Ecosystems
https://doi.org/10.1007/s10021-022-00783-4

Prevalence of Autotrophy in Non-humic African Lakes

Cédric Morana,[1,2] * Alberto V. Borges,[1] Loris Deirmendjian,[1,3] William Okello,[4] Hugo Sarmento,[5] Jean-Pierre Descy,[1] Ismael A. Kimirei,[6] and Steven Bouillon[2]

[1]*Chemical Oceanography Unit, Université de Liège, Liège, Belgium;* [2]*Department of Earth and Environmental Sciences, KULeuven, Leuven, Belgium;* [3]*Géosciences Environnement Toulouse (GET, CNRS, IRD), Université de Toulouse Paul Sabatier, Toulouse, France;* [4]*Limnology Unit, National Fisheries Resources Research Institute, Jinja, Uganda;* [5]*Departamento de Hidrobiologia, Universidade Federal de São Carlos, São Carlos, Brazil;* [6]*Tanzania Fisheries Research Institute, Dar es Salaam, Tanzania*

Abstract

Heterotrophic respiration of organic matter (OM) is thought to dominate over aquatic primary production (PP) in most freshwater lake ecosystems. This paradigm implies that lateral transport of OM from the terrestrial biosphere subsidize the major fraction of aquatic respiration and that many lakes are a net source of carbon dioxide (CO_2) to atmosphere. Nevertheless, African lakes were absent of the datasets upon which this paradigm was built. Here, we report a comprehensive and methodologically consistent data set of pelagic PP and community respiration (CR) obtained over the last decade in contrasting non-humic African lakes including 5 of the East African Great lakes (Tanganyika, Kivu, Edward, Albert, Victoria) and smaller shallow lakes located in Eastern Africa. Also, we determined the partial pressure of CO_2 in surface waters and examined the sources and dynamics of organic and inorganic carbon by means of stable isotope tools across a wide range of physical and chemical conditions and productivity status. Our observations revealed that the threshold value at which the equivalence between PP and CR is met is substantially lower in Africa (10 mmol C m^{-3} d^{-1}) than at higher latitude (25 mmol C m^{-3} d^{-1}), suggesting that non-humic African lakes tend to be more autotrophic than expected from empirical relationships derived from data collected in boreal and temperate regions. Integrated at the regional scale, we estimate that PP is about 20 times higher than the organic carbon burial in sediments. It implies that a large fraction (< 90%) of PP is effectively recycled in the warm water column of non-humic African lakes.

Introduction

Inland waters play a central role in the biogeochemical cycling of carbon in the Earth system. Considering the limited surface of the Earth covered by inland water bodies, they represent ''hotspots'' of C processing, and their relative contribution to the global C budget is therefore substantial compared with marine and terrestrial ecosystems (Cole and others 2007). The balance between rates of organic matter (OM) consumption (heterotrophy) and autochthonous production by

Received 11 December 2021; accepted 30 July 2022

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s10021-022-00783-4.

Author Contributions: CM, AVB and SB conceived and designed the study. CM, AVB, LD, HS performed the experiments. All co-authors contributed to the data analysis. CM drafted the manuscript with inputs from all co-authors.

*Corresponding author; e-mail: cedric.morana@uliege.be

Published online: 26 August 2022

photosynthesis (autotrophy) in an aquatic ecosystem is representative of its metabolism. Odum (1956) postulated that at sufficiently large spatio-temporal scale, ecosystem production and consumption of OM rates are close to equilibrium. Indeed, in a relatively closed system, any increase in ecosystem productivity yields OM which would eventually be respired proportionally, and alternatively, any increase in OM mineralization will release inorganic nutrients that would stimulate primary production (Staehr and others 2012). According to this theory, only lakes characterized by high concentration of terrestrially derived colored dissolved OM (humic lakes) or lakes polluted by waste water would be expected to be net heterotrophic (Odum 1956; Duarte and Prairie 2005). This view is supported by the results of del Giorgio and Peters (1994) who found that the balance between photosynthesis and heterotrophic respiration is strongly influenced by lake water color which decreases underwater light penetration. Therefore, they came up with the hypothesis that lake net metabolism is primarily determined by environmental variables controlling phytoplankton production, such as water color, which is in turn directly related to humic substances concentration, nutrient availability (del Giorgio and Peters 1994, lake morphometry and stratification pattern (mean depth, watershed to surface area ratio) (Rawson 1953; Fee 1979), and temperature (Robarts and Zohary 1987).

Since the late 1990's, a new paradigm progressively emerged proposing that respiration of OM predominantly exceeds autochthonous production in oligotrophic freshwaters ecosystems regardless of their humic contents, meaning that they are predominantly net heterotrophic because they receive substantial allochthonous inputs of OM from adjacent ecosystems, in particular from the terrestrial biosphere (Del Giorgio and others 1997; Duarte and Agusti 1999; Duarte and Prairie 2005). This paradigm was supported by contemporary reports of lakes and rivers as significant sources of CO_2 to atmosphere (Cole and others 1994; Prairie et L. 2002; Richey and others 2002). In lakes, a productivity threshold at which heterotrophic respiration is balanced by primary production has been proposed at a primary production rate of 25 mmol m^{-3} d^{-1} (82 lakes, Duarte and Agusti 1998). This paradigm shift has important implications because net heterotrophy has been recognized as one of the main causes for the net CO_2 emissions from freshwaters ecosystems to the atmosphere (Cole and others 2007). However, the vast majority of the data included in these studies were gathered in small or medium size lakes located in temperate or boreal regions where relatively unproductive, humic lakes are common. Furthermore, the apparent prevalence of net heterotrophy in seemingly unproductive lakes could come from a ''plankton-centric'' perspective that usually does not count into account benthic primary production (Brothers and Vadeboncoeur 2021), which could be especially important in oligotrophic, clearwater.

For several reasons, the statement that most lakes are net heterotrophic may not apply to African tropical lakes. Indeed, net primary production in tropical lakes is typically three times higher than in their temperate and boreal counterparts due to the combination of year-round high light and temperature conditions (Sarmento 2012; Kraemer and others 2017a), and a less stable water column favorable for episodical nutrient inputs (Lewis 1996). Also, tropical lakes are generally characterized by an overall stronger contribution of cyanobacteria to the phytoplankton assemblage as some species can overcome nitrogen limitation through atmospheric N_2 fixation (Kosten and others 2012). In productive lakes, cyanobacteria are able to cope with the limitation of CO_2 availability through photosynthetic assimilation of HCO_3^- (Morales-Williams and others 2017) and through carbon dioxide concentration mechanisms (CCM). Additionally, because of higher light harvesting capabilities than most other phytoplankton groups, cyanobacteria can generally cope better with the prevalence of light limitation in shallow eutrophic lakes and attain extremely high biomass (Reynolds 2006). Conversely, enhanced metabolic activity due to higher temperatures in tropical lakes (Kraemer and others 2017b) could lead to higher OM mineralization rates and CO_2 production and emission to the atmosphere (Marotta and others 2009; Pinho and others 2016).

Here, we report a comprehensive and methodologically consistent data set of pelagic primary production (PP) and community respiration (CR) obtained over the last decade in 12 contrasting non-humic African lakes including 5 of the East African Great lakes (L. Tanganyika, L. Kivu, L. Edward, L. Albert, L. Victoria) and 7 smaller shallow lakes located in Eastern Africa. Also, we determined the partial pressure of CO_2 (pCO_2) in surface waters and examined the sources and dynamics of organic and inorganic C by means of stable C isotope tools across a wide range of physical and chemical parameters and productivity status. We test the hypothesis that the water column in non-humic African lakes tends to net autotro-

phy, contrasting with the predictions drawn from studies carried out in boreal or temperate systems.

Material and Methods

Sampling and Analytical Methods

We gathered new data in 12 different lakes located in Equatorial Africa (Uganda, Tanzania), sampled on several occasions between October 2016 and October 2019 (Figure 1), and compiled existing data from previous studies carried out with a similar methodology (but using radiocarbon instead of ^{13}C as C flow tracer) in Lake Kivu (Darchambeau and others 2014) and Lake Tanganyika (Sténuite and others 2007). The sampled lakes cover a wide range of size (< 1 to 68,100 km^2), mean depth (3–550 m), mixing regimes (holomictic and meromictic) and trophic status (oligotrophic to eutrophic). Table S1 summarizes some of the major limnological features of these ecosystems. All lakes were located in the same climatic region. Sampling in Lake Edward and Lake George, and several smaller lakes located in Western Uganda was carried out during three sampling campaign held in October 2016 and March 2017 (rainy season), and January 2018 (short dry season). Lake Victoria was sampled in April 2018 and November 2018 (rainy season), and June 2019 (dry season) at several sites

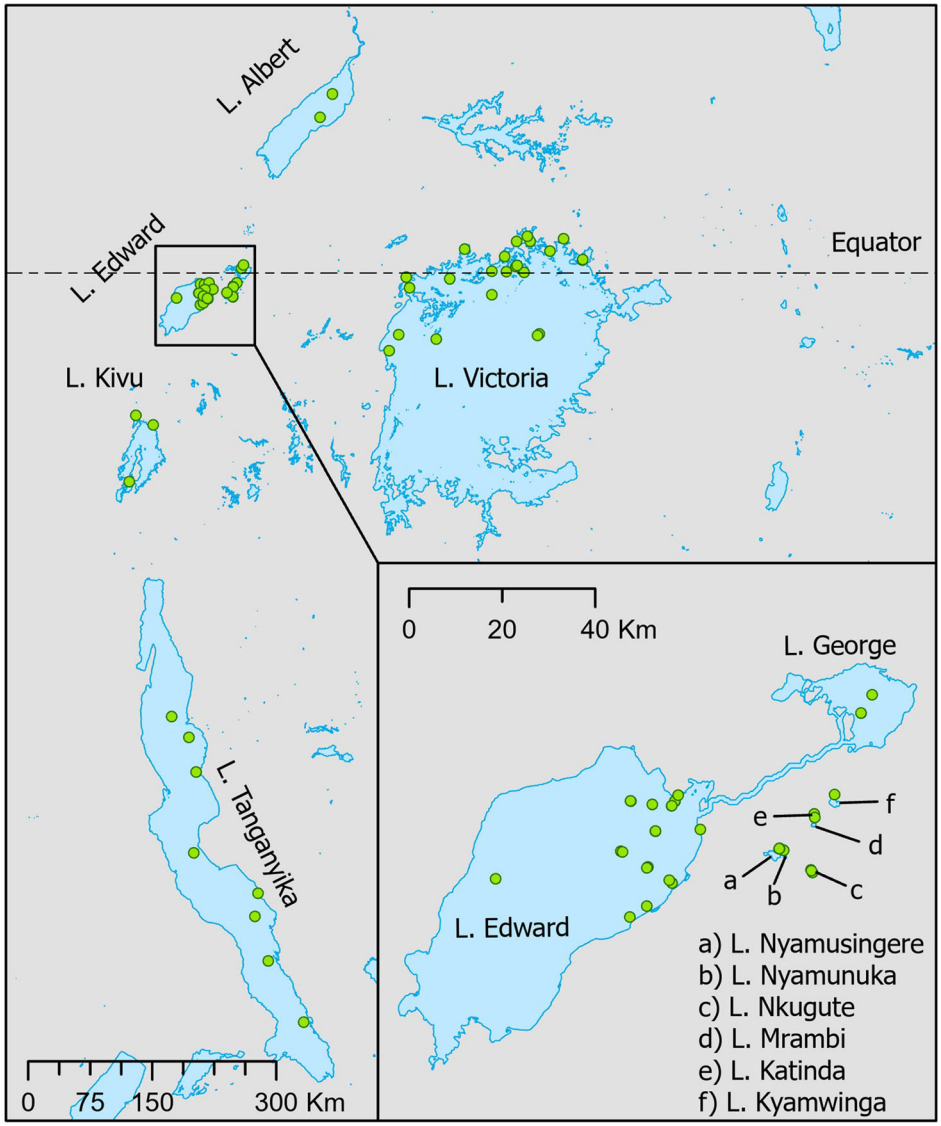

Figure 1. Map showing the location of the sampling sites (green circles) distributed in 12 African lakes where primary production and community respiration measurements were conducted. The sampling of L. Kivu was carried out between 2002 and 2008, the sampling of every other lakes was carried out between 2016 and 2019.

located in embayment and coastal area (hereafter L. Victoria – coastal) or offshore (hereafter L. Victoria – Pelagic). Lake Albert was sampled once, in June 2019 (dry season). Lake Tanganyika was sampled in October 2019 (early rainy season) during a north to south transect.

Vertical temperature and conductivity profiles were obtained with an YSI EXOII multiprobe. Incident photosynthetically active radiation (PAR) was continuously measured with a Li-Cor® LI-190 quantum sensor during the sampling campaign. The vertical light attenuation coefficient in the water column was estimated with a Secchi disk (30 cm) at every sampling site. Precision of the of the Secchi disk measurement was regularly assessed by comparison with depth profile of underwater PAR measurement performed concomitantly with a spherical quantum sensor (Li-Cor Li-193SA). The euphotic depth, Z_{eu}, was defined as the depth at which light is 1% of incident irradiance.

Chlorophyll *a* concentration was determined by high performance liquid chromatography (HPLC). At each sampling site, lake water was filtered on a Macherey-Nägel GF-5 filter (nominal porosity of 0.4 µm). Pigment extraction was carried out in 5 mL of 90% HPLC grade acetone. After two sonication steps of 15 min separated by an overnight period at 4 °C, the extracts were stored in 2 mL amber vials at− 25 °C. HPLC analysis was performed rapidly after samples collection following the method described in Sarmento and others (2008), with a Waters system comprising photodiode array and fluorescence detectors. Calibration was made using commercial external standards (DHI Lab Products). Precision for chlorophyll *a* measurement was better than ± 7%.

Samples for the determination of the pCO_2 were taken in triplicate, in 60 mL polypropylene syringes, directly from the Niskin bottle (5L). After headspace equilibration with atmospheric air directly in the syringes, pCO_2 was measured with an infra-red gas analyzer (Licor®, Li-840). The Li-840 was calibrated with N_2 and certified CO_2:N_2 mixtures (Air Liquide, Belgium) of 388, 813, 3788 and 8300 ppm CO_2. The precision of measurements was ± 4.1%. Measurements of total alkalinity (TA) were carried out by open-cell titration with HCl 0.1 mol L^{-1} on 50 mL water samples, and data were quality checked with Certified Reference Material acquired from Andrew Dickson (Scripps Institution of Oceanography, University of California, San Diego). Typical precision for TA measurements was better than ± 3 µmol L^{-1}. DIC concentration was computed from pCO_2 and TA measurements using the carbonic acid dissociation constants of Millero and others (2006) and the CO_2 solubility from Weiss (1974), as implemented in the CO2SYS software (Lewis and Wallace 1998).

Samples for the C stable isotope composition of the dissolved inorganic carbon (δ^{13}C-DIC) were collected by filling 12 mL headspace vials (Labco Exetainer®) with water directly from the Niskin bottles, avoiding air bubbles. Samples were preserved with the addition of 20 µL of a saturated $HgCl_2$ solution. Prior to the analysis of δ^{13}C-DIC, a 2 ml helium headspace was created with N_2 and 100 µL of phosphoric acid (H_3PO_4, 99%) was added in the vial to convert all inorganic C species to CO_2. After overnight equilibration, 200 µL of the headspace gas was injected with a gastight syringe into an EA-IRMS (Thermo FlashHT® with Thermo DeltaV Advantage). The obtained data were corrected for isotopic equilibration between dissolved and gaseous CO_2 as described in Gillikin and Bouillon (2007). Calibration of δ^{13}C-DIC measurements was performed with the international certified standards IAEA-CO1 and LSVEC. The reproducibility of δ^{13}C-DIC measurement was typically better than ± 0.2 ‰.

The samples for the particulate organic C (POC) and particulate nitrogen (PN) concentrations and stable carbon and nitrogen isotope compositions (δ^{13}C-POC; δ^{15}N-PN) were obtained by filtering a known volume of water on pre-combusted (overnight at 450 °C) 25 mm glass fiber filters (Sartorius, 0.7 µm nominal porosity), and kept frozen until subsequent processing. Subsequently, the filters were decarbonated with HCl fumes for 4 h, dried and packed in silver cups prior to analysis on an EA-IRMS (Thermo FlashHT with Thermo DeltaV Advantage). Calibration of δ^{13}C-POC, δ^{15}N-PN, POC and PN measurements was performed with caffeine (δ^{13}C = − 27.77 ‰ ± 0.04 ‰; δ^{15}N = 1.00 ‰ ± 0.05 ‰), leucine (δ^{13}C = − 13.47 ‰ ± 0.07 ‰; δ^{15}N = 0.92 ‰ ± 0.06 ‰), and tuna fish tissue ((δ^{13}C = − 18.72 ‰; δ^{15}N = 13.27 ‰ ± 0.04 ‰) as standards. Our caffeine standard (IAEA-600) is certified, leucine and tuna fish tissues were internally calibrated against the international standard IAEA-C6, IAEA-600, IAEA-N1 and IAEA-N_2. Reproducibility of δ^{13}C-POC and δ^{15}N-PN measurements was typically better than ± 0.2 ‰ and relative standard deviations for POC and PN measurements were always below 5%.

Water samples for DOC concentrations were filtered through pre-flushed 0.2 µm syringe filters in 40 mL borosilicate vials with Teflon-coated screw caps and preserved with 0.1 mL of H_3PO_4 (50%). DOC concentrations were measured with a cus-

tomized OI Analytical Aurora 1030 W coupled to a Delta + XP isotope ratio mass spectrometer (IRMS) via a GasBench II interface and with a cryofocussing trap. Quantification and calibration were performed with standard solutions of two in-house standards. Typical reproducibility for DOC analyses was below 5%.

Phytoplankton Primary Production and Community Respiration Measurements

PP rates were determined from stable isotope photosynthesis-irradiance experiments using $NaH^{13}CO_3$ (Eurisotop) as tracer for incorporation of dissolved inorganic carbon (DIC) into the biomass. Three subsamples were preserved with $HgCl_2$ in 12-mL Exetainers vials (Labco) for the determination of the exact initial ^{13}C-DIC and enrichment. The rest of the sample was divided into nine 50-ml polycarbonate flasks, filled without headspace. Eight flasks were placed into a floating incubation device providing a range of light intensity (from 0 to 80% of natural light) using neutral density filter screen (Lee). The last one was immediately amended with neutral formaldehyde (0.5% final concentration) and served as sacrificed control sample. Samples were incubated in situ for 2 h around midday just below the surface at lake surface temperature. After incubation, biological activity was stopped by adding neutral formaldehyde into the flasks, and the nine samples were filtered on precombusted GF/F filters when back in the lab. Filters were decarbonated with HCl fumes overnight, dried, and their δ^{13}C-POC value was determined with an EA-IRMS (Thermo FlashHT – Delta V Advantage) following the procedure described above. Initial enrichment of ^{13}C-DIC was measured in the lab as described above.

Photosynthetic (P_i) rates in individual bottles were calculated following Hama and others (1983) and corrected for any abiotic tracer incorporation by subtraction of the sacrificed control value. For each experiment, the maximum photosynthetic (Pmax) and the irradiance at the onset of light saturation (Ik) were determined by fitting P_i the light intensity gradient provided by the incubator (I_i) using the following equation (Vollenweider 1965). Fitting was performed using the Gauss–Newton algorithm for nonlinear least squares regression using the JMP Pro 15 software (SAS). Coefficient of determination (r^2) was typically better than 0.9.

$$P_i = 2 * P\max\left(I_i/(2*Ik)\right)/\left(1+\left(I_i/(2*Ik)\right)^2\right) \quad (1)$$

Daily depth-integrated primary production (mg C m^{-2} d^{-1}) was determined using the photosynthetic parameters Pmax and Ik and assuming a vertically homogenous chlorophyll *a* profile with the equation of Kirk (1994).

$$P(z,t) = 2 * P\max\left(I(z,t)/(2*Ik)\right)/\left(1+\left(I(z,t)/(2*Ik)\right)^2\right) \quad (2)$$

where P(z, t) is the photosynthesis at depth z and time t, and I(z, t) is the underwater light determined from vertical light attenuation parameter (k, see below) and surface irradiance recorded every 5 min with a Li-COR Li-190 instrument. The vertical homogeneity of the water column was assessed with depth profile of chlorophyll a concentration in every lakes where primary production was measured, which confirmed our assumption. Vertical profiles of photosynthetic active radiation (PAR) were measured with an underwater quantum sensor (Li-COR Li-192) mounted on a PME data logger (MiniPAR) attached to the CTD. Given the low variability of water temperature and solar irradiance in the tropics, annual rates were calculated multiplying daily rate by 365. The variable k was estimated from the slope of the semilog relationship between $\ln(PAR_z/PAR_0)$ against the depth (z), where PAR_z and PAR_0 are the PAR measured at a specific depth or at the surface, respectively. When only Secchi disk depth (SD) were available, k was estimated after the conversion of SD with the following relationships for L. Victoria (Eq. 3) and L. Edward (Eq. 4):

$$k = 1.5 * (1/SD) - 0.01 \left(r^2 = 0.90, n = 19\right) \quad (3)$$

$$k = 1.141 * (1/SD) \left(r^2 = 0.97, n = 9\right) \quad (4)$$

The euphotic zone depth (Zeu), defined as the depth illuminated by 1% of incoming surface light, was then determined as follows:

$$\mathrm{Zeu} = -\ln(0.01)/k \quad (5)$$

Community Respiration

CR was determined from the decrease in dissolved O_2 concentrations in 60 mL biological oxygen demand (BOD) bottles (Wheaton®) over about 24 h incubation periods. At each sampling site, 6 bottles were gently filled using a silicone tube connected to the Niskin bottle, overflowed approximately 3 times the BOD bottles volume, and directly sealed with a glass stopper. The bottles were kept in the dark and close to in situ temperature in a cooler

filled with lake water. The O_2 decrease was determined from triplicate measurements at the start (typically less than 15 min after sampling) and at the end of the incubation (typically 24 h after the initiation of the incubation). Measurements were performed with an optical O_2 probe (YSI ProODO). At the end of incubation, the sealed samples were homogenized with a magnetic bar during to the measurement of O_2. Student t-test ($p < 0.05$) were used to assess the statistical significance of the O_2 concentration decrease during the 24 h end-point incubations.

Phytoplankton Primary Production Upscaling Approach

We used the HydroLAKES database (Messager and others 2016) of lake morphology for lakes with a surface area of at least 0.1 km^2 to compute the African lake primary production at the regional scale. This database is publicly accessible unlike other database used in the literature, and is the only one to include average depth.

The general approach to scale up the primary production for African tropical lakes (24°N-24°S) followed several steps:

1 – We classified the objects in Hydrolakes for natural lakes (that is, excluding reservoirs – category 2) into strongly humic lakes and non-humic lakes as extensively described in Borges and others (2022). Briefly, individual lake watershed was computed with HydroSHED (Lehner and others 2008) and the wetland coverage on each lake watershed was computed with the GIEMS-D15 dataset (Fluet-Chouinard and others 2015). We hypothesized that wetlands fringing lakes were the major source of humic DOM to the lakes as suggested by the data presented in Borges and others (2022). Only lakes located in the intertropical zone and identified as non-humic ($n = 6211$) were considered further for the upscaling as the underwater light attenuation is expected to be uncorrelated to chlorophyll a in humic lakes.

2 – Estimation of chlorophyll *a* concentration in surface waters based on an empirical relationship between African lakes mean depth and chlorophyll *a* concentration (Table S2). The relationship was established combining new data presented in this work and a compilation of previous African lake studies.

3 – Estimation of the light extinction coefficient (k) and photosynthesis parameters (Pmax and Ik) based on the African lakes-specific empirical relationships of these variables with chlorophyll *a* concentration (Table S3); these relationships were established based on data acquired during this study.

4 – Estimation of the daily depth-integrated primary production in each individual lake as a function of Eq. 2, using estimated Pmax, Ik, k, and annual mean of hourly photosynthetically active radiation irradiance (CAMS radiation data – Jade, Copernicus) for the years 2016–2019 as input parameters. Lake specific shortwave radiation data were retrieved for each lake center point and converted into PAR flux with a conversion factor of 0.368 and then to photon flux with a conversion factor of 4.56 (Sayers and others 2020). The uncertainties of primary production rates estimation were assessed by Monte Carlo simulations (1000 iterations) during which each inputs parameter used to calculate the daily depth primary production (Table S2) was randomly picked from a normal distribution described by the mean and 1 standard deviation values. Mean percentage of uncertainty of primary production estimation derived from the empirical model was ± 33%.

Organic Carbon Burial Calculation Based on the Geostatistical Model of Mendonça and Others (2017)

Organic carbon burial in the sediments was estimated for each of the 6211 African lakes identified as non-humic, based on the statistical model of Mendonça and others (2017) which link organic carbon burial with several key watershed characteristics:

$$\text{Log OC burial} = 1.307 + 0.105*Cr - 0.330*SI - 0.142*Ar + 0.134*Ru + 0.027*Tp - 0.310.$$

Where OC burial is in gC m^{-2} y^{-1}, Cr is the log-cropland coverage (%), SI is the log-average slope of the catchment (degrees), Ar is the log-lake area (km^2), Ru is the log-runoff (mm y^{-1}), and Tp is the annual average temperature (°C), and lake surface area (km^2). Data on lake surface area and lakes pour point were obtained from HydroLAKES database. Watershed slope and altitude were obtained from HydroSHEDS (3 arc-second resolution). Data on the cropland coverage were extracted for each lake catchment from the Global Land Cover 2000 database (European Commission, Joint Research Centre 2003). The annual average of air temperature was extracted for each lake from WorldClim (Fick and others 2017), and the surface lake water temperature was computed from air temperature using a linear regression as a function of the latitude of the difference of air and water temperature as described by Borges and others (2022). Runoff

data were derived from UNH/GRDC Composite Runoff Fields.

Statistical Analysis

Statistical approach used for the determination of photosynthesis parameters, community respiration and primary production upscaling are provided in their respective sections above. Statistical analyses were performed using the JMP Pro 15 software (SAS) at the exception of the Monte Carlo simulations which were done using Microsoft Excel 2013. Correlation between variables reported below were assessed by Pearson's correlation coefficient and simple linear regression (model I). Correlations were considered statistically significant where two-tailed p-value was < 0.05.

Results and Discussion

Phytoplankton Biomass and Isotopic Characterization of C Pools

Our dataset covered a wide range of lake trophic status, with chlorophyll *a* concentration ranging from 1.0 µg Chla L^{-1} in the deep L. Tanganyika to 619.2 µg Chla L^{-1} in the shallow, polymictic L. Kyashanduka. The higher phytoplankton biomass was measured in the shallower and polymictic lakes (L. George, L. Nyamusingere, L. Kyanshanduka). Indeed, a significant negative relationship between lake mean depth and chlorophyll *a* concentration in surface waters was observed in our dataset, in good agreement with data compiled from other studies carried out in Africa (Figure 2 and Table S2).

POC and chlorophyll *a* were positively related in the surface waters (Figure S1), and POC was found to contribute to a large fraction of the total suspended matter (44 ± 12%), revealing that the seston was predominantly composed of organic material. Pigment analyses revealed that cyanobacteria dominated the phytoplankton assemblage in all lakes, representing at least 55% of the phytoplankton biomass (Table S4). In eutrophic lakes, Cyanobacteria accounted for more than 90% of biomass in the shallow L. Kyashanduka, George, and Nyamusingere, and deeper crater lakes Katinda and Mrambi (Table S4). L. Victoria, and the mesotrophic L. Edward, L. Albert, L. Nkugute, and L. Kyambura harbored a more diverse phytoplankton community (Table S4) with a higher proportion of diatoms (between ~ 10% and ~ 30%). Finally, the phytoplankton composition in the oligotrophic L. Tanganyika was characterized by a higher contribution of Chlorophytes (~ 30%).

Phytoplankton abundance played an important role in controlling underwater light as reflected by the positive correlation found between the light vertical attenuation coefficient and chlorophyll a concentration (Figure 3). Because of this strong underwater light attenuation by phytoplankton, the vast majority of the sediment area of the studied lakes was not located in the photic zone (Figure S2). Nearshore-offshore transects carried out in two large mesotrophic lakes (L. Edward and L. Victoria) revealed shallower photic zone depth and a parallel increase in water column chlorophyll a when moving toward nearshore, in shallower waters (Figure S3). It implies that the percentage of sediment area in the photic zone is not necessarily

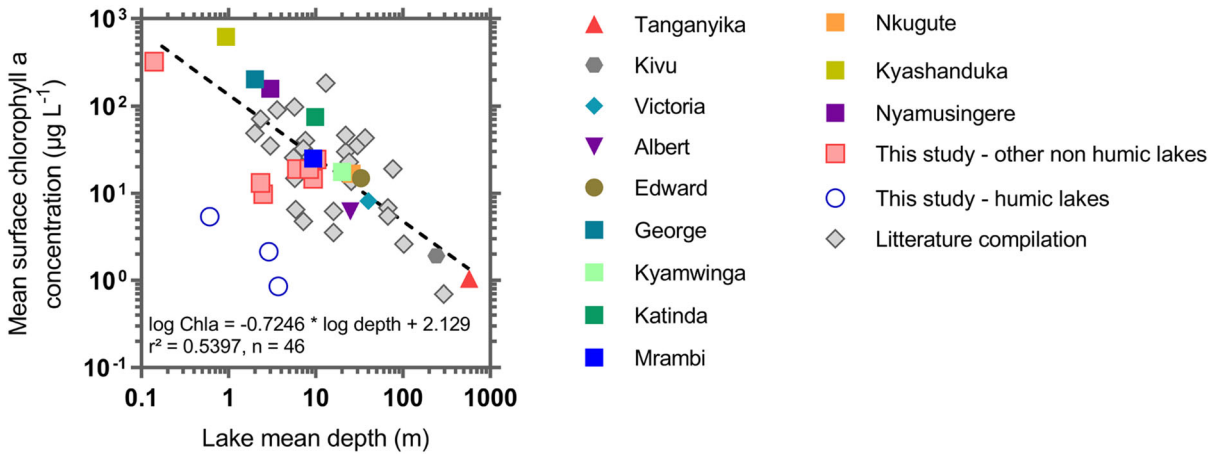

Figure 2. Relationship between lake mean depth (m) and chlorophyll *a* concentration in surface waters of diverse African lakes sampled during this study and in a literature compilation. Humic lakes (empty blue circles) differed from the pattern showed by non-humic lakes and were excluded of the linear regression analysis.

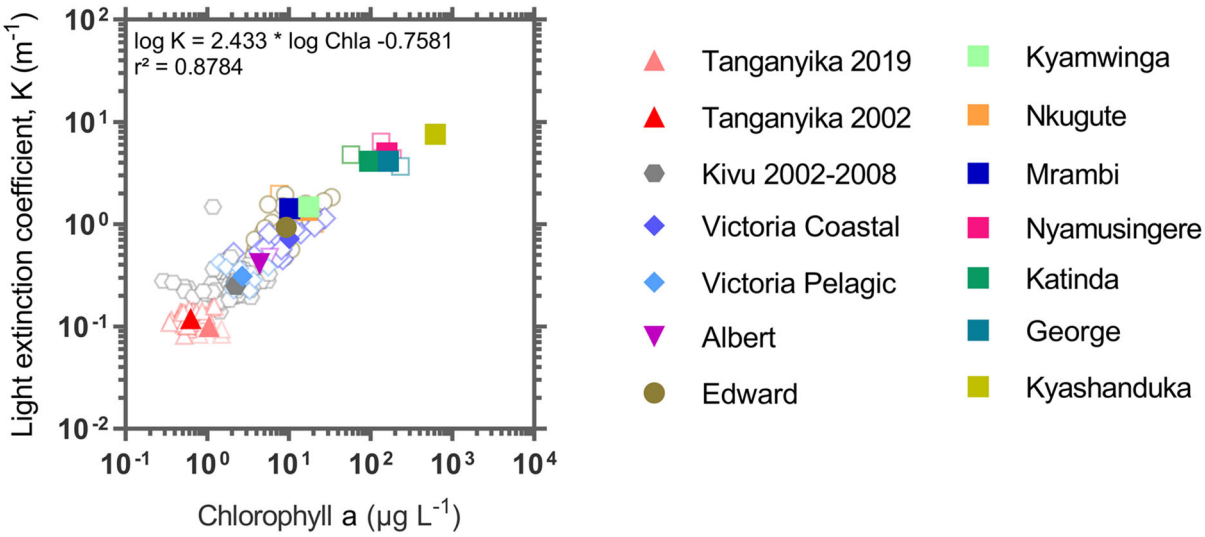

Figure 3. Relationship between lake chlorophyll *a* concentration in surface waters and vertical light attenuation (k) in the water of diverse African lakes sampled during this study. Plain symbols represent mean value for each lake and empty symbols represent individual values.

higher in shallow areas because they are also more productive, with higher planktonic biomass and more turbid waters. Overall, this pattern suggest that benthic primary production would be of minor importance, even in the shallower lakes of our dataset (Figures 2,3). Counterintuitively, it also implies that a higher fraction of sediment in the photic zone might be found in the oligotrophic, usually deepest lakes, such as L. Tanganyika and L. Kivu. For instance, substantial periphyton production rates have been reported in littoral zone down to about 10 m depth in L. Tanganyika (Vadeboncoeur and others 2014). However, L. Tanganyika and L. Kivu are African Valley rift lakes, both characterized by a very steep coastline so that benthic primary production averaged on the entire lake area would be relatively minor compared to planktonic phytoplankton rates, even if it can sustain a particularly diverse and productive littoral food web (Mcintyre and others 2006).

The pCO_2 was inversely related to chlorophyll *a* concentration and was below atmospheric equilibrium in all lakes except in the larger and deeper L. Tanganyika and L. Kivu, and some pelagic stations of L. Edward, L. Albert and L. Victoria, where average pCO_2 (415 ppm) was slightly above the atmospheric equilibrium (388 ppm) (Figure 4). Lakes exhibited a broad range of δ^{13}C-DIC and δ^{13}C-POC values, which were strongly correlated with chlorophyll *a* concentration. With the exception of L. Kyashanduka and L. George, both characterized by extremely low pCO_2 values, δ^{13}C-POC was linearly related to δ^{13}C-DIC with a slope not significantly different from 1 (Figure 4). The phytoplankton assemblage in the CO_2-depleted L. Kyashanduka and L. George was almost exclusively dominated by cyanobacteria (> 95% of phytoplankton assemblage, Table S4), among which the ability to use bicarbonate as an alternative C source in case of widespread CO_2 limitation (Badger and Price 1994). Indeed, the apparent isotopic fractionation between DIC and POC was substantially lower in the lakes with pCO_2 lower than 100 ppm (Figure 4). Bicarbonate being about 10 ‰ enriched in ^{13}C relative to aqueous CO_2 (Mook and others 1974), an increasing contribution of bicarbonate as a C source is likely to shift the isotopic composition of phytoplankton toward more positive values. Finally, δ^{13}C-DOC was found to follow closely the δ^{13}C-POC (Deirmendijan and others 2020) and was substantially ^{13}C-enriched in lakes with high chlorophyll *a* concentration (Figure 4). This pattern suggests that the dissolved and particulate pools of OM share a same origin – likely phytoplanktonic – in the more productive lakes of the dataset (Figure 4). A notable exception to this pattern is observed in L. George, where relatively low δ^{13}C-DOC values (~ -20‰) were recorded despite higher δ^{13}C-POC values (-10 ‰). This pattern does not necessary hold true for the deeper and usually large, less productive lakes of the dataset where the δ^{13}C-DOC could not be distinguished from the terrestrial δ^{13}C signature of terrestrial vegetation (~ -22 ‰ to -34‰ for C3 plants).

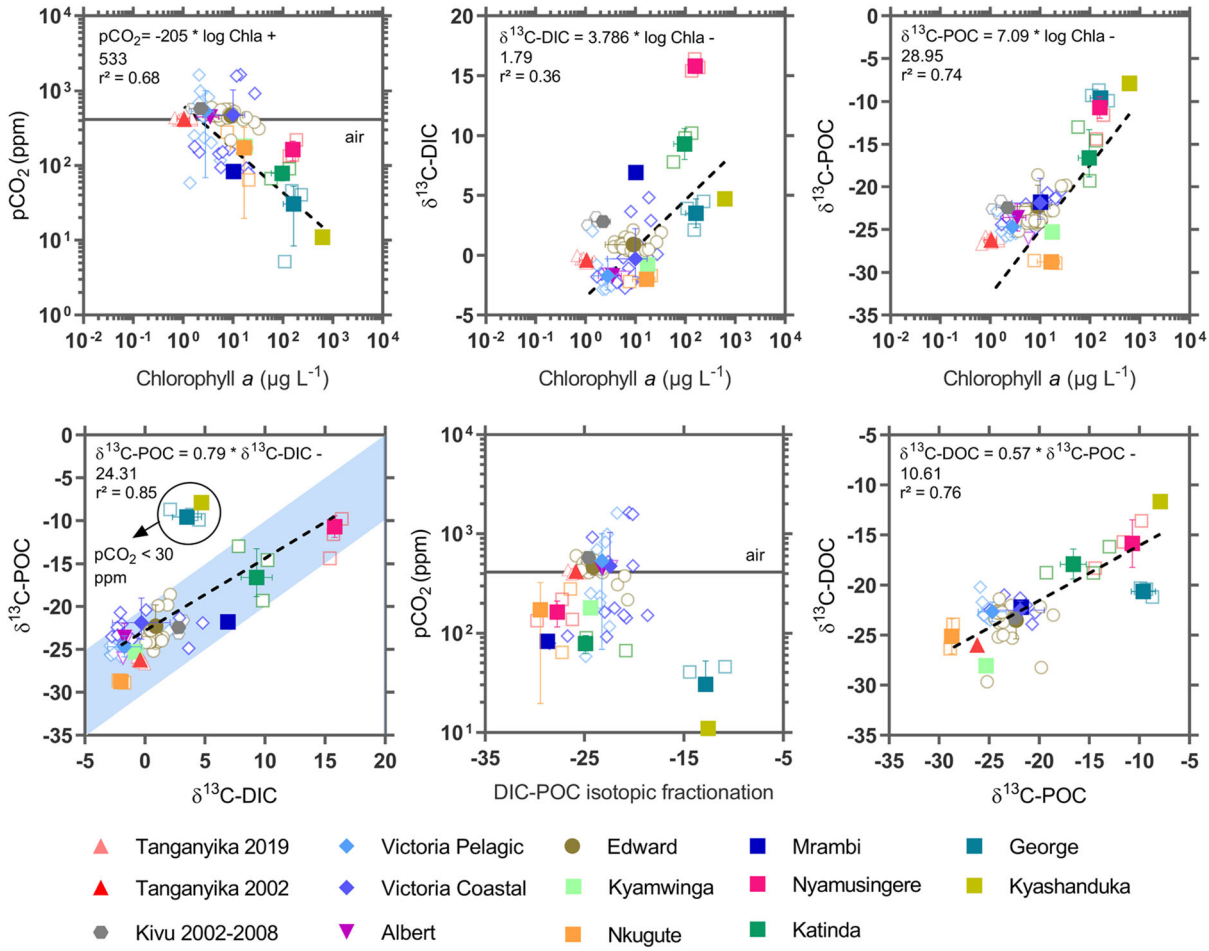

Figure 4. Relationships between chlorophyll *a* concentration pCO_2 in surface waters, between δ^{13}C-DIC and δ^{13}C-POC, between δ^{13}C-DIC and δ^{13}C-POC, and between δ^{13}C-POC and δ^{13}C-DOC. Plain symbols represent mean value for each lake and empty symbols represent individual values. Error bars indicate 1 standard deviation. Blue shaded area in the plot of δ^{13}C-POC against δ^{13}C-DIC represents the expected δ^{13}C-POC assuming a conservative ^{13}C fractionation during photosynthesis ranging between 20 ‰ and 30 ‰.

Phytoplankton Primary Production

A significant positive relationship between the maximum photosynthetic rate Pmax and chlorophyll *a* concentration (Figure 5, Table S3) was observed. The slope (1.127) of the log–log relationship was not statistically different from 1 (95% confidence interval: 0.9228 – 1.332) meaning that the photosynthetic capacity (PBmax, that is, Pmax normalized to chlorophyll *a* concentration) did not vary significantly across the wide range of chlorophyll *a* concentration, and indeed, no significant correlation (Pearson correlation test) was found between PBmax and any other variables. Observations of seemingly steady PBmax values in contrasting African lakes might be related to the low variability of lake surface temperature in the intertropical zone. Indeed, many phytoplankton cellular processes are temperature-dependent with optima at about 25 °C (Robarts and Zohary 1987) and temperature has been frequently shown to be the main driver controlling PBmax in globally distributed lakes (Lewis 2011; Sayers and others 2020), even if temperature effects are likely to be synergistic with other factors, such as nutrients availability (Geider and others 1998). PBmax in L. Kivu (1.8 ± 0.1 µg C µg Chla h^{-1}; $n = 98$) appeared significantly lower than in the rest of the dataset (6.8 ± 0.5 µg C µg Chla h^{-1}; $n = 102$). This could be linked to the peculiar food web structure of L. Kivu, with a strong top-down pressure of the planktonic fish *Limnothrissa miodon* on zooplankton, leading to a lower grazing pressure from metazooplankton on phytoplankton (Isumbisho and others 2006). This feature might explain why phytoplankton biomass observed in Lake Kivu is

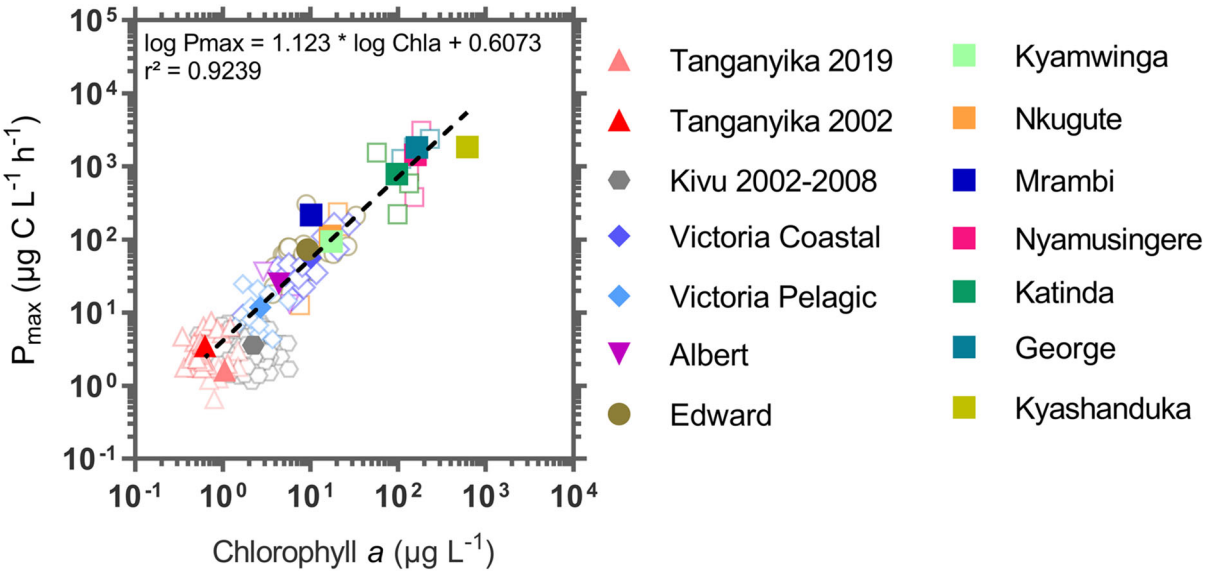

Figure 5. Relationship between chlorophyll *a* and the photosynthetic rate of phytoplankton at light saturation (Pmax). Plain symbols represent mean value for each lake and empty symbols represent individual measurements.

relatively high (Sarmento and others 2006), despite phytoplankton productivity is of the same magnitude as in Lake Tanganyika (Darchambeau and others 2014).

The irradiance at the onset of saturation (Ik) was significantly correlated to the vertical light attenuation (k) and chlorophyll *a* concentration in the water column (Table S3). Lower Ik values in eutrophic, turbid waters, reflects the adaptation of phytoplankton community to the low-light conditions, being able to reach their maximal photosynthetic capacity at the modest irradiance induced by self-shading effect. In contrast, higher Ik values were observed in oligotrophic, clear waters where the community was dominated by high light adapted phytoplankton. The higher phytoplankton biomass and the good photosynthetic efficiency at low-light intensities allowed substantially higher daily depth-integrated phytoplankton primary production rates in the shallow eutrophic lakes than in the deeper, oligo- mesotrophic lakes despite the reduced photic zone depths.

Phytoplankton Primary Production and Community Respiration Balance in African Lakes

CR rates varied over two orders of magnitude across the dataset and were highly correlated to the mean primary production in the mixed layer (Figure 6). The slope of the log-log relationship was significantly lower than 1, implying that the ratio between photosynthesis and respiration (P:R) decreases with ecosystem productivity, in agreement with previous observations in boreal and temperate lakes (Del Giorgio and Peters 1994; Duarte and Agusti 1998). However, only the most oligotrophic and unproductive lake of our dataset, the deep and permanently stratified L. Tanganyika, showed epilimnion P:R ratio consistently lower than 1. Based on an extensive set of measurements in freshwater lakes ($n = 82$), Duarte and Agusti (1998) proposed that a volumetric daily gross primary production rate of at least 25 mmol C m^{-3} d^{-1} (31 mmol O_2 m^{-3} d^{-1} converted with a photosynthesis quotient of 1.25) is required to balance the bacterial carbon demand in the photic zone, or in other words, for a freshwater system to be net autotrophic. The significantly lower slope of the regression line fitted on our non-humic African lake dataset indicates that this threshold value is lower for African freshwater ecosystems (10 mmol C m^{-3} d^{-1}) and suggests that oligotrophic African lakes are more prone to exhibit a net autotrophic status than their temperate or boreal counterpart.

The empirical relationships found in our study between lake mean depth and chlorophyll *a* (Figure 2, Table S3), and between chlorophyll *a* and the photosynthesis parameters Pmax and Ik, and k (Figure 3, Figure 5, Table S3), allow the use of a simple mechanistic model to upscale the primary production at the tropical Africa continental scale. Only data from lakes identified as non-humic ($n = 6211$) were considered further for the upscaling as the underwater light attenuation is expected to be uncorrelated to chlorophyll *a* in

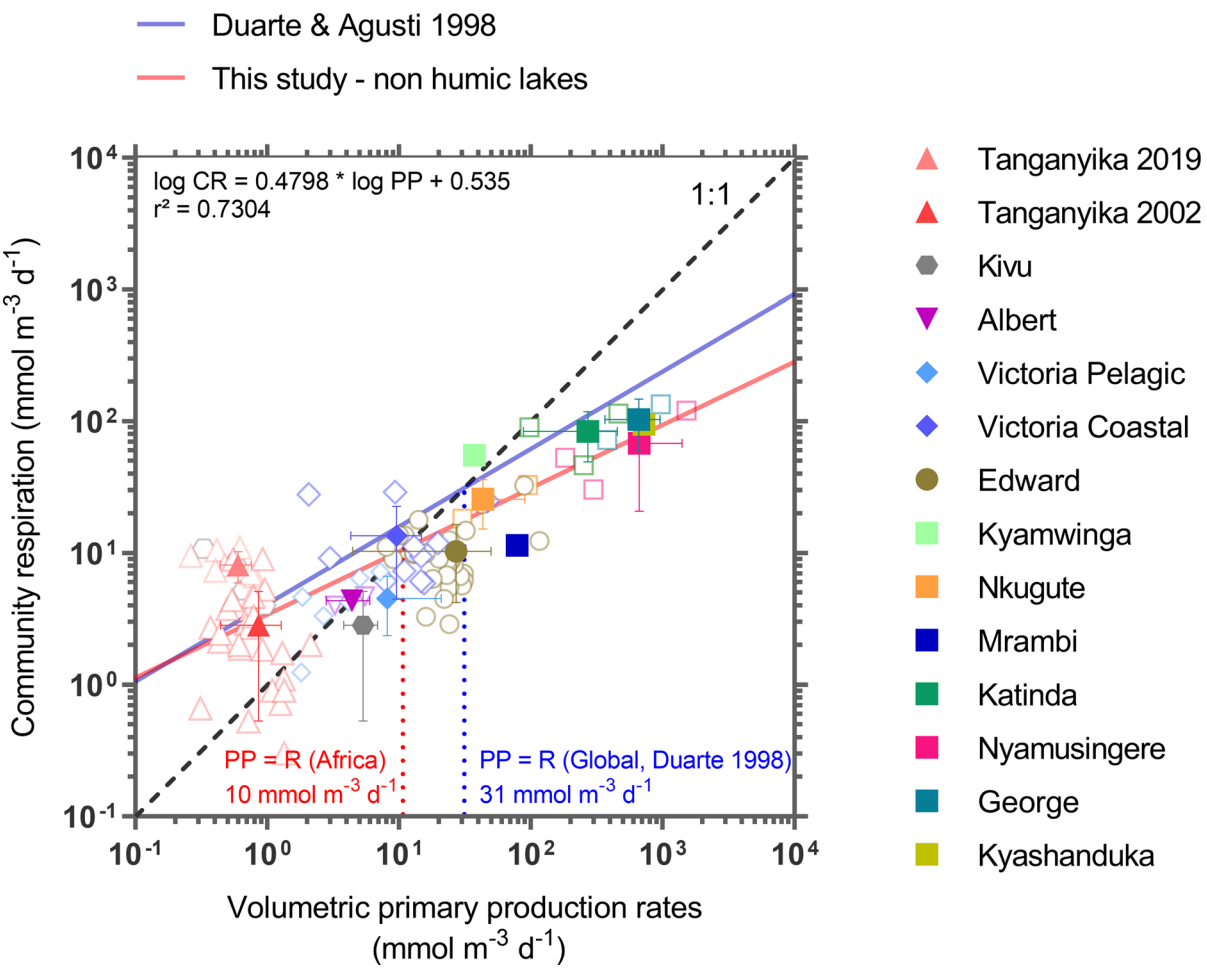

Figure 6. Relationship between the mean primary production and community respiration rates in the surface mixed layer of diverse African lakes. Plain symbols represent mean value for each lake and empty symbols represent individual measurements. Error bars indicate 1 standard deviation. Dashed line is the 1:1 line, red line represent the log–log regression line for African lakes and blue line represents the log–log regression line for the lakes included in the extensive data compilation of Duarte and Agusti (1998).

humic lakes. Indeed, in humic lakes high cDOM content decreases light penetration in the water column, strongly limiting phytoplankton growth and planktonic production, and the high content of terrestrial DOC should also sustain microbial degradation of organic matter del Giorgio and Peters (1994). In addition, African humic lakes were characterized by important wetland coverage (Table S1) that should have sustained a large lateral input to the lakes of CO_2 from flooded soils (Borges and others 2022). Mean areal primary production rates for non-humic African lakes determined with our field-data driven statistical model (629 g C m^{-2} y^{-1}) is in good agreement with the value obtained by Lewis (2011) for tropical latitude with a mechanistic model approach (median values ranging between 340–932 g C m^{-2} y^{-1}, depending on the latitude bin considered). It is also of the same order of magnitude as the value reported by Alin and Johnson (2007) in a compilation of primary production measurements carried out in large lakes of the world (234–795 g C m^{-2} y^{-1}). Integrated at the continental scale, we estimated the non-humic African lakes primary production would reach 117 Tg C y^{-1}, which is substantially higher than the continental CO_2 emission flux previously estimated at 35.6 Tg C y^{-1} (Raymond and others 2013), but recently revised down to 6.3 Tg C y^{-1} for all African lakes, or 0.1 Tg C y^{-1} for African non-humic lakes (Figure 7, Borges and others 2022).

Organic carbon burial in the sediments was estimated for each of the 6211 African lakes identified as non-humic, based on the statistical model of Mendonça and others (2017) Using this model, we estimated the mean areal organic carbon burial in African non-humic lakes was 25 g C m^{-2} y^{-1}, a

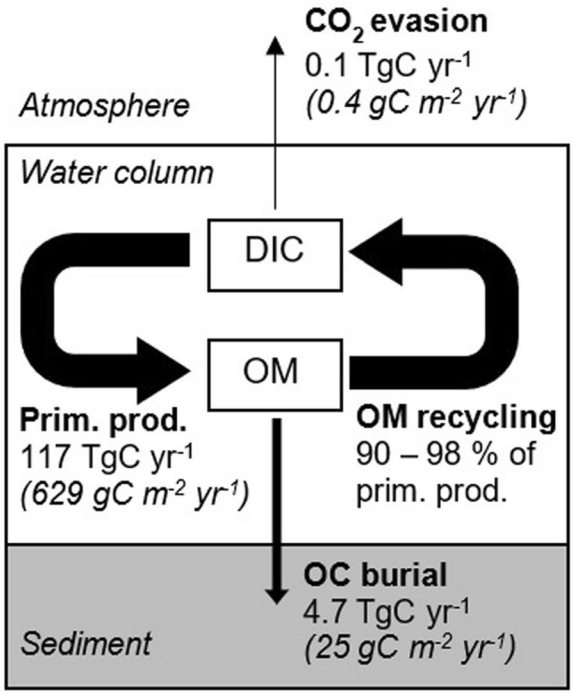

Figure 7. Simplified view of the carbon cycle in African (non-humic) lakes showing the primary production and OM recycling rates (this study), CO_2 evasion rate (Borges and others 2022), OC carbon burial rate (calculated with the model of Mendonça and others 2017). Numbers in brackets are the mean areal rates.

value close to the global average (22 g C m^{-2} y^{-1}, Mendonça and others 2017) but substantially higher than reported for large lakes of the world (range 1–20 g C m^{-2} y^{-1}) in the data compilation of Alin and Johnson (2007). Nevertheless, some cautions are needed in the interpretation of the results provided by the organic carbon burial model for African lakes because of the scarcity of data collected in tropical lakes. Mendonça and others (2017) found that organic carbon burial was overall higher in tropical area, probably related to the overall higher productivity of tropical aquatic ecosystems. However, despite the extensive data compilation of Mendonça and others 2017, their model integrates only 34 datapoints from intertropical region (total n = 344) and 90% of the data were gathered in Europe or North America. At the African continental scale, organic carbon burial in non-humic lakes would reach 4.7 Tg C y^{-1}, a value substantially higher than the CO_2 evasion from non-humic African lakes (0.1 Tg C y^{-1}, Borges and others 2022) but substantially lower than phytoplankton primary production (117 TgC y^{-1}) (Figure 7). Phytoplankton primary production would be ~ 20 times higher than the loss of C via organic carbon burial and CO_2 evasion to the atmosphere, implying that a large fraction (90–98%) of the African lake primary production is effectively recycled in the warm water column of tropical lakes (Figure 7). We propose that internal processes predominantly control CO_2 levels in these lakes, particularly planktonic primary production in non-humic shallow lakes. This is also supported by the lack of relation between pCO_2 in the sampled lakes and terrestrial vegetation biomass on the catchment (Borges and others 2022). Nevertheless, several abiotic processes also affect the CO_2 dynamics in lakes so that the net metabolic status of the ecosystem might appear in contradiction with its carbon source or sink balance. For instance, several hard-water lakes were identified as net autotrophic but acting as a source of CO_2 to the atmosphere (McDonald and others 2013). In Africa, the oligotrophic and alkaline L. Kivu is an example of a tropical lake acting as a source of CO_2 to the atmosphere, despite having a net autotrophic epilimnion.

Duarte and Prairie (2005) proposed that a mean volumetric primary production rate of at least 25 mmol C m^{-3} d^{-1} is required to balance the bacterial carbon demand, or in other words, for a freshwater system to be net autotrophic. This threshold value exceeds the primary production rates in 14 of the largest and deepest African lakes, implying that 77% of the cumulated African lake surface area would have been considered as net heterotrophic, according to Duarte and Prairie (2005) data. However, the PP and CR experimental data (Figure 6) gathered on the field during this study indicate that the Africa-specific threshold value at which PP equals CR rates would be substantially lower (10 mmol C m^{-3} d^{-1}) than proposed by Duarte and Prairie (2005). Thus, we determined that only the 3 deepest lakes (L. Tanganyika, L. Malawi, L. Kivu; representing 35% of the cumulated surface area of African lakes) would be characterized by CR rates higher than PP. Thus, our results suggest that non-humic African lakes are predominantly net autotrophic systems despite the common assumption that relatively oligotrophic waters are usually net heterotrophic (del Giorgio and Peters 1994; Cole 1999; Duarte and Prairie 2005; Cole and and others 2007). This finding is supported by several others biogeochemical observations during our field study. The vast majority of the sampled lakes were CO_2 undersaturated compared to the atmosphere, acting thus as a carbon sink, while only the larger (deeper lakes) were close to saturation (Figure 4). Stable isotope data suggest that the particulate OM

pool is primarily derived from in situ primary production, as illustrated by the strong relationships between chlorophyll *a* concentration, δ^{13}C-DIC and δ^{13}C-POC (Figure 4). Furthermore, the significant relationship between δ^{13}C-POC and δ^{13}C-DOC indicate these two OM pools share the same autotrophic origin in at least the meso- and eutrophic lakes of our dataset (Figure 4).

This discrepancy between our results and the predictive model of Duarte and Prairie (2005) can be explained by the fact that the data they compiled and used to construct this relationship between the metabolic status and the phytoplankton production rates were gathered in small to medium sized lakes (< 250 km^2) located in the temperate or boreal regions, and cannot directly apply to African tropical lakes which are characterized by year-round high light and temperature conditions (Sarmento 2012; Kraemer and others 2017a), and a less stable water column favorable for episodical nutrient inputs (Lewis 1996). Also, podzols, a soil group characterized by particularly rich in organic matter content, are extensive in Québec (Canada) and Scandinavia but are much less common at lower latitude (Sanborn and and others 2011). In case of poor drainage of podzols, organic matter bounded on metal ions can be transported laterally in the catchment over considerable distance (Driessen and others 2000) and could supply boreal lakes with a relatively high amount of terrestrially derived humic compounds. However, high humic substance concentrations directly affect water color which in turn has a strong negative impact on phytoplankton productivity (del Giorgio and Peters 1994).

In comparison with temperate lakes, tropical lakes experience ''endless summer'' environmental conditions (Kilham and Kilham 1990) due to constantly high temperature and sunlight irradiance throughout the year. Our findings may seem contradictory with theoretical predictions drawn from metabolic ecology theory which propose that the phytoplankton biomass should decline with temperature due to increased metabolic rates and hence higher resource requirements in warm tropical waters (Yvon-Durocher and others 2011). However, elevated temperature conditions do not only affect phytoplankton and bacterial metabolism but also the trophic interactions and the availability of inorganic nutrients to phytoplankton which could alleviate the warming induce metabolic deficit (Kraemer and others 2017b). Indeed, in addition to the stimulating effect on phytoplankton metabolism (Robarts and Zohary 1987), warm water temperature favors also the metabolism of heterotrophic prokaryotes which are then able to recycle a larger amount of nutrients in the water column, increasing resource availability for phytoplankton growth in the mixed layer. The comparison with our primary production results and the organic C burial rates calculated from the equations of (Mendonça and others 2017) indicate that the vast majority (90–98%) of the OM fixed by PP is efficiently recycled in the water column. This observation agrees with the view that biological control of the elemental cycles dominates in tropical lakes instead of physical processes (thermal stratification, transport from littoral sediments), thought to dominate in temperate lakes for a large part of the year (Kilham and Kilham 1990). Further, tropical lakes are usually characterized by weaker water column stratification due to the lower thermal amplitude under the tropics. Hence, the mixed layer can be twice as thick compared to temperate counterparts (Lewis 2011). Their mixed layer depth could deepen episodically in response to punctual variation of heat flux resulting in a better connectivity between the illuminated surface and bottom layers of water, as shown in L. Victoria (Deirmendjian and others 2021). Also, high solar irradiance enhances the excretion of labile organic molecules by healthy phytoplankton cells, particularly in case of nutrient limitation (Myklestad 2000). The active release of recently produced organic molecules by phytoplankton cells can be viewed as a protection mechanism occurring under nutrient limitation, when the synthesis of molecules containing N or P is not possible (Moran and others 2002). Consequently, the percentage of extracellular release of primary production appears substantially higher in oligotrophic tropical lakes than in their temperate and boreal counterparts (Morana and others 2014), supporting a tight coupling between phytoplankton and heterotrophic prokaryotes in tropical lakes.

Our calculation also highlights the importance of the East African Rift lakes (L. Victoria, Tanganyika, Malawi, Turkana, Rukwa, Albert, Mweru, Tana, Edward, Kivu) in the African inland waters C budget, where phytoplankton would fix 79 Tg C each year. In addition, substantial periphyton primary production have been reported in the littoral zone of L. Tanganyika where it sustains an important littoral foodweb (McIntyre and others 2006; Vadeboncoeur and others 2014). Together, these 10 lakes account for 68% of the total African non-humic lake primary production. The East African Rift is the second major locus of large lakes on Earth after North America, but despite a lower cumulated surface area, they sustain a much larger

fisheries (Sterner and others 2020) owing to their higher areal phytoplankton productivity (494 g C m^{-2} y^{-1}, this study, against 87 g C m^{-2} y^{-1} in the upper Laurentian Great Lakes, Fahnenstiel et al 2016).

Conclusions

The prevailing paradigm of lakes as net heterotrophic systems (sustaining CO_2 emissions to the atmosphere) is mainly based on data collected in lakes in North America and Scandinavia, where the net heterotrophy is tightly associated with low PP and lateral transport of colored OM from the terrestrial biosphere. Here, we show that African lakes aquatic primary production balance a larger fraction of OM respiration than in temperate and boreal lakes (Figure 6), and net heterotrophy could only be observed in the few deepest, largest and most oligotrophic lakes. This is in line with the recent estimate of very low air–water CO_2 emissions of 0.1 Tg C y^{-1} from non-humic African lakes by Borges and others (2022), which is two orders of magnitude lower than the estimate of 36 Tg C y^{-1} from all African lakes by Raymond and others (2013). A nearly neutral emission of CO_2 from non-humic African lakes is consistent with our finding of a close coupling between phytoplankton and heterotrophic prokaryotes. Despite a lacustrine primary production of 117 Tg C y^{-1}, only 5 Tg C y^{-1} are potentially buried in lake sediments (Mendonça and others 2017). This implies that nearly all of the primary production is internally recycled, but also that allochthonous OM inputs are low in these lakes, and do not sustain a large CO_2 emission to the atmosphere. This is also consistent with lower threshold value for the equivalence of PP and CR in these 12 non-humic African lakes (10 mmol C m^{-3} d^{-1}) than the one reported by Duarte and Agusti (1998) for 82 mainly boreal lakes (25 mmol m^{-3} d^{-1}). This means that allochthonous OM inputs need sustain additional CR in boreal lakes reported by Duarte and Agusti (1998) and Duarte and Prairie (2005) compared to African lakes at equivalent levels of PP.

Acknowledgements

We are grateful to crews of RV Hammerkop and the Maman Benita for support during the sampling expeditions in Lakes Victoria and Tanganyika, to the team from the Institut Supérieur Pédagogique Bukavu for help during the sampling in Lake Kivu, to the Katwe marine police officers, Angela Nankabirwa and Erina Nabafu for help during sampling in Lakes Edward and George and Western Uganda lakes, to Marc-Vincent Commarieu, Bruno Leporcq, Zita Kelemen and Yannick Stroobandt for analytical support. This work was funded by the Belgian Federal Science Policy Office (BELSPO, HIPE project, BR/154/A1/HIPE, and EAGLES project, SD/AR/02A), by the Fonds National de la Recherche Scientifique (FNRS, LAVIGAS project, contract T.0156.18, and TANGAGAS project) and by the Spanish Ministry of Science and Technology (AGLOM project CGL2010-11556-E). Field expeditions were supported by FNRS with travel grants awarded to AVB, by the Fonds Agathon de Potter with travel grants awarded to CM and LD, by the Fonds Leopold III with a travel grant awarded to LD and by the Fonds Wetenschappelijk Onderzoek (FWO-Vlaanderen, Belgium) with travel grants awarded to CM and SB. HS was supported by Conselho Nacional de Desenvolvimento e Pesquisa Tecnológica (CNPq productivity grant 303906/2021-9). CM and LD are post-doctoral researchers at the FNRS, and AVB is a Research Director at the FNRS.

References

Alin SR, Johnson TC. 2007. Carbon cycling in large lakes of the world: A synthesis of production burial and lake-atmosphere exchange estimates. Global Biogeochemical Cycles. https://doi.org/10.1029/2006GB002881.

Badger MR, Price GD. 1994. The role of carbonic anhydrase in photosynthesis. Annual Review of Plant Biology 45(1):369–392.

Brothers S, Vadeboncoeur Y. 2021. Shoring up the foundations of production to respiration ratios in lakes. Limnology and Oceanography 66(7):2762–2778

Borges AV, Deirmendjian L, Bouillon S, Okello, W, Lambert T, Roland FA, Razanamahandry VF, Voarintsoa NRG, Darchambeau F, Kimirei IA, Descy J-P, Allen GH, Morana C. 2022. Greenhouse gas emissions from African lakes are no longer a blind spot. Science Advances 8(25):eabi8716.

Cole JJ. 1999. Aquatic microbiology for ecosystem scientists: new and recycled paradigms in ecological microbiology. Ecosystems 2(3):215–225.

Cole JJ, Caraco NF, Kling GW, Kratz TK. 1994. Carbon dioxide supersaturation in the surface waters of lakes. Science 265:1568–1570.

Cole JJ, Prairie YT, Caraco NF, McDowell WH, Tranvik LJ, Striegl RG, Melack J. 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. Ecosystems 10(1):172–185.

Darchambeau F, Sarmento H, Descy JP. 2014. Primary production in a tropical large lake: The role of phytoplankton composition. Science of the Total Environment 473:178–188.

Deirmendjian L, Lambert T, Morana C, Bouillon S, Descy JP, Okello W, Borges AV. 2020. Dissolved organic matter composition and reactivity in Lake Victoria, the world's largest tropical lake. Biogeochemistry 150(1):61–83.

Deirmendjian L, Descy J-P, Morana C, Okello W, Stoyneva-Gärtner MP, Bouillon S, Borges AV. 2021. Limnological changes in Lake Victoria since the mid-20th century. Freshwater Biology 66(8):1630–1647.

Del Giorgio PA, Peters RH. 1994. Patterns in planktonic P: R ratios in lakes: influence of lake trophy and dissolved organic carbon. Limnology and Oceanography 39(4):772–787.

Del Giorgio PA, Cole JJ, Cimbleris A. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. Nature 385(6612):148–151.

Driessen, P., Deckers, J., Spaargaren, O., and Nachtergaele, F. (2000). Lecture notes on the major soils of the world Food and Agriculture Organization 94

Duarte CM, Agustí S. 1998. The CO2 balance of unproductive aquatic ecosystems. Science 281(5374):234–236.

Duarte CM, Prairie YT. 2005. Prevalence of heterotrophy and atmospheric CO 2 emissions from aquatic ecosystems. Ecosystems 8(7):862–870.

Fahnenstiel GL, Sayers MJ, Shuchman RA, Yousef F, Pothoven SA. 2016. Lake-wide phytoplankton production and abundance in the Upper Great Lakes: 2010–2013. Journal of Great Lakes Research 42(3):619–629.

Fee EJ. 1979. A relation between lake morphometry and primary production and its use in interpretating whole-lake experiments. Limnology and Oceanography 24:401–416.

Fick SE, Hijmans RJ. 2017. WorldClim 2: New 1km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37:4302–4315.

Fluet-Chouinard E, Lehner B, Rebelo L-M, Papa F, Hamilton SK. 2015. Development of a global inundation map at high spatial resolution from topographic downscaling of coarse-scale remote sensing data. Remote Sensing of Environment 158:348–361.

Geider RJ, MacIntyre HL, Kana TM. 1998. A dynamic regulatory model of phytoplanktonic acclimation to light, nutrients, and temperature. Limnology and Oceanography 43(4):679–694.

Gillikin DP, Bouillon S. 2007. Determination of delta O-18 of water and delta C-13 of dissolved inorganic carbon using a simple modification of an elemental analyzer-isotope ratio mass spectrometer: an evaluation. Rapid Communications in Mass Spectrometry 21(8):1475–1478.

Hama T, Miyazaki T, Ogawa Y, Iwakuma T, Takahashi M, Otsuki A, Ichimura S. 1983. Measurement of photosynthetic production of a marine phytoplankton population using a stable 13 C isotope. Marine Biology 73(1):31–36.

Isumbisho M, Sarmento H, Kaningini B, Micha JC, Descy JP. 2006. Zooplankton of Lake Kivu, East Africa, half a century after the Tanganyika sardine introduction. Journal of Plankton Research 28(11):971–989.

Kilham P, Kilham SS. 1990. Endless summer: internal loading processes dominate nutrient cycling in tropical lakes. Freshwater Biology 23(2):379–389.

Kirk JT. 1994. Light and photosynthesis in aquatic ecosystems. Cambridge University Press.

Kosten S, Huszar VL, Bécares E, Costa LS, van Donk E, Hansson LA, Scheffer M. 2012. Warmer climates boost cyanobacterial dominance in shallow lakes. Global Change Biology 18(1):118–126.

Kraemer BM, Chandra S, Dell AI, Dix M, Kuusisto E, Livingstone DM, McIntyre PB. 2017a. Global patterns in lake ecosystem responses to warming based on the temperature dependence of metabolism. Global Change Biology 23(5):1881–1890.

Kraemer BM, Mehner T, Adrian R. 2017b. Reconciling the opposing effects of warming on phytoplankton biomass in 188 large lakes. Scientific Reports 7(1):1–7.

Lehner B, Verdin K, Jarvis A. 2008. New global hydrography derived from spaceborne elevation data. Eos, Transactions American Geophysical Union 89(10):93–94.

Lewis WM Jr. 1996. Tropical lakes: how latitude makes a difference. Perspectives in Tropical Limnology 4364:43–64.

Lewis WM Jr. 2011. Global primary production of lakes: 19th Baldi Memorial Lecture. Inland Waters 1(1):1–28.

Lewis, E. R., and Wallace, D. W. R. (1998). Program developed for CO_2 system calculations (No. cdiac: CDIAC-105). Environmental System Science Data Infrastructure for a Virtual Ecosystem

Marotta H, Duarte CM, Sobek S, Enrich-Prast A. 2009. Large CO2 disequilibria in tropical lakes. Global Biogeochemical Cycles. https://doi.org/10.1029/2008GB003434.

McDonald CP, Stets EG, Striegl RG, Butman D. 2013. Inorganic carbon loading as a primary driver of dissolved carbon dioxide concentrations in the lakes and reservoirs of the contiguous United States. Global Biogeochemical Cycles 27(2):285–295.

McIntyre PB, Michel E, Olsgard M. 2006. Top-down and bottom-up controls on periphyton biomass and productivity in Lake Tanganyika. Limnology and Oceanography 51(3):1514–1523.

Mendonça R, Müller RA, Clow D, Verpoorter C, Raymond P, Tranvik LJ, Sobek S. 2017. Organic carbon burial in global lakes and reservoirs. Nature Communications 8(1):1–7.

Messager ML, Lehner B, Grill G, Nedeva I, Schmitt O. 2016. Estimating the volume and age of water stored in global lakes using a geo-statistical approach. Nature Communications 7(1):1–11.

Millero FJ, Graham TB, Huang F, Bustos-Serrano H, Pierrot D. 2006. Dissociation constants of carbonic acid in seawater as a function of salinity and temperature. Marine Chemistry 100(1–2):80–94.

Mook WG, Bommerson JC, Staverman WH. 1974. Carbon isotope fractionation between dissolved bicarbonate and gaseous carbon dioxide. Earth and Planetary Science Letters 22(2):169–176.

Morales-Williams AM, Wanamaker AD Jr, Downing JA. 2017. Cyanobacterial carbon concentrating mechanisms facilitate sustained CO 2 depletion in eutrophic lakes. Biogeosciences 14(11):2865–2875.

Morán XAG, Estrada M, Gasol JM, Pedrós-Alió C. 2002. Dissolved primary production and the strength of phytoplankton–bacterioplankton coupling in contrasting marine regions. Microbial Ecology 44(3):217–223.

Morana C, Sarmento H, Descy JP, Gasol JM, Borges AV, Bouillon S, Darchambeau F. 2014. Production of dissolved organic matter by phytoplankton and its uptake by heterotrophic prokaryotes in large tropical lakes. Limnology and Oceanography 59(4):1364–1375.

Myklestad SM. 2000. Dissolved organic carbon from phytoplankton. Marine chemistry, . Springer: Berlin Heidelberg. pp 111–148.

Odum HT. 1956. Primary production in flowing waters 1. Limnology and Oceanography 1(2):102–117.

Pinho L, Duarte CM, Marotta H, Enrich-Prast A. 2016. Temperature dependence of the relationship between pCO 2 and

dissolved organic carbon in lakes. Biogeosciences 13(3):865–871.

Prairie YT, Bird DF, Cole JJ. 2002. The summer metabolic balance in the epilimnion of southeastern Quebec lakes. Limnology and Oceanography 47:316–321.

Rawson DS. 1953. Morphometry as a dominant factor in the productivity of large lakes. Internationale Vereinigung Für Theoretische Und Angewandte Limnologie:verhandlungen 12(1):164–175.

Raymond PA, Hartmann J, Lauerwald R, Sobek S, McDonald C, Hoover M, Guth P. 2013. Global carbon dioxide emissions from inland waters. Nature 503(7476):355–359.

Reynolds CS. 2006. The ecology of phytoplankton. Cambridge, United Kingdom: Cambridge University Press.

Richey JE, Melack JM, Aufdenkampe AK, Ballester VM, Hess L. 2002. Outgassing from Amazonian rivers and wetlands as a large tropical source of atmospheric CO_2. Nature 416:617–620.

Robarts RD, Zohary T. 1987. Temperature effects on photosynthetic capacity, respiration, and growth rates of bloom-forming cyanobacteria. New Zealand Journal of Marine and Freshwater Research 21(3):391–399.

Sanborn P, Lamontagne L, Hendershot W. 2011. Podzolic soils of Canada: Genesis, distribution, and classification. Canadian Journal of Soil Science 91(5):843–880.

Sarmento H, Descy JP. 2008. Use of marker pigments and functional groups for assessing the status of phytoplankton assemblages in lakes. Journal of Applied Phycology 20(6):1001–1011.

Sarmento H, Gasol JM. 2012. Use of phytoplankton-derived dissolved organic carbon by different types of bacterioplankton. Environmental Microbiology 14(9):2348–2360.

Sarmento H, Isumbisho M, Descy J-P. 2006. Phytoplankton ecology of Lake Kivu (East Africa). Journal of Plankton Research 28(9):815–829.

Sayers M, Bosse K, Fahnenstiel G, Shuchman R. 2020. Carbon Fixation Trends in Eleven of the World's Largest Lakes: 2003–2018. Water 12(12):3500.

Staehr PA, Testa JM, Kemp WM, Cole JJ, Sand-Jensen K, Smith SV. 2012. The metabolism of aquatic ecosystems: history, applications, and future challenges. Aquatic Sciences 74(1):15–29.

Stenuite S, Pirlot S, Hardy MA, Sarmento H, Tarbe AL, Leporcq B, Descy JP. 2007. Phytoplankton production and growth rate in Lake Tanganyika: evidence of a decline in primary productivity in recent decades. Freshwater Biology 52(11):2226–2239.

Sterner RW, Keeler B, Polasky S, Poudel R, Rhude K, Rogers M. 2020. Ecosystem services of Earth's largest freshwater lakes. Ecosystem Services 41:101046.

Vadeboncoeur Y, Devlin SP, McIntyre PB, Vander Zanden MJ. 2014. Is there light after depth? Distribution of periphyton chlorophyll and productivity in lake littoral zones. Freshwater Science 33(2):524–536.

Vollenweider RA. 1965. Calculations models of photosynthesis-depth curves and some implications regarding day rate estimates in primary production measurements. Memorie Dell'istituto Italiano Di Idrobiologia 18:425–457.

Yvon-Durocher G, Montoya JM, Trimmer M, Woodward GUY. 2011. Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. Global Change Biology 17(4):1681–1694.