Seasonal Variability of Carbon Dioxide in the Rivers and Lagoons of Ivory Coast (West Africa)

Y. J. M. Koné · G. Abril · K. N. Kouadio · B. Delille · A. V. Borges

Abstract We report partial pressure of CO_2 (pCO_2) and ancillary data in three rivers (Bia, Tanoé, and Comoé) and five lagoons (Tendo, Aby, Ebrié, Potou, and Grand-Lahou) in Ivory Coast (West Africa), during four cruises covering the main climatic seasons. The three rivers were oversaturated in CO_2 with respect to atmospheric equilibrium, and the seasonal variability of pCO_2 was due to dilution during the flooding period. Surface waters of the Potou, Ebrié, and Grand-Lahou lagoons were oversaturated in CO_2 during all seasons. These lagoons behaved similarly to the oligohaline regions of macrotidal estuaries that are CO_2 sources to the atmosphere due to net ecosystem heterotrophy and inputs of riverine CO_2 rich waters. The Aby and Tendo lagoons were undersaturated in CO_2 with respect to the atmosphere because of their permanent haline stratification (unlike the other lagoons) that seemed to lead to higher phytoplankton production and export of organic carbon below the pycnocline.

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Introduction

Despite the small surface area covered by coastal ecosystems (7% of the global ocean surface area), they host between 10% and 30% of the global marine primary production, and they account for 80% of oceanic organic matter burial (Gattuso et al. 1998; Wollast 1998). Overall continental seas are net sinks for atmospheric CO_2 although there are strong regional differences in the direction of the air–sea CO_2 fluxes, with tropical and subtropical systems acting as sources of CO_2 to the atmosphere and mid- and high-latitude systems acting as sinks for atmospheric CO_2 (Borges 2005; Borges et al. 2005; Cai et al. 2006; Chen and Borges 2008). However, near-shore coastal ecosystems are in general sources of CO_2 to the atmosphere due to the influence of inputs from land (Abril and Borges 2004; Borges 2005; Borges et al. 2005, 2006; Chen and Borges 2008). There is a scarcity of air–water CO_2 flux data in coastal environments at subtropical and tropical latitudes that receive about 60% of the global freshwater discharge and an equivalent fraction of riverine organic inputs (e.g., Ludwig et al. 1996a; Richey 2004). There is also a lack of information on air–water CO_2 fluxes in some coastal ecosystems, such as lagoons where the few studies of carbon cycling have focused solely on the ecosystem metabolism (e.g., Boucher et al. 1994; Carmouze et al. 1998; Sidinei et al. 2001; McGlathery et al. 2001; Hung and Hung 2003).

Lagoons are among the most common near-shore coastal environments occupying 13% of the World's coastline (Kjerfve 1985). These ecosystems are difficult to define,

and there are no generally accepted criteria which unambiguously separate them from bays, estuaries, marshes, and other parts of the coastal zone. In general, they are characterized by their shallow depth (<5 m), limited exchanges with the adjacent ocean and a high net primary production (Boynton et al. 1996). Like the coastal zone of which they are an integral part, lagoons are subjected worldwide to increased nutrient inputs due to anthropogenic activities such as modification of land use, effluent disposal, and aquaculture (Caumette et al. 1996). The resulting eutrophication leads to the proliferation of macrophytes and the enhancement of phytoplankton blooms in lagoons (Sidinei et al. 2001). The decomposition of the increased plant biomass and of the anthropogenic carbon may lead to the emission of CO_2 to the atmosphere from lagoons.

The input of dissolved inorganic carbon (DIC) from rivers contributes to the CO_2 dynamics in estuaries and lagoons. Rivers are in general oversaturated in CO_2 with respect to atmospheric equilibrium (Kempe 1982; Cole and Caraco 2001) due to the input of soil CO_2 by rain and groundwater and to the in situ degradation of organic matter in excess of primary production. Dynamics of pCO_2 in rivers are modulated seasonally by primary production, temperature effect on the CO_2 solubility, dilution during flooding periods, and exchange of CO_2 with the atmosphere.

In the present work, we report DIC and ancillary data obtained in five lagoons (Tendo, Aby, Ebrié, Potou, and Grand-Lahou) in Ivory Coast (West Africa) and three rivers (Bia, Tanoé, and Comoé) flowing into these lagoons

(Fig. 1), during the four characteristic seasons (Fig. 2). The three studied rivers are the most important in Ivory Coast in terms of freshwater discharge excepted for the Bandama (Table 1). The studied lagoons differ by the variable density of the riparian population, by different freshwater inputs (Table 1), and by physical settings (permanent or seasonal stratification). Hence, the studied lagoons are representative of most of the kinds of lagoons that can be encountered in West Africa and at tropical latitudes. The present study allows characterizing the differences in the cycling of CO_2 in a wide range of types of tropical lagoons, provides the range of seasonal variability of pCO_2 and air–water CO_2 fluxes over an annual cycle.

Material and Methods

Description of Study Area

Lagoons are the most prominent coastal ecosystems of Ivory Coast (Fig. 1) covering an area of 1,200 km², which corresponds to a large fraction of the surface area of lagoons in West Africa (5,000 km²; Binet et al. 1995). They are gathered in three systems (Ebrié, Grand-Lahou, and Aby) and stretch along some 300 km of the coastline. The density of the riparian population is variable ranging from 3.5 inhabitants km^{-2} around the Aby lagoon system to ~100 inhabitants km^{-2} around the Ebrié lagoon system (Jallow et al. 1999).
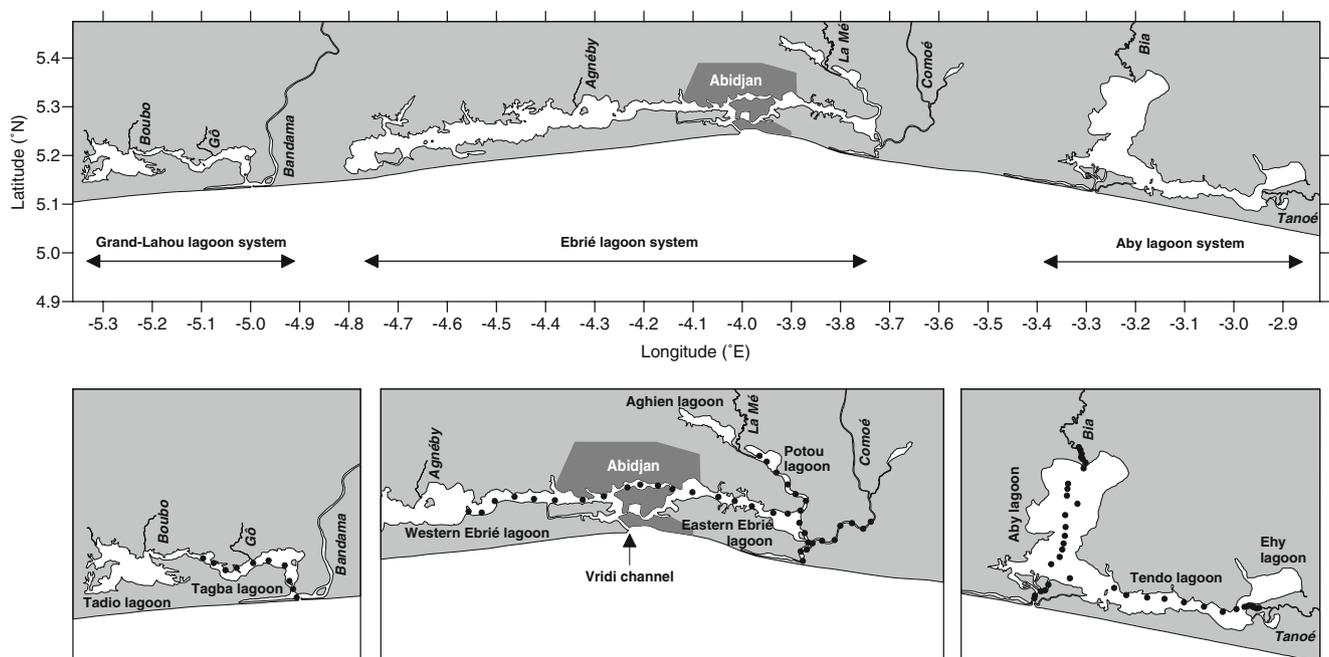

Fig. 1 Map showing the location of lagoons and rivers in Ivory Coast and the sampling stations (*bottom panels*)
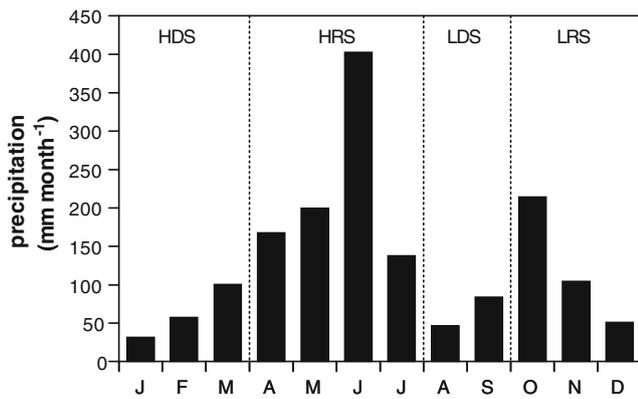
Fig. 2 Average monthly rainfall (mm month^{-1}) during 2000–2006 at Adiaké station (−3.3° E 5.28° N) close to Aby lagoon, obtained from the Direction Météorologique d'Adiaké. *HDS* high dry season, *HRS* high rainy season, *LDS* low dry season, *LRS* low rainy season

The climate is close to equatorial, with an annual rainfall ranging from 1,500 to 1,800 mm, characterized by two rainy seasons and two dry seasons (Durand and Skubich 1982). The high dry season extends from January to March, the high rainy season from early April to late July, the low dry season from August to September, and the low rainy season from October to December (Fig. 2).

The rivers flowing into these lagoons have two different hydrological regimes (Iltis and Lévêque 1982; Jallow et al. 1999). The Tanoé, the Bia, the La Mé, and the Agnéby rivers have an equatorial transition regime with two flooding periods in June–July and October–November. The Comoé and Bandama rivers have a mixed regime with only one flooding period during September–October. The lithology of the drainage basin of the three rivers is different: In the Comoé, it is composed of 63% plutonic acids, 26% of Precambrian basement, and 11% consolidated siliciclastic rocks; in the Bia, it is composed of 67% of Precambrian basement, 17% plutonic acids, and 16% semi- to unconsolidated sedimentary; in the Tanoé, it is exclusively composed of Precambrian basement (Dürr et al. 2005).

The Ebrié lagoon system (Fig. 1) is the largest lagoon in West Africa (Adingra and Arfi 1998). It is an elongated

lagoon system with a total area of 566 km^2, and it stretches for ~130 km, with a maximum width of ~7 km. The average depth is of 4.8 m, with a few deep areas especially around Abidjan (27 m south of Boulay Island). It is divided into three lagoons—Potou, Aghien, and Ebrié—and receives freshwater from the Comoé, Agnéby, and La Mé rivers (Fig. 1; Table 1). Annual freshwater input from the Comoé river is estimated to ~7 km^3 that represents approximately three times the total volume of the lagoon system (Table 1), while the flow of seawater is ~14 times this volume (Durand and Guiral 1994). Salinity in the system varies between 0 and 35. Before 1951, the Ebrié lagoon system was only connected to the Atlantic Ocean through the Bassam inlet in the far east of the lagoon system (40 km away from Abidjan). The Vridi Channel was built in 1951 allowing a connection to the sea closer to Abidjan, greatly modifying the hydrological environment since the Bassam inlet has progressively closed, and nowadays, the Comoé river discharges into the lagoon system rather than directly to the sea. The Ebrié lagoon system is strongly polluted by domestic and industrial waste water inputs (Kouassi et al. 1995; Adingra and Arfi 1998). The waters around Abidjan are highly eutrophicated leading to frequent oxygen depletion, massive fish kills, and repelling sulfuric smells (Kouassi et al. 1995; Scheren et al. 2004) and have been included in a recent compilation of coastal "dead zones" (Diaz and Rosenberg 2008).

The Aby lagoon system consists of the main Aby lagoon, the Tendo lagoon, and the Ehy lagoon and receives freshwater from the Bia and the Tanoé rivers, respectively, in the northwest and in the east (Fig. 1). The Aby lagoon system is located in the far east of Ivory Coast and forms a natural border with Ghana, extends over 30 km of the coastline and occupies over an area of 424 km^2. The main Aby lagoon (hereafter Aby lagoon) is the largest and covers 305 km^2, with a total shoreline of 24.5 km and a maximal width of 15.5 km. The Tendo lagoon has a length of 22 km and a width varying between 1.5 and 3.5 km and a surface area of 74 km^2. The Ehy lagoon has a mean depth of 1.5 m and a surface area of 45 km^2. The Aby and Tendo lagoons

Table 1 Some relevant characteristics of the Tendo, Aby, Ebrié, Potou, and Grand-Lahou lagoons and of the main rivers (Tanoé, Bia, Comoé, La Mé, Agnéby, and Bandama) flowing into these lagoons, based on Chantraine (1980), Durand and Chantraine (1982), and Durand and Skubich (1982)

Lagoons	Area (km^2)	Volume (km^3)	Mean depth (m)	Surface salinity	Rivers	Total length (km)	Drainage area (km^2)	Mean water discharge (m^3 s^{-1})
Tendo	74	0.2	2.7	0–8	Tanoé	625	16,000	132
Aby	305	1.3	4.2	1–8	Bia	290	9,650	59
Ebrié	524	2.6	4.8	0–35	Comoé	1,160	78,000	224
					Agnéby	200	8,900	27
Potou	22	0.03	2.7	0–6	La Mé	140	4,300	47
Grand-Lahou	190	0.5	2.0	0–26	Bandama	1,050	97,000	298

pH, DIC (mmol kg⁻¹), pCO₂ (ppm), chlorophyll-a (µg L⁻¹), NO₃⁻
(µmol L⁻¹), PO₄³⁻ (µmol L⁻¹), and Si (µmol L⁻¹) in Aby (−3.231° E
5.228° N) and Tendo (−3.110° E 5.142° N) lagoons during the high
dry season (March)

are characterized by permanent haline stratification (Fig. 3)
unlike the other two lagoon systems that are seasonally
stratified.

The Grand-Lahou lagoon system (Tagba and Tadio
lagoons) is located in the far west of the coast and is the
smallest of the Ivory Coast lagoon systems with an area of
190 km² (Fig. 1; Table 1). It receives freshwater from the
Bandama river and from the smaller Gô and Boubo rivers.

Sampling, Analytical Techniques, and Statistics

Four cruises were carried out (08 June to 07 July 2006, 06–
22 September 2006, 24 November to 13 December 2006,
08–30 March 2007) to sample five lagoons (Tendo, Aby,
Ebrié, Potou, and Grand-Lahou) and three rivers (Tanoé,
Bia, and Comoé). The cruise in June–July is representative
of the high rainy season, the cruise in September of the low
dry season, the cruise in November–December of the low
rainy season, and the cruise in March of the high dry season
(Fig. 2). On average for each cruise, eight samples were
obtained in the Comoé river, eight samples in the Bia river,
eight samples in the Tanoé river, ten samples in the Grand-
Lahou lagoon, 16 samples in the Aby lagoon, six samples
in the Potou lagoon, 23 samples in the Ebrié lagoon, and
eight samples in the Tendo lagoon (Fig. 1).

Subsurface waters (depth ~30 cm) were sampled with a
1.7-L Niskin bottle and pH measurements were carried out
immediately after collection, with a combined electrode
(Metrohm 6.0232.100) calibrated on the US National
Bureau of Standards scale as described by Frankignoulle
and Borges (2001), with a precision and estimated accuracy
of ±0.001 and ±0.005 pH units, respectively. Salinity and
water temperature were measured in situ using a portable
conductivity meter (WTW Cond-340) with a precision of
±0.1 and ±0.1°C, respectively. A volume of 100 mL was
filtered through 0.2 µm pore size polysulfone filters and
was stored at ambient temperature in polyethylene bottles
for the determination of total alkalinity (TA). TA was
measured within 1 month after sampling, on 50 mL samples
by automated Gran electro-titration with 0.1 M HCl as
titrant, with a reproducibility of ±3 µmol kg⁻¹. Measure-
ments of TA and pH were used to compute pCO₂ and DIC,
with an estimated accuracy of ±4 ppm and ±4 µmol kg⁻¹,
respectively (Frankignoulle and Borges 2001).

Air–water fluxes of CO₂ were calculated according to:

$$F = \alpha k \Delta pCO_2$$
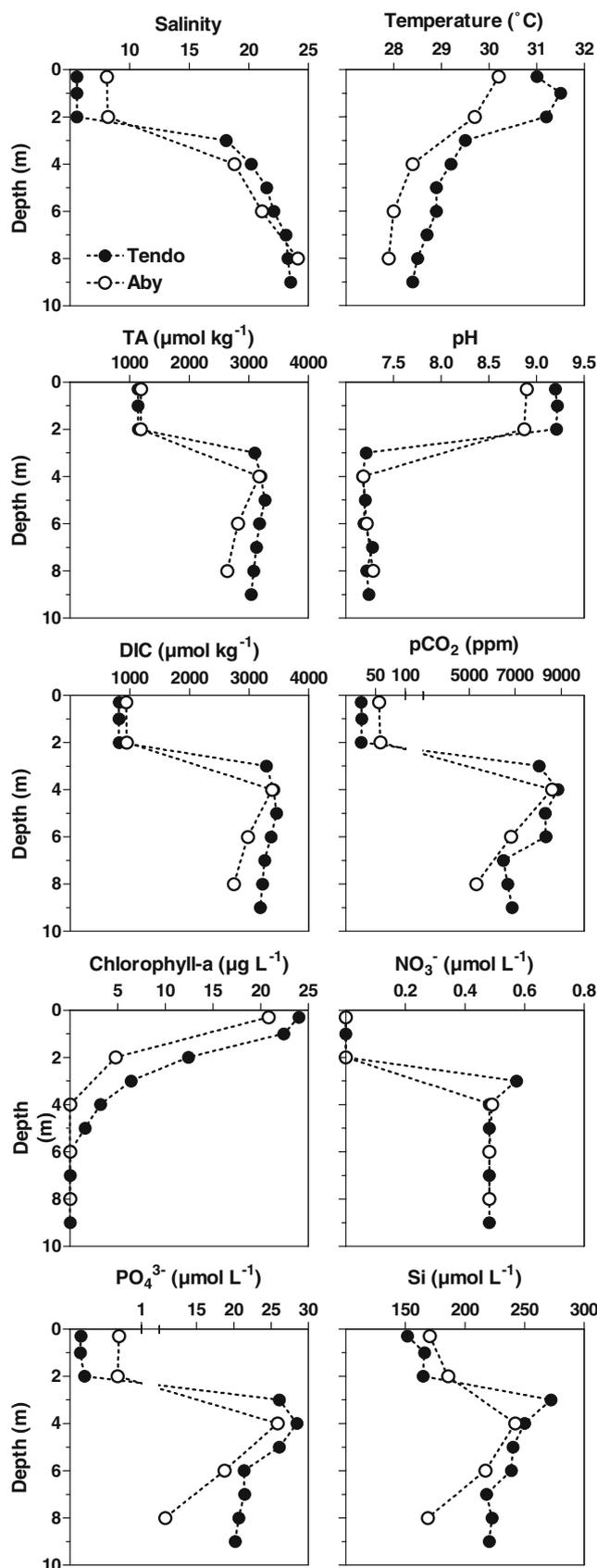
where α is the solubility coefficient of CO_2, k is the gas transfer velocity of CO_2, and ΔpCO_2 is the air–water gradient of pCO_2.

We computed k using the wind speed field measurements and the "tracers only" parameterization given by Raymond and Cole (2001). Wind speed was measured at each sampling station with a hand-held anemometer.

Water samples for nitrate (NO_3^-), phosphate (PO_4^{3-}), and silicate (Si) measurements were filtered through cellulose acetate filters (Sartorius), refiltered through 0.2 μm pore size polysulfone filters, and preserved with $HgCl_2$ (for NO_3^- and PO_4^{3-}) and HCl for Si. Concentrations of NO_3^- were measured on a Technicon Auto Analyser II (Tréguer and Le Corre 1975), with an estimated accuracy of ±0.1 μmol L^{-1}. Concentrations of PO_4^{3-} and Si were measured with the standard colorimetric methods (Grasshoff et al. 1983), with an estimated accuracy of ±0.01 μmol L^{-1} and ±0.1 μmol L^{-1}, respectively.

Total suspended matter (TSM) data were obtained by filtering a known volume of water (250 to 500 mL) on preweighted glass fibber filters (Whatman GF/F), rinsed with deionized water to avoid salt contributions (for lagoon samples), and subsequently dried. Samples for chlorophyll-a concentrations were obtained by filtering a known volume of water (250 to 500 mL) on glass fibber filters (Whatman GF/F) that were frozen until analysis (−40°C). The pigments were extracted between 12 and 24 h in 15 mL of 90% acetone at 4°C, and after centrifugation, absorbance was measured at 665 and 750 nm, before and after acidification with 100 μL of HCl 0.1 M, according to the spectrophotometric method described by Lorenzen (1967). The estimated accuracy of chlorophyll-a concentration is ±5%.

Sample means were compared (across sampling sites in each season and across seasons within each site) statistically using a two-tailed unpaired Student t test, using Prism 4.00 (GraphPad). P values are not explicitly mentioned hereafter but "significant(ly)" refers to $P<0.05$, "very significant(ly)" refers to $P<0.01$, "highly significant(ly)" refers to $P<0.001$, and "not significant(ly)" refers to $P>0.05$ at 0.05 level.

Results and Discussion

Inorganic Carbon and Nutrient Dynamics in the Bia, Tanoé, and Comoé Rivers

Inorganic Nutrients and Suspended Matter Dynamics in the Three Rivers

Average Si concentration values in the three rivers ranged from 63 to 190 μmol L^{-1} (Fig. 4) in agreement with those reported in the same rivers by Iltis and Lévêque (1982). In the Tanoé and Bia rivers, average Si concentrations were very significantly to highly significantly higher during the high dry season than during the other seasons. In the Bia and Tanoé rivers, Si concentrations decreased during the flooding period due to dilution, while in Comoé river, Si concentrations increased during the flooding period. This different pattern could be due to the characteristic vegetation on the three drainage basins. The Comoé drainage basin is dominated by savannah and flooding most likely increases the export of vegetal debris that are rich in biogenic silica (phytoliths; Wilding et al. 1977; Conley et al. 2006). The Bia and Tanoé drainage basins are dominated by forests where there is a relatively efficient recycling and retention of silica by the vegetation (e.g., Conley 2002; Conley et al. 2006).

The average concentrations of NO_3^- and PO_4^{3-} in the three rivers ranged from 1.8 to 17.7 μmol L^{-1} and from 0.2 to 2.0 μmol L^{-1}, respectively (Fig. 4). Unlike Si, NO_3^- and PO_4^{3-} increased very significantly in the three rivers during the high rainy season (flooding) period due to increased leaching from soils. The average concentrations of NO_3^- were maximal in the three rivers during the high rainy season, while the average PO_4^{3-} concentrations showed a second seasonal maximum during the low rainy season in the Bia and Tanoé rivers but not in the Comoé river. This difference is related to the fact that the Comoé river has only one flooding period due to the more extended drainage basin, while the Bia and Tanoé rivers have two flooding periods. The average concentration of NO_3^- and PO_4^{3-} values are low compared to other rivers due to the fact that the Comoé, Bia, and Tanoé rivers do not receive domestic or industrial waste waters and because the use of agricultural fertilizers in the drainage basin is low.

TSM values in the three rivers ranged from 0 to 50 mg L^{-1} and were significantly to highly significantly higher during the flooding periods due to a substantial soil erosion (Fig. 4). In the three rivers, chlorophyll-a values were generally higher during the flooding periods, when inorganic nutrient availability was also higher. Chlorophyll-a showed a lower seasonal amplitude in the Tanoé and the Comoé rivers than in the Bia river. During the high rainy season and the low dry season, average chlorophyll-a concentrations were higher in the Bia river than in the Tanoé and the Comoé rivers. This is related to the fact that sampling in the Bia river was carried out 60 km downstream of the Ayamé dam. Hence, in the unregulated Comoé and Tanoé rivers, phytoplankton is flushed by the flow, while downstream of the Ayamé dam phytoplankton accumulates in the Bia river, due to a higher residence time of freshwater related to much lower (regulated) water discharge.
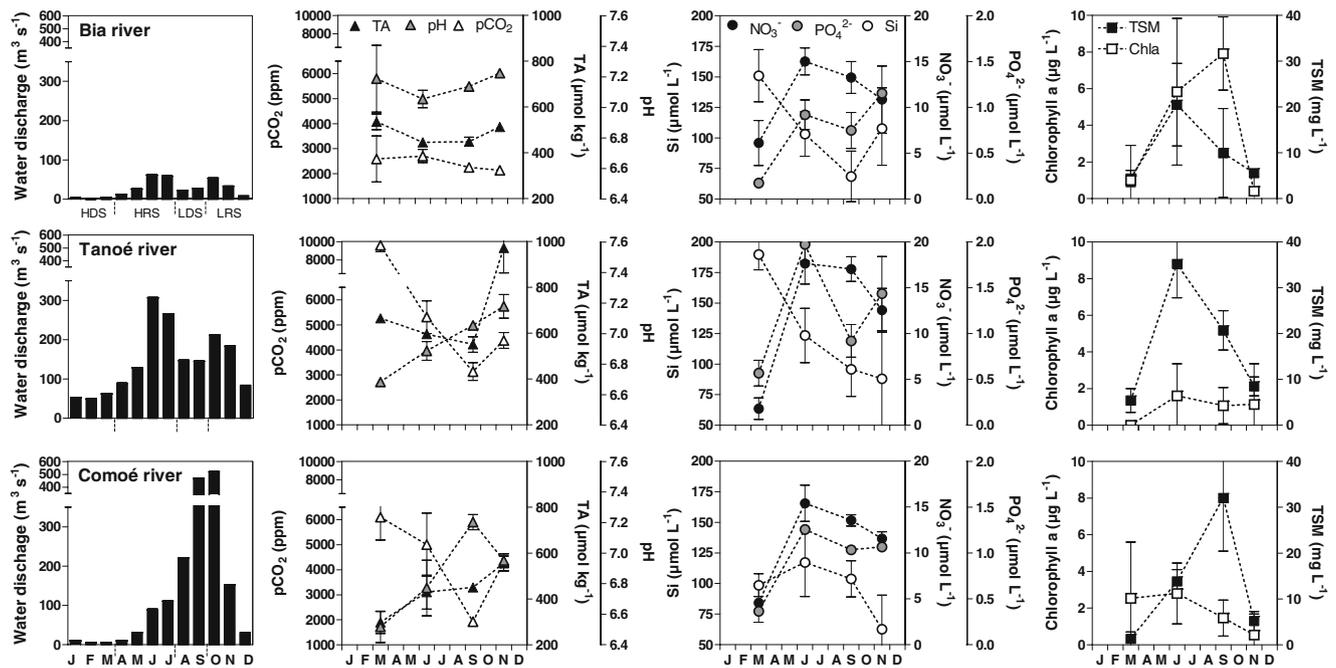
Fig. 4 Seasonal variations of average monthly freshwater discharge, TA (μmol kg^{-1}), pCO$_2$ (ppm), pH, NO$_3^-$ (μmol L^{-1}), PO$_4^{3-}$ (μmol L^{-1}), Si (μmol L^{-1}), chlorophyll-a concentration (μg L^{-1}), and TSM (mg L^{-1}) in the Bia ($n=8$), the Tanoé ($n=8$), and the Comoé ($n=8$) rivers, during the high dry season (March), the high rainy season (June), the low dry season (September), and the low rainy season (December). Average monthly freshwater discharge values during 2000–2005 measured at Bianou and Yakassé stations for Bia and Comoé rivers, respectively (data from the Direction de l'Eau d'Abidjan). Average monthly freshwater discharge values in Tanoé river are only available for 1978, at Alanda station (from the University of New Hampshire Global Runoff Data Centre database available at http://www.grdc.sr.unh.edu/). *Error bars* correspond to standard deviation on the mean

DIC Dynamics in the Three Rivers

The TA values in the three rivers were low (<1,000 μmol kg^{-1}; Fig. 4) due to the dominance of lateritic soils in the drainage basin (Mangin et al. 1966; Perraud, 1971), depleted in alterable minerals leading to low specific HCO$_3^-$ fluxes, as in most tropical rivers (Ludwig et al. 1996b; Cai et al. 2008). During the high dry season (March), average TA values in the Comoé river were highly significantly lower than in the other two rivers. The Comoé river has no large tributaries, so during the high dry season, its small tributaries become dry or form ponds, resulting in a very low freshwater discharge compared for instance with the Tanoé river (Fig. 4). The TA varied inversely with water discharge in the Tanoé and Bia rivers due to dilution during the flooding period. In the Comoé river, TA increased with water discharge probably due to the different lithology of the drainage basins: The drainage basin of Comoé is dominated by acid plutonic rocks with a small contribution from consolidated siliciclastic rocks, while the Bia and the Tanoé drainage basins are dominated by Precambrian basement.

The average pH values in the three rivers ranged from 6.52 to 7.22, and pH followed the reverse temporal variations of pCO$_2$ except during the low rainy season (December) in the Tanoé river when both pH and pCO$_2$ increased compared to the value during low dry season (September; Fig. 4). This is related to the increase of the buffering capacity of the water due to almost twofold increase of TA values in the Tanoé river from the low dry season (September) to the low rainy season (December). The average values of pCO$_2$ in the three rivers ranged from 1,925 to 9,595 ppm, always above atmospheric equilibrium. Seasonal variations of pCO$_2$ were large in the Tanoé and Comoé rivers, with the highest average values obtained during the high dry season (highly significantly) and lowest values during the flooding period (highly significantly), due to dilution (Fig. 4). It is unlikely that planktonic primary production contributed to the decrease of pCO$_2$ during the flooding period because of relatively low seasonal variability of chlorophyll-a and relatively low values of chlorophyll-a (average <3 μg L^{-1}) in the Tanoé and Comoé rivers. Further, the lowest pCO$_2$ values did not coincide with the maximal chlorophyll-a values in these rivers. Also, pCO$_2$ values during the flooding period were highly significantly lower in the Comoé river (<2,000 ppm) than in the Tanoé river (~3,000 ppm) due to the twice higher freshwater discharge in the Comoé river. In the Bia river, the decrease of pCO$_2$ during the flooding period was much less marked than in the Comoé and the Tanoé rivers due to flow

regulation by the Ayamé dam 60 km upstream of the sampling site. The dam strongly decreases the seasonal variations of freshwater discharge and smoothes over the annual cycle the impact of drainage of soil CO_2 by groundwater leading to lower amplitude of seasonal pCO_2 variations in the Bia compared to the other two rivers.

The seasonal cycle of pCO_2 in the Comoé and the Tanoé rivers followed the same pattern (strong decrease of pCO_2 during the flooding period due to dilution) as reported from the subtropical Xijiang river (pCO_2 range 600–7,200 ppm; Yao et al. 2007) and the tropical Niger river (pCO_2 range 1,210–6,310 ppm; Martin and Probst, 1991). This seasonal pattern is distinctly different from the one reported by Richey et al. (2002) in the Amazon where pCO_2 increases with rising water (up to 44,000 ppm) due to carbon inputs to the water during the inundation of the floodplain. The difference in seasonal patterns of pCO_2 between these subtropical and tropical rivers is related to the very large freshwater discharge of the Amazon river ($\sim$175,000 m^3 s^{-1}) and very extensive floodplains (up to 20 times the surface area of the mainstream channel). Furthermore, the seasonal pCO_2 cycle in the Comoé and the Tanoé rivers is also distinctly different from temperate rivers, where pCO_2 can be maximal during low water (summer) due to the effect of temperature change on the CO_2 solubility like in the York river (Raymond et al. 1997), or where pCO_2 can be minimal in summer in highly eutrophied rivers like the Loire due to intense phytoplankton blooms (Abril unpublished).

Role of Floating Macrophytes on DIC and Inorganic Nutrient Dynamics in the Rivers

In tropical rivers, the respiration and decomposition from floating and emerged macrophytes can constitute an important source of CO_2 to the water column. For instance, in the Amazon river, root respiration from and decomposition of floating and emerged macrophytes contribute to 25% of CO_2 evasion to atmosphere from the water column (Richey et al. 2002; Engle et al. 2008). Different macrophytes are present in the Comoé, Bia, and Tanoé rivers, such as *Eichhornia crassipes*, *Pistia stratoties*, and *Salvinia molesta* (Guiral and Etien 1994). The biomass of these macrophytes is $\sim$90 gC m^{-2} in the rivers and ranges between $\sim$90 and $\sim$150 gC m^{-2} in the lagoons (Guiral and Etien 1994) and can occupy between 1 and 100% of surface waters (Etien and Arfi 1996). The water hyacinth *E. crassipes* is an invasive species originating from the Amazon river with a capacity for growth and propagation that raises serious socioeconomic issues (Holm et al. 1991). *E. crassipes* affects water chemistry (temperature, pH, oxygen, and nutrients concentrations; Rai and Datta Mushi 1978) and organic matter flows (Poi de Neiffa et al. 1994).

During our sampling cruises, low densities of macrophytes were observed in the main stream and the inundation plains of the Bia and Comoé rivers. In the Comoé river, due to the large freshwater discharge, macrophytes are transported downstream to the adjacent lagoons, and in the Bia river, macrophytes accumulate upstream of our sampling site in Ayamé dam. In the Tanoé river, a strong proliferation of *E. crassipes* occurred during the high dry season (March), because of the low freshwater discharge, and macrophytes completely covered the mainstream of the river.

During the period of *E. crassipes* proliferation in the Tanoé, the average NO_3^- concentration was significantly lower (1.8±1.2 µmol L^{-1}; Fig. 4) than in the Bia and Comoé rivers at the same period (6.1±2.5 and 4.6± 2.1 µmol L^{-1}, respectively), most likely due to the efficient uptake of nutrients from the water column by the macrophytes (Reddy and De Busk 1985; Petrucio and Esteves 2000). Also, the shading effect of the macrophytes on the water column lead to undetectable chlorophyll-a concentrations in the Tanoé compared to 1 and 2 µg L^{-1} in the Bia and Comoé rivers, respectively, at the same period of the year. The combination of NO_3^- uptake by macrophytes and light limitation of phytoplankton production lead to a significantly higher Si/NO_3^- ratio (168) in the Tanoé than in the Bia and Comoé rivers at the same period of the year (52 and 31, respectively). The presence of macrophytes in the Tanoé river also lead to highly significantly higher pCO_2 values ($\sim$9,600 ppm) compared to the Comoé and Bia rivers during the same period ($\sim$6,100 and $\sim$2,600 ppm, respectively), due to root respiration and degradation of macrophyte organic matter. The presence of these emerged macrophytes leads to a net built up of CO_2 in the water column, since photosynthesis fixes atmospheric CO_2, while root respiration and degradation of macrophyte organic matter lead to a release of CO_2 in the water column.

Inorganic Carbon and Nutrient Dynamics in the Aby, Tendo Potou, Ebrié, and Grand-Lahou lagoons

Salinity and TA Variations in the Five Lagoons

Surface salinity in the five lagoons was highly significantly lower during the high rainy season (June) than the high dry season (March; Table 2), due to the higher freshwater input during this period of the year. Yet, salinity in the Aby lagoon was highly significantly higher during the high rainy season (June) than during the low dry season (September) and the low rainy season (December), unlike the Tendo, Ebrié, and Grand-Lahou lagoons. This could be due to the fact that, in the Aby lagoon, the high freshwater inputs during the high rainy season (June) lead to an erosion of the pycnocline due to the turbulence from the

flow and the partial mixing with surface waters of deep water with a much higher salinity (Fig. 3).

Whatever the season, surface salinity was significantly to highly significantly lower in the Potou, Aby, and Tendo lagoons than in the Ebrié and Grand-Lahou lagoons (except for the Aby lagoon during the high rainy season (June); Table 2). This is due to the fact that the Potou, Aby, and Tendo lagoons are in the direct continuation of the La Mé, Bia, and Tanoé rivers, respectively, hence strongly influenced by freshwater inputs, and they have a shallow connection with the adjacent marine systems. The surface salinity in the Grand-Lahou system was significantly to highly significantly higher than in the other lagoons during all seasons (except the high rainy season) because sampling was carried out close to the opening with the sea.

Surface salinity was high in the Ebrié lagoon (Table 2) because it is connected to the sea by the Vridi Channel. Surface salinity in the Ebrié lagoon had strong longitudinal gradients, with the highest salinities at the vicinity of the Vridi Channel (near Abidjan) and decreasing eastward due to the freshwater inputs from the La Mé and the Comoé rivers and westward due to the freshwater input from the Agnéby river (Fig. 5). The relative importance of the different freshwater inputs on the water masses in the Ebrié lagoon can be seen on the TA distribution as a function of salinity (Fig. 6). Whatever the season, TA was higher at a given salinity in the western side than in the eastern side of the Ebrié lagoon. This was due to the influence of the Agnéby river that had higher TA values than the Comoé and La Mé rivers. Indeed, the y-intercept of the linear regression of TA as a function of salinity for the western side of the Ebrié lagoon (indicative of TA in the Agnéby river) ranged from 670 to 777 μmol kg^{-1}, above the observed TA values in the Potou lagoon (influenced by the La Mé river) and the Comoé river (Fig. 6). In December and September, the TA values in the eastern side of the Ebrié lagoon, suggest that the Comoé river had a much larger influence on the oligohaline Ebrié lagoon than the La Mé river, in agreement with the very different average annual discharge values (47 and 224 m^3 s^{-1}, respectively). In June, the oligohaline region of the eastern Ebrié lagoon seemed to be a mixture of both the Comoé and La Mé river end members. Finally, in March when the
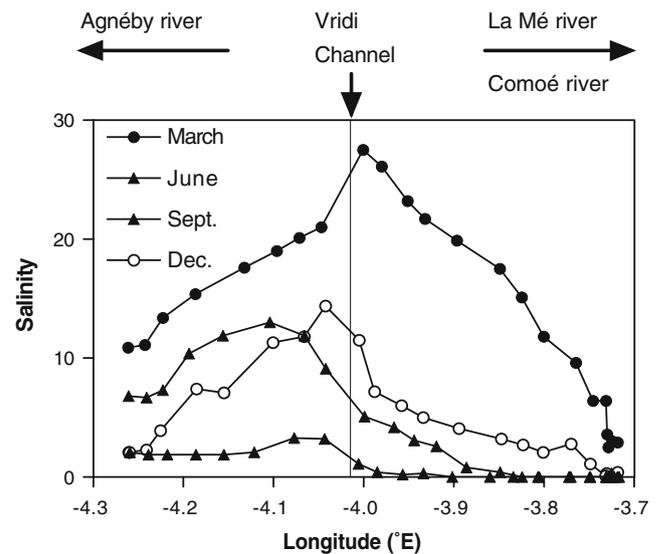

Fig. 5 Latitudinal variations of salinity in the Ebrié lagoon during the during the high dry season (March), the high rainy season (June), the low dry season (September), and the low rainy season (December)

freshwater inputs from the La Mé river were lowest, the Potou lagoon was dominated by brackish waters, and the y-intercept of the linear regression of TA as a function of salinity (381 μmol kg^{-1}) suggests that the La Mé river had a higher freshwater TA than the measured value in the Comoé river (268 μmol kg^{-1}).

Inorganic Nutrients and Suspended Matter Dynamics in the Five Lagoons

Average NO$_3^-$ concentrations in the five lagoons were very significantly to highly significantly higher during the high rainy season (June) than the high dry season (March; Fig. 7) due to strong freshwater inputs (Table 2). Average NO$_3^-$ concentrations in the Tendo, Ebrié, and Potou lagoons during the high rainy season (June) were also significantly to highly significantly higher than during the low dry season (September) and the low rainy season (December).

At a given salinity, whatever the season, NO$_3^-$ and PO$_4^{3-}$ were higher in the Ebrié, Potou, and Grand-Lahou lagoons

Table 2 Seasonal variations of the average salinity (±standard deviation) in surface waters in the Tendo (*n*=8), Aby (*n*=11), Ebrié (*n*=23), Potou (*n*=6), and Grand-Lahou (*n*=10) lagoons, during the high dry season (March), the high rainy season (June), the low dry season (September), and the low rainy season (December)

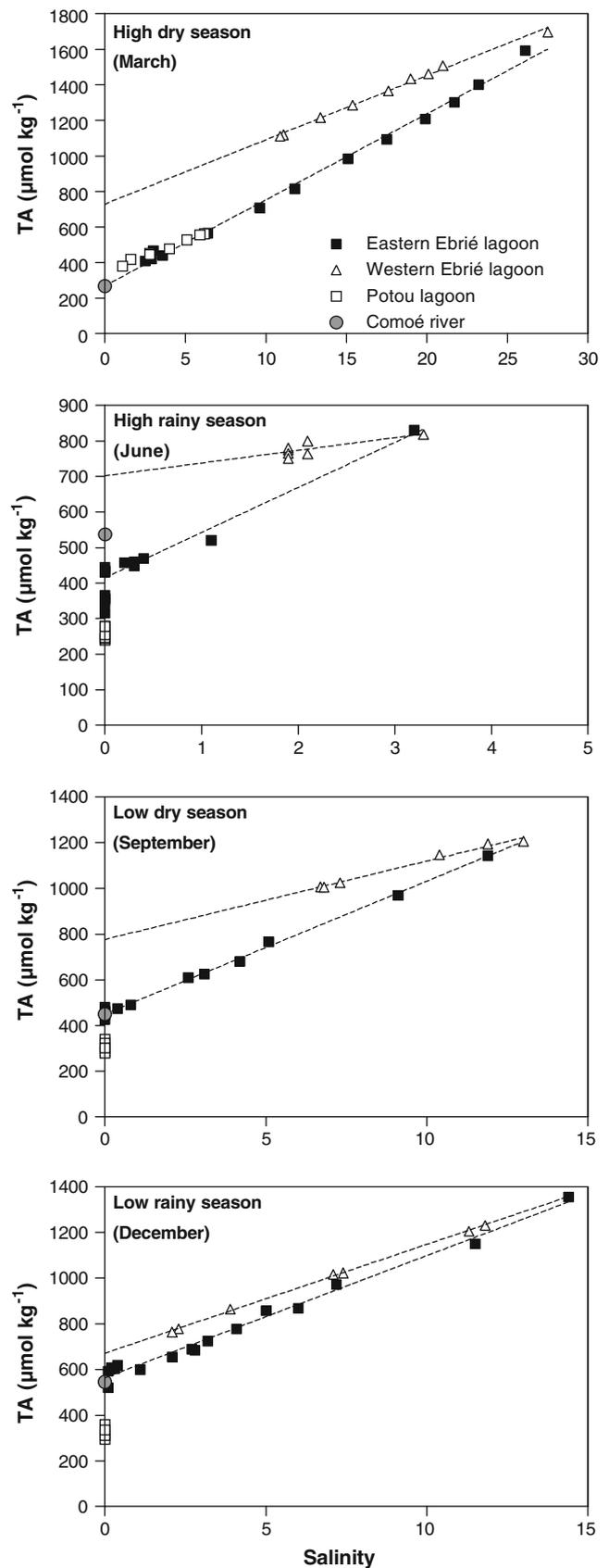|	High dry season (March)	High rainy season (June)	Low dry season (September)	Low rainy season (December)
Tendo	4.9±2.7	0.0±0.1	0.5±0.7	0.1±0.2
Aby	6.5±0.9	2.0±0.2	1.1±0.5	1.2±0.4
Ebrié	14.2±7.7	0.9±1.1	4.1±4.6	4.7±4.3
Potou	3.7±1.9	0.0±0.0	0.0±0.0	0.0±0.0
Grand-Lahou	19.4±5.0	0.6±0.3	8.0±1.6	9.2±3.5

Fig. 6 TA as a function of salinity in the Comoé river and in the Ebrié ▶
and the Potou lagoons during the during the high dry season (March),
the high rainy season (June), the low dry season (September), and the
low rainy season (December). *Dotted line* indicate the regression lines
of TA as a function of salinity for salinities >0. Note that the *x*-axis
scale is variable from one season to another

than in the Aby and Tendo lagoons, except in March when
strong NO_3^- depletion was observed in most lagoons
(Fig. 8). In June and September, NO_3^- and PO_4^{3-} at a given
salinity were higher in the eastern Ebrié lagoon than in the
Grand-Lahou lagoon that is relatively pristine. In September,
at a given salinity, both NO_3^- and PO_4^{3-} were higher in the
eastern Ebrié lagoon than in the western Ebrié lagoon, and
this was also the case of PO_4^{3-} in March. This was the case
for the sampling stations in the eastern Ebrié lagoon in the
vicinity of Abidjan showing the effect of eutrophication
related to ~3.8 million inhabitants living in this city.

Average Si concentrations were always high in the five
lagoons, and the seasonal cycles in the Tendo and Aby
lagoons differed from that in the Ebrié lagoon (Fig. 7). In
the Tendo and Aby lagoons, the average Si concentrations
were highly significantly higher during the high dry season
(March) because of the inputs from the Tanoé and the Bia
rivers that were characterized during this period of the year
by the highest Si concentrations (Fig. 4). In the Ebrié
lagoon, average Si concentrations were very significantly to
highly significantly higher during the high rainy season
(June) than the other seasons due to the higher inputs of
freshwater (Table 2) and because Si concentrations were
highest at this period of the year in the Comoé river
(Fig. 4). In the Potou and the Grand-Lahou lagoons, no
clear seasonality was apparent in the average Si concen-
trations. The Si:NO_3^- ratios ranged between 2:1 and
5,691:1, and the Si/PO_4^{3-} ratios ranged between 16:1 and
1,800:1, well above the Redfield ratio for the average
phytoplankton composition (1:16 and 1:1, respectively).

At a given salinity, Si concentrations in the Grand-Lahou
lagoon were generally higher than in the Ebrié lagoon in
June, September, and March (Fig. 8). In March, September,
and December, Si concentrations were higher in the eastern
side of the Ebrié lagoon than in the western side confirming
the different influences of freshwater inputs from the
Comoé and Agnéby rivers highlighted above from TA
variations (Fig. 6).

During the high dry season (March) and the low dry
season (September), the average TSM values were very
significantly to highly significantly higher in the Ebrié
lagoon (Fig. 7) than in the Comoé river and very
significantly to highly significantly higher in the Aby
lagoon (Fig. 7) than in the Bia river. In the five lagoons,
average TSM values were not significantly different or in
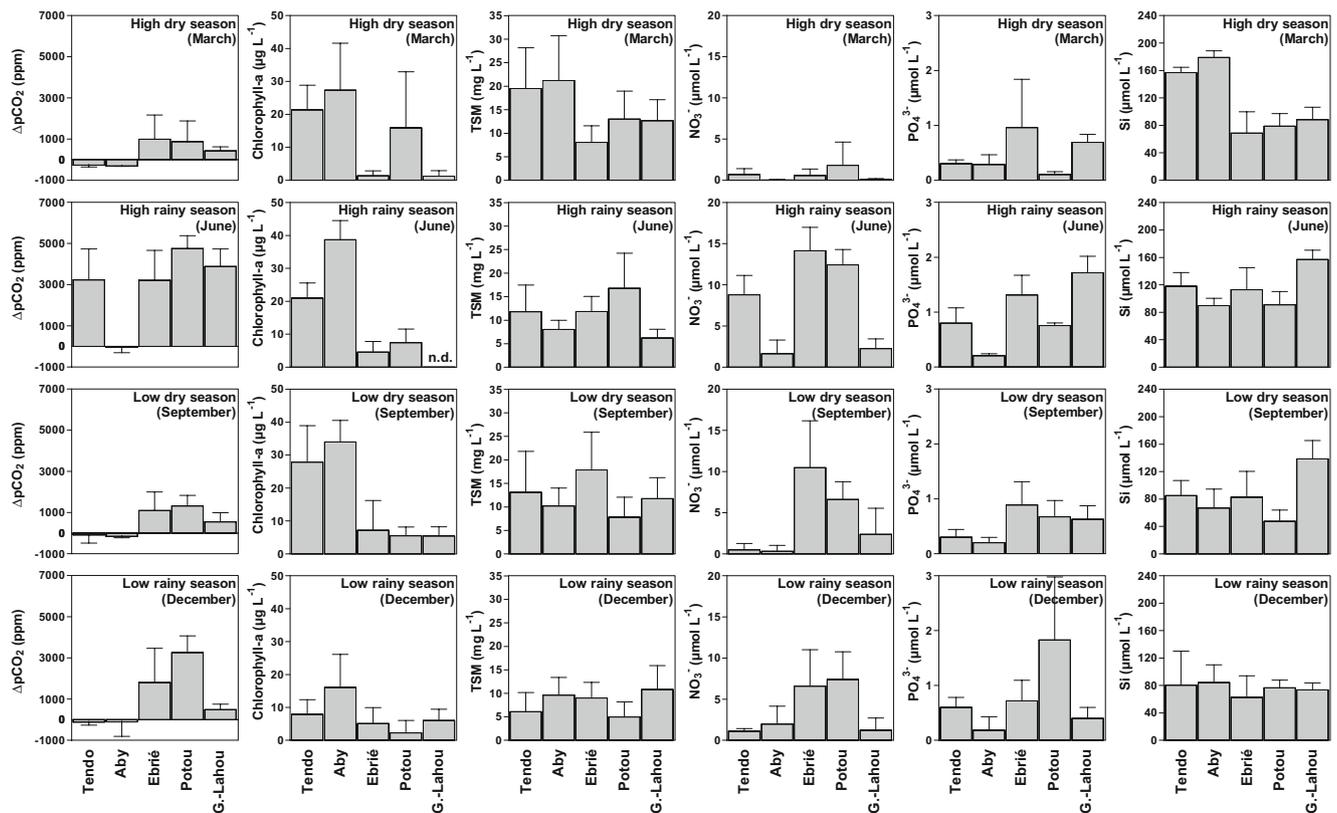some cases significantly lower during the high rainy season

Fig. 7 Seasonal variations of average ΔpCO_2 (ppm), chlorophyll-a concentration ($\mu g\ L^{-1}$), TSM ($mg\ L^{-1}$), NO_3^- ($\mu mol\ L^{-1}$), PO_4^{3-} ($\mu mol\ L^{-1}$), and Si ($\mu mol\ L^{-1}$) in the Tendo ($n=8$), Aby ($n=11$), Ebrié ($n=23$), Potou ($n=6$), and Grand-Lahou ($n=10$) lagoons, during the high dry season (March), the high rainy season (June), the low dry season (September), and the low rainy season (December). *Error bars* correspond to standard deviation on the mean. *n.d.* no data, *G.-Lahou* Grand-Lahou

(June) than during the high dry season (March). This suggests that spatial and temporal variations of TSM in the lagoons were unrelated to riverine inputs of TSM. The TSM content in the lagoons was then related to sediment resuspension and coastal erosion. The comparison between the five lagoons of average TSM (Fig. 7) or as a function of salinity (Fig. 9) does not show any systematic patterns.

Whatever the season, the Aby lagoon was characterized by significantly to highly significantly higher average chlorophyll-a concentrations compared to the Ebrié, Potou, and Grand-Lahou lagoons (Fig. 7); this was also the case when chlorophyll-a concentrations in these lagoons are compared at similar salinities (Fig. 9). The average chlorophyll-a values in the Tendo lagoon were highly significantly higher than in the Ebrié and Grand-Lahou lagoons during all seasons, except during the low rainy season (December). The average chlorophyll-a values in the Tendo lagoon were also highly significantly higher than in the Potou lagoon during the high rainy season (June) and the low dry season (September).

The high chlorophyll-a concentrations in the Aby and Tendo seemed to be related to local production in the lagoons, rather than phytoplankton inputs from the rivers, since chlorophyll-a concentrations were four- to 44-fold higher according to the season in the Aby lagoon than in the Bia river and seven to 26-fold higher according to the season in the Tendo lagoon than in the Tanoé river. These two lagoons are permanently stratified (Fig. 3) unlike the other lagoons, and this probably enhances light availability for phytoplankton and leads to a higher primary production. The enhancement of light availability is probably related to a shallower mixed layer (~2 m deep; Fig. 3) than the other lagoons, since average TSM levels were similar for a given season in all five lagoons (Fig. 7). This is also consistent with the fact that in the Tendo and Aby lagoons, average NO_3^- values were very significantly to highly significantly lower (Figs. 7 and 8) than in the in the Ebrié and Potou lagoons, whatever the season, except in March when strong NO_3^- depletion was apparent in most of the lagoons (Figs. 7 and 8). Also, in the Tendo and Aby lagoons, average ΔpCO_2 were very significantly to highly significantly lower than the other three lagoons (Figs. 7 and 9), whatever the season, except during the high rainy season (June) when strong river runoff led to high pCO_2 values in the Tendo
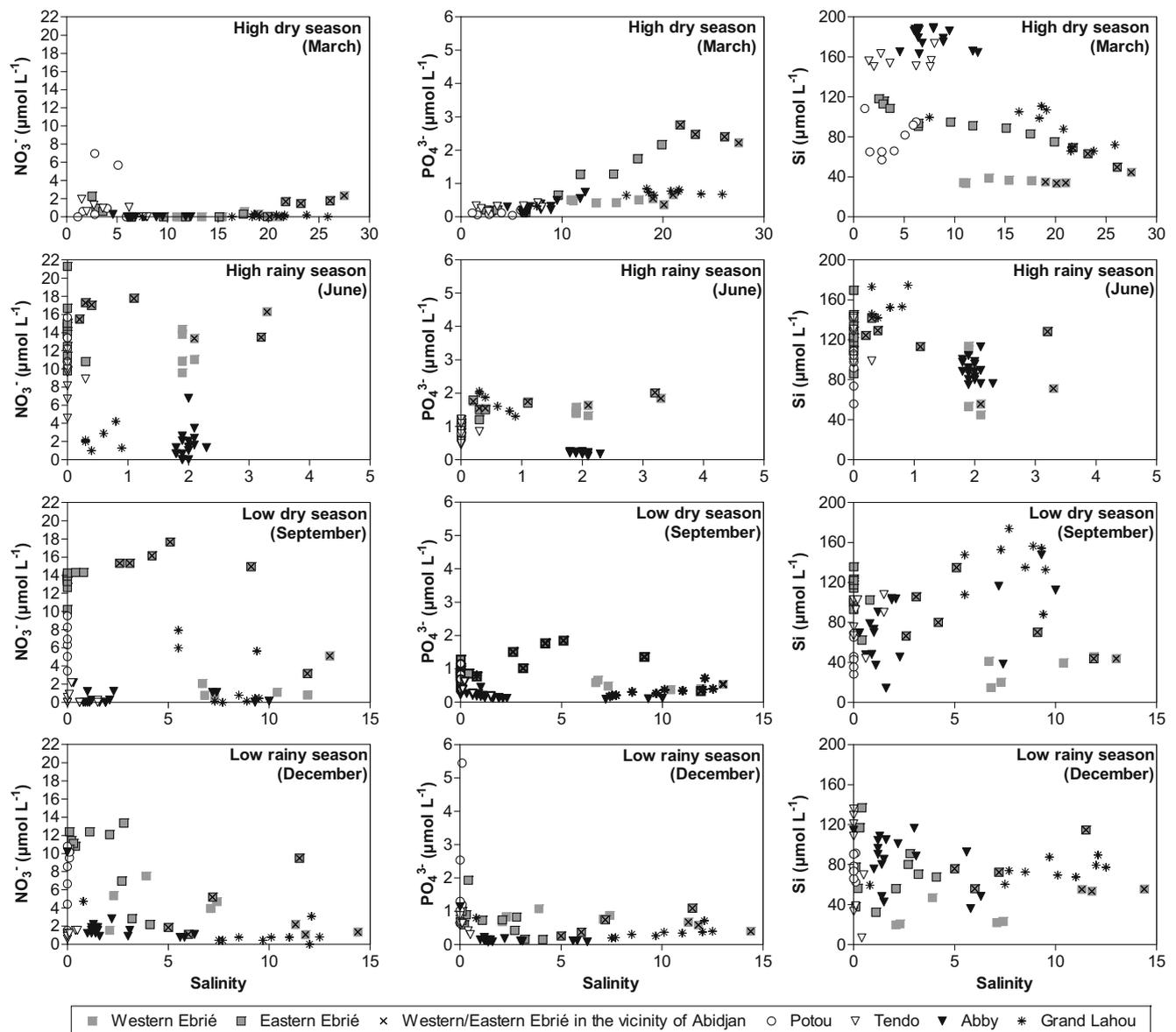
Fig. 8 NO_3^- (μmol L^{-1}), PO_4^{3-} (μmol L^{-1}), and Si (μmol L^{-1}) as a function of salinity in the Ebrié, Potou, Tendo, Aby, and Grand-Lahou lagoons during the high dry season (March), the high rainy season (June), the low dry season (September), and the low rainy season (December). Note that the x-axis scale is variable from one season to another

lagoon. This is due to the fact that in the permanently stratified Tendo and Aby lagoons, DIC and inorganic nutrient uptake by phytoplankton in the mixed layer is strongly decoupled from DIC and inorganic nutrient remineralization below the pycnocline, leading to strong vertical gradients of these quantities (Fig. 3). There was no clear seasonality in the chlorophyll-a concentration in the five lagoons. No clear difference in chlorophyll-a concentration was apparent between the eastern and western Ebrié lagoon, except in September when higher values were observed in the western side than in the eastern side.

DIC Dynamics in the Five Lagoons

In the Tendo, Ebrié, Potou, and Grand-Lahou lagoons, the average ΔpCO_2 values were very significantly to highly significantly higher during the high rainy season (June) than the other seasons (Fig. 7), due to strong inputs from the rivers that were oversaturated throughout the year (Fig. 4). The Ebrié, Potou, and Grand-Lahou lagoons were oversaturated in CO_2 whatever the season, as observed in the oligohaline and mesohaline regions of macrotidal estuaries worldwide (Frankignoulle et al. 1998; Abril and
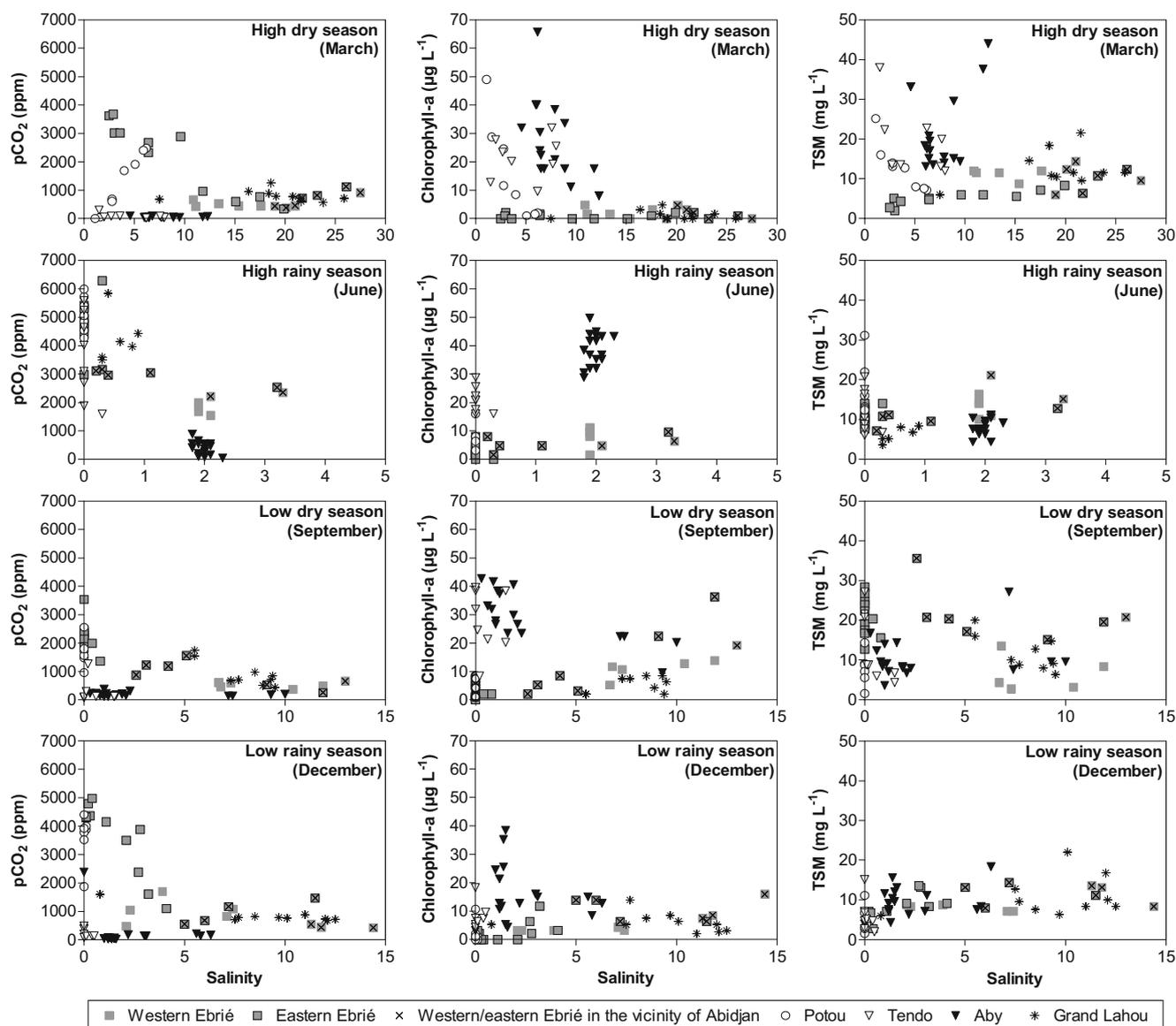
Fig. 9 pCO₂ (ppm), TSM (mg L⁻¹), and chlorophyll-a (µg L⁻¹) as a function of salinity in the Ebrié, Potou, Tendo, Aby, and Grand-Lahou lagoons during the high dry season (March), the high rainy season (June), the low dry season (September), and the low rainy season (December). Note that the x-axis scale is variable from one season to another

Borges 2004), while the Tendo and Aby lagoons were undersaturated in CO₂ through the year (except for the Tendo during the high rainy season (June) due the inputs from the Tanoé river).

The Aby lagoon is connected to the sea by a very shallow channel (<1 m) while the Grand-Lahou and the Ebrié lagoons are connected to the sea by much deeper channels that are used for navigation. This implies that wave and tidal action from the ocean do not propagate as intensely in the Aby lagoon system than in the Ebrié and Grand-Lahou lagoon systems, leading to a strong and permanent haline stratification (Fig. 3), resulting in anoxic conditions in bottom waters (Chantraine 1980). The

freshwater residence time in the Aby lagoon is probably higher compared to the Ebrié and Grand-Lahou lagoons, due to the much shallower connection to the sea. The combination of permanent stratification and long freshwater residence time promotes the export from the mixed layer across the pycnocline of organic matter that is degraded in the bottom waters leading to an increase of DIC, pCO₂, inorganic nutrients, and the decrease of pH (Fig. 3). At the base of pycnocline (3–4 m), a maximum of DIC, pCO₂, and inorganic nutrients suggests an enhanced organic matter degradation due to the accumulation of organic matter sedimenting from the surface, as indicated by the presence of chlorophyll-a at these depths in the Tendo lagoon

(Fig. 3). The strong permanent haline stratification in the Aby lagoon probably also promotes light availability throughout the year when compared to the other seasonally stratified lagoons. This could lead to higher rates of primary production as suggested by the higher chlorophyll-a concentrations and lower inorganic nutrients in the Aby and Tendo lagoons when compared to the other three lagoons. This is in agreement with measurements of primary production based on O_2 incubations reported by Chantraine (1980) that yield annual averages of 3.8 g O_2 m^{-2} day^{-1} in the Tendo lagoon and 6.3 g O_2 m^{-2} day^{-1} in the Aby lagoon, well above the annual average of 2.5 g O_2 m^{-2} day^{-1} in the Ebrié lagoon (in the area we sampled). The combination of higher primary production and efficient export of organic matter across the pycnocline in the Aby and Tendo lagoons can explain why they were undersaturated in CO_2 throughout the year (except during the high rainy season (March) in the Tendo lagoon due to strong river inputs) unlike the other lagoons.

Values of pCO_2 in the Grand-Lahou lagoon and the eastern and western Ebrié lagoons were relatively similar whatever the season (Fig. 9). While evidence for the impact of the Abidjan population on the water quality was found for inorganic nutrients, this did not seem to be the case for pCO_2.

Air–Water CO_2 Fluxes in the Three Rivers and Five Lagoons

The average values of k and F obtained in the three rivers and the five lagoons are given per season and integrated on an annual basis in Table 3. The u and k values were generally higher in the wider Comoé river than in the narrower Bia and Tanoé rivers. The unregulated Tanoé and Comoé rivers were characterized by higher annual F values (137 and 170 mmol C m^{-2} day^{-1}, respectively) than the Bia river (49 mmol C m^{-2} day^{-1}) where the freshwater discharge is regulated by the Ayamé dam. Annual F values in the Comoé, Bia, and Tanoé rivers (ranging from 49 to 170 mmol C m^{-2} day^{-1}) are within the range reported by Cole and Caraco (2001) for worldwide rivers (20 to 1,026 mmol C m^{-2} day^{-1}) and for tropical rivers (60 to 1,026 mmol C m^{-2} day^{-1}).

The F values in the five lagoons showed strong seasonal variability in agreement with the seasonal changes of ΔpCO_2 (Table 3). The Ebrié, Potou, and Grand-Lahou lagoons were net sources of CO_2 to the atmosphere, since they were oversaturated in CO_2 throughout the year, and the annual F values (range from 51 to 101 mmol C m^{-2} day^{-1}) are consistent with those reported for macrotidal estuaries worldwide (range from 14 to 202 mmol C m^{-2} day^{-1}) and higher than those reported so far at subtropical and tropical latitudes (range from 14 to 39 mmol C m^{-2} day^{-1}; Frankignoulle et al. 1998; Abril and Borges 2004; Borges

Table 3 Seasonal variations of the mean (±standard deviation) of wind speed (u in m s^{-1}), gas transfer velocity (k in cm h^{-1}) and air–water CO_2 flux (F in mmol C m^{-2} day^{-1}) obtained in the rivers (Bia, Tanoé, and Comoé) and lagoons (Tendo, Aby, Ebrié, Potou, and Grand-Lahou)

		High dry season (March)			High rainy season (June)			Low dry season (September)			Low rainy season (December)			Annual F
		u	k	F	u	k	F	u	k	F	u	k	F	
Rivers	Bia	1.7±0.8	2.7±0.7	58.7±31.8	1.0±1.1	2.3±0.8	48.5±17.3	1.2±1.8	2.7±2.2	45.5±33.7	1.2±1.3	2.4±1.0	40.0±18.1	49.2±24.3
	Tanoé	1.5±2.1	2.8±1.9	233.1±141.6	1.2±1.5	2.5±1.4	119.3±79.4	1.6±1.4	2.8±1.4	72.7±44.3	0.7±0.7	2.0±0.4	73.5±16.9	137.4±97.1
	Comoé	4.3±1.2	6.0±2.3	311.4±88.7	2.4±1.3	3.5±1.2	148.1±71.4	3.5±1.8	5.1±2.5	73.7±37.7	0.7±0.6	2.0±0.4	73.1±16.4	170.4±112.8
Lagoons	Tendo	4.8±2.0	7.7±4.6	−17.7±12.6	1.8±1.1	2.8±0.8	75.5±29.3	5.3±0.7	7.8±1.6	−4.9±29.1	2.5±1.4	3.6±1.3	−3.0±4.9	19.3±45.0
	Aby	4.3±2.7	7.3±4.6	−20.0±13.2	3.7±2.6	6.4±4.8	1.2±16.4	4.7±1.7	7.3±4.0	−11.3±8.0	1.2±1.5	2.5±1.5	−4.1±12.9	−7.4±15.4
	Ebrié	4.5±2.1	7.7±5.7	56.4±59.8	2.8±2.0	4.3±2.6	109.4±61.3	4.3±2.4	7.2±4.9	61.9±63.7	2.1±1.2	3.1±1.1	48.0±47.0	72.9±62.3
	Potou	3.7±0.9	4.9±1.6	40.4±54.4	2.4±2.4	4.0±2.9	186.2±155.6	2.0±1.6	3.3±1.9	45.6±46.7	1.5±1.3	2.6±1.0	82.7±45.4	100.7±95.5
	Grand-Lahou	3.1±1.5	4.4±2.1	18.1±15.3	2.1±1.1	3.1±1.1	114.1±51.2	4.8±1.3	7.2±2.6	28.4±15.0	2.0±1.3	3.1±1.2	13.2±7.6	50.7±53.4

The annual F values (in mmol C m^{-2} day^{-1}) were integrated annually based on the average duration of the seasons (90 days for high dry season, 122 days for the high rainy season, 61 days for the low dry season, and 92 days for the low rainy season)

2005; Borges et al. 2005, 2006; Chen and Borges 2008). The Aby lagoon acted as a sink of atmospheric CO_2 (-7 mmol C m^{-2} day^{-1}) on an annual basis since undersaturation of CO_2 was observed throughout the year. The Tendo lagoon could be a net source of CO_2 to the atmosphere on an annual basis, although the annual efflux of CO_2 (19 mmol C m^{-2} day^{-1}) is driven by a large efflux during the high rainy season (June) of 76 mmol C m^{-2} day^{-1}, while the flux was negative the rest of the year (range from -3 to -18 mmol C m^{-2} day^{-1}).

The surface area weighted annual CO_2 flux in the five lagoons yields a net CO_2 emission to the atmosphere at a rate of 44 mmol C m^{-2} day^{-1}. This value is lower than the average values reported in other near-shore coastal ecosystems such as macrotidal estuaries (118 mmol C m^{-2} day^{-1}), mangrove surrounding waters (51 mmol C m^{-2} day^{-1}), and salt marsh surrounding waters (64 mmol C m^{-2} day^{-1}) compiled by Borges (2005).

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