Diel variation of bacterial abundance and productivity in tropical coastal lagoons: the importance of bottom-up factors in a short-time scale.

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ABSTRACT: Diel variation of bacterial abundance and productivity in tropical coastal lagoons: the importance of bottom-up factors in a short-time scale. We analyzed the diel variation of some limnological variables and its effects on the abundance and secondary productivity of bacterioplankton in two tropical coastal lagoons located in Southeastern Brazil (Rio de Janeiro State). Bacterial abundance and secondary productivity remained constant throughout the day in Cabiúnas lagoon, as the water temperature and the dissolved oxygen concentration. On the other hand, Garças lagoon showed a wide diel variation in water temperature, reaching values close to 39 °C at 16:00 h. The oxygen concentration varied throughout the day, surpassing 10 mg O_2.L^{-1} at noon and dropping to less than 3 mg O_2.L^{-1} during the night in Garças lagoon. Despite the fact that bacterial abundance remained constant in Garças lagoon, bacterial productivity varied throughout the day. Bacterial productivity was higher at night, in the period of oxygen depletion and lower temperatures. The high temperatures observed in Garças lagoon during the day seem to be detrimental to bacterial metabolism, probably due to denaturation of bacterial enzymes. Thus, in shallow tropical ecosystems, as is particularly the case for most of coastal lagoons, the daily temperature variation may be an important factor regulating bacterial production in a short-time scale, with great implications for the metabolism of these ecosystems.
Key-words: planktonic bacteria, bacterial production, diel variation, bottom-up factors, coastal lagoons.

RESUMO: Variação diária da abundância e produtividade bacteriana em lagoas costeiras tropicais: a importância dos fatores ascendentes em curta escala de tempo. Foram analisadas as variações diárias de alguns parâmetros limnológicos e seus efeitos sobre a densidade e produtividade secundária do bacterioplâncton em duas lagoas costeiras tropicais localizadas no Sudeste do Brasil (Rio de Janeiro). A abundância e a produtividade bacteriana permaneceram constantes ao longo do dia na Lagoa Cabiúnas, bem como a temperatura da água e a concentração de oxigênio dissolvido. De modo inverso, a Lagoa das Garças apresentou uma ampla variação diária da temperatura da água, atingindo valores próximos a 39 °C às 16:00 h. A concentração de oxigênio também variou ao longo do dia, superando 10 mg O_2.L^{-1} às 12:00 h e decaindo para valores inferiores a 3 mg O_2.L^{-1} durante a noite, na Lagoa das Garças. Embora a densidade bacteriana tenha permanecido constante na Lagoa das Garças, a produtividade bacteriana variou ao longo do dia. A produtividade bacteriana foi maior no período de déficit de oxigênio e de temperaturas mais baixas. As altas temperaturas observadas durante o dia na lagoa Garças parecem ter um efeito negativo sobre a atividade bacteriana, provavelmente devido à desnaturação de enzimas bacterianas. Portanto, em ecossistemas aquáticos tropicais rasos, como é o caso da maioria das lagoas costeiras, a variação térmica diária pode ser um importante fator regulando a

produção bacteriana em uma escala de tempo curta, tendo grandes implicações para metabolismo destes ecossistemas
Palavras-chave: bactérias planctônicas, produção bacteriana, variação diária, fatores ascendentes, lagoas costeiras.

Introduction

Bacteria have been considered important organic matter mineralizers in aquatic ecosystems. In the middle 1970's, a new framework attributed a major role as secondary producers in the water column to planktonic bacteria. By this idea, initially formalized by Pomeroy (1974), planktonic bacteria could recover dissolved organic matter (DOM) to the microbial food web through grazing sequentially by protozoans, larger zooplankters and fishes. The advances in fluorescence and radioisotopes techniques (e.g. Hobbie et al., 1977; Fuhrman & Azam, 1980) in early 80's showed that these organisms were much more abundant in aquatic ecosystems than previously thought, and accounted for a significant amount of secondary production using DOM as substrate (Fuhrman & Azam, 1982). Therefore, the concept of the "microbial loop" (Azam et al., 1983) could be formalized in a more sound basis, becoming a major paradigm for the research on aquatic food webs (for a review, see Søndergaard, 1997).

Further studies showed that planktonic bacteria could account for as much or even more production as phytoplankton in some ecosystems (e.g. Simon et al., 1992). This seems to be specially the case for oligotrophic systems, where bacteria are competitively more favoured than planktonic algae (Cotner & Biddanda, 2002). The carbon flux through bacterioplankton is also higher when the inputs of organic carbon are mainly from allochthonous sources (Biddanda & Cotner, 2002).

Bacterioplankton abundance and production can be controlled by either top-down or bottom-up processes and the importance of each process varies among ecosystems, bacterial populations and time-scales. Top-down control is exerted by higher trophic levels, via grazing or viral activity, and its importance is relatively higher in bacterial abundance regulation and in eutrophic ecosystems (Cotner & Biddanda, 2002; Auer et al., 2004, Jacquet et al., 2005). Bottom-up control is related to resource availability and abiotic conditions that directly affect bacterial activity (Felip et al., 1996; Cotner et al., 1997). Most studies on bottom-up control of bacterioplankton focus on resource limitation. Phosphorus seems to be the main limiting nutrient to bacterial growth in most aquatic ecosystem, including tropical coastal lagoons (Cotner et al., 1997; Farjalla et al., 2002a; 2002b). Other nutrients, such as nitrogen and iron, may limit bacterial production in some aquatic ecosystems (Pakulski et al., 1996). In aquatic ecosystems, where phytoplankton exudates are the main source of DOC, bacterial production may be strongly related to algal exudates production (Cole et al., 1988). Where the input of allochthonous terrestrial DOC predominate, only a small fraction of DOC is readily metabolized by bacteria and the DOC composition has a strong influence on bacterial metabolism (Cotner & Biddanda, 2002; Farjalla et al., 2002a; in press).

However, other bottom-up factors may regulate bacterial activity in aquatic ecosystems, mainly in a short time scale. Studies in temperate ecosystems showed that temperature is a major modulator and predictor of bacterial production in a seasonal perspective, overwhelming other factors, such as nutrient concentrations (Søndergaard, 1997; Biddanda & Cotner, 2002; McManus et al., 2004). Tropical aquatic ecosystems are not subject to strong seasonal temperature fluctuations, but daily temperature variations may have significant effects on bacterioplankton abundance and activity (Jugnia et al., 1998). Bastviken et al. (2001) observed the influence of dissolved oxygen concentration on bacterial growth, considering that changes on dissolved oxygen concentration are usually observed between night and day. Furthermore, the DOC photo-degradation by solar radiation can produce labile organic

compounds that enhance bacterial growth in humic waters during the day (Lindell et al., 2000). Therefore, to a better understanding of bacterial growth limitation in aquatic ecosystems, both large- and small-time scale factors must be considered.

In this study we evaluated diel variation of bacterial abundance and production and some limnological variables in two coastal lagoons in Southeastern Brazil (Rio de Janeiro State). We aim to relate diel changes of bacterial activity to other limnological variables, identifying the main limiting factors to bacterial activity in a short-time scale in these lagoons.

Material and methods

Study Area

This study was carried out in Restinga de Jurubatiba National Park, in the outskirts of Macaé, in the Northern Rio de Janeiro State (22° - 22°30' S and 41°15'- 42° W), in January 2001. We performed the diel variation surveys in two lagoons, Cabiúnas and Garças (Fig. 1), with contrasting abiotic features (see Tab. I). Cabiúnas is a humic, freshwater, oligotrophic lagoon and its littoral zone is densely colonized by aquatic macrophytes, mainly Typha domingensis. Garças lagoon is more shallow and saltier than Cabiúnas lagoon, and generally shows higher DOC and nutrients concentration. In addition, in January 2001, we observed a very well-defined microbial mat in Garças lagoon. Both lagoons are separated from sea by a sandbar of roughly 20 meters length. Garças lagoon is very influenced by marine water, which is also evident by its alkaline pH and high conductivity, mainly because its main axis is parallel to the sea (Farjalla et al., 2001a). Cabiúnas lagoon, instead, has its main axis perpendicular to the sea, with a smaller area of potential marine influence. Finally, planktonic bacteria seems to be phosphorus limited in both lagoons (Farjalla et al. 2001a; 2002b)

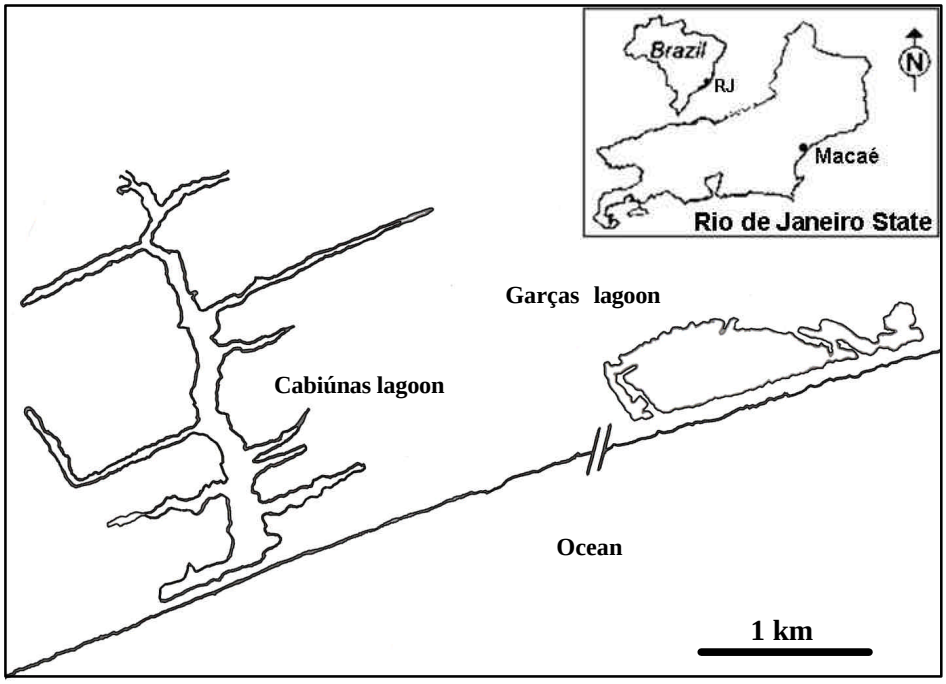

Figure 1: Geographical location of Cabiúnas and Garças lagoons.

Table I: Abiotic and biotic variables in Cabiúnas and Garças lagoons: salinity, electrical conductivity, pH, depth, total dissolved nitrogen (TDN), total dissolved phosphorus (TDP), N:P molar ratio (N:P) and chlorophyll-a in Cabiúnas and Garças lagoons in the beginning of diel variations. Phytoplanktonic Primary Production (PPP) in the 10-16 h interval. Meand wind speed and sunlight intensity of values measured every 4 h (standard deviations in parenthesis).

Variables	Cabiúnas Lagoon	Garças Lagoon
Salinity	0.3	64.3
Conductivity ($mS.cm^{-1}$)	0.61	94.06
pH	6.93	7.66
Depth (m)	3.5	0.2
TDN (mM)	27.62	28.69
TDP (mM)	0.076	0.110
N:P	356.05	260.82
Chlorophyll-a ($mg.L^{-1}$)	2.68	4.04
PPP ($mg\ O_2.L^{-1}.h^{-1}$)	0.02	0.20
Wind speed ($m.s^{-1}$)	3.33 (2.64)	1.83 (1.72)
Sunlight ($mE.cm^{-1}$)	1,471.43 (149.60)	1,485.71 (167.62)

Samplings

Samplings were made in the central limnetic region of both lagoons. Initial measurements of salinity and electrical conductivity were performed with a multifunctional probe (YSI – 30, YellowSpring) and the depth of each lagoon was also recorded. Water samples from each lagoon were collected in acid-washed polyethylene bottles and frozen at – 20 °C for further analysis of total dissolved nitrogen and total dissolved phosphorus. Water samples were also filtered through glassfiber filters (1.2 mm, Ø = 47 mm, Whatman) and the filters were frozen for further determination of chlorophyll-a concentration.

The water temperature and the wind speed were recorded every 4 hours during 24 h with a multifunctional sound (YSI-30, YellowSpring) and an anemometer (Kestrel 1000), respectively. At the same time, water samples were collected in BOD flasks for dissolved oxygen concentration determination. Water samples were fixed with buffered formaline (3.7 %, final concentration, saturated with $Na_2B_4O_7$) for bacterial abundance estimations. Samples were also incubated with ^3H-leucine for bacterial production rate estimations.

Finally, water samples were incubated in BOD flaks (4 treatments and 4 dark controls) in the sub-surface of each lagoon for phytoplanktonic primary production evaluation in the period of highest sunlight intensity (10:00 – 16:00 h). Phytoplanktonic primary production was estimated by the difference in oxygen concentration between treatments and dark controls after 6 h-incubation. Sunlight intensity was measured by a radiometer (Li-Cor 350b) during incubation in each lagoon.

Analytical methods

Total dissolved nitrogen concentrations were measured as NH_4^+ through digestion at 320 °C and distillation (Mackereth et al., 1978). Total dissolved phosphorus was measured by potassium persulphate oxidation and reaction with molybdic acid (Golterman et al., 1978). Chlorophyll-a concentrations were determined after hot 90 % Ethanol extraction (Nusch & Palme, 1975). Dissolved oxygen was determined by Winkler method, modified by Golterman et al. (1978).

Bacterial abundance was ascertained through the method proposed by Hobbie et al. (1977). Samples stained with acridine orange (0.005 %, final concentration)

were filtered through black polycarbonate filters (0.2 mm Nuclepore® filter) and the bacteria were counted in an epifluorescence microscope (Axiovert Zeiss Universal), at 1,600-fold magnification. At least 300 bacteria or 30 fields were counted in each filter. The controls were prepared with sterilized water.

Bacterial production rate was obtained from the incorporation of ^{3}H-leucine, according to Smith & Azam (1992). A 1.3 mL aliquot of each sample was incubated in Eppendorff tubes (4 replicates) containing 10 nM of ^{3}H-leucine (5-fold diluted solution, 159 Ci mM, Amersham), in the dark, for 40 minutes. Controls were prepared adding 90 mL of 100 % TCA (Trichloric Acetic Acid) to the mixture. After incubation, 90 mL of 100 % TCA were added to each sample to halt the reaction. Each tube was sequentially washed with 5 % TCA and 80 % Ethanol. After addition of 500 mL of Scintillation Cocktail (Aquasol 2, Dupont) to each tube, the radioactivity was measured by a Beckman LS-5600 Liquid Scintillation System. Bacterial production rates were calculated by assuming an intracellular leucine dilution factor of 2 and a cellular carbon-to-protein ratio of 0.86, according to Wetzel & Likens (1991).

Statistical Analyses

In order to detect the increase in oxygen concentration by phytoplankton primary production, we compared the treatments and dark controls with Mann-Whitney test. A paired t-test was applied to test for differences in wind and cell-specific bacterial production between lagoons. A two-way ANOVA was used to test the bacterial production between lagoons and time samplings. We used the STATISTICA 6.0 (StatSoft, Inc., 2001) to perform all tests. A probability level of $\pm = 0.05$ was used throughout to determine statistical significance.

Results

Cabiúnas and Garças lagoons showed remarkably different depths, salinities and electrical conductivities, despite being similar in dissolved nutrient concentrations (Tab. I). During the samplings, Garças lagoon was extremely shallow (0.2 m), with high salinity (61.3), high electrical conductivity (94.06 mS.cm^{-1}) and slightly alkaline pH (7.66), while Cabiúnas was much deeper (3.5 m) and showed lower values of salinity (0.3),electrical conductivity (0.61 mS.cm^{-1}) and close to neutral pH (6.93). Both Cabiúnas and Garças lagoons showed low nutrient concentrations, however, the N:P molar ratio was somewhat lower in Garças lagoon. Chlorophyll-a concentration was low in both lagoons (Tab. I) and the wind speed was higher, on average, in Cabiúnas lagoon (Tab. I, $p < 0.05$). A significant phytoplanktonic primary production was observed in Garças lagoon (Tab. I, $p < 0.05$), although it was very low comparing to the variations in dissolved oxygen concentration during the day in the same lagoon (Fig. 2B). The dissolved oxygen concentrations were not different between treatments and dark controls in Cabiúnas lagoon, indicating no significant phytoplanktonic primary production in this lagoon (Tab. I, $p > 0.05$).

Despite the similar incidence of sunlight in both lagoons (Tab. I), they showed very distinct patterns of diel variation in water temperature (Fig. 2A). Water temperature remained fairly constant (c.a. 28.0 ^{o}C) in Cabiúnas lagoon. In contrast, Garças lagoon showed a great temperature oscillation during the day (26.5 – 38.8 ^{o}C), with a sharp heating close to noon. Both lagoons showed similar temperatures during the night (Fig. 2A). The dissolved oxygen concentrations showed a similar pattern, being roughly constant during the day in Cabiúnas lagoon (c.a. 7.00 mg O_2.L^{-1}, Fig. 2B) and ranging from 2.45 mg O_2.L^{-1} (during the night and in the beginning of the morning) to 10.24 mg O_2.L^{-1} (close to noon) in Garças lagoon (Fig. 2B). Therefore, Garças lagoon presented almost anoxic conditions during the night as well as hiperoxic conditions close to noon.

Bacterial abundance remained constant in both lagoons during the day, although it was more than two-fold higher in Garças lagoon than in Cabiúnas lagoon (Fig. 3).

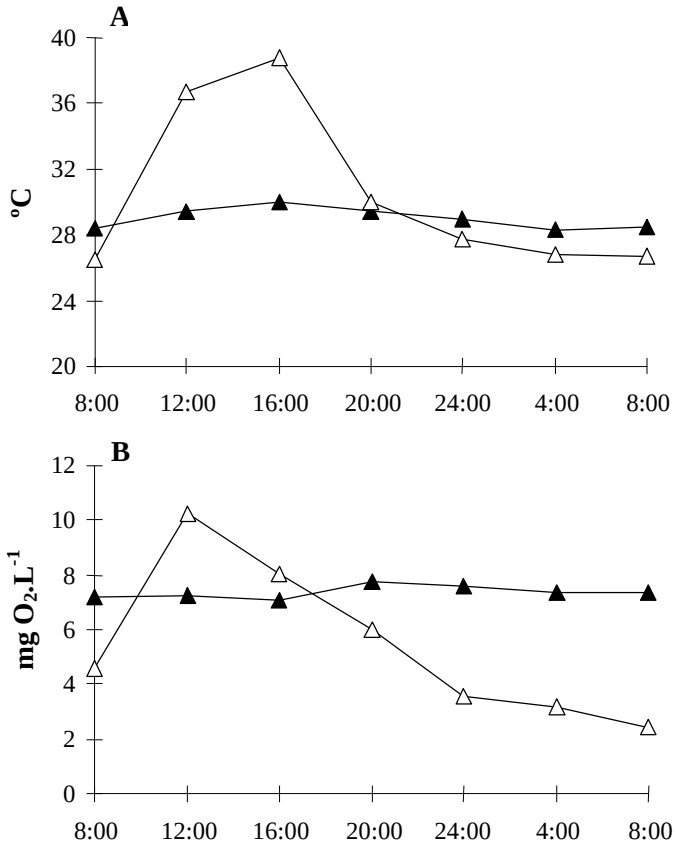

Figure 2: Diel variation of (A) water temperature (°C) and (B) dissolved oxygen concentration (mg.L^{-1}) in Cabiúnas and Garças lagoons.

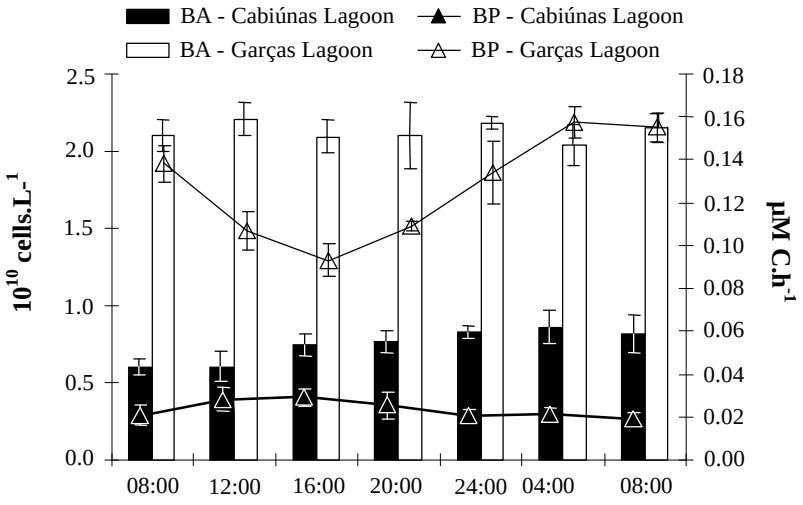

Figure 3: Diel variation of bacterial abundance (BA, cells.L^{-1}) and bacterial production rate (BP, mM C.h^{-1}) in Cabiúnas and Garças lagoons. Bars account for the standard deviations.

Bacterial production rate was also constant in Cabiúnas lagoon, but in Garças lagoon it showed a pattern of diel variation inverse to those of water temperature and dissolved oxygen (Fig. 3). Thus, bacterial production rates in Garças lagoon were higher when the values of dissolved oxygen concentration and temperature were lower and vice-versa. Bacterial production rates were always more than two-fold higher in Garças lagoon than in Cabiúnas lagoon (Fig. 3).

Discussion

Water temperature and dissolved oxygen concentration remained fairly constant throughout the day in Cabiúnas lagoon (Fig. 2A). It seems that, as a joint effect of higher wind incidence and depth, the continuous mixing of the water column buffered Cabiúnas lagoon against variation in water temperature. Furthermore, Cabiúnas lagoon is a humic lagoon, with dark water and low nutrient and chlorophyll-a concentration when compared to other coastal lagoons (Farjalla et al., 2001), resulting in low phytoplanktonic primary production. Humic lagoons typically show a net heterotrophic metabolism, as was reported, for instance, by Thomaz et al. (2001) for Comprida lagoon. Dissolved oxygen concentration was kept constant during the day probably through diffusive input from atmosphere, similar to the results found by Melack & Fisher (1983) in Calado Lake. The absence of diel variation on temperature and dissolved oxygen is also consistent with the constant bacterial abundances and production rates during the day in Cabiúnas lagoon. Farjalla et al. (2002b) found an expressive variation on bacterial production in Cabiúnas and other coastal lagoons over the year due to changes in nutrient availability. Thus, we suggest that bacterioplankton in Cabiúnas lagoon is less susceptible to short-term regulation, such as diel changes on water temperature and dissolved oxygen concentration, than to other bottom-up factors, such as the dissolved phosphorus availability.

On the other hand, Garças lagoon showed a marked variation in water temperature and in dissolved oxygen concentration during the day (Fig. 2). The variation in dissolved oxygen seems to result from the balance between primary production during the day and heterotrophic activity during the night. However, chlorophyll-a concentration and phytoplanktonic primary production were low in Garças lagoon. The increased dissolved oxygen concentration during the day was probably provided by the photosynthetic activity of benthic microalgae present in Garças lagoon, specially due to the extremely low depth of the water column (0.2 m). These phytobenthic producers are usually associated with heterotrophic bacteria in a layer over the sediment, known as "microbial mat" (Fenchel et al., 1998). The microbial mat may be particularly important for the metabolism of shallow aquatic ecosystems, causing a massive oxygen increase during the day but also a rather high oxygen uptake during the night. Thus, the oxygen depletion observed during the night in Garças lagoon (Fig. 2B) may be largely due to heterotrophic activity of the microbial mat.

Along with this variation on water temperature and oxygen, Garças lagoon presented a well marked diel variation on bacterial production rates, in a pattern opposite to those variables (Fig. 2 and 3). The lowest values of bacterial production rates occurred when water temperature were higher, indicating that high temperatures reached during the day may have a detrimental effect on bacterioplankton activity in Garças lagoon, probably due to denaturation of bacterial enzymes. Other factors, such as the direct damage by UV radiation of bacterial cells, that are more sensitive to the negative effects of UV radiation than eucharyotic cells (Hader et al., 1998), and the nutrient competition with the microbial mat cells, could also have limited the bacterioplankton production during the day. Finally, it is also known that toxic compounds such as H_2O_2 are produced by sunlight-induced photo-reactions (Scully et al., 1995). These compounds show low half-life in water column, being completely

degraded in few hours after produced (Farjalla et al., 2001b). Although we did not measure the photo-production of H_2O_2, it might have affected bacterial activity negatively during the day in Garças lagoon, with a decreasing effect toward night as it is was degraded.

The high bacterial production at night was also certainly responsible for the dissolved oxygen depletion, along with the microbial mat, as suggested above. However, it must be noted that the values recorded for dissolved oxygen concentration are the results of the net balance of production and uptake in the in-between intervals. Bacterial production rates, on the other hand, are instantaneous rates of bacterial activity. Therefore, our results indicate that bacterial activity was rather insensitive to oxygen depletion (Fig. 2 and 3). Although anaerobic bacterial metabolism has a lower energetic yield, recent studies have shown that bacterial growth in anoxic conditions may be similar or even higher than in the presence of oxygen (Bastviken et al., 2001). Thus, it is likely that bacterioplankton switch between aerobic and anaerobic metabolism in Garças lagoon during the day.

Studies on diel variation of bacterioplankton production are extremely rare, specially for tropical ecosystems. Torréton et al. (1994), for instance, working in a tropical eutrophic lagoon, found a pattern of diel variation for bacterial production rates similar to that found in Garças lagoon in the present study, with higher rates during the night (Fig.3). These authors attributed this fact to nocturnal upward migration of zooplankton, which could enhance bacterial activity through 1) increased nutrient release due to sloppy feeding and excretion of egestion or 2) increased predation of bacterivores. We did not analyzed zooplankton dynamics in the present study, but a similar explanation is not reasonable for Garças lagoons, since it was very shallow during our survey (0.2 m). Moreover, as reported by Pedrós-Alió (2000), the importance of top-down regulation on bacterioplankton decreases with increasing salinity, since eukaryotic bacterivores (flagellates and ciliates) are also increasingly rare through this gradient. We believe, therefore, that changes in bacterial production rates were mainly driven by bottom-up factors in Garças lagoon in this study.

Despite the fact that bacterial abundance remained constant during the day in both lagoons, bacterial abundance was always more than two-fold higher in Garças than in Cabiúnas lagoon (Fig. 3). This seems to reinforce the above suggestion that grazing pressure upon planktonic bacteria is probably lower in Garças lagoon. Higher bacterial abundances, per se, could explain the higher bacterial production rates found in Garças lagoon, but even calculating the cell-specific bacterial production (by dividing the bacterial production rate by the bacterial abundance at each time sampling), Garças lagoon still showed higher rates of bacterial production per cell. Thus, not only the bacterial abundances but also the bacterial metabolism per cell seem to be favoured in Garças lagoon. Based on the limnological features of Garças and Cabiúnas lagoons reported in the study and previous papers (Farjalla et al. 2001a; 2002b, Suhett et al., 2004), we suggest that labile organic compounds excreted by benthic algae from the microbial mat during the day support heterotrophic bacterial metabolism in Garças lagoon, while humic substances, more refractory organic compounds, are the main carbon substrates to bacterial growth in Cabiúnas lagoon.

Most of the studies concerning the control of bacterial growth in aquatic ecosystems deal with factors that vary on time scale of months or seasons. In temperate ecosystems, seasonal changes in temperature, organic matter and nutrient inputs by snowmelt or mixing of water column, phytoplankton blooms, among others, drive changes in bacterioplankton abundance and production rates (Søndergaard, 1997; Biddanda & Cotner, 2002; McManus et al., 2004). In tropical ecosystems, bacterioplankton growth seems to be primarily related to seasonal alternation between allochthonous and autochthonous (i.e. algal) carbon sources (Anesio et al., 1997; Farjalla et al., in press) and availability of limiting nutrients (Farjalla et al., 2002a; Farjalla et al., 2002b).

This work shows that water temperature may have a crucial role in the short-time regulation of bacterial production in very shallow tropical aquatics ecosystems, as Garças lagoon. Although tropical ecosystems are not subject to strong seasonal variations in sunlight radiation, as temperate ecosystems are, the within-a-day variation in water temperature can have a marked effect on bacterioplankton production rates. Since most of tropical lagoons are shallow and small, and this is specially the case of many coastal lagoons, this pattern of diel variation in bacterial production rates may also be widely found, and should be accounted for in the study of the metabolism of these ecosystems.

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