



# Dissolved organic matter composition and reactivity in Lake Victoria, the world's largest tropical lake

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**Abstract** We report a data set of dissolved organic carbon (DOC) concentration and dissolved organic matter (DOM) composition (stable carbon isotope signatures, absorption and fluorescence properties) obtained from samples collected in Lake Victoria, a large lake in East Africa. Samples were collected in 2018–2019 along a bathymetric gradient (bays to open waters), during three contrasting seasons: long rainy, short rainy and dry, which corresponded to distinctly water column mixing regimes, respectively, stratified,

semi-stratified and mixed regimes. Eight DOM components from parallel factor analysis (PARAFAC) were identified based on three-dimensional excitation–emission matrices (EEMs), which were aggregated into three main groups of components (microbial humic-like, terrestrial humic-like, protein-like). Spatially, the more productive bays were characterized by higher DOM concentration than deeper more offshore waters (fluorescence intensity and DOC were  $\sim 80\%$  and  $\sim 30\%$  higher in bays, respectively). Seasonally, the DOM pool shifted from protein-like components during the mixed regime to microbial humic-like components during the semi-stratified regime and to terrestrial humic-like components during the stratified regime. This indicates that pulses of autochthonous DOM derived from

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phytoplankton occurred when the lake was mixing, which increased the availability of dissolved inorganic nutrients. Subsequently, this freshly produced autochthonous DOM was microbially processed during the following semi-stratified regime. In the open waters, during the stratified regime, only terrestrial refractory DOM components remained because the labile and fresh stock of DOM created during the preceding mixed season was consumed. In the bays, the high terrestrial refractory DOM during the stratified regime may be additionally due to the allochthonous DOM input from the runoff. At the scale of the whole lake, the background refractory DOM probably comes mainly from precipitation and followed by river inputs.

**Keywords** Colored dissolved organic matter · Fluorescent dissolved organic matter · Dissolved organic carbon · Carbon cycle · Lake Victoria · Tropical lake

## Introduction

Dissolved organic matter (DOM) is present in all natural aquatic environments and is operationally defined as organic matter that passes filtration with a given pore size (typically 0.7, 0.45 or 0.2  $\mu\text{m}$ ) and includes dissolved organic carbon (DOC), nitrogen and phosphorous. DOM is the largest bioavailable organic carbon source across the Earth's aquatic ecosystems and, consequently, its dynamics have great implications for carbon cycling on local to global scales (Benner 2003; Battin et al. 2009; Tank et al. 2013). A minor fraction of DOM consists of simple compounds such as sugars, lipids or free amino acids (Benner 2002), and the rest consists of a complex mixture of organic molecules that vary greatly in molecular weight and chemical composition. This makes the chemical characterization of DOM difficult and thus a large fraction of DOM remains uncharacterized. The chemical heterogeneity of DOM is due to the variety of sources and its reactivity to physical, chemical and microbial degradation processes (Stedmon and Markager 2005a). In lakes, DOM can be of allochthonous (i.e., terrestrial and anthropogenic) or of autochthonous (i.e., aquatic) origins (Leenheer and Croué 2003). Specifically, the major DOM sources are

the release of soil organic matter; extracellular release of organic matter by algae; release via grazing and excretion by zooplankton; viral lysis of bacteria and algae cells; degradation and exudation of macrophytes and release from sediments (e.g., Aitkenhead-Peterson et al. 2003; Nagata 2000). Allochthonous and autochthonous DOM inputs to freshwaters are the result of complex interplays between catchment soil properties (Autio et al. 2016), land cover (Lambert et al. 2017; Xenopoulos et al. 2009) and water residence time (Kothawala et al. 2014), which all are affected by human disturbance (Carpenter et al. 2011).

DOM plays a critical role in freshwater ecosystems because it supplies carbon and nitrogen to heterotrophic respiration, which affects energy flow through food webs (Cole et al. 2006; Keil and Kirchman 2007; Wetzel 1992). This is reflected in the relations in lakes between dissolved  $\text{CO}_2$  and  $\text{CH}_4$  concentrations and DOC (Lapierre and del Giorgio 2012; Sanches et al. 2019). In addition, DOM in freshwaters affects the mobility and transport of contaminants and heavy metals, pH buffering capacity and light attenuation (Bracchini et al. 2007; Diercks et al. 2010; McKnight et al. 1985; Patidar et al. 2015; Soto Cárdenas et al. 2017). The absorption of ultra violet (UV) radiation by DOM leads to its degradation, which can be described as photodegradation or photobleaching, and this process is considered important in terms of carbon cycling in temperate lakes (Bertilsson and Tranvik 2000; Kellerman et al. 2014), as well as in tropical lakes (Bittar et al. 2015). In two inner bays of Lake Victoria, using vertical diffusive irradiance measurements of the lake water column, Bracchini et al. (2006) showed that the release of terrestrial DOM by the surrounding wetlands led to photosynthetic active irradiance (PAR) attenuation, which in return had a possible negative feedback on phytoplankton growth. The extent to which DOM can affect freshwaters ecosystems functioning depends on DOM concentration, age, structure and chemical composition (Benner 2003; Jaffé et al. 2008).

The optically active fraction of DOM can trace compositional changes because biochemical characteristics of DOM can be related to its optical properties (Hernes et al. 2009; Stedmon et al. 2003). Compositional changes of DOM are related to the DOM sources, which makes DOM composition a useful tracer to understand variability of allochthonous versus autochthonous DOM sources in aquatic

ecosystems (Coble 1996; Fellman et al. 2010). The optically active fraction of DOM is called colored dissolved organic matter (CDOM), which is that part of the DOM that absorbs irradiance in the solar ultraviolet and visible spectral bands. Another property of CDOM is to emit fluorescence when excited by light in the ultraviolet and blue region of the spectrum. Fluorescent DOM (FDOM) is colored, but not all CDOM is fluorescent (Coble 2007). The two major DOM components that have been found to fluoresce are humic materials (i.e., a blue fluorescence) and protein fractions (i.e., a UV fluorescence) (Coble 1996). DOM measurements acquired as three-dimensional excitation–emission matrices (EEMs) are analyzed with parallel factor analysis (PARAFAC), a multivariate statistical method that enables developing models to decompose individual EEMs, and provides additional benefits for the characterization of composition of DOM from diverse sources (Stedmon and Bro 2008). These sources including terrestrial plants and soils, microbial communities in freshwater and marine ecosystems and from wastewaters (Cawley et al. 2012; Fellman et al. 2010; Murphy et al. 2008; Stedmon et al. 2003; Stedmon and Markager 2005b; Yamashita and Jaffe 2008).

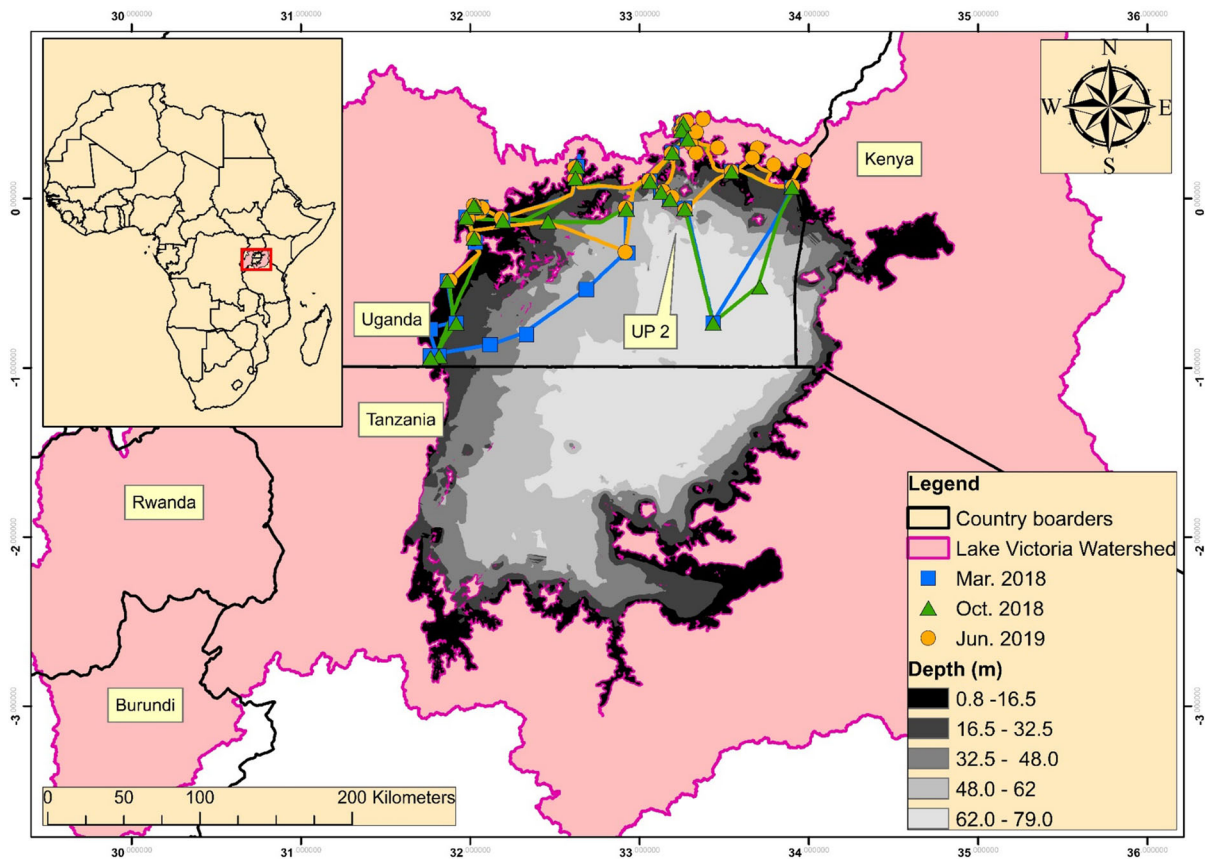
Lake Victoria is considered one of the critically important water and fisheries resources in East Africa, providing life support requirements to more than 47 million habitants from three riparian countries, i.e., Uganda, Kenya, Tanzania (UNEP 2008). Despite Lake Victoria being the world's third largest freshwater body in terms of surface area (68,800 km<sup>2</sup>; Bootsma et al. 2003), it remains largely underrepresented in large-scale studies on DOM processing. To the best of our knowledge, there are few studies dealing with DOM in Lake Victoria (Bracchini et al. 2006, 2007; Loiselle et al. 2010); these studies focused specifically on DOM absorbance in inner bays, not representative of DOM variability for the whole lake. In the present study, we applied absorbance and fluorescence measurements to DOM samples obtained from Lake Victoria in Ugandan waters. We chose sampling stations to be representative of the whole lake spatial variability, from shallow bays to deeper open waters, during three contrasting seasons that mainly differed in terms of stratification. From EEMs, we developed a PARAFAC model for Lake Victoria to describe DOM chemical composition, reactivity and its spatio-temporal dynamics. To the best of our

knowledge, our study represents the first time that PARAFAC analysis has been used in Lake Victoria. Consequently, the main goal of this study was to characterize DOM composition in Lake Victoria. The second goal was to investigate the spatial and seasonal variations of the DOM pool. We hypothesized that spatio-temporal variations of DOM resulted mostly from different rates of aquatic primary production, which likely was the major source of fresh and labile DOM, while rain and rivers were sources of terrestrial DOM that we assumed mainly refractory (e.g., Lambert et al. 2016). On the one hand, irrespective of the seasons, we hypothesized that horizontal variations of DOM were likely a result of mixing between bays and open waters, both exhibiting different rates of aquatic primary production. On the other hand, seasonal variations of DOM were a product of different water column stratification, which influenced the availability of nutrients in surface waters that in turn affected aquatic primary production.

## Material and methods

### Study site

Lake Victoria, source of the White Nile, is located in the upper Nile basin in East Africa within latitudes 3.05° S to 0.55° N and longitudes 31.5° to 34.88° E (Fig. 1). The shorelines of Lake Victoria are shared across three riparian East African countries: Tanzania (49%), Uganda (45%) and Kenya (6%; Fig. 1). The present lake surface area is large (68,800 km<sup>2</sup>) but the basin is relatively shallow with a mean depth of 40 m and a maximum depth of 80 m (Fig. 1; Bootsma et al. 2003; Johnson et al. 2009). Lake Victoria surface is at an average elevation of approximately 1135 m above sea level (Bootsma et al. 2003). The complex shoreline length is approximately 3440 km and it is composed of several gulfs and bays (Fig. 1; Akurut et al. 2017; Balirwa 1995). Wetlands dominated by papyrus are sporadically present along the shoreline of Lake Victoria. In addition, several islands fringe the shore with combined surface area of approximately 1500 km<sup>2</sup> (Fig. 1; Lehman 2009). The long lake residence time (~ 23 years) makes Lake Victoria susceptible to climate change and water quality deterioration (Akurut et al. 2017; Bootsma et al. 2003).



**Fig. 1** Map of Lake Victoria showing the watershed, the lake water depth, the sampling stations and the boat cruise-tracks during the three different field campaigns. The first campaign was conducted during the long rainy period corresponding to strongly stratified water column conditions (March 2018), the second one during the short rainy period corresponding to partly

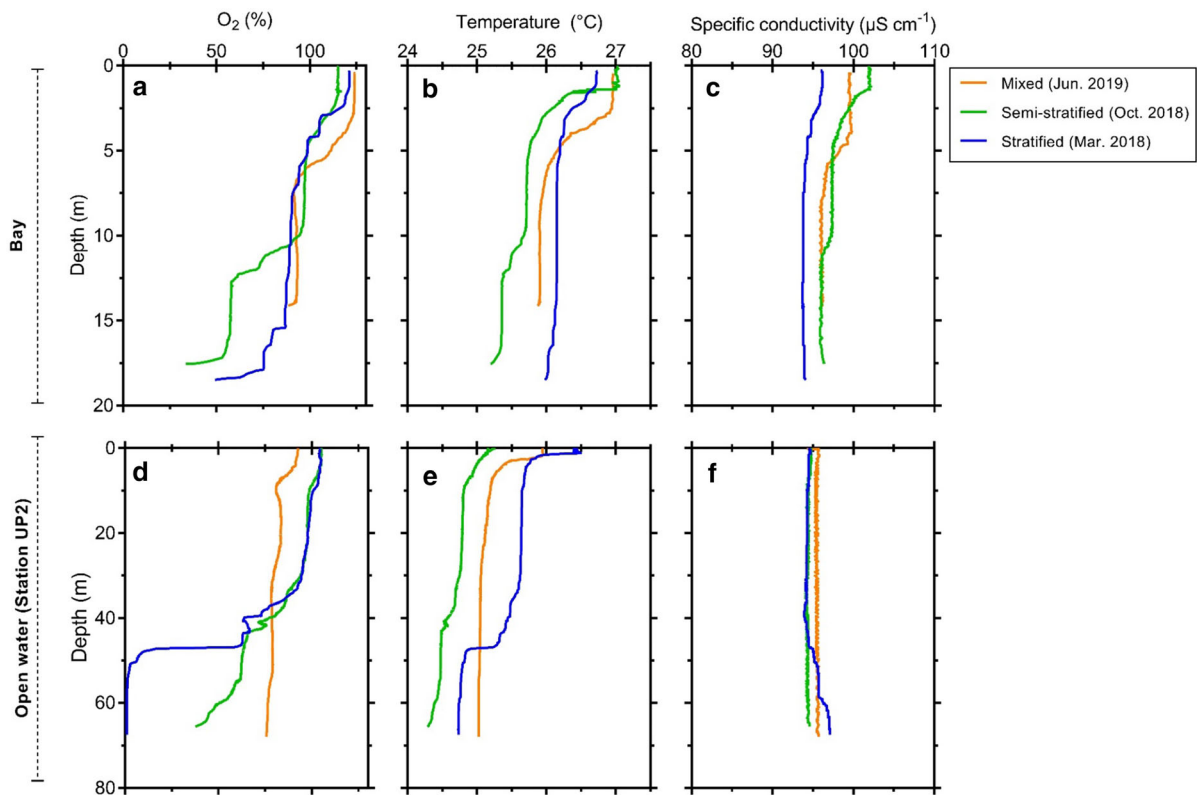
stratified water column conditions (October 2018) and the third one during the dry season corresponding to mixed water column conditions (June 2019). UP2 is the open water sampling station from which vertical physico-chemical profiles are presented in Fig. 2

The general climate of the Lake Victoria basin, whose seasonal variation is governed by migration of the intertropical convergence zone, ranges from a modified equatorial type to a semiarid type (Anyah et al. 2006; Nicholson 1996). Consequently, the Lake Victoria basin experiences two rainy seasons yearly. The ‘long rains’ occur from March to May and the ‘short rains’ are from October to November. There are 23 rivers draining into the lake but only one effluent: the White, or Victoria Nile with an outflow of  $462 \text{ mm year}^{-1}$ , approximately equivalent to the combined river inflow of  $480 \text{ mm year}^{-1}$  (Vanderkelen et al. 2018). The water mass balance of Lake Victoria is thus largely dominated by the balance between rainfall input ( $+ 1525 \text{ mm year}^{-1}$ ) and evaporation output ( $- 1539 \text{ mm year}^{-1}$ ;

Vanderkelen et al. 2018). The evaporative losses accounting for  $\sim 80\%$  of the water leaving the lake. Not only does evaporation represent a major water loss process in Lake Victoria, it is also a large heat budget component, and therefore plays an important role in the annual mixing regime, by means of evaporative cooling and turbulence (Bootsma et al. 2003). Thermal stratification is either absent or extremely modest from mid-May to mid-August, after which a definite stratification develops (Talling 1957).

### Sampling

To capture the seasonal variations of the studied parameters, sampling was conducted during three field cruises that were characterized by three distinct



**Fig. 2** Vertical profiles at an open water (UP2; Fig. 1) and a bay sampling site showing the water temperature ( $^{\circ}\text{C}$ ), dissolved oxygen saturation (%) and specific conductivity ( $\mu\text{S cm}^{-1}$ ) obtained with a CTD multiprobe during the three cruises on

Lake Victoria (during the long rainy season in March 2018, the short rainy season in October 2018 and the dry season in June 2019)

hydrological conditions: in March 2018 (long rainy period), October 2018 (short rainy period) and June 2019 (dry period), from the *MV Hammerkop*, the research vessel from the Ugandan National Fisheries Resource Research Institute (Jinja). Sampling was carried out along a bathymetric gradient, from shallow inner bays to deeper open waters (Deirmendjian et al. 2020; Fig. 1). Vertical profiles (data acquisition 2 s) of water temperature, specific conductivity and dissolved oxygen saturation were obtained with a Yellow Springs Instrument (YSI) EXO-2 multiparameter probe. Calibration of sensors was carried out prior to the cruises and regularly checked during the cruises. The conductivity cell was calibrated with a  $1000 \mu\text{S cm}^{-1}$  ( $25^{\circ}\text{C}$ ) YSI standard. The oxygen optical probe was calibrated with humidity saturated ambient air. Lake water was sampled using a 3 L Niskin bottle at a depth interval of 10 m, from the lake surface ( $\sim 1$  m below the surface) to the lake bottom ( $\sim 2$  m above the lake sediment). The water depth was

recorded continuously with a Humminbird® echo sounder (Helix 5 G2). The Secchi disk depth was determined at every sampling site with a homemade Secchi disk. Samplings of dissolved organic carbon (DOC), stable isotopic signature of DOC ( $\delta^{13}\text{C}$ -DOC) and CDOM/FDOM were performed after two successive filtrations, on pre-combusted GF/F glass fiber filters ( $0.7 \mu\text{m}$  porosity) and then on  $0.2 \mu\text{m}$  polyethersulfone syringe filters. Samples for the measurement of DOC concentration and  $\delta^{13}\text{C}$ -DOC were stored in 40 mL amber borosilicate vials with polytetrafluoroethylene (PTFE)-coated septa with addition of  $50 \mu\text{L}$  of  $\text{H}_3\text{PO}_4$  (85%) and stored at ambient temperature. Samples for CDOM and FDOM analyses were stored in 20 mL amber borosilicate vials with PTFE-coated septa but without  $\text{H}_3\text{PO}_4$  addition and stored in a refrigerator ( $4^{\circ}\text{C}$ ). At each sampling depth, a variable amount of water was filtered on a pre-combusted 25 mm glass fibre filters (Sartorius GF5,  $0.7 \mu\text{m}$  nominal pore size) for



particulate organic carbon (POC) and on Macherey-Nägel GF-5 filters (0.7  $\mu\text{m}$ ) for Chlorophyll-a. For POC, filters were dried and then kept in small Petri dishes. For Chlorophyll-a, filters were immediately frozen in liquid nitrogen and then kept at  $-25\text{ }^{\circ}\text{C}$  until the extraction was performed during the field trip. All samples were brought back to the home laboratory in Belgium and analyzed within 4–12 weeks after sampling.

### Chemical analyses and PARAFAC modelling

DOC and  $\delta^{13}\text{C}$ -DOC were analyzed with an Aurora1030 total organic carbon analyzer (OI Analytical) coupled to a Delta V Advantage isotope ratio mass spectrometer (KU Leuven, Belgium). Typical precision observed in duplicate samples was in  $>95\%$  cases  $<5\%$  for DOC, and  $0.2\text{‰}$  for  $\delta^{13}\text{C}$ -DOC. Quantification and calibration was performed with series of standards prepared in different concentrations, using both IAEA-C6 ( $\delta^{13}\text{C} = -10.4\text{‰}$ ) and in-house sucrose standard ( $\delta^{13}\text{C} = -26.9\text{‰}$ ). All data are reported in the notation relative to VPDB (Vienna Pee Dee Belemnite).

Filters for  $\delta^{13}\text{C}$ -POC were decarbonated with HCl flumes for 4 h, re-dried and packed in silver cups prior to analysis on a EA-IRMS (Thermo FlashHT with Thermo DeltaV Advantage). Calibration of  $\delta^{13}\text{C}$ -POC measurements was performed with a combination of IAEA-600 (caffeine,  $\delta^{13}\text{C} = -27.77\text{‰}$ ) and two in-house standards, leucine and tuna tissue ( $\delta^{13}\text{C} = -13.47$  and  $-18.72\text{‰}$ , respectively). Reproducibility of  $\delta^{13}\text{C}$ -POC measurements was typically better than  $\pm 0.2\text{‰}$ .

Chlorophyll-a was determined by high performance liquid chromatography (HPLC). Chlorophyll-a extraction was carried out in 3.5 mL of 90% HPLC grade acetone. After two sonication steps in cold water of 15 min separated by an overnight period at  $4\text{ }^{\circ}\text{C}$ , Chlorophyll-a extracts were stored in 2 mL amber vials at  $-25\text{ }^{\circ}\text{C}$ . HPLC analysis was performed following the gradient elution method described in Wright (1991), with a Waters system comprising a 600E pump, a 717 auto sampler and a 2996 photodiode array and detector. Calibration was made using commercial external standards (DHI Lab Products, Denmark). Reproducibility for pigment concentration measurement was better than 7%. Pigment concentrations were processed with the CHEMTAX software

(CSIRO Marine Laboratories; Mackey et al. 1996) using input ratio matrices adapted for freshwater phytoplankton (Descy et al. 2005).

For dissolved inorganic nutrients ( $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$ ), 50 mL of water was filtered on a  $0.2\text{ }\mu\text{m}$  polyethylsulfone syringe filter and preserved frozen until measurement by colorimetry according to standard techniques. The sum of  $\text{NO}_3^-$ ,  $\text{NO}_2^-$  and  $\text{NH}_4^+$  was considered as the dissolved inorganic nitrogen content (DIN).  $\text{NH}_4^+$  concentration was determined using the dichloroisocyanurate-salicylate-nitroprussiate colorimetric method (Westwood 1981).  $\text{NO}_3^-$  and  $\text{NO}_2^-$  were determined with the sulphanilamide colorimetric method, after cadmium reduction for  $\text{NO}_3^-$  (APHA 1998).  $\text{PO}_4^{3-}$  was determined by spectrophotometry using the ammonium molybdate-potassium antimonyl tartrate method (Murphy and Riley 1962).

Absorbance was recorded on a Perkin-Elmer UV/Vis 650S spectrophotometer using a 1 cm quartz cuvette. Absorbance spectra were measured between 190 and 900 nm at 1 nm increments, and instrument noise was assessed by using ultrapure (Type 1) Milli-Q (Millipore) water as the blank. After subtracting the blank spectrum, the correction for scattering and index of refraction was performed by fitting the absorption spectra to the data over the 200–700 nm range according to the following equation:

$$A_{\lambda} = A_0 \exp(-S(\lambda - \lambda_0)) + K$$

where  $A_{\lambda}$  and  $A_0$  are the absorbance measured at a defined wavelength and at a reference wavelength of  $\lambda_0 = 375\text{ nm}$ , respectively,  $S$  the spectral slope ( $\text{nm}^{-1}$ ) that describes the approximate exponential decline in absorption with increasing wavelength and  $K$  a background offset. The fit was not used for any purpose other than to provide an offset value  $K$  that was then subtracted from the whole spectrum (Lambert et al. 2016).

The spectral slope for the intervals 275–295 nm ( $S_{275-295}$ ) was determined from the linear regression of the log-transformed absorbance spectra vs. wavelength. Parameter  $S_{275-295}$  is both inversely related to the percent of terrigenous DOC and the average molecular weight and it is also considered to be an excellent indicator of photobleaching, which increases  $S_{275-295}$  (Fichot and Benner 2012; Helms et al. 2008).

Fluorescence intensity was recorded on a Perkin-Elmer LS45 fluorescence spectrometer using a 1 cm

quartz cuvette across excitation wavelengths of 220–450 nm (5 nm increments) and emission wavelengths of 230–600 nm (0.5 nm increments) to build EEMs. Before each measurement session (i.e., each day), a Milli-Q water sample was also measured and subtracted from EEMs. Fluorescence intensities measured at specific excitation wavelengths were used to derive several proxies of FDOM composition. The fluorescence index (FI) was calculated as the ratio of the emission intensities at 470 and 520 nm at an excitation wavelength of 370 nm (McKnight et al. 2001). FI is inversely related to the lignin content and to the aromaticity of DOM and is indicative of the contribution of microbially derived compounds to the DOM pool. FI values typically range from 1.3 to 2.0, i.e., from terrestrial, higher-plant DOM sources to predominant microbial DOM sources. The biological index (BI or  $\beta:\alpha$  ratio) was calculated as the ratio of the emission intensity measured at 380 nm ( $\beta$  region) divided by the emission intensity maximum recorded between 420 and 435 nm ( $\alpha$  region) at an excitation wavelength of 310 nm (Huguet et al. 2009; Parlanti et al. 2000). The  $\beta:\alpha$  ratio typically ranges from 0.4 to 1.0 and it is an indicator of recently produced microbial DOM, with higher values representing a higher proportion of fresh DOM.

EEMs preprocessing (including removing first and second Raman scattering, standardization to Raman units, absorbance corrections and inner filter effects) was performed prior the PARAFAC modeling. The scans were standardized to Raman units (noted RU; normalized to the integral of the Raman signal between 390 and 410 nm in emission at a fixed excitation of 350 nm) with a Milli-Q water sample run the same day as the samples (Zepp et al. 2004). PARAFAC model was built using MATLAB (MathWorks, Natick, MA, USA) and the drEEM Toolbox version 1.0 (Murphy 2013) and included additional EEMs collected in wetlands and tributaries surrounding Lake Victoria as well as EEMs collected in riverine and lacustrine Ugandan waters (total number of EEMs > 1000). The database includes 350 EEMs from Lake Edward, 225 from Lake Victoria, 80 from Lake George and various crater lakes, 300 from rivers draining into these different lakes, and 200 from degradation experiment carried out in these waters. All EEMs were collected using the same sampling,

preservation and analytical procedures. In addition, Lakes Victoria, Edward and George are shallow tropical lakes that are geographically, climatically and geomorphically close: tropical lakes with low-depth. Including a greater diversity of DOM fluorescence signatures acquired in similar environments can lead identifying components that would not have been detected otherwise (Lapierre and Frenette 2009; Massicotte and Frenette 2011; Stedmon and Markager 2005b) and moreover identify large-scale patterns in DOM origin and dynamic in inland waters (Kothawala et al. 2014; Mann et al. 2016; Williams et al. 2016). Validation of the model was performed by split-half analysis and random initialization and visual validation of residual matrices. The normalization step was applied to scale each EEM to its total signal, thus ensuring the model focused entirely on compositional rather than concentration gradients. The positions of maximums peaks of the eight PARAFAC components (i.e., fluorophores) determined to adequately model the data set were compared to the classical nomenclature and to other PARAFAC models built in other environments using the OpenFluor database (Murphy et al. 2014), in an attempt to provide a general description from previous studies (Table 1). The maximum fluorescence ( $F_{\text{Max}}$ ) values of each component for a particular sample provided by the model were summed to calculate the total fluorescence signal ( $F_{\text{Tot}}$ ) of the sample in Raman unit. The relative abundance of any particular PARAFAC component X was then calculated as  $\%C(X) = (F_{\text{Max}}(X)/F_{\text{Tot}}) \times 100$ .

#### Statistical and data analyses

The data set contained 219 observations from the three sampling cruises (77, 68 and 74 for the first-, second- and third-cruise, respectively). The water samples considered as surface samples corresponded to samples collected in the epilimnion approximately 1 m below the lake surface. We collected 26, 23 and 30 surface water samples for the first, second and third cruise, respectively (Deirmendjian et al. 2020). In addition, we separated the data set into two classes: bay vs. open water sites. The bay sites corresponded to sampling stations located in inner bays but as well to sampling stations located outside the bays but very close to nearshore. The water depth for these bay sampling

**Table 1** Spectral properties (excitation and emission maxima) of the eight components identified using PARAFAC modeling, matching entries in Open Fluor database (95% of similarity), correspondence with peak classification, and comparison with previously identified components in different environments

Component (matching-entries in Open Fluor database from Murphy et al. 2014)	Ex <sub>max</sub> / Em <sub>max</sub> (nm/ nm)	Peak name (Coble et al. 1998)	Comparison with other environments							
			Rivers in Maine, USA (Cawley et al. 2012)	Prairie saline lakes of the U.S Great Plains (Christopher L Osburn et al. 2011)	Congo Basin (Lambert et al. 2016)	Boreal Lakes in Greenland (Osburn et al. 2017)	Brackish salt marsh (Osburn et al. 2015)	Fjord in Denmark (Asmala et al. 2018)	Storm water ponds in Ontario, Canada (Williams et al. 2013)	Coastal waters in Florida, USA (Yamashita et al. 2013)
C1 (66)	305/396	M	C4	C2	C2	None	C8	C2	None	C1
C2 (37)	< 260(320)/ 438	C	C2	C1	None	C2	C2	C1	None	None
C3 (28)	< 260/434	A	C1	C3	C4	C3	C3	C3	C3	None
C4 (58)	270(375)/ 482	A and C	C3	C4	C1	C1	C4	C4	C1	None
C5 (4)	< 260(355)/ 418		None	None	None	None	None	None	C5	None
C6 (16)	275/340	T	C5	None	C6	None	C7	None	None	None
C7 (20)	300/346		None	None	None	None	None	None	None	C5
C8 (25)	270/298	B	None	None	None	None	None	C6	None	C3



stations ranged from 8.4 to 31 m and the mean water depth was 13 m. The open water sites corresponded to sampling stations located in open waters offshore the several islands fringing the shore. The water depth for these open water sampling stations ranged from 29 to 73 m and the mean water depth was 52 m. In addition, in surface waters along the bathymetric gradient, we found the best curve fit on the different data set with CurveExpert Professional2.6® software's.

Principal component analysis (PCA) was performed to condense multivariate information on several parameters to a set of few new variables called principal components (further referred as dimensions). PCA was performed with the data set of the PARAFAC modelling (i.e., relative abundance of the different PARAFAC components) and the different DOM proxies. All data were log-transformed prior to PCA. Redundancy discriminant analysis (RDA) was performed to test relationships between PARAFAC components and few predictive environmental variables. All data were log-transformed prior to RDA. All statistical analyses were performed with R software version 3.1.4 (R Core Team 2018). The vegan package was used for RDA (Oksanen et al. 2019). For PCA, the FactoMineR package was used for analysis (Kassambara and Mundt 2017; Lê et al. 2008).

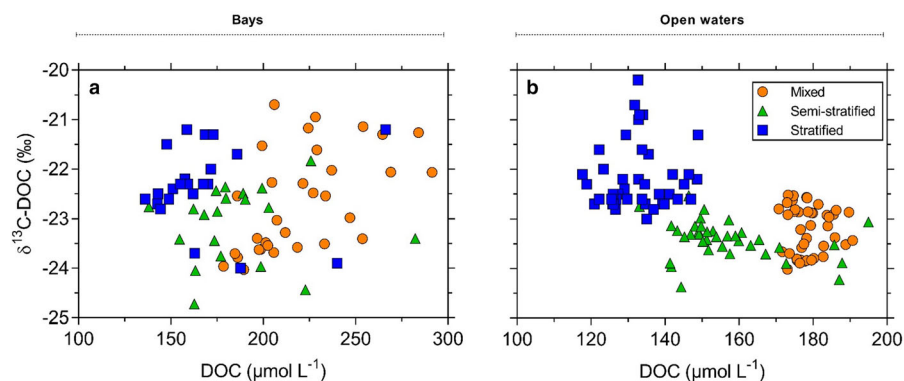
We used the Pearson's correlation for data normally distributed and Spearman's rank correlation for data that were not normally distributed. Normality was tested with the Agostino & Pearson normality test. All tests were made with Golden Software Prism (version 7).

## Results

### Seasonal trends of physico-chemical water column characteristics

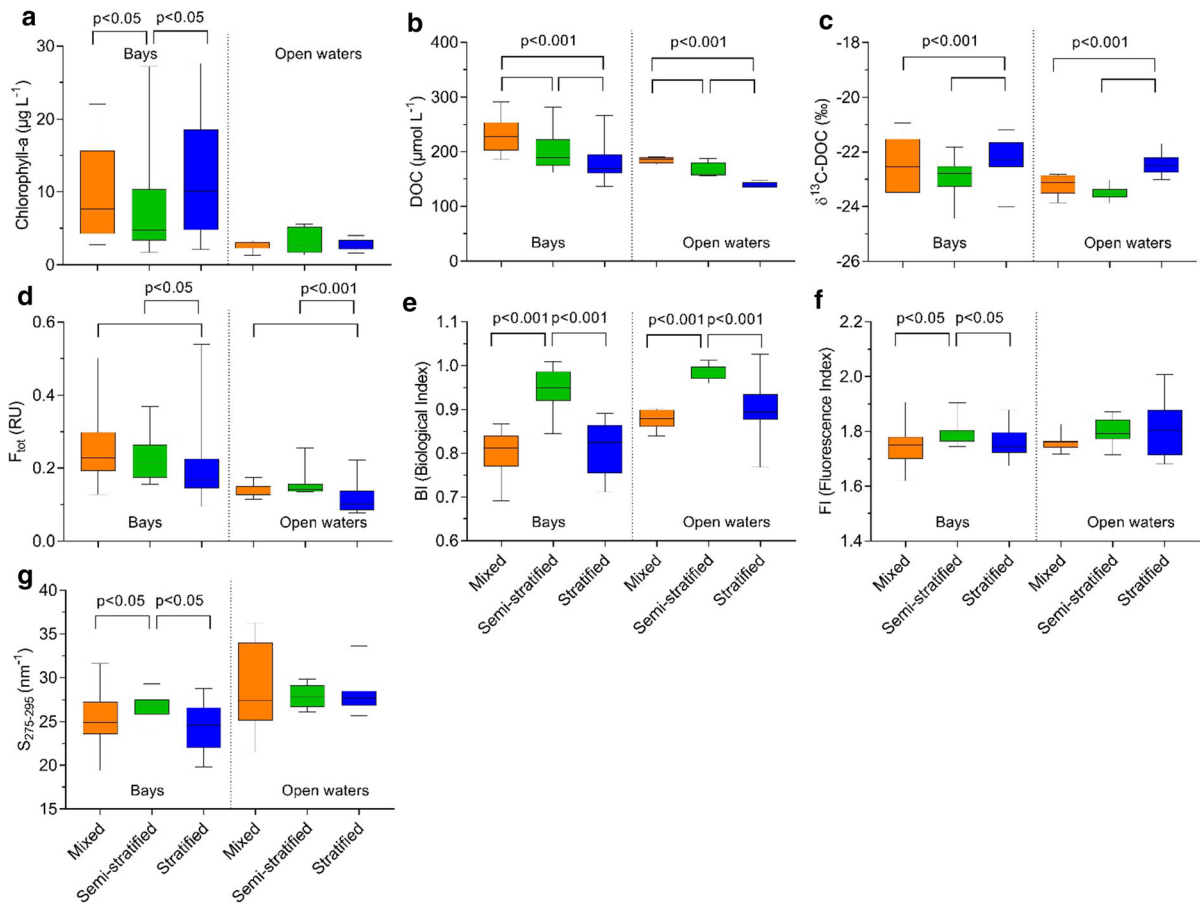
During the dry season (i.e., mixed regime, June 2019), the water column of the open waters exhibited a near absence of a thermal gradient (the water temperature range was 25.0–25.9 °C; Fig. 2e), leading to a vertically well mixed and well oxygenated (the dissolved oxygen saturation range was 76–93%; Fig. 2d) water column. During the short rainy season (i.e., semi-stratified regime, October 2018), the water column was weakly stratified; both a modest thermal gradient (the water temperature range was 24.3–25.3 °C; Fig. 2e) and a modest oxycline (the dissolved oxygen saturation range was 38–105%; Fig. 2d) were apparent between 30 and 45 m depth. During the long rainy season (i.e., stratified regime, March 2018), a marked thermal stratification was observed (the water temperature range was 24.7–26.5 °C; Fig. 2e) and was associated with a strong oxycline below which the water was anoxic, and with a chemocline as indicated by a gradient of specific conductivity (Fig. 2d, f). In the open waters, the mixed layer depth was somewhat similar (approximately 35 m) during the two rainy seasons (Fig. 2e).

In the bays, the thermal gradient was weak or absent during the three sampled seasons and, as consequence, the mixed layer depth in these shallow environments was equivalent to the total depth, regardless of the season (even though a diurnal stratification could develop; Fig. 2b). In the bays, the bottom water was



**Fig. 3** Seasonal relationships between DOC ( $\mu\text{mol L}^{-1}$ ) and  $\delta^{13}\text{C-DOC}$  (‰) in surface waters of **a** bays and **b** open waters of Lake Victoria during the long rainy season corresponding to strongly stratified water column conditions (March 2018), the

short rainy season corresponding to partly stratified water column conditions (October 2018) and the dry season corresponding to mixed water column conditions (June 2019)



**Fig. 4** Seasonal (mixed vs. semi-stratified vs. stratified periods) and spatial (bay vs. open waters) variations of Chlorophyll-a ( $\mu\text{g L}^{-1}$ ), DOC ( $\mu\text{mol L}^{-1}$ ),  $\delta^{13}\text{C}$ -DOC (‰),  $F_{\text{tot}}$  (RU), BI, FI and  $S_{275-295}$  ( $\text{nm}^{-1}$ ), in surface waters of Lake Victoria.

never anoxic, although there was a decreasing pattern of dissolved oxygen saturation with depth that ranged between 49 and 121%, 33 and 116% and 88 and 124%, in the stratified, semi-stratified and mixed regimes, respectively (Fig. 2a). In surface waters of bays, oversaturation of dissolved oxygen with respect to atmospheric equilibrium was recurrently observed, indicative of intense primary production (Fig. 2a).

#### Seasonal variations of DOC and DOM composition

DOC concentrations changed seasonally, being significantly higher during the mixed season (mean  $230 \pm 30 \mu\text{mol L}^{-1}$  and  $185 \pm 5 \mu\text{mol L}^{-1}$  in bay and open waters, respectively; Figs. 3, 4b) than during

Significant differences within bays and within open waters have been tested with a Mann–Whitney statistical test. p-values are shown on the figure

the semi-stratified ( $197 \pm 35$  and  $165 \pm 13 \mu\text{mol L}^{-1}$ ) and stratified seasons ( $180 \pm 40$  and  $140 \pm 5 \mu\text{mol L}^{-1}$ ). Seasonal variations of  $\delta^{13}\text{C}$ -DOC exhibited an opposite pattern to those of DOC with significant higher values (i.e., less negative) during the stratified season ( $-22.3 \pm 0.8$  and  $-22.4 \pm 0.4$ ‰ in bay and open waters, respectively; Figs. 3, 4c) than during the semi-stratified ( $-22.9 \pm 0.6$  and  $-23.5 \pm 0.3$ ‰) and mixed ( $-22.5 \pm 1.0$  and  $-23.2 \pm 0.4$ ‰) seasons.

During the mixed season, the composition of the DOM pool was mainly driven by the relative abundance of components C6 and C8 (Table 2; Fig. 5a). Components C6 (tryptophan-like) and C8 (tyrosine-like) are categorized as protein-like materials (Peaks T and B; Coble et al. 1998) derived from phytoplankton

**Table 2** Positive correlations of the eight DOM components obtained from PARAFAC with its origins (protein-like, microbial humic-like, terrestrial humic-like), hydrologicalregimes (mixed, semi-stratified and stratified), DOM proxies (Chlorophyll-a, DOC,  $F_{\text{tot}}$ , BI, FI,  $\delta^{13}\text{C}$ -DOC) and nutrients ( $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$ )

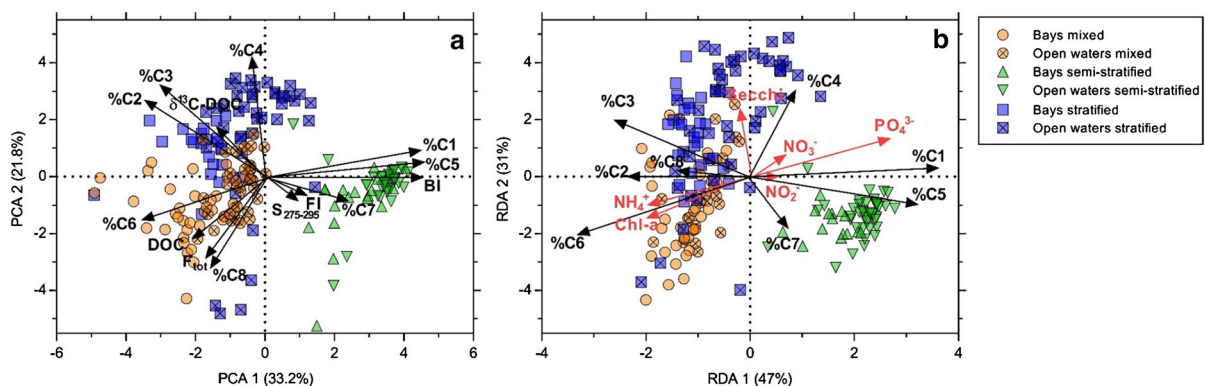
	C6	C8	C1	C5	C7	C2	C3	C4
Protein-like (amino acids derived from primary production, aliphatic, LMW) <sup>a</sup>	+	+						
Microbial humic-like (microbially transformed humic-like material) <sup>b</sup>			+	+	+			
Terrestrial humic-like (from terrestrial environments, aromatic, HMW) <sup>c</sup>						+	+	+
Mixed season	+	+						
Semi-stratified season			+	+	+			
Stratified season						+	+	+
Chlorophyll-a	+	+						
DOC	+	+						
$F_{\text{tot}}$	+	+						
$\text{NH}_4^+$	+	+						
BI			+	+	+			
FI			+	+	+			
$\text{PO}_4^{3-}$			+	+	+			
$\delta^{13}\text{C}$ -DOC						+	+	+

The positive correlations denoted the results obtained in the PCA and the RDA (Fig. 5)

<sup>a</sup>Deduced from Fellman et al. (2010) and Stedmon and Markager, (2005a, b)

<sup>b</sup>Deduced from Cawley et al. (2012), Lambert et al. (2016), Osburn et al. (2011, 2015)

<sup>c</sup>Deduced from Asmala et al. (2018), Cawley et al. (2012), Fellman et al. (2010), Lambert et al. (2016). LMW and HMW for low and high molecular weight, respectively

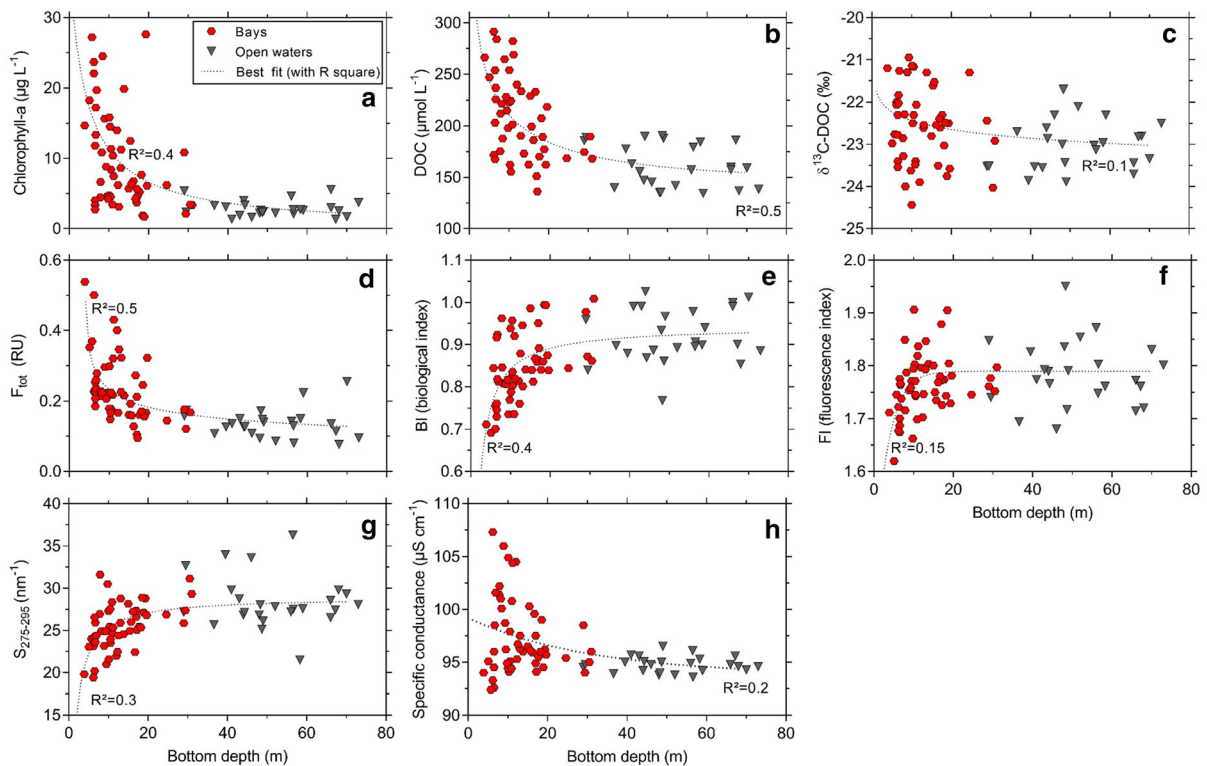


**Fig. 5** **a** Principal component analysis (PCA) of Lake Victoria water samples (all sampling depths combined, and using datasets of PARAFAC components in relative abundance % and DOM proxies) including loadings plot for the input variables and scores plot for water samples. **b** Redundancy discriminant analysis (RDA) of Lake Victoria water samples, using the PARAFAC dataset and few predictive environmental

variables: plot of variables and individuals on the two first RDA dimensions. The environmental variables are indicated as red vectors (red arrows) whereas the PARAFAC variables are indicated in black solid lines and represented the relative abundance (in %) of a given PARAFAC component. Individuals have been clustered in qualitative groups corresponding to the three seasons. (Color figure online)

indicative of biologic activity and DOM bioavailability (Tables 1, 2). Components C6 and C8 were clustered with  $F_{\text{tot}}$ , DOC,  $\text{NH}_4^+$  and Chlorophyll-a

(Table 2; Fig. 5). During the semi-stratified season, the composition of the DOM pool was mainly driven by the relative abundance of C1 and C5 (Table 2;



**Fig. 6** Horizontal variations of Chlorophyll-a ( $\mu\text{g L}^{-1}$ ), DOC ( $\mu\text{mol L}^{-1}$ ),  $\delta^{13}\text{C-DOC}$  (‰),  $F_{\text{tot}}$  (RU), BI, FI and  $S_{275-295}$  ( $\text{nm}^{-1}$ ), in surface waters of Lake Victoria (data from all

sampling campaigns combined). The best regression line, with associated  $R^2$  value, for each data set is represented by a black dashed curve

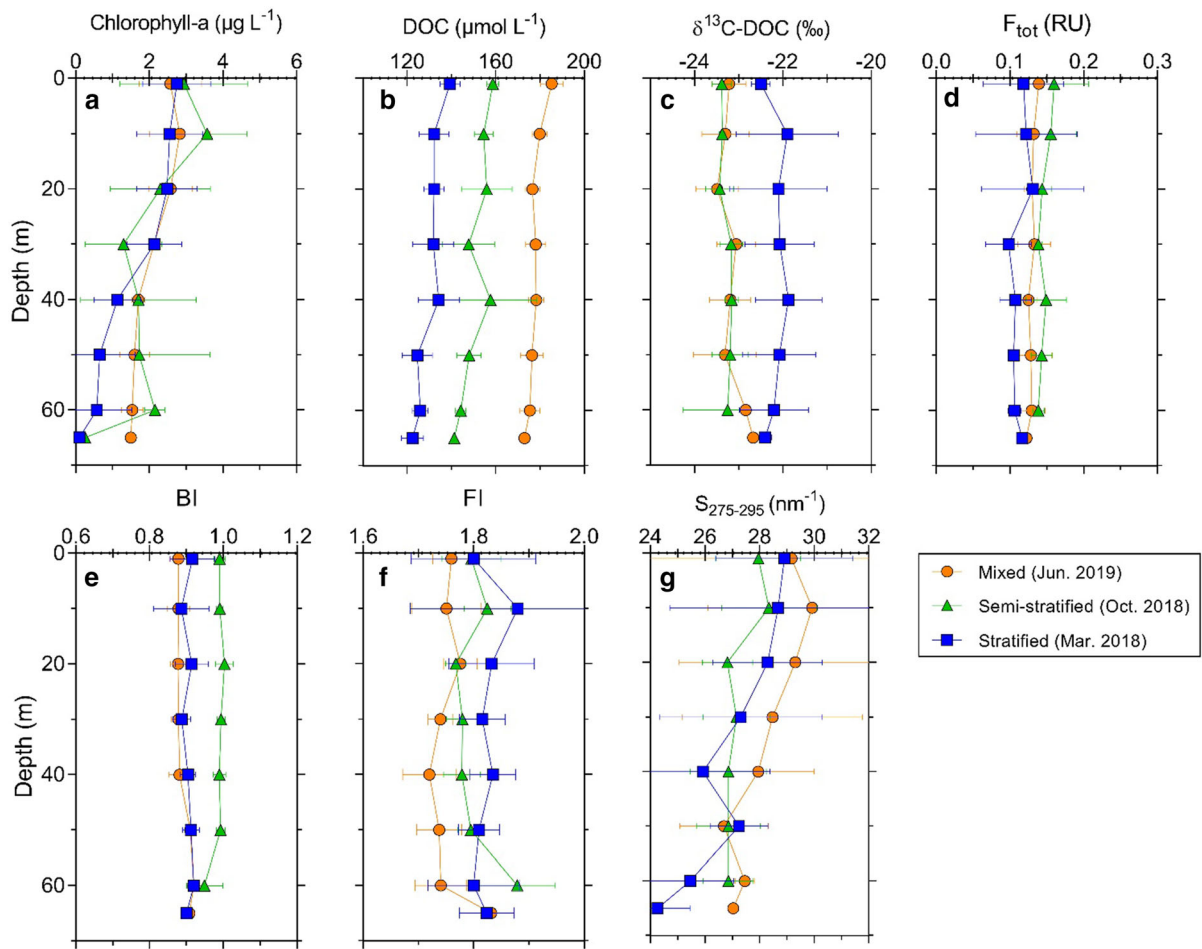
Fig. 5a). Components C1 and C5 are categorized as microbially transformed humic-like material (Peak M, Tables 1, 2). Components C1 and C5 were clustered with  $\text{PO}_4^{3-}$  and BI and to a lesser extent with FI and  $S_{275-295}$  (Table 2; Fig. 5). During the stratified season, the composition of the DOM pool was mainly driven by the relative abundance of components C2, C3 and C4 (Fig. 5). Components C2, C3 and C4 originates from terrestrial environments (Peaks A and C; Tables 1, 2) and C4 were clustered with  $\delta^{13}\text{C-DOC}$  (Fig. 5a).

#### Horizontal and vertical variations of Chlorophyll-a, DOC and DOM composition

In surface waters, Chlorophyll-a concentration decreased spatially along the bathymetric gradient: Chlorophyll-a ranged between 1.6 and  $27.2 \mu\text{g L}^{-1}$  (mean  $9.7 \pm 6.9 \mu\text{g L}^{-1}$ ) in bays and between 1.3 and  $5.7 \mu\text{g L}^{-1}$  (mean  $2.8 \pm 1.1 \mu\text{g L}^{-1}$ ) in open waters (Figs. 6a, S2). Secchi disk depth was  $170 \pm 65 \text{ cm}$

and  $350 \pm 86 \text{ cm}$  in bays and open waters, respectively (Fig. S3a). Consequently, according to Chlorophyll-a and Secchi disk depth, bays can be considered as being eutrophic whereas open waters can be considered as being mesotrophic, based on classification developed for temperate lakes (e.g., Vollenweider and Kerekes 1982). In surface waters, DOC ( $208 \pm 38$  and  $161 \pm 21 \mu\text{mol L}^{-1}$  in bays and open waters, respectively),  $F_{\text{tot}}$  ( $0.24 \pm 0.1$  and  $0.14 \pm 0.04 \text{ RU}$ ) and the fluorescence intensity of the eight PARAFAC components mirrored the decreasing spatial pattern of Chlorophyll-a with bottom depth (Figs. 6, S2, S4). In contrast, BI ( $0.84 \pm 0.08$  and  $0.92 \pm 0.06$ ), FI ( $1.76 \pm 0.05$  and  $1.80 \pm 0.08$ ) and  $S_{275-295}$  ( $25.4 \pm 2.7$  and  $28.4 \pm 3.1 \text{ nm}^{-1}$ ) exhibited an increasing pattern with bottom depth (Figs. 6, S2).

We only focused on pelagic waters for the description of vertical patterns (Figs. 7, S5) because the sampled bays were shallow and irrespective of the season, the water column of bays was always mixed (Fig. 2). Chlorophyll-a and DOC concentrations



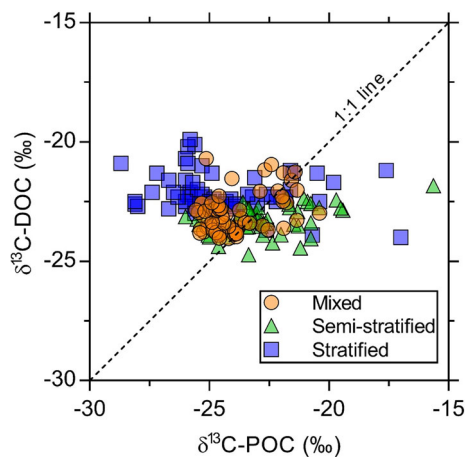
**Fig. 7** Vertical profiles in open waters of Chlorophyll-a ( $\mu\text{g L}^{-1}$ ), DOC ( $\mu\text{mol L}^{-1}$ ),  $\delta^{13}\text{C-DOC}$  (‰),  $F_{\text{tot}}$  (RU), BI, FI and  $S_{275-295}$  ( $\text{nm}^{-1}$ ), for the different seasons in Lake Victoria. One

point represents the mean and the associated standard deviation of all open water stations at a specific depth

tended to decrease vertically, regardless of the season; suggesting that degradation processes occurred in the water column (Fig. 7a, b). The two latter parameters seemed to decrease in two steps: a first decrease occurred in the first 20 m suggesting photooxidation and/or more active microbial activity, whereas second decrease occurred below 40 m in stratified and semi-stratified seasons, which suggested additional microbial degradation below the thermocline. In contrast,  $\delta^{13}\text{C-DOC}$ ,  $F_{\text{tot}}$ , BI and FI were relatively homogeneous in the water column (Fig. 7c–f). During the stratified season, the microbial humic-like components C1 and C5 tended to increase with depth whereas

protein-like components C6 and C8 tended to decrease with depth (Fig. S5). This suggests microbial degradation of C6 and C8 below the thermocline. In addition, during the stratified season, the terrestrial humic-like component C4 increased with depth whereas parameter  $S_{275-295}$  decreased with depth (Figs. 7g, S5).  $S_{275-295}$  is inversely related to the molecular weight and the percent of terrigenous DOC, indicative of heavier refractory organic terrestrial materials being concentrated (accumulation of residual compounds) below the thermocline where labile organic materials were depleted.





**Fig. 8** Seasonal relationships between  $\delta^{13}\text{C}$ -DOC (‰) and  $\delta^{13}\text{C}$ -POC (‰)

## Discussion

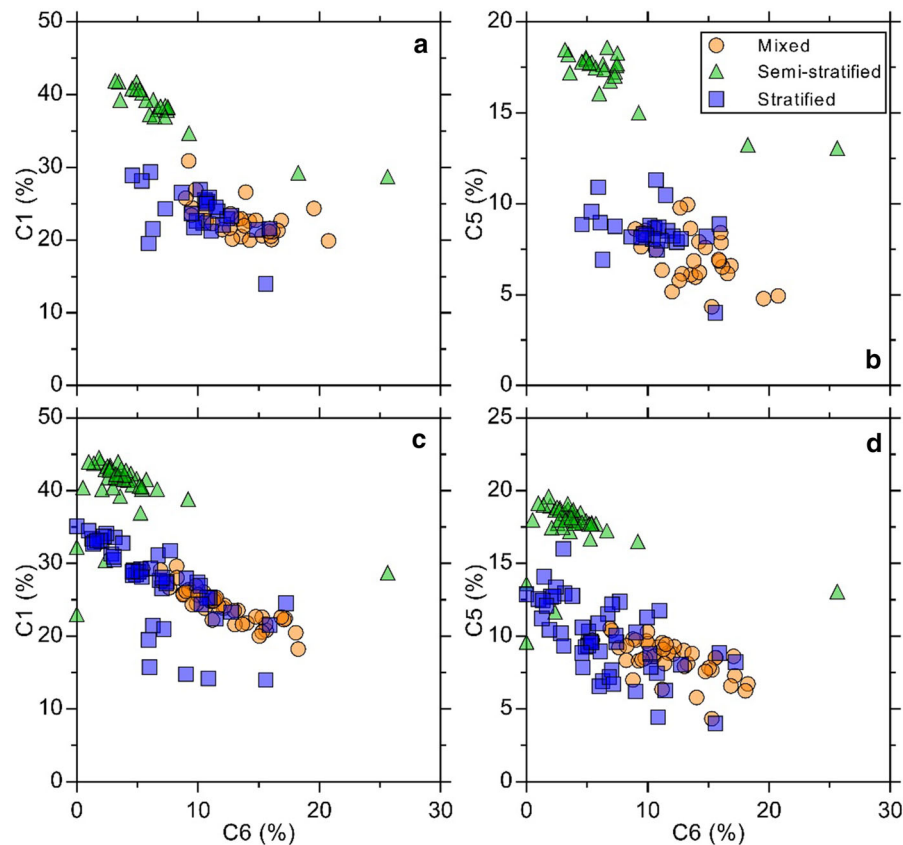
### Seasonality of the DOM pool

DOM composition was different among the three sampled seasons, following the sequence of DOC production related to changes in vertical stratification, from the replenishment of the DOC stock during the mixed conditions to its collapse during the most stratified conditions, with a parallel increase of the impact of the microbial processing and reworking of DOM. In addition, DOM composition was dominated by autochthonous sources, as evidenced by the different DOM proxies: BI ( $0.9 \pm 0.05$ ), FI ( $1.8 \pm 0.05$ ) and  $S_{275-295}$  ( $27 \pm 2.9 \text{ nm}^{-1}$ ); those values are much higher to values found in typical terrestrially-dominated ecosystems.

During the mixed season, the availability of DIN, particularly ammonia, increased (Figs. 5b, S3b), consequently, aquatic primary production in Lake Victoria was  $\sim$  twice higher during the mixed season in comparison to the two other seasons (unpublished data) as generally observed in tropical lakes (e.g. Petrucio and Barbosa 2004; Stenuite et al. 2009). The RDA also evidenced this, where data points corresponding to the mixed season were clustered with Chlorophyll-a and  $\text{NH}_4^+$  (Fig. 5b). In addition, the positive relationship between DOC,  $F_{\text{tot}}$ , protein-like components (C6 and C8) and Chlorophyll-a showed that aquatic primary production led to an increase in the stock of DOC and was also a major source of

fluorescence of protein-like components (Fig. 5). Indeed, the tryptophan-like component (C6) is generally associated with the dominance of algal-derived DOM and its abundance is larger in more productive systems (Cammack et al. 2004; Thottathil et al. 2013; Yamashita and Tanoue 2003). During the mixed and semi-stratified seasons, there was a closer correspondence between  $\delta^{13}\text{C}$ -POC and  $\delta^{13}\text{C}$ -DOC, whereas during the stratified season, much wider variations in  $\delta^{13}\text{C}$ -POC were not associated with similar variability in  $\delta^{13}\text{C}$ -DOC (Fig. 8). The POC pool was mainly phytoplankton-derived, as indicated by a strong overall correlation between  $\delta^{13}\text{C}$ -POC and  $\delta^{13}\text{C}$ -DIC (Spearman coefficient of 0.51,  $p$ -value  $< 0.001$ , unpublished data). The  $\delta^{13}\text{C}$ -DOC and  $\delta^{13}\text{C}$ -POC variations suggest that the bulk DOC pool was strongly tied to in situ phytoplankton production during the mixed and semi-stratified seasons but not during the stratified season. Morana et al. (2014) investigated phytoplankton extracellular release and its microbial uptake in four African tropical lakes distributed along a gradient of a productivity, including Lake Victoria. They concluded that phytoplankton extracellular release was the the main mechanism of DOC release rather than cell lysis or trophic processes such as zooplankton grazing. This freshly excreted DOC is quickly processed by microbes (Morana et al. 2014), yet, protein-like components did not originate from microbial sources as evidenced by the negative correlation between protein-like components and FI (Fig. 5a).

During the semi-stratified season, significantly higher values of microbial humic-like components (C1 and C5), BI and FI indicate that the DOM pool was fresher and more microbially transformed than during the preceding mixed season (Table 2; Fig. 5a). The peak of microbial humic-like components did not correspond with the peak of protein-like components (non-humic DOM; Fig. 5), suggesting condensation reactions of non-humic DOM were not the mechanism for the observed occurrence of microbially derived humic DOM (Kieber et al. 1997). The negative linear relationships in surface and deeper waters between the tryptophan-like component C6 and the microbial humic-like components C1 and C5 suggested that C6 might be degraded into C1 and/or C5 (Fig. 9). To explain this pattern we can exclude photobleaching because the majority of photobleaching occur in peaks A, C and M whereas peaks T and B (protein-like

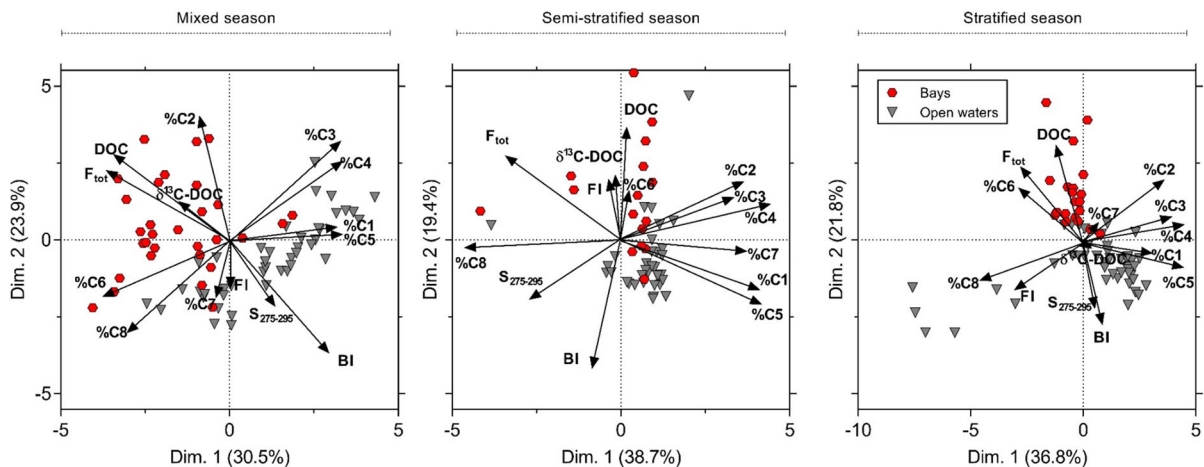


**Fig. 9** Seasonal relationships between the relative abundance of C1 and C6, and of C5 and C6, horizontally in surface waters (**a** and **b**), and vertically in open waters (**c** and **d**) in Lake Victoria. We performed an outlier elimination on the datasets and then we explored correlations with Pearson correlation test. The results showed strong correlation with  $p < 0.001$  or

$p < 0.05$ . In the figure **a**) Pearson's coefficient was  $-0.83$ ,  $-0.57$ ,  $-0.9$  for the stratified, semi-stratified and mixed regimes, respectively. Pearson's coefficient was  $-0.45$ ,  $-0.42$ ,  $-0.5$ ;  $-0.43$ ,  $-0.82$ ,  $-0.52$  and  $-0.6$ ,  $-0.6$ ,  $-0.6$ ; in **b–d**, respectively

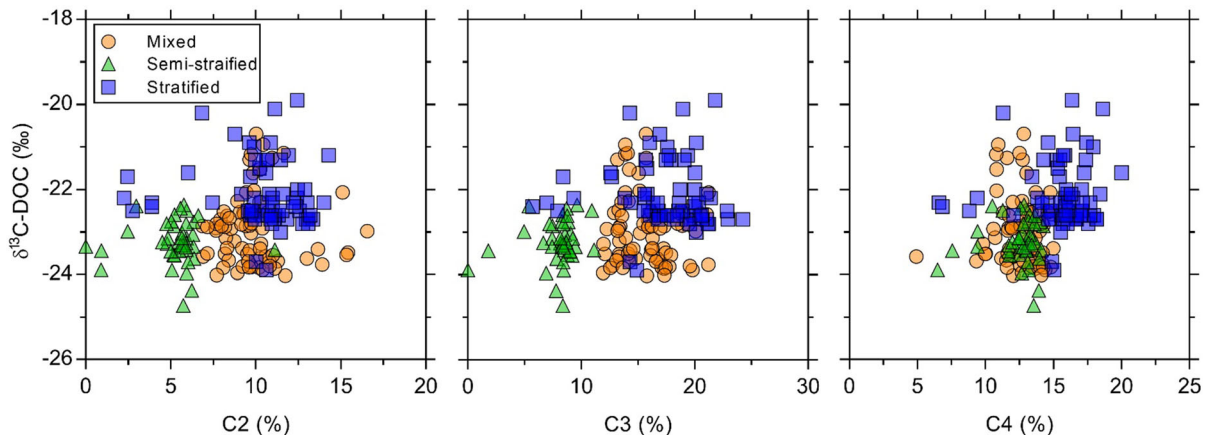
materials) usually exhibit the least amount of photo-bleaching among all the components (Cory et al. 2007; Osburn et al. 2011; Winter et al. 2007). Cammack et al (2004) observed that tryptophan-like component degradation exceeds its production in nutrient depleted conditions. These results are in agreement with ours, where tryptophan-like components increased in nutrient rich waters during the mixed season and decreased in the following semi-stratified season when surface waters were nutrient depleted (Fig. S3b). This suggests a lag time between phytoplankton and bacterioplankton blooms (Wambeke et al. 2002) as also observed in Lake Tanganyika (Stenuite et al. 2009). In tropical Lake Kariba in Zimbabwe, Lindell and Edling (1996) showed that bacterial abundance and production was inhibited by

solar irradiance because light had a negative effect on bacterial enzyme production. In Lake Victoria, the euphotic layer (based on Secchi disk measurements; Fig. S3a) strongly decreased in the semi-stratified season, which might have positive effects on bacterial abundance and subsequent microbial humic-like production. In addition, the RDA showed that the dataset of the semi-stratified season was positively correlated with  $\text{PO}_4^{3-}$  and negatively with Chlorophyll-a (Fig. 5b). On a yearly basis, Chlorophyll-a was also strongly negatively correlated with  $\text{PO}_4^{3-}$  (Spearman coefficient of  $-0.7$ ,  $p$ -value  $< 0.001$ ). Considering a twice-lower aquatic primary production during this season in comparison to the mixed season, this showed that more  $\text{PO}_4^{3-}$  was available for microbes due to a lower competition with phytoplankton, which boosted



**Fig. 10** Principal component analysis (PCA) of Lake Victoria water samples (all sampling depths combined, and using datasets of PARAFAC components in relative abundance %

and DOM proxies) for the **a** mixed, **b** semi-stratified and **c** stratified seasons. Individuals have been clustered in qualitative groups corresponding to the bays and open waters

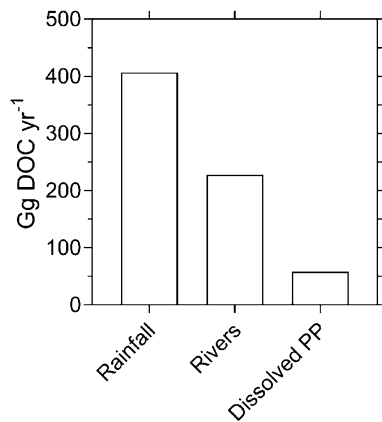


**Fig. 11** Seasonal relationships between the relative abundance of terrestrial humic-like components (C2, C3 and C4) and  $\delta^{13}\text{C-DOC}$  (‰)

microbial activity, in agreements with the emergence of components C1 and C5 and the increase in BI. Lapierre and Del Giorgio (2014) showed that component C5 was highly photodegradable; however, we found high relative abundance of this component during the semi-stratified season, showing that production of component C5 was higher than its photodegradation, confirming high bacterial production and abundance. During the the semi-stratified season, a large portion of the dataset falls close the 1:1 line for  $\delta^{13}\text{C-POC}$  vs.  $\delta^{13}\text{C-DOC}$  (Fig. 8) and there was no statistical difference between both pools. Consequently, during the semi-stratified season, the

autochthonous DOM was produced by intense bacterial processing of DOM (very likely protein-like components) that derived from aquatic primary production.

During the stratified season, DOC was lowest ( $\delta^{13}\text{C-DOC}$  was highest) and the variability of the DOM pool was dominated by terrestrial humic-like components (C2, C3 and C4). Some authors (e.g., Parlanti et al. 2000; Osburn et al. 2011) argued strongly for peak C (C2) having autochthonous origin (degradation of peak M: C1). In Lake Victoria, we found no significant relationships between C2 and C1 that could argue for peak C having an autochthonous



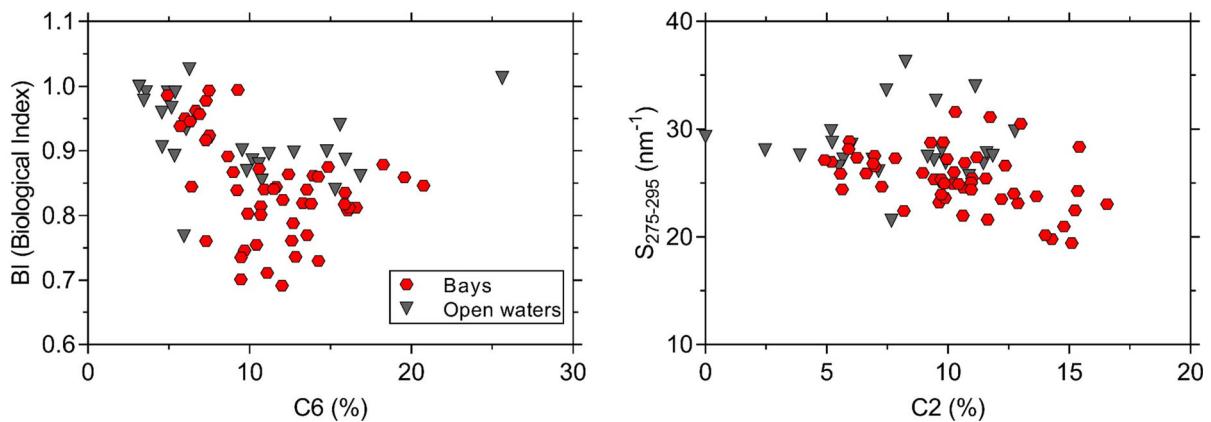
**Fig. 12** Annual DOC inputs into Lake Victoria from rain, rivers and dissolved primary production. Dissolved primary production was estimated from particulate primary production (Morana et al. 2014) and particulate primary production measurements during the cruises upscaled to the whole lake (unpublished data). DOC inputs from rain were estimated with a mean value of DOC in rain over the lake derived from a global model ( $3.47 \text{ mg L}^{-1}$ ; Safieddine and Heald, 2017) and the rainfall over the lake for the 1950–2004 period ( $3719 \text{ m}^3 \text{ s}^{-1}$ ; Sewagudde 2009). DOC inputs from rivers were estimated with a mean value of DOC in two main rivers draining into the lake and measured during the three cruises ( $8.9 \text{ mg L}^{-1}$ , unpublished data) and the basin discharge for the 1950–2004 period ( $814 \text{ m}^3 \text{ s}^{-1}$ ; Sewagudde 2009)

origin (Fig. S6). In Lake Victoria, considering the large volume and the long residence time, it appears unlikely that, on a seasonal basis, rivers (or precipitation) can deliver sufficient organic material to shift the variability of the DOM pool (in the entire lake) towards terrestrial humic-like components. This is confirmed by the PCA showing the variability of the DOM pool for the stratified season where the terrestrial components were clustered with open waters rather than with bays that are directly influenced by terrestrial inputs from rivers and surface runoff (Fig. 10c). The relationships between  $\delta^{13}\text{C}$ -POC and  $\delta^{13}\text{C}$ -DOC exhibited more disconnection of the two pools during the stratified season in comparison to the two other seasons (Fig. 8). Therefore, the DOM pool was not directly related to freshly excreted DOM from phytoplankton during this season but was rather composed of a mixture of older and highly degraded DOM from phytoplankton and refractory terrestrial components. The dominance of refractory components during the stratified season would be a consequence of the degradation of higher quality DOC during the preceding seasons by a highly active

microbial community. During the stratified season, the accumulation of residual refractory compounds was evidenced by the positive relationships between  $\delta^{13}\text{C}$ -DOC and terrestrial components (Fig. 11). DOC inputs to the lake were estimated to 407, 228 and 58  $\text{Gg year}^{-1}$ , from rainfall, rivers and dissolved primary production, respectively (Fig. 12). This suggests that residual DOM, which was apparent during the stratified season when the labile and fresh stock of DOC created during the preceding mixed season was consumed, is mainly allochthonous and of terrestrial origin with a strong dominance of rain inputs on river inputs.

#### DOM in the epilimnion: mixing of eutrophic bays and mesotrophic open waters

In surface waters, the relationship between specific conductivity (assuming it is a conservative tracer) and bottom depth (Fig. 6h) suggested that lateral variations are likely due to water mixing between two end-members: bays and open waters. In Lake Victoria, inshore–offshore exchange is indeed mediated by wind and by lateral convection that could occur year round (Macintyre et al. 2014). Bays continuously receive nutrients from the drainage of land and/or from anthropogenic activity as well as from the sediments since the water column is permanently mixed vertically (Fig. 2b). In the deeper part of the lake, inputs of nutrients are due mainly to internal loading whereas aquatic primary production was light-limited due to the deeper mixing layer depth (Fig. 2b, e; Njuru 2009). On a yearly basis, aquatic primary production was indeed  $\sim 30\%$  higher in bays in comparison to open waters (unpublished data). Consequently, bays exhibited Chlorophyll-a up to twenty times higher than in open waters (Fig. 6a) and DOM was more abundant in eutrophic bays (DOC and  $F_{\text{tot}}$  were up to two times higher, Fig. 6b, d) than in mesotrophic open waters. This was particularly true for component C6, which was highly correlated with DOC and  $F_{\text{tot}}$  in bays in the PCAs, regardless of seasons (Fig. 10). In the bays, this showed a larger contribution of algae derived component (C6), which is negatively related to BI (Pearson coefficient =  $-0.5$ ,  $p < 0.001$ ; Fig. 12), reflecting higher phytoplankton activity in bays in comparison to microbial activity whereas the opposite pattern occur in open waters. Indeed, in open waters, bacteria undergo lower competition with



**Fig. 13** Spatial relationships in surface waters of Lake Victoria between the relative abundance of C6 and BI (Biological Index) and between the relative abundance of C2 and  $S_{275-295}$  ( $\text{nm}^{-1}$ )

phytoplankton because phytoplankton is light-limited. This also agrees with DOM characterization, with higher values of  $S_{275-295}$ , FI and BI, and higher C1 and C5 components in relative abundance in open waters compared to bays (Figs. 10, S2, S7); which indicates that DOM in open waters is slighter, fresher and more microbially produced. The terrestrial-like component C2 exhibited a significant contribution in bays but this was not the case for the two other terrestrial like-components C3 and C4 (Figs. 10, S7). A lower  $S_{275-295}$  in bays in comparison to open waters is driven by higher content of terrigenous component C2 (Spearman coefficient =  $-0.4$ ,  $p < 0.001$ ; Fig. 13). Moreover, light limitation in open waters led to respiration dominating over primary production (Hecky et al. 2010), which in turn caused concomitant accumulation of refractory compounds (C3 and C4) and it is also coherent with higher microbial-like components (C1 and C5) and BI in open waters (Figs. 10, S2, S7).

#### Limitation of the study and perspectives

Even though further information on the characterization of photochemical degradation would be needed to obtain a complete understanding of DOM dynamics and cycling in this important tropical freshwater ecosystem, we hypothesize it was not the main process regulating DOM dynamics in the lake. In surface waters, we showed that fluorescence followed a conservative mixing pattern, excluding photodegradation as a significant sink for DOM, as reported by

Loiselle et al. (2010) in some inner bays of the lake. On the contrary, bays where there was a reduced exchange of water can undergo photodegradation of DOM (Loiselle et al. 2010). However, those type of inner bays are not representative of the hydrological variability of the entire lake. In the open waters, photodegradation is light-limited (as for the primary production) because the mixing depth is deeper than the euphotic depth whereas in bays photodegradation is limited by self-shading (Hecky et al. 2010). In tropical reservoirs, DOM exudation by cyanobacteria (that represented 60% of the phytoplankton during our cruises, unpublished data) was highly bioavailable, implying high biological alteration and turnover rates of this DOM pool (Bittar et al. 2015).

In the study, we observed a cross-shore variability of DOM (from inner bays to open waters), but we did not observe a long-shore variability. This was supported by the multivariate analyses (Figs. 5, 10) for which the bays sampling points were often strongly clustered together. In one bay surrounded by wetlands (Katonga Bay), we did observed higher fluorescence than in other bays, in line with the study of Loiselle et al. (2010). Nowadays, most of the coastal wetlands have been drained and converted to agriculture land (Crisman 2001): this bay is not representative of other bays around the lake. In addition, the fresh organic matter originating from the drainage of the land (anthropogenic inputs) should be quickly processed when it enters the bays, making its observation difficult.



We highlighted that terrestrial DOM components emerged during the stratified regime because the labile and fresh stock of DOM created during the preceding mixed season was consumed. In the bays, allochthonous DOM inputs from the runoff could play an additional role in seasonally shifting the DOM pool towards terrestrial DOM components but our study design does not allow for a clear identification of this process. Future studies are needed to characterize and quantify the allochthonous DOM inputs from runoff and precipitation.

## Conclusions

Organic matter corresponds to the largest reactive reservoir of carbon-based compounds on Earth and, as consequence; DOM is a key component of the local and global carbon cycles. In Lake Victoria, the present study showed that DOM was a very active carbon reservoir, which varied greatly in terms of sources and reactivity, both in time (seasonally) and in space (vertically and laterally). We highlighted that in such a large lake, the difference in DOM composition in surface waters was mainly related to different aquatic primary production rates. Eutrophic bays had higher DOM stocks derived both from aquatic primary production and from terrestrial inputs, while in mesotrophic open waters, light limitation decreased the intensity of aquatic primary production and resulted in a larger fraction of DOM derived from the microbial loop. Using PARAFAC analysis, the data has shown that DOM in Lake Victoria is dominated by eight fluorophores belonging to three main classes (i.e., terrestrial humic-like, microbial humic-like and protein-like). The most significant result was the seasonal shift of these three main DOM classes, which is highly related to the physico-chemical characteristics (i.e., stratification, light and nutrients) of the lake. This study supports the view that African Great Lakes are very active in terms of carbon cycling and must be better considered in global models.

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**Data availability** The full data-set is publically available at zenodo.org (Deirmendjian et al. 2020).

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