., Cambridge University Press, Cambridge, 2007.

10 Jensen, J. and Revsbech, N. P.: Photosynthesis and respiration of a diatom biofilm cultured in a new gradient growth chamber, *FEMS Microbiol. Lett.*, 62, 29–38, 1989.

Krause-Jensen, D. and Sand-Jensen, K.: Light attenuation and photosynthesis of aquatic plant communities, *Limnol. Oceanogr.*, 43, 396–407, 1998.

15 Kremp, A., Godhe, A., Egardt, J., Dupont, S., Suikkanen, S., Casabianca, S., and Penna, A.: Intraspecific variability in the response of bloom-forming marine microalgae to changed climate conditions, *Ecol. Evol.*, 2, 1195–1207, 2012.

Kromkamp, J., Barranguet, C., and Peene, J.: Determination of microphytobenthos PSII quantum efficiency and photosynthetic activity by means of variable chlorophyll fluorescence, *Mar. Ecol-Prog. Ser.*, 162, 45–55, 1998.

20 Kruschel, C. and Castenholz, R. W.: The effect of solar UV and visible irradiance on the vertical movements of cyanobacteria in microbial mats of hypersaline waters, *FEMS Microbiol. Ecol.*, 27, 53–72, 1998.

Kuhl, M., Glud, R. N., Ploug, H., and Ramsing, N. B.: Microenvironmental control of photosynthesis and photosynthesis-coupled respiration in an epilithic cyanobacterial biofilm, *J. Phycol.*, 32, 799–812, 1996.

25 Lassen, C., Ploug, H., and Jorgensen, B. B.: Microalgal photosynthesis and spectral scalar irradiance in coastal marine-sediments of Limfjorden, Denmark, *Limnol. Oceanogr.*, 37, 760–772, 1992.

Latifi, A., Ruiz, M., and Zhang, C. C.: Oxidative stress in cyanobacteria, *FEMS Microbiol. Rev.*, 33, 258–278, doi:10.1111/j.1574-6976.2008.00134.x, 2009.

30 Low-Decarie, E., Fussmann, G. F., and Bell, G.: The effect of elevated CO₂ on growth and competition in experimental phytoplankton communities, *Global Change Biol.*, 17, 2525–2535, doi:10.1111/j.1365-2486.2011.02402.x, 2011.

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Marotta, H., Duarte, C. M., Sobek, S., and Enrich-Prast, A.: Large CO₂ disequilibria in tropical lakes, *Global Biogeochem. Cy.*, 23, Gb4022, doi:10.1029/2008gb003434, 2009.

Oakes, J. M., Eyre, B. D., Middelburg, J. J., and Boschker, H. T. S.: Composition, production, and loss of carbohydrates in subtropical shallow subtidal sandy sediments: rapid processing and long-term retention revealed by C-13-labeling, *Limnol. Oceanogr.*, 55, 2126–2138, doi:10.4319/lo.2010.55.5.2126, 2010.

Oliveira, V. P., Bento, L., and Enrich-Prast, A.: Short-term spatial and temporal variation of sediment oxygen dynamics in a tropical tidal salt flat, *Wetlands Ecol. Manage.*, 19, 389–395, 2011.

Oren, A.: Diversity of organic osmotic compounds and osmotic adaptation in cyanobacteria and algae, in: *Algae and Cyanobacteria in Extreme Environments, Cellular Origin, Life in Extreme Habitats and Astrobiology*, edited by: Seckbach, J., Springer, Dordrecht, 641–655, 2007.

Rasmussen, M. B., Henriksen, K., and Jensen, A.: Possible causes of temporal fluctuations in primary production of the microphytobenthos in the Danish Wadden Sea, *Mar. Biol.*, 73, 109–114, 1983.

Raven, J. A.: Putting the C in phycology, *Eur. J. Phycol.*, 32, 319–333, 1997.

Raven, J. A. and Jhonston, A. M.: Mechanisms of inorganic-carbon acquisition in marine phytoplankton and their implications for the use of other resources *Limnol. Oceanogr.*, 36, 1701–1714, 1991.

Revsbech, N. P. and Jorgensen, B. B.: Photosynthesis of benthic microflora measured with high spatial-resolution by the oxygen microprofile method – capabilities and limitations of the method, *Limnol. Oceanogr.*, 28, 749–756, 1983.

Revsbech, N. P., Jorgensen, B. B., and Brix, O.: Primary production of microalgae in sediments measured by oxygen microprofile, H-Co-14(3)-fixation, and oxygen-exchange methods, *Limnol. Oceanogr.*, 26, 717–730, 1981.

Revsbech, N. P., Madsen, B., and Jorgensen, B. B.: Oxygen production and consumption in sediments determined at high spatial-resolution by computer-simulation of oxygen micro-electrode data, *Limnol. Oceanogr.*, 31, 293–304, 1986.

Riebesell, U.: Effects of CO₂ enrichment on marine phytoplankton, *J. Oceanogr.*, 60, 719–729, 2004.

Riebesell, U., Schulz, K. G., Bellerby, R. G. J., Botros, M., Fritsche, P., Meyerhofer, M., Neill, C., Nondal, G., Oschlies, A., Wohlers, J., and Zollner, E.: Enhanced biological carbon consumption in a high CO₂ ocean, *Nature*, 450, 545–548, doi:10.1038/nature06267, 2007.

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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

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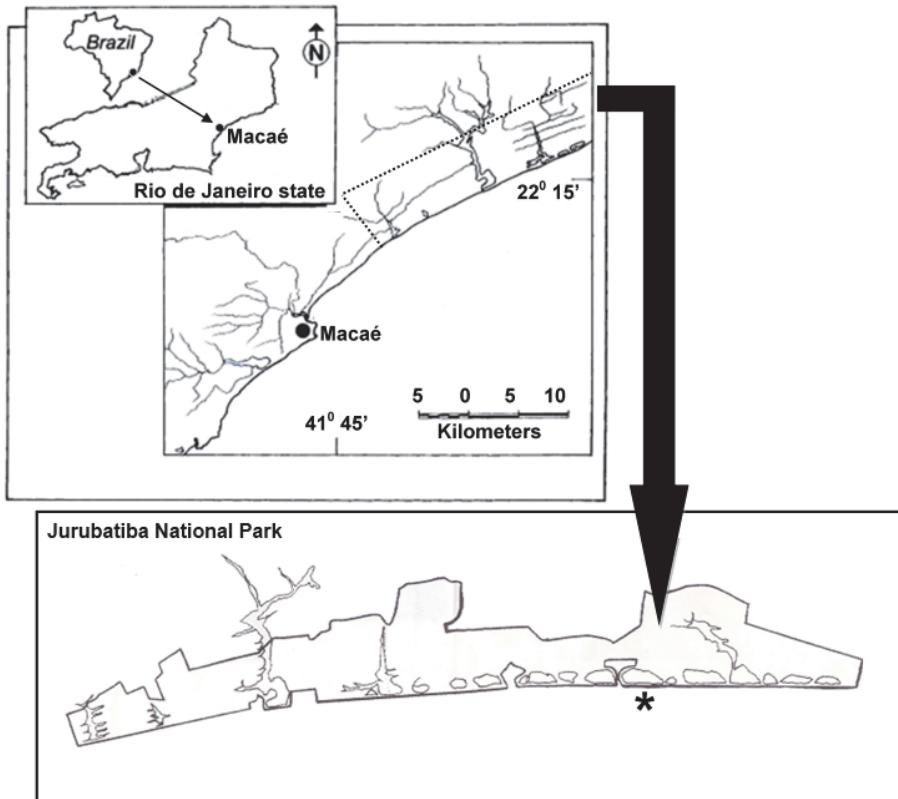


Fig. 1. Geographic localization of the studied area. Visqueiro lagoon is identified by an asterisk.

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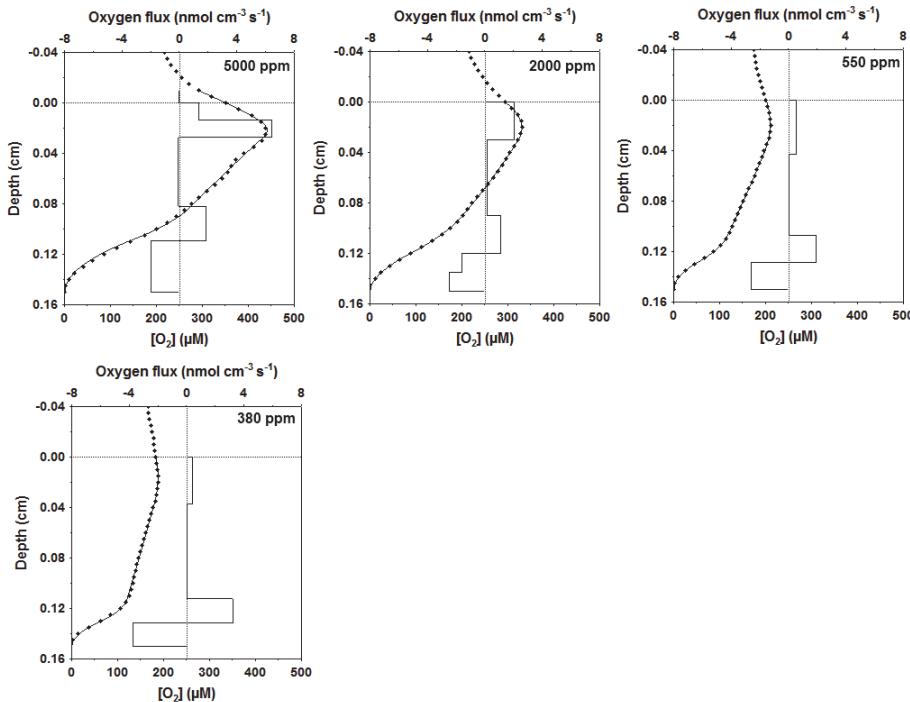


Fig. 2. Measured oxygen concentration (circles), modeled oxygen profile (line connecting circles) and modeled net primary production (NPP, square line) of the first set experiments. All graphs represent steady-state profiles of each treatment. Light is $550 \mu\text{E}$ for all treatments.

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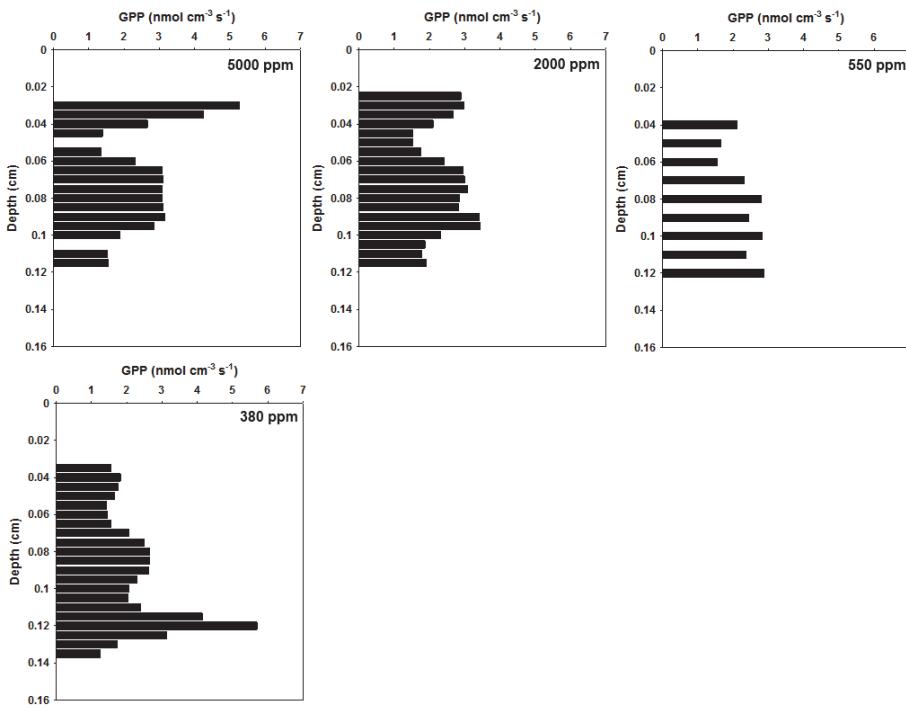


Fig. 3. Steady-state profiles of the microbial mat gross primary production (GPP) submitted to different atmospheric CO₂ concentrations of the first set of experiments. Light is 550 μE for all treatments.

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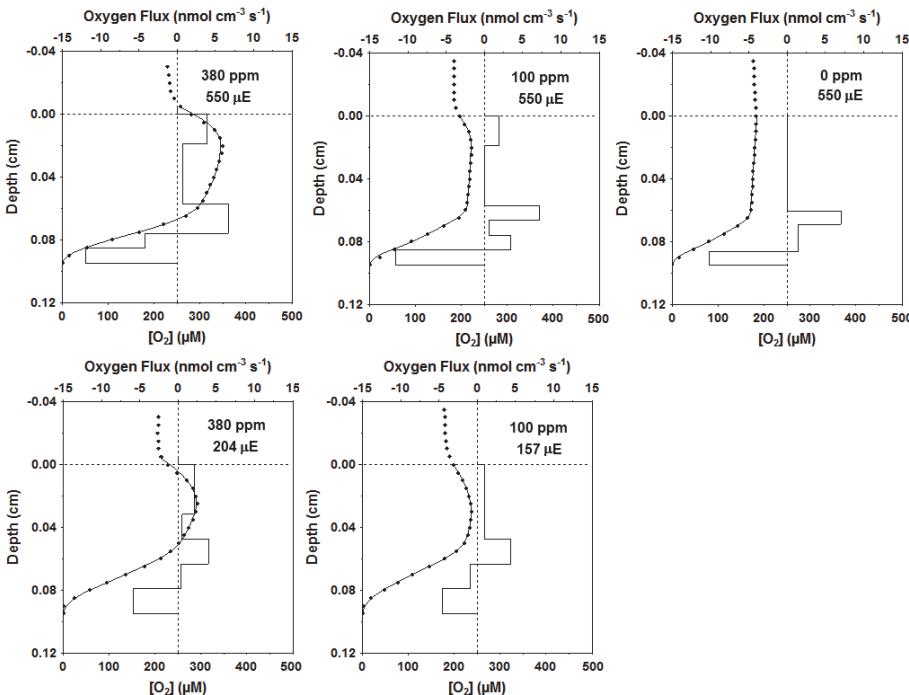


Fig. 4. Measured oxygen concentration (circles), modeled oxygen profile (line connecting circles) and modeled net primary production (NPP, square line) of the second set experiments. All graphs represent steady-state profiles of each treatment.

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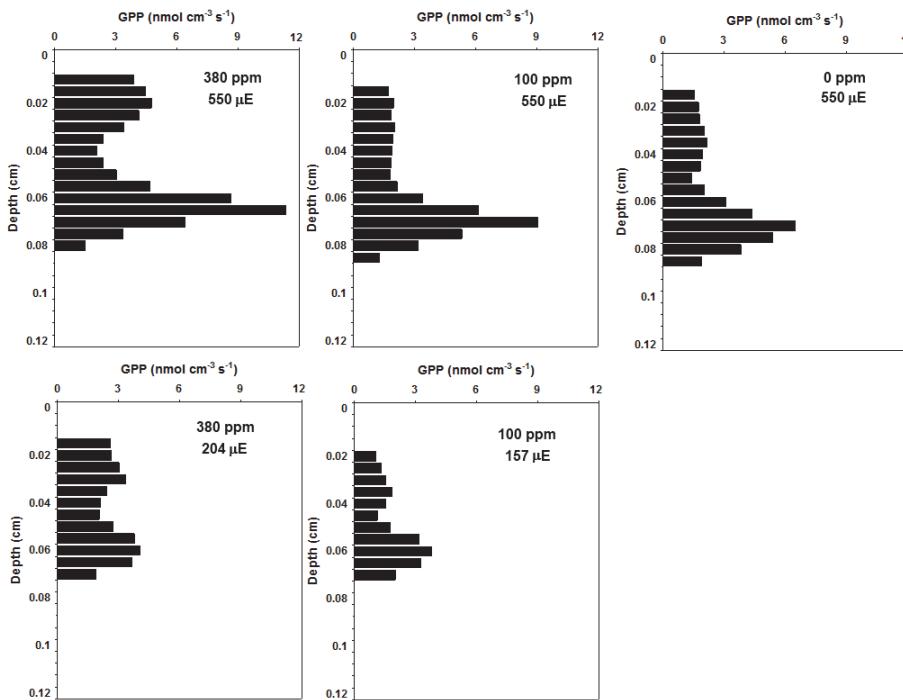


Fig. 5. Steady-state profiles of the microbial mat gross primary production (GPP) submitted to different atmospheric CO_2 concentrations and light of the second set of experiments.

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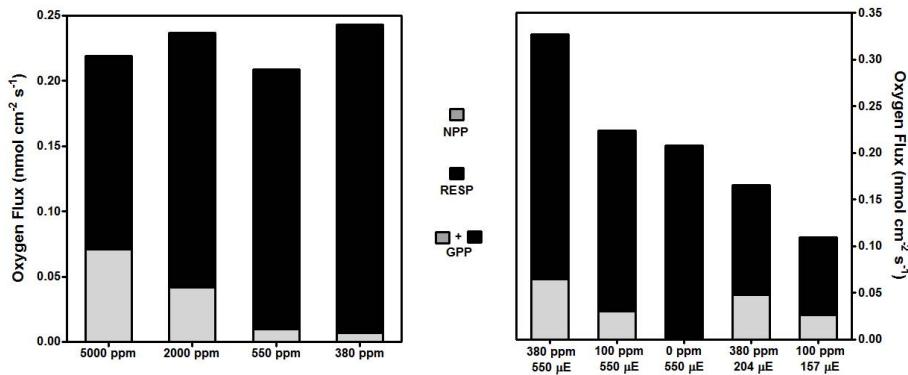


Fig. 6. Depth integrated net primary production (NPP), respiration (R) and gross primary production (GPP) of the microbial mat samples of the two sets of experiments. Each graph represents different mat samples from the same studied area.

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