Title: Natural Events of Anoxia and Low Respiration Index in Oligotrophic Lakes of the Atlantic Tropical Forest

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Abstract. Hypoxia is a well-recognized condition reducing biodiversity and increasing greenhouse gases emissions in aquatic ecosystems, especially under warmer temperatures of tropical waters. Anoxia is a natural event commonly intensified by human-induced organic inputs in inland waters. Here, we assessed the partial pressure of O_2 (pO_2) and CO_2 (pCO_2), and the ratio between them (represented by the respiration index, RI) in two oligotrophic lakes of the Atlantic Tropical Forest, encompassing dry and rainy seasons over 19 months. We formulated the hypothesis that thermal stratification events could be coupled to natural hypoxia in deep waters of both lakes. Our results indicated a persistence of CO_2 emissions from these tropical lakes to the atmosphere, on average ± standard error (SE), 2.3 (± 0.3) mmol m^{-2} h^{-1} probably subsided by terrestrial C inputs from the forest. Additionally, the thermal stratification during the end of the dry season and the rainy summer was coupled to anoxic events and very low RI in deep waters, and to significantly higher pO_2 and RI at the surface (about 20,000 μatm and 1.0, respectively). In contrast, the water mixing during dry seasons in the beginning of the winter was related to a strong destratification in pO_2, pCO_2 and RI in surface and deep waters, without reaching any anoxic conditions throughout the water column. These findings confirm our hypothesis, suggesting that lakes of the Atlantic Tropical Forest could be dynamic, but especially sensitive to organic inputs. Natural anoxic events indicate that tropical oligotrophic lakes might be highly influenced by human land uses, which increase organic discharges into the watershed.

1 Introduction

Lakes are small but broadly distributed at low altitudes (Downing et al., 2006), representing a common fate for organic and inorganic inputs from large areas in the watershed (Tranvik et al., 2009). These ecosystems show intense metabolic activity supported by the availability of water, nutrients and organic matter in both pelagic (Biddanda et al., 2001) and benthic (Downing et al., 2008) compartments. Globally, important pool of carbon (C) fixed in organic compounds by terrestrial plants may be buried (von Wachenfeldt and Tranvik, 2008) or mineralized to C gases (Cole et al., 2007) within lakes, a crucial component of the C cycle.

Oxygenic photosynthesis and aerobic respiration are the major metabolic pathways by which organic matter is produced and destroyed in the biosphere (Cole et al., 2000), corresponding to the overall metabolic balance of an ecosystem (Howarth et al., 1996). Carbon dioxide (CO_2) and oxygen (O_2) are metabolic gases involved in both processes, as oxygenic photosynthesis absorbs CO_2 producing O_2, while aerobic respiration demands O_2 releasing CO_2 (Clarke and Fraser, 2004). In this way, lakes may show net autotrophy uptaking atmospheric CO_2, or net heterotrophy with subsequent CO_2 evasion to atmosphere. However, most lakes are heterotrophic due to terrestrial organic inputs subsiding the aquatic decomposition (Duarte and Prairie, 2005;Cole et al., 1994) and food web (Pace et al., 2004).

Respiration is the most efficient biological process of organic degradation, but is strongly limited by the O_2 supply (Sobek et al., 2009). The O_2 depletion following high respiration of the excessive organic loading is a typical cause of organism death and severe decline in the species (Vaquer-Sunyer and Duarte, 2008), which also stimulates the anaerobic organic decomposition in natural waters (Conrad et al., 2011). These anaerobic processes have important implications to global warming, producing more powerful greenhouse gases than CO_2 (Bastviken et al., 2011), as well to create “dead zones” by releasing toxic substances for major aquatic organisms (Diaz and Rosenberg, 2008). Besides aerobic conditions (Diaz and Rosenberg, 2008;Vaquer-Sunyer and Duarte, 2008), the high ratio between partial pressures of O_2 and CO_2 (pO_2:pCO_2), named respiration index (RI), is also crucial to support biological diversity, as provides a simple numerical constraint related to available energy in natural waters (Brewer and Peltzer, 2009).

Along the latitudinal gradient, warmer annual temperatures may contribute to higher diversity of organisms (Amarasinghe and Welcomme, 2002) and more intense metabolic processes (Brown et al., 2004;Davidson and Janssens, 2006) in tropical lakes, including those involved in the organic mineralization with subsequent production of greenhouse gases (Marotta et al., 2009a;Bastviken et al., 2010). The magnitude of metabolic responses following common changes in resource availability or conditions may be substantially enhanced under higher temperatures, resulting in a high variability either among (Marotta et al., 2009a) or within tropical lakes (Marotta et al., 2010a) and over time in these ecosystems (Marotta et al., 2010b;Marotta et al., 2010a).

The Atlantic Tropical Forest is a very productive and threatened biome in Brazil (Metzker et al., 2011). Lakes surrounded by this forest show a persistent CO_2 evasion to the atmosphere attributable to terrestrial C inputs (Marotta et al., 2009b), despite large changes related to seasonal events of water stratification and mixing, especially during the winter and summer, respectively (Tundisi, 1997). The aim of the present study was to assess pO_2, pCO_2 and RI fluctuations following seasonal water column stratification and mixing periods over 19 months in two oligotrophic lakes of the Atlantic Tropical Forest. We tested the hypothesis that thermal stratification events could be coupled to natural hypoxia in deep waters of both lakes.

2 Material and Methods

2.1 Study Area

Barra (19º47’45”S; 42º36'53”W) and Aguapé (19º51’32”S; 42º38'32”W) are lakes situated relatively close to one another (distance 6 km) at 300-m altitude in the south border of the Rio Doce State Park (Southeast Brazil; Fig. 1). This protected area includes one of most important conserved remnant of the Atlantic Tropical Forest in Brazil (36,000 ha). Lake Barra and Lake Aguapé are shallow (maximal depth of 10 m) and small (areas of 1.350 and 1.372 km^2, respectively); showing organic and oligotrophic waters (total phosphorus around 1 μmol L^{-1}, chlorophyll-a about 15 μg L^{-1}, and total organic carbon above 5 mg L^{-1} during this study). Despite any human interference in the margins (abandoned eucalyptus plantation in regeneration to native forest and few field houses), both lakes receive natural inputs from the watershed dominated by the Atlantic Tropical Forest with low human use and preserved natural conditions. Terrestrial inputs from the protected tropical forest commonly affect aquatic organisms and metabolic processes in lakes of this region (Petrucio and Barbosa, 2004;Petrucio et al., 2006).

The climate of the study area is tropical wet and dry (Koppen climate classification Aw), characterized by a strong seasonality in rainfall (Metzker et al., 2011), which includes dry winters from June to September and rainy summers from December to March showing 25-year monthly mean precipitation (± SE) around, respectively, 10 (± 2) and 198 (± 13) mm (data of the National Institute of Meteorology for 1987-2011). Lakes of this region show a well-described seasonal stratification during the rainy season, caused by less water circulation, higher air temperatures and inputs of slightly colder and denser groundwaters, contrasting with a typical mixing during the dry winter by lower air temperatures and more windy conditions (Tundisi, 1997).

2.2 Study design

Water samples for O_2, pH, alkalinity, temperature, nutrients, chlorophyll-a and total organic carbon (TOC) were collected in the morning, using a 3-L Van Dorn bottle, at approximately monthly intervals from March 2004 to October 2005 (19 months). Additionally, one daily variation in O_2, pH, alkalinity and temperature (12:00 p.m., 6:00 p.m., 6:00 a.m. and 12:00 p.m. the day after) was simultaneously assessed in three periods: (a) rainy season in the end of the summer (March 2005), (b) dry season in the beginning of the winter (June 2005) and (c) dry season in the end of the winter (September 2005). Four sampling depths at the central station in both lakes were chosen assuming the light penetration by a 20-cm diameter Secchi disk: 100% (surface waters), 10% (the Secchi depth), 1% (three times the Secchi depth), and 0% (aphotic zone below the 1% light penetration depth and above the bottom sediment).

2.3 Analytical Methods

Dissolved O_2 concentrations by the Winkler method, pH using a pHmeter Marconi PA-200 (precision of 0.01 unities of pH), and the total alkalinity by the Gran titration were immediately analyzed after the sampling (APHA, 1992). At the laboratory, pre-filtered (0.7 μm, Whatman GF/F) water samples were analyzed for chlorophyll-*a* concentrations by extraction with 90% acetone (Lorenzen, 1967), and for TOC concentrations by high-temperature catalytic oxidation using a TOC-5000A Shimadzu Analyzer (samples pre-acidified to pH < 2.0).

CO_2 concentrations were estimated from measurements of pH and alkalinity (Stumm and Morgan, 1996) with corrections for temperature, altitude, and ionic strength (Cole et al., 1994). pCO_2 and pO_2 were calculated from the Henry's law with appropriated adjustments for temperature and salinity for CO_2 (Weiss, 1974) and O_2 (Garcia and Gordon, 1992) solubility. The respiration index was calculated as the ratio $pCO_2{:}pO_2$ in log 10 following Brewer and Peltzer (2009).

2.4 Statistical Analyses

Log-transformed data of pO_2 and pCO_2 or raw data of RI from the same sampling depth or period for each lake showed significant Gaussian distribution (Kolmogorov-Smirnov, $p<0.05$), homogeneity of variances (Bartlett, $p>0.05$) and significant matching (F test, $p<0.05$). Hence, these variables in different sampling depths and periods were compared using parametric tests (Zar, 1996), repeated measures one-way ANOVA followed by Tukey-Kramer multiple comparisons (significance level set at $p<0.05$). In contrast, non-parametric statistics were used to test for differences in pO_2, pCO_2 and RI between the lakes, repeated measures Friedman test followed by Dunn's post-test (significance level set at $p<0.05$), as the transformed data set including all measurements of each variable from the same lake did not meet parametric assumptions. Consequently, pO_2, pCO_2 and RI were correlated with chlorophyll-*a* and TOC concentrations using Spearman correlations (significance level set at $p<0.05$). All statistics were conducted using the software Statistica 7.0.

3 Results

Our study included the end of the rainy season in 2004 (March-April) followed by two dry periods in 2004 and 2005 (May-October) with a whole rainy season between them (November 2004-April 2005; Fig. 2a). The dry season in the beginning of the winter (June-August 2004 and 2005) was characterized by lower water temperatures (around 23-24 ^{o}C) coupled to an overall thermal mixing in waters of both lakes (Figs. 2b and 2c). In contrast, the end of the dry season in 2004 and 2005 (September-October) showed an initial stratification in temperature, reaching 29 ^{o}C in warmer surface waters and 26 ^{o}C in those colder deep before a stronger thermal stratification during the rainy summer (December 2004-March 2005), reaching 31 (surface) and 26 ^{o}C (deep) in both lakes (Figs. 2b and 2c).

Lake Barra and Lake Aguapé showed similar fluctuations in pO_2, pCO_2 and RI during 19 months (Figs. 3a, 3b and 3c), and non-significant differences for these variables comparing monthly (from March 2004 to October 2005) or 24-h cycle (in March, June and September 2005) measurements

(Paired t-test, $p<0.05$). From the end of the rainy seasons to the beginning of the dry winters in 2004 and 2005, pO_2 and RI decreased in surface and increased in deep waters following the thermal mixing (Figs. 3a and 3c), while pCO_2 showed the opposite trend, increasing in surface and decreasing in deep waters (Figs. 3b). Additionally, a reversal increase in surface and decline in deep pO_2 and RI followed the thermal stratification in both lakes during the end of the dry seasons and during the rainy summer in 2004 and 2005, (Figs. 3a and 3c), also contrasting with the opposite trend observed for pCO_2 (Figs. 3b).

In this way, the stronger thermal stratification over the 24-h cycle in the rainy summer (March 2005) was coupled to more intense differences for metabolic variables in the vertical profile, which showed, on average, pO_2 values about 50-fold higher, pCO_2 about sixfold lower, and RI around twofold higher in surface (at 100 or 10% light penetration) than in deep (at 1% or 0% light penetration) waters of both lakes (Fig. 4; Tukey-Kramer, $p<0.05$). RI values were ≤ 0 in deep waters of both lakes during this strong thermal stratification (Fig. 4). On the other hand, a persistent thermal mixing over the 24-h cycle in the beginning of the dry winter (June 2005) was related to non-significant differences for pO_2, pCO_2 and RI at both surface and deep depths (Fig. 5; Repeated-measures one-way ANOVA, $p>0.05$). Lastly, the initial thermal stratification over the daily variation in the end of the dry season (September 2005) significantly showed, on average, pO_2 about eightfold higher, pCO_2 about 2.5-fold lower, and RI around twofold higher comparing surface (100 or 10% light penetration) and deep (1% or 0% light penetration) waters of both lakes (Fig. 6; Tukey-Kramer, $p<0.05$), with RI values once again ≤ 0 in the deep waters (Figs. 4 and 6).

Lake Aguapé showed significantly higher (almost two-fold) chlorophyll-a and TOC concentrations, on average (± SE), 19.1 (± 1.7) $\mu g\ L^{-1}$ and 10.4 (± 0.3) $mg\ L^{-1}$ respectively, than Lake Barra, on average (± SE), 12.0 (± 1.0) $\mu g\ L^{-1}$ and 5.5 (± 0.2) $mg\ L^{-1}$ respectively (Dunn, $p<0.05$). Any significant difference was not observed among sampling depths for TOC and chlorophyll-a in each lake (Dunn, $p>0.05$).

The negative relationship between pO_2 and pCO_2 were significant but weak for waters from Lake Barra and Lake Aguapé ($R_{Spearman}$ = -0.37 and -0.38 respectively; Spearman correlation, $p<0.05$). Additionally, pO_2, pCO_2 and RI in waters from all depths showed non-significant relationships with chlorophyll-a̲ and TOC in both lakes (Spearman correlation, $p>0.05$), except weak significant correlations of pO_2 with chlorophyll-a̲ and TOC ($R_{Spearman}$ = 0.33 and -0.23 respectively) or RI with chlorophyll-a̲ ($R_{Spearman}$ = 0.17) in Lake Aguapé (Spearman correlations, $p<0.05$).

4 Discussion

Overall, Lake Barra and Lake Aguapé showed a consistent prevalence of pCO_2 above and pO_2 below the equilibrium with the atmosphere, resulting in low RI to aquatic organisms. The persistence of CO_2 emissions to the atmosphere during the study reached, on average (± SE), 2.3 (± 0.3) mmol m^{-2} h^{-1}, assuming air-water fluxes calculated as Cole and Caraco (1998), a pCO_2 in equilibrium with the atmosphere of 380 µatm and a mean 10-m wind speed over land of 3.28 m s^{-1} (Archer and Jacobson, 2005). This confirms that the typical role of terrestrial C inputs subsiding organic degradation and CO_2 supersaturation in most lakes around the world (Cole et al., 1994;Cole et al., 2007;Duarte and Prairie, 2005) might be also found in inland waters of the Atlantic Tropical Forest.

Indeed, the negative relationship between pO_2 and pCO_2 also supported the potential role of the balance between aquatic respiration and photosynthesis in regulating the production and consumption of metabolic gases in waters of both lakes studied here. This was confirmed in the lake with higher chlorophyll-a̲ and TOC concentrations (Lake Aguapé), as expected significant relationships were found between chlorophyll-a̲ (algal biomass) and increases in O_2 and RI, probably from oxygenic photosynthesis (Carignan et al., 2000). However, all these significant correlations were weak, coupled to other non-significant relationships between chlorophyll-a̲ or TOC with pO_2, pCO_2 or RI in Lake Barra and Lake Aguapé. These weakly significant and non-significant correlations suggest that other dynamics than the balance between aquatic photosynthesis and respiration might drive high fluctuations in metabolic gases, strongly reducing the negative relationship between metabolic gases, pO_2 and pCO_2, in both lakes. The C inputs from the watershed (Marotta et al., 2010b), and anaerobic (Conrad et al., 2011) or physical-chemical (Amado et al., 2007) organic degradation processes may enhance CO_2 without consuming O_2 in natural waters. In addition, anoxygenic photosynthesis may be responsible for the decoupling between CO_2 fixation and O_2 production (Fontes et al., 2011). After the aerobic organic degradation reducing O_2 supply (Vaquer-Sunyer and Duarte, 2008;Sobek et al., 2009), intense anaerobic pathways subsidized by high allochthonous organic inputs may decrease RI to negative values ($RI \leq 0$) (Brewer and Peltzer, 2009) or release toxic compounds (Diaz and Rosenberg, 2008) to critical levels to major organisms in aquatic ecosystems.

The prevalence of high pCO_2 and low pO_2 also revealed highly dynamic fluctuations in metabolic gases and RI in waters of both lakes during 19 months. Substantial changes in pCO_2, pO_2 and RI were closely related to seasonal patterns of water stratification and mixing. Natural shifts from stratified and anoxic to oxic and mixed conditions were observed throughout the year in deep waters of both lakes. On the other hand, surface waters showed a contrasting decline in O_2 and RI following the mixing with deep waters during a mixing period in the beginning of the dry winter. Higher temperatures in the summer stimulating biological activity (Brown et al., 2004;Clarke and Fraser, 2004) might explain more intense increases reported here for O_2 and RI in the surface photic zone, probably by primary producers, and stronger decreases for both (O_2 and RI) in deep waters, probably by light limitation to oxygenic photosynthesis (Gu et al., 2011;Fontes et al., 2011). These results confirm the high temporal variability of metabolic gases described in previous studies on tropical lake waters, which related typical warmer temperatures at low latitudes to large shifts in biological processes, following common changes in meteorological and physical-chemical conditions over time (Marotta et al., 2010b;Marotta et al., 2010a).

In conclusion, we confirm the hypothesis, as thermal stratification events were coupled to hypoxia, reaching anoxia in deep waters of both studied lakes. Indeed, our results consistently suggest a natural susceptibility of deep waters in oligotrophic lakes of the Atlantic Tropical Forest to anoxia and low RI (reaching values < 0) mainly during the summer. These conditions in aquatic ecosystems typically result in low biological diversity (Brewer and Peltzer, 2009;Diaz and Rosenberg, 2008;Vaquer-Sunyer and Duarte, 2008) and high production of CO_2 and other more powerful greenhouse gases (Conrad et al., 2011;Bastviken et al., 2011). Here, the natural water mixing during the beginning of the dry winter showed a reversal oxygenation and increase of RI in deep waters, coupled to the opposite trend at the surface without reaching severe hypoxia throughout the water column. This illustrates that tropical lakes could be very dynamic, but also especially sensitive to organic inputs, which are commonly intensified by human activities in the watershed, like from untreated discharges of sewage and animal manure (Downing and McCauley, 1992). Natural events of anoxia under warm temperatures in tropical waters indicate, therefore, that human-induced organic inputs could potentially contribute to persistence of low O_2 supply and RI resulting in CO_2 evasion to the atmosphere. Studies on the fluctuations of metabolic gases, like O_2 and CO_2, related to hypoxia at low latitudes are crucial to a better knowledge on the controls and feedbacks of two relevant topics that are often intensified by human activities in broad areas, the organism's death and greenhouse gases emissions in aquatic ecosystems.

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Figure Legends

Figure 1: Geographic locations of the studied lakes surrounded by Atlantic Tropical Forest in Southeast Brazil: (1) Lake Barra and (2) Lake Aguapé.

Figure 2: Monthly fluctuations in 30-day precipitation (A) and water temperature in Lake Barra (B) and Lake Aguapé (C) during 19 months from March 2004 to October 2005. Four depths were sampled in the morning assuming the light penetration in lake waters: 100% (unbroken line, filled circle), 10% (unbroken line, filled triangle), 1% (dashed line, open circle), and 0% (dashed line, crosses). See material and methods for details on the determination of each sampling depth. Arrows point to the thermal mixing events during the dry season in the beginning of the winter (2004 and 2005), and the dotted frame indicate the rainy seasons (between 2004 and 2005) in each lake.

Figure 3: Monthly fluctuations in pO_2 (A and D), pCO_2 (B and E) and respiration index (C and F) in Lake Barra and Lake Aguapé, respectively, during 19 months from March 2004 to October 2005. Symbols, arrows and the dotted frame are as defined in Fig. 2. The dash-dot line represents the pO_2 (A and D) or pCO_2 (B and E) in equilibrium with the atmosphere and the critical limit for RI (C and F) to major aquatic organisms (Brewer and Peltzer, 2009). Negative values of RI indicate a ratio $pO_2{:}pCO_2 < 1.0$.

Figure 4: Vertical profiles of daytime pO_2, pCO_2 and respiration index from the lake surface to deep waters for Lake Barra (unbroken line, filled squares) and Lake Aguapé (dashed line, crosses) during a thermal stratification event in the rainy season (March/2005). Values are the average ± standard error (SE). The same letters indicate non-significant differences among treatments ($p<0.05$, Tukey–Kramer).

Figure 5: Vertical profiles of daytime pO_2, pCO_2 and respiration index from the lake surface to deep waters for both lakes during a thermal mixing event in the dry winter (June/2005). Values are the average ± SE. Symbols and letters are as defined in Fig. 4.

Figure 6: Vertical profiles of daytime pO_2, pCO_2 and respiration index from the lake surface to deep waters for both lakes during initial thermal stratification events in the end of the dry season (September/2005). Values are the average ± SE. Symbols and letters are as defined in Fig. 4.

Figure 1

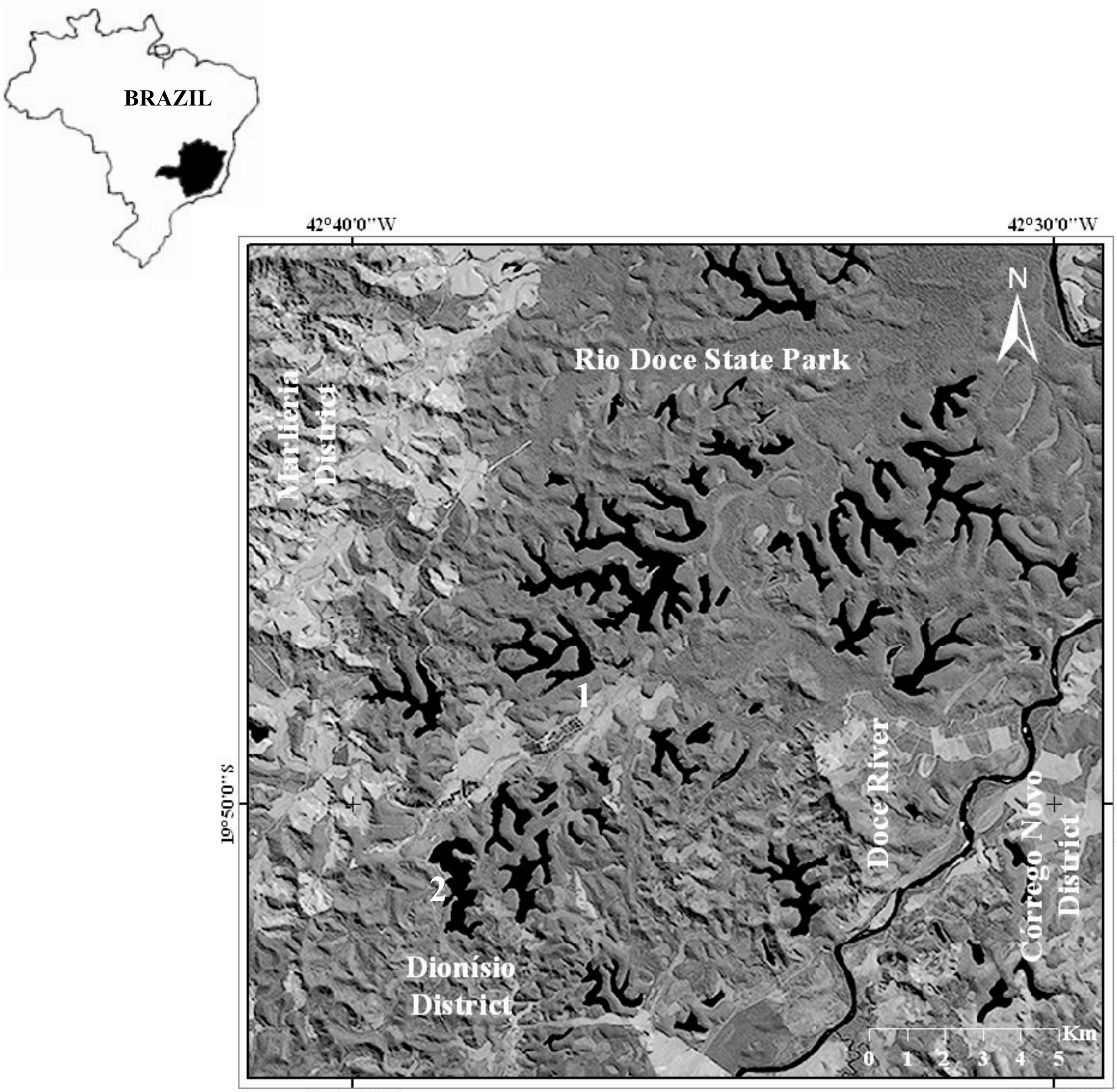

BRAZIL
42°40'0''W
42°30'0''W
N
Rio Doce State Park
Marliéria District
1
Doce River
19°50'0''S
2
Córrego Novo District
Dionísio District
Km
0
1
2
3
4
5

Figure 2

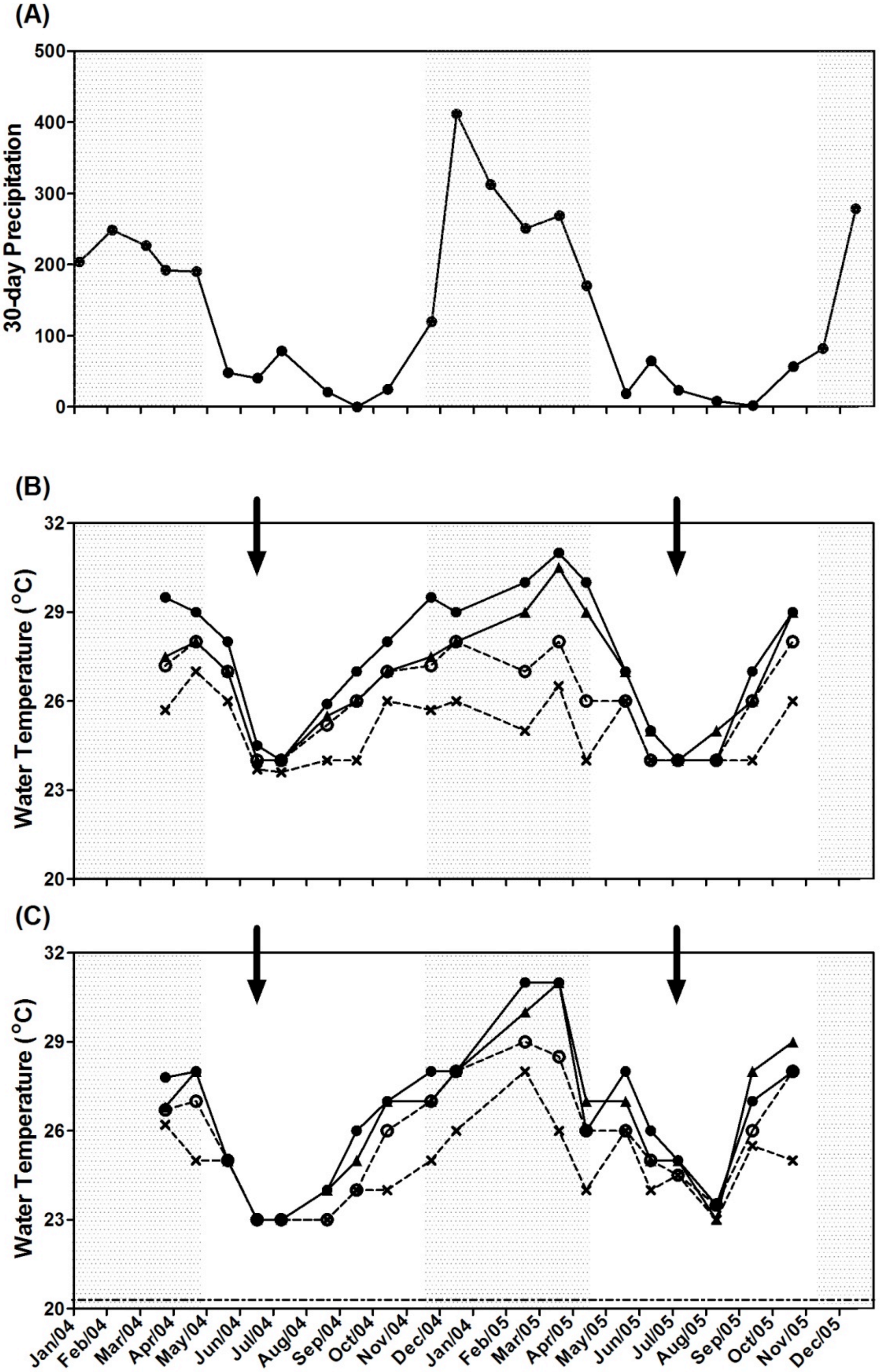

(A)
500
400
300
200
100
0
30-day Precipitation
(B)
32
29
26
23
20
Water Temperature (°C)
(C)
32
29
26
23
20
Water Temperature (°C)
Jan/04
Feb/04
Mar/04
Apr/04
May/04
Jun/04
Jul/04
Aug/04
Sep/04
Oct/04
Nov/04
Dec/04
Jan/04
Feb/05
Mar/05
Apr/05
May/05
Jun/05
Jul/05
Aug/05
Sep/05
Oct/05
Nov/05
Dec/05

Figure 3

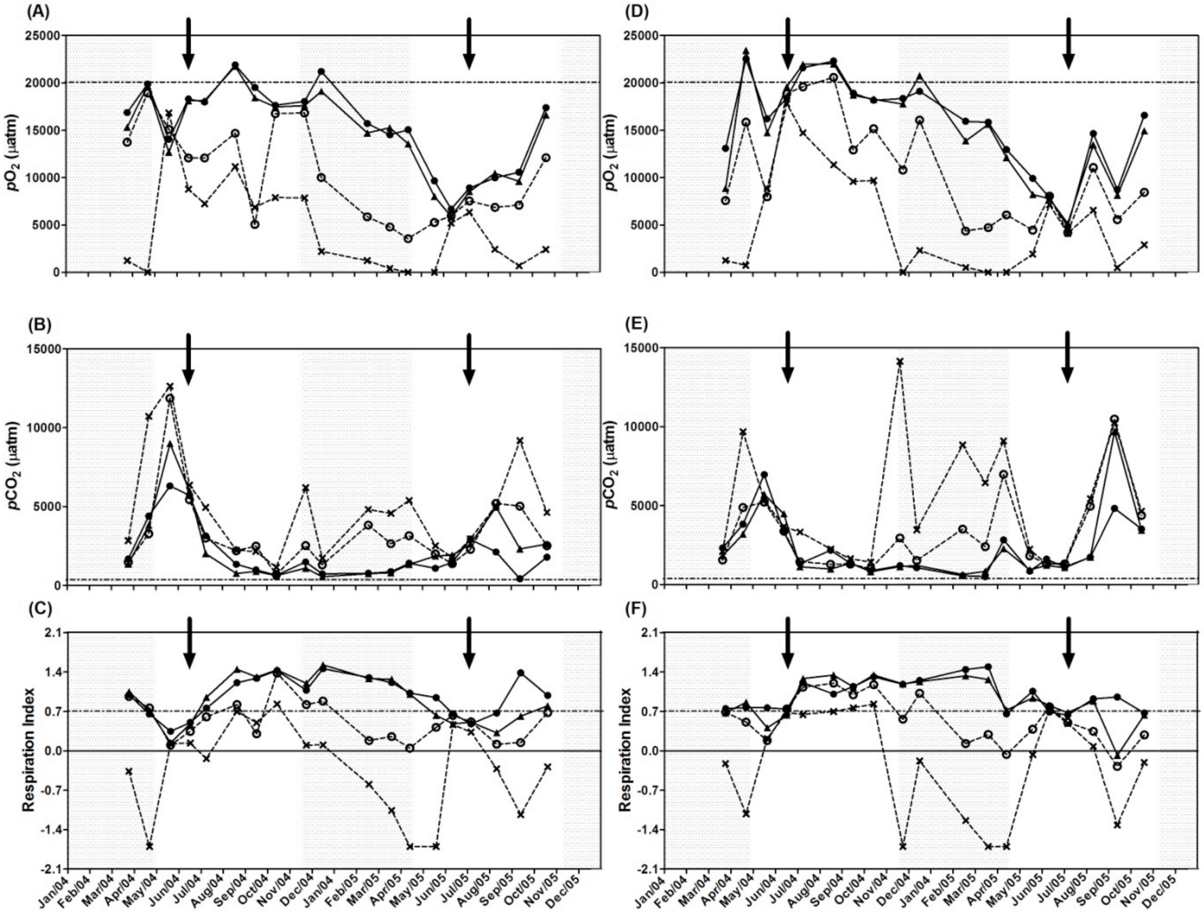
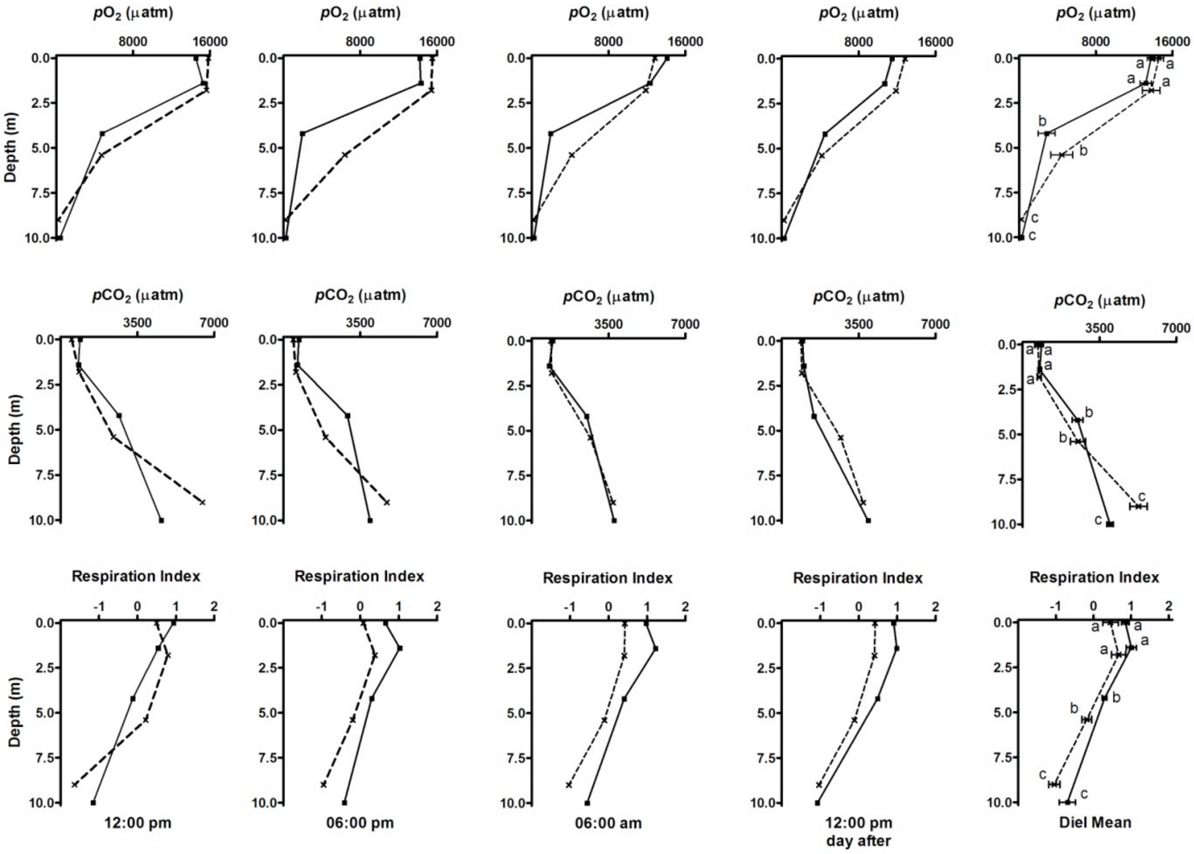

(A)
(B)
(C)
(D)
(E)
(F)
pO_2 (μatm)
pCO_2 (μatm)
Respiration Index
25000
20000
15000
10000
5000
0
15000
10000
5000
0
2.1
1.4
0.7
0.0
-0.7
-1.4
-2.1
Jan/04
Feb/04
Mar/04
Apr/04
May/04
Jun/04
Jul/04
Aug/04
Sep/04
Oct/04
Nov/04
Dec/04
Jan/04
Feb/05
Mar/05
Apr/05
May/05
Jun/05
Jul/05
Aug/05
Sep/05
Oct/05
Nov/05
Dec/05

Figure 4



pO2 (μatm)
8000
16000
pCO2 (μatm)
3500
7000
Respiration Index
-1
0
1
2
Depth (m)
0.0
2.5
5.0
7.5
10.0
a
b
c
12:00 pm
06:00 pm
06:00 am
12:00 pm
day after
Diel Mean

Figure 5

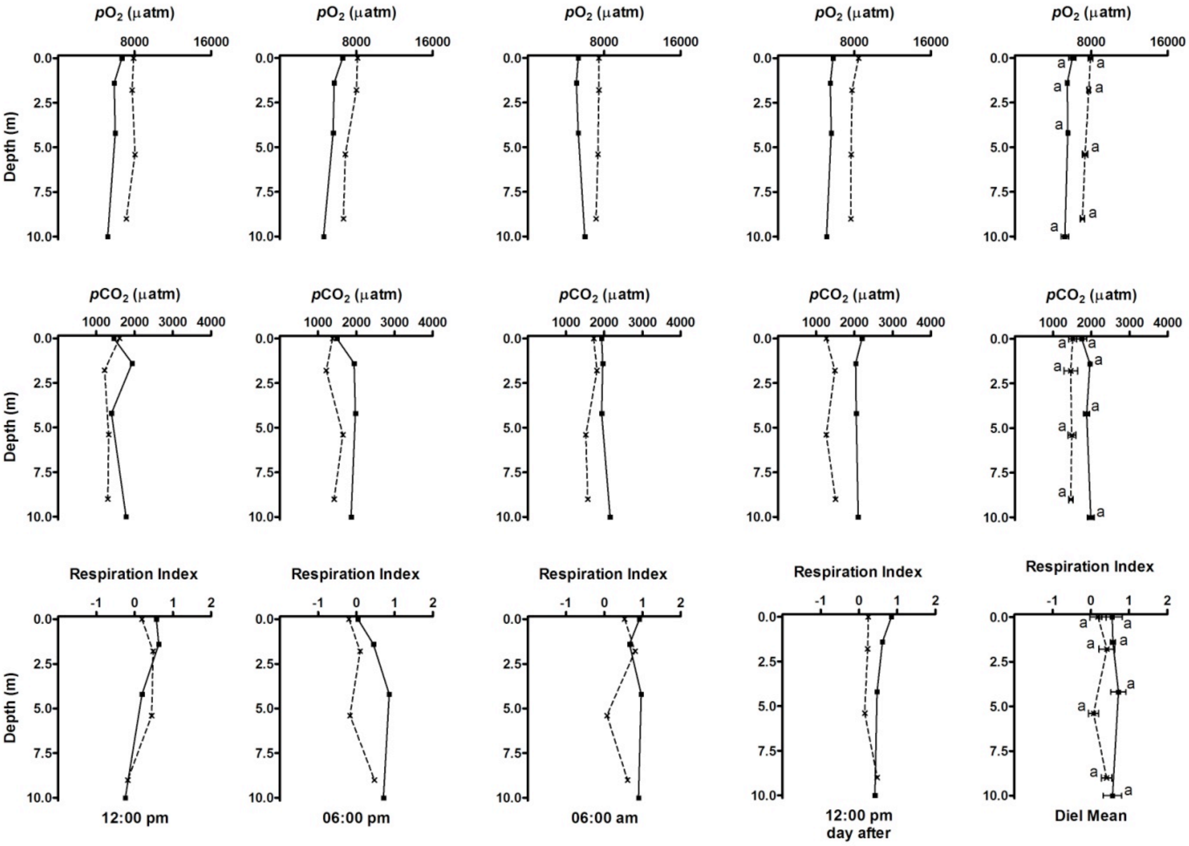
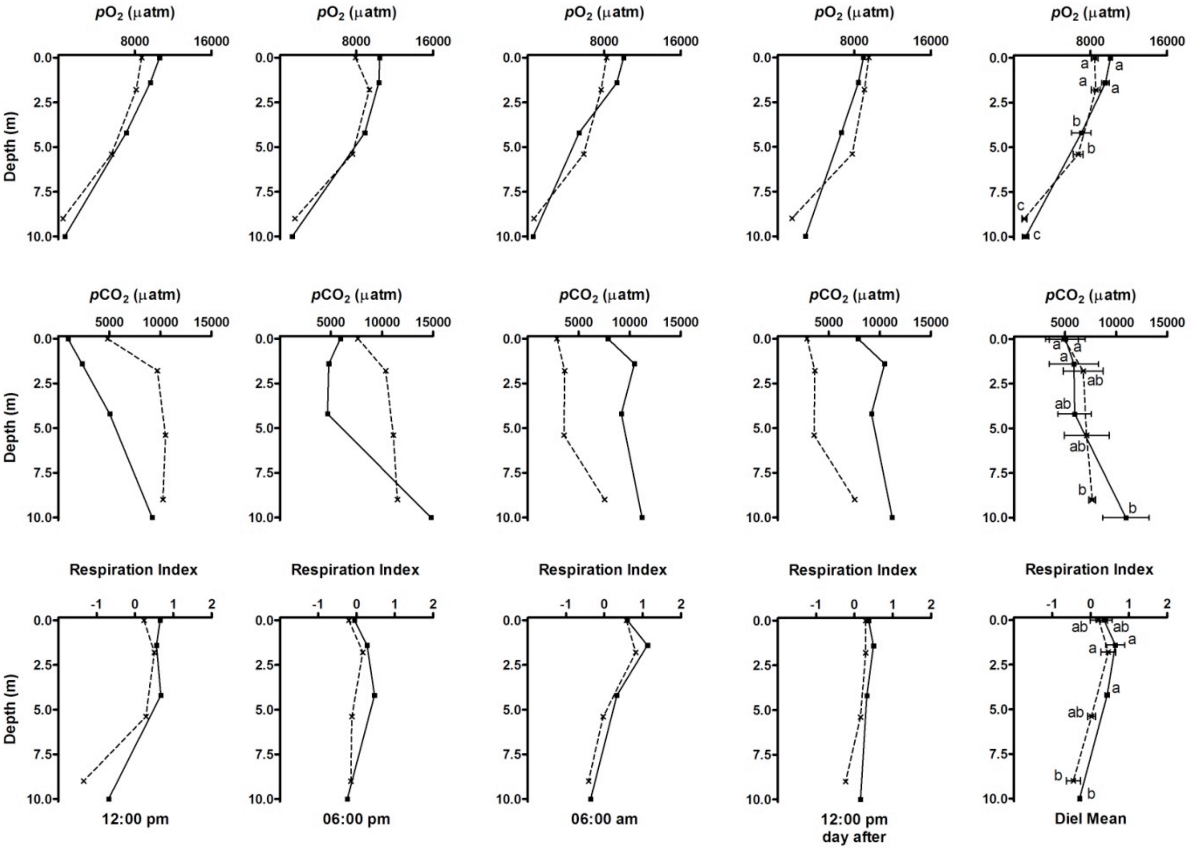

pO₂ (μatm)
8000
16000
pCO₂ (μatm)
1000
2000
3000
4000
Respiration Index
-1
0
1
2
Depth (m)
0.0
2.5
5.0
7.5
10.0
a
12:00 pm
06:00 pm
06:00 am
12:00 pm
day after
Diel Mean

Figure 6



pO$_2$ (μatm)
8000
16000
pCO$_2$ (μatm)
5000
10000
15000
Respiration Index
-1
0
1
2
Depth (m)
0.0
2.5
5.0
7.5
10.0
a
b
c
ab
12:00 pm
06:00 pm
06:00 am
12:00 pm day after
Diel Mean