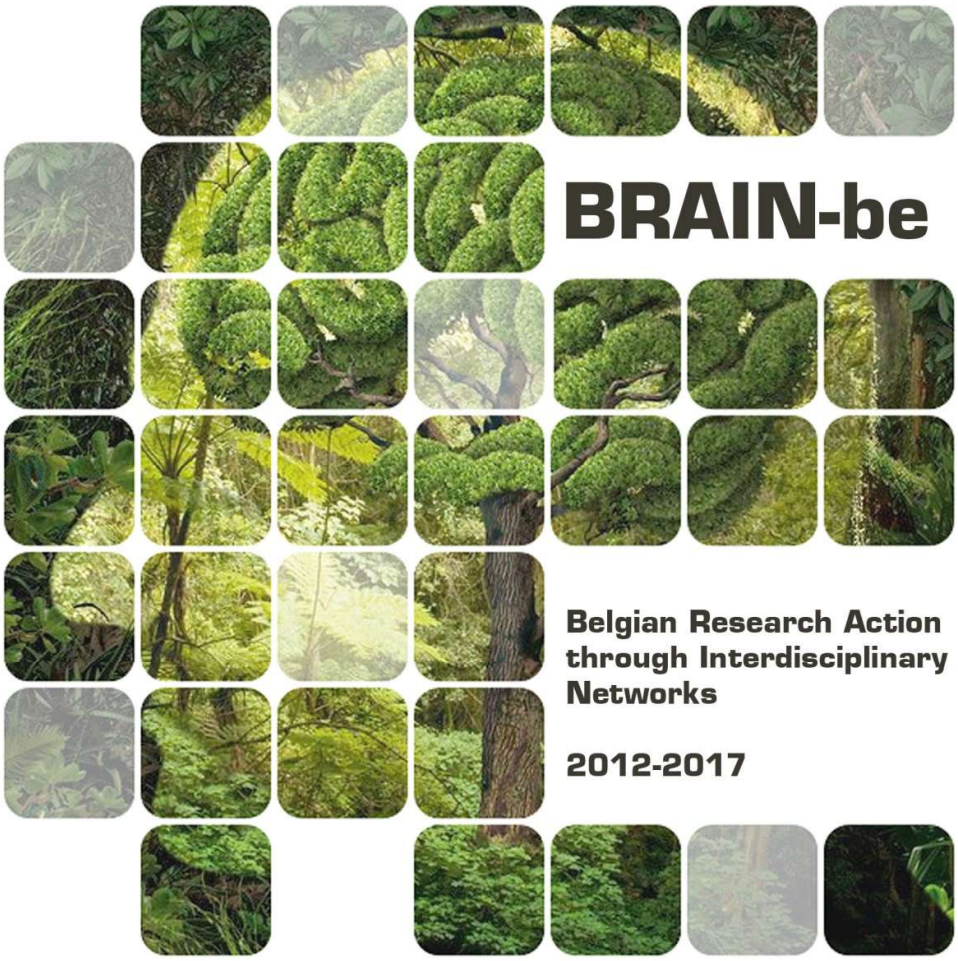

HIPE

Human impacts on ecosystem health and resources of Lake Edward

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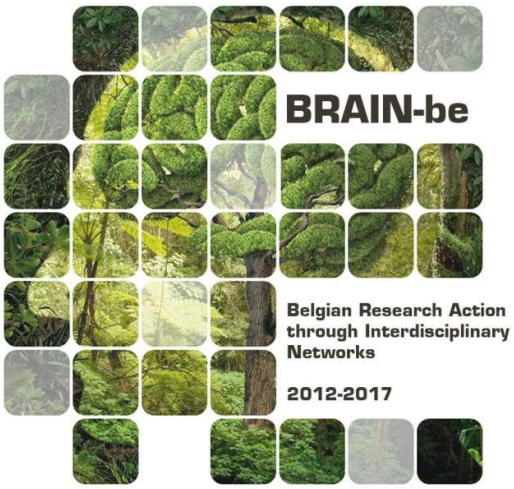

NETWORK PROJECT

HIPE

Human impacts on ecosystem health and resources of Lake Edward

Contract - BR/154/A1/HIPE

FINAL REPORT

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ABSTRACT

Context

Lake Edward is one of the East African Rift lakes (surface 2325 km^2, maximum depth 112 m), is located on the border between the Democratic Republic of Congo (DRC) and Uganda. It is connected to the smaller lake George (surface 250 km^2, maximum depth 3m) through Kazinga Channel, and is part of the Nile watershed. On both sides of the border, Lake Edward is bordered by two major natural reserves, the Virunga National Park, Queen Elisabeth National Park. A collapse of the fisheries of Lake Edward was observed from the 1960's to 1980's that matched the reduction of the numbers of hippos observed from the 1960s and 1970s. The reason of this collapse is unknown, nor if fisheries continued to decline until present.

Objectives

The aim of HIPE was to test the causal relationship between the recent environmental changes and the drastic reduction of fisheries productivity. Our working hypothesis was that several environmental pressures in the watershed of Lake Edward have disrupted the biogeochemical, structural and functional links between the terrestrial and aquatic ecosystems, leading to a collapse of the main ecosystem service provided by Lake Edward. The fishing effort has dramatically increased since the 1960s. This in combination with a relaxed enforcement, resulted in an overexploitation of the fish stock and a spread of the use of damaging fishing techniques around the lake. Other potential causes are changes in the hydrological cycle, which could have also modified the transfer of nutrients from the watershed to the lake, and climate variability affecting nutrient cycling and availability in the Great Lakes.

Conclusions

Shallow sediment cores from Lake Edward show a shift in stable carbon isotope composition in the upper 10 cm of the core (approximately last 40 yrs) that could be explained by (i) an increase in the delivery of C3-derived organic matter to the lake, and/or (ii) a decrease in phytoplankton productivity, which would increase isotope fractionation in phytoplankton due to alleviation of diffusive CO2 limitation. Museum-archived fish specimens confirm a shift in the baseline δ13C values in the lake, corresponding to a lower productivity or a change in the composition of terrestrial organic matter input to L. Edward over the past century. A range of bivalve shells analyzed for C and O isotope ratios along their growth lines indicate these are excellent tools to differentiate habitats, but this compromises their use as archives for paleo-environmental reconstruction in the area since exact provenance of museum collection specimens is typically not sufficiently well documented. The data from tooth enamel from Hippopotamus canines show a long-term trend towards decreasing δ13C values of the Hippopotamus diet in the region, although showing a high inter-individual variability in δ13C values, most pronounced in more recent specimens, indicating that dietary differences exist on small spatial scales. As Hippopotamus are thought to be rather indiscriminate grazers, this

should reflect local differences in relative C3-C4 cover. The oxygen stable isotope data of Hippopotamus were shown to be likely good proxies for their lacustrine versus riverine habitat use.

The phytoplankton community in Lake Edward was largely dominated cyanobacteria (60% of the phytoplankton biomass), followed by diatoms (25% of the phytoplankton biomass), and by green algae, chrysophytes and cryptophytes. 248 taxa phytoplankton were identified with clear prevalence of cyanobacteria (104 taxa), from the morphological groups of coccal and filamentous species (non-heterocytous and heterocytous). Compared to historical data from the 1930's it seems a shift in algal diversity (number of species) from diatoms to cyanobacteria. Lack of historical data does not allow to determine if a change in total phytoplankton biomass occurred. The primary production measured in Lake Edward during the three cruises was approximately 4 times lower than the single historical value (June 1960), but values seemed comparable in Lake George compared to those from the 1960's. This is consistent with an overall decrease of present phosphorus loading compared to historical data (1990's).

Primary production rates were high, and in excess of community respiration, indicating a net autotrophic status leading to low values of dissolved CO_2. Consequently, Lake George and the part of Lake Edward influenced by the outflow from Lake George acted as sinks for atmospheric CO_2. This challenges the paradigm that inland waters are systematically sources of atmospheric CO_2 that was derived from data mostly collected in boreal and temperate lakes. The sampled sites were in some cases very strong CH_4 emitters to the atmosphere, although a very strong spatial variability was observed due to a combination of several factors such as the occurrence of anoxia in bottom waters and productivity, both related to depth (the shallowest systems being the most productive and devoid of bottom anoxia). Most systems were sinks of atmospheric N_2O due to denitrification.

Data on stable C, N and H isotope composition indicate that aquatic primary production is the dominant energy source at the basis of the foodweb, but the wide variability in consumer stable isotope signatures also indicates that a wider variety of sources is used, with contributions of terrestrial and possibly CH_4-derived carbon.

The basin of Lake Edward has a fish fauna that is typical for East Africa and consists of two components: a species-rich assemblage of *Haplochromis* species and a relatively species-poor assemblage of non-*Haplochromis* species. A total of 34 non-*Haplochromis* species belonging to 10 families and 21 genera are recorded from the system. These include six species of major importance to the fisheries. Three non-Haplochromis species are endemic to the system and two others have been introduced in the region. Six species are new records for the Lake Edward system. The *Haplochromis* species diversity was seriously underreported and went from 27 species known to 56, of which 13 new ones have been or are being described. We have currently no indication that species have disappeared from the system in the last few decades, though one catfish species known from historical records, *H. longifillis*, could not be retrieved during the recent expeditions. Substantial dietary niche overlaps were found between several commercially important fish species, while niche overlaps between *Haplochromis* species were small, which suggests that they display a high trophic differentiation in accordance with their specialised morphologies. We did not find indications that different stocks exist for the commercial species. However, we found that the populations

in the lakes were separated from those inhabiting the rivers. We did find intraspecific differences in morphology and ecology between populations from Lake Edward and Lake George (including the Kazinga Channel) of some *Haplochromis* species. No signs of large-scale hybridization were found between the two important tilapias.

Recent reports on the state of the fisheries of the Lake Edward system remain scarce. Lakes Edward and George are almost completely within protected areas. However, occupied land area, the number of inhabitants and the number of boats has risen substantially during the last decades. Total annual yields have been increasing in the last ten years, but Catch Per Unit Effort (CPUE) appears to be continuously decreasing. Tilapias, which were traditionally dominant in the catches, seem to have crashed in the eighties and their share in the catches keeps decreasing.

Recent estimates showed poor stock status for most commercially important species with most stocks defined as either collapsed, recruitment impaired or overfished. Higher catches could be obtained under sustainable management. The immediate target of management should be rebuilding biomass to the biomass at maximum sustainable yield (*B*msy). A survey was conducted at the different landing sites along lakes Edward and George. This revealed that fishers were aware of the changes in the state of the fishery. Fishers attributed declining catches to excessive effort, fishing malpractices, destruction of breeding grounds, and pollution. Communities reported large-scale non-compliance with fisheries regulation, especially at Lake George.

Keywords

Biodiversity, Biogeochemistry, Fish diversity, Fish ecology, Food webs, Lake Edward, Lake George, Virunga National Park, Queen Elisabeth National Park

1. INTRODUCTION

HIPE (Human impacts on ecosystem health and resources of Lake Edward) is a multi-disciplinary project that combines the expertise of researchers in biology, ecology, biogeochemistry, limnology, fisheries and socio-economics. The main objective of HIPE is to test the causal relationship between the recent environmental changes and the drastic reduction of fisheries productivity using innovative paleo-proxies, coupled to a study of the present lake functioning. Assessing the validity of the various hypotheses, linked to a better understanding of ecosystem function and a thorough estimation of the socio-economic benefits, will help to develop appropriate management actions to mitigate present and future impacts. Our working hypothesis is that several environmental pressures on the watershed of Lake Edward have disrupted the biogeochemical, structural and functional links between the terrestrial and aquatic ecosystems, leading to a collapse of the main ecosystem service provided by the lake.

2. STATE OF THE ART AND OBJECTIVES

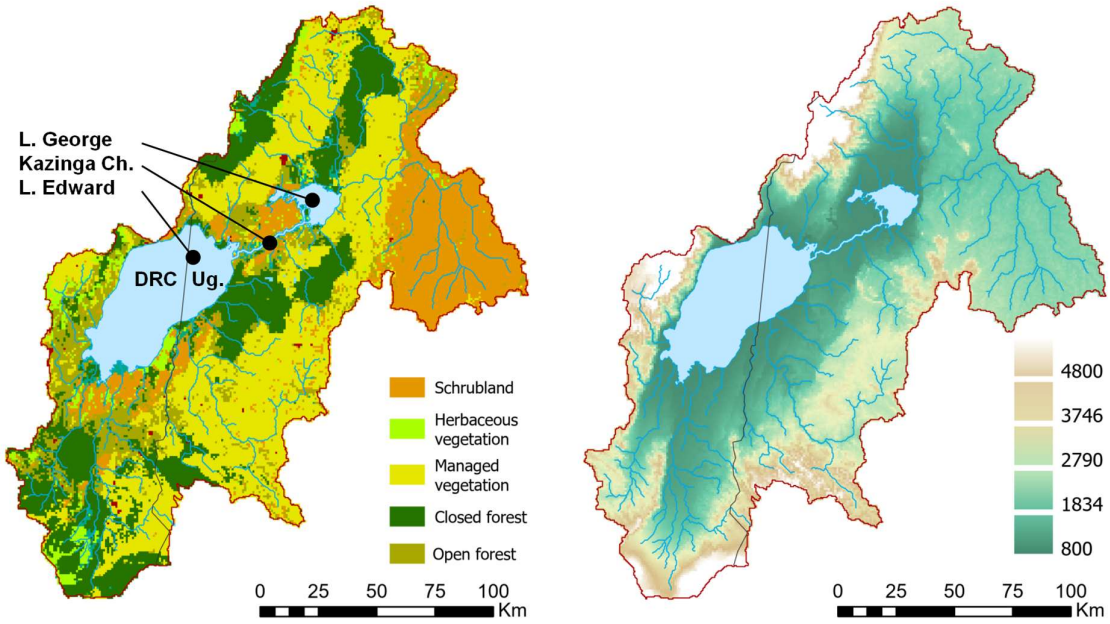

Figure 1: Lake Edward, Lake George, and Kazinga Channel, and land cover and elevation on the respective catchments. DRC = Democratic Republic of Congo; Ug. = Uganda

Lake Edward (0°-0°40'S, 29°20'-29°50'), along with lakes Albert and Victoria, constitutes the major lake sources of the White Nile and contributes to the rich limnology of central East Africa. Lake Edward occupies a large (2325 km²) and deep (112 m) tilted basin across the Congo-Uganda border at an altitude of about 900 m (Fig. 1). The lake drains the southern Virunga volcanoes, the Kigezi highlands to the east and the northern Ruwenzori Mountains (Russell & Johnson 2006). Some inflow occurs through the Kazinga Channel from Lake George, a shallow, productive, northeastern basin. The lake is presently open, draining north into Lake Albert via the Semliki River, but loses ~50% of its water inputs through evaporation (Russell & Johnson 2006). Lake Edward is anoxic below ~30 m water depth, is only weakly stratified (Beadle 1981) and is presently mesotrophic (Cohen et al. 1996). Lake Edward has not been subject to comparative examination of limnological properties for over four decades, despite changes in land use, fisheries exploitation, population growth, and regional climate (Cohen et al. 1996).

HIPE seeks to understand the recent collapse of productivity and fisheries in Lake Edward in response to pressures, and how this has changed and will continue to change ecosystem functions and delivery of goods and services. **To achieve this, a multi-disciplinary approach was used combining biology, ecology, biogeochemistry, and socio-economics in order to understand the recent past and present ecosystem functioning and the delivery of goods and services, in responses to pressures**.

In the 1960s, the population of *Hippopotamus amphibius* located in the vicinity of Lakes Edward and George was the most numerous and dense on Earth (Cornet d'Elzius 1996). The populations were severely depleted in the 1980s and 1990s through poaching (Languy & de Merode 2006; Eltringham 1999). Hippos are aquatic but feed at night upon distant (1-3 km)

savanna grass, and return to shallow waters well before dawn (Eltringham 1999), where they spend 1-2 days before revisiting their grazing grounds. As a consequence, defecation mainly occurs in the water, leading to a high transfer of organic matter and nutrients from land to water (Grey & Harper 2002). A first-order estimate of the nutrient supply from the hippos population in the vicinity of Lake Edward indicates that, before the 2000s, they contributed much more to the nutrient budget of the lake than the natural riverine inputs, and that the recent poaching may have drastically reduced the amount of nutrients reaching the lake. In support to this hypothesis, Lehman et al. (1998) reported a total phosphorus reduction in Lake Edward between the 1950s and the 1990s of about one half.

In parallel, there is growing evidence of a recent collapse of the fishery of Lake Edward (Languy & de Merode 2006). According to the official reports until the 1980s (Russell & Werne 2009), the decline in fish catch started in 1960s and followed the reduction of the numbers of hippos observed in the 1960s and 1970s. Rarely, fish catch data have been officially published for the Congolese waters since.

Thus, different indicators suggest that the grazing by large mammals, and especially by the hippos, in the watershed of Lake Edward was responsible for the nutrient enrichment during the previous century, and that the lake is currently experiencing a drastic decline of productivity jeopardizing the sustainable access to a critical source of local livelihoods. This phenomenon accentuates the pressure on other land resources, drastically modifying local land-use (Languy & de Merode 2006). Additional and/or alternative phenomena might also explain the reduction of fish catch in Lake Edward. First, the number of fishing boats has dramatically increased since the 1960s (Languy & Kujirakwinja 2006), without any management, so that overexploitation of the fish stock and use of damaging fishing techniques have spread around the lake. Other potential causes are changes in the hydrological cycle (Lyon & DeWitt 2012), which could have also modified the transfer of nutrients from the watershed to the lake, and climate variability affecting nutrient cycling and availability in the Great Lakes (Lehman et al. 1998). Hence further limnological research is highly and urgently needed.

The main objective of HIPE is to test the causal relationship between the recent environmental changes and the drastic reduction of lake productivity using innovative paleo-proxies coupled to a study of the present lake functioning. Assessing the validity of the various hypotheses, linked to a better understanding of the ecosystem functioning and a thorough estimation of the socio-economic benefits, will help to develop appropriate management actions to mitigate present and further impacts.

The fish fauna of the Lake Edward/George system has not been reviewed since the publication of ‘The fishes of Uganda’ by Greenwood (1966). In addition, while the other larger lakes in the East African Rift Valley received much scientific attention because of their endemic cichlid radiations, the cichlid assemblages of the Lake Edward system have received very little scientific attention. So in short, little up-to-date information was available at the start of the project on the fish diversity of the system and its biology. The Royal Museum for Central Africa (RMCA) is well placed to engage in such a study as for decades it is world leader in studies on African freshwater fishes, in particular those of the African Rift Valley region. Data on fisheries are also scarce, scattered in time and over the two countries, and encompassing different methodologies to estimate catches and catch per unit effort (CPUE). Hence, a clear picture of the situation was lacking at the start of the project.

3. METHODOLOGY

3.1 Paleolimnology

Sediment cores were collected at different sites within Lake Edward (and Lake George) during the different HIPE field campaigns. Cores were retreived by an UWITEC gravity corer, with typically a maximum section of 40-50 cm sampled. Sediment cores were retreived at lake water depths between 5 and 30 m for lake Edward (Ugandan side), with one additional core collected at the 90 m depth station (DRC portion of the lake). Sediment cores were subsectioned in the field lab at high resolution (between 2 and 5 mm), and stored frozen for shipment to Belgium. They were analysed for total, organic and inorganic carbon (and its $\delta^{13}C$ composition), nitrogen stable isotope ratios, total phosphorus content, water content, pigment concentrations (by HPLC), and a number of subsamples were analysed for major element composition and hydrogen isotope ratios in the organic, non-exchangeable H fraction.

Hippopotamus teeth were collected by UWA and NaFIRRI from carcasses of hippos which died of natural causes in the vicinity of the QENP headquarters (Katwe and Mweya peninsula). A total of 7 recent specimens were collected. The canines were stored in the field lab, and subsamples of the tooth enamal were drilled with a manual Dremmel drill during different HIPE field campaigns (see Figure 2). The powdered samples were transported to Belgium, and analysed for C and O stable isotope ratios following the methods described in Souron et al. (2012). In addition to the recently collected specimens, we gained access to four speciments from the Lake Edward region in the KMMA-MRAC collection. Three of these were collected in the southern part of L.Edward (DRC), one close to the outlet of the lake on the northwestern side (also DRC). These specimens date back to the 1920's and 1950's.

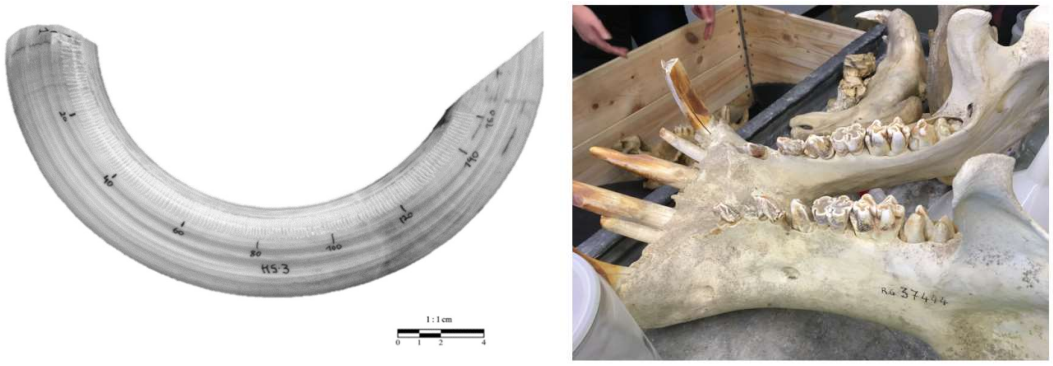

Figure 2: Example of recent hippo canine sampled along its growth axis for tooth enamel (left panel), and a Hippopotamus specimen from the MRAC-KMMA collected in Tervuren from the Lake Edward region (right panel)

A large collection of **bivalve shells** was made during the different HIPE campaigns. Shells were collected from both Lake George and Lake Edward, and were mostly found abundantly in shallow waters, such as near the mouth of Nyamugasani River (northwestern side of Lake George) or along the northeastern shores in shallow protected waters. A selection of these bivalve shells were sectioned along their maximal growth axis, and subsampled using

a NewWave Micromill to allow C and O isotope analyses along their growth period. Several historical specimens were obtained from museum collections, but so far no analyses have been made on these given the uncertaintly on their exact sampling locatation, and the fact that there are clear spatial gradients in the proxy information (see further).

Furthermore, we have collected a range of **museum-archived fish specimens**. These fish samples have been analysed for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{2}H$ – which offers a comparison to the contemporary fish stable isotope data collected (see WP2 & 3).

Finally, several **tree cores** have been collected during one of the HIPE sampling campaigns for an explorative analyses of whether carbon and oxygen stable isotope data suggest any trends in local climatic conditions in the region. We focused on *Acacia* spp. Given that this was not part of the HIPE workplan initially, we only managed to analyze one of these tree cores so far, but these preliminary results are extremely promising and offer good prospect for further work.

3.2 Greenhouse gases

We sampled Lake Edward, Kazinga Channel and Lake George on four occasions (20/10-07/11/2016, 23/03-08/04/2017, 18/01-02/02/2018, 21/03-30/03/2019). The first two cruises corresponded to the start and the end of the rainy season, respectively. The last two cruises corresponded each time to the end of the dry season. The two first cruises were characterized by lower air temperature and wind, but higher humidity and precipitation than the two last cruises (Fig. 3). During each cruise, sampling was designed to cover spatial variability horizontally and was mainly confined to Ugandan territorial waters, allowing sampling only down to 30m, which exception of the sampling cruise in January 2018 when the deepest part of the lake was sampled in the territorial waters of the Democratic Republic of Congo (DRC) (Fig. 4). From January 2017 to December 2019, a shallow station (3 m bottom depth) and a deeper station (22 m bottom depth) were regularly sampled, every 15 d in 2017 and 2018, and every 30 d in 2019. Water collection was carried out with the speed boat of the Katwe Marine policy.

Meteorological data were acquired (10 minute interval) with a Davis Instruments Weather Station (Vantage Pro2) in Mweya on top of a Uganda Wildlife Authority building, 4m above ground (-0.190384°N 29.899103°E).

During the March 2019 cruise, continuous measurements (1 min interval) of partial pressure of CO_2 (pCO_2) and of partial pressure of CH_4 (pCH_4) were made with an equilibrator designed for turbid waters (Frankignoulle et al. 2001) coupled to a Los Gatos Research off-axis integrated cavity output spectroscopy analyzer (Ultraportable Greenhouse Gas Analyzer with extended range for CH_4). In parallel water temperature, specific conductivity, pH, dissolved oxygen saturation level ($\%O_2$), turbidity, chlorophyll-*a* (Chl-*a*), and fluorescent dissolved organic matter (FDOM) were measured with an YSI EXO-II multi-parameter probe, position with a Garmin geographical position system (Map 60S) portable probe, and depth with a Hummingbird Helix 5 echo-sounder. Water was pumped to the equilibrator and the multi-parameter probe (on deck) with a 12V-powered water pump (LVM105) attached to the side of the boat at about 0.5 m depth.

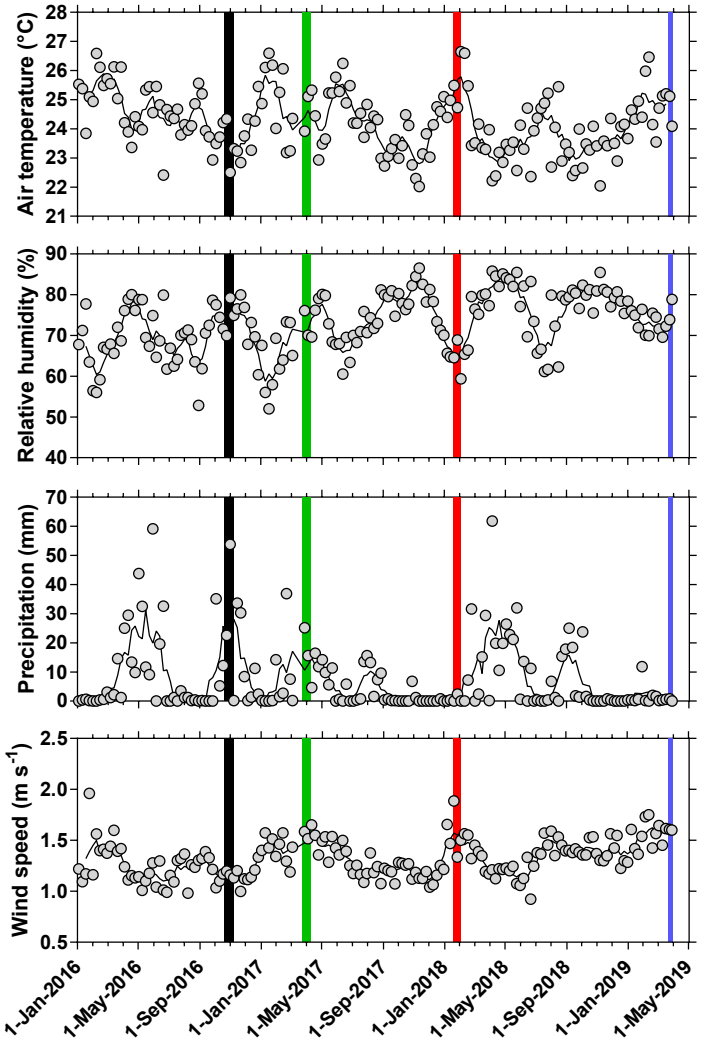

Figure 3: Air temperature (°C), relative humidity (%), precipitation (mm), wind speed (m s^{-1}) in Mweya (-0.1904°N 29.8991°E) from January 2016 to late March 2019. Coloured vertical lines indicate the sampling cruises for greenhouse gases.

Sampling was done from the side of the boat with a 5.0L Niskin bottle (General Oceanics). During the first cruise, vertical profiles of water temperature, specific conductivity, pH, $\%O_2$ and Chl-*a* were measured with a Hydrolab DS5 multi-parameter probe, while during the other three cruises and also during the monitoring, turbidity and FDOM were measured additionally with a YSI EXO-II multi-parameter probe. Both multi-parameter probes were calibrated according to manufacturer's specifications, in air for $\%O_2$ and with standard solutions for other variables: commercial pH buffers (4.00 and 7.00), a 1000 µS cm^{-1} standard for conductivity. pCO_2 was measured directly after water sampling with a Li-Cor Li-840 infra-red gas analyser (IRGA) based on the headspace technique with 4 polypropylene 60 ml syringes (Borges et al. 2015). The Li-Cor 840 IRGA was calibrated before and after each cruise with ultrapure N_2 and a suite of gas standards (Air Liquide Belgium) with CO_2 mixing ratios of 388, 813, 3788 and 8300 ppm. The overall precision of pCO_2 measurements was ±2.0%.

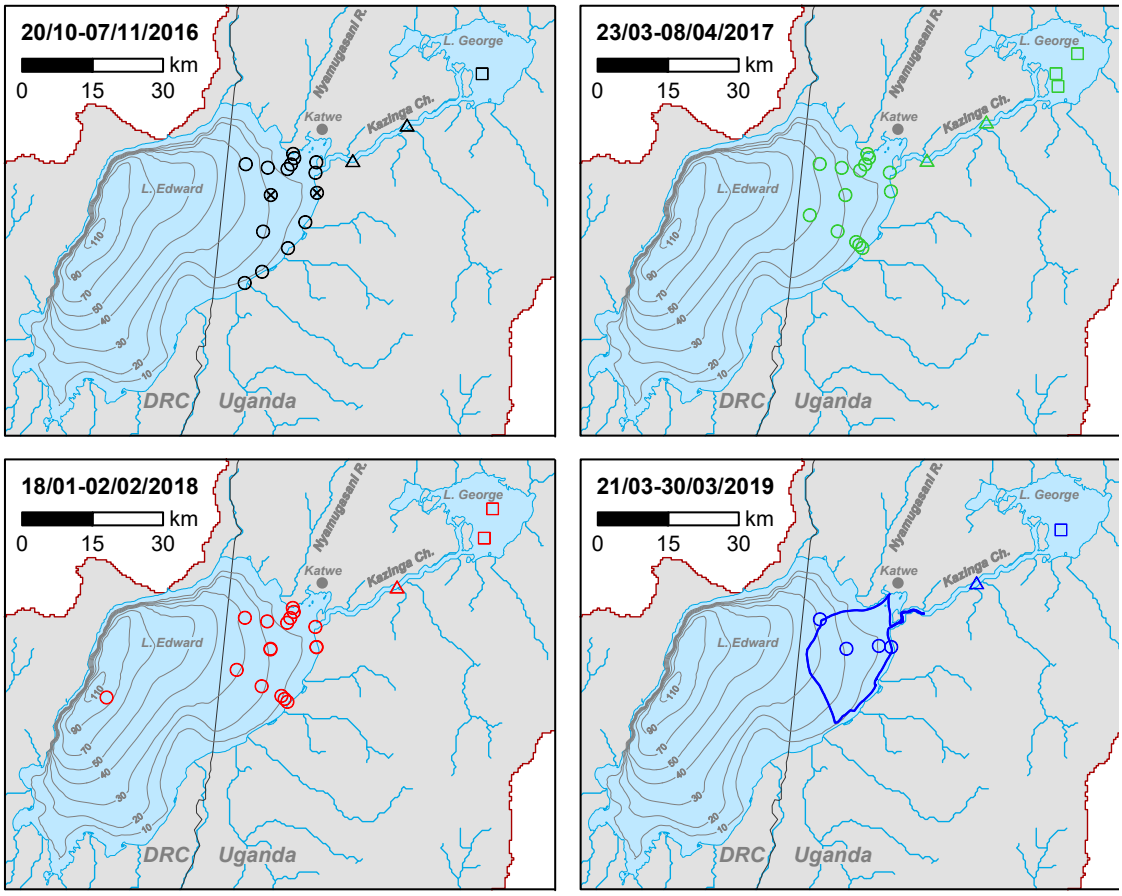

Figure 4: Map of Lake Edward and George showing catchment (grey), and large rivers (Strahler order ≥2), border between Uganda and Democratic Republic of Congo (RDC, black line), bathymethy and sampling stations (circles) in October 2016, March 2017, January 2018, March 2019, as well as continuous measurements in surface waters in March 2019. Crosses in the map of October 2016 indicate the two stations that were chosen for the regular monitoring (2017-2019).

Samples for CH_4 and N_2O were collected from the Niskin bottle with a silicone tube in 60 ml borosilicate serum bottles (Weathon), poisoned with 200 µl of a saturated solution of $HgCl_2$ and sealed with a butyl stopper and crimped with aluminium cap. Measurements were made with the headspace technique (Weiss 1981) and a GC (SRI 8610C) with a flame ionisation detector for CH_4 (with a methanizer for CO_2) and electron capture detector for N_2O calibrated with CO_2:CH_4:N_2O:N_2 gas mixtures (Air Liquide Belgium) with mixing ratios of 1, 10 and 30 ppm for CH_4, 404, 1018, 3961 ppm for CO_2, and 0.2, 2.0 and 6.0 ppm for N_2O. The precision of measurement based on duplicate samples was ±3.9% for CH_4 and ±3.2% for N_2O. The CO_2 concentration is expressed as partial pressure in parts per million (ppm) and CH_4 as dissolved concentration (nmol L^{-1}), in accordance with convention in existing topical literature. Variations of N_2O were modest and concentrations fluctuated around atmospheric equilibrium, so data are presented as percent of saturation level (%N_2O, where atmospheric equilibrium corresponds to 100%), computed from the global mean N_2O air mixing ratios given by the Global Monitoring Division (GMD) of the Earth System Research Laboratory (ESRL) of the National Oceanic and Atmospheric Administration (NOAA)

(https://www.esrl.noaa.gov/gmd/hats/combined/N2O.html), and using the Henry's constant given by Weiss and Price (1982).

3.3. Phytoplankton diversity and production

Vertical profile of temperature, conductivity, dissolved oxygen concentration (DO) and pH were measured in situ with a YSI EXO2 multiparametric probe. The depth of the mixed layer (Zm) was determined from the temperature and DO profiles at every sampling station. Secchi disk depth (SD) was determined at every sampling site. The vertical light attenuation coefficient in water (k; m^{-1}) was directly measured at different sites with a spherical underwater quantum sensor (Li-COR Li-193SA). Intercalibration with Secchi depth measurements enabled to obtain the following equation (R^2=0.97):

k = 1.141*(1/SD), with Secchi depth expressed in m.

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

Zeu = -ln(0.01)/k

At each sampling depth, a variable amount of water was filtered on a pre-combusted 25 mm glass fibre filters (Sartorius GF5, 0.7 µm nominal pore size) for particulate organic carbon (POC), particulate nitrogen (PN) and particulate organic phosphorus (POP) analyses. Filters were dried and then kept in small Petri dishes until later analysis. Filters for POC and PN concentration and their isotopic composition determination were decarbonated with HCl fume prior to measurement using an EA 1110 elemental analyser coupled to a Delta V Advantage isotope ratio mass spectrometer (Thermo). Calibration of δ^{13}C-POC measurements was performed with a combination of IAEA-600 (caffeine, δ^{13}C= -27.77 ‰) and two in-house standards, leucine and tuna tissue (δ^{13}C= -13.47 and -18.72 ‰, respectively). Reproducibility of δ^{13}C-POC measurements was typically better than ±0.2‰. POP was measured by spectrophotometry of phosphate using the molybdate blue-ascorbic acid reaction (APHA, 1998) after persulphate digestion (Valderrama, 1981). Molar C:N and C:P ratios were used as indicators of phytoplankton nutrient status.

An exetainer vial (12 ml, Labco) was filled without headspace at each sampling depth and preserved with $HgCl_2$ in order to determine the stable isotope C composition of DIC. Analysis of the δ^{13}C-DIC was carried out with an EA 1110 elemental analyser coupled to a Delta V Advantage isotope ratio mass spectrometer (Thermo). Prior to the analysis of δ^{13}C-DIC, a 2 mL helium headspace (He) was created, and 100 µL of phosphoric acid (H_3PO_4, 99 %) was added in the vial in order to convert all inorganic C species to CO_2. After overnight equilibration, a subsample of the headspace was injected with a gastight syringe into an elemental analyzer–isotopic ratio mass spectrometer (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).

Samples for total suspended matter (TSM) concentration were filtered on a pre-weighed 47mm glass fibre filters (Sartorius GF5, 0.7 µm nominal pore size), dried, and subsequently weighed to determine the TSM load.

For dissolved inorganic nutrients (NO_3^- ; NO_2^- ; NH_4^+; soluble reactive phosphorus (SRP)), 50 mL of water was filtered on a 0.2 µm polyethylsulfone syringe filter and preserved frozen until measurement by colorimetry according to standard techniques. The sum of NO_3^-, NO_2^- and NH_4^+ was considered as the dissolved inorganic nitrogen content (DIN). NH_4^+ concentration was determined using the dichloroisocyanurate-salicylate-nitroprussiate colorimetric method. NO_3^- and NO_2^- - were determined with the sulphanilamide colorimetric method, after cadmium reduction for NO_3^- (APHA, 1998). SRP was determined by spectrophotometry using the ammonium molybdate-potassium antimonyl tartrate method (Murphy and Riley, 1962). The sum of POP and SRP was considered as total phosphorus (TP).

Measurements of total alkalinity (TA) were performed by automated electrotitration on 50 mL filtered (0.2 µm) samples with HCl 0.1 mol L^{-1} as the titrant. The equivalence point was determined from pH between 4 and 3 with the Gran method. In addition, data were quality checked with certified reference material obtained from Andrew Dickinson (Scripps Institution of Oceanography, University of California, San Diego, USA). Typical reproducibility of TA measurements was better than ±3 µmol L^{-1}. The dissolved inorganic carbon (DIC) concentration was computed from water temperature, pH and TA measurements using the carbonic acid dissociation constants of Millero et al. (2006) and the CO_2 solubility from Weiss (1974), implemented in the CO2SYS software.

Primary production and N_2 fixation rates were determined from dual stable isotope photosynthesis-irradiance experiments using $NaH^{13}CO_3$ (Eurisotop) and dissolved $^{15}N_2$ (Eurisotop) as tracers for incorporation of dissolved inorganic carbon (DIC) and dinitrogen into the biomass. A dissolved $^{15}N_2$ solution was prepared following the recommendation of Mohr et al. (2010). At each station a sample of surface waters (500 ml) was spiked with the tracers (final enrichment in the heavy isotope of ~5%). Three subsamples were preserved with HgCl2 in 12-mL Exetainers vials (Labco) for the determination of the exact initial ^{13}C-DIC and $^{15}N_2$ 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 killed control sample. Samples were incubated in situ during 2 hours around mid-day just below the surface at lake surface temperature. A Li-Cor (Lincoln, Nebraska, USA) quantum sensor (LI-190; 5 min interval acquisition) monitored incident light for the daylight period. After incubation, biological activity was stopped by adding neutral formaldehyde into the flasks, and the nine samples were filtered on pre-combusted GF/F filters when back in the lab. Filters were decarbonated with HCl fumes overnight, dried, and their δ^{13}C-POC and δ^{15}N-PN values were determined with an EA-IRMS (Thermo FlashHT – delta V Advantage) following the procedure described above. For the measurement of the initial ^{15}N enrichment, a 2-ml helium headspace was created, and after 12h equilibration, a fraction of the headspace was injected into the above-mentioned EA-IRMS equipped with a Cu column warmed at 640°C and a CO_2 trap. Initial enrichment of ^{13}C-DIC was measured as described above.

Photosynthetic (P_i) and N_2 fixation (N2i) rates in individual bottles were calculated following Hama et al. (1983) and Montoya et al. (1996), respectively, and corrected for any abiotic tracer incorporation by subtraction of the killed control value. For each experiment, the maximum photosynthetic and N_2 fixation rates (Pmax, N2fixmax) and the irradiance at the onset of light saturation (Ik_PP, Ik_N2fix) were determined by fitting Pi and N2fixi to the light intensity gradient provided by the incubator (Ii) using the equation (1) for photosynthesis activity, and (2) for N_2 fixation.

$$Pi = 2*Pmax\ (Ii/(2*Ik\_PP))/(1+(Ii/(2*Ik\_PP))^2)$$
$$N2i = 2*N2fixmax\ (Ii/(2*Ik\_N2fix))/(1+(Ii/(2*Ik\_N2fix))^2)$$

Fitting was performed using the Gauss–Newton algorithm for nonlinear least squares regression with the JMP® software.

Daily depth-integrated primary production and N_2 fixation was determined assuming a vertically homogenous chlorophyll-a profile over the euphotic zone with the photosynthetic parameters Pm and Ik, the extinction coefficient k, and continuous surface irradiance data (Kirk, 1994). These measurements were integrated from averaged daily surface irradiance during the cruise. In addition, we defined the average light experienced by the phytoplankton in the mixed layer (I_{Zm}) according to Riley (1957):

$$I_{Zm} = I_s\ (1 - \exp(-Zm \times k)) / (Zm \times k)$$

where I_s is the mean incident light at the surface of the lake during the entire cruises and measured with a Li-Cor quantum sensor. The sensor continuously recorded light throughout the day during the entire cruises and then we estimated a mean light for the daylight.

Nutrient limitation of phytoplankton in a pelagic site in Lake Edward (M20 in Fig. 5) was assessed during the rainy (March-April 2017) and dry (January 2018) seasons. Twelve 500-mL polycarbonate bottles (Nalgene) were filled with water collected in the epilimnion and amended in triplicate with either 1 mL of a solution of $NaNO_3$ (+N treatment, 55 µmol L^{-1} final concentration), NaH_2PO_4 (+P treatment, 55 µmol L^{-1} final concentration), $NaNO_3$ and NaH_2PO_4 (+NP, 55 µmol L^{-1} final concentration), or 1 mL of mQ water (control treatment). Directly after the nutrient addition, every bottle was spiked with 1 mL of a solution of $NaH^{13}CO_3$ (10% final ^{13}C enrichment) and incubated for 24h at in situ temperature (26°C) and under constant light conditions provided by a Philips 55W PLL-deluxe bulb (250 µmol photons m^{-2} s^{-1}). Prior starting the incubation, an exetainer vial (12 mL, Labco) poisoned with 50 µL of $HgCl_2$ was filled with water from every bottle in order to determine the exact ^{13}C enrichment of the dissolved inorganic carbon pool (%^{13}C-DICi). The stable C isotope composition of the DIC was determined as described above. The initial concentration (POC) and stable C isotope composition of the POC (%^{13}C-POCi) was also determined filtering 50 mL of water through a precombusted 25 mm glass fibre filter (0.7 µm nominal porosity). At the end of the incubation (24h), the incorporation of the 13C tracer into the POC (%^{13}C-POC) was assessed in every bottle filtering 50 mL of water in duplicate through precombusted 25 mm glass fibre filter (0.7 µm nominal porosity). Filters were dried, decarbonated with HCl fumes and analysed with the

above-mentioned EA 1110 elemental analyser coupled to a Delta V Advantage isotope ratio mass spectrometer (Thermo).

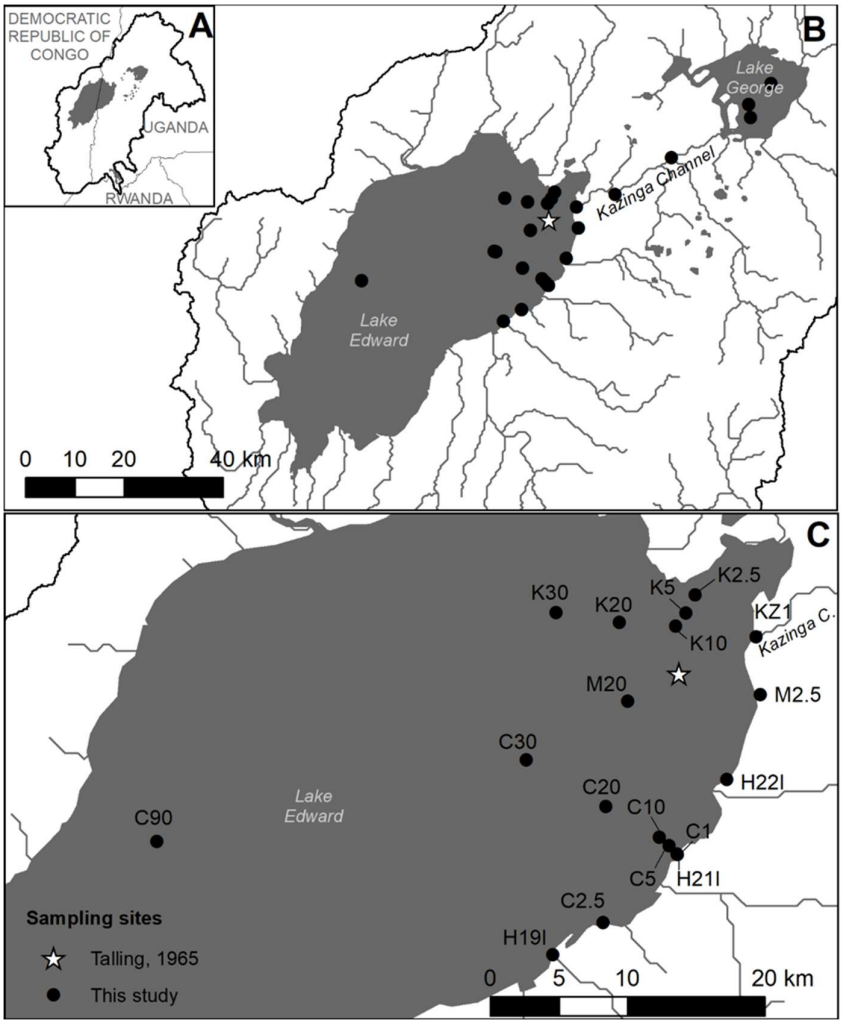

Figure 5: Location of Lake Edward and of the study sites. A. Location of Lake Edward in East Africa; B: Lake Edward basin, with the inflowing rivers, Lake George and the Kazinga Channel; C: Location of the sampled sites. The dots indicate the study sites (figures giving depth at the sampling site); the star shows the location of Talling's (1965) sampling site.

The amount of C incorporated into the POC (CFix) during the incubation (t = 24h) was calculated as:

$$CFix = (POC * (\%^{13}C\text{-}POC - \%^{13}C\text{-}POCi))/(t \times (\%^{13}C\text{-}DICi - \%^{13}C\text{-}POCi))$$

A variable volume of water was filtered on Macherey-Nägel (Düren, Germany) 47 mm GF5 filters (nominal pore size 0.7 µm) on which pigment extraction was performed in 90% HPLC-grade acetone, following Sarmento et al. (2006). Phytoplankton biomass and composition were assessed throughout the study by determination of chlorophyll a (Chla) and marker pigments by high performance liquid chromatography (HPLC). HPLC analysis of phytoplankton extracts was performed using the Wright et al. (1991) gradient elution method,

with a Waters system comprising a Photodiode DA detector and a fluorescence detector. Calibration was made using commercial external standards (DHI, Denmark). For estimating phytoplankton abundance at the class level, pigment concentrations were processed with the CHEMTAX software (Mackey et al., 1996), following a procedure similar to that of Descy et al. (2005), allowing estimating Chla biomass of green algae, chrysophytes, diatoms, cryptophytes, dinoflagellates and cyanobacteria, taking into account possible variation of pigment ratios with depth. Phytoplankton biomass was expressed per unit volume (µg Chla L^{-1}). Based on knowledge of the phytoplankton composition in Lake Edward analyzed using microscopy (see below), the following phytoplankton groups were considered according to their pigment composition:

• Diatoms and chrysophytes, which have chlorophylls c and share fucoxanthin as main marker pigment; diatoms also have diadinoxanthin and diatoxanthin; due to analytical problems of the HPLC technique (i.e. the incomplete separation of myxoxanthophyll and violaxanthin or diadinoxanthin), the two classes could not be separated by the CHEMTAX processing; however, as no chrysophytes were detected by microscopy in the lake samples, “diatoms + chrysophytes” could be safely considered as diatoms;
• Green algae, which have chlorophyll b, lutein, neoxanthin, zeaxanthin, and violaxanthin
• Cyanobacteria type 1 (T1), which have zeaxanthin at high concentration
• Cyanobacteria type 2 (T2), which have echinenone and often aphanizophyll and/or myxoxanthophyll in addition to zeaxanthin
• Cryptophytes, with chlorophyll c, alloxanthin, and α–carotene
• Dinoflagellates, with chlorophyll c, peridinin, and diadinoxanthin

Twenty-nine additional 500 mL water samples were taken at 1 m depth in the sites sampled during the three campaigns, preserved with formalin and settled to a final volume of approximately 25 mL for microscopical analysis of phytoplankton composition. The algal identification was based on conventional light microscopy (LM) in combination with scanning electron microscopy (SEM) for diatom determination. The work was done on fixed material on non-permanent slides using LM microscopes Motic BA 4000. Images were taken with Moticam 2000 camera supplied by Motic Images 2 Plus software program. Diatom permanent slides were obtained after digestion with hydrogen peroxide and mounting with Naphrax, and examined with a 100X objective under phase contrast on a Leitz Diaplan standard microscope, equipped with a Euromex camera using the Image Focus 4 software. The determination was based on standard taxonomic sources (Krammer and Lange-Bertalot, 1991, 1997a,b, 2004; Komárek & Fott, 1983, Komárek & Anagnostidis, 1999, 2005; Komárek, 2013, Moestrup and Calado, 2018) with use of recently published updating papers (for details see Stoyneva-Gärtner and Descy, 2018). The latin names were checked using AlgaeBase (Guiry and Guiry, 2019), CyanoDB 2.0 (Hauer and Komárek, 2019) and DiatomBase (Kociolek et al., 2018). A detailed analysis of the algal flora of the lake, with comparison with earlier reports can be found in Stoyneva-Gärtner and Descy, (2018).

3.4. Fish diversity and ecology

The four fieldtrips (2016–2019) resulted in some 30 000 specimens (± 22 000 haplochromines and ± 8000 non haplochromines), and some 4354 samples for genetic research from more than 50 localities in the system (Figure 6). Commercial species were mostly bought on local markets. Experimental fishing (gill nets, hand nets and electrofishing) complemented these samples with commercial and nearly all non-commercial fish species. Fish were identified in the lab using all relevant literature and comparisons with reference specimens in collections. Taxonomic studies were based on standard and geometric morphometrics and DNA barcoding. The presence of stocks of the commercial species was evaluated using microsatellite data. Stomach contents were studied of the main commercial species. The specimens examined corresponded as much as possible to those selected for the Stable Isotopes (SI) study. The frequency of occurrence and prey-specific abundance based on dry weight were calculated to determine the trophic niche of each species. In addition, dietary niche widths and niche overlap between species was also estimated. Size at first maturity was studied in the two tilapia species, based on the macroscopical examination of the gonads.

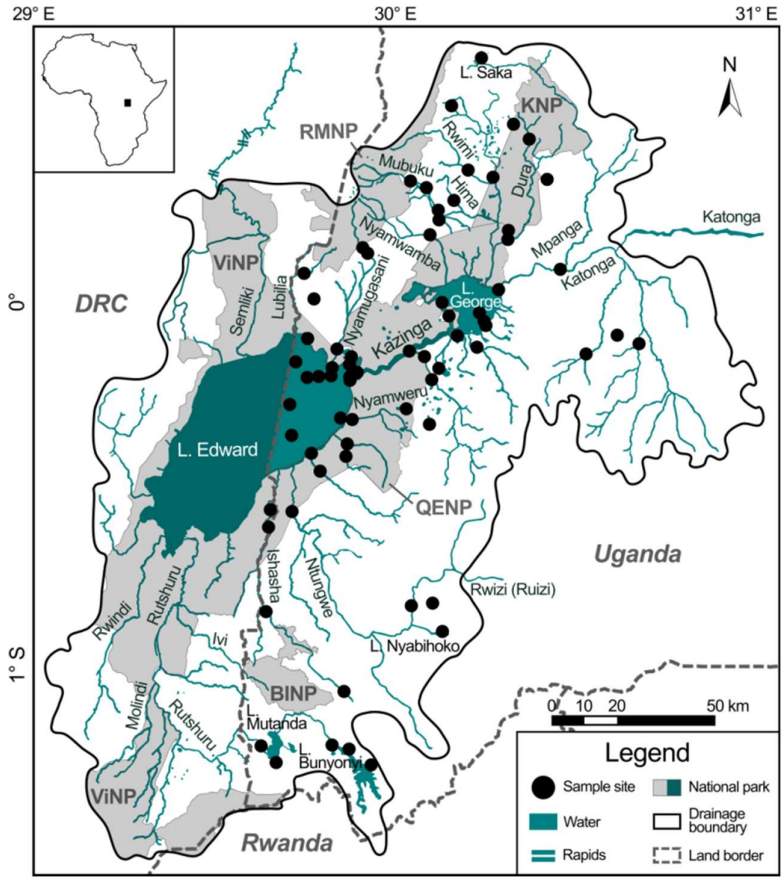

Figure 6: Overview of all 30 non-*Haplochromis* species and 50 *Haplochromis* species (including some species to be described) from the Lake Edward system that were all collected during the HIPE expeditions. Of these, 32 species (3 non-*Haplochromis* and 29 *Haplochromis*) were not known to inhabit the system prior to the HIPE project.

3.5. Fisheries

We have scanned all relevant literature available and made a state of the art synthesis of the data available on fisheries. In a recent publication, we determined Fisheries Reference Points (FRP) using recently developed stock assessment methods for data-limited fisheries for the Ugandan part of Lake Edward and for Lake George. The FRP were based on four stock assessment methods for data-limited fisheries: Length-based Bayesian biomass (LBB), abundance-based maximum sustainable yield (AMSY), catch-based maximum sustainable yield (CMSY), and a Bayesian Schaefer model (BSM). The major FRP determined for the stocks assessed were MSY (maximum sustainable yield), *B*msy (biomass that supports MSY), *B*/*B*msy (current biomass relative to *B*msy), *F*msy (fishing mortality rate at MSY), *F*/*F*msy (fishing mortality rate relative to *F*msy), and *B/B0 (*current biomass relative to unfished biomass).

3.6. Ecosystem services

Socio-economic data were collected between December 2017 and February 2018 on nine landing sites on the Ugandan part of Lake Edward and on Lake George respectively. The objective was to determine how the environmental and socio-economic changes over the last 30 to 50 years had affected fisheries productivity and benefits. Key Informant Interviews were done with the leaders of the landing sites, and 152 randomly selected respondents were interviewed using Individual Sample Surveys. Additionally, Focus Group Discussions were held at four of the landing sites. Enquiries related to i) the demography and living conditions at the landing sites, ii) the potential conflict with wildlife conservation, iii) the perceived changes in the fisheries, iv) the compliance with fisheries regulations, v) the effect of declining fisheries on livelihoods and vi) the potential conflicts with foreign fishermen.

4. SCIENTIFIC RESULTS AND RECOMMENDATIONS

4.1 PAST ECOSYSTEM FUNCTIONING

We retrieved modelled climate data over the catchment of Lake Edward from different sources as a complement the paleo-proxy data derived from other archives (Fig.7). There was a significant warming trend over the last decades, as well as a decreasing trend in precipitation, in particular since the 1960's. Other data sources confirm this trend (e.g. Funk et al. 2012). The magnitude of these trends leads us to anticipate that they have potentially changed the hydrological cycle, productivity of the lake, and vegetation over the catchment.

Several **sediment cores** have been analyzed for a number of key parameters. These were sectioned in the field (in most cases 3 mm increments for the upper 10 cm, 5 mm resolution at higher depths; the core from the deepest sampling point was subsampled at 0.5 cm resolution), during which occasionally encountered other relevant material (e.g. chironomid larvae, gastropods or bivalves) were picked out and stored separately. The sediment core from L. George shows a uniform pattern of $\delta^{13}C_{OC}$ (-10.5 ± 0.5 ‰, Fig.8), values consistent with those measured in the lake POC pool during the different HIPE cruises, and was dominated by organic matter (%OC: 31.1 ± 3.2 %). Thus, the organic carbon accumulating in Lake George appears to be predominantly derive from in situ cyanobacterial production, and our sediment cores do not show any signs of drastic changes in e.g. productivity (primary productivity is expected to affect the degree of isotope fractionation in aquatic primary producers: faster growth rates lead to diffusion limitation and thus, less isotope fractionation, hence higher $\delta^{13}C$ values of other factors remain constant).

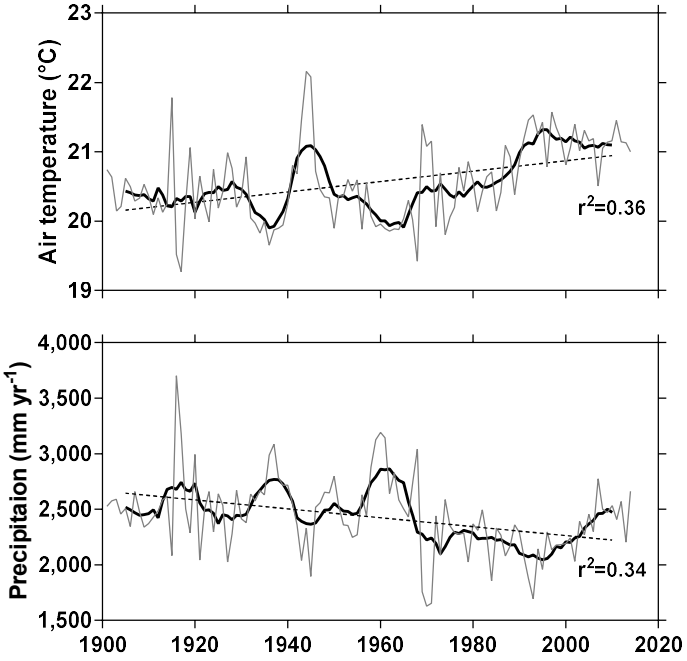

Figure 7: Evolution from 1900 to 2014 of annual air temperature and precipitation over the catchment of Lake Edward based on the National Oceanic and Atmospheric Administration Twentieth Century Reanalysis (20CR). Grey line corresponds to annual values, thick black line to 10yr running average and dotted line to the linear regression of the latter over time.

Three sediment cores from Lake Edward, in contrast, show marked gradients in $\delta^{13}C$: for the 5m and 30m cores, $\delta^{13}C$ shifts from values between -21.5 and -20.5 ‰ in the deeper part of the cores to ~-24‰ in the upper 10 cm of the core, the change starting at about 20 cm depth. This shift is higher than can be explained by the Suess effect (i.e. the decrease in atmospheric $\delta^{13}C$-CO_2 due to fossil fuel combustion) and hence points towards a general change in the $\delta^{13}C$ value of the lake organic matter inputs. Two hypotheses (not mutually exclusive) could explain such a decreasing trend in $\delta^{13}C$: (i) an increase in the delivery of C3-derived organic matter to the lake, and/or (ii) a decrease in phytoplankton productivity, which would increase isotope fractionation in phytoplankton due to alleviation of diffusive CO_2 limitation. In the core collected at 90m water colum depth, however, the trends are quite different: $\delta^{13}C$ is lower then in other cores near the surface (-25.5 ±) for the first 10 cm, and then shows an excursion towards more negative values (-26.5 ‰) up to ~20 cm depth, then increases again to ~-25 ‰ (Fig.8).

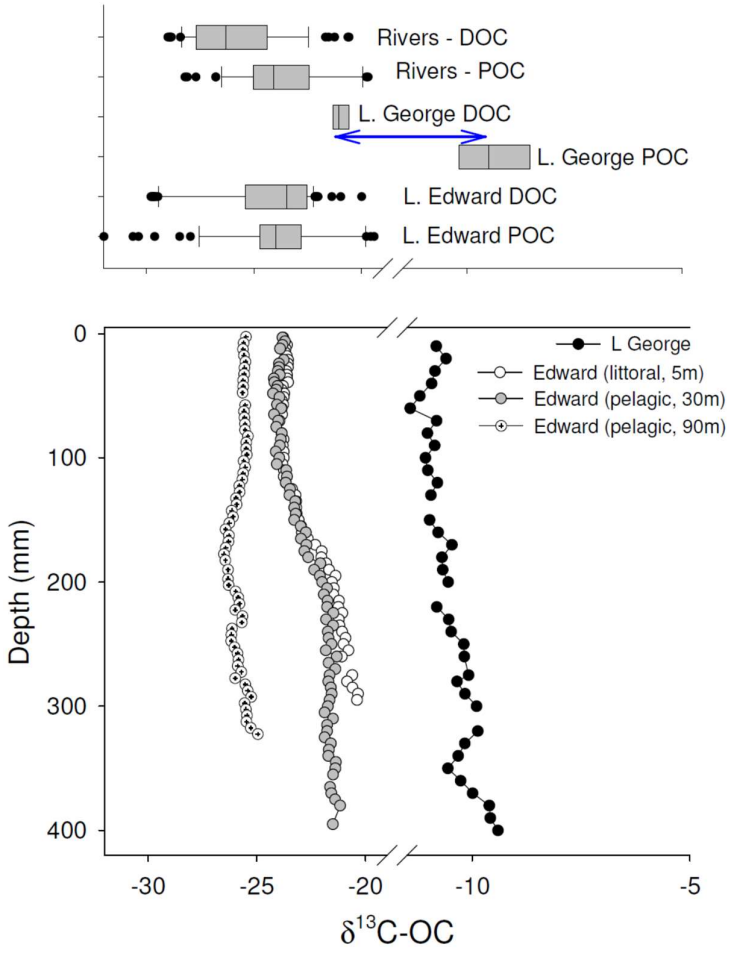

Figure 8: $\delta^{13}C$ profiles in 4 sediment cores (lower panel: littoral and pelagic station in Lake Edward; one central location in Lake George), and summary of $\delta^{13}C$ values measured in particulate and dissolved organic carbon pools in both lakes and inflowing rivers (upper panel – compilation of data from different seasons).

This trend contrasts with those observed in the two more shallow sites. Attempts to date the sediment cores using $^{210}Pb_{xs}$ activities were unsuccessful, unfortunately: activities were

often not higher than background values and could not be used for reliable dating. We can, however, assume lower sedimentation rates in the deep station, which is also characterized by permanently anoxic deep waters, affecting the post-depositional preservation of sediment organic matter: %OC is indeed more stable throughout the depth of this cores (11.8 ± 0.9 %), while the OC content shows a clear decrease in the more shallow sites (Fig.9). Differences in organic matter preservation/processing are likely also partially responsible for the general increase in TOC/TN ratios from shallow water to deepwater sediment cores (Fig.10).

An approximation for dating the sediment cores from L. Edward can, however be made based on data from Russell et al. (2003) and Russell & Johnson (2007), who dated several cores from L. Edward based on a combination of ^{14}C ages obtained on terrestrial macrofossils or charcoal, and ^{210}Pb from other sediment cores that were visually similar. An average sedimentation rate of ~3.5 mm y^{-1} was reported for a core taken at 100 m depth in L. Edward. The core was sampled on the Congolese side of L. Edward in the deepest section of the lake close to the sampling site of sediment core #26 (90 m depth). A similar average sedimentation rate for our sediment core #26 can thus be assumed, which would put the shift to higher $\delta^{13}C$-TOC values at about 40 years BP. One sediment core described by Russel & Johnson (2007) was retrieved at 30 m depth and the average sedimentation rate in the upper part of the core (53-83 cm) was determined at 2 mm y^{-1}. Our sediment core #8 was retrieved at the same depth in L. Edward (however, the two locations are not near to each other) and, applying this sedimentation rate to our sediment core results in an age of about 200 years BP for the deepest section.

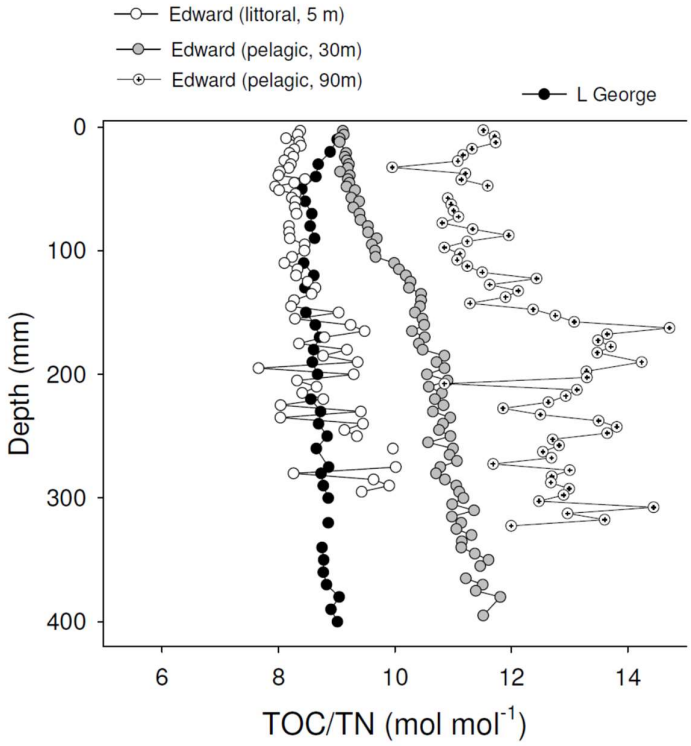

Figure9: Depth profiles of organic carbon content (%OC, upper panel), and TOC/TN (molar ratios, lower panel) in 4 sediment cores from Lake Edward and L. George.

Phytoplankton pigments have been extracted from these sediment cores and analysed by HPLC, and also reveal different trends between the more shallow-water sediment cores and the 90m core. These results are, however, pending a more in-depth analysis in order to shed more light on their interpretation.

An explorative study was also performed to investigate to which extent hydrogen stable isotope ratios (δ^2H) on non-exchangeable H in sediment organic matter could shed some light on further distinguishing terrestrial and aquatic C sources to sediment sources (Fig.10). This is a novel approach which has so far only been tried in a single marine study (Häggi et al. 2021) and in 2 explorative soil studies (Ruppenthal et al. 2013, 2015). This approach is rather cumbersome from an anlytical point of view, since it requires 4 separate analysis per sample (a dual equilibration with ^2H-enriched and ^2H-depleted water, respectively, for both a bulk subsample and a mineral subsample where the organic fraction is removed by pre-combustion at 450°C). The expectation was that aquatic sources would be strongly ^2H-depleted relative to terrestrial organic matter sources, which was indeed the case (see Fig.10, middle panel), whereas δ^2H values of water in the lake proper is relatively homogeneous (Fig.10, top panel). Besides source information, we also expect that mineralization of organic matter leads to a gradual 2H-enrichment in the non-exchangeable H, given that processing by heterotrophic bacteria integrates H from environmental H_2O into the organic fraction. If we consider the gradient of L. Edward sediment cores from 5m over 30m to 90m water column depth, we notice a constent trend towards lower δ^2H in OM (by ~90 ‰ overall between 5 and 90m). This trend is consistent with two mutually non-exclusive mechanisms: (i) a gradually higher contribution of in situ aquatic production (i.e. phytoplankton biomass) from littoral to deepwater sites, and (ii) stronger preservation of organic matter inputs towards deepwater sites (i.e. less microbial processing). We consider this to be a highly relevant methodological output of the project, which we hope to follow up on and develop new experimental work to explore this further.

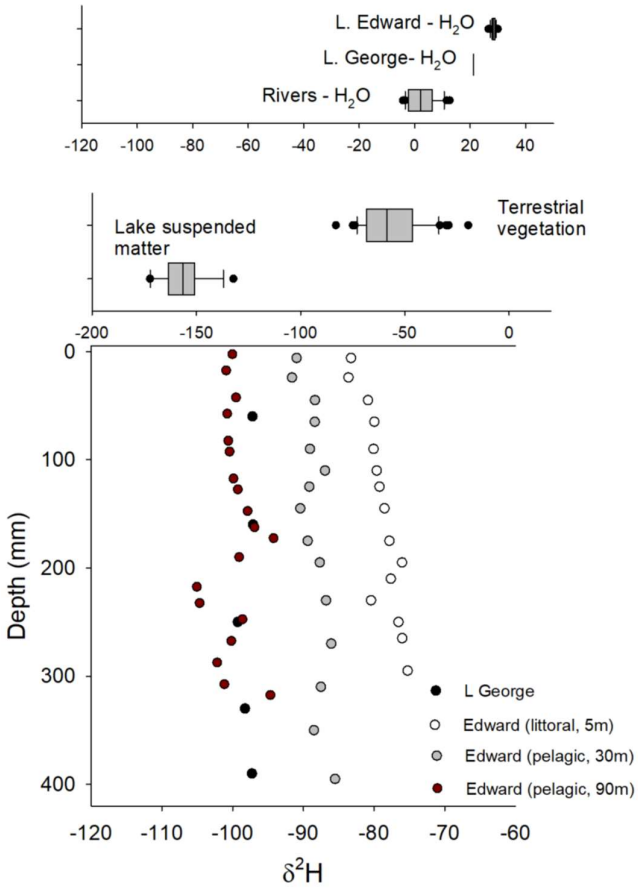

Figure 10: Overview of hydrogen stable isotope data (δ^2H) on surface waters from L. Edward, L. George and a range of inflowing rivers (top panel), δ^2H values of non-exchangeable H in vegetation and suspended matter samples from L. Edward, and δ^2H values of non-exchangeable H measured in sediment cores from L. Edward and George.

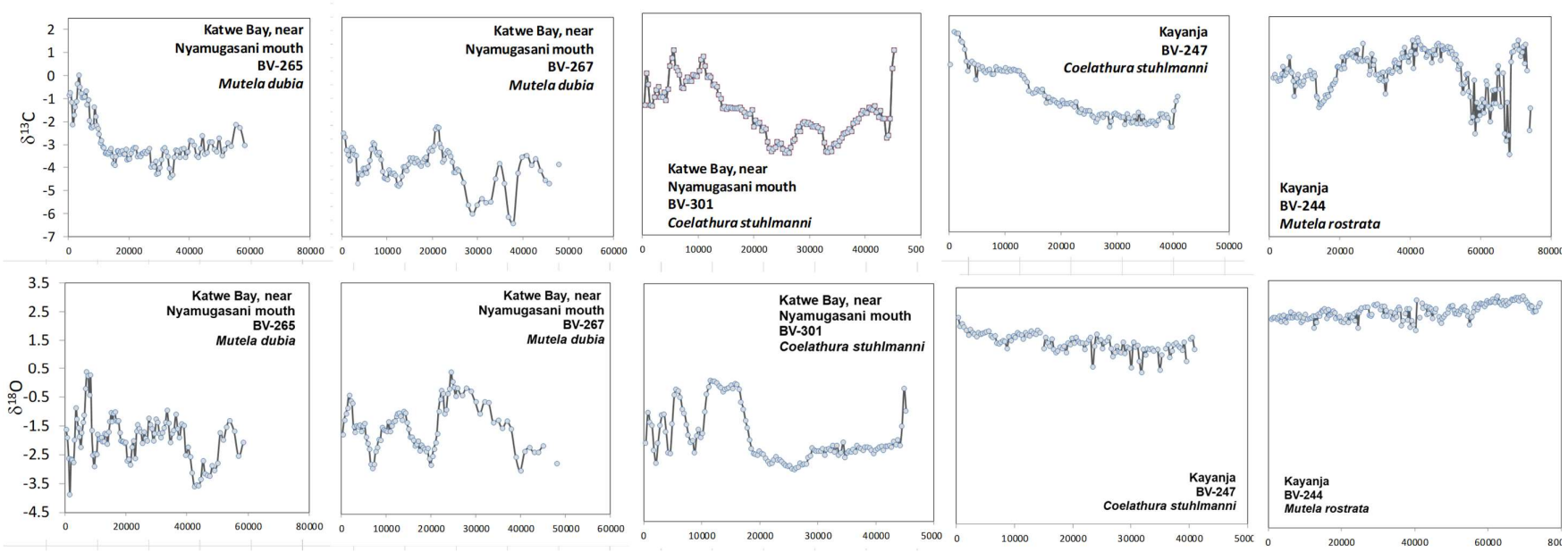

Figure 11: High-resolution $\delta^{13}C$ and $\delta^{18}O$ measurements in bivalve shells collected in 2016 and 2017 from Lake Edward.

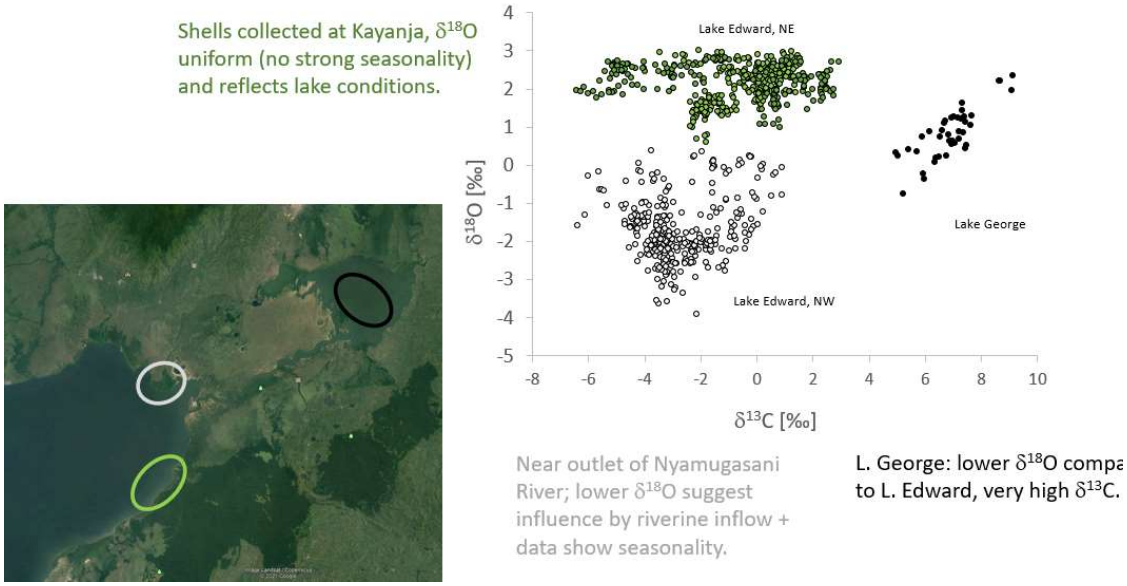

Figure 12: Oxygen versus carbon isotope ratios measured along the maximal growth axis of bivalve shells collected in from Lake Edward and Lake George.

The collection of live **bivalve shells** has been inventorized, and $\delta^{13}C$, $\delta^{15}N$ and $\delta^{2}H$ analyses on the organic tissues were made (see WP2). At the moment, eight shells (7 from L. Edward, one from L. George) have been fully analyzed for $\delta^{13}C$ and $\delta^{18}O$ along the maximal growth axis (Fig. 11 and 12). $\delta^{13}C$ values in the Lake Edward specimens varied widely between -6.5 and 0.0 ‰, and in most specimens showed a gradual increase through ontogeny, with no clear annual cyclicity. The latter is not surprising, since $\delta^{13}C$ values in freshwater bivalve shells are influenced not only by the $\delta^{13}C$ of the external DIC pool, but also by a variable contribution of metabolic CO_2, which is typically strongly depleted in ^{13}C. Values of $\delta^{18}O$ in contrast, do show a clear cyclicity for specimens collected near the outlet of Nyamugasani River, ranging between -3.9 and +0.3 ‰, and suggest a growth period of 4-5 years (note that the spread of a single cycle over a wider distance further away from the tip is due to the fact that this is the early growth stage, when shells typically grow faster). Assuming the carbonate is secreted in oxygen isotope equilibrium with the environmental water, and using an average lake temperature of 26.5 °C, these values correspond to $\delta^{18}O_{water}$ values of -0.7 ± 0.8 ‰ (range: -2.7 to +1.6 ‰). $\delta^{18}O_{water}$ data from the monitoring on Lake Edward show a much more restricted range, however (mostly between +3.2 and +3.8 ‰), showing a clear riverine influence on this sampling site. $\delta^{18}O$ data on shells from Kayanja (see Fig.12) are much more stable and in line with $\delta^{18}O_{water}$ data from the Lake Edward monitoring. The shell material from L. George (Fig.12) differs strongly from those in different parts of L. Edward, in particular for $\delta^{13}C$, with average values of +6.9 ‰ across the growth axis – this strong ^{13}C enrichment reflects the high $\delta^{13}C$-DIC values measured in L.George and the high aquatic primary production. In summary, we found a strong local influence on both $\delta^{13}C$ and $\delta^{18}O$ values recorded in lacustrine bivalve shells – which was not anticipated. While this reflects the potential of bivalve shell proxies to infer information on the local habitat and geographical origin of shell material, it strongly compromises the use of (museum) archived shell material

to reconstruct lake hydrological or geochemical conditions, when no detailed sampling site information is provide on such specimens – as is the case for the museum-held specimens we were able to obtain. Given the limited prospect to derive relevant information to contribute to the project objectives, analyses of the archived specimens was therefore put on hold.

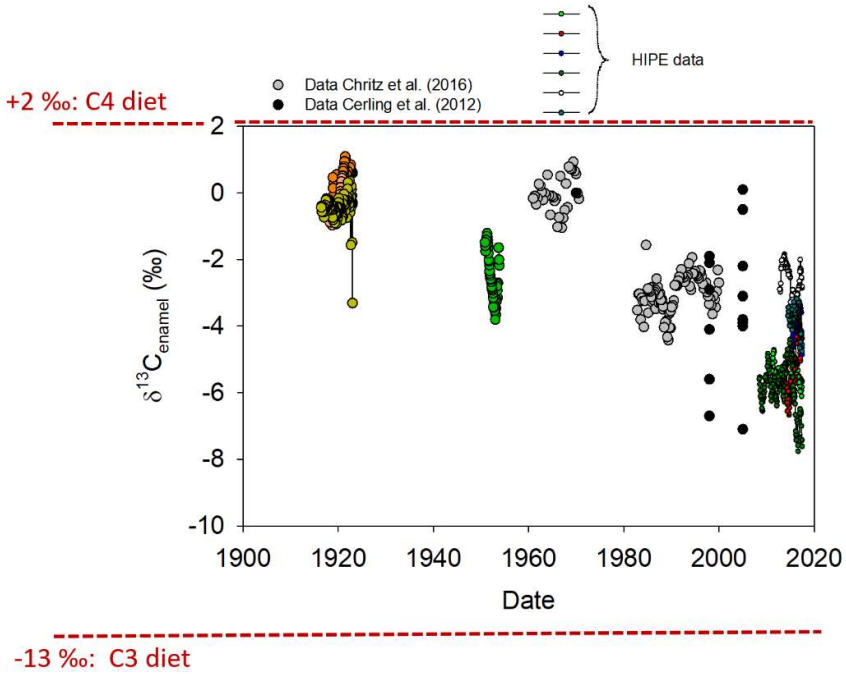

Figure 13: $\delta^{13}C$ values of *Hippopotamus* canine tooth enamel from Lake Edward: historical data from the literature (Cerling et al. 2008; Chritz et al. 2016) and data on six specimens collected during HIPE.

The analyses made on **tooth enamel from *Hippopotamus*** canines (Figures 13,14,15) were inspired by the report by Chritz et al. (2016), who reported a shift in *Hippopotamus* diet in the northern part of Lake Edward, based on high-resolution sampling of canines of two *Hippopotamus* specimens (one covering the 1960's, one covering the 1990's). The lower $\delta^{13}C$ data in the late 20th century specimen was interpreted as reflecting a shift in the catchment vegetation towards more C3 vegetation, i.e. open C4 grasslands gradually being encroached or closing in by shrubs and trees (note: grasses in this region follow the C4 pathway, shrubs and trees all follow the C3 pathway), and linked to the declining large herbivore populations in the area. Given the broad implications of their conclusions – based on only 2 specimens, we compiled both additional literature data from the region (Cerling et al. 2008), collected canines from recent *Hippopotamus* along the northern shores of L. Edward, and obtained 4 specimens from the region from the KMMA-MRAC collection. Assuming a fractionation of ~14 ‰ between diet and tooth enamel, $\delta^{13}C$ values of +2 ‰ correspond to a pure C4 diet, while a pure C3 diet would correspond to $\delta^{13}C_{enamel}$ values around -13 ‰. Several relevant trends emerge from large dataset (see Figures 13, 14, 15):

(i) Overall, the data confirm a long-term trend towards decreasing $\delta^{13}C$ values of the *Hippopotamus* diet in the region

(ii) There is a high inter-individual variabilty in $\delta^{13}C$ values, most pronounced in more recent specimens, indicating that dietary differences exist on small spatial scales. As *Hippopotamus*

are thought to be rather indiscriminate grazers, this should reflect local differences in relative C3-C4 cover.

(iii) Oxygen stable isotope data of Hippopotamus are likely good proxies for their lacustrine versus riverine habitat use: the lowest $\delta^{18}O_{enamel}$ values are found in specimens originating from the Rwindi River area (KMMA-MRAC collection).

Thus, our data generally support the conclusions by Chritz et al. (2016) that C3 vegetation has an increasing importance in the diet of hippos, in line with the hypothesis of a strong change in vegetation over the past decades. However, we advise caution in making interpretations based on a limited number of individual specimens, since large inter-individual differences in dietary contributions are found.

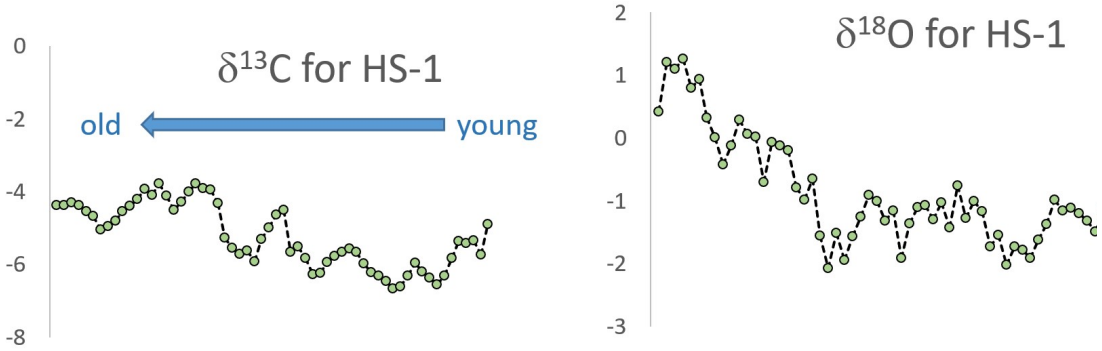

Figure 14: More detailed view of $\delta^{13}C$ and $\delta^{18}O$ values of canine tooth enamel from one of *Hippopotamus* specimen recently collected near Lake Edward.

Furthermore, we have collected a range of **museum-archived fish specimens**. The fish samples have been analysed for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{2}H$, covering >40 fish specimens from the L. Edward watershed (mostly from the 1930's). These museum specimens include the following fish commercial species from the lake: *Bagrus docmak*, *Clarias gariepinus*, *Labeobarbus altianalis*, *Protopterus aethiopicus*, *Oreochromis niloticus*, and *Oreochromis leucostictus*. Isotope values were corrected by the confounding effect of solvent used for storage and conservation. Their combined isotopic composition was higher for $\delta^{13}C$ (-16.4 ± 1.3 ‰), but no significant differences were found for $\delta^{15}N$ (9.8 ± 2.4 ‰), relative to data from the same species collected at present in L. Edward, at locations with no influence of other large contributing systems such as the Kazinga Channel (-18.5 ± 1.0 ‰ for $\delta^{13}C$ and 10.2 ± 1.6 ‰ for $\delta^{15}N$). These results would be consistent with a shift in the baseline $\delta^{13}C$ values in the lake, corresponding to a lower productivity or a change in the composition of terrestrial OM input to L. Edward over the past century.

Finally, a number of *Acacia* spp. **tree cores** were collected, one of which was analyzed for $\delta^{13}C$ and $\delta^{18}O$ in cellulose along the growth axis ($\delta^{13}C$ data shown in Figure 16). $\delta^{13}C$ values recorded in tree rings mainly reflect changing water availability (e.g. Gessler et al. 2014), but long-term trends are influenced also by the Suess effect, which refers to the decrease in $\delta^{13}C$ in atmospheric CO_2 due to anthropogenic (mostly fossil fuel-derived) CO_2 emissions. The data obtained were thus corrected for the Suess effect in order for interannual variations to mainly related to water availability: lower water availability leads to less isotope fractionation (due to lower stomatal opening, therefore leading to diffusion limitation) and

hence higher $\delta^{13}C$ values. The data show a clear shift towards higher $\delta^{13}C$ (hence: lower water availability) in recent decades, consistent with climatic data (Fig 7).

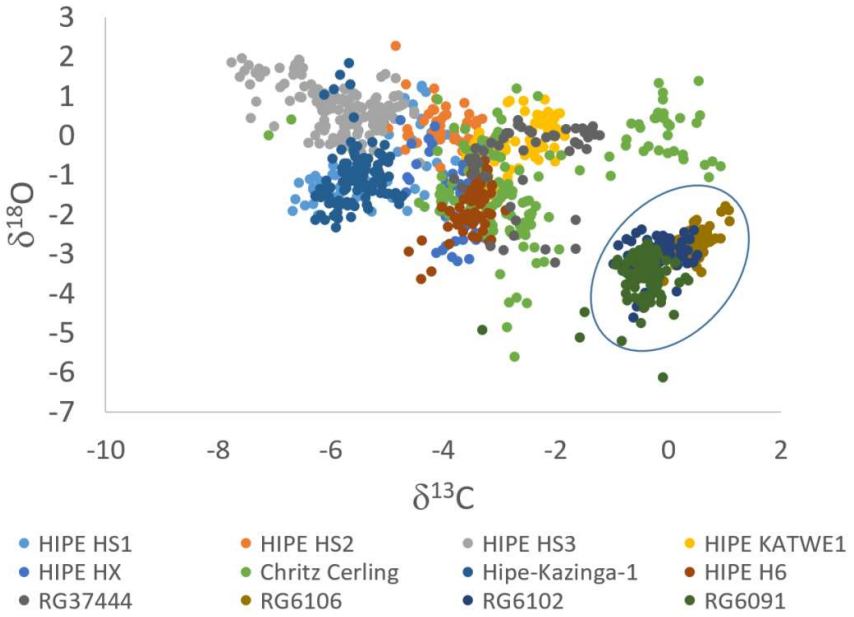

Figure 15: Overview of combined $\delta^{13}C$ and $\delta^{18}O$ values of *Hippopotamus* canine tooth enamel from Lake Edward: historical data from the literature (Cerling et al. 2008; Chritz et al. 2016), data on six recent specimens collected during HIPE, and 4 specimens sampled from the MRAC-KMMA collection from the L. Edward region dating back to the 1920's and 1950's. The encircled data are specimens from the Rwindi River area.

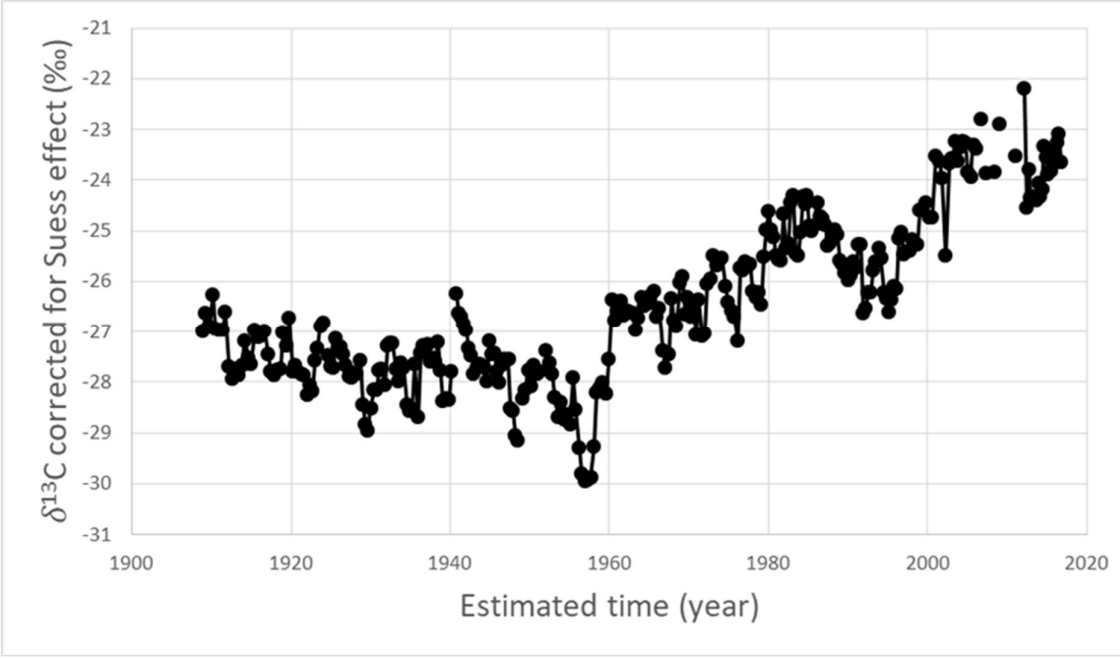

Figure 16: $\delta^{13}C$ values of bulk tree core samples on an *Acacia* spp. collected in the crater lake area on the NW side of Lake Edward. Age estimates are preliminary and approximate, based on average stem growth increments reported for *Acacia* spp. $\delta^{13}C$ data were corrected for the Suess effect (i.e. change in $\delta^{13}C$ of atmospheric CO_2 due to anthropogenic CO_2 emissions).

4.2 CARBON AND NUTRIENT CYCLING

4.2.1 Dynamics of greenhouse-gases (CO_2, CH_4, N_2O)

Vertical variations

Figure 17 shows the vertical profiles at 32 m depth obtained during the four cruises (Fig. 4). Conditions were stratified in October 2016 and March 2017 corresponding to the rainy season (Fig. 3) with a thermocline situated at between ~16 and ~22 m, and anoxic conditions in bottom waters (Fig. 17). Partly mixed and fully mixed conditions were observed in March 2019 and January 2018 (Fig. 17), respectively, corresponding to the two cruises carried out at the end of the dry season (Fig. 3). During the stratified conditions, pCO_2, CH_4 and NH_4^+ (Fig. 17) strongly increased with depth, with the highest values in March 2017. CH_4 and NH_4^+ were nearly homogeneous with depth during the two dry season conditions – January 2018 and March 2019 (Fig. 17). pCO_2, $\%N_2O$ and NO_3^- increased slightly with depth in March 2019 (partly mixed conditions) indicating some organic matter degradation and nitrification in bottom waters. $\%N_2O$ in bottom waters was very different during the two rainy seasons, with a very marked over-saturation in October 2016 (10,389%, start of the rainy season) and a very marked under-saturation in March 2017 (7%, end of the rainy season). We hypothesize this pattern resulted from duration of the anoxic bottom waters.

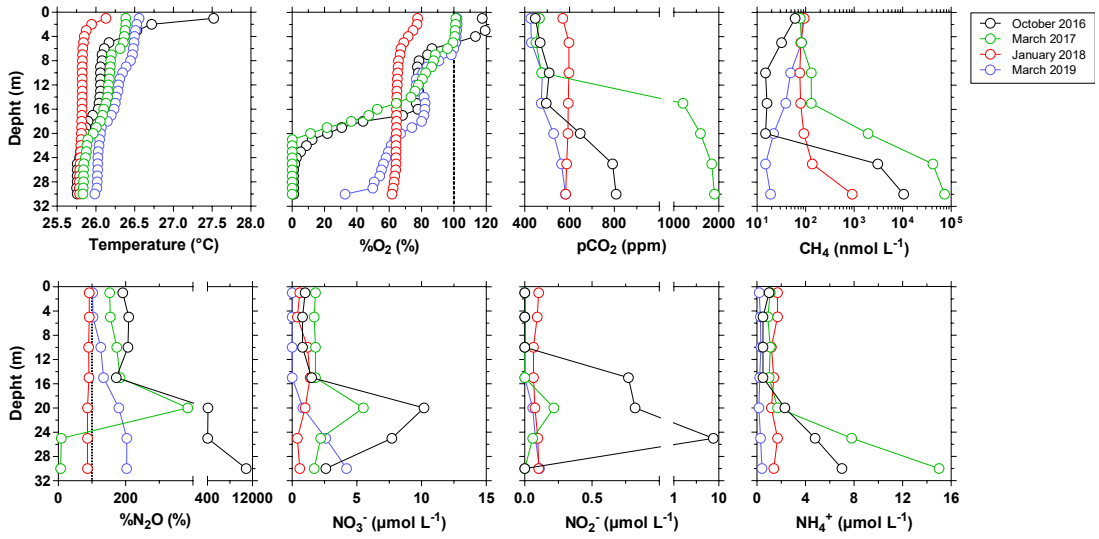

Figure17: Vertical profiles of water temperature (°C), O_2 saturation level ($\%O_2$, %), partial pressure of CO_2 (pCO_2, ppm), CH_4 concentration (nmol L^{-1}), N_2O saturation level ($\%N_2O$, %), NO_3^-, NO_2^- and NH_4^+ concentrations (µmol L^{-1}) in Lake Edward (32 m bottom depth) in October 2016, March 2017, January 2018, March 2019. Vertical dotted line indicates the atmospheric equilibrium value.

During the early rainy season (October 2016) anoxic conditions were recently established, while anoxic conditions were well established during the late rainy season (March 2017). This could explain intense N_2O production in bottom water from nitrification that also resulted in a very large peak in NO_2^- and higher NO_3^- in bottom water in October 2016 compared to March 2017. Under well established anoxic conditions (March 2017), in bottom

waters N_2O was removed from the water column by sedimentary or pelagic denitrification leading to under-saturation in N_2O. In March 2017, under partly mixed conditions, N_2O peaked at the oxycline along with NO_2^- and NO_3^-, while $\%N_2O$, NH_4^+, NO_3^- and NO_2^- were relatively homogeneous throughout the water column, under fully mixed conditions in January 2018.

Variations from cruise to cruise were much more modest in surface water than at depth. The values of CH_4 in surface waters were very close among the four cruises (61-94 nmol L^{-1}). pCO_2 was higher during fully mixed conditions (January 2018, 570 ppm) compared to the other three cruises (427-466 ppm), while $\%$N2O was higher during the two stratified conditions (with anoxic bottom waters, 192-152%) compared to the other cruises with more mixed conditions (with oxic bottom waters, 92-102%).

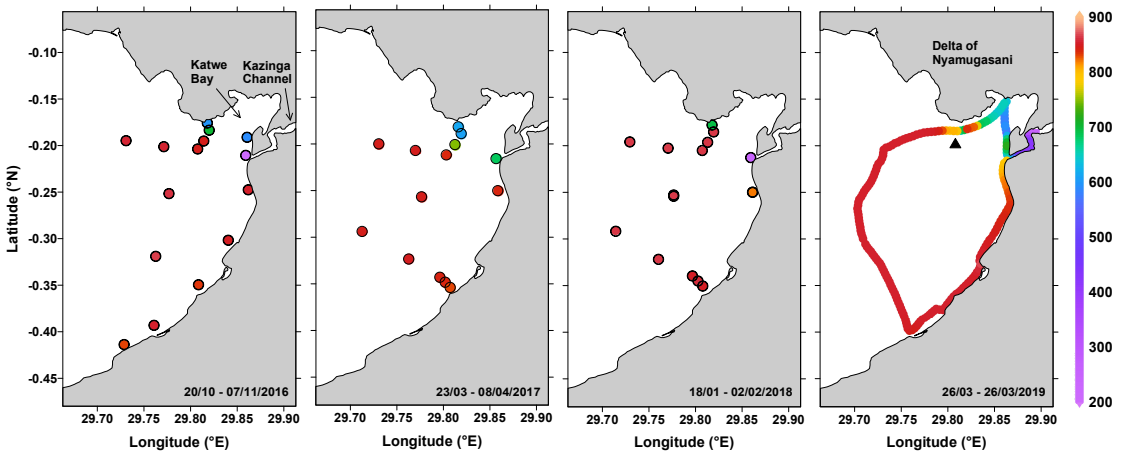

Figure 18: Variations in surface waters of Lake Edward of specific conductivity (µS cm^{-1}) in October 2016, March 2017, January 2018, March 2019. Vertical dotted line indicates the atmospheric equilibrium value. Black triangle indicates an area presumably influenced by inputs from the Nyamugasani river.

Horizontal variations

Surface water with a lower specific conductivity (202-726 µS cm^{-1}) was observed at the mouth of the Kazinga Channel, and this water mass propagated Northward towards Katwe Bay and also to lesser extend southward of the mouth of the Kazinga Channel during the two cruises at the end of the dry season (Fig. 18). Elsewhere in Lake Edward, specific conductivity in surface waters was higher and relatively homogenous (~ 853±10 µS cm^{-1}). Surface water from the Kazinga Channel had characteristics very close to those as Lake George, with high Chl-*a* (177±125 µg L^{-1}), low pCO_2 (28±13 ppm), CH_4 (135±102 nmol L^{-1}) and $\%N_2O$ (77±10%) (Fig. 19). The high phytoplanktonic biomass in Lake George sustained by cyanobacteria was related to its shallowness (<3 m) (Stoyneva-Gaertner et al. 2020) and led to a strong uptake of CO_2 and consequently low pCO_2 values down to 13 ppm, among the lowest values reported in literature (e.g. Sobek et al. 2005). The high phytoplanktonic biomass should also provide substantial quantities of organic matter to the sediment that should lead to intense denitrification and removal of N_2O from the water column leading to N_2O under-saturation in surface waters. The high phytoplanktonic biomass also led to CH_4 fluxes from the sediment to water column (by both diffusion and dissolution of rising bubbles) that were one order of magnitude higher in Lake George compared to Lake Edward (Morana et al. 2020).

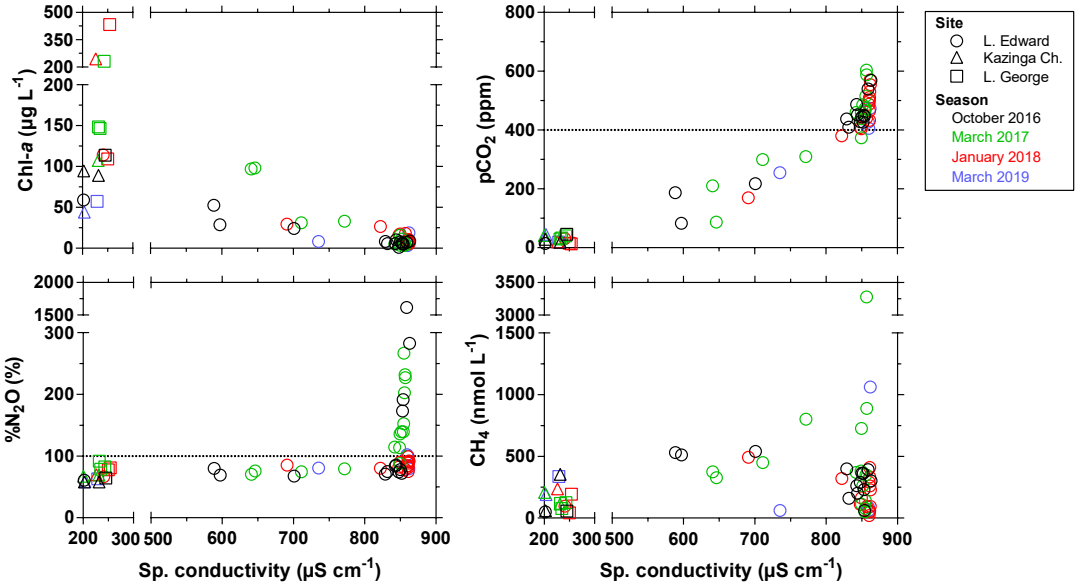

Figure 19: Variations in surface waters of Lake Edward, Kazinga Channel and Lake George of Chlorophyll-*a* (Chl-*a*, µg L^{-1}), partial pressure of CO_2 (pCO_2, ppm), N_2O saturation level (%N_2O, %), and CH_4 concentration (nmol L^{-1}) as function of specific (Sp.) conductivity (µS cm^{-1}) in October 2016, March 2017, January 2018, March 2019. Horizontal dotted line indicates the atmospheric equilibrium value.

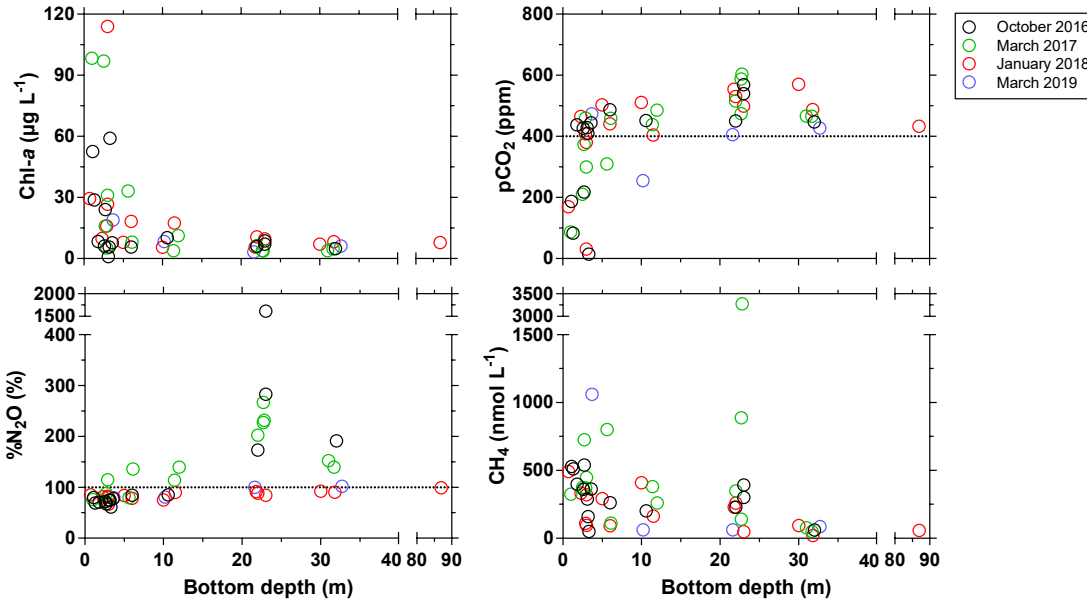

Figure 20: Variations in surface waters of Lake Edward (for specific conductivity > 800 µS cm^{-1}) of Chlorophyll-*a* (Chl-*a*, µg L^{-1}), partial pressure of CO_2 (pCO_2, ppm), N_2O saturation level (%N_2O, %), and CH_4 concentration (nmol L^{-1}) as function of bottom depth (m) in October 2016, March 2017, January 2018, March 2019. Horizontal dotted line indicates the atmospheric equilibrium value.

Surprisingly, the CH_4 concentrations in surface waters of Lake George and Kazinga Channel were of the same order of magnitude than in Lake Edward (Fig. 19). This contradiction was related to much higher CH_4 microbial oxidation measured with incubations (data not shown) in Lake George than in Lake Edward, that seemed related to the activity of methanotrophs fixed on aggregates (Borges et al. in prep.).

In Lake Edward "proper" (samples with a specific conductivity > 800 µS cm^{-1}), Chl-*a*, pCO_2, CH_4 and $\%N_2O$ varied as function of depth (Fig. 20). With higher Chl-*a* values in surface waters at shallower bottom depths resulting from higher primary production sustained by nutrient inputs from sediments (Del Giorgio and Peeters 1994). Higher primary production at shallower bottom depths led low surface water pCO_2 and concomitant organic matter delivery to sediment probably sustained high benthic diagenesis. This in turn led to low $\%N_2O$ values due to sedimentary denitrification and high CH_4 values due to sedimentary methanogenesis. Patterns with depth of surface water $\%N_2O$ and CH_4 as a function of bottom depth were to some extent obscured in some cases higher values at a bottom depth of 22 m that will discussed below.

Short-term variations

In March 2017, an extremely high value of CH_4 concentration (3277 nmol L^{-1}) was observed in surface waters of Lake Edward at 22m bottom depth (Fig. 20). Compared to other samples in surface waters collected during this cruise, the high CH_4 concentration was related to lower water temperature and $\%O_2$ and higher pCO_2 (Fig. 21). This indicated that the high CH_4 concentration was related to a mixing event. Indeed, the sampling was carried in the morning of March 30, a few hours after a night-time storm as indicated by high wind speeds and coinciding to a sudden decrease of air temperature of ~1.9°C in about 20 minutes (Fig. 22).

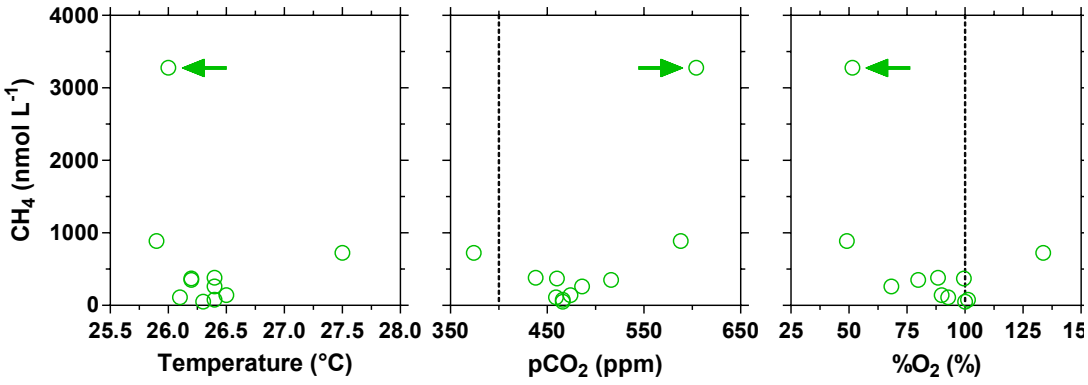

Figure 21: Variations in surface waters of Lake Edward (for specific conductivity > 800 µS cm^{-1}) of CH_4 concentration (nmol L^{-1}) as function of water temperature (°C),, partial pressure of CO_2 (pCO_2, ppm), O_2 saturation level ($\%O_2$, %) in March 2017. Vertical dotted line indicates the atmospheric equilibrium value. Arrow indicates a particularly elevated CH4 concentrations measured at a station with a bottom depth of 22 m on March 30.

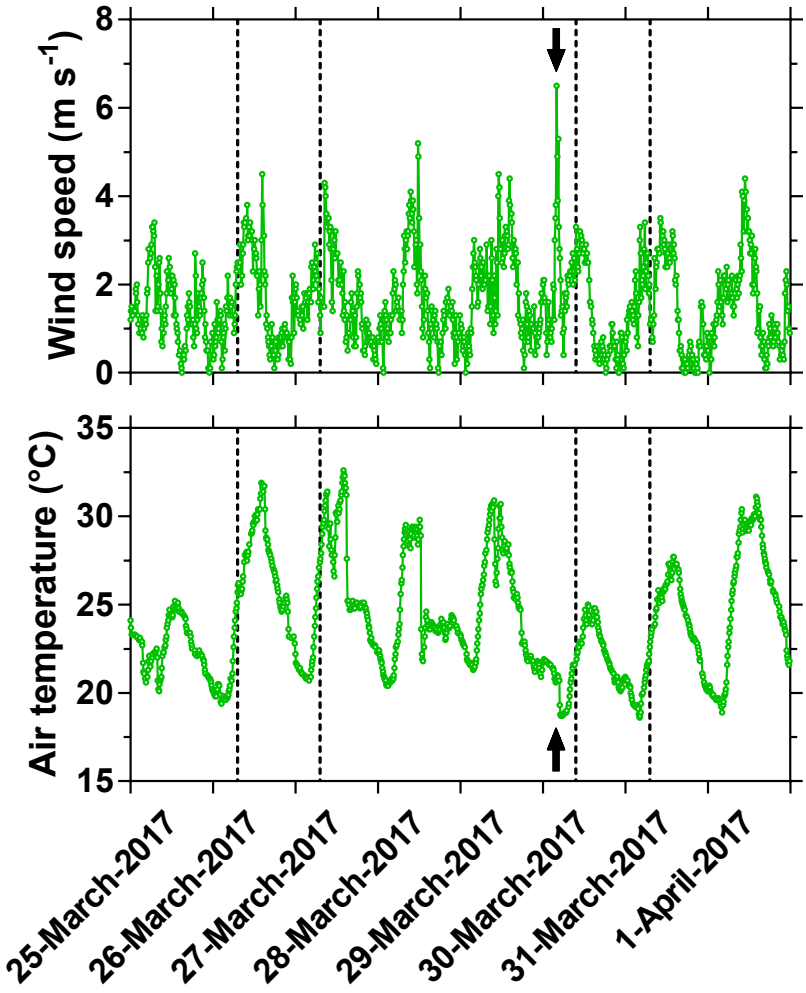

Figure 22: Wind speed (m s^{-1}) and air temperature (°C), in Mweya (-0.1904°N 29.8991°E) from March 25 to April 1 2017. Vertical dotted lines indicate the sampled profiles shown in figure 10. Arrow indicates a storm on March 30.

In October 2017, an extremely high value of $\%N_2O$ (1616 %) was observed in surface waters of Lake Edward at a station with 22 m bottom depth (Fig. 20). Compared to other samples in surface waters collected during this cruise, the high $\%N_2O$ value was related to lower water temperature and $\%O_2$ and higher pCO_2, indicating that the high $\%N_2O$ was related to a mixing event (Fig. 23). The sampling was carried on November 4, two days after a 3-day spell of very windy conditions, and the day after a severe drop of air temperature (decrease of 4.4°C of the maximum daily value compared to the day before) (Fig 24).

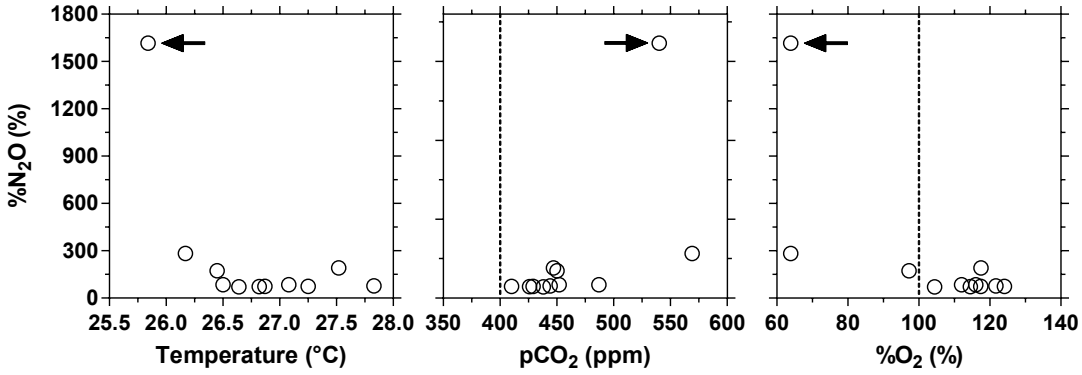

Figure 23: Variations in surface waters of Lake Edward (for specific conductivity > 800 µS cm^{-1}) of N_2O saturation level (%N_2O in%) as a function of water temperature (°C),, partial pressure of CO_2 (pCO_2, ppm), O_2 saturation level (%O_2, %) in October 2016. Vertical dotted line indicates the atmospheric equilibrium value. Arrow indicates a particularly elevated %N_2O value measured at a station with a bottom depth of 22 m on November 4.

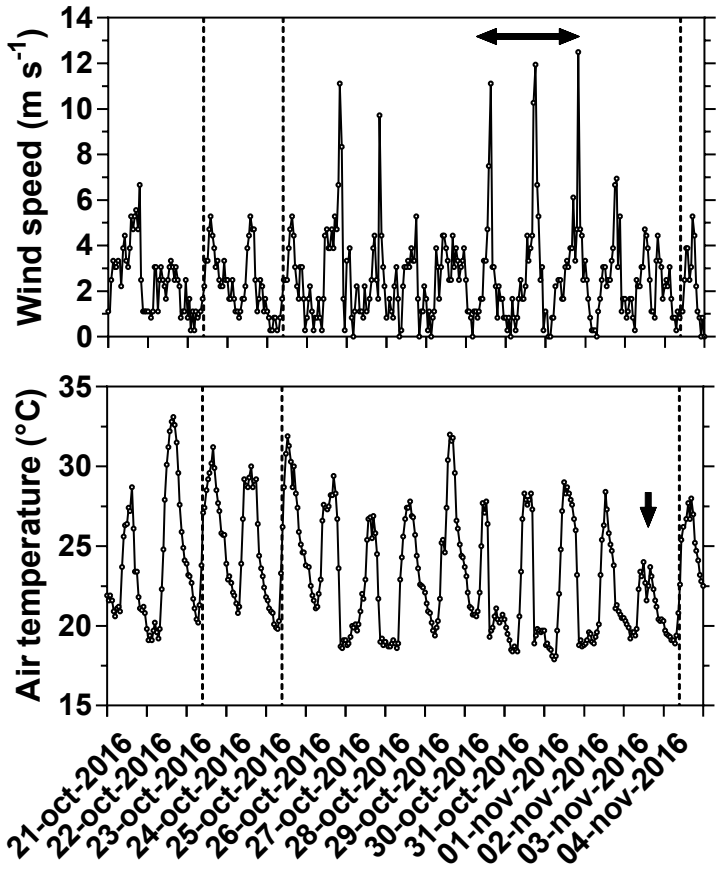

Figure 24: Wind speed (m s^{-1}) and air temperature (°C), in Mweya (-0.1904°N 29.8991°E) from October 21 to November 4 2016. Vertical dotted lines indicate the sampled profiles shown in Figure 12. Horizontal double arrow indicates 3 consecutive days of windy conditions, and vertical arrow indicates a cooling prior to sampling on November 4.

During both mixing events (March 2017 and October 2016), pCO_2 levels in surface waters increased by ~90 ppm, which corresponded to a modest increase of ≤20% from the pCO_2 levels prior to the mixing event, specially compared to CH_4 and $\%N_2O$ that both increased by an order of magnitude in response to the mixing. This is in consistent with the fact that at 20 m, the increase of pCO_2 between surface and bottom waters was also modest (~100 ppm) compared to $\%N_2O$ and CH_4 (Fig. 17).

It is notable that this short-term changes surface water N_2O and CH_4 content related to storm induced mixing were observed on both occasions at stations sampled at 22 m. This corresponds to the depth of the seasonal thermocline (Fig. 17), meaning that locations shallower than 22 m were mostly permanently vertically mixed and locations deeper than 22 m probably remained partly stratified and did not fully mix to the bottom, after a short-term mixing event during the rainy season.

Seasonal variations

From January 2017 to December 2019, a shallow station (3 m bottom depth) and a deeper station (22 m bottom bepth) were regularly sampled, every 15 d in 2017 and 2018, and every 30 d in 2019. At the deeper station, irregular changes between stratified and mixed conditions (indicated by the SSI) were observed without a clear seasonally (Fig. 25), possibly related to the fact that the depth of the seasonal thermocline was located at around 22 m, as mentioned above, so small changes in weather conditions allowed the establishment or on the contrary the erosion of stratification at 22 m bottom depth. Two periods of marked and relatively sustained mixed conditions were observed in January-April 2018 and August-September 2018 (Fig. 25). During these two periods, water temperature, $\%O_2$, CH_4 and $\%N_2O$ were relatively homogeneous vertically. During the other sampled periods, moderate to strong vertical gradients were observed in all sampled variables. Maximum bottom water CH_4 values were 14,994 and 23,760 nmol L^{-1} in June 2017 and May 2018, respectively, and corresponded to fully anoxic conditions (Fig. 25). The maximum $\%N_2O$ values were also observed on these two occasions with a value of 833% located at the oxycline in June 2017 at 15 m, while the anoxic bottom waters were characterized by lower $\%N_2O$ (32%). In May 2018, a value of 1,032% in $\%N_2O$ was observed at 20 m depth in the anoxic layer.

Figure 26 shows the variations of pCO_2, CH_4, and $\%N_2O$ in surface waters at the shallow and deeper stations. CH_4 in surface waters was distinctly higher at the shallow station (720±424 nmol L^{-1}) than at the deeper station (121±151 nmol L^{-1}), while the opposite pattern was observed for $\%N_2O$ (90±19% versus 133±40%). Differences in pCO_2 between the two stations were less marked, yet the average value was lower at the shallower station (466±126 ppm) where values below atmospheric equilibrium were observed on 12 occasions than in the deeper station (540±103 ppm) where values below atmospheric equilibrium were only observed on one occasion. The variations between samplings of pCO_2 were related to phytoplankton biomass, as shown by the negative relation between pCO_2 and Chl-*a* and POC (Fig. 27), consistent with the uptake of CO_2 by photosynthesis. The average Chl-*a* was distinctly higher at the shallower station (17±8 µg L^{-1}) than at the deeper station (8±3 µg L^{-1}). Overall, these differences among the two stations of pCO_2, CH_4 and $\%N_2O$ were consistent with the patterns as a function of depth derived from the spatial surveys (Figs. 20).

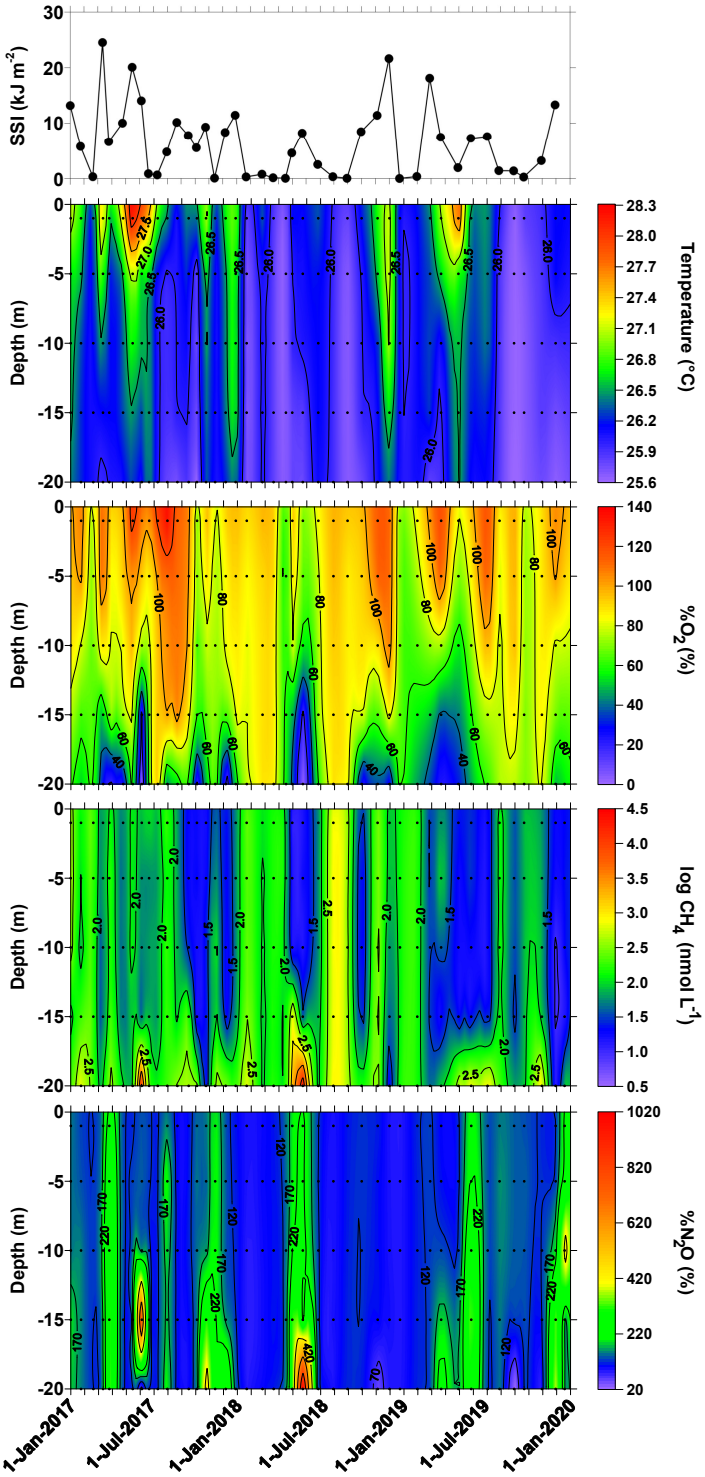

Figure 25: Schmidt stability index (SSI, kJ m^{-2}) calculated from 5 to 20 m (excluding top 5m to avoid accounting for diurnal stratification), and vertical profiles of water temperature (°C), O_2 saturation level (%O_2, %), log of CH_4 concentration (nmol L^{-1}), N_2O saturation level (%N_2O, %) from January 2017 to December 2019 in Lake Edward at a station with bottom depth of 22m.

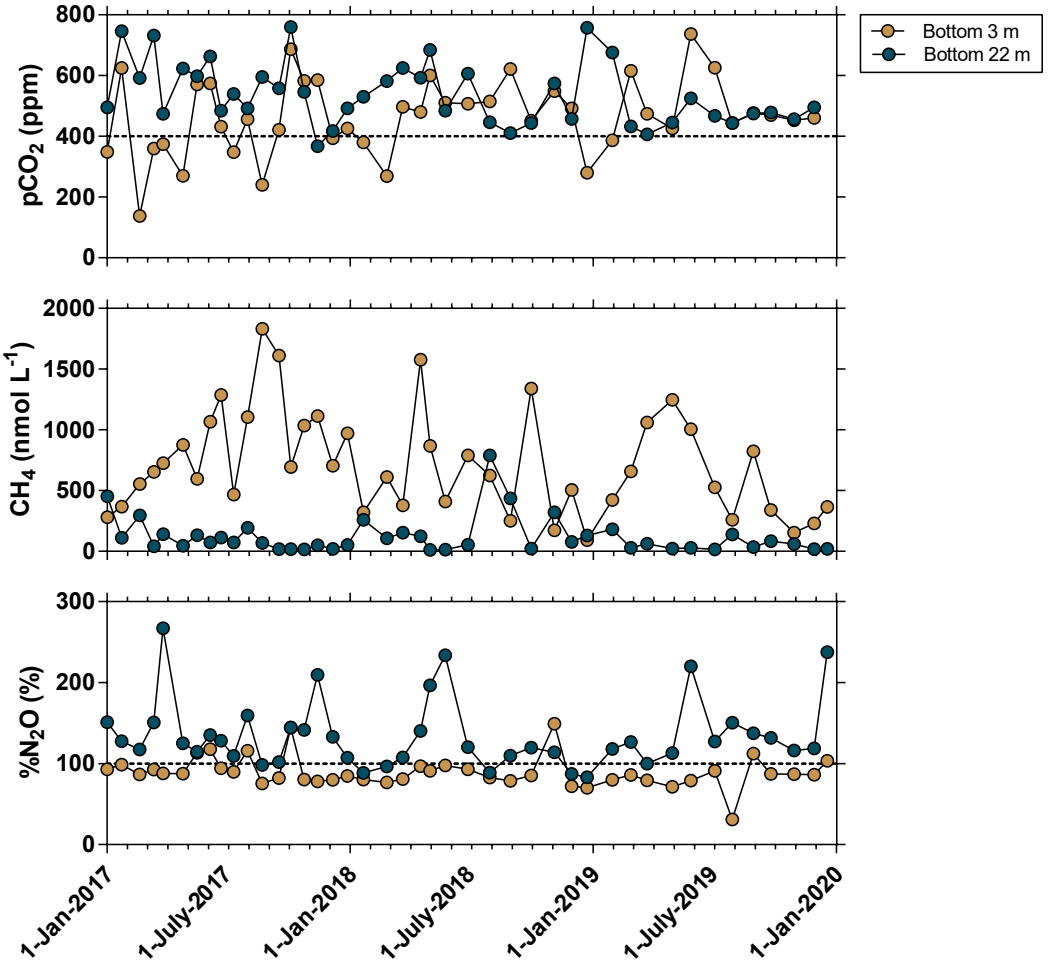

Figure 26: Variations in surface waters of Lake Edward of the partial pressure of CO_2 (pCO_2, ppm), CH_4 concentration (nmol L^{-1}), N_2O saturation level (%N_2O, %) from January 2017 to December 2019. two stations with bottom depth of 3m and 22m.

Yet, CH_4 concentration at the shallower station did not correlate with Chl-*a* and in fact negatively correlated to POC (Fig. 27). This could be in part related to the fact that the samplings at the most littoral station with a high Chl-*a* might have been partly influenced by water from the Kazinga Channel, which also had a lower CH_4 content (Fig. 19). Given the strong contribution of the cyanobacteria to total phytoplankton biomass in Lake Edward (Stoyneva-Gaertner et al. 2020) that are producers of CH_4 according to Bižić et al. (2020), the lack of correlation between CH_4 and Chl-*a* indirectly confirms that CH_4 production in aerobic conditions is a very marginal flux compared to other input fluxes of CH_4 from the sediments (Morana et al. 2020).

The variations among samplings at the deeper station of %N_2O in surface waters and the water column average of %N_2O correlated negatively with %O_2 in the bottom layer (20m) (Fig. 28). The %O_2 in the bottom layer was in turn correlated to the SSI (not shown). This indicates that the lowering of O_2 content in bottom waters related to stratification promotes the production of N_2O.

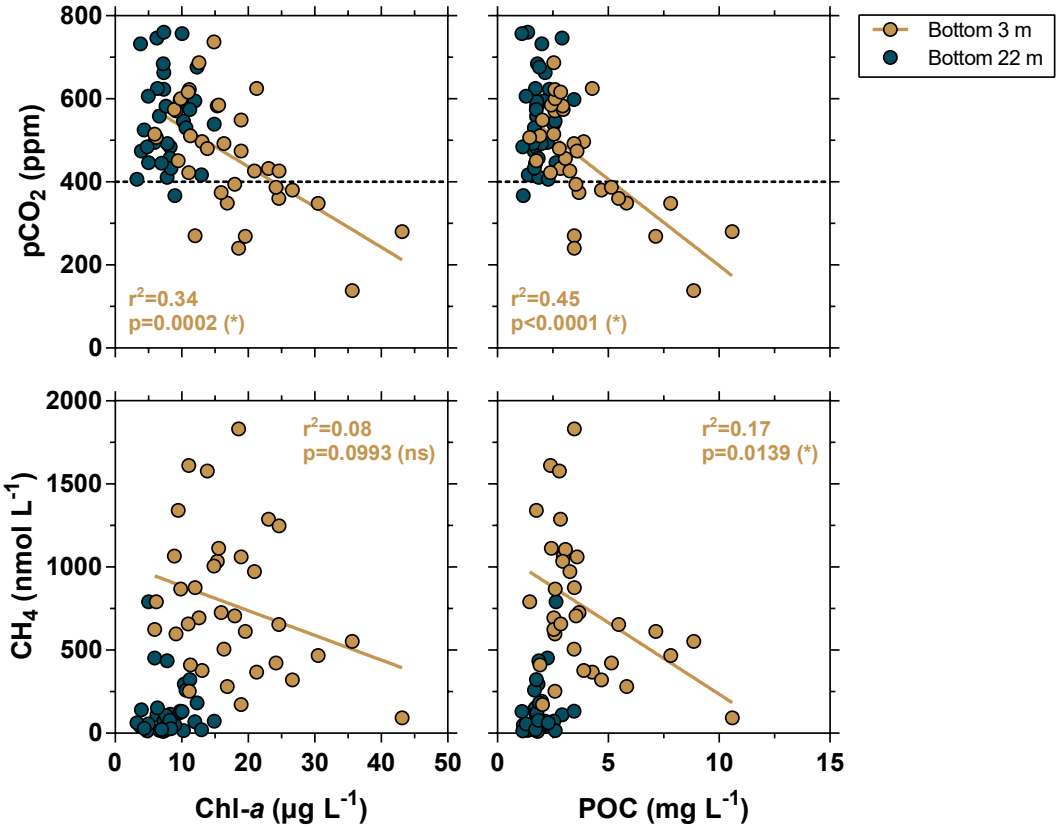

Figure 27: Partial pressure of CO_2 (pCO_2, ppm) and CH_4 concentration (nmol L^{-1}) versus Chlorophyll-a (Chl-*a*, µg L^{-1}) and particulate organic carbon (POC, mg L^{-1}), N_2O saturation level ($\%N_2O$, %) in surface waters of Lake Edward, from January 2017 to December 2019, at two stations with bottom depth of 3m and 22m.

A remarkable HIPE result was the observation of short-term extreme mixing events related to storms that led to the increase of CO_2, CH_4 and N_2O content in surface waters that was particularly marked on some occasion for CH_4 and N_2O but more modest than for CO_2, as vertical gradients of CH_4 and N_2O (on some occasions) were much more intense than for CO_2. This indicates that CH_4 and N_2O emissions to the atmosphere from tropical lakes can have hot moments that could be very frequent, as vertical thermal gradients are usually were weak, and stratification can frequently be eroded by storm events. **We recommend further investigation and quantification of these hot moments that will require a mooring based approach rather than a punctual survey approach as used in the present study in the present study.**

Another remarkable HIPE result is that average pCO2 levels in both Lake George (30 ppm) and Edward (449 ppm) were lower than values previously attributed in literature to tropical lakes in general of 1800-1900 ppm (Marotta et al. 2009; Audenkampe et al. 2011; Raymond et al. 2013) and for tropical African lakes specifically of 2300 ppm (Cole et al. 1994). This discrepancy is probably related to an over-representation in literature of studies of South

American floodplain lakes and/or of small water bodies, as well as possible methodological over-estimation of pCO2 values in older studies. **We recommend a large scale sampling effort to better characterize CO_2, CH_4 and N_2O across the full range of tropical lakes in terms of climate, watershed characteristics, and morphology (size and depth). This should allow to derive statistical models that could help to more accurately evaluate the emissions of greenhouse gas (GHG) emissions (instead of using literature data mainly from South America) that should be included in the national inventory report (NIR) of GHG emissions required annually from nations by the United Nations Framework Convention on Climate Change (UNFCCC).**

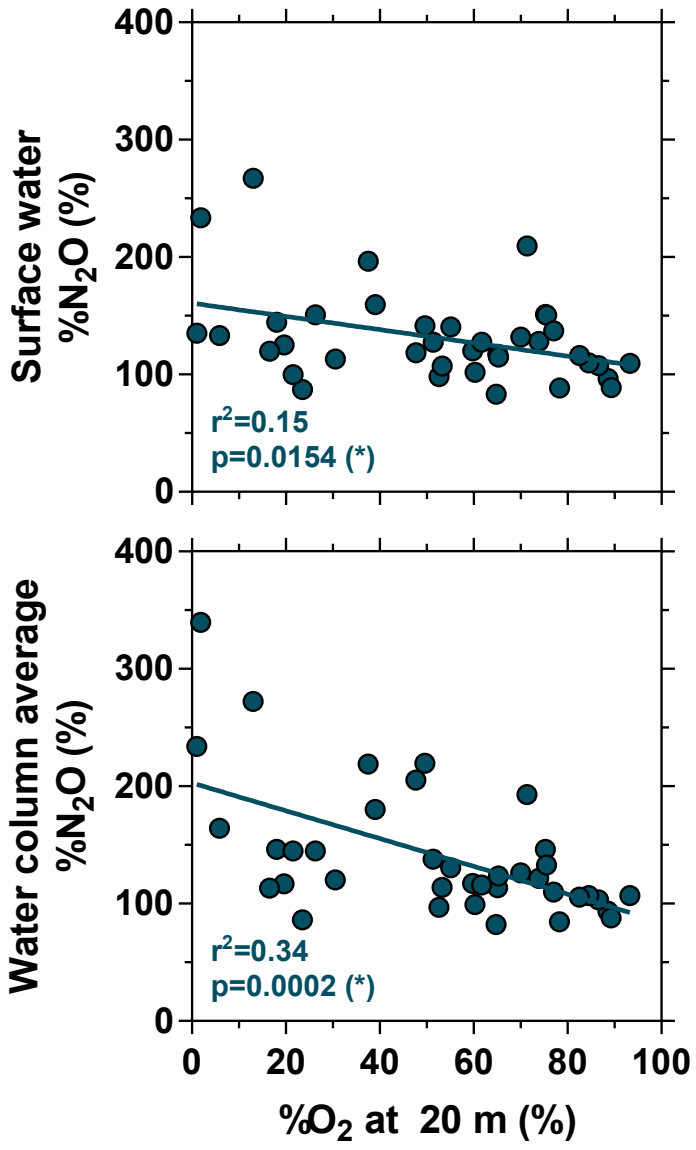

Figure 28: N_2O saturation level (%N_2O, %) in surface waters and the water column average versus the O_2 saturation level (%O_2, %) in bottom waters (sampled at 20 m depth) in Lake Edward, at a station with bottom depth of 22m, from January 2017 to December 2019.

4.2.2 Phytoplankton diversity and primary production

Limnological characteristics

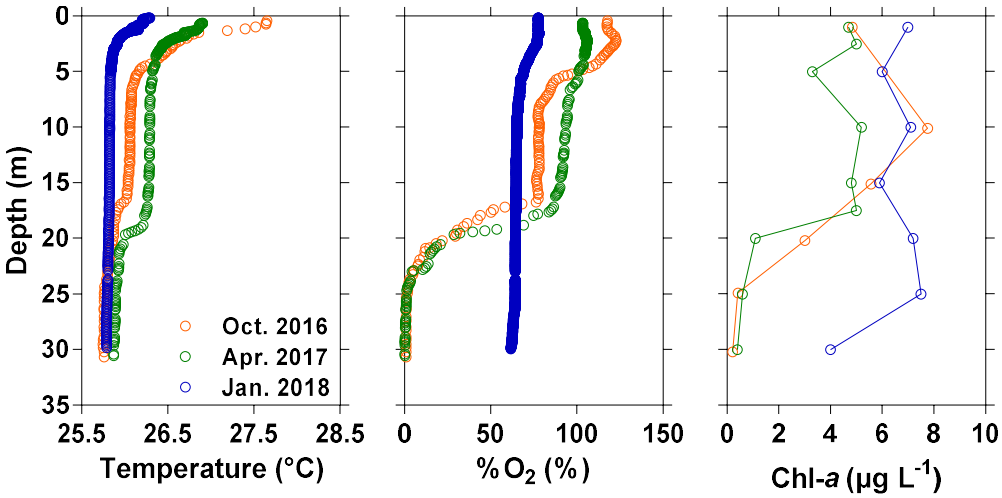

Figure 29: Depth profile of temperature, dissolved O_2, and chlorophyll a concentration in a pelagic station (C30) in L. Edward.

Here we summarize results of the phytoplankton study from Lake Edward, with a focus on the pelagic zone: further detail can be found in Stoyneva et al. (2020). Representative limnological profiles of the pelagic zone of Lake Edward (at site C30, see Fig. 5) are presented in Figure 29, which essentially shows the difference in mixed layer depth (MLD) between the rainy and dry seasons. Temperature (range was 25.5-27.8°C) and DO profiles indicated a weak thermal gradient between 15 m and 20 m depth in rainy season conditions, and the absence of gradient in dry season conditions. Accordingly, DO, conductivity, soluble substances and biomass were distributed in a mixed layer of maximum 18 m in the rainy season and of 55 m in the dry season (not shown). The depth of the euphotic layer, Zeu, did not vary significantly depending on seasons (Fig. 30, Zeu was 6.2±1.7 m and 5.8±2.2 m in the rainy and dry seasons, respectively). The exposure of the phytoplankton to light in the water column differed greatly between sites but did not between seasons: considering the mean surface irradiance during the 3 sampling series (736 – 832 µE m^{-2} s^{-1}, data not shown), the mean irradiance in the water column was 60-68 µE m^{-2} s^{-1} in the pelagic sites. In the deepest site (90 m) sampled in the dry season, the exposure of phytoplankton to light in the mixed layer was ~20 µE m^{-2} s^{-1}, with a Zm:Zeu ratio of 8.4.

Phytoplankton diversity

Based on biomass estimates from the marker pigments, phytoplankton was dominated in the whole lake by two classes (Fig. 31), cyanobacteria and diatoms. Cyanobacteria were most abundant in Katwe Bay, with 90% of Chla, and also dominated in the littoral and pelagic sites (~60 % of Chla on average). Cyanobacteria T1 were always more abundant than cyanobacteria T2 (Fig. 31). Diatoms were represented in similar proportion in the pelagic (27.7

% of Chla on average) and the littoral sites (24.7 % of Chla), and less abundant in the Katwe Bay (7.7 % of Chla on average).

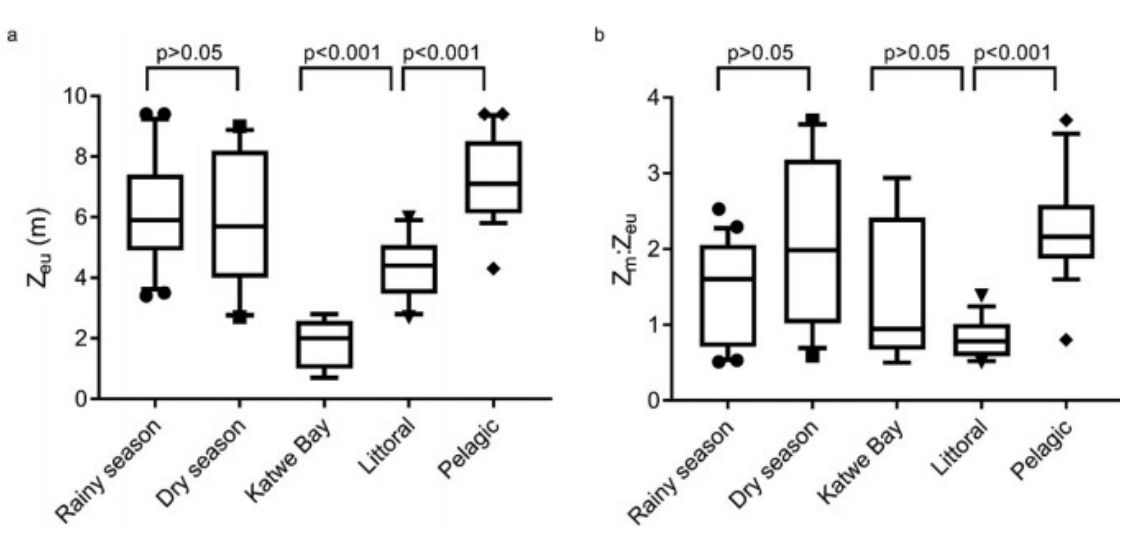

Figure 30: Photic zone depth (a) and its ratio with the mixed layer (b) in L. Edward.

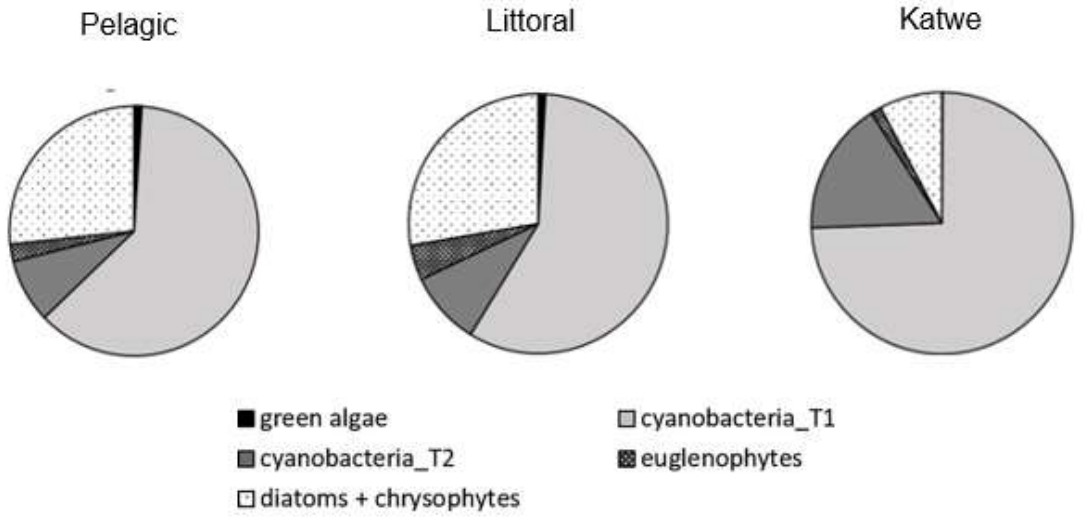

Figure 31: Mean relative abundance of phytoplankton classes in Lake Edward, expressed as percentage contribution to chlorophyll a concentration.

In the different sampling sites, green algae were the least abundant group, followed by cryptophytes and euglenophytes. Microscopical examinations of the lake phytoplankton confirmed the dominance of cyanobacteria and diatoms in Lake Edward, and recorded a total of 248 species, varieties and forms from 6 divisions. The heterocytous species from the filamentous genera *Raphidiopsis* and *Anabaenopsis* were abundant, in combination with small coccoid colonial algae from the genera *Microcystis*, *Merismopedia*, *Aphanocapsa*, *Aphanothece* and *Anathece*. For diatoms, the most important were species of the genus *Nitzschia*, the most abundant being the needle-like *N. spiculum* and *N. bacata*, although *N.* cf.

lacuum (= N. *fonticola* sensu Hustedt 1949) and *N. tropica* could occur in large numbers in some samples. Centric diatoms were represented by *Cyclostephanos damasii* and *Stephanodiscus* cf. *minutulus*; they occurred in a relatively high number of samples, but they were much less abundant than the needle-like *Nitzschia*. Lake George and presumably the Kazinga Channel had a different species composition from that of Lake Edward: both water bodies were dominated by *Microcystis*, with high proportion of small coccal (*Gloeothece*, *Chroococcus*) and tiny filamentous non-heterocytous cyanoprokaryotes (*Planktolyngbya*) with very low contribution of heterocytous genera like *Raphidiopsis* and *Anabaenopsis*. Despite the connection through Kazinga Channel, the floristic similarity between lakes George and Edward was very low (only 11%). Whatever the water column conditions (stratified in HIPE I and II; deep mixing in HIPE III), phytoplankton were exposed to low light level due to the relatively shallow photic zone in comparison with the mixed layer depth. This may explain the low biomass of the mostly photophilic green algae, and the success of the shade-adapted cyanobacteria and diatoms.

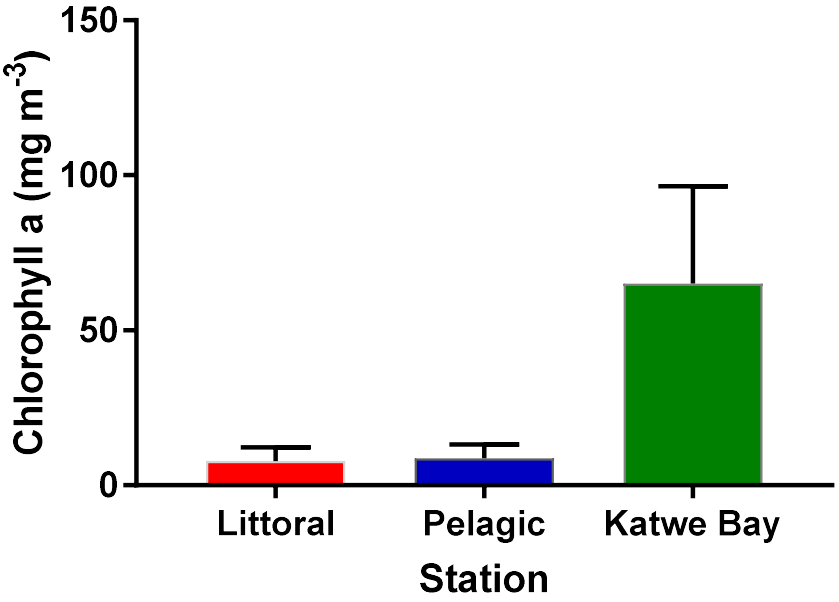

Figure.32: Chlorophyll a concentration in different sites of L. Edward : littoral (< 5m), pelagic and Katwe Bay

Phytoplankton biomass

The median chlorophyll a concentration measured during the HIPE sampling campaign was 7.4 µg L^{-1}. Chlorophyll a concentration variability was larger in the littoral zone (> 5m) and was higher in the Katwe Bay and at proximity of the Kazinga channel (Fig. 32), TSM, POC and chlorophyll a concentrations were all positively related (Fig. 33). POC contributed to a high fraction of TSM (mean 36 ± 11%), revealing that the seston was predominantly composed of organic material. This value did not differ significantly between littoral and pelagic zone. We found that the underwater light attenuation (k, m^{-1}), and therefore the depth of the photic zone, was linearly related to chlorophyll a concentration (Fig. 34). However this relationship was

mostly driven by higher chlorophyll a concentration in some littoral sites located close to the Kazinga channel. There was no relationship between chlorophyll a concentration and water transparency when considering pelagic sites alone. The contrasting patterns could highlight the importance of self-shading effect in limiting light intensities in the water column in littoral sites located closer to the Kazinga, characterized by high chlorophyll a concentration. In other littoral sites with moderate chlorophyll a concentration, sediment resuspension or lateral inputs of suspended particles could have played a larger role in determining water transparency.

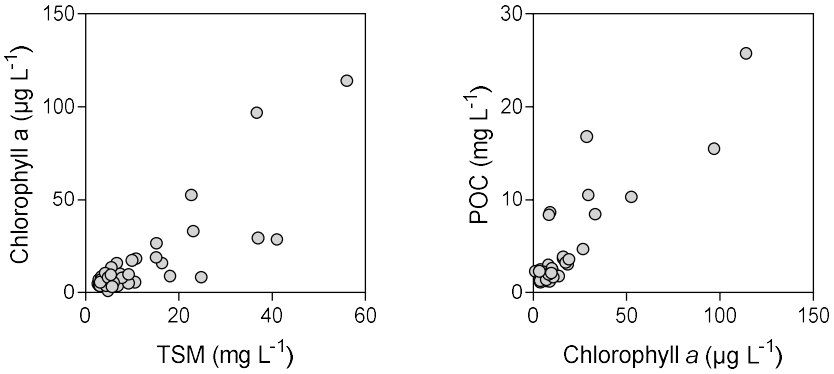

Figure 33: Relationship between TSM and chlorophyll a and between chlorophyll a and POC.

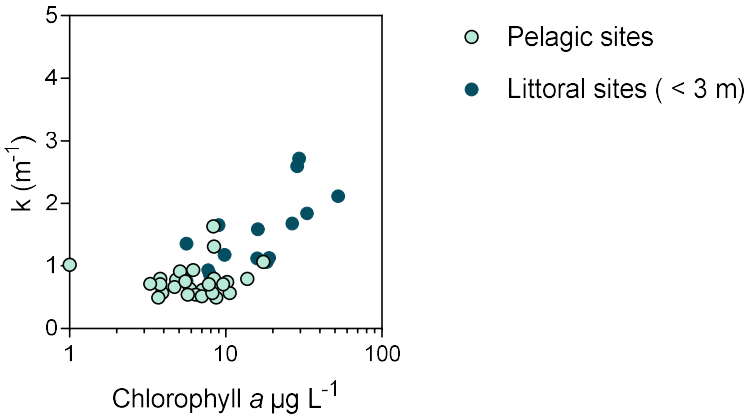

Figure 34: Relationship between chlorophyll a and water transparency in pelagic and littoral sites (including Katwe Bay)

Stable isotope composition of the particulate organic matter averaged -24.1 ‰ in the epilimnion. It varied in function of chlorophyll a concentration, being sometimes substantially higher in littoral zone, where phytoplankton biomass was also higher (Fig. 35). This isotopic enrichment of the particulate organic matter pool is linked to higher photosynthetic activity under CO_2 undersaturation conditions. Indeed, as CO_2 availability decrease in consequence of high C uptake by photosynthesis, isotopic fractionation during photosynthesis tend to decrease, as illustrated by Figure 35.

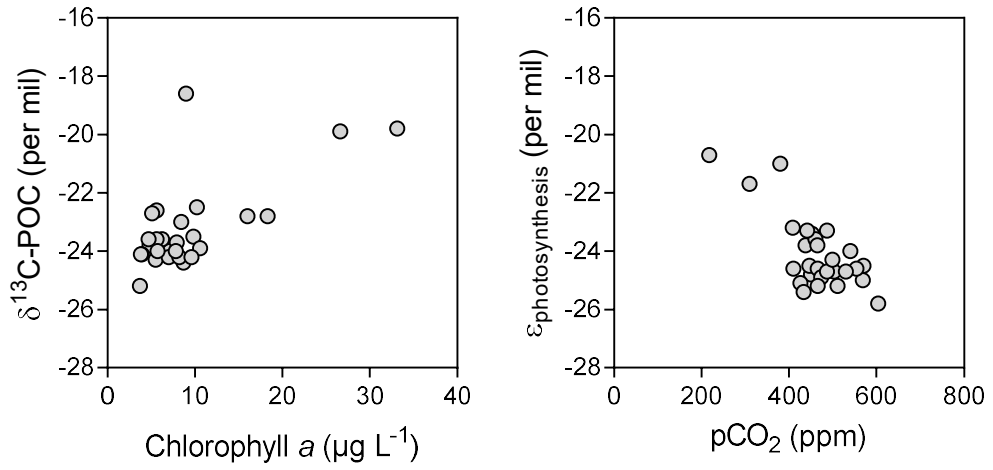

Figure 35: Relationship between chlorophyll a concentration and the stable C isotope composition of particulate organic carbon and between the partial pressure in CO_2 in surface waters and the apparent fractionation coefficient between dissolved inorganic carbon and particulate organic carbon pools.

Primary production

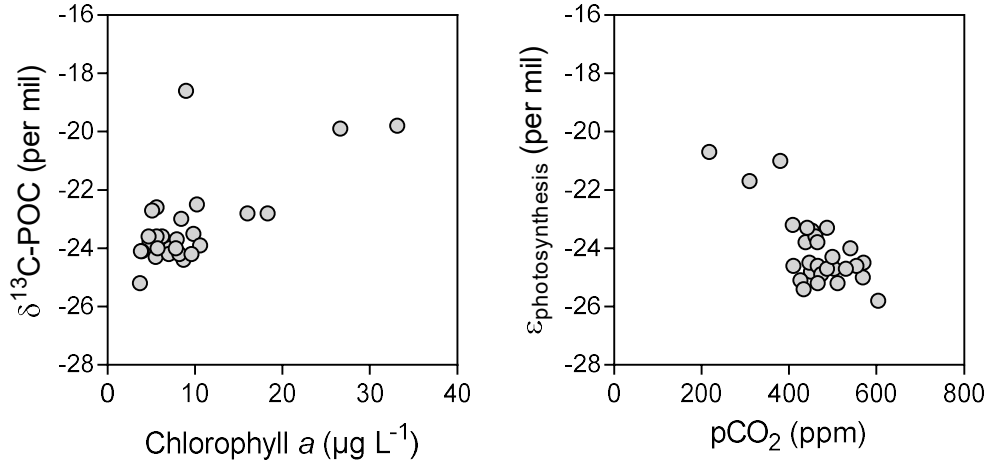

Figure 36: Relationship between chlorophyll a concentration and maximum photosynthetic capacity of phytoplankton in L. Edward.

Primary production in the littoral zone was significantly higher in the northern part (near Katwe) than in the rest of the lake, due to the influence of the Kazinga channel inflow. The water column primary production measured during three sampling campaign (133 ± 71 mmol C m^{-2} d^{-1}, n = 28 observations) was approximately 4 times lower than the single historical value of primary production available for L. Edward (431 mmol O_2 m^{-2} d^{-1} measured in June 1960 at a 5m-depth station, reported by Talling (1965)). The light-saturated (maximum) rate of photosynthesis parameter (P*max*) was also significantly higher in June 1960 (P*max* = 22 µmol C l^{-1} h^{-1}) than during HIPE sampling campaign ((P*max* = 6 ± 4 µmol C l^{-1} h^{-1}) but note the observations of significantly higher value near-shore (< 5m depth) in Katwe Bay, with values as high as 17 µmol C l^{-1} h^{-1}. By contrast, the phytoplankton primary production of L. George

(2016 & 2017) 648 ± 133 mmol C m^{-2} d^{-1} (n=2) was comparable with the value reported for the 1960's (489 ± 2 mmol O_2 m^{-2} d^{-1} and 375 mmol C m^{-2} d^{-1}; Talling 1965; Ganf & Horne 1975). Overall, we observed a positive relationship between the chlorophyll a concentration and the P*max* parameter (Fig. 36). The specific maximum photosynthesis rate (P*max* normalized with chlorophyll a concentration) was fairly constant across our L. Edward dataset (0.68 ± 0.28 µmol µg $Chla^{-1}$ h^{-1}, or 8.1 ± 3.3 mgC $mgChla^{-1}$ h^{-1}). The L. Edward values were much slightly higher than in the oligotrophic L. Kivu, L. Tanganyika and L. Malawi (< 5 mgC $mgChla^{-1}$ h^{-1}, Guilford et al. 2007, Sténuite et al, 2007, Darchambeau et al. 2014) but closer to values reported for the L. Victoria at equivalent chlorophyll a concentration (~ 8.25 mgC $mgChla^{-1}$ h^{-1}, Silsbe et al. 2006). Several environmental factors such as temperature and nutrient availability, and also the composition of the phytoplankton assemblage (Darchambeau et al, 2014), are to known to directly affect the specific maximum photosynthesis rate, and could explain its variability across lake of different trophic status. Mean value for the Ik parameter (irradiance at onset of saturation) was 222 µmol photon m^{-2} s^{-1}, which is much higher than the mean irradiance in the mixed layer depth, highlighting the importance of the light limitation of phytoplankton.

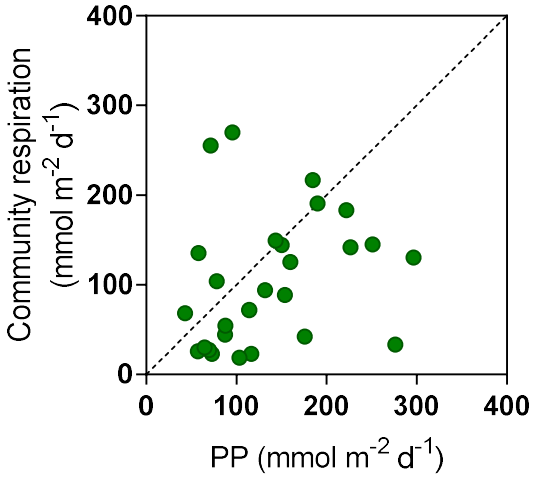

Figure 37: Comparison between depth integrated primary production rates (PP) and community respiration rates. Dashed line is the 1:1 line. Symbols higher than the line indicate an excess of respiration, symbols below indicate a predominance an excess of primary production. Predominance of symbols below the line highlight the overall net autotrophic status of L. Edward.

Comparison of the depth-integrated PP rates with depth integrated community respiration rates show that primary production exceeds respiration in > 80% of the observations (Fig. 37). Note that community respiration was estimated by extrapolating measurements in surface waters to the entire water column, they are then likely over-estimated, respiration being usually higher in surface waters were the availability of labile dissolved organic molecules released by phytoplankton is higher.

We deploy an oxygen sensor at a littoral station (2.5m depth max depth, sensor at 1m depth) in order to investigate the importance of benthic primary production (Fig. 38). We found that the total (net) primary production estimated from the net dissolved O_2 production we measured (6.4 µmol L^{-1} h^{-1}, 215 µmol m^{-2} d^{-1}) was comparable with the water column

phytoplankton primary production measured in parallel using ^{13}C labelling approach as described above. This observation imply that benthic primary production would play only a minor role in the overall C budget of the lake, more than likely because the higher phytoplankton biomass that is typically observed near-shore reduce significantly the light penetration in the water, limiting then the amount of light illuminating the bottom of the lake (photic zone always shallower than bottom water column depth).

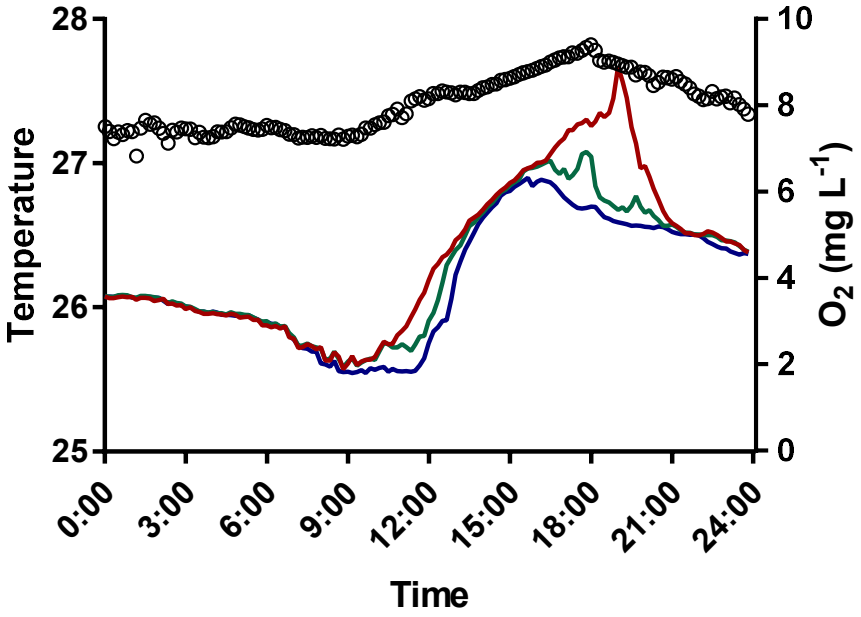

Figure 38: Evolution of the temperature at 0.3 (red), 1.3 (green) and 2.3 m (blue) (littoral station, 2.5 m bottom depth) and of the dissolved O_2 concentration (empty circle) during 1 day (local time).

A key ecological factor affecting phytoplankton biomass and community composition in L. Edward may be N supply, as indicated by the relatively high C:N molar (10.3±1.9: values in this range indicate moderate N-limitation (Guildford & Hecky, 2000). To investigate further phytoplankton nutrient limitation in L. Edward, nutrient limitation assays were conducted during the HIPE sampling campaign with addition of phosphorus and nitrogen, alone and in combination. We observed a doubling of photosynthetic C uptake when N was added, providing evidence of significant N limitation (Fig. 39). By contrast, phosphorus addition alone did not stimulate photosynthetic activity, suggesting that phytoplankton were primarily limited by N availability and overall low light conditions.

N_2 fixation

N_2 fixation was measured in parallel with the measurement of phytoplankton primary production in several occasion in L. Edward and L. George. Substantial rates of light-driven N_2 fixation were detected. In addition, a time-course experiment (6h) was carried out to

investigate the occurrence of dark N_2 fixation. It showed that significant amount of N_2 were never incorporated in the dark during the 6h long incubation, suggesting that N_2 fixation was exclusively a light-driven process in the L. Edward and L. George. The biological reduction of N_2 is catalyzed by nitrogenase, an enzyme complex abundant in cyanobacteria but absent in eukaryotic cells, which is irreversibly inhibited by molecular oxygen. Cyanobacteria should hence separate (1) temporally or (2) spatially photosynthesis and N_2 fixation to avoid that the O_2 produced during photosynthesis inhibits the N_2 fixation process. The absence of N_2 fixation in the dark suggest that the second strategy was used by cyanobacteria, in good agreement with the observation of heterocyst cells in the lake. N_2 fixation is an energy consuming process, with around 30 mol of ATP consume per mol of N reduced. Coexistence of photosynthesis with N_2 fixation in separate cells allows then photosynthesis to directly provide the energy required for N_2 fixation if the heterocyst cells of the colony. Nutrient limitation experiments revealed that primary production was nitrogen limited, hence N_2 fixation could represent an important N source at the scale of the ecosystem.

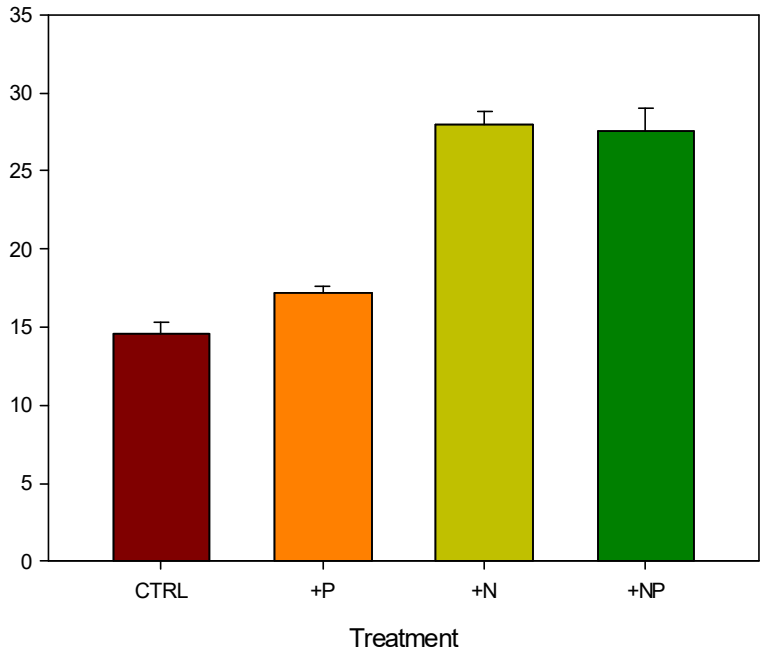

Figure 39: Photosynthetic C fixation rates measured during a nutrient limitation experiment (24h incubation under constant light irradiance) carried out with samples from a pelagic station in L. Edward (20 m max depth). Bottles were incubated without any amendment (CTRL treatment), or amended with an excess amount of NO_3^- (+N treatment), PO_4^{3-} (+P treatment), or both NO_3^- and PO_4^{3-} (+NP treatment). Error bars are the standard deviation calculated on triplicates.

The concentration of NO_3^- and NH_4^+ was measured in the major rivers flowing into L. Edward. Mean annual river discharge were extracted from the RiverAtlas database (Hydroshed) in order to estimate the N inputs from the rivers. If summed and integrated over the water column, N_2 fixation in L. Edward (0.7 mmol m^{-2} d^{-1}, n = 22 observations) would be one order of magnitude higher than the N inputs from the rivers (~0.04 mmol m^{-2} d^{-1}). Despite its potential importance in the N budget of the L. Edward, N_2 fixation would be sufficient to supply only ~10% of the phytoplankton N demand (8 ± 4 mmol N m^{-2} d^{-1}), estimated based on

the mean phytoplankton primary production measured during the project and a C:N ratio of 16. These rather low values suggest that N is effectively recycled in the system and the N cycle is mostly driven by internal sources, as frequently hypothesized in African lakes (Kilham & Kilham 1991).

Seasonal and interannual variability

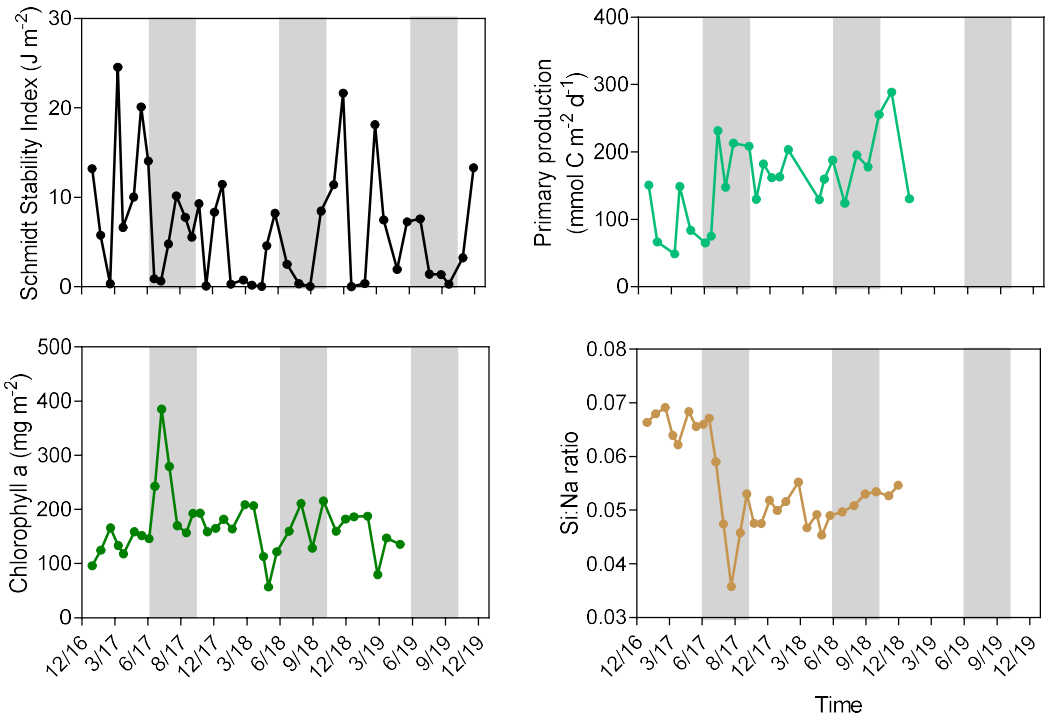

Figure 40: Temporal variation of the Schmidt stability index and several variables related to the phytoplankton dynamic (water column chlorophyll a concentration, primary production rates, Si:Na ratio)

The monitoring data set offers the opportunity to look at temporal variations (Fig. 40) in the pelagic zone of the lake, in 2017 and 2018. mean chlorophyll a concentration in the euphotic zone was 8.1±3.0 µg L^{-1} (168 mg Chla m^{-2}), and cyanobacteria T1 dominated with largest contribution to chlorophyll a (74.2±10.5 %); diatoms were second, with 19.3±9.8 % of chlorophyll a. In 2017, a distinct peak of chlorophyll a concentration (up to 18.5 µg L^{-1} on average over the 0-20 m water column) occurred in the dry season (July to September), corresponding to a depth integrated chlorophyll a concentration of 385 mg Chla m^{-2}. We observed a sharp increase of both diatoms and cyanobacteria biomass, whereas chlorophyll a was < 10 µg L^{-1} before and after this dry season peak. On average, in terms of phytoplankton biomass and composition, the peak corresponded to a consistent deep-water column mixing related to a weakening of the temperature gradient following a stratification period in May-June. By contrast, no such clear alternation between stratification and mixing occurred in 2018, as shown by variations of the Schmidt's Stability index (Fig. 40), and no clear increase

of phytoplankton abundance occurred that year (Fig 40). Primary production measurements does not follow any clear patterns as well, being slightly lower during the end of the rainy season 2017, but oscillating around 180 mmol C m^{-2} d^{-1} after. We hypothesized this to result from the frequent mixing of the water column, often down to the maximum 21 m depth: with a euphotic depth only a fraction of this total depth, phytoplankton spent most of the time in the dark. This points to the strong light limitation experienced by the lake phytoplankton. It is also evidenced by the relatively low Ik (onset of light saturation, mean ~222 µE m^{-2} s^{-1}) which was most of the time higher than I_{zm}, the mean light in the mixed layer (mean ~140 µE m^{-2} s^{-1} at noon).

The increase of diatoms biomass during the dry season 2017 is also reflected in the Si:Na ratio, which show a pronounced decrease during the phytoplankton bloom. Interestingly, the Si:Na ratio did not recover to pre-bloom values during the following rainy season, which was characterized by frequent mixing even (low SSI values throughout the season). Dissolved Si concentration were never lower than 120 µmol L^{-1} (i.e. far from limiting concentration), but the deeper water column mixing conditions during the dry season 2017 and the following rainy season could have been more favorable to diatoms growth, explaining the lower Si:Na ratio throughout the year (Fig. 40).

Major conclusions

- No clear seasonal patterns in terms of phytoplankton dynamics. This is probably related to the overall weak stratification of the water column that allow episodical mixing event to occur. Note also that with a mean depth 35m, L. Edward is relatively shallow in comparison with others East African Great Lakes.

- Higher phytoplankton abundance as reflected by the higher chlorophyll a concentration in Katwe Bay than in the rest of the lake. However, depth integrated primary production rates appeared only slightly higher than in the rest of the lake due to the lower water transparency of Katwe Bay (self-shading effect).

- Photic zone is always shallow in comparison with the mixed layer depth and the irradiance at the onset of saturation is 2-3 times higher than the mean irradiance of the mixed layer, suggesting that phytoplankton is constantly light limited in L. Edward. Secondly, the results of nutrient limitation assay experiments and C:N ratio of the seston indicate that N limitation occur at all times (little seasonal variation). Together with the reduced light availability in the water column they may be drivers explaining the success of cyanobacteria over diatoms and other phytoplankton groups.

- Results suggest that primary production is ~ 4X lower than during the 1960's. This result should however be taken with great caution given the paucity of historical data (only 1 measurement in 1961).

- N_2 fixation is an important process at the scale of the ecosystem, being 1 order of magnitude higher than the N inputs by rivers.

4.3 FISH BIODIVERSITY, BIOLOGY AND ECOLOGY

Fish species diversity

Figure 41: Overview of all 30 non-Haplochromis species and 50 Haplochromis species (including some species to be described) from the Lake Edward system that were all collected during the HIPE expeditions. Of these, 32 species (3 non-Haplochromis and 29 Haplochromis) were not known to inhabit the system prior to the HIPE project

The fish fauna of the Lake Edward/George system has not been reviewed since the book on the fishes of Uganda by Greenwood (1966). We reviewed all available information in the literature, verified the RMCA, RBINS and NHM-UK collections, and those of the three recent expeditions (2016-2018), which is a time-consuming exercise requiring a lot of effort, certainly for such a poorly known system as the Lake Edward system. Based on all this information, we finalized an annotated species list of 34 non-*Haplochromis* species belonging to 10 families and 21 genera (Decru et al., 2020). Three of these are endemic to the system, *Amphilius* sp. 'Bwindii' (undescribed species), *Labeobarbus ruwenzorii* and *Laciris pelagica*, and two others have been introduced in the region, *Poecilia reticulata* and *Coptodon zillii*. In addition, we also found the introduced red swamp crayfish (*Procambarus clarkii*) in the smaller lakes within the system. This species is known to spread rapidly and cause severe harm to ecosystems. The checklist also contains six species that are new records for the system. A species accumulation curve has been compiled (Figure 42), indicating that for the area sampled, we probably covered most of the non-*Haplochromis* species. Yet, undetected species might still be present in areas not sampled during the expeditions (such as the Congolese part of the system). Being situated on the border of three ichthyofaunal provinces (the East Coast, Nilo Sudan, and Congo Provinces), the ichthyo-geographic position of the Lake Edward system has regularly been debated. A comparison of the species list with those of neighbouring basins confirmed the placement of the Lake Edward system within the East-Coast ichthyofaunal province.

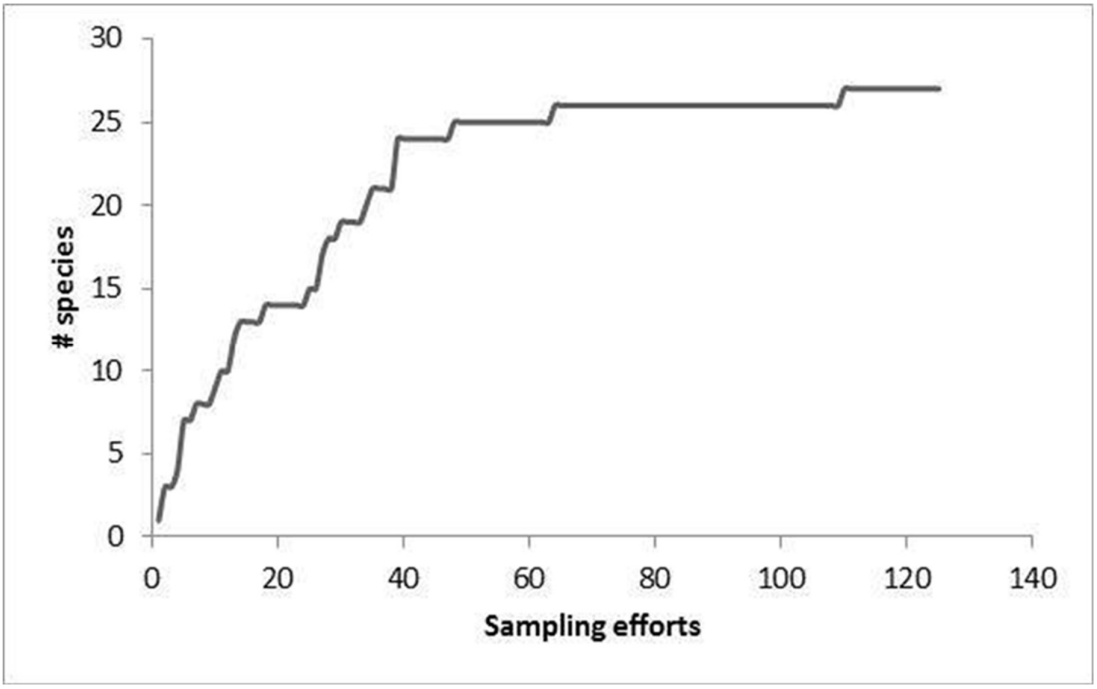

Figure 42: Species accumulation curve for the non-*Haplochromis* species of the Lake Edward system caught between 2016 and 2018. A single unit of sampling effort corresponded with one sampling locality per day.

The small barbs (*Enteromius*) as a new model for evolutionary research

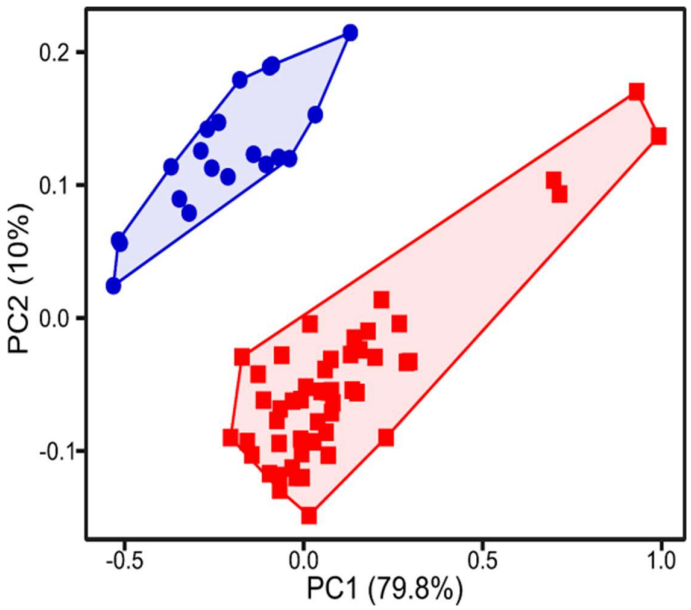

Figure 43: Scatterplot of Principal Axis 2 (PC2) against PC1 of a Principal Component Ananlysis (PCA) on 24 log-transformed measurements of 71 specimens, illustrating the difference found between the two genetic clades that were found to represent *E. alberti* (●) and *E. cf. mimus* (■). Numerous of such multivariate analyses have been executed during the project as they represent an ideal tool to explore the multivariate dataset of a large number of specimens by reducing the number of variables to a few axes that account for most of the relevant information in the dataset.

A particularly interesting and complicated group turned out to be the species of the small African barbs, *Enteromius*. Five morphospecies were listed in the checklist, of which two have a smooth third unbranched dorsal fin ray and the other three have serrations on the back of the ossified third unbranched dorsal fin ray. A revision was carried out based on morphometric and genetic analyses (see below). The two morphospecies with a smooth third unbranched dorsal fin ray were initially identified as *E. perince* and *E. stigmatopygus* (Decru et al., 2020). Both species were very difficult to distinguish but formed two genetic clades (mtCOI) with a large genetic distance (8.5%). Upon a detailed morphometric study, morphological characteristics were found that allowed specimens to be assigned to one of the genetic groups (Figure 43). The two groups, however, did not correspond to *E. perince* and *E. stigmatopygus*, but could be identified as *E. alberti* and *E.* cf. *mimus* (expressing its strong resemblance to *E. mimus*, a species from coastal basins in Kenya). The three morphospecies with a serrated third dorsal fin ray were initially identified as *E.* cf. *apleurogramma*, *E.* cf. *kerstenii* and *E.* cf. *pellegrini* (Decru et al., 2020). We found multiple genetic clades within each of these species based on COI: two in *E.* cf. *apleurogramma*, two in *E.* cf. *kerstenii* and three in *E.* cf. *pellegrini* (Figure 44). The genetic distances between the intraspecific genetic clades range from 2.4% to 5.2%. Although indistinguishable with the naked eye, morphological differences were found between the intraspecific clades within each of the three morphospecies based on multivariate analyses. Also geographical meaningfull patterns were found. Based on these results, the

number of *Enteromius* species with a serrated dorsal fin ray from the Lake Edward system may rise from three to seven. However, further examination with the inclusion of species from neighbouring regions is necessary to solve this problem. This unexpected and unrecognised diversity in *Enteromius* appears to mirror to some extent the cryptic diversity found in the Congo Basin (Van Ginneken et al. 2017). The discovery of large genetic divergences with almost a morphological stasis unveils the genus *Enteromius* as a new model group for evolutionary research in tropical riverine fish species. At present, we continue the work on this group to evaluate which speciation events have led to such an extra-ordinary species richness.

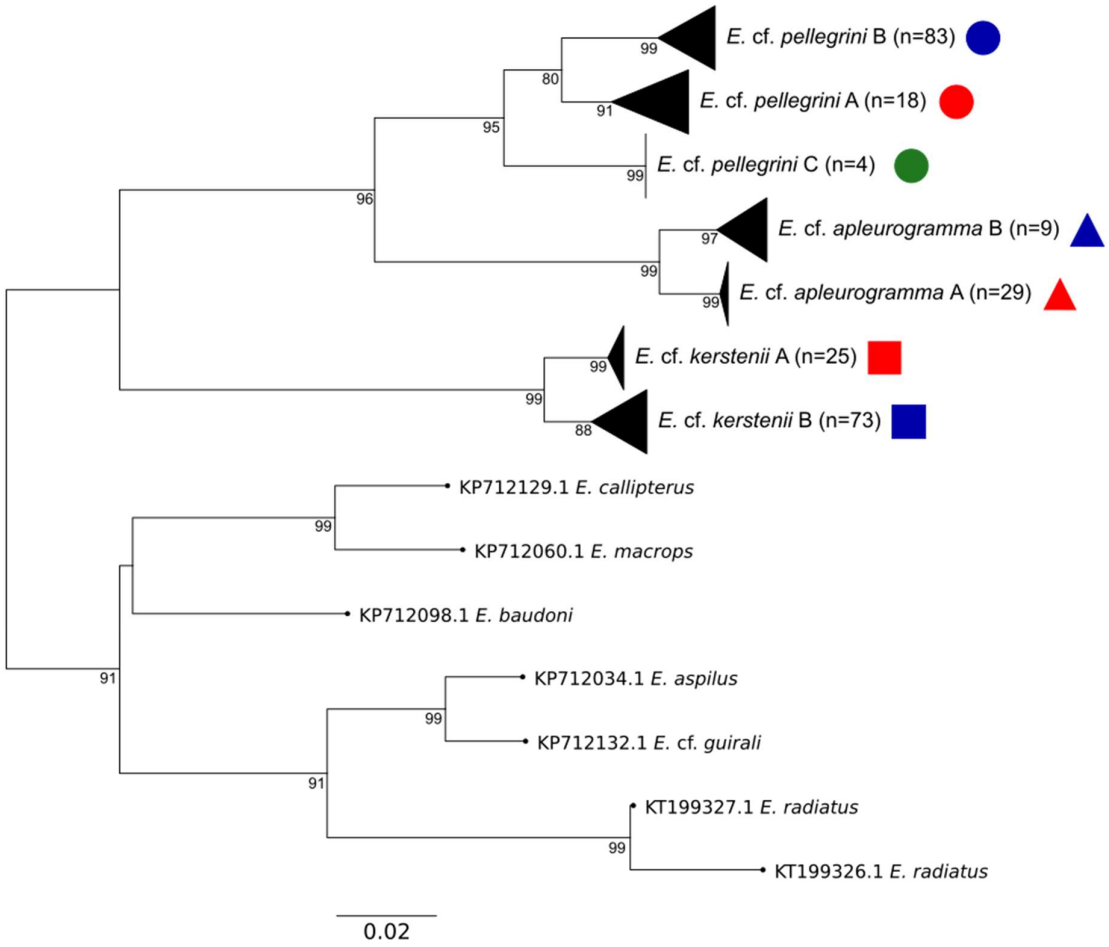

Figure 44: COI-based ML tree of 243 specimens of *Enteromius* from the Lake Edward system and seven specimens of other *Enteromius* species as outgroup. Lineages within each morphospecies with less than 2% genetic variance are collapsed. Statistical node support (1000 bootstrap replications) is illustrated under the branches (bootstrap values > 75% are shown). Specimens of the genetic clade *E.* cf. *apleurogramma* A (▲), *E.* cf. *apleurogramma* B (▲), *E.* cf. *kerstenii* A (■), *E.* cf. *kerstenii* B (■), *E.* cf. *pellegrini* A (●), *E.* cf. *pellegrini* B (●) and *E.* cf. *pellegrini* C (●). This is a typical output of a barcode analysis that permits in contrasting the delineation of groups based on morphology with the grouping of specimens based on genetic markers in monophyletic clades.

The endemic *Haplochromis* radiation untangled

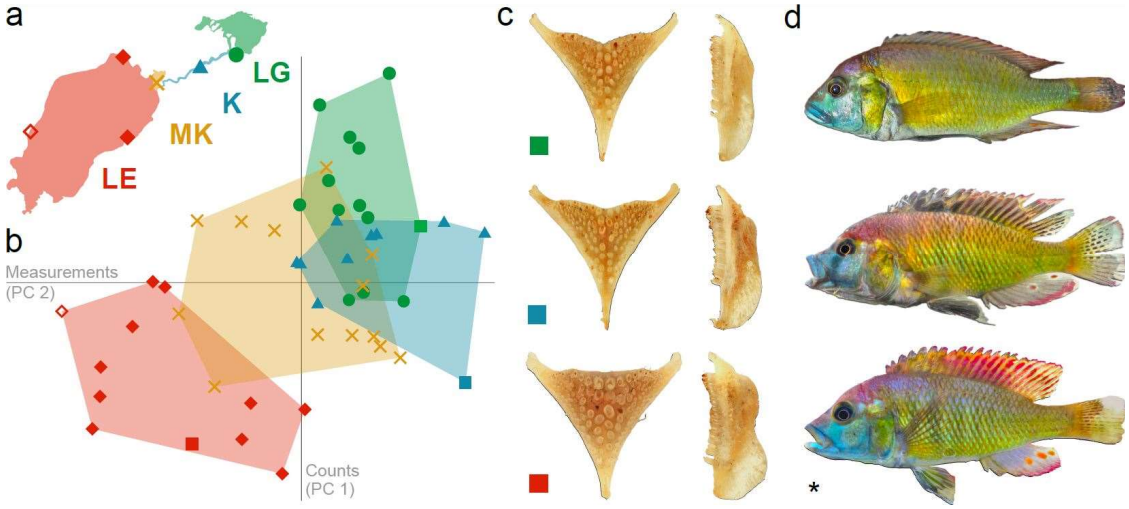

Figure 45: Geographical variation in morphology in *Haplochromis pharyngalis*. (a) The Lake Edward system with catch localities: Lakes Edward (LE; ◆, ◇ lectotype) and George (LG; ●) and the Kazinga Channel (K; ▲) and its mouth (MK; ×). (b) Plot of PC 2 of the PCA of 25 log-transformed measurements against PC 1 of a PCA of 22 raw counts. (c) Pictures of dorsal and lateral views of the lower pharyngeal bones of the specimens indicated with a square: LG (■), K (■), and LE (■). (d) Colour patterns of dominant males as in (c) except for *, which represents a specimen from the same catch.

The system harbours an estimated 60–100 endemic *Haplochromis* cichlids, which were very poorly studied. These fishes are part of a larger Lake Victoria Region Superflock (LVRS), a large radiation of ca. 700 eco-morphologically specialised species, nearly all endemic to one particular lake. Their systematics is notoriously difficult and only few teams in the world have been studying their taxonomy. Over decades, the Africa Museum has acquired the necessary expertise to tackle such species assemblages. As a first approach, all collected *Haplochromis* specimens were examined and twelve eco-morphological groups delineated. For each of these groups, a taxonomic revision has been or is being performed. A revision of the paedophages (i.e., highly specialised consumers of cichlid eggs and larvae) revealed that the system harbours not two but five species (Vranken et al., 2019). The lobed-lipped insectivores and the oral mollusc shellers were found to contain two and three species, respectively (Vranken et al., 2020 a,b). From the piscivores and the offshore benthic insectivores two species were known each, while the revisions of these groups revealed twelve and four species, respectively. Of the zooplanktivores, only one species was known. However, two species were found, both with a high degree of sexual dimorphism. The intraspecific morphological variation between the sexes within both species proved to be comparable to the interspecific variation. Of the *H. pharyngalis*-complex, two species were known, *H. pharyngalis* and *H. petronius*. About 40 specimens were investigated and a large variation was found in the size of the lower pharyngeal jaw (Vranken et al., 2020c; Figure 45). This variation was found to correlate with habitat. Species from Lake George have slender pharyngeal jaws, those from Lake Edward strongly hypertrophied pharyngeal jaws, and intermediate morphologies were observed in specimens from intermediate habitats. Other

morphological and qualitative differences were absent and therefore *H. petronius* was placed into synonymy with *H. pharyngalis* (Vranken et al., 2020c).

The six remaining eco-morphological groups are still under investigation and contain a total of 14 known species and 9 putative new species. These consist of the generalists that contain about 9 species, the slender insectivores about 4 species, the phytoplanktivores about 4 species, and the algae grazers about 4 species. In addition, we found one species of pharyngeal mollusc crusher and one presumed parasite eater.

In conclusion, before this study, 27 species of *Haplochromis* were known from the system. Within this project, we placed one species into synonymy, described 7 new species and are currently describing an additional 13 species (in review), and recognise a further 9 putative new species. This result is exemplary for the complexity of such endemic cichlid assemblages and at the same time represents a much larger output than anticipated at the start of the project. At present, a total of 56 species of *Haplochromis* is known from the area (see part of Figure 41).

DNA barcoding as a useful tool for fish identification

For the DNA barcoding study (COI, mtDNA), 696 samples were successfully sequenced, representing a nearly complete coverage of the non-*Haplochromis* species (31 of 34) that are known from the system. With the recent morphology-based review of the ichthyofauna of the system as a backbone, the DNA barcoding library proved to be a very effective tool for future species identifications. The COI barcodes were largely in accordance with the morphology-based identifications and thus high identification successes were obtained. As expected, COI failed to discriminate species of *Haplochromis*. This is because these species speciated too recently for the genetic differences to have accumulated. Surprisingly, *Laciris pelagicus* and *Micropanchax vitschumbaensis*, two morphologically distinct species, shared identical COI sequences, while in the genus *Enteromius* (see above) the existence of possible cryptic species was revealed. In both *Coptodon zillii* (a tilapia) and *Protopterus aethiopicus* (a lungfish), within-species sequence divergence exceeded that of other species in the basin, which in both cases was due to a single divergent sequence. For *Coptodon zillii*, an introduced species, this might point to two independent introduction events. As the fisheries of the system are under pressure, the provided reference library of DNA barcodes is a valuable tool for future conservation actions. The barcoding study resulted in the one of the most complete reference libraries for a tropical basin so far.

Trophic ecology and biology of the fishes

The trophic ecology of the six economically most important species of the Lake Edward system was studied via stomach analyses, the results of which are contrasted with the results from the stable isotopes (SI) analyses. Stomach analyses revealed that all species appear to be opportunistic to a certain extent, which is illustrated by the fact that stomachs contain a large variety of prey items in low proportions (Figure 46).

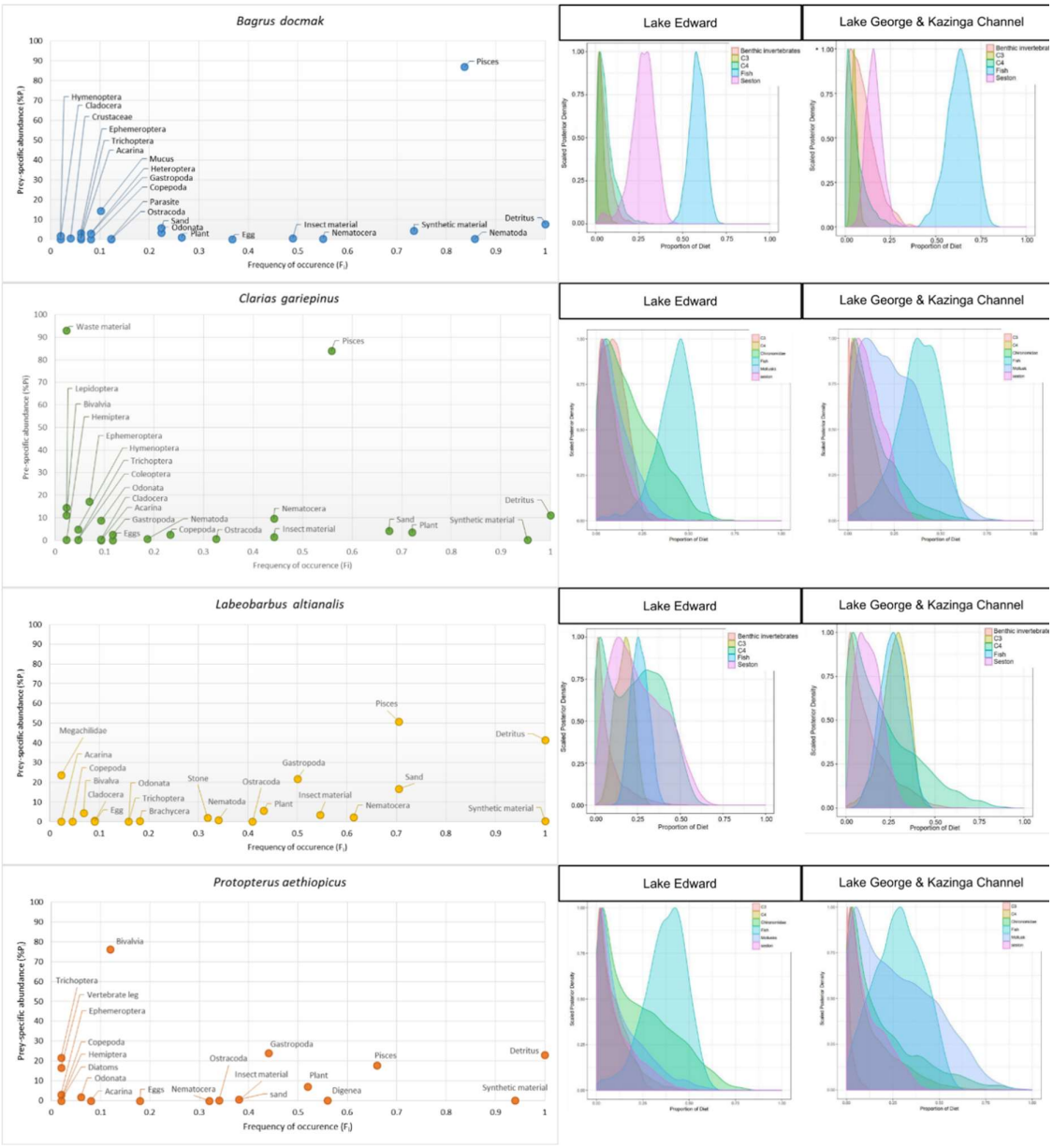

Figure 46 The prey specific abundance (%Pi) and frequency of occurrence (%Fi) calculated on dry weights of stomach contents (left) illustrate that *B. docmak* is piscivorous, *L. altianalis* is omnivorous and *C. gariepinus* and *P. aethiopicus* are opportunistic with a preference for fish. While the Bayesian mixing model based on the stable isotopes δ13C and δ15N (right) confirmed the diets for *B. docmak, C. gariepinus* and *P. aethiopicus*, the model suggested a largely herbivorous diet for *L. altianalis,* though plant material was hardly found in the stomachs.

The stomach content analyses in combination with the SI results revealed that *Bagrus* is piscivorous. *Clarias* and *Protopterus* have opportunistic diets with preferences for fish. *Labeobarbus* has an opportunistic diet with an ontogenetic shift: small specimens prefer insects, while larger specimens have a preference for fish. The two species of *Oreochromis* are phytoplanktivorous. Substantial dietary niche overlap was found between several species. SI results are generally in accordance with the stomach analyses, except for *L. altianalis,* for which the mixing model (SI) suggested a largely herbivorous diet, though plant material was

hardly found in the stomachs (Figure 46). Furthermore, *B. docmak, P. aethiopicus, C. gariepinus* and *L. altianalis* have been studied in more detail to study possible influences of season, locality and size. So far, no significant influences of seasonality or locality have been observed in the diets of these fishes. SI results, however, revealed a difference in $\delta^{13}C$ and $\delta^{15}N$ patterns for all six species between Lake George and Lake Edward.

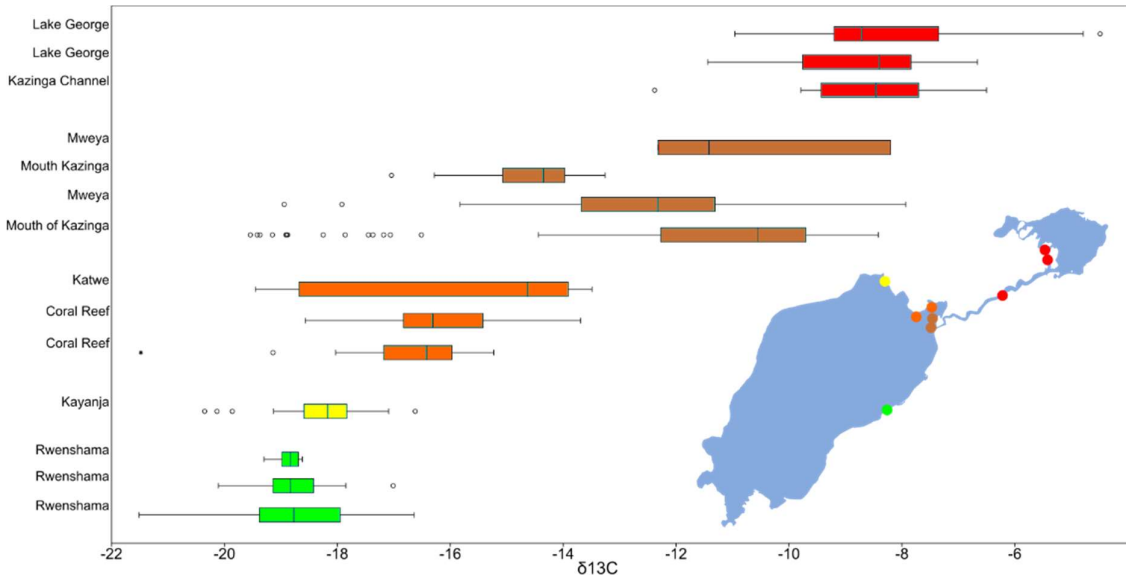

Figure 47: $\delta^{13}C$ profiles across all *Haplochromis* samples illustrating the effect of locality.

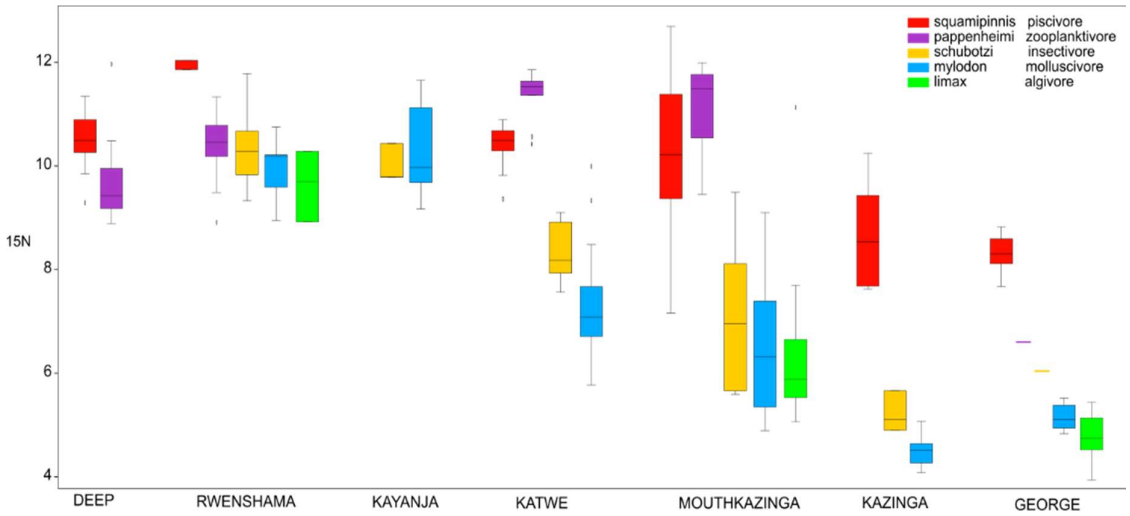

Figure 48: δ15N profiles for five Haplochromis species representing each a different trophic group. Within species, specimens from Lake George and the Kazinga Channel have lower values than those from the Lake Edward system

We are preparing a manuscript on the trophic ecology of the commercially species, combining stomach contents and SI data of the same specimens. As far as we know, such an approach has not been documented for an African freshwater system. An integrated synthesis of these data is not easy, because stomach contents reflect a short term view on the diet, while stable isotope signals reflect diet over a longer time.

Stable isotope analyses were done on *Haplochromis*, resulting in 693 SI profiles for C and N, and 383 for H. In contrast to the commercially important species, niche overlaps between most species of *Haplochromis* were small, which suggests that they display a high trophic differentiation in accordance with their specialised morphologies. The data showed a strong effect of locality (e.g. Figure 47) on top of a difference between species/trophic groups (e.g. Figure 48). We also analysed the *Haplochromis* assemblage within one location (near Akika Island at Lake George). A plot of in $\delta^{13}C$ and $\delta^{15}N$ signatures of 15 species of *Haplochromis* from this locality indicated that species clustered per trophic group (Figure 49).

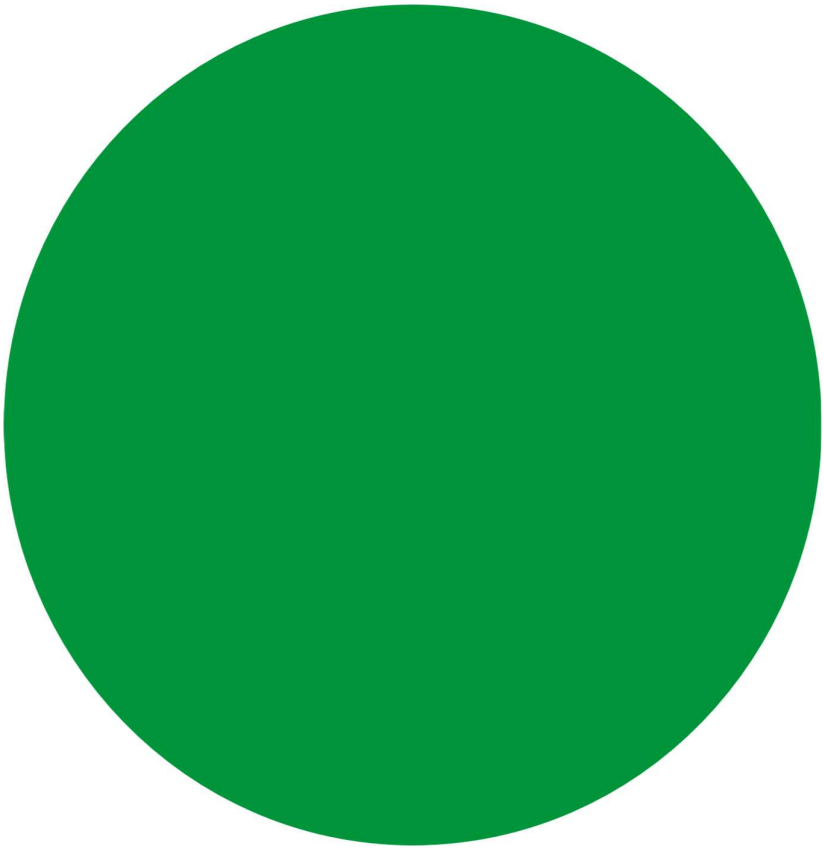

Figure 49: Plot of $\delta^{13}C$ against $\delta^{15}N$ signatures of 15 *Haplochromis* species from Akika Island from Lake George, illustrating the associations between the species at a given locatily. Species clustered per trophic group; most species that largely overlap have the same diet.

Size at first maturity has been studied in the two tilapias, *O. niloticus* and *O. leucostictus,* based on the macroscopical examination of the gonads. The results indicated that *O. leucostictus* appears to mature faster in Lake Edward than in Lake George. The sample size of *O. niloticus* in Lake Edward was too small to calculate the size at first maturity.

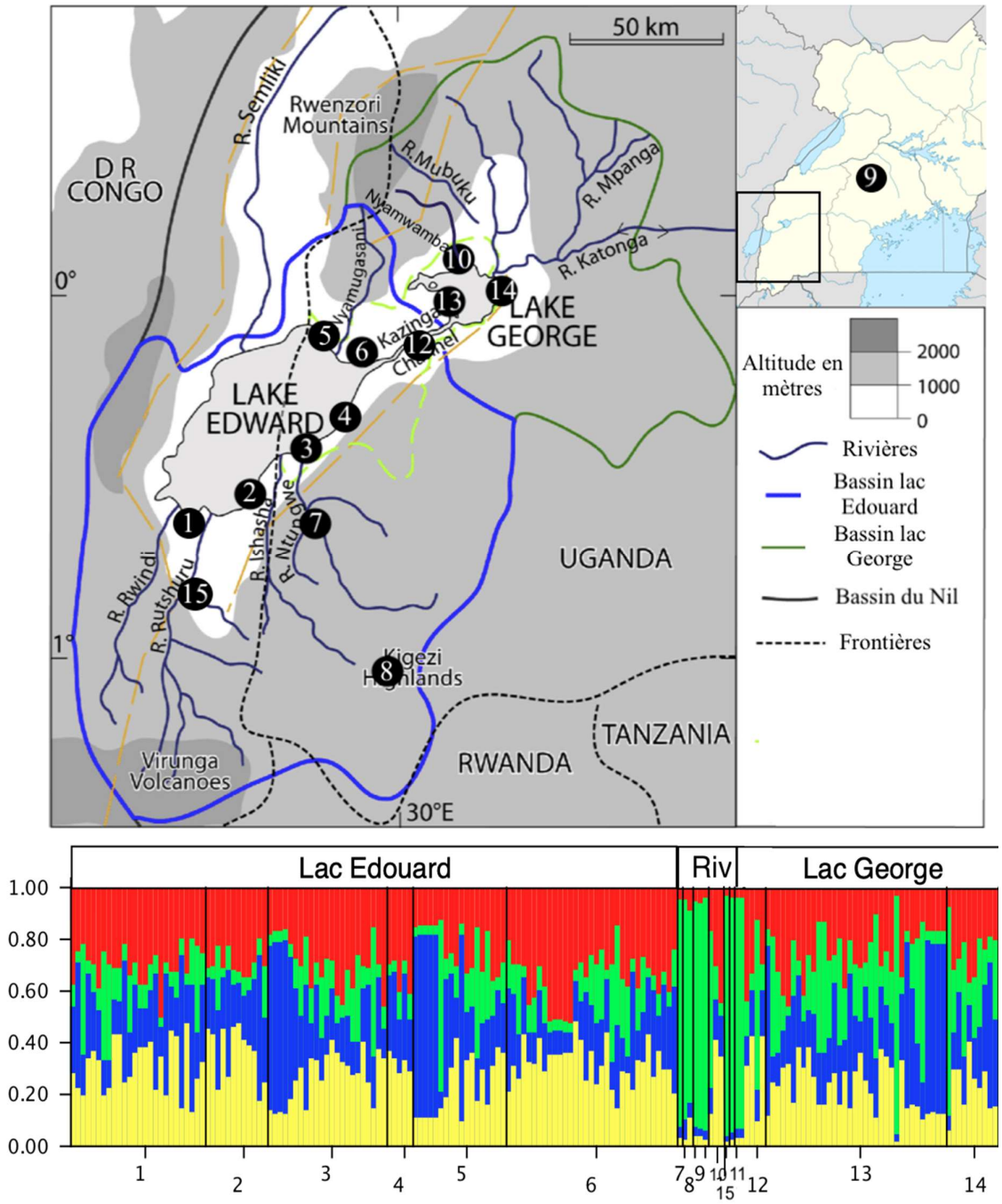

Figure 50: Sampling localities of *C. gariepinus* used for the microsatellite analysis (above) and results of STRUCTURE analysis (K=4) performed on 166 specimens (below). Numbers indicate sampling localities whereas colours indicate membership to one of 4 suggested groups.

The genetic population structure of the commercial fish species has important implications for stock and fisheries management. Hence, we conducted population genetic studies on the commercially important species. For this, an additional sampling scheme was set up during which samples were collected on a monthly basis at each of the main landing sites in Uganda and the DRC. Hitherto, a population genetic study was performed on four of the five commercial species: the two tilapias (*O. niloticus* and *O. leucostictus*) and the two

catfishes (*C. gariepinus* and *B. docmak*). Given the technical difficulties of studying *P. aethiopicus* (large genome size) and *L. altianalis* (hexaploidy), approaches to study the latter two species are still being developed. For *C. gariepinus*, 166 specimens from 14 localities were studied using seven microsatellite markers. STRUCTURE analysis suggested that Lakes Edward and George shared a panmictic population (Figure 50).

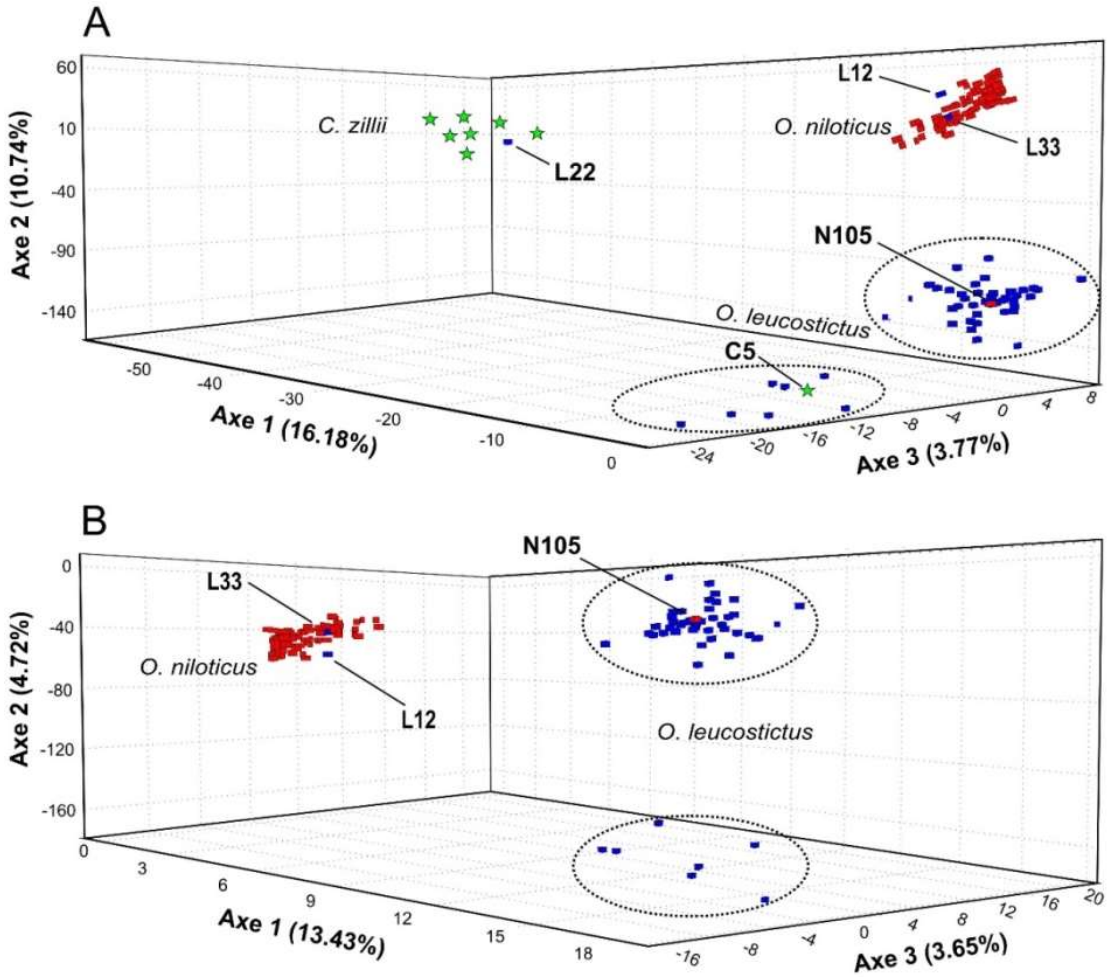

Figure 51: 3D Factorial Components Analysis (FCA) for (A) *C. zillii* (stars), *O. niloticus* and *O. leucostictus* (squares) and (B) *O. niloticus* and *O. leucostictus* microsatellite genotypes, respectively. Colours correspond to species. N105 represents a misidentified specimen. Ovals indicate two groups in *O. leucostictus*.

Strangely, a differentiation was observed between the lacustrine and the riverine specimens. This questions the role of rivers as breeding areas and nurseries of the species. For the tilapias, extracts were made of a total of 181 specimens and 14 microsatellite markers were used. Also for *O. niloticus* and *O. leucostictus*, no differentiation between specimens of the different lakes was found. However, a Factorial Components Analysis revealed the *O. leucostictus* population from the Lower Mpanga river, an affluent of Lake George to differ from the population in the lakes (Figure 51). This echoes the results of the study of *C. gariepinus*. These results underline the importance of managing the stocks of Lake Edward and George jointly, and suggest that riverine populations should be managed and protected separately.

Although *O. niloticus* and *O. leucostictus* are known to hybridise at several locations within their distribution range, no indications were found that hybridisation events have occurred in the Lake Edward basin. These findings show that the stock at Lake Edward still consists of genetically pure *O. niloticus*. In view of the importance of the species in global aquaculture, this gives an additional reason to protect this population. For *B. docmak*, extractions were performed and seven microsatellites were amplified successfully. The results still have to be analysed.

Putting the results of our fish diversity and biology study in a wider perspective, we can start with the premise that no indication was found of the existence of separate fisheries stocks within the Lake Edward system except for a small genetic divergence between lake and river populations in two of the three intensively studied commercial species. Since river fisheries appear to be negligible (no data exist) in comparison with fisheries in the lake, from a fisheries perspective, the populations of both lakes can be regarded a one unit. From a biological and conservation point of view, the riverine populations may, however, be important. This could be an interesting avenue for further research. Conversely, the ecology of the commercial species, and also of some *Haplochromis* species studied, seems to differ between Lake Edward on the one hand and Lake George and the Kazinga Channel on the other. This is almost certainly linked to the fact that both lakes represent a very different environment to which the populations have adapted. Therefore, anthropogenic pressures may act differently on the populations of the two environments, again an avenue of research that should be explored further to support sustainable management plans. The six most commercial species to a large extent seem to be opportunistic feeders, with three of them being partially piscivorous (thanks to the large biomass of small and medium-sized haplochromines) and two (the tilapias) mainly phytoplanktivorous. In both groups species present a large overlap in niche. Such rather generalist feeders may display a better resilience to anthropogenic pressures than specialist feeders.

Fisheries

Data on the historical fisheries on Lake Edward and George are very scarce and seldomly published in peer-reviewed publications. Moreover, information is scattered as often no comparable information is available of landing sites on the Congolese side and the Ugandan side. In addition, different methods were used to estimate catches and fisheries effort in various reports. In our synthesis below, these discrepancies also become obvious, though the general picture of overexploitation emerges very clearly.

Fisheries on Lake Edward underwent a huge evolution over the past decades. For the Congolese side of the lake, records date back to 1934, when fisheries was very small. Vitshumbi, for example, which is now the most important landing site on the Congolese side, then counted only 92 fishermen (Languy & Kujirakwinja, 2006). In 1940, fisheries activities were established as co-operative fisheries. Two legal fisheries were recognizes within the Virunga National Park, Vitshumbi and Kyavinyonge, while a third, Nyakakoma, was tolerated. These three landing sides expanded greatly over the years in terms of surface occupied and number of inhabitants (Languy & Kujirakwinja, 2006). Moreover, next to these three legal landing sites, illegal fisheries also greatly expanded between 1990 and 2000, mostly on the

western shore, occupying an area of 11,685 ha in 2006 (Languy & Kujirakwinja, 2006) with an estimated 27,850 inhabitants (Languy & Kujirakwinja, 2006).

Similar data on the landing sides on the Ugandan side are lacking. Recent estimates of the situation at Lake George, the Ugandan part of Lake Edward and the Kazinga Channel, indicate a substantial increase in the number of boats and fishermen between 2011 and 2013 (Bassa et al., 2015). In Uganda, nine landing sites became established after the creation of the Queen Elisabeth National Park (QENP). Initially, fishing was the sole allowed economic activity (together with salt mining in Katwe) and no permanent settlement of families was allowed. However, starting from the 1970's, families became established at the sites, which transformed into villages (see below, socio-economic survey).

Together with the growth of the landing sites and riparian populations, fishing effort also greatly increased over the past decades. According to Vakily (1989), the maximum sustainable yield (MSY) of Lake Edward is 14,000-16,000 tons per year, of which 3,000-4,000 tons can be obtained from the Ugandan side of the lake. Annual catches in the two registered landing sites at the Congolese side (Vitshumbi and Kyavinyonge) varied between 1,227 and 6,010 tons between 1949 and 1964. Later estimates referred to a total of 10,000-11,000 tons on the Congolese side in 1988 (Vakily, 1989), a minimum of 15,000 tons in 2006 (Petit, 2006) and up to 19,000 in 2013 (Kambere et al., 2015), thus largely exceeding the estimated capacity of the Congolese part of Lake Edward.

After the study of Vakily (1989) on the lake's capacity, the number of allowed canoes was fixed at 700 for the three official landing sites at the DRC. However, in 1994 already 1,100 canoes were counted (Kasonia & Mushenzi, 2006). A survey in 1995 obtained a total of 2150 canoes at the Congolese side of Lake Edward. In 2006, the number was already estimated to be at least 2300, but probably over 3000 (Petit, 2006). In 2013, the number of fishing units at the Congolese side was at 275% of the recommended limit (Balole-Bwami Lubala et al., 2018).

In Uganda, the number of fishing boats was set at 297 and 280 for the Ugandan part of Lake Edward and for George, respectively (Kamanyi and Mwene, 1992). However, currently the number of boats present on the lakes is a multiple of this (Figure 52).

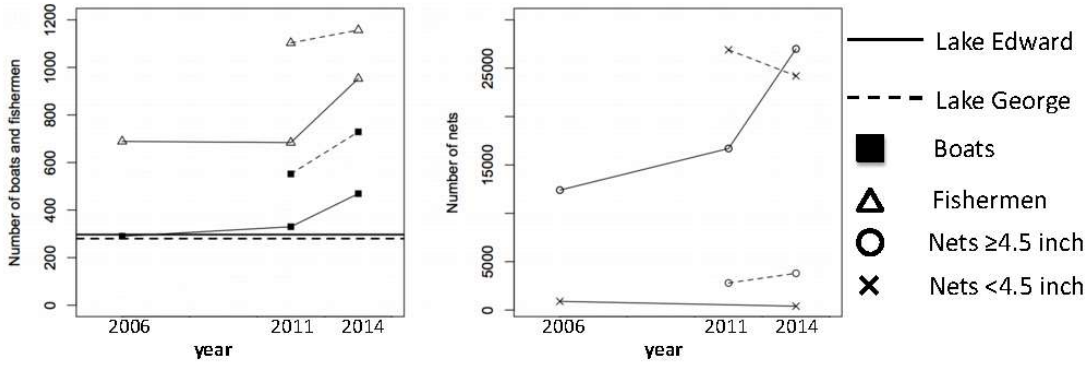

Figure 52: Trends in the fisheries in the Ugandan part of Lake Edward and in Lake George. A) The number of boats and fishermen active on the two lakes, the horizontal lines denote the number of authorised boats. B) the number of legal (≥4.5 inch) and illegal (<4.5 inch) gill nets deployed in the two lakes. Source: Bassa et al., 2015.

Although Vakily (1989) estimated the capacity of the Ugandan side of Lake Edward to be 3,000-4,000 tons, Dunn (1989) estimated the maximum sustainable yield in Uganda to be 7,000 tons on Lake Edward and 3,000 on Lake George.

Crespi & Ardizzone (1995) reported a major decrease in the late seventies with a progressive increase again in catches at the Ugandan side of Lake Edward after 1985, mainly as a consequence of political and economic stability. This lead to an increase in fishing effort, reflected in an increase in the numbers of fishers, canoes and fishing gear. They calculated a total of 5844.2 tons a year in the Ugandan fishing villages of Lake Edward for 1995. More recent estimates exist for the Ugandan part of Lake Edward, Lake George and the Kazinga Channel (Bassa et al., 2015). For Lake Edward, these figures varied between 1386 and 3192 tons a year between 2011 and 2013, which is much lower than the estimated annual yield by Crespi & Ardizzone (1995). This could be due to the different methodology used. The data of Bassa et al. (2015) were obtained via surveys, while the values of Crespi & Ardizzone (1995) were calculated by multiplying the total number of canoes by the average catches/canoes day and the number of fishing days per year. The latter method may have led to an overestimation, while during surveys maybe not all fisheries activities are reported. Many data on annual catches are based on official fisheries statistics (by COPEVI at the DRC and the Ugandan Fisheries Department at Uganda). Illegal fisheries, however, form a large part of the fishery activities, mainly at the DRC, which means that the reported numbers are probably an underestimation.

Fishing practices and catch per unit effort

Although the total annual yields are increasing to meet the increasing demand of the growing populations, the catch per unit effort (CPUE) is actually decreasing. Changes in CPUE are one of the best indicators to quickly evaluate the health of fisheries and in this case changes are quite significant. While in 1988 on average about 145 fish per canoe were captured on the Congolese side (Vakily, 1989), only an average of 30 fish per canoe were captured in 2006 (Petit, 2006). In addition, also the size of the captured fishes has decreased, adding to the decrease in the total weight of each catch. Although it was reported that in 1990 at the Ugandan side, most captured fishes were of mature size and that the fishing techniques did not cause any harm to the fishes (Crespi & Ardizzone, 1995), a more recent study revealed that in 2011-2013 a significant amount of the captured fish were below length at 50% maturity (Bassa et al., 2015). On the Congolese side a decrease in CPUE was found over the years, with the mean weight of *O. niloticus* in catches decreasing from 0.60 to 0.52 kg from 1970 to 1989, and to 0.49 kg in 2016 (Balole-Bwami Lubala et al., 2018). An increase in fishing effort was noticed since 1985 linked to an increase in fishermen and canoes, and a change in fishing gear (Crespi & Ardizzone, 1995). The smallest mesh size currently allowed is 5 inches, but most observed mesh sizes are of 4 inches and some even of 3, and also mosquito nets are used. This trend is observed on both sides of the lake (Crespi & Ardizzone, 1995, Petit, 2006; Bassa et al., 2015; Balole-Bwami Lubala et al., 2018). This results in a much larger share of immature and juvenile fish being caught. Between 2011-2013, there was an upsurge of (illegal) basket traps, which really intensified fish exploitation. During that period, an increase in the

number of gillnets (from 49,085 in 2011 to 59,356 in 2013) and of hooks (from 166,050 in 2011 to 365,200 in 2013), was also observed in the Edward-George system.

Changes in catch composition

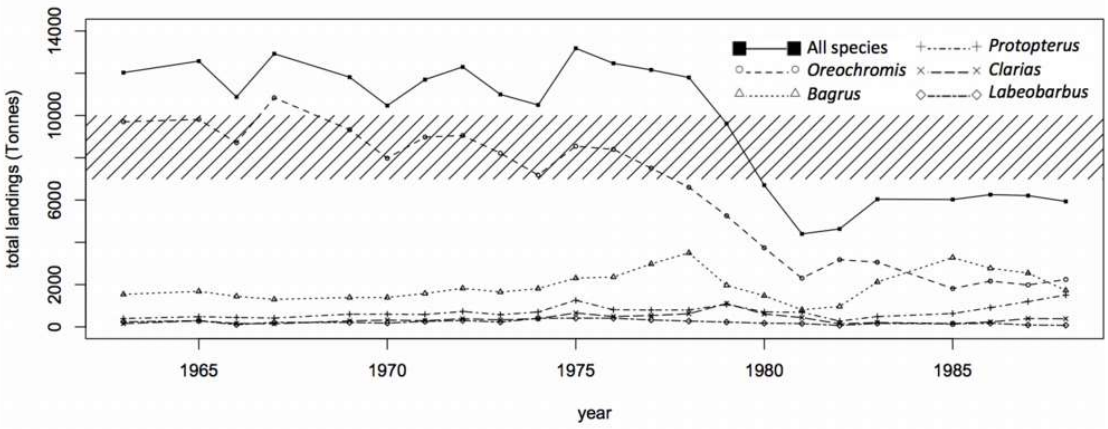

Figure 53: Evolution of the catches in the Ugandan part of Lake Edward and in Lake George between 1963 and 1988. The barred region denotes the ranges of the maximal sustainable yield capacity of these waters given the estimates of 7,000-10,000 Tonnes by Vakilyn (1989) and Dunn (1989). Symbols and lines denote the five main fisheries target species, as well as the total catch. (data from Orach-Meza *et al*., 1989).

Over the years, a change in species composition in the catches was observed. Tilapia (mainly *O. niloticus*) used to dominate the catches in weight and number, but a steep decrease was observed in the late seventies, at the same time as a general decrease in total catches (Figure 53 Orach-Meza et al., 1989). Balole-Bwami Lubala et al. (2018) illustrated the relative increase in *Bagrus* coupled with the decrease in *O. niloticus* in the Congolese catches between 1970 and 2016 (Figure 54). On the Ugandan side, *Bagrus* became the most important fish species in the catches at Lake Edward in 1990 (Crespi & Ardizzone, 1995).

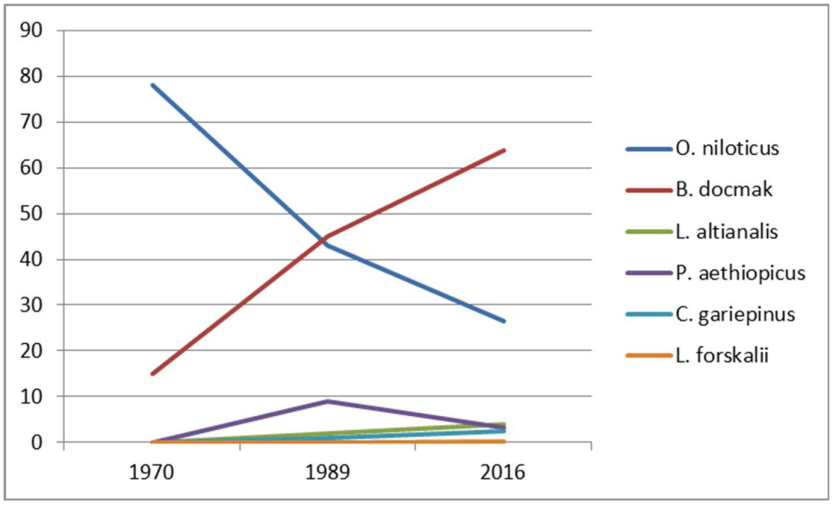

Figure 54: Evolution of contribution per catch (in %) in Vitchumbi, Kyavinyonge and Nyakakoma (DRC). Based on data from Balole-Bwami Lubala et al. (2018).

A new assessment of exploited fish species

In a recent publication (Musinguzi et al., 2021), we determined Fisheries Reference Points (FRP) using recently developed stock assessment methods for data-limited fisheries for Lake George and the Ugandan part of Lake Edward. This is the first time this method has been applied to African freshwater systems. Fisheries reference points were estimated for five exploited fish species (11 stocks). The assessed fish species are responsible for >80% of the catches in each of the waterbodies. The aim was to ascertain the status of the fisheries and establish reference points for effective management. The reference points were based on four linked stock assessment approaches for data-limited fisheries. Estimates showed poor stock status with the stocks defined as either collapsed, recruitment impaired or overfished. Estimates of maximum sustainable yield (MSY) and supporting biomass (*B*msy) are provided for 10 of the stocks as targets for rebuilding plans. We highlighted the possible implications for sustainable management. The immediate target of management should be rebuilding biomass to *B*msy. Applicable measures include shifting length at first capture to the length that maximizes catch without endangering size structure and biomass, and livelihood diversification out of fisheries.

Further issues

In addition to the fisheries-related results presented above, two issues that remain underreported need some discussion. First is the introduction of invasive species in the area. Invasive species constitute one of the major anthropogenic threats to African freshwater biodiversity (Snoeks et al., 2011). The presence of introduced species was highlighted in this project (Decru et al., 2020). Given that we found two fish species (*Poecilia reticulata* and *Coptodon zillii*) and the red swamp crayfish (*Procambarus clarkii*) to be present in various parts of the system, it would be good to study their impact.

Another important issue is that of Illegal, Unreported and Unregulated (IUU) fishing. It is a worldwide problem for which virtually no data exist for Africa. For most African countries, catches are estimated to be over 200%, and for many over 400% of what was officially reported (Fluet-Chouinard et al., 2018). Without any doubt there is substantially IUU fishing in the area. This is mentioned in recent reports and has been forwarded as an important concern by the interviewees in the socio-economic study (see below). The extent of this phenomenon in the region studies has never been estimated (and off course is very difficult to do), but certainly deserves more attention by those involved in fisheries research. As discussed above, all indicators point to a severe overfishing. If then catches in reality are double the size or even more of what is reported, the problem is much worse than documented.

4.4 EVALUATION OF ECOSYSTEMS SERVICES

This part of the report is based on a socio-economic survey carried out by NaFIRRI, the results of which were synthesised in collaboration with the Tervuren team (Odongkara Okecha et al., in review). During the study, all nine authorised landing sites within the boundary of the QENP at Lake George and Lake Edward were visited. The study had five main objectives: (1)

to identify the demography and living conditions on the landing sites, (2) to identify the relations between fishing communities with wildlife and park authorities, (3) to identify the changes in the fisheries, (4) to investigate the compliance with fisheries regulations, (5) to investigate the effects of declining fisheries resources on livelihoods, and (6) to investigate conflicts between Ugandan and DRC fishermen that share Lake Edward.

For all objectives, the study was designed to measure the changes respondents witnessed during their stay at the landing sites, during which they were active in the fisheries (18 years on average, with a maximum of 30 years).

Data was gathered using three methodologies: A) Key Informant Interviews (KII); Individual Sample Surveys (ISS), and Focus Group Discussions (FGD). KIIs were held with leaders of landing sites, using a checklist. ISSs were conducted with 152 respondents that were randomly selected by the chairpersons. ISSs were performed using a semi-structured questionnaire. Finally, FGD were performed at four of the landing sites, two at Lake Edward (Kazinga and Kishenyi), and two at Lake George (Kashaka and Kahendero). FDG were done with 12 participants at each of the landing sites, which were selected by the chairpersons of the landing sites to represent the key stakeholders of fisheries: boat owners, crewmembers and traders. At least 30% of the respondents were women.

Demography and living conditions. The demography of the landing sites is summarised in Table I. The study revealed how the population of the landing sites increased drastically in 30 years' time. Additionally, as the landing sites were initially set up to serve only as centres for fisheries, families were originally not allowed at the sites. Respondents stated that since the 1970's fishermen gradually started to bring their families to the landing sites. Currently, these sites have developed into villages with household sizes of 7 on average (for our respondents). Additionally, landing sites officials estimated high numbers of refugees, i.e. people stemming from other districts in Uganda or from the neighbouring DRC that were drawn to the landing sites to join the fisheries, or that fled their home because of the war. Respondents mentioned an increase in pollution in and near the sites.

Table I: Demographic characteristics of the landing sites. With landing sites at Lake Edward: KZ = Kazinga, RW = Rwenshama, KS = Kishenyi, KY = Kayanja, KT = Katwe; and at Lake George: KH= Kahendero, HM = Hamukungu, KA = Kasenyi, KK = Kashaka; Sources: UBOS, 2017* and this study, 2018**

	Lake Edward					**Lake George**			
	KZ	**RW**	**KS**	**KY**	**KT**	**KH**	**KK**	**KA**	**HM**
Male*	517	1,315	672	812	529	2,400	900	650	2,000
Female*	412	943	566	768	362	1,600	300	350	1,000
Total *	**929**	**2258**	**1,238**	**1,580**	**891**	**4,000**	**1,200**	**1,000**	**3,000**
Households*	273	672	488	394	332	700	200	500	500
Immigrants**	800	1,200	600	100	900	1,500	300	650	1,000
Population 30 years ago**	400	800	800	900	1,000	2,400	1,600	400	1,000

Relations between fishing communities with wildlife and park authorities. Communities had mixed views on the presence of the park around the landing sites. They mentioned a constant conflict with wild animals and the park authority, mostly due to fatal

conflicts with wild animals without compensation. Additional conflicts were due to trespassing prohibited areas of the park by fishers. The major benefits received from the park were the 25% of revenue, and the permission to collect firewood, floats, roofing materials and herbs from the park. We found a difference between communities living around Lake Edward and Lake George. Most respondents at Lake Edward said it was a good thing while at Lake George, about half thought it was not.

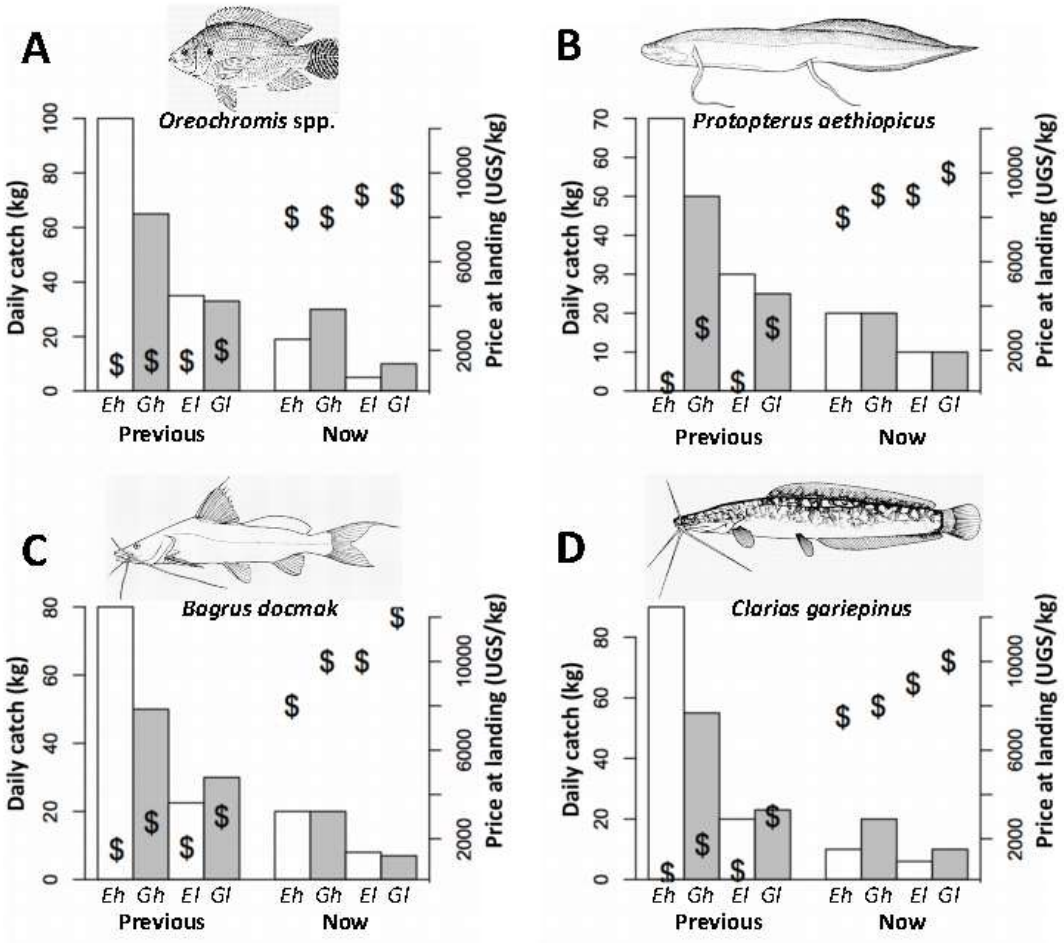

Figure 55: Perceived tendencies of the fisheries in lakes Edward and George. Reported daily catches (bar plots, scale left) and obtained prices at landing sites ($ signs, scale right) per kg when respondents first joined the fisheries (Previous) and at the time of study (Now) for A.) *Oreochromis* sp., B.) *Protopterus aethiopicus*, C.) *Bagrus docmak*, D.) *Clarias gariepinus*, with Eh: Lake Edward, high season; Gh: Lake George, high season; El: Lake Edward, low season; Gl: Lake George, low season. Drawings of the fisheries target species from Eccles (1992).

Changes in the fisheries. Respondents both reported a decline in catches and a shift in fisheries target species (Fig. 55). Several respondents had changed targeted fish species since they joined the fisheries, with the shifts being more pronounced on Lake George than on Lake Edward. On Lake Edward, tilapias remained the preferred species (ISS), followed by *B. docmak*. On Lake George, respondents targeting tilapias decline from 69% to 21% since they joined the fisheries. Now, most respondents targeted *P. aethiopicus*, followed by *B. docmak*. ISSs also revealed that average weight of fishes in the catches decreased. For tilapia

a decline was seen from 0.8 to 0.5 kg on Lake Edward and from 1.0 to 0.3 kg on Lake George. For *B. docmak,* this went from 3.0 to 2.0 kg on Lake Edward and from 5.0 to 3.0 kg on Lake George. Similar trends were reported for other commercial species although the changes were less dramatic. FGDs mentioned that *Labeobarbus altianalis* (Enjunguli), *Mormyrus kannume* (Elephant snout fish/Kasulubana), and *Labeo forskalli* (Ningu) became scarce since the 1990s.

Respondents of ISSs on both lakes admitted using gillnets with an average mesh size of 2 inches (5cm), much smaller than the allowed 4.5 inches. FGDs revealed that the number of hooks had risen from the authorized 100 to 1,000 per boat, and that fishermen exceeded the number of authorised nets per boat.

Fishing is restricted to night time only. However, FGDs revealed that fishing time regulations were no longer complied with at the time of the study. Some fishers even maintained two sets of crew per fleet, one for the night and the other for the day. Others stayed on the lake fishing for days before coming to shore. FGDs at KT revealed that hook and basket trap fishers maintained their gear in the lake almost permanently, only shifting position when necessary.

Effects of declining fisheries resources on livelihoods. Respondents of the ISSs answered that due to limited availability, fish was consumed on average three days a week, down from seven when respondents joined the fisheries (18 years ago on average). Given its nutritional value, the dwindling consumption of fish could lead to malnourishment, especially among children. ISSs were used to inquire about the financial situation of the fishermen. This revealed that an average fisherman at Lake Edward earned UShs 15,000; compared to UShs 30,000 when he joined the fisheries, representing a 50% decline. At Lake George, incomes went down to UShs 10,000 compared to UShs 15,000 before, representing a 33.3% decline. Although the decline in income was attributed to reduced catch-rates, fish prices had gone up, which was believed to have saved the fishermen from greater reductions in incomes (Figure 55). On average, respondents stated that two household members were involved in fisheries while four were engaged in non-fishery activities, like crop and livestock farming. However, restrictions imposed by park authorities limited alternative income opportunities. For example, some communities wanted to engage in activities such as crop farming, which is not allowed in the park.

Conflicts between Ugandan and DRC fishersmen. KII revealed that cross-border fishing was common with fishermen from DRC operating on the Ugandan part of Lake Edward, but that it was not common for Ugandan fishermen to cross to the DRC side. However, we should stress that we only collected the viewpoints of the Ugandan fishermen. Respondents stated that most DRC fishermen were using illegal fishing gears, and feared that this could result in reduced catches in Uganda. They also reported that DRC fishermen usually stole fishing gears from the Ugandan fishermen. Although the Ugandan fishermen stated not to be hostile to the DRC fishermen, it was reported that Ugandan fishermen who crossed to operate on the DRC part of Lake Edward were harassed and sometimes killed. Efforts aimed at stopping DRC fishers from fishing in Ugandan waters were minimal in spite of this being a major source of conflict between the two countries.

Added values, broad relevance and collaborations. The spill-over effects of the fish part of the project are larger than expected. On the national level, the project has intensified

collaboration with the various partners and in particular with the Royal Belgian Institute of Natural Sciences (RBINS), where a previous collaborator of the project at the Royal Museum for Central Africa (RMCA) (Maarten Van Steenberge) has been employed as a senior scientist. Another former collaborator (Eva Decru) is now employed at the KU Leuven. The RMCA continues to work closely with both institutes in a new Brain project (KEAFish, see below).

During the current project, a new line of collaboration has started within the Joint Experimental Molecular Unit (JEMU) of the RMCA and the RBINS, and with Prof. Hannes Svardal of the University of Antwerp. Now that we have set up a state-of-the-art taxonomic framework for the fish diversity of the Lake Edward system and found challenging issues especially in the systematics of the haplochromines and the small barbs, the next step is to unravel the evolutionary history of these taxa, which possibly is linked to the turbulent geological history of the region. In this new collaboration, we have already started the work on the genomics of the haplochromines via a FWO PhD study of Nathan Vranken (also a former HIPE collaborator) and are starting a genomic study on *Enteromius* within the new KEAFish project, concentrating on a larger region encompassing the whole region of Lakes Kivu, Edward and Albert.

On the international level, the collaboration with NaFIRRI (Uganda), started during the current project, is expanding on two fronts. NaFIRRI has become a partner within the above mentioned KEAFish project and an employee of NaFIRRI became a PhD student at the KU Leuven studying the fisheries and ecosystem services of the Lake Edward system, within the FishBase-for-Africa project of the RMCA. Mbalassa Mulongaibailu (Université de Bukavu, DRC), who became the main collaborator for the fish diversity part in the DRC, is also partner in the same FishBase-for-Africa project and will study the fisheries and ecosystem services of the Lake Edward system from the Congolese side.

The project also contributed to the mission statement of the RMCA and RBINS in other ways than the activities discussed above. During the project, a large number of unregistered specimens from historical collections from the Lake Edward system have been identified, hence valorising these sleeping collections. Furthermore, the data produced during the project will be integrated in FishBase by the RMCA team members. The project also provided guidance to several FishBase trainees that studied fishes of the region during their case study.

With regard to further links with federal competences, both Uganda and the DRC are important partner countries for the Belgian Development Cooperation. The results of our study are directly relevant in reaching several of the sustainable development goals (SDG), especially SDG 2 and 14: zero hunger and life below water.

5. DISSEMINATION AND VALORISATION

5.1. Presentations at international meetings

Decru E, M Van Steenberge, S Bouillon, AV Borges & J Snoeks HIPE: Human impacts on ecosystem health and resources of Lake Edward; exploring a poorly known ichthyofaunal, Zoology 2016, Royal Dutch and Belgian Zoological Societies, University of Antwerp, Belgium, 16-17 December 2016, poster

Borges AV, & Bouillon S (2017) Globally significant greenhouse-gas emissions from African inland waters. EGU General Assembly, Vienna, April 2017.

Borges AV, Morana C, Lambert T, Okello W, & Bouillon S (2017) Distribution of dissolved greenhouse gases (CO2, CH4, N2O) in Lakes Edward and George: results from the first field cruise of the HIPE project. EGU General Assembly, Vienna, April 2017.

Bouillon S (2017) Carbon cycling in tropical rivers and lakes: insights from carbon isotope analyses. University of Toulouse, invited talk, May 2017.

Lambert T, Bouillon S, Morana C, Okello W & Borges AV (2017) Environmental drivers on dissolved organic matter concentration and composition in tropical inland waters. Biogeomon symposium, Litomyšl, Czech Republic, August 2017.

Soto DX, Morana C, Borges AV, Wassenaar LI, Okello W, Nabafu E, Nankabirwa A, and Bouillon S. Hydrogen isotopic analysis of sediment and suspended particulate matter using online equilibration systems. The Advances in Stable Isotope Techniques and Applications Conference (ASITA 2017). Waterloo, Canada. June 2017.

Soto DX (2018) Animal migration and food web ecology using stable isotopes: applications and challenges, The Doñana Biological Station (EBD-CSIC), Spain, invited talk, Feb 2018.

Soto DX, Morana C, Borges AV, Okello W, Nabafu E, Nankabirwa A, and Bouillon S. An update (2nd) on stable isotope studies from African river basins. Third IAEA Research Coordination Meeting, Vienna, Sep 2017.

Vranken N., Van Steenberge M., Snoeks J. (2017). Grasping ecological opportunities: not one but five paedophages in the Lake Edward system. Cichlid Science 2017. Prague, Czech Republic, 4-7 September 2017.

Vranken N., M. Van Steenberge, J. Snoeks. 2018. Exploring the diversity of haplochromines in the Lake Edward system. Zoology 2018. Antwerp, Belgium, 13–15 December 2018.

Vranken N., M. Van Steenberge, J. Snoeks. 2018. Exploring the unexpected diversity of haplochromines in the Lake Edward system. PAFFA 6. Mangochi, Malawi, 24–28 September 2018

Decru E., N. Vranken, M. Van Steenberge, W. Okello, L. Cox, A. Heylen, S. Heeren, A. Mertens, A. Kayenbergh, H. Maetens, M. Mulongaibailu, A. Balagizi, G. Okito & J. Snoeks. 2018. HIPE: Human impacts on ecosystem health and resources of Lake Edward: the ichthyofauna of the Lake Edward system. Zoology 2018. Antwerp, Belgium, 13–15 December 2018.

Decru E., N. Vranken, M. Van Steenberge, W. Okello, L. Cox, A. Heylen, S. Heeren, A. Mertens, A. Kayenbergh, H. Maetens, M. Mulongaibailu, A. Balagizi, G. Okito & J. Snoeks. 2018. HIPE: Human impacts on ecosystem health and resources of Lake Edward: the ichthyofauna of the Lake Edward system. Poster presentation at Sixth International Conference of the Pan African Fish and Fisheries Association. Mangochi, Malawi, 24-28 September 2018.

Decru E, Van Ginneken M, Vreven E, Kimbembi A, Verheyen E, Snoeks J. Hidden diversity in the small African barbs. Sixth International Conference of the Pan African Fish and Fisheries Association (PAFFA 6), Mangochi (Malawi), 17 – 21 September 2018. Oral presentation.

Mbalassa, M., Snoeks, J., Van Steenberge, M. (2018). A systematic study of the pelagic Haplochromis species from the Lake Edward-George system. Presented at the Sixth International Conference of the Pan African Fish and Fisheries Association (PAFFA 6), Mangochi, Malawi, 24 Sep 2018-28 Sep 2018.

Snoeks, J. (2018). African fish diversity in fisheries and conservation: a happy marriage or conflicting extremes? Invited lecture presented at the Sixth International Conference of the Pan African Fish and Fisheries Association (PAFFA 6), Mangochi, Malawi, 24 Sep 2018-28 Sep 2018.

Decru E., M. Van Steenberge, K. Odongkara, N. Vranken, L. Cox, S. Heeren, A.Mertens, A. Kayenbergh, M. Mulongaibailu & J. Snoeks 2018. The non-haplochromine fishes of Lake Edward: diversity, biology and fishery. Poster presentation at Speciation in Ancient Lakes (SIAL 8), 29 July-3 August, 2018 in Entebbe, Uganda

Vranken N., M. Van Steenberge & J. Snoeks 2018. Tackling a forgotten species flock: The haplochromine cichlids of the Lake Edward system. SIAL 8. Entebbe, Uganda, 29 July-3 August 2018.

Morana C, Bouillon S, Nolla-Ardèvol V, Roland F, Okello W, & Borges AV (2018) Phytoplankton metabolism sustains microbial CH4 production in oxygenated lake surface waters. BASIS meeting, Liège, April 2018.

Descy JP, M.P. Stoyneva, C. Morana, S. Bouillon & A.V. Borges. Human Impacts on ecosystem health and resources of Lake Edward (HIPE): the phytoplankton study. IAGLR meeting, Evian, September 2018.

Rosentreter JA, AV Borges, CM Duarte, PA Raymond, PA Del Giorgio, YT Prarie, D Olefeldt, E Bradley, Methane Emissions across Aquatic Systems - From Headwater Streams to the Open Ocean, Goldsmith 2019, Barcelona, Spain, 18-23 August 2019, oral

Maetens H., E. Decru, M. Van Steenberge & J. Snoeks (2019). The *Enteromius* species (Cyprinidae) from the Lake Edward system (East Africa): geographic variation or cryptic diversity?. Young Systematists' Forum. London, United Kingdom, 22 November 2019.

Vranken N., M. Van Steenberge & J. Snoeks 2019. Exploring the cichlid diversity of Lake Edward (East Africa). Young Systematists' Forum. London, UK, 22 November 2019.

Rosentreter JA, AV Borges, PA Raymond, BR Deemer, M Holgerson, S Liu, C Song, CM Duarte, D Olefeldt, T Battin, P del Giorgio, Y Prairie & B Eyre, Methane Emissions across Aquatic Ecosystems - From Headwater Streams to the Open Ocean, AGU Fall Meeting 2019, 9-13 December 2019, San Francisco, USA, oral

Rosentreter JA, AV Borges, PA Raymond, BR Deemer, M Holgerson, S Liu, C Song, CM Duarte, GH Allen, D Olefeldt, T Battin, JM Melack & B Eyre, Aquatic Ecosystems are the Largest Source of Methane on Earth, AGU/ASLO Ocean Sciences 2020, 16-21 February 2020, San Diego, USA, poster

Rosentreter JA, AV Borges, PA Raymond, BR Deemer, MA Holgerson, CM Duarte, S Liu, C Song, GH Allen, J Melack, B Poulter, D Olefeldt, TI Battin, BD Eyre, Aquatic Ecosystems are the Most Uncertain but Potentially Largest Source of Methane on Earth, AGU Fall Meeting 2020, 7 – 11 December 2020, Online

Nankabirwa A, W Okello, J-P Descy, I Nabafu, L Deirmendjian, S Bouillon, AV Borges & C Morana, Impact of mixing on the seasonal variations of productivity and phytoplankton communities of Lake Edward (East Africa), 64th annual Conference on Great Lakes Research (IAGLR 2021) May 17–21, 2021, virtual

Morana C, S Bouillon, V Nolla-Ardèvol, FAE Roland, W Okello, J-P Descy, A Nankabirwa, E Nabafu, D Springael & AV Borges Methane paradox in tropical lakes? Sedimentary fluxes rather than pelagic production in oxic conditions sustain methanotrophy and emissions to the atmosphere, ASLO 2021 Aquatic Sciences Virtual Meeting, 22-27 June 2021.

5.2 Scientific publications

See section 6

5.3. Others

Nathan Vranken was awarded the public prize of the Kets Award for his MSc thesis on the thick-lipped haplochromine cichlids of the Lake Edward system (see http://rbzs.be/kets-award/) and was invited for a special lecture at the 25th Benelux Congress of Zoology: Zoology in the Anthropocene. Furthermore, he was invited on the Africa Museum podcast, where he talked about the haplochromine cichlids of the system (Africa Museum Podcast #3: A fish tale from Lake Edward; https://www.africamuseum.be/en/learn/podcasts).Maarten Van Steenberge participated in the ACARE workshop (Nov 2019, Entebbe) and became founding member of the Lake Edward-Albert advisory committee (https://www.agl-acare.org/2019-workshop-resources).

Maarten Van Steenberge was interviewed by the VRT regarding possible conflicts between fishers from Uganda and the DRC on Lake Edward (Vissersoorlog tussen Congo en Oeganda: hoe conflict en bevolkingstoename de vissers tot wanhoop drijven | VRT NWS: nieuws).

Rosentreter J, AV Borges, B Poulter, B Eyre (2021), Half of global methane emissions come from aquatic ecosystems - much of this is human-made, The Conversation, https://theconversation.com/half-of-global-methane-emissions-come-from-aquatic-ecosystems-much-of-this-is-human-made-156960

DailyScience : Les milieux aquatiques responsables de la moitié des émissions mondiales de methane (https://dailyscience.be/20/04/2021/les-milieux-aquatiques-responsables-de-la-moitie-des-emissions-mondiales-de-methane/)

ULiège press release : "Methane emissions from aquatic systems contribute half of global emissions" (https://www.sciences.uliege.be/cms/c_7180859/en/methane-emissions-from-aquatic-systems-contribute-half-of-global-emissions)

On the web:

https://www.co2.uliege.be/cms/c_5639396/en/hipe
https://www.researchgate.net/project/HIPE-Human-impacts-on-ecosystem-health-and-resources-of-Lake-Edward
https://www.africamuseum.be/en/learn/podcasts, podcast#3
http://rbzs.be/kets-award/
https://www.vrt.be/vrtnws/nl/2018/09/15/de-visserij-oorlog-tussen-congo-en-oeganda-of-hoe-conflict-en-b/

6. PUBLICATIONS

6.1. PEER-REVIEWED

Stoyneva-Gärtner M. P., Descy, J.-P. (2018) Cyanoprokaryote and algal biodiversity in the tropical Lake Edward (Africa) with notes on new, rare and potentially harmful species. – Annual of Sofia University, Faculty of Biology, Book 2-Botany, 102, pp. 1–28.

Vranken N., M. Van Steenberge & J. Snoeks (2019) Grasping ecological opportunities: not one but five paedophagous species of Haplochromis (Teleostei: Cichlidae) in the Lake Edward system. Hydrobiologia, 832, 105–134, https://doi.org/10.1007/s10750-018-3742-5

Stoyneva-Gaertner M, C Morana, AV Borges, W Okello, S Bouillon, L Deirmendjian, T Lambert, F Roland, A Nankabirwa, E Nabafu, F Darchambeau, J-P Descy (2020) Diversity and ecology of phytoplankton in Lake Edward (East Africa): present status and long-term changes, Journal of Great Lakes Research, 46(4), 741-751, https://doi.org/10.1016/j.jglr.2020.01.003

Morana C, S Bouillon, V Nolla-Ardèvol, FAE Roland, W Okello, J-P Descy, A Nankabirwa, E Nabafu, D Springael & AV Borges (2020) Methane paradox in tropical lakes? Sedimentary fluxes rather than pelagic production in oxic conditions sustain methanotrophy and emissions to the atmosphere, Biogeosciences, 17, 5209-5221, https://doi.org/10.5194/bg-17-5209-2020

Decru E., N. Vranken, P. H. N. Bragança, J. Snoeks & M. Van Steenberge (2020) Where ichthyofaunal provinces meet: the fish fauna of the Lake Edward system. Journal of Fish Biology, 96 (5) 1186-1201, https://doi.org/10.1111/jfb.13992

Maetens, H., Van Steenberge, M., Snoeks, J., Decru, E. (2020). Revalidation of Enteromius alberti and presence of Enteromius cf. mimus (Cypriniformes: Cyprinidae) in the Lake Edward system, East Africa. *EUROPEAN JOURNAL OF TAXONOMY*, *700*, 1-28. doi: 10.5852/ejt.2020.700

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Van Steenberge M, Vanhove M, Chocha Manda A, Larmuseau M, Swart B, Khang'Mate F, Arndt A, Hellemans B, Van Houdt J, Micha JC, Koblmuller S, Roodt-Wilding R, Volckaert, FAM, 2020. Unravelling the evolution of Africa's drainage basins through a widespread freshwater fish, the African sharptooth catfish *Clarias gariepinus*. Journal of biogeography 47 (8) , 1739 -1754. https://doi.org/10.1111/jbi.13858

Vranken N., M. Van Steenberge & J. Snoeks (2020) Similar ecology, different morphology: the oral mollusc shellers from Lake Edward. Journal of Fish Biology, 96(5), 1202-1217, https://doi.org/10.1111/jfb.14107

Vranken N, M Van Steenberge, A Balagizi, J Snoeks (2020) The synonymy of *Haplochromis pharyngalis* and *Haplochromis petronius* (Cichlidae), Journal of Fish Biology, 97(5), 1554-1559, https://doi.org/10.1111/jfb.14455

Musinguzi L, S Bassa, V Natugonza, M Van Steenberge, W Okello, J Snoeks, R Froese (2021) Assessment of exploited fish species in the Lake Edward System, East Africa. Journal of Applied Ichthyology, *37* (2), 216-226, https://doi.org/10.1111/jai.14161

Rosentreter JA, AV Borges, PA Raymond, BR Deemer, MA Holgerson, CM Duarte, S Liu, C Song, GH Allen, J Melack, B Poulter, D Olefeldt, TI Battin, BD Eyre (2021) Aquatic ecosystems are the most uncertain but potentially largest source of methane on Earth, Nature Geoscience, https://doi.org/10.1038/s41561-021-00715-2

Stoyneva-Gärtner M, Gärtner G, Uzunov B, J-P Descy & W Okello (in press) Cyanocystopsis kitagatae gen. et sp. nov. (Cyanoprokaryota/Cyanobacteria) from the tropical lake Kitagata (Uganda, Africa), Wulfenia

Borges AV, L Deirmendjian, S Bouillon, W Okello, T Lambert, FAE Roland, VF Razanamahandry, NRG Voarintsoa, F Darchambeau, J-P Descy, GH Allen, C Morana (in revision) Greenhouse gas emissions from African lakes are no longer a blind spot

Vranken, N. Van Steenberge, M., Heylen, A, Decru, E & J. Snoeks (in review) From a pair to a dozen: the piscivorous species of *Haplochromis* (Cichlidae) from the Lake Edward system. European Journal of Taxonomy.

Diedericks G., Maetens, H. Van Steenberge M. & J. Snoeks (in review) Testing for hybridization between Nile tilapia (*Oreochromis niloticus*) and blue spotted tilapia (*Oreochromis leucostictus*) in the Lake Edward system. Journal of Great Lakes Research.

Decru E, Vranken N, Maetens H, Mertens De Vry A, Kayenbergh A, Snoeks J, &M. Van Steenberge (submitted). DNA barcoding the Lake Edward basin: high taxonomic coverage of a tropical freshwater ichthyofauna. Biodiversity and Conservation

Odongkara Okecha K, Bwambale M, Akumu J, Okura R, Aroni I, Nasuuna A, Okello W, Ocaya H, Decru E, Snoeks J & M Van Streenberge (submitted) Perceptions on fisheries and socio-economic conditions of fishing communities at Lakes Edward and George, Queen Elisabeth National Park, Uganda. Journal of Great Lakes Research

6.2. OTHERS

M.Sc.theses

- The thick-lipped haplochromine cichlids of the Lake Edward system: a morphometric revision, by Nathan Vranken, 2016-2017, KU Leuven.
- The piscivorous haplochromine cichlids of the Lake Edward system: a morphometric revision, by Annelies Heylen, 2016-2017, KU Leuven.
- Diet analyses of the six most commercial fish species in the Lake Edward system, by Lindsay Cox, 2017-2018, KU Leuven.
- A revision of the *Enteromius* species (Cyprinidae) from the Lake Edward basin (East Africa) by Heleen Maetens, 2018-2019, KU Leuven.
- Revising the generalist *Haplochromis* species (Cichlidae) from Lake Edward (East Africa) by Annelies Kayenbergh, 2018-2019, KU Leuven.
- Reconstructing the food web of the Lake Edward basin by Thom Kusters, 2018-2019, KU Leuven.
- A revision of the algae-scraping haplochromines from the Lake Edward system, by Sara Vandersteen, 2019-2020, KU Leuven.
- A revision of the offshore insectivorous haplochromines from the Lake Edward system, by Pieter Morlion, 2020-2021, KU Leuven.
- Janssens, A (2019). Recent changes in the ecology and biogeochemistry of Lake Edward as recorded in isotope proxies in sediment cores. MSc thesis, KULeuven.

B.Sc. reports

- Sara Vandersteen (2016-2017): The piscivorous *Haplochromis* species (Teleostei, Cichlidae) of the Lake Edward system: a geomorphometric approach, KU Leuven.
- Amber Mertens (2016-2017): Diversiteit van het genus *Enteromius* (Teleostei, Cypriniformes) in het stroombekken van het Edwardmeer, Centraal-Afrika, KU Leuven.
- Annelies Kayenbergh (2016-2017): De diversiteit van *Clarias* (Teleostei, Siluriformes) en tilapias (Teleostei, Cichliformes) in het Edwardmeerbekken (DR Congo, Oeganda) , KU Leuven.
- Senne Heeren (2017-2018): Reproductive biology of two *Oreochromis* species from the Lake Edward-George system, KU Leuven.
- Stef Jans (2018-2019): Een geometrisch morfometrische studie op enkele *Enteromius*-soorten van het Edwardsysteem, KU Leuven.
- Caitlin Man (2018-2019): A geometric-morphometric study of the pelagic *Haplochromis* species of the Lake Edward system, KU Leuven.
- Vincent Van Obbergen (2018-2019): Geometrisch- morfometrische studie van het *Haplochromis schubtoziellus* complex uit het Edwardmeersysteem, KU Leuven.
- Marlies Laethem (2019-2020): A geometric morphometric analysis of the *Enteromius alberti* complex (Cyprinidae) from the Lake Edward system, KU Leuven.
- Liz Vanderhaeghe (2019-2020): A geometric morphometric analysis of the generalised *Haplochromis* species (Cichlidae) from the Lake Edward system, KU Leuven.

- Amber Matté (2020-2021): The thick-lipped haplochromine cichlids of the Lake Edward system: a geometric morphometric approach, KU Leuven.
- Isabelle Splengler (2020-2021): The offshore insectivorous haplochromine cichlids of the Lake Edward system: a geometric morphometric approach, KU Leuven.
- Rémi Shair. (2019): Structuration de populations de *Clarias gariepinus* (Burchell, 1822) du lac Edouard et du lac George par microsatellites. BSc thesis. Institut Roger Lambion, Anderlecht.
- Charlotte Willems. (2020): Optimalisatie van microsatelliet analyse op Nijl Tilapia (Oreochromis niloticus). BSc thesis. Vives hogeschool, Roeselare.
- Aerts R, De Bock A, Dewaele M, & Van Campenhout H (2018) Climate variation in the Lake Edward region: an isotope study in cellulose of a tree core. BSc integrated project report, KU Leuven.
- Braekmans J, Langenberg C, Mng'ong'o M, & Simons J (2020) Vegetation changes in the Lake Edward region: using stable isotopes in Hippopotamus teeth as a natural archive. BSc integrated project report, KU Leuven.

Fishbase internship and study visit reports

- Mulongaibalu Mbalassa (2017): Study of the pelagic *Haplochromis* species from Lake Edward, Albertine rift valley.
- Laban Musinguzi (2018): A possibility of two new haplochromine cichlid species and sexual dimorphism in *Haplochromis eduardii*, Regan 1921 in Lake Edward.
- Désiré Balagizi (2019): *Haplochromis pharyngalis* et *Haplochromis petronius*, quelle différence?
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7. ACKNOWLEDGEMENTS

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