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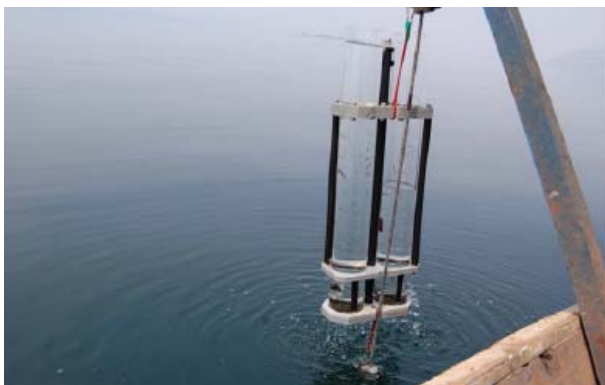
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**Hydrological variability and biogeochemistry
of particulate organic matter of a large
tropical rift lake, Lake Kivu (East Africa)**



A dissertation submitted by
Fabrice Amisi Muvundja
In partial fulfillment of the
requirements for the degree of
PhD in Biological Sciences
March 2015



Faculty of Sciences
Department of Biology
Research Unit in Environmental and
Evolutionary Biology

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Edith Munyiragi M.

Eliane Mangomindja M.

Preface

Kivu, the Heart of the Wonderland of Eastern Congo

When you think of Kivu, think of a vast land embellished by large lakes, rivers and streams; active, sleeping and dead volcanoes (“Virunga”); mountains (Rwenzori or the “Mountains of the Moon”, the Mitumba mountain chains, etc.), cascading hills, plateau and escarpments; valleys and ravines; forests and savannahs; unusual high biodiversity density (among the highest, if not the highest on Earth) both for human (lots of tribes and clans) and non-human (plant and animal species), etc., dwelling on a seldom mineral-rich underground. This is a land where life has learned to coexist with the fury of the Earth made of a continuously threatening and hazardous environment, fortunately softened by a marvellous and fertile landscape.

The literature is full of romantic stories from contemplators and travellers which illustrate the wonderful features of the Kivu highland region as quoted below:

“From the southern end of the lake a dull-red glare in the night sky became stronger as they (Ndlr, Sir Alfred Sharpe and Hon. Mountstuart Elphinstone) went north and there were dense black clouds by day in the same direction. From Bobandana, at the north-west corner of the lake, a splendid view was obtained of the erupting volcano seven miles away, [...]. A broad, swift river of lava flowing into the Kabino [Ndlr Kabuno bay] inlet of Lake Kivu, three miles from the volcano (Ndlr, Nyamulagira). The water in that part of the lake was heated to boiling point....Thousands of dead fish were floating in the northern end of Lake Kivu. Twelve miles from the volcano the water was too hot to bathe in. For miles the land was black, with no green leaf or blade to be seen, and many dead birds and small mammals were found, evidently killed by the showers of volcanic material. Hundreds of natives were killed. The eruption was audible at Beni 140 miles away to the north, and at Bukoba (Ndlr, Tanzania), on the Victoria-Nyanza, 190 miles East, while ashes fell heavily for two days at Walikali (Ndlr, Walikale), in the Congo forest, 100 miles to the West” (In: A new volcano in the Kivu Country, Nature 30, 1916).

....

“I spent six weeks of a really hard work hunting gorillas between the volcanoes of Mikeno and Karisimbi and chasing chimpanzees in the bamboo-covered ravines of the Bugoie [Ndlr, Bugoyi] Forest, after which I was glad enough to rejoin my wife, whom I had left at Kisenyies [Ndlr, Gisenyi]. As this place is one of the loveliest spots in Africa, both as regards to climate and scenery, where the lotus life” is really possible, I found my wife had been really enjoying herself in my absence” (Round Lake Kivu-Rwakataraka and the fairy forest of Rugega, In: Barns, T.A., Across the Great Craterland to the Congo, Salzwasser Verlag, 1923).

According to the local culture legend, the space occupied by Lake Kivu was originally a wonderful land before a cataclism occurred ordered by God to punish human indiscretion [Pagès , In Ruanda, sur les bords du lac Kivou (Congo), Ethnologie, Histoire et Religion, 1933]

That is a briefing welcome to the complex environmental settings of the lake studied in this thesis.

« La patience est amère mais son fruit est délicieux ».

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Summary

The conservation of Great Lakes for sustainable ecosystem service benefits has become an important research question. Lakes can be sensitive to climate variability and changes as well as human intervention. Perturbations of a lake's hydrology affect the limnology and biogeochemical cycles and induce important consequences on the ecosystem functioning. This thesis analyzed the recent hydrological records of Lake Kivu in relationship to meteorological variation as well as the dynamics of particulate organic matter (POM) cycling with focus on sources, vertical export and fate, and paleolimnological significance. Lake Kivu is better known due to its enormous and hazardous dissolved gases ($\text{CO}_2 + \text{CH}_4$). The important CH_4 resource is biogeochemically produced at the water-sediment interface under anoxic conditions thanks to methanogenic bacteria by two pathways: (1) the reduction of geogenic CO_2 ($\sim 2/3$) in which OM may serve as electron donor, and (2) by OM fermentation ($\sim 1/3$).

The water level of Lake Kivu was estimated based on an extensive precipitation dataset using a relatively simple water balance model for both the catchment and the lake. For the time period with a good availability of rainfall data, the predicted water levels as well as their seasonal variation agreed well with observations, indicating that the observed variations in the water level were mainly driven by the variation in precipitation. The lack of rainfall data after 1991 seriously impaired the predictive capability of the model. This highlights the importance of hydrometric and meteorological monitoring data for reconstructing the lake water balance of East African Great lakes. The construction of a hydropower dam at the outlet at the end of 1950s did not show any clear effect on the lake water level dynamics, whereas a modification of the outlet in 1977 seems to have induced some interannual variability in the lake levels.

The subaquatic groundwater system is an important hydrological component for this Rift Lake in terms of water, dissolved solid and heat inputs beneath the lake surface sustaining the permanent lake stratification and nutrient uplift to the mixolimnion from the deep waters. The nutrients made available by internal loading feed the phytoplankton growth. Prior to this work, little was known about the decaying POM, the relative importance of its export and its fate into the monimolimnion as well as on how the presence of organic molecules and the elemental/stable isotope signatures in sedimentary material can be interpreted to reconstruct the historical records

of the lake productivity, the origin and preservation of POM, the phytoplankton community structure, nutrient cycling and mixing regime.

Organic matter (OM) in Lake Kivu is essentially autochthonous as evidenced by stable isotopes and molecular biomarkers. Its production and sedimentation fluxes are highly seasonal. They depend on the mixing status of the water column. Most of the pigment degradation occurs between 30 and 60 m water depth. The particulate organic carbon export to the monimolimnion is closer to 6% of the primary production indicating a high conversion rate of POM into dissolved organic matter and thus an efficient recycling of nutrients within the mixolimnion.

Some phytoplankton pigments such as lutein, alloxanthin and zeaxanthin were preserved throughout the water column and within the sediment archives suggesting that they are good paleolimnological proxies for tracing the history of phytoplankton group distribution in the lake. However peridinin, fucoxanthin and diadinoxanthin were completely degraded prior to settlement. This study also showed that Lake Kivu underwent alternating periods of high and low productivity caused by nutrient availability changes forced by subaquatic groundwater dynamics. An intermittent dynamics of carbonate was also observed. Periods of organic carbon-rich sediment accumulation characterized by low carbonate concentrations alternated with periods of low to moderate carbon concentrations and high carbonate preservation. A high carbonate flux to the monimolimnion occurred during periods with strong stratification. The low carbonate content in organic-rich sediments was interpreted as a consequence of re-dissolution caused by acidogenesis during diagenetic sedimentary OM fermentation.

Résumé

La conservation de grands lacs dans le but de pérenniser leurs services écologiques est devenue une question importante de recherche. Les lacs peuvent être sensibles aux variations et changements climatiques ainsi qu'aux modifications imposées par l'homme. Les perturbations hydrologiques d'un lac affectent sa limnologie et ses cycles biogéochimiques, pouvant conduire à des conséquences notables dans son fonctionnement en tant qu'écosystème. Cette thèse analyse les données hydrologiques récentes du lac Kivu en relation avec les variations météorologiques de son bassin versant. Elle étudie en plus la dynamique du cycle de la matière organique particulaire en se focalisant sur ses sources, son transport vertical et son devenir lors de la sédimentation, ainsi que son importance dans la reconstruction de l'histoire du lac Kivu. Le lac Kivu est mieux connu grâce à son énorme contenu en gas dissous ($\text{CO}_2 + \text{CH}_4$). Cette importante ressource en CH_4 est produite biogéochimiquement par des bactéries méthanogènes en milieu anaérobie suivant deux voies à savoir : (1) la réduction du CO_2 géogénique ($\sim 2/3$) pouvant utiliser la matière organique comme donneur d'électron et (2) la fermentation de celle-ci ($\sim 1/3$).

Le niveau d'eau du lac Kivu a été reconstitué sur base d'une importante base de données de précipitations en utilisant un modèle mathématique simple de bilan d'eau aussi bien pour le bassin versant que pour le lac lui-même. Pour la période avec une bonne couverture par de données de pluies, les niveaux d'eau calculés ainsi que leur variation saisonnière ont reflété les observations enregistrées sur le terrain ; ce qui signifie que les variations observées dans les niveaux d'eau du lac étaient essentiellement liées aux variations des précipitations. Le manque de données pour la période d'après 1991 a sérieusement impacté la capacité du modèle à prédire les niveaux d'eau du lac. Ceci démontre sans équivoque la nécessité d'un monitoring hydrométrique et météorologique du lac et du bassin versant afin d'améliorer la précision des estimations de bilan hydrique des Grands lacs de l'Afrique de l'Est. La construction d'un barrage hydroélectrique à l'exutoire du lac à la fin des années 1950 n'a pas eu d'effet manifeste sur la dynamique du niveau d'eau du lac. Cependant la modification apportée à la morphologie de l'exutoire en 1977 semble avoir induit une certaine variabilité interannuelle des niveaux d'eau.

Le système d'eaux souterraines subaquatiques est une composante importante de l'hydrologie de ce lac du Rift en termes d'apports en eau, en sels dissous et en chaleur injectés en dessous de la surface du lac permettant ainsi une stratification permanente du lac et un flux ascendant de

nutriments en provenance des eaux profondes vers le mixolimnion. Ces nutriments apportés par une recharge interne des eaux de surface stimulent la croissance du phytoplancton. Bien avant cette étude, relativement peu d'informations étaient connues à propos du devenir de la matière organique particulaire, ni sur l'importance de son exportation vers les eaux profondes comparativement à la production primaire, lors de la sédimentation dans la colonne d'eau et de la formation des dépôts sédimentaires. Rien n'était connu non plus sur la signification paléolimnologique de différentes archives sédimentaires, comme les molécules organiques préservées dans les sédiments et les signatures isotopiques et élémentaires. Ces « proxies » peuvent donner des informations sur les changements de productivité, de composition de la communauté phytoplanctonique, ainsi que sur l'origine et la préservation de la matière organique, le cycle des nutriments et le régime de mélange des eaux.

Ainsi que l'indiquent des biomarqueurs isotopiques et moléculaires, la matière organique du lac Kivu est essentiellement d'origine autochtone. Sa production et son accumulation dans les eaux profondes varient en fonction des saisons, qui déterminent les alternances de périodes de mélange et de stratification de la partie supérieure, oxygène, de la colonne d'eau, appelée mixolimnion. Des mesures de pigments phytoplanctoniques, dont la chlorophylle a et ses dérivés, montrent qu'une dégradation importante se produit sous la zone photique, entre 30 m et 60 m de profondeur. L'analyse de la matière organique dans des trappes à sédiments disposés sous le mixolimnion suggère que le flux de carbone vers les sédiments représente environ 6% de la production primaire. Ceci suggère qu'une fraction majeure de la matière organique produite par le plancton de la zone pélagique est recyclée dans le mixolimnion par les microorganismes hétérotrophes.

L'analyse de la matière particulaire accumulée dans les trappes montre une bonne préservation des pigments caroténoïdes du phytoplancton. Ainsi, la lutéine, l'alloxanthine et la zéaxanthine sont bien préservés dans la colonne d'eau et dans les sédiments, indiquant leur potentiel en tant qu'outils paléolimnologiques utilisables comme traceurs des modifications de la composition du phytoplancton du lac au cours du temps. D'autres pigments comme la péridinine, la fucoxanthine et la diadinoxanthine, présents dans les trappes, ne sont pas retrouvés dans les sédiments, suite à leur dégradation au cours de la sédimentation dans les eaux profondes ou à la surface du sédiment. Les différents marqueurs paléolimnologiques étudiés montrent que le lac Kivu a

présenté, au cours de l'Holocène, des variations de productivité, résultant de changements de disponibilité de nutriments. Une variation dans l'accumulation des carbonates dans les sédiments est aussi observée. Des périodes d'accumulation de sédiments riches en carbone organique mais pauvres en carbonates alternent avec des périodes de concentrations plus faibles de carbone organique mais beaucoup plus riches en carbonates. Il est possible qu'une forte déposition de carbonates dans le monimolimnion se soit produite pendant des périodes de forte stratification. La faible concentration en carbonate de la strate sédimentaire très riche en carbone organique était interprétée comme une conséquence de la re-dissolution provoquée par l'apparition d'une acidité relativement forte due à la fermentation, lors de la diagenèse, de l'abondante matière organique enfouie dans les sédiments.

Chapter 1. General introduction

1.1. Overview

The present thesis addresses recent changes in the hydrology and the biogeochemistry of Lake Kivu, a lake with many exceptional properties located in the East African rift. Several topical studies indicated significant recent changes in this lake which had been previously thought to be in a near-steady state, where important alterations in the biogeochemistry would occur only on time scales of centuries or longer. The reasons for these changes have been widely discussed, but the complexity of the system, concurrent alterations in different external factors such as climate, population growth, and the introduction of an alien fish species, as well as the lack of long-term data despite large efforts made in the past decades, make it difficult to draw definite conclusions on the causes and the extent and importance of the observed changes. The present thesis aims at shedding light on some aspects of these changes and their causes. In the following sections, first Lake Kivu and its special properties are described, followed by a general introduction on the hydrology of East African lakes and of the proxies used in the present to assess recent changes in the biogeochemistry of Lake Kivu.

1.2. Geological settings, limnology and biogeochemistry of Lake Kivu

1.2.1 Geology and hydrology

The East African great lakes are located in the vast East African Rift System (EARS, $\sim 4.5 \times 10^6$ km²; Hall and Diggins, 2011) which consists of two branches, namely the Western Branch, known as Albertine Rift (e.g., Lakes Albert, Edward, Kivu, Tanganyika) and the Eastern Branch, called Gregory Rift (e.g., Lakes Victoria, Turkana and Malawi/Nyassa). In this region, intense tectonism and volcanism have led to land depressions, geological thrusts and terrain subsidence. The resulting depressions were filled by water from precipitation and runoff exceeding evaporation (Sene and Plinston 1994; Bergonzini, 1998; Crétaux et al., 2011). The region harbors the largest and deepest lakes in Africa and some of the most important in the world.

The hydrological regime of these lakes is determined by the local climatic conditions which are marked by alternating wet and dry seasons (Becker et al., 2010). Modern East African lakes are open lakes with considerable outflow. Fluctuations in the lake water volume reflect changes of precipitation to evaporation over the lakes' surfaces and their catchments, meaning that these fluctuations may serve as indicators of a lake's sensitivity to past and present climate changes at local and regional scales (Becker et al. 2010).

The hydrogeology of rift lakes is often complex due to the potential influence of faults and porous volcanic and volcanoclastic media on groundwater (Olaka 2011). Stream flow infiltration is common in rift region, and other rivers in the catchment disappear and reappear along their course to the lakes (Olaka 2011).

Specifically for Lake Kivu, the most elevated lake of the African rift (1460 m a.s.l.; 2370 km² of area; 485 of maximum depth), the water balance components include rainfall, runoff (made of a hundred of small rivers and streams, Muvundja et al. 2009) and subaquatic groundwater discharge (SGD) as inputs, and evaporation and outflow as outputs (Bergonzini 1998; Schmid and Wüest 2012; this thesis, chap. 2). The Ruzizi River is the outflow (2.7 km³ yr⁻¹; this thesis, chap. 2) and links the lake to Lake Tanganyika southward (~30% of the total inflow to Lake Tanganyika; Vandellanote et al. 1999). Subaquatic water inputs (1.3 km³ yr⁻¹, Schmid et al., 2005), heat and salt inputs (Schmid et al., 2005) from groundwater sources to the monimolimnion play an important role in the thermohaline stratification (Damas, 1937; Degens et al., 1973) of this volcanic lake and therefore in its chemistry and microbiology (Schmid et al., 2005; Pasche et al., 2009; Schmid and Wüest, 2012; Bhattarai et al., 2012; Llíros et al., 2012; Ross et al., 2015a) making it a unique and fascinating crenogenic lake for limnologists and biogeochemists.

1.2.2. Limnology

Lake Kivu is meromictic with a mixolimnion down to ~60 m and an anoxic monimolimnion (Fig. 1, Schmid et al., 2004, 2005; Sarmiento et al., 2006, Isumbisho et al., 2006) rich in dissolved CO₂ (~300 km³, STP) and CH₄ (~60 km³, STP) (Schmitz and Kufferath, 1955; Capart and Kufferath, 1956; Tietze et al., 1980; Schmid et al., 2004, 2005; Wüest et al. 2012). As in other African great lakes, internal loading has been found to be the most prominent factor of the

nutrient fluxes sustaining primary production in the epilimnion (Hecky and Kilham, 1988; Kilham and Kilham, 1990; Muvundja et al., 2009; Pasche et al., 2012). In Lake Kivu, an important subaquatic groundwater discharge (SGD), which consists of hot and cold waters depending of the inflow depths (Ross et al., 2014), drives a slow upwelling which entrains nutrients towards the mixolimnion (Schmid et al. 2010; Schmid and Wüest, 2012; Carpenter et al., 2012; Ross et al., 2015a). The SGD is also the main source of salts, CO₂ and heat to the deep waters and is the cause for the permanent thermohaline stratification in the lake.

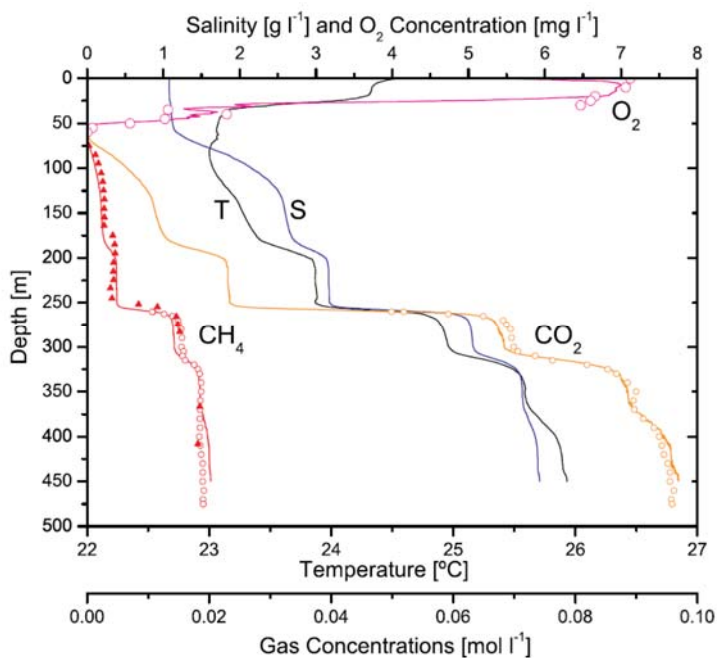


Figure 1. Vertical profiles of temperature (T), salinity (S), and dissolved gas concentrations in Lake Kivu (from Schmid et al., 2005)

The permanent thermohaline stratification allowed the accumulation of the dissolved gases (CO₂, CH₄, H₂S, etc.) in the monimolimnion. The residence time of methane in the lake has been estimated at ~800 yrs (Schmid et al., 2005). Two thirds of the methane originate from the microbial reduction of geogenic CO₂ while the remaining part is produced from organic matter fermentation via acetoclastic methanogenesis (Tietze et al., 1980; Schoell et al., 1988; Pasche et al., 2011). Recently, Pasche et al. (2011) estimated the CH₄ formation rate to 72 g C m⁻² yr⁻¹ or

0.27 km³ yr⁻¹ and the net accumulation to 0.14 km³ yr⁻¹ (which represents 50% of the annually formed CH₄), or 0.2% of the total methane reservoir of the lake (Wüest et al., 2012). The major sink of CH₄ was found to be aerobic oxidation by methanotrophs (Jannasch et al., 1975; Pache et al., 2011)

The ongoing plans for methane resource exploitation for power production are believed to be the most convenient way of dealing with the potential natural hazards borne by this gas accumulation within the lake towards saturation (Schmid et al., 2004, 2005; Tietze, 2007; Wüest et al., 2009, 2012) because the pending threat to human population can be avoided and wealth generated meanwhile, if proper extraction management practices are applied.

Compared to other East African lakes, Lake Kivu's flora and fauna are poorly diversified (Cunnington, 1920; Verbeke, 1957; Isumbisho et al., 2006; Sarmiento et al., 2007, 2008; Snoeks et al., 2012). Massive fish extinctions are believed to have occurred in the lake several times in past geological times (Haberyan and Hecky, 1987; Verheyen et al., 2003).

In total only 42 taxa of pelagic phytoplankton were recorded in the lake flora: 14 taxa for cyanobacteria, 3 for Cryptophyceae, 3 for Dinophyceae, 7 for Bacillariophyceae, 1 for Chrysophyceae, 7 for Chlorophyceae, 3 for Trebouxiophyceae and 4 for Charophyceae (Sarmiento et al., 2008). The most common phytoplankton taxa in Lake Kivu are the pennate diatoms *Nitzschia baccata* and *Fragilaria danica* and the cyanobacteria *Planktonlyngbya limnetica* and *Synechococcus sp.* (Sarmiento et al., 2008). Near the surface under stratified conditions, some development of the centric diatom *Urosolenia sp.* and the cyanobacterium *Microcystis sp.* has been reported by Sarmiento et al. (2008). Vertical stratification seemed to be the most important factor driving taxonomic and functional diversity in the phytoplankton of Lake Kivu.

The phytoplankton community in Lake Kivu is dominated by diatoms, cryptophytes, chrysophytes, chlorophytes, cyanophytes and dinoflagellates (Fig. 2 A&B; Sarmiento et al., 2012; Darchambeau et al., 2014). The interannual fluctuation of the lake surface water mixing regime (Fig. 2C) and nutrient upwelling (Pasche et al., 2012), that of the euphotic zone (Fig. 2D) and light penetration (Fig. 2 E) are linked to that of the algal production (Fig. 2F). Seasonality is clearly expressed in algal specific dominance: Diatoms are favored by the dry season (June to

September) with a maximum specific photosynthetic rate of $7.21 \text{ g C g Chla}^{-1}\text{h}^{-1}$, and cyanobacteria by the rainy season (September to June) with a maximum specific photosynthetic rate of $1.13 \text{ g C g Chla}^{-1}\text{h}^{-1}$ (Darchambeau et al., 2014).

Heterotrophic bacteria (HB) and photosynthetic picoplankton (PPP) cell numbers were found to be always high in the mixolimnion but PPP concentrations ($10^5 \text{ cell. ml}^{-1}$) were higher than HB (Sarmiento et al., 2006). Stenuite et al. (2009) reported that the contribution of bacterial production by HB to the particulate matter in the top 60 m of Lake Tanganyika was equivalent to $93\text{-}735 \text{ mg C m}^{-2} \text{ day}^{-1}$ compared to $150\text{-}1687 \text{ mg C m}^{-2} \text{ day}^{-1}$ for photosynthetic production. For Lake Kivu, the mean bacterial production was estimated to $336 \text{ mg C m}^{-2} \text{ day}^{-1}$ (Llirós et al., 2012) against $620 \text{ mg C m}^{-2} \text{ day}^{-1}$ of photosynthesis (Sarmiento et al., 2012; Darchambeau et al., 2014). Morana et al. (2014a) estimated that in Lake Kivu, the bacterial carbon demand should range between $1680 \text{ mg C m}^{-2} \text{ d}^{-1}$ and $3360 \text{ mg C m}^{-2} \text{ d}^{-1}$ against $1550\text{-}3100 \text{ mg C m}^{-2} \text{ d}^{-1}$ for Lake Tanganyika.

Three populations of picocyanobacteria were identified by Sarmiento et al. (2006) namely: *Synechococcus* and two other colonial categories. The *Synechococcus* biomass in the euphotic zone (from the surface to 15-18 m depth) was estimated to 24.7 mg C m^{-3} whereas the mean HB biomass in the same zone was 31.5 mg C m^{-3} corresponding (Sarmiento et al., 2006).

Previous studies (Damas, 1937; Verbeke, 1957; Dumont, 1986; Isumbisho et al., 2006) revealed also a low diversity of zooplankton species. Current mesozooplankton is dominated by cyclopoid copepods (*Thermocyclops consimilis*, *Mesocyclops aequatorialis* and *Tropocyclops confinis*) but cladocerans and rotifers are also present (Isumbisho et al., 2006). The seasonal dynamics closely responds to variations of chlorophyll a concentrations and to the dry season phytoplankton peak (Darchambeau et al., 2012). The mean annual production rate of crustaceans was estimated to $23 \text{ g C m}^{-2} \text{ yr}^{-1}$ which represents a trophic transfer efficiency of 6.8% between phytoplankton and zooplankton grazers (Darchambeau et al., 2012).

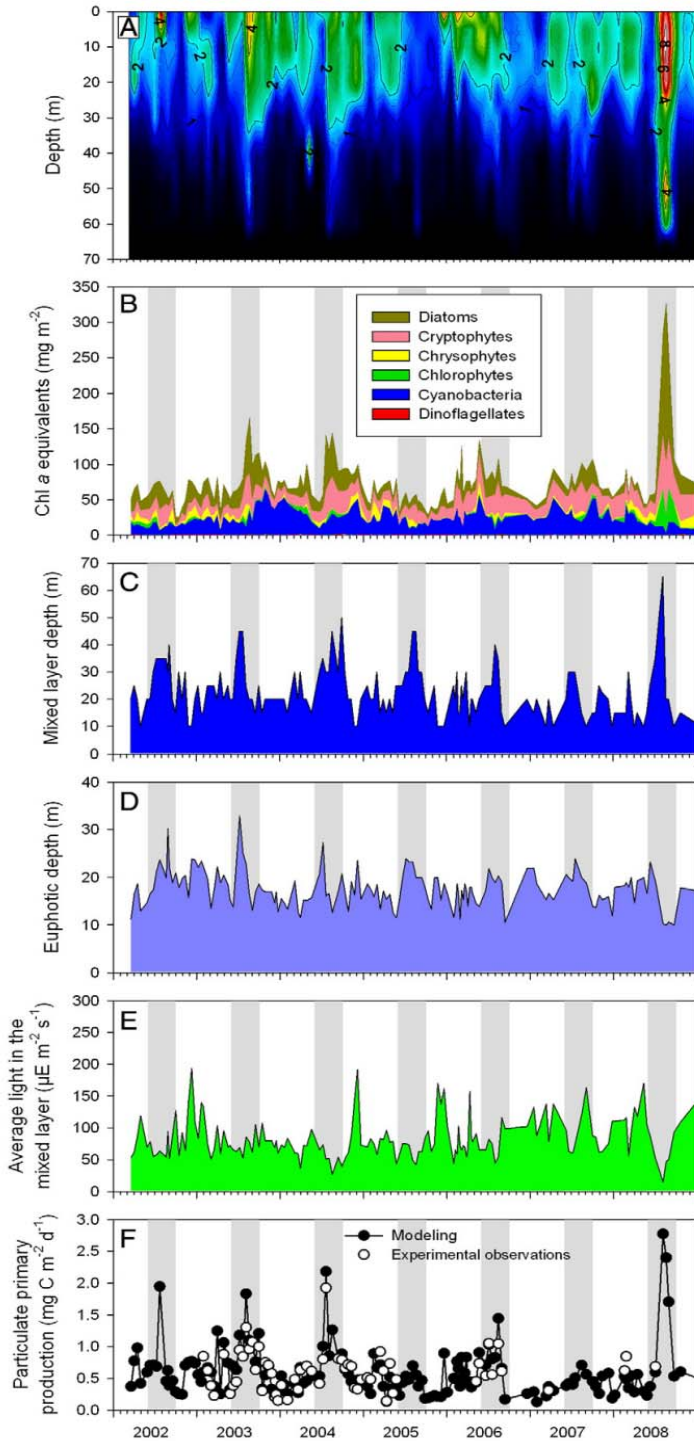


Figure 2. Interannual variation of phytoplankton biomass and production and of some physical parameters relevant for primary production in Lake Kivu (from Darchambeau et al., 2014): (A) Vertical distribution of phytoplankton biomass (Chlorophyll a, mg m^{-3}), (B) areal chlorophyll a concentrations and biomass composition from marker pigment analysis, (C) depth of the mixed layer, (D) depth of the euphotic layer, (E) average light in the mixed layer, (F) daily depth-integrated primary production with photosynthetic parameters. The gray boxes identify the main dry season periods.

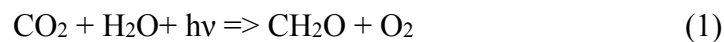
1.3. Geochemistry of organic matter in aquatic environments

1.3.1. Organic matter cycling

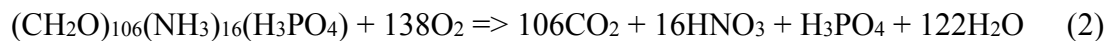
The distributions of major chemical elements C, N, S, P and O between living and non-living organic matter are linked to various inorganic reservoirs by dynamic biogeochemical cycles (Pantoja and Wakeham 2000). In aquatic environments, primary organic matter is biosynthesized from inorganic nutrients by phytoplankton, using light as the major energy source via photosynthesis.

The photosynthetic reactions generating aquatic OM differ from those of terrestrial OM because the proportions of C, N, S and P in aquatic algae are different from those of land plants (Mackenzie 1999). The ratio C:N:S:P in marine algae, known as the Redfield ratio is 106:16:1.7:1 (Redfield, 1963). In lakes, this ratio is known to vary significantly as a function of the nutrient status of the ecosystem (Guildford and Hecky 2000). In comparison, the C:N:S:P ratio for terrestrial plants averages 882:9:6:1 and is even more variable (Mackenzie, 1999). Land plants have higher carbon content because a larger fraction of their OM consists of carbohydrates rather than proteins.

The generalized photosynthesis equation for higher plants where the electron donor is H₂O is:



The chemical composition of marine phytoplankton can be expressed by the formula: (CH₂O)₁₀₆(NH₃)₁₆(H₃PO₄). Dead phytoplankton decays by reacting with O₂ in oxygenated environments to yield carbon dioxide, nitric acid, phosphoric acid and water:



The respiration and decay of phytoplankton by bacteria in anoxic environments requires other electron acceptors such as SO₄²⁻. Therefore equation (2) becomes:



Thus anoxic environments in meromictic lakes experience an accumulation of sulfide in case of low iron concentrations. Apart from these autochthonous sources of OM, aquatic ecosystems

may receive other organic inputs from their catchment (allochthonous sources). In aquatic ecosystems where respiration exceeds autochthonous gross primary production, net heterotrophy can be sustained only if aquatic respiration is subsidized by organic material from the terrestrial environment (Cole and Caraco, 2001).

Allochthonous sources of OM are composed of terrestrial plant detritus, soil humic substances and anthropogenic inputs whereas autochthonous sources consist of algal biomass which is biosynthesized from inorganic nutrients using light as the major source of energy (Wetzel, 2001). The resulting particulate organic matter (POM) is either consumed by various consumers (zooplankton in lakes, as well as various grazers) or decomposed by heterotrophic bacteria, yielding secondary production of OM (Legendre 1999; De La Rocha and Passow, 2007). Grazing, excretion, cell lysis and enzymatic hydrolysis of cellular material convert an important fraction of POM to the dissolved organic matter (DOM) pool (Pantoja and Wakeham, 2000; Morana et al. 2014b).

A fraction of the DOM and POM is embedded in the refractory phase depending on the environment but a significant fraction feeds the microbial loop involving heterotrophic bacteria and protozoa (Sarmiento, 2012; Alcocer et al., 2014). Furthermore a fraction of POM is not grazed by zooplankton and is only slightly altered by chemical processes during its sinking process as it aggregates and coagulates (De La Rocha and Passow, 2007). Therefore OM undergoes other chemical reactions such as hydrolysis, rearrangement, demetalation, oxidation, precipitation and complexation as well as photo-oxidation (Reuss, 2005).

Table 1. Nutrient biogeochemical processes and involved organisms in aquatic environments (modified after Stolz et al., 1989)

Nutr.	Process	Chemical equations (simplified)	Example of organisms involved
	CO ₂ fixation	CO ₂ + H ₂ O => CH ₂ O + O ₂	Photoautotrophs: cyanobacteria, purple and green sulfur Bacteria; chemoautotrophs (S and Fe oxidizing bacteria)
C	Methanogenesis	CO ₂ + 4H ₂ => CH ₄ + 2H ₂ O CH ₃ -COOH => CH ₄ + CO ₂	Methanogenic bacteria Methanogenic bacteria
	Methanotrophy	CH ₄ + 2O ₂ => CO ₂ + 2H ₂ O CH ₄ + SO ₄ ²⁻ => HCO ₃ ⁻ + HS ⁻ + H ₂ O CH ₄ + 4Fe(OH) ₃ => 4Fe ²⁺ + HCO ₃ ⁻ + 3OH ⁻ + 6 H ₂ O	Aerobic methanotrophic bacteria Archaea, sulfate-reducing bacteria Anaerobic heterotrophic bacteria
		5CH ₄ + 8NO ₃ ⁻ + 8H ⁺ => 5CO ₂ + 4N ₂ + 14H ₂ O	Crenarchaeota
	Biodegradation	2CH ₂ O => CO ₂ + CH ₄	Anaerobic heterotrophic bacteria
	Respiration	CH ₂ O + O ₂ => CO ₂ + H ₂ O	Aerobic heterotrophic bacteria
S	Sulfur reduction	SO ₄ ²⁻ + 5H ₂ => 2HS ⁻ + 4H ₂ O	Sulfur-reducing bacteria
	Sulfur oxidation	H ₂ S => S+ H ₂ 2S + 3O ₂ + 2H ₂ O => 2SO ₄ ²⁻ + 4H ⁺	Purple and green sulfur phototrophs Sulfur oxidizing bacteria
	N ₂ fixation	N ₂ + 3H ₂ => 2NH ₃	Phototrophic bacteria, nitrogen-fixing heterotrophic bacteria
N	Nitrification	R-NH ₂ + H ₂ O => NH ₃ + R-OH NH ₃ +H ₂ O => NH ₄ ⁺ +OH ⁻ 2NH ₄ ⁺ + 3O ₂ => 2NO ₂ ⁻ + 4H ⁺ + 2 H ₂ O NO ₂ ⁻ + O ₂ => 2 NO ₃ ⁻	Nitrifying bacteria Nitrifying bacteria Nitrifying bacteria
	Denitrification	NO ₂ ⁻ , NO ₃ ⁻ => N ₂ O, N ₂	Denitrifying bacteria

These processes which are collectively known as fermentation, respiration and decomposition consist of different steps: hydrolysis, acidogenesis, acetogenesis and methanogenesis. These biodegradation processes occur throughout the water column and in the sediments.

During the hydrolysis stage, particulates are solubilized and polymers (carbohydrates, esters, proteins) are split into simple molecules (monomers) which can be taken up by microbes (Morgenroth et al., 2002). During acidogenesis, these monomers (simple sugars, amino-acids and fatty acids) are converted into volatile fatty acids whereas in acetogenesis, volatile fatty acids are transformed into acetic acid, carbon dioxide and hydrogen (Ruel et al., 2002). Finally acetic acid

is converted into methane and carbon dioxide during methanogenesis, the final stage of anaerobic OM biodegradation (Ruel et al., 2002). These complex biochemical processes are mediated by a consortium of microorganisms (bacteria and archaea) specialized in transforming high weight organic compounds into end products of CO₂ and CH₄ (Table 1).

At the water/sediment interface, OM undergoes early diagenesis during which some labile molecules are resuspended and redissolved into the water column where they can become subject to microbial uptake. Within the sediments, most OM remains associated with particles or adsorbed on sediment grains such as clay. Freshly deposited materials, in particular after sedimentation of phytoplankton blooms, often form a thin detritus layer at the water/sediment interface (Jorgensen, 2000). This detritus layer is a site of high microbial activity and rapid organic matter degradation and mineralization following a number of biogeochemical processes (Table 1). At the end of these processes, simple molecules, such as CO₂, CH₄, H₂S, N₂O or N₂, etc., are formed (Table 1). CO₂ is a product of various organisms which utilize fermentation, anaerobic or aerobic respiration to produce energy (Brock and Madigan, 1991). Methane is generated by methanogenic bacteria from oxidation of primary organic compounds in surface anoxic sediments using SO₄²⁻, NO₃⁻, FeOOH, MnO₂, CO₂, etc. as source of oxygen (Lovley and Philips, 1988; Wehrli et al., 1995; Jørgensen, 2000; Macalady and Walton-Day, 2011). It can also be oxidized into CO₂ by methanotrophs (e.g. archaea) when it enters oxic waters. Sulfide [R-S-R(H), H₂S, HS⁻, S²⁻] accumulation in deep stratified anoxic waters is a product of these degradation pathways.

The sedimentary material remains subject to further diagenetic degradation whereas the refractory material is simply buried and sequestered into the sediment mud (Alcocer et al. 2014). Preservation of OM in aquatic environments depends on prevailing conditions such as light penetration, oxic/anoxic conditions, temperature, acidity/alkalinity, salinity, mixing regime, lake bathymetry, etc. (Canfield, 1994; Ingalls et al., 2000; Killops and Killops, 2005; Reuss, 2005).

Tropical lakes are constantly exposed to high temperatures and radiation compared to temperate lakes. Metabolism can be expressed in terms of metabolic potential which is regulated by temperature, solar irradiance and chemical reservoir (nutrients, electron acceptors, organic matter; Lewis, 2010). Therefore tropical lakes are considered more efficient in producing

phytoplankton on a similar nutrient base than temperate lakes but inefficient in cascading primary production to higher trophic levels (Lewis 1996). The decomposition processes such as microbial uptake (e.g., denitrification in deep waters) and photo-oxidation are assumed to be more relevant in the tropics than in the temperate regions but the scarcity of data do not allow any strong conclusion about any significant difference of microbial process magnitude between tropical and temperate lakes (Lewis, 2010; Sarmiento, 2012).

Furthermore in deep and permanently stratified tropical lakes, the rapidly sinking particulate matter quickly escapes aerobic mineralization due to the persistence of anoxic conditions in the hypolimnion (Lewis, 2010). Thus important nutrient (N and P) release occurs in deep waters (e.g., meromictic lakes) leading to nutrient accumulation within the hypolimnion but to less export to the sediments in contrast to holomictic (shallow) lakes which are easily fed in nutrients by seasonal complete mixing and upwelling (Bootsma and Hecky 1993; Hamblin et al. 2003). Internal nutrient cycling and upwelling are the main processes which supply nutrients to the epilimnetic zones of most East African deep lakes such as Lakes Malawi, Tanganyika and Kivu (Hamblin et al. 2003; Corman et al. 2010; Pasche et al. 2012).

1.3.2. Bulk biogeochemical proxies used in tracing organic matter dynamics in freshwaters

a) Carbon, nitrogen and biogenic silica

Different sources of organic matter have also different carbon to nitrogen ratios (Meyers, 1994; Meyers and Lallier-Verges, 1999). Autochthonous OM of sedimentary material in lakes are enriched in proteins, low molecular weight compounds rich in H and N atoms, thus, low C/N ratios (typically $C/N < 10$, Meyers and Ishiwatari, 1993; Meyers, 1994; Dean, 1999). Allochthonous terrestrial OM is enriched in humic, high molecular weight, C-rich compounds, and their C/N ratios tend to be much higher with values typically comprised between 20 and 30 (Meyers and Ishiwatari, 1993). Intermediate values of C/N may indicate either mixed sources of OM (Bouillon et al., 2007; Das et al., 2007; Thevenon et al., 2012) or a poor preservation due to advanced diagenetic degradation (authigenic C/N ratios) within the sediments (Rullkötter et al., 1998; Das et al., 2007).

Furthermore, biogenic silica composition of sediment archives is an important tool to trace siliceous algae such as fossil diatom abundance and environmental conditions during sedimentation and burial of phytoplankton (Conley, 1988; Pasche et al., 2010; Berg et al., 2013).

b) Carbon, nitrogen and oxygen stable isotopes

Carbon has two stable isotopes, namely ^{12}C and ^{13}C . Their natural abundance is about 98.9% and 1.1%, respectively (Nier, 1950). Nitrogen has also two natural stable isotopes, ^{14}N and ^{15}N , with relative abundances of 99.63% and 0.37% respectively; Nier, 1950; Rosman and Taylor, 1998). Oxygen has three stable isotopes, ^{16}O , ^{17}O , and ^{18}O with natural abundances of 99.757%, 0.038% and 0.205% respectively (Hoefs, 2009). Oxygen ratios are measured relative to Vienna Standard Mean Ocean Water (VSMOW) or Vienna Pee Dee Belemnite (VPDB) but VPDB is preferred for paleoclimate and hydrological studies (Drever, 2002). $^{18}\text{O}/^{16}\text{O}$ is preferred to $^{17}\text{O}/^{16}\text{O}$ in isotope geochemical proxy analyses because of the higher abundances of the two isotopes compared to ^{17}O .

The shifts in these isotopic ratios, noted $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{18}\text{O}$ respectively, are calculated relative to the VPDB and N_2 atmospheric compositions as standards respectively, as following:

$$\delta^{13}\text{C}(\text{‰}) = \left[\frac{(^{13}\text{C}/^{12}\text{C})_{\text{sample}}}{(^{13}\text{C}/^{12}\text{C})_{\text{standard}}} - 1 \right] \times 1000 \quad (1)$$

$$\delta^{15}\text{N}(\text{‰}) = \left[\frac{(^{15}\text{N}/^{14}\text{N})_{\text{sample}}}{(^{15}\text{N}/^{14}\text{N})_{\text{standard}}} - 1 \right] \times 1000 \quad (2)$$

$$\delta^{18}\text{O}(\text{‰}) = \left[\frac{(^{18}\text{O}/^{16}\text{O})_{\text{sample}}}{(^{18}\text{O}/^{16}\text{O})_{\text{standard}}} - 1 \right] \times 1000 \quad (2)$$

The VPDB is an international standard consisting of references normalized to the original PDB (calcium carbonate from a Cretaceous belemnite rostrum from the Pee Dee River in South Carolina, USA) with a $^{13}\text{C}/^{12}\text{C}$ isotope ratio of 0.0112372 (Nier, 1950; Hoefs, 2009). Atmospheric N_2 is the standard for $^{15}\text{N}/^{14}\text{N}$ analysis. $^{15}\text{N}/^{14}\text{N}$ in atmospheric air is 0.00367647 (Ryabenko, 2013).

Stable isotope data of OM can be used for addressing biogeochemical processes relevant to the carbon cycle of individual ecosystems (Meyers, 1994; Hayes et al., 1990; Leng and Marshall,

2004, Berg et al., 2013). Living organisms preferentially utilize lighter isotopes because of lower energy costs associated with breaking the chemical bonds, which results in significant isotope fractionations between the substrate (heavier) and the biologically mediated product (lighter) (Kendall and Caldwell, 1998). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are also useful proxies in discriminating between land plants and aquatic sources of organic carbon because these two sources bear different isotopic signatures (Street-Perrott, 2004; Das et al., 2007; Kristen et al., 2010).

Among land plants, C_3 plants are characterized by $\delta^{13}\text{C} = \sim -26\text{‰}$ whereas C_4 plants have $\delta^{13}\text{C}$ signatures between -14 to -10‰ , and CAM between -33 to -10‰ (O'Leary, 1981; Fry and Sherr, 1984; Schidolowski, 1988). Lake sediments have $\delta^{13}\text{C}$ values ranging from -36‰ to -16‰ (Fogel and Cifuentes, 1993; Goericke and Fry, 1994; Opperman, 2010).

1.3.3. Organic molecules as paleoecological biomarkers

Despite the various degradation pathways of sedimentary organic matter, some molecules are chemically stable and quite well preserved, so that they constitute valuable paleoecological indicators of many non-siliceous algae and other microorganisms (Reuss, 2005). These molecules are called biological markers or biomarkers. They are either fossil molecules, meaning that they originated from formerly living organisms or contemporary biogenic molecules if they are identified in fresh organisms (Eganhouse, 1997). Thus the prevailing phototrophic community is reflected by the sedimentary records of pigments and lipids, which can be used to track long-term changes in algae and bacterial populations (Leavitt and Hodgson 2001; Sinninghe-Damsté et al., 2002; Wright and Jeffrey, 2006; Volkman, 2006; Bechtel and Schubert, 2009a,b).

a) Pigment biomarkers in aquatic ecosystems

In aquatic environments, pigments are chemotaxonomically biosynthesized by phytoplankton (Table 2) in the euphotic layers, and therefore make an important tool for tracing phytoplankton organisms (Wright and Jeffrey, 2006; Schlüter et al., 2006; Descy et al., 2000, 2005, 2009). Pigment markers have been widely and successfully used to identify and quantify the various algal groups and even photosynthetic bacteria in all types of aquatic environments (e.g. marine, estuarine; Wright and Jeffrey 2006; freshwaters, Descy et al., 2009). In this technique, algal group biomass is estimated from pigment concentrations in the water column by calculations

based on molecular marker/Chlorophyll a ratios (e.g zeaxanthin/Chl a ratio for cyanobacteria and chlorophytes).

Several methods have been developed to derive the contribution of algal “classes” to chlorophyll a. The most popular is CHEMTAX (Mackey et al., 1996), a computing algorithm which can handle the presence of some markers in different phytoplankton groups, such as fucoxanthin in both diatoms and freshwater chrysophytes.

Thanks to such methods, pigment markers make it possible to distinguish a broad range of algal groups within a phytoplankton population, with many applications in oceanography and limnology (Mackey et al., 1996; Wright and Jeffrey, 2006; Descy et al., 2009; Jeffrey and Wright, 2006). The pigment approach has been applied to tropical lakes (e.g Lake Tanganyika; Descy et al., 2005; Descy and Sarmiento, 2008) and elsewhere both for marine and freshwaters (e.g., Wilmotte et al., 2002; Rodriguez et al., 2002; Yacobi, 2003). All of these studies have shown strong and interesting results. However CHEMTAX is not appropriate to sediment pigment assemblages due to selective degradation of the pigment biomarkers (Reuss, 2005).

Pigment biomarkers are restricted to chloropigments and carotenoids (Table 2). Phycobiliproteins are not used as chemical markers because algal classes that contain them are also easily recognized and counted by other techniques that detect biliprotein fluorescence directly in situ (Wright and Jeffrey, 2006; Jeffrey and Wright 2006). In addition, biliproteins are water soluble, and therefore are not extracted by organic solvents used in analyses of chlorophylls and carotenoids.

A study of pigment geochemistry in East-African lakes has shown a large variability in some pigment ratios with depth in deep stratifying lakes as well as seasonal variation relating to changes in water column structure (Descy et al., 2005, 2009). Pigment ratios correlated well with indicators of nutrient availability and light penetration (Descy et al., 2009). Chlorophyll a concentrations decreased with depth whereas its degradation products (phaeophytins and phaeophorbides) show an increasing trend (Descy et al., 2005).

Table 2. Main phytoplankton pigments and distribution among taxonomic groups

Pigment marker	Phytoplankton group	Reference
Alloxanthin	Chryptophyta, Dinophyta Type 4, Haptophyta Type 8, Chrysophyta Type 3	Descy et al. 2000; Schlüter et al. 2006
Antheraxanthin	Chlorophyta	Descy et al. 2000; Schlüter et al. 2006
Canthaxanthin	Euglenophyta	Descy et al. 2000; Schlüter et al. 2006
Chl a	all phytoplankton	Hurley and Armstrong 1990; Jeffrey et al. 1997
Chl b	Euglenophyta, Chlorophyta	Descy et al. 2000; Wright and Jeffrey 2006
Chl c1	Bacillariophyta Type 1, Dinophyta Type 1-4	Strain et al. 1971; Wright and Jeffrey 2006
Chl c2	Haptophyta Type 1,6-8	Strain et al. 1971; Wright and Jeffrey 2006
Crocoxanthin	Chlorophyta, Cryptophyta, Dinophyta Type 1-4 Haptophyta Type 1,6-8, Bacillariophyta Type 1, Cryptophyta Type 3,	Jeffrey et al. 1997; Wright and Jeffrey 2006
Diadinoxanthin	Euglenophyta	Hurley and Armstrong 1990; Descy et al. 2000
Diatoxanthin	Bacillariophyta	Schlüter et al. 2006; Wright et al. 2006
Divinyl Chl a & b	Prochlorophyta	Jeffrey et al. 1997; Wright and Jeffrey 2006
Echinenone	Cyanophyta Type 2 Bacillariophyta Type 1, Dinophyta Type 2&3, Haptophyta Type 1,6-8,	Descy et al. 2000; Schlüter et al. 2006
Fucoxanthin	Chrysophyta Type 3	Hurley and Armstrong 1990; Descy et al. 2000
Isorenieratene	Green sulphur bacteria	Koopmans et al. 1996; Dieser et al. 2010
Lutein	Chlorophyta, Prasinophyta Type 1	Descy et al. 2000; Wright and Jeffrey 2006
Myxoxanthophyll	Cyanophyta Type 1	Descy et al. 2000; Wright and Jeffrey 2006
Oscillaxanthin	Cyanophyta	Jeffrey et al. 1997; Schlüter et al. 2006
Peridinin	Dinophyta Type 1	Descy et al. 2000; Yacobi 2003
Violaxanthin	Chlorophyta, Chrysophyta, Bacillariophyta	Descy et al. 2000; Schlüter et al. 2006
Zeaxanthin	Cyanophyta Type 1&2, Chlorophyta	Jeffrey et al. 1997; Wright and Jeffrey 2006
β -carotene	Bacillariophyta, Chlorophyta, Prochlorophyta, Cryptophyta	Descy et al. 2000; Schlüter et al. 2006

In Lake Tanganyika, most pigments were located at 0-60 m with depth-integrated concentrations ranging from 36.4-41.3 mg m⁻² (representing concentrations 0.3-3.4 mg m⁻³), and decreased sharply downward while chlorophyll a degradation products were only detected at 100 m among 0-100 m sample sets (Descy et al., 2005). In Lake Kivu, Chl a concentrations in the mixolimnion were estimated at 2.2 mg m⁻³ (Sarmiento et al., 2006; Darchambeau et al., 2014) indicating a higher Chl a concentration for Lake Kivu than in Lakes Tanganyika and Malawi (Sarmiento et al., 2008 and references therein). In a preliminary study, the analysis of pigments showed a dominance of cyanobacteria pigments throughout the water column as well as a significant presence of bacteriochlorophyll and bacterial carotenoids in sediments, indicators of strong stratification conditions during the last 40 years (Knops, 2010).

b) Lipid biomarkers

Lipids are biochemical compounds soluble in organic solvents but insoluble in water. In contrast to carbohydrates and proteins which undergo hydrolysis to yield water soluble products of low molecular weight, chemically or biochemically degradable, lipids are preserved intact or converted into stable products (Breger, 1963). Lipids are major components of OM as energy storage (triacylglycerol esters of fatty acids) and/or membrane structural molecules (phospholipids and sterols).

The class of lipids can be divided into a variety of functional groups such as fatty acids esters, isoprenoids and terpenoids, alcohols and sterols, fatty acids and esters, hydrocarbons (n-alkanes, n-alkenes and cyclic compounds), etc.

Fatty acids and esters

Fatty acids are an important class of lipid tracers (Table 3) and exist in the nature mostly as esters. The specificity of some fatty acids has been used to assess the origins of organic matter in natural water samples (Saliot et al., 1991; Volkman et al., 1989; Bechtel and Schubert 2009a,b). For example, it is known that plankton derived OM inputs to POM lead to a mixture of 14:0,

16:0, 16:1w7, 18:1w9, 18:0, 20:5w3 and 22:6w3 (Saliot et al., 1991). In addition, high values of $\Sigma C_{16}/\Sigma C_{18}$ (Σ : sum of saturated and unsaturated fatty acids) and $C_{16:1}/C_{16:0}$ ratios are characteristic of diatoms (Claustre et al., 1988). Branched 15:0 and 17:0 iso- and anteiso-fatty acids as well as 18:1w7 are commonly used as bacterial biomarkers because of their strong predominance in microorganisms (Volkman et al., 1980; Bechtel and Schubert, 2009a,b).

Table 3. Selected lipid biomarkers used in tracing sedimentary organic matter sources

Lipid biomarker	Sedimentary OM sources	References
Phytol, n-alknols (nC14 to nC16), Campesterol, stigmasterol, sitosterol	Phototrophic organisms (algae)	Baker and Louda 1983; Tolossa et al. 2003; Rontani and Volkman 2003
Iso and anteiso C15:0 to C17:0 FAs	Heterotrophic bacteria (e.g. SRB)	Kaneda 1991
nC16:0 FA, Dinosterol and Dinostanol	Diatoms	Robinson et al. 1984, Bechtel and Schubert 2009a
C18:0 and C18:1 FAs	Cyanobacteria and bacteria	Tolosa et al. 2003&2008
Cholesterol, dehydrocholesterol, 24-methyl and 24-ethylcholesterol, cholestenol	Algal grazing/zooplankton	Bechtel and Schubert 2009b; Kristen et al. 2010
Tetrahymanol	Anoxia, Ciliates or phtosynthetic sulfur bacteria	Naeher et al. 2012
Hopanoids, hopanoic acid, diplopterol	Methanotrophic bacteria	Kristen et al. 2010
Alkylthiopene	Intense diagenesis under anoxic conditions	Marlow et al. 2001
Archaeol	Archaea	Zhang et al. 2003

Isoprenoids, terpenoids and steroids

Isoprene (2-methylbuta-1, 3-diene), a branched diunsaturated C₅ hydrocarbon, is the building unit of a large family of open-chain and cyclic isoprenoids and terpenoids. Phytol, an acyclic diterpene, is probably the most abundant isoprenoid on Earth. It occurs as an esterified

isoprenoid to Chl a and to some bacteriochlorophylls, and thus, it is widely distributed in the green pigments of aquatic plants (Rullkötter, 2000).

Sesterpenes (C₂₅) are of relatively minor importance except in some methanogenic bacteria (Volkman and Mawell, 1986). The geochemically most important and widespread triterpenes are from the hopane series (hopanoids) like diploptene which occurs in cyanobacteria and other bacteria (Rullkötter, 2000; Saito and Suzuki, 2007). Hopanoids are mainly from bacterial membranes and can be divided into two groups namely biohopanoids and geohopanoids (Saito and Suzuki, 2007). Biohopanoids such as bacteriohopanetetrol (BHT) are pentacyclic triterpenoids synthesized by a diverse range of bacteria as cell membrane rigidifiers (Ourisson et al., 1987; Rullkötter, 2000). Geohopanoids, including hopanols, hopanoic acids, most hopenes and hopanoidal aldehydes and ketones, are products of diagenetic processes which modify the side chain structure of biohopanoids after the death of bacteria (Saito and Suzuki, 2007).

Steroids are tetracyclic compounds that are also biochemically derived from squalene epoxide cyclization but have lost in most cases three methyl groups. Cholesterol (C₂₇) is the most important sterol in animals and of some plants as well (Table 3). Higher plants frequently contain C₂₉ sterols, for example sitosterols, as the most abundant compound of this group. Steroid together with terpenoids are typical examples of lipid biomarkers (Table 3).

1.4. Research problem

Lake Kivu is most famous for its methane reservoir (Schmitz and Kufferath, 1955; Tietze et al., 1980; Schmid et al., 2004, 2005). It is also known to have a poor (faunal and floral) biodiversity, and a simple pelagic foodweb without a predatory fish. These features led it to attract more and more attention of researchers during the past decades (Descy et al., 2012). Recent biological investigations dealt mainly with the investigation of the dynamics of the introduced Tanganyika sardine (Capart 1959; Kaningini, 1995), *Limnothrissa miodon*, and that of its preys and diet (Isumbisho, 2006; Masilya, 2011) as well as the ecology of phytoplankton of Lake Kivu (Sarmiento, 2006; Darchambeau et al., 2014) in order to better understand the sustainability of the fisheries of the lake and its functioning.

Recently many authors reported that the lake was undergoing several environmental changes evidenced by the alteration of the foodweb due to the impact of the introduced *Limnothrissa miodon* (Capart, 1959) on the zooplankton abundance and diversity (Dumont, 1986; Isumbisho et al., 2006; Darchambeau et al., 2012), the recent increase in methane gas accumulation into the deep waters (Schmid et al. 2004, 2005), the abrupt resumption of carbonate precipitation in the lake (Pasche et al., 2010) and the high lake water level stands since the 1960s (this thesis, chap. 2) under an increase of human population and urbanization conditions in the basin (Muvundja et al. 2009). Yet further potential changes are predicted regarding the soaring demography in the catchment (Muvundja et al. 2009), the development of the methane exploitation industry (Wüest et al. 2012), and the recent introduction of *Lamprichtys tanganicanus* which shows an overlap in diet and habitat with the previously introduced *L. miodon* (Masilya et al. 2011).

Although the fish resources of Lake Kivu are not as large as in other East African lakes, Lake Kivu fisheries still play an important role in ensuring food security to more than a million of riparian population (Guillard et al. 2012) which mostly live under poverty and rely exclusively on natural resources for their livelihoods. Therefore, particular attention should be given to the sustainability of the fisheries by monitoring the foodweb dynamics and by determining the sensitivity of the lake to environmental changes. Another important issue is the extraction of the methane gas resource which has to be performed in a manner that complies with environmental and safety requirements.

Therefore many aspects of the lake functioning still need to be examined in order to solve the Lake Kivu puzzle. They comprise - but are not restricted to - the dynamics of the hydrological system, the microbial pool and its contribution to the foodweb, the biogeochemical cycles of dissolved and particulate organic matter, the historical records of the lake mixing processes, nutrient supply, productivity and producer community structure (Descy et al., 2012).

A hydrological model of the lake is needed for the assessment of the lake basin water budget as well the establishment of the lake response to climatic and anthropogenic stressors. The use of some biogeochemical tools such as elemental and stable isotope, pigment and lipid marker composition samples from different lake compartments (suspended, sinking, settled and buried sediments) can provide useful information on how these changes may have impacted the lake

functioning. Such information will allow interpreting future limnological pattern changes of the lake as well as drawing the attention of stakeholders and policy-makers for a sustainable management of the ecosystem.

Briefly, in this study we explored the following research questions: What are the causes of modern Lake Kivu water level variability? What are the current patterns of the biogeochemistry of POM in Lake Kivu? Which lessons can be learned from the history of the lake to understand better the present and envisage the future of the functioning of Lake Kivu's ecosystem? What are the links between the limnology of Lake Kivu and some external stressors at the catchment level?

1.5. Objectives and thesis structure

In this work, we aimed to study the recent hydrological variability, the sources and fate of particulate organic matter in Lake Kivu as well as to address their recent history in relation to environmental changes within the lake system. This study specifically aims at determining

- (i) the factors which underpinned the lake hydrological variability during the last century;
- (ii) the fluxes and the fate of particulate organic matter in the lake;
- (iii) the lake response to environmental changes with reference to water chemistry, the lake productivity and organic matter cycling.

Beside the general introduction (Chapter 1) and the general conclusion (Chapter 5), this thesis consists of three main chapters and three appendices. In Chapter 2, «Modelling Lake Kivu water level variations over the last seven decades», a simple mathematical model was used to reconstruct the history of the lake water levels and address the contribution of each hydrological component to the lake water budget as well as to explain the causes of the lake level variability since 1941. Chapter 3: «Fate and downward fluxes of phytoplankton pigments in a deep tropical lake (Lake Kivu, East Africa) », examines the fluxes and preservation of the particulate organic matter during its export from the productive layers to the sediments using pigment biomarkers.

Chapter 4, « Biogeochemical proxies indicating the response of a tropical crenogenic and meromictic large lake (Lake Kivu, East Africa) to recent environmental changes», infers from paleolimnological records the biogeochemical status of nutrients and the lake productivity as well as the phytoplankton assemblages which prevailed within the lake during the last 700-1000 yrs.

The appendices to this dissertation are published or accepted papers from companion studies in which I was involved as collaborator. They include:

- (i) Chapter 6, «Biogeochemistry of a large and deep tropical lake (Lake Kivu, East Africa): insights from a stable isotope study covering an annual cycle» by Morana et al. (2014b), presents data and interprets the OM cycling in the water column with regard to the seasonal variability of the (C, N) concentration and stable isotope composition in several inorganic and organic matter reservoirs (DIC-, POC- and zooplankton-pools);
- (ii) Chapter 7, « The history and the role of the subaquatic volcanism recorded in the sediments of Lake Kivu; East Africa» by Ross et al. (2015a), where seismic stratigraphy and sediment core geochemistry were used to track the history of subaquatic groundwater discharge and volcanism in the basin and make implications on how they affected the geochemistry of the lake;
- (iii) Chapter 8, «Abrupt onset of carbonate deposition in Lake Kivu during the 1960s: response to recent environmental changes» by Pasche et al. (2010) which discusses the recent changes in carbonate geochemistry of Lake Kivu.

1.6. Contributions from different authors

Chapter 2: Modelling Lake Kivu water levels variations over the last seven decades:

Muvundja F.A.: Data collection and analysis, model application, result interpretation, writing and publication process.

Wüest A., Result interpretation and writing supervision, manuscript reviews

Isumbisho M.: Data collection, supervision and manuscript review

Kaningini M. B.: Data collection and manuscript review

Pasche N.: Data collection and analysis (partially), manuscript review.

Rinta P.: Data collection and analysis (partially)

Schmid M.: Data analysis, supervision, model set up and validation, and manuscript reviews.

Chapter 3 Fate and downward fluxes of phytoplankton pigments in a deep tropical lake (Lake Kivu, East Africa):

Muvundja F.A.: Data analysis (partially), result interpretation, writing.

Darchambeau F.: Experimental design, field sampling (partially), chemical analyses (partially) and data analysis (partially).

Rugema E.: Field sampling and sample treatment

Leporcq B.: Field sampling (partially), HPLC pigment analysis

Morana C.: Field sampling (partially), elemental and isotope analyses

Schmid M.: Data interpretation and writing supervision, manuscript reviews.

Descy J.P.: Experimental design, field sampling (partially), CHEMTAX processing, data interpretation and writing supervision, manuscript reviews.

Chapter 4 Biogeochemical proxies indicating the response of a tropical crenogenic and meromictic large lake (Lake Kivu, East Africa) to recent environmental changes

Muvundja F.A.: GIS-KV10-3 coring, sample treatment and chemical analyses, both studied core data analysis and result interpretation, writing.

Herman M.: GIS-KV11-4 core sample preparation and chemical analyses (partially)

Morana C.: GIS-KV11-4 core sampling, treatment and chemical analyses, manuscript review

Schmidt S.: Core ²¹⁰Pb dating

Ssemanda I.: Core pollen dating

Steigüber C.G.: GIS-KV11-4 sample preparation for dating, data analysis (partially) and manuscript review.

Verleyen E.: Data analysis (partially) and manuscript review

Anselmetti F.: GIS-KV10-3 coring, Inorganic carbon analysis supervision, manuscript review

Isumbisho M: Fieldwork supervision, manuscript review

Darchambeau: GIS-KV11-4 coring, chemical analyses

André L.: Lithological analyses

Bouillon S.: Chemical analysis supervision, data interpretation, manuscript review

Schubert C.: Chemical analysis supervision of GIS-KV10-3 core, data interpretation, manuscript review.

Descy J.P.: Pigment analysis and data interpretation supervision, manuscript reviews.

Schmid M.: data processing and interpretation supervision, manuscript reviews

My contributions to the chapters in appendices:

Chapter 6. Biogeochemistry of a large and deep tropical lake (Lake Kivu, East Africa): insights from a stable isotope study covering an annual cycle :

Fieldwork, sample pre-treatment, conditioning, and expedition, chemical treatment prior to EA-IRMS analyses (partial), manuscript review.

Chapter 7. The history and the role of the subaquatic volcanism recorded in the sediments of Lake Kivu; East Africa:

Core sampling, sample preparation and chemical analyses (partial), manuscript review.

Chapter 8. Abrupt onset of carbonate deposition in Lake Kivu during the 1960s: response to recent environmental changes:

Field work, sample pre-treatment, conditioning and expedition, manuscript review.

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Chapter 2. Modelling Lake Kivu water level variations over the last seven decades

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2.1. Abstract

This study aimed at analysing the hydrological changes in the Lake Kivu Basin over the last seven decades with focus on the response of the lake water level to meteorological factors and hydropower dam construction. Historical precipitation and lake water levels were acquired from literature, local agencies and from global databases in order to compile a coherent dataset. The net lake inflow was modelled using a soil water balance model and the water levels were reconstructed using a parsimonious lake water balance model. The soil water balance shows that 370 mm yr⁻¹ (25%) of the precipitation in the catchment contributes to the runoff and baseflow whereas 1100 mm yr⁻¹ (75%) contributes to the evapotranspiration. A review of the lake water

balance resulted in the following estimates of hydrological contributions: 55%, 25%, and 20% of the overall inputs from precipitation, surface inflows, and subaquatic groundwater discharge, respectively. The overall losses were 58% and 42% for lake surface evaporation and outflow discharge, respectively. The hydrological model used indicated a remarkable sensitivity of the lake water levels to hydrometeorological variability up to 1977, when the outflow bed was artificially widened.

2.2. Introduction

The variations of water level of natural (unregulated) lakes are an indicator of changes in the hydrological budget of the lake catchment. Such changes may be caused by climatic variations (precipitation, evapotranspiration and other meteorological components) or by changes in the runoff characteristics (such as land-use changes) in the catchment (Vuglinskiy et al. 2009). Depending on the ratio of the catchment area per lake surface area, lake levels change within time scales ranging from hours to years (Mason et al. 1994). Also the sensitivity of lake water levels to rainfall evidently depends on the catchment to lake surface ratio (Vuglinskiy et al. 2009). For example, a significant relationship has been observed between rainfall variability and lake water level in the Lake Victoria Basin (Mistry and Conway 2003). The sensitivity of lake water levels to rainfall changes depends on the catchment-to-lake surface ratios (Vuglinskiy et al. 2009).

The seasonal rainfall distribution in the East-African region is bimodal due to the twice-annual passage of the Intertropical Convergence Zone (Verschuren et al. 2009). A recent study suggests that long-term variations in East-African rainfall are mainly driven by sea surface temperatures in the Indian Ocean (Tierney et al. 2013). East-African lakes experienced a rise in their water levels, the so-called “*Centennial rising of River Congo and Nile water levels*” during the course of 1961 to 1964 due to an increase in rainfall (Lake Victoria: 2.25 m; Mistry and Conway 2003; Lake Tanganyika: ~3 m; Kite 1981; Bergonzini 2002; Lake Kivu: 0.97 m, Pasche et al. 2010, 2012). Confusingly, for Lake Kivu, this period of higher rainfall coincided with the construction of a hydropower dam (1958/59) at the Ruzizi outflow, 3 km downstream of the lake (SINELAC 1989) as well as with the beginning of increased human activities in the catchment (Muvundja et

al. 2009). Unfortunately continuous hydrological data of this basin are lacking as the catchment remains ungauged except for the lake level. In addition, records from most rain gauge stations in the catchment are discontinuous.

For Lake Kivu, in addition subaquatic groundwater discharge (SGD) that enters the lake below 100 m is of high relevance. The SGD drives a slow upwards advective transport within the lake that is the main source of nutrients for primary production in the lake surface layer (Pasche et al. 2012; Schmid and Wüest 2012). An increase in precipitation may be expected to also lead to an increase of the SGD and thus an increase in the availability of nutrients for primary production.

The hydrological modelling of the lake water levels has already been identified as a relevant information because the lake serves as the principal reservoir for the downstream hydropower dam cascade. In addition, lake level variability has an impact on fisheries, especially the littoral zone ecological functions such as fish breeding and feeding. In the case of Lake Kivu, the littoral zone plays an important role as it is the permanent habitat for 27 of the only 29 fish species of this lake (Snoeks et al. 2012). The littoral zone is the breeding and growing area of *Limnothrissa miodon* on which the fisheries resource is largely based (Isumbisho et al. 2004; Masilya et al. 2011).

This study aimed to evaluate the lake level response to the hydrological variability in the catchment and to dam operation. The importance of Lake Kivu as a source of water resources, in the context of increasing demography and demand, is expected to increase in the forthcoming decades for further electricity production, irrigation as well as domestic and industrial uses. Thus, the assessment of the hydrological patterns and their effect on the water resource is crucial for monitoring and predicting the evolution of the water level of Lake Kivu and the discharge of the Ruzizi River (Vodacek et al. 2010). This analysis will contribute in providing the information needed to allow policy-making for an integrated water resource management in the lake catchment.

2.3. Study site

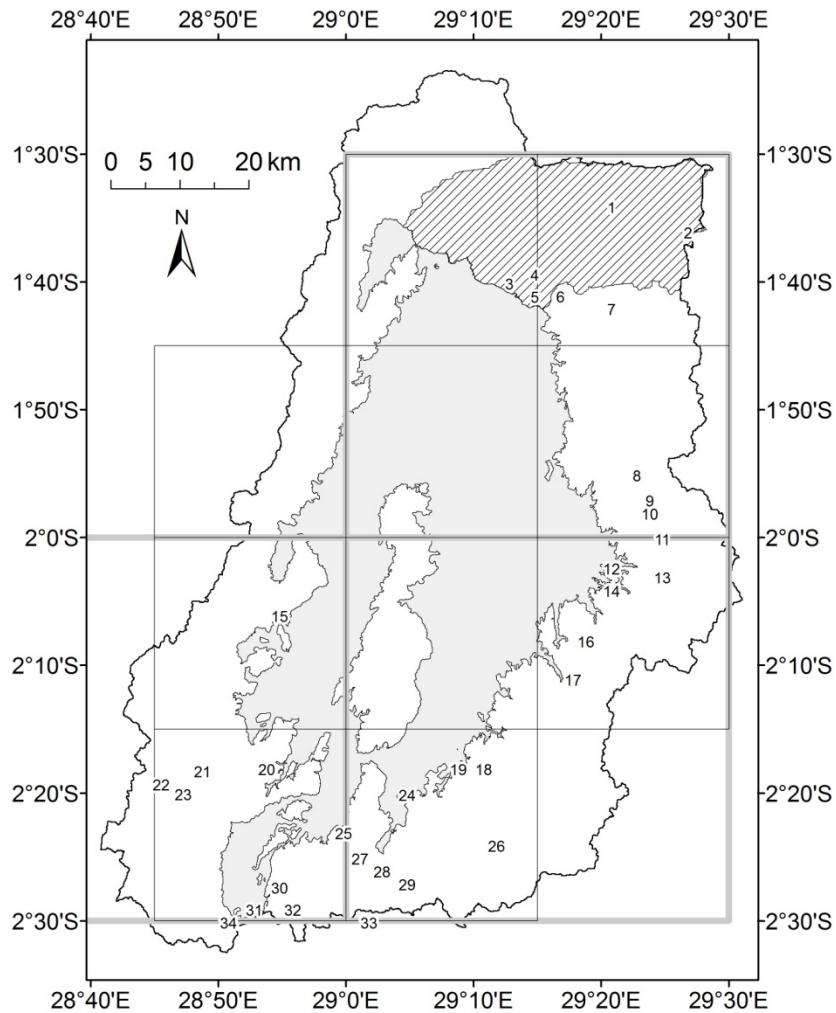


Figure 1. Map of Lake Kivu and its catchment. The numbers indicate the locations of the meteorological stations used in this study as listed in Table 1. The hatched area represents the river-free catchment area to the North of the lake. The large grey squares and the small black squares indicates the grid cells of the GPCP and the TRMM data, respectively, that were used to calculate average precipitation in the catchment.

Lake Kivu is one of the equatorial East-African rift lakes (Fig. 1). The lake is situated at the feet of the volcanically active region of Nyiragongo between the Democratic Republic of the Congo and Rwanda. The lake surface is 2370 km² with a drainage basin of 4940 km² (excluding the lake, Ballatore 2012). Most of the drainage basin consists of a river-active area (4255 km²) dominated by Haplic Acrisols (clay-rich but nutrient- and mineral-deficient acidic soils) in the Northwest and Southeast, by Humic Ferralsols (lateritic soils rich in iron, low clay soils; IUSS Working Group WRB 2007) in the Southwest and by Humic Acrisols in the East. A river-free area (685 km²) is situated in the North of the lake and dominated by Mollic Andosols (Muvundja et al. 2009) which are black volcanic ash soils and consist of a mixture of volcanic ashes, stones and gases (Driessen et al. 2001). The SGD into the lake is most probably at least partially fed by infiltration in this river-free area. The land-use in the catchment is currently dominated by Dryland Cropland and Pasture (65%) whereas Evergreen Broadleaf Forest accounts for only 17%, Shrubland for 11% and other land-uses for 7% (Muvundja et al. 2009).

The climate is humid with a bimodal precipitation regime (~1400 mm yr⁻¹ over the lake catchment; Muvundja et al. 2009). The rainy season spans from September to May and the dry season from June to August (Bultot 1971; Fehr 1984; Bergonzini 1998). The evaporation over the lake surface was estimated to ~1530 mm yr⁻¹ (CGIAR-CSI, <http://www.cgiar-csi.org/data/global-aridity-and-pet-database>). For comparison, Bultot (1971) estimated evaporation to ~1410 mm yr⁻¹, while estimates from other sources ranged from 800 to 1800 mm yr⁻¹ (Tractionel and Rhein-Ruhr-Ingenieur (RRI) 1980). The potential evapotranspiration in the catchment estimated by different authors ranges from 900 to 1500 mm yr⁻¹ (Kilauli 1976; Vangu 1981; Bigororande 1982; Kombi 1982; CGIAR-CSI, <http://www.cgiar-csi.org/data/global-aridity-and-pet-database>). An increase in evaporation and evapotranspiration is expected as a response to global warming (Verburg et al. 2003; Taylor et al. 2006). The surface runoff coefficient for this region is ~0.3 according to Shahin (2002) which contributes to feed the more than 100 rivers and streams that flow into the lake (Muvundja et al. 2009; Schmid and Wüest 2012).

In previous studies, the water balance of Lake Kivu was estimated to be composed of inputs of 3.3 km³ yr⁻¹ by precipitation, 2.0 km³ yr⁻¹ by river inflows, 1.3 km³ yr⁻¹ by SGD and outputs of 3.6 km³ yr⁻¹ by lake surface evaporation and 3.0 km³ yr⁻¹ by the Ruzizi River outflow (Muvundja

et al. 2009; Schmid and Wüest 2012). The SGD are permanent underground water springs with most of the discharge attributed to cool and fresh SGD that mainly drive the upwelling in the lake, and a smaller contribution of hydrothermal sources that maintain the permanent stratification of the lake (Degens et al. 1973; Schmid et al. 2005; Ross et al. 2014, 2015a, b).

Regarding the outlet, it is important to consider the construction and the operation of the Ruzizi I Hydropower Dam since 1959, located 3 km downstream of the lake (Tractionel and RRI 1980, Fichtner 2008). In 1977, dredging and widening operations were conducted, and a by-pass was erected at the lake outlet to regulate the amount of water in the river channel (Fichtner 2008). However the by-pass did not work properly and was decommissioned shortly afterwards. All these operations may have induced some bias to the “natural” lake level versus discharge relationship (Bergonzini 1998; Tractionel and RRI 1980; Fichtner 2008) and sometimes to an unknown extent.

2.4. Data

Rain data from 34 meteorological stations (1928 to 1993; Fig. 1 and Table 1) were compiled from the literature (Bultot 1954, 1971; INEAC 1960; Kilauli 1976; Bitacibera and Gasimbanyi 1978; Vangu 1981; Bigorarande 1982; Bikoba 1984) and local meteorological services (Météo-Rwanda as well as Division Provinciale de Météorologie and Division Provinciale d’Agriculture, Pêche et Elevage in D.R. Congo; Fig. 1). Arithmetic means were used as the variation between the individual stations was comparably small (coefficient of variation: 17.8%).

Furthermore, two global precipitation databases were used for the analysis: the Global Precipitation Climatology Centre database (GPCC; Rudolf and Schneider 2005; Rudolf et al. 2010; <http://gpcc.dwd.de>) and the satellite-based Tropical Rainfall Measuring Mission 3B43 product (TRMM; Jiang et al. 2011 and references therein; <http://trmm.gsfc.nasa.gov/>) which combines estimates generated by the TRMM and other satellite products as well as available rainfall gauge data from various sources available at: http://disc.sci.gsfc.nasa.gov/precipitation/documentation/TRMM_README/TRMM_3B43_readme.shtml

Table 1. Meteorological stations used in this study as located in Fig.1

Station No.	Station name	Altitude (m asl)	Rainfall (mm yr ⁻¹)	# of years
1	Tamira	2300	1196	9
2	Kora	2500	1272	11
3	Goma	1493	1196	44
4	Gisenyi –Airport	1554	1164	23
5	Prefecture	1540	1185	67
6	Pfunda	1480	1326	21
7	Kanama	1900	1477	8
8	Murunda	1875	1348	49
9	Rutsiro	2300	1482	13
10	Crête Congo-Nil	2300	1231	3
11	Mushumbati	1800	1197	3
12	Kibuye	1470	1259	32
13	Rubengera	1700	1200	44
14	Nyamishaba	1470	1100	18
15	Kalehe	1500	1728	19
16	Mubuga	1650	1361	53
17	Mugonero	1600	1406	51
18	Gatare	1800	1511	7
19	Maseka	1465	1221	49
20	Mushweshwe	1700	1270	19
21	Nyamunyunye	1746	1548	32
22	Tshibinda	2070	1860	21
23	Mulungu	1715	1607	21
24	Nyamasheke	1500	1209	62
25	Shangi	1600	1418	27
26	Kamatsira	1500	1729	12
27	Bumazi	1600	1621	29
28	Mwaga	1850	1877	11
29	Gisakura	1946	2191	16
30	Kamembe- Airport	1591	1390	42
31	Cyangugu	1525	1411	49
32	Shagasha	1700	1612	14
33	Bugutu	2025	1846	31
34	Bukavu	1635	1317	50

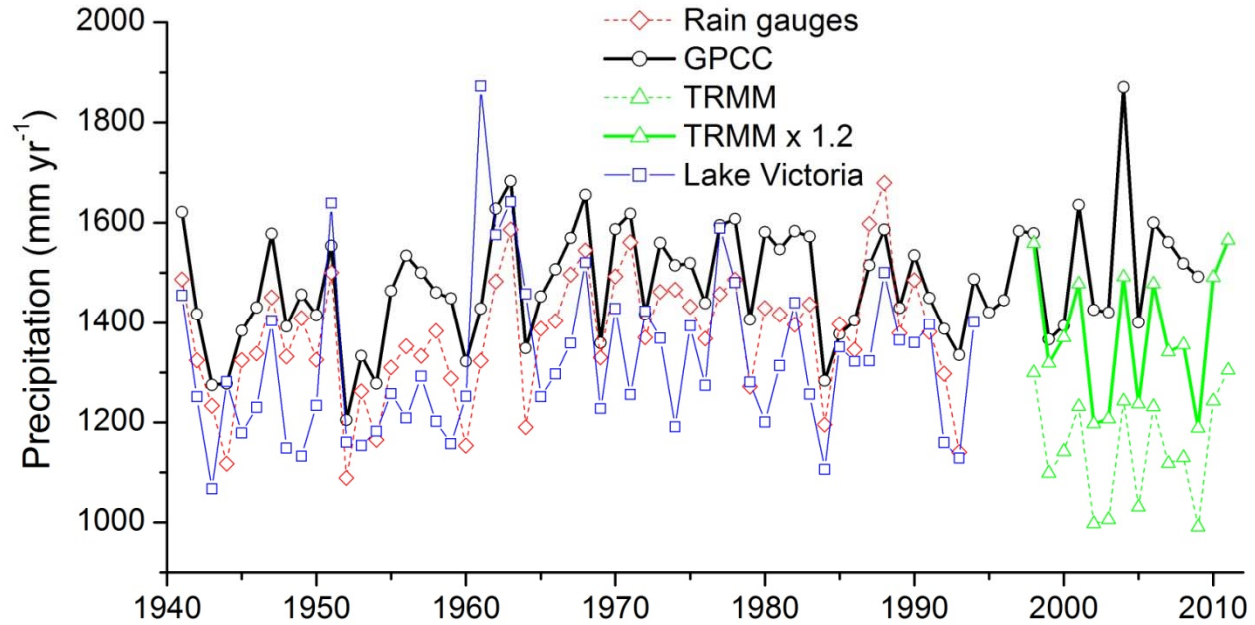


Figure 2. Time series of annual precipitation for the basins of Lake Victoria (blue line; calculated back using lake surface precipitation data and relationship provided by Nicholson and Yin (2002)) and of Lake Kivu (different sources indicated by the other lines). For other data sources, see text. TRMM data are corrected by a factor of 1.2.

The monthly GPCC data were averaged for the three grid cells covering most of the catchment area of the lake and compared to the average of the rain gauge measurements for the years 1941 to 1993 (Fig. 2). The correlation between the two time series is excellent ($R^2 = 0.94$; Fig. 3), with the GPCC data being on average $\sim 7\%$ higher. After 1993, both the rain gauge and the GPCC data cannot be considered reliable due to the absence of a sufficiently dense local *in-situ* measurement network. For the water balance calculations, the GPCC data were used until 1997, while for the years 1998 to 2012 the average values of the TRMM 3B43 products for the grid cells shown in Fig. 1 were used. However, the TRMM data had to be multiplied by a constant factor of 1.2 to maintain the agreement with the mean lake levels.

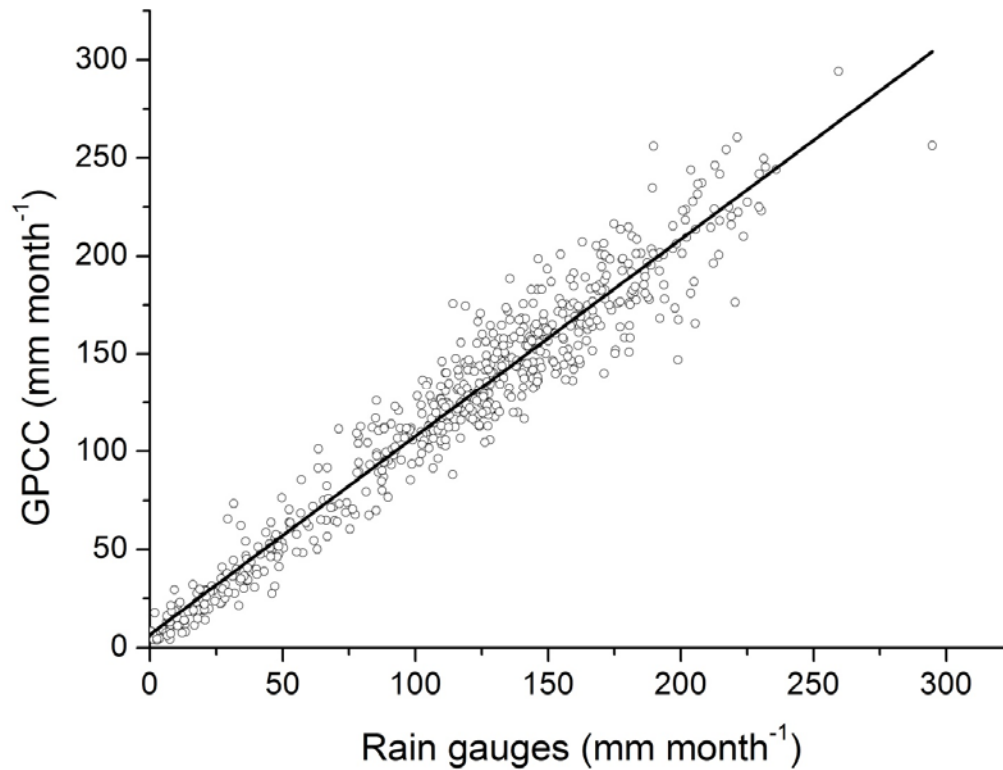


Figure 3. Correlation between monthly rainfalls calculated from the rain gauge data (Table 1) and average rainfall in the GPCC dataset for the three grid cells marked in Fig. 1. The regression line is defined by the equation $P_{GPCC} = 1.01 \times P_{gauge} + 7 \text{ mm month}^{-1}$; $R^2 = 0.94$.

In fact, TRMM's performance and uncertainties for Africa (e.g., Nicholson et al. 2003; Beighley et al. 2011; Liechti et al. 2012; Sylla et al. 2013) and elsewhere (Wolf et al. 2005; Franchito et al. 2009; Javanmard et al. 2010; Cheema and Bastiaanssen 2012) have been widely discussed, and its uncertainties were estimated to reach up to 30% and more in some cases. Topography has been found to be a major source of error for TRMM data which has been shown to moderately underestimate rainfall over highland regions compared to gauged data in East Africa and abroad (e.g., Ebert et al. 2007; Asadullah et al. 2008; Dinku et al. 2011, Ward et al. 2011). The reason given is the failure of the satellite to pick up the orographic enhancement of rainfall (Ebert et al. 2007). An underestimation of rainfall by TRMM in the mountainous region of Lake Kivu is in agreement with these findings. Nevertheless, the TRMM dataset is one of most reliable satellite products in the tropics, and even ground gauged meteorological data have similar uncertainties (of up to ~30%; WMO 2006).

Table 2. Parameter values used for the runoff model and the lake water balance model

Model parameter	Symbol	Value	Unit	Comment / Reference
Lake surface area	A_L	2370	km ²	
Lake basin area	A_B	7310	km ²	Ballatore (2012)
Catchment area (without lake)	$A_C (= A_B - A)$	4940	km ²	
Volcanic area without rivers	A_V	685	km ²	Ballatore (2012)
River-active area	$A_r (= A_C - A_V)$	4255	km ²	
Subaquatic spring inflow	Q_{sp}	1.3	km ³ yr ⁻¹	Schmid et al. (2005)
Soil storage capacity	S_{max}	300	mm	Bultot (1971)
Coefficient 1 in runoff model	α_1	2.2		Model calibration
Coefficient 2 in runoff model	α_2	2.0		Wang et al. (2011)
groundwater storage parameter	β	0.6		Model calibration
groundwater residence time	k	5	months	Model calibration
Rating curve slope 1941-1976	a_1	78.9	m ² s ⁻¹	SNEL (pers. comm.)
Rating curve intercept 1941-1976	b_1	124.6	m ³ s ⁻¹	SNEL (pers. comm.)
Rating curve slope 1977-2011	a_2	82.3	m ² s ⁻¹	SNEL (pers. comm.)
Rating curve intercept 1977-2011	b_2	131.7	m ³ s ⁻¹	SNEL (pers. comm.)

Catchment potential evapotranspiration (PET) data as well as lake surface evaporation data were downloaded from the Consortium of Spatial Information (CGIAR-CSI) Database of the CGIAR-Global Research Partnership for a Food Secure Future (Zomer et al. 2008; <http://www.cgiar-csi.org/data/global-aridity-and-pet-database>). These data had been generated by Zomer et al. (2008) using the data available from the WorldClim Global Climate data (Hijmans et al. 2005) as input parameters. WorldClim is based on a high number of climate observations and the NASA Shuttle Radar Topography Mission which is a 90 m resolution digital elevation database and provides a major advance in the accessibility of high quality elevation data for tropical regions (FAO 2004). Monthly potential evapotranspiration (PET) data have been characterized and tested for Africa and South America using different temperature-based methods applied to the WorldClim Global Climate data (available at <http://worldclim.org>; Zomer et al. 2008). The Hargreaves model (Hargreaves et al. 1985) yielded the best agreement and was applied (Zomer et al. 2008). The model was validated by these authors using PET measurements calculated from direct observations provided by the FAOCLIM 2 Climate station dataset (Allen et al. 1998) available on the FAO website. Many other studies have successfully used these global PET data (e.g., Trabucco et al. 2008; MacDonald et al. 2013; Metzger et al. 2013).

Historical records of lake water levels (1941- 1993) and the outflow discharge calibration curves were collected from the Ruzizi I Hydropower Dam Company in Bukavu-Mururu (Société Nationale d'Electricité, SNEL). Furthermore, lake levels determined by remote sensing measurements were retrieved from the global hydrological database HYDROWEB (Crétaux et al. 2011) and compared to ground measurements. Discharges of the Ruzizi outflow were calculated from the lake water level using the calibration curves provided by Tractionel and RRI (1980) and by Bergonzini (1998) as summarized in Table 2.

2.5. Model description

2.5.1. Runoff model

The water balance of Lake Kivu and its catchment was calculated with a monthly time step Δt based on the meteorological data described above. Since only few actual discharge measurements from the tributaries of Lake Kivu were available (Bergonzini 1998; Muvundja et al. 2009), we used a runoff model for estimating the monthly runoff from the catchment as an input to the lake water balance model.

Many authors have used hydrological models based on the Budyko framework (Budyko 1958) in their studies for various purposes. For example, Zhang et al. (2008) applied the Budyko framework to develop and test a water balance model over variable time scales which allows predicting streamflow for ungauged catchments. Donohue et al. (2010) studied the importance of vegetation dynamics to improve Budyko's model. Chen et al. (2013) used modified Budyko-type equations to estimate the seasonal evaporation and annual water storage in catchments. Van der Velde et al. (2013) used Budyko's framework to identify regions with contrasting hydroclimatic change during the past 50 years in Sweden. In this study, we estimated the runoff of the Lake Kivu catchment by applying a monthly hydrological model based on the Budyko framework, the water partition and balance (WAPABA) model developed for diverse ungauged catchments by Wang et al. (2011).

The model comprises five steps summarized as below:

1. Rainfall, $P(t)$ (mm month⁻¹), is partitioned into the catchment water yield, $Y(t)$ (mm month⁻¹) and the catchment water consumption, $X(t)$ (mm month⁻¹):

$$Y(t) = P(t) - X(t) \quad (1)$$

$Y(t)$ comprises surface runoff, $Q_s(t)$ (mm month⁻¹) and groundwater recharge, $R(t)$ (mm month⁻¹) such as:

$$Q_s = Y(t) - R(t) \quad (2)$$

A supply-demand-consumption equation is applied to calculate $X(t)$ from rainfall:

$$X(t) = P(t) \left\{ 1 + \frac{X_0(t)}{P(t)} - \left[1 + \left(\frac{X_0(t)}{P(t)} \right)^{\alpha_1} \right]^{\frac{1}{\alpha_1}} \right\} \quad (3)$$

Here, α_1 is the catchment consumption curve coefficient; $X_0(t)$ (mm month⁻¹) is the potential catchment water consumption or water demand limit given by:

$$X_0(t) = ET_0(t) + \frac{(S_{max} - S_{(t-1)})}{\Delta t} \quad (4)$$

where $ET_0(t)$ (mm month⁻¹) is the catchment potential evapotranspiration; S_{max} (mm) is the maximum water holding capacity of the soil in the catchment; $S_{(t-1)}$ is the amount of water held in the soil for the prior time step t-1; and $\Delta t = 1$ month is the simulation time step.

2. The amount of water available for evapotranspiration, $W(t)$ (mm month⁻¹), is then given by:

$$W(t) = \frac{S_{(t-1)}}{\Delta t} + X(t) \quad (5)$$

The actual evapotranspiration is calculated from:

$$ET(t) = W(t) \left\{ 1 + \frac{(ET_0(t) + \frac{S_{max}}{\Delta t})}{W(t)} - \left[1 + \left(\frac{(ET_0(t) + \frac{S_{max}}{\Delta t})}{W(t)} \right)^{\alpha_2} \right]^{\frac{1}{\alpha_2}} \right\} \quad (6)$$

where α_2 is the catchment evapotranspiration curve coefficient. The soil water storage at the end of the time t, $S(t)$ is:

$$S(t) = S(t - 1) + [W(t) - ET(t)]\Delta t \quad (7)$$

3. The catchment water yield at time step t , $Y(t)$ is partitioned into $R(t)$ (mm month⁻¹) and $Q_s(t)$ (mm month⁻¹) by:

$$R(t) = \beta Y(t) \quad (8)$$

where β is the proportion of the water yield and the groundwater recharge rate, $G(t)$.

The rest of $Y(t)$ contributes to the surface runoff, $Q_s(t)$ given by :

$$Q_s = Y(t) \times (1-\beta) \quad (9)$$

4. The groundwater storage is drained to generate a baseflow $Q_b(t)$ (mm month⁻¹) given by:

$$Q_b(t) = \frac{G(t)}{k} \quad (10)$$

where $G(t)$ (mm) is the groundwater storage and k (months) the groundwater residence time. The baseflow here indicates the amount of infiltrated groundwater which returns to the surface. Given the steepness of the basin topography, the residence time of the groundwater should be comparably short. However, we have no concrete observational evidence for the residence time. We therefore chose to estimate this parameter during the model calibration (see section 4.3). Thus the remaining water in the groundwater storage at the end of time t is:

$$G(t) = G(t - 1) + \Delta t(R(t) - Q_b(t)) \quad (11)$$

5. The sum of surface runoff and the baseflow results in the total flow, $Q(t)$, during the time step Δt and closes the hydrological cycle by:

$$Q(t) = Q_s(t) + Q_b(t) \quad (12)$$

The catchment runoff coefficient, k_r is calculated by:

$$k_r = \frac{Q(t)}{P(t)} \quad (13)$$

Finally, the inflow into the lake, $Q_r(t)$ (m³ s⁻¹), is calculated from $Q(t)$ by

$$Q_r(t) = c \times Q(t) \times A_r \quad (14)$$

Here A_r (m^2) is the river-active area of the catchment, and c is a conversion factor to convert from mm month^{-1} to m s^{-1} . The procedures for estimating or calibrating the five model parameters α_1 , α_2 , β , k , and S are described in Section 4.3 below and the values of the parameters are given in Table 2.

2.5.2. Lake water balance model

A parsimonious water balance model was used to reconstruct the lake level dynamics from the knowledge on lake hydrological and morphological parameters (Table 2). The calculations of the hydrological inputs to the model were made from January 1941 to December 2011.

The model used is based on the following equation:

$$\Delta Q(t) = A_L \times [P(t) - E(t)] + Q_r(t) + Q_{SGD}(t) - Q_{out}(t) \quad (15)$$

where ΔQ ($\text{m}^3 \text{s}^{-1}$) is the net water inflow to the lake; A_L is the lake surface area (m^2), $P(t)$ is the rainfall (m s^{-1}) on the lake surface at time t (s), and $E(t)$ is the evaporation rate (m s^{-1}) from the lake surface.

$Q_r(t)$ ($\text{m}^3 \text{s}^{-1}$) is the total catchment flow to the lake (except SGD) calculated from the sum of catchment runoff and baseflow as given by Equations 12 and 14.

The long-term mean total discharge of the SGD, $Q_{SGD}(t)$, is relatively well constrained by the salt balance of the lake (Schmid and Wüest 2012), but nothing is known about the residence time of the water before entering the lake or the temporal dynamics of the SGD. We therefore used two different approaches for estimating Q_{SGD} , either as constant:

$$Q_{SGD}(t) = \overline{Q_{SGD}} = 41.2 \text{ m}^3 \text{s}^{-1} (= 1.3 \text{ km}^3 \text{yr}^{-1}) \quad (16)$$

or as variable in time as a function of the precipitation previous during the previous year:

$$Q_{SGD}(t) = \overline{Q_{SGD}} \times \gamma \left[1 + \frac{(P_n - \overline{P})}{\overline{P}} \right] \quad (17)$$

where P_n is the mean precipitation during the past year, and, \bar{P} is the average long-term precipitation; γ is a non-dimensional fit parameter describing the extent to which the SGD discharge varies with precipitation.

$Q_{out}(t)$ ($\text{m}^3 \text{s}^{-1}$) is the discharge of the outflow given by:

$$Q_{out}(t) = aH(t) + b \quad (18)$$

where $H(t)$ is the lake water level gauged at the outflow (m, above 1460 m asl); a ($\text{m}^2 \text{s}^{-1}$) and b ($\text{m}^3 \text{s}^{-1}$) are the slope and the intercept of the rating curve, respectively (Table 2). Two different rating curves were used for the periods before and after the year 1977 when the outflow was modified by dredging and widening.

The lake water level was then calculated from the net water inflow by:

$$H_i = H_{i-1} + \frac{(\Delta Q)_{i-1}}{A_L} \Delta t \quad (19)$$

Where H_i is the simulated water level for the month i ; H_{i-1} is the simulated water level for the previous month $i-1$; $(\Delta Q)_{i-1}$ the net inflow of the previous month calculated using Equation (14), Δt the time elapsed from the first day of the previous month to the first day of the month under consideration.

2.5.3. Model parameterization and calibration

The model parameters were defined or calibrated as follows: For the soil water holding capacity, S_{max} , a value of 300 mm was used, which is the value given for the region by Bultot (1971) and agrees with average values around Lake Kivu in the FAO Soil Map of the World. Of the two parameters α_1 and α_2 only one could be used for model calibration, as their effects on the total runoff from the catchment are qualitatively very similar. Therefore parameter α_2 was arbitrarily set to 2.0, a typical value observed in 331 test catchments by Wang et al. (2011). Then, α_1 was optimized to set the mean difference between observed and calculated lake levels for the entire time series to zero. This resulted in $\alpha_1 = 2.2$.

Finally, the parameters β and k were calibrated to reduce the difference between the observed and simulated seasonality of the lake level. Here, seasonality is defined as the difference between

the monthly lake levels and their 12-months running mean, averaged for the period 1942 to 1997, i.e. not including the years for which the TRMM data were used. The best fit between observed and simulated seasonality was achieved with $\beta = 0.6$ and $k = 5$ months, meaning that 60% of the water yield is contributed by the baseflow, which resides on average 5 months in the catchment (the value of 5 months was chosen to optimize the model but we have no concrete observational evidence).

2.5.4. Model evaluation

The predictive power of the model was assessed using the Nash-Sutcliffe efficiency (NSE) index (Nash and Sutcliffe 1970) as well as the ratio of the root mean square error and the standard deviation of the observations (RSR) as described by Moriasi et al. (2007).

2.6. Observations and results

2.6.1. Precipitation

The precipitation record for Lake Kivu shows a shift towards wetter conditions around 1961. Similar observations were made for the Lake Victoria Basin (Nicholson and Yin, 2002; Kizza et al., 2009; Fig. 2) indicating that rainfall in the catchment of Lake Kivu is driven by the same regional meteorological patterns as for Lake Victoria. In order to support this, we give in the following the respective values for Lake Kivu (in italics) and Lake Victoria (in parentheses, data are from Nicholson and Yin 2002). The annual mean precipitation (\pm standard deviation) in the rain gauge data for the period 1941-1960 was *1417* \pm 112 mm yr⁻¹ for the Lake Kivu Basin (1244 \pm 129 mm yr⁻¹). The minimum precipitation of *1090* mm yr⁻¹ (1070 mm yr⁻¹) was observed in 1952 (*1943*), the maximum of *1500* mm yr⁻¹ (1640 mm yr⁻¹) occurred in 1951 (Fig. 2). Subsequently, the mean rainfall rose to *1415* \pm 118 mm yr⁻¹ (1367 \pm 167 mm yr⁻¹), in the period 1961 to 1993, corresponding to an increase by 8% (10%) compared to the average before 1961. The minimum values for this period were *1140* mm yr⁻¹ (1110 mm yr⁻¹) in *1993* (*1984*), whereas the maxima were *1590* mm yr⁻¹ in 1963 and *1680* mm yr⁻¹ in 1988 (1870 mm yr⁻¹ in 1961 and 1640 mm yr⁻¹ in 1963).

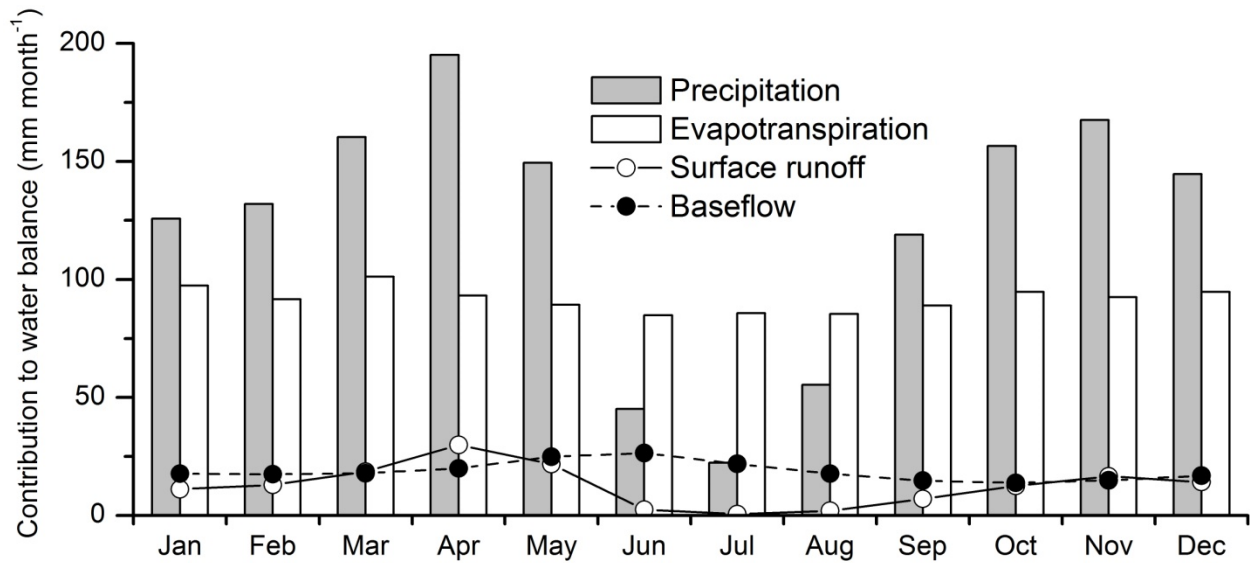


Figure 4. Monthly components of the soil water balance (precipitation, potential evapotranspiration, surface runoff and baseflow) calculated with the runoff model for the catchment of Lake Kivu for the period 1941 to 1991 (the period with reliable precipitation data).

Based on the classification of Fehr (1984), the long-term series indicate that June to August are dry months with 46, 29 and 57 mm month⁻¹ respectively whereas the months from September to May are wet with precipitation ranging between 121 and 199 mm month⁻¹ (Fig. 4). Among the wet months, September and January are the least wet with 121 and 128 mm month⁻¹, respectively, while November and April are the wettest with 171 and 199 mm month⁻¹, respectively, according to a bimodal rainfall regime (Fig. 4).

2.6.2. Runoff

The runoff model indicated an annual mean land potential evapotranspiration rate of 1100 mm yr⁻¹ and mean baseflow of 220 mm yr⁻¹ (Table 3; Fig. 4). The surface runoff was 150 mm yr⁻¹ (Table 3; Fig. 4). Except for the baseflow, all soil water balance components showed lower values in the dry season (Fig. 4). The average runoff coefficient for the entire basin was estimated at $k_r = 0.25$ (Table 3). The runoff was estimated to have increased by 19% in the period 1961- 1993 compared to 1941- 1960.

Table 3. Soil water balance in the catchment of Lake Kivu for the years 1941 to 1991

Soil water balance	Value (mm yr ⁻¹)
Precipitation	1470
Evapotranspiration	1100
Surface runoff	150
Baseflow	220

2.6.3. Lake water levels

A comparison of lake levels observed *in-situ* and with remote sensing confirmed that both time series are accurate within a few cm (Fig. 5). Remotely sensed lake levels for neighbouring Lakes Edward and Victoria show very similar temporal dynamics as for Lake Kivu, indicating that the lake level fluctuations are driven mainly by regional meteorological variations. This is also supported by a comparison of historical trends of lake levels and rainfall in the drainage area (Fig. 6).

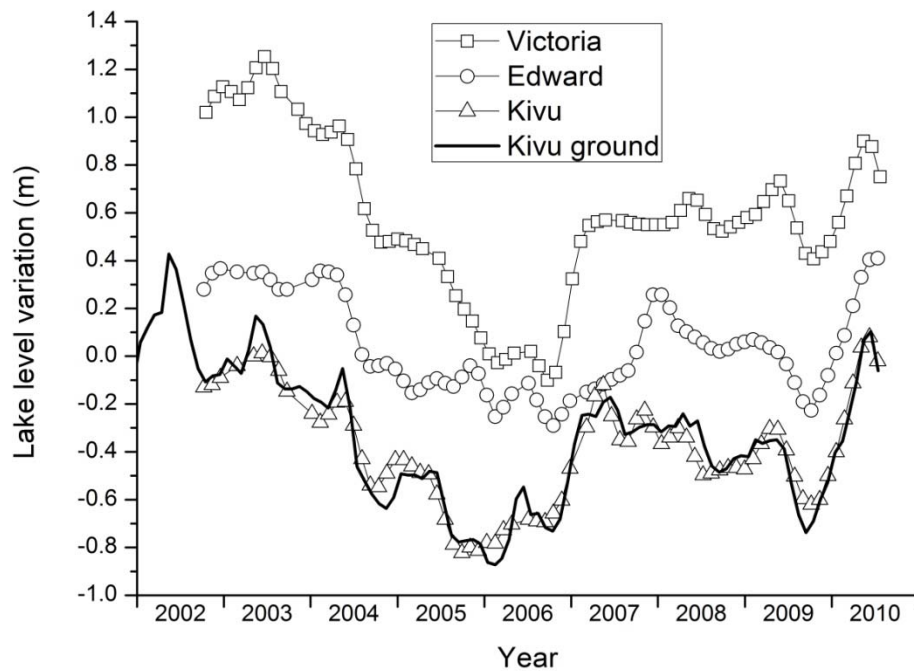


Figure 5. Comparison of satellite (Créaux et al. 2011) water level variation (relative to an arbitrary average level) of selected East-African great lakes with the levels observed *in-situ* for Lake Kivu. “Kivu” indicates the satellite-based data and “Kivu ground” the *in situ* gauged data.

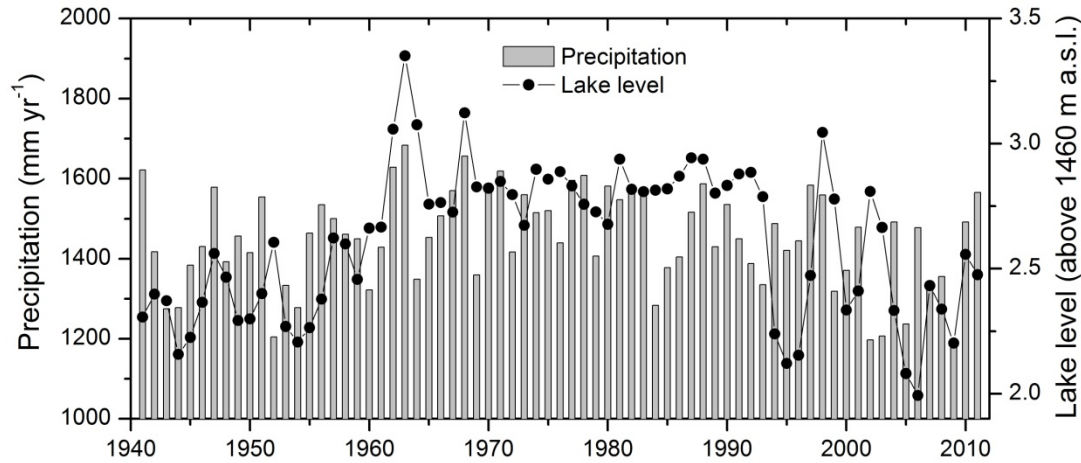


Figure 6. Annual mean Lake Kivu water level (grey line with circles; data from SNEL) and precipitation (black bold line, data from GPCP until 1997 and TRMM multiplied with a factor 1.2 afterwards). The lake water levels are relative to a height of 1460 m asl. Note that the lower number of precipitation data (Fig. 7) affected the quality of the agreement after 1993.

Periods of high annual precipitation matched with high lake water levels and vice versa both before and after the dam construction of 1959 (Fig. 6). Both curves indicate higher water levels for the period after 1960 with a maximum peak in 1963. The average lake levels increased from 1462.40 m asl for 1941 to 1960 to 1462.86 m for 1961 to 1993, and fell back to 1462.41 m in the years 1994 to 2011, albeit with a twice as large interannual variability than before.

2.6.4. Lake water balance

Observed and simulated lake levels are compared in Fig. 7. The absolute difference between observed and simulated monthly lake levels in the model with constant SGD inflow was 0.17 m. Adding a variable SGD inflow depending on the precipitation of the previous years (Eq. 17), improved the agreement extreme (maximum and minimum) lake levels between observations and simulations, but did not remarkably decrease the mean absolute differences or strongly modify their relationship. We therefore do not see sufficient justification in the observed data to support or reject the hypothesis of a variable SGD inflow depending on precipitation. For the study analysis we used the results of the model with constant SGD inflow, but none of the conclusions would have been different using the model with variable SGD inflow.

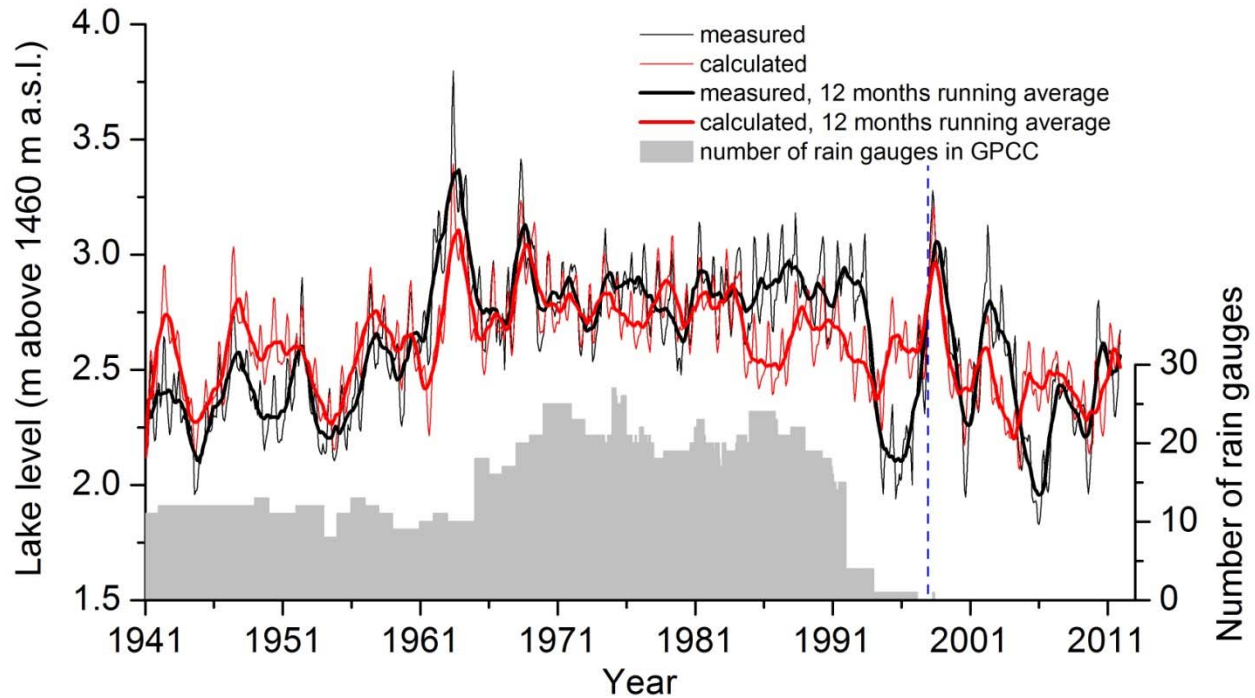


Figure 7. Comparison between observed and simulated (model output) lake water levels generated by assuming a constant subaquatic groundwater discharge to the lake. The calculated and measured curves are compared with their 12 months running average curves (see curves (see legend)). The shaded curve indicates the number of rain gauges used in this study.

The model evaluation suggested that its performance was satisfactory ($NSE = 0.60$ and $RSR = 0.64$) for 1941 to 1958 and good ($NSE = 0.72$ and $RSR = 0.53$) for 1959 to 1976. However for the period after 1977, the predictive power of the model was lower ($NSE = 0.34$ and $RSR = 0.81$) most likely due to turbine operating problems (Tractionel and RRI 1980; Fichtner 2008) which induced large uncertainties in the lake discharge.

The correlation between mean annual observed and simulated water levels was good before the outlet of the river was modified in 1977, for both periods before and after the dam construction (Fig. 8). The same was true for the correlations between observed and simulated lake level increase during the rainy season from October to May (Fig. 9). Correlations for the lake level decrease during the dry season were weaker, and the slope was only 0.42 before dam construction and 0.34 thereafter (Fig. 10).

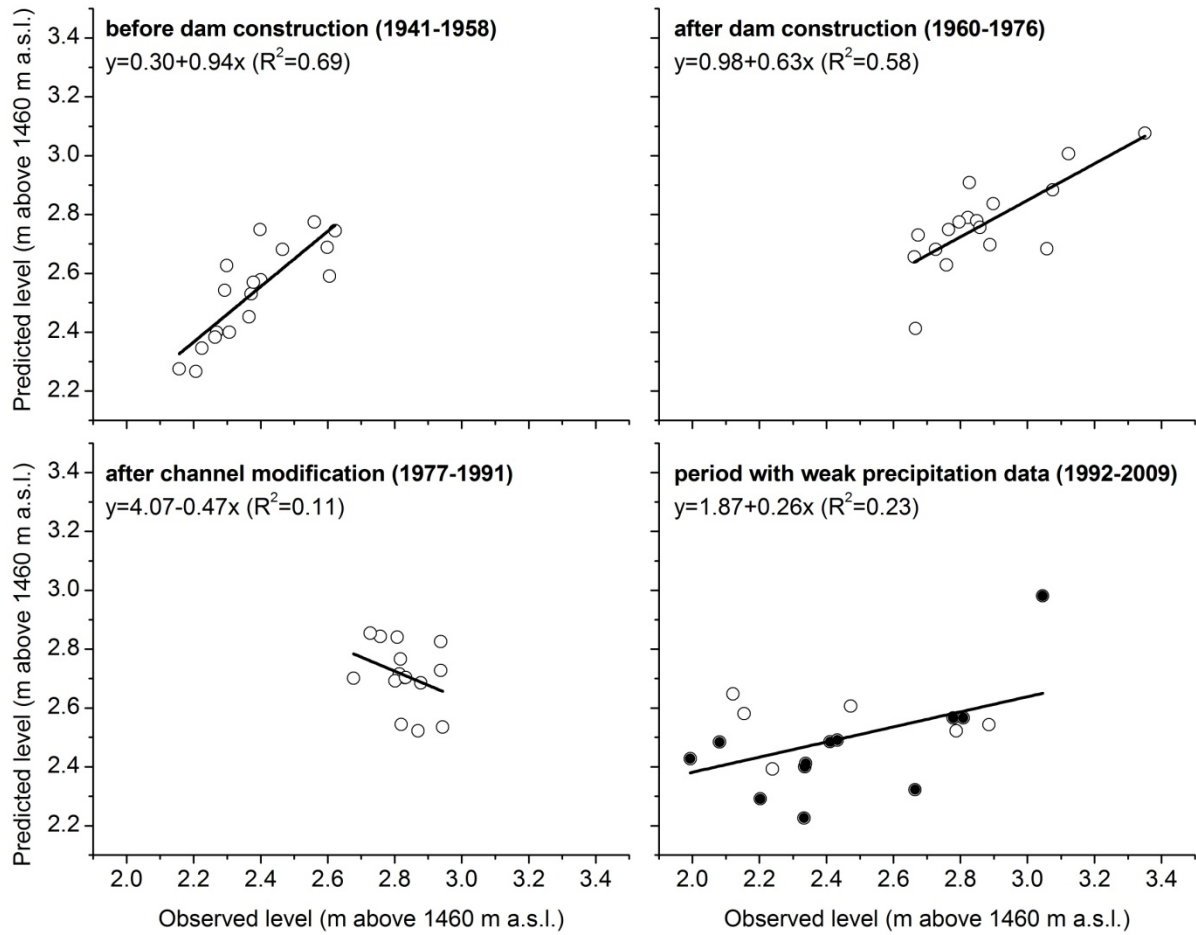


Figure 8. Correlations between predicted and observed lake levels for different periods. The black dots indicate the years where the TRMM data was used.

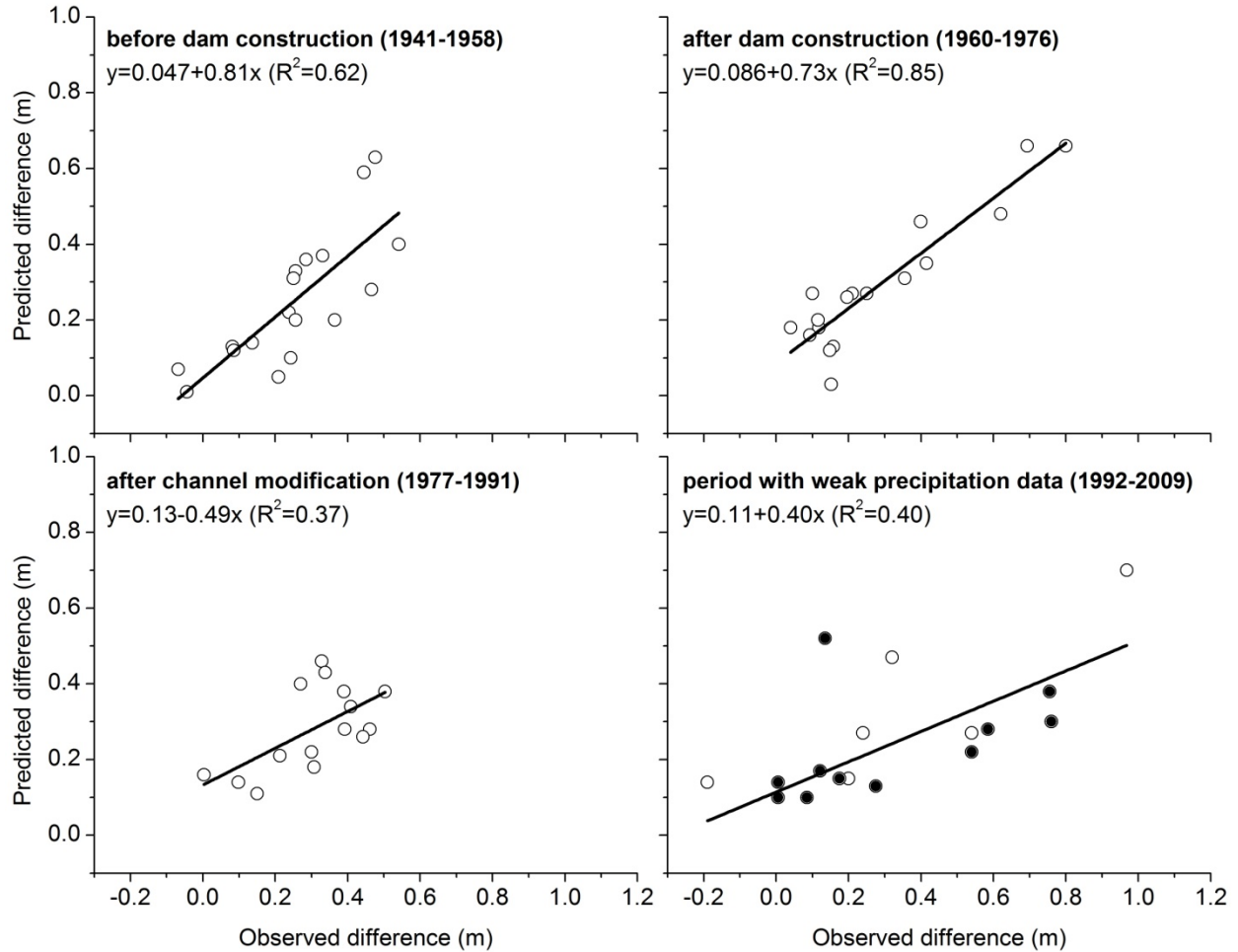


Figure 9. Comparison of simulated and observed lake level differences between 1 October and 1 May next year (Wet Season)

After the modification of the outlet, the predictive capability of the model for all three quantities (mean annual level, increase during the wet and decrease during the dry season) became consistently weaker, both for the period 1977- 1991 when still sufficient precipitation data was available, and for the period after 1992 for which almost no rain gauge data was available (Figs. 9 and 10).

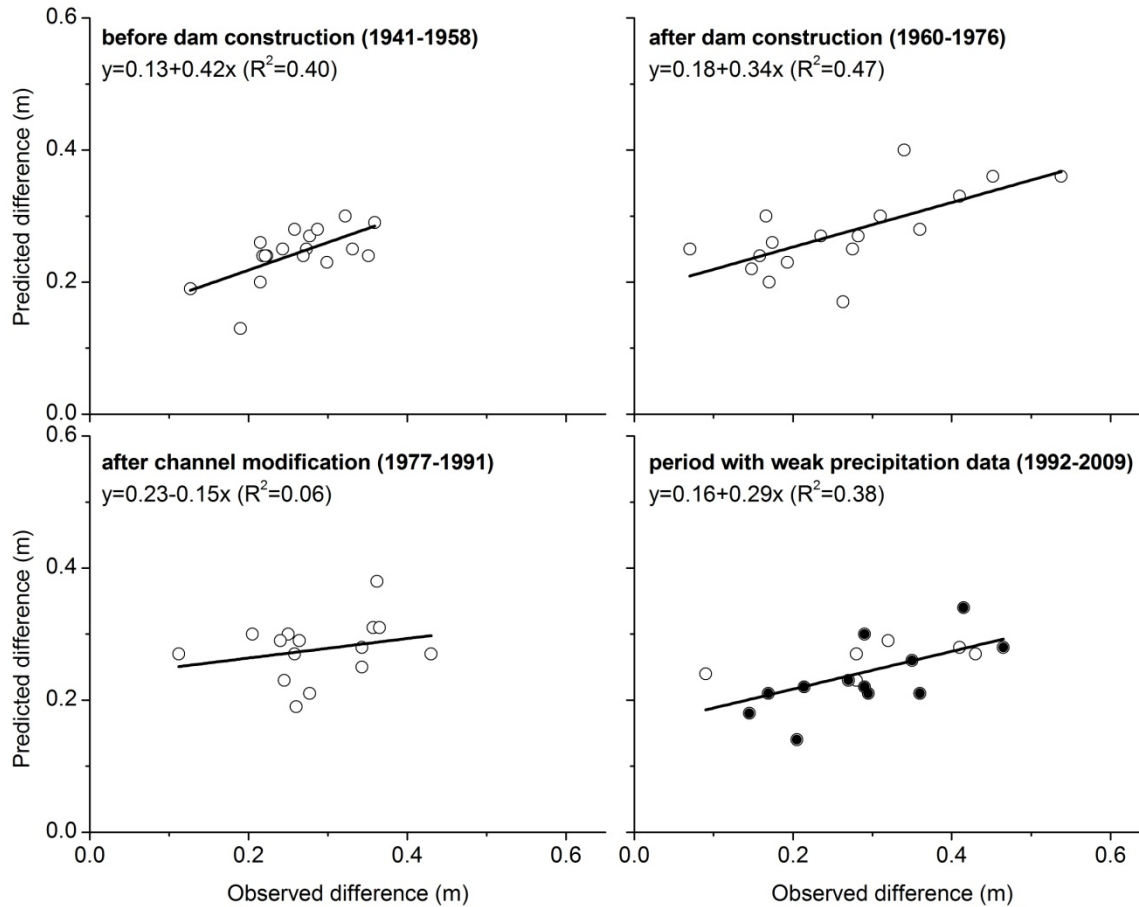


Figure 10. Comparison of simulated and observed lake level differences between 1 June and 1 September (Dry Season)

The observed and simulated lake levels show a consistent seasonality. Maximum lake levels are reached in May (0.16 m above annual average) and minimum lake levels in September (0.10 m below annual average; Fig. 11). Interestingly, the reproduction of the mean seasonal lake water level was equally good (with residuals generally lower than 0.02 m) for all periods, independent of dam construction or modification of the river outlet (Fig. 11). It is only somewhat worse for the period where TRMM data was used for driving the model, which might indicate a seasonal bias in the TRMM data. The mean annual flows of the calculated lake water balance are summarized in Table 4 and their seasonal variability is shown in Fig. 12. Table 4 highlights the importance of direct precipitation on the lake surface and evaporation (3.5 and 3.6 km³ yr⁻¹, respectively), which contribute more than half to the total inputs and outputs.

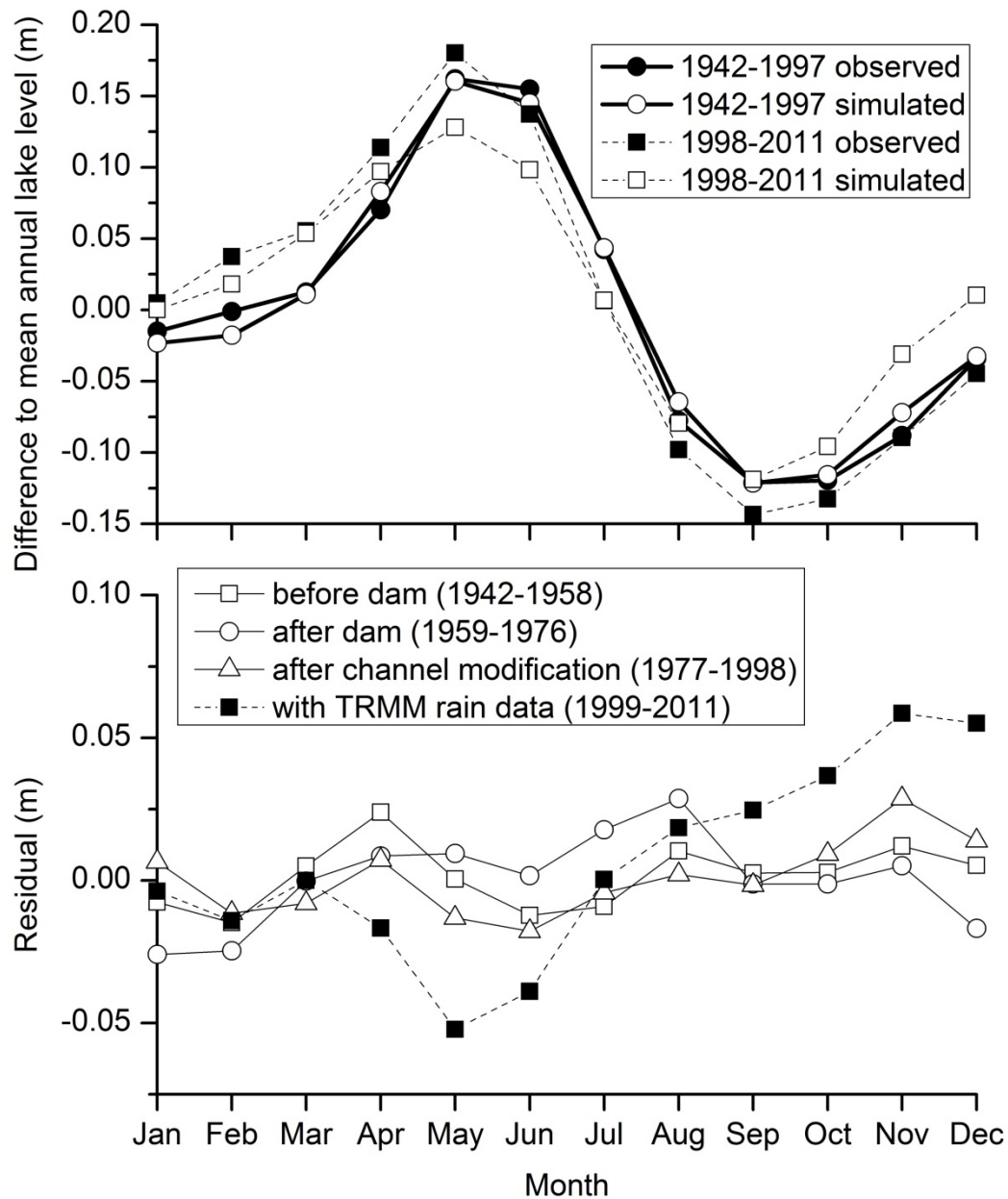


Figure 11. Above: Monthly deviation from the annual mean of the observed and simulated lake levels, averaged for the periods where the GPCP (1942-1997) and the TRMM data (1998-2011) were used, respectively. Below: Monthly residuals (differences between calculated and observed lake levels) for different past periods.

Table 4. Lake Kivu water balance as calculated with the model for the years 1941 to 1991

Lake water balance	$\text{m}^3 \text{s}^{-1}$	$\text{km}^3 \text{yr}^{-1}$	$\text{mm yr}^{-1 \text{ a)}$	Contribution (%)
Precipitation	111	3.5	1470	55
Inflows	50	1.6	670	25
Subaquatic springs	41	1.3	550	20
Evaporation	115	3.6	1530	57
Discharge	86	2.7	1150	43

^{a)} related to the lake surface area.

The estimated surface inflows ($1.6 \text{ km}^3 \text{ yr}^{-1}$) are lower than the previous estimates of $2.4 \text{ km}^3 \text{ yr}^{-1}$ (Muvundja et al. 2009) and of 1.6 to $2.4 \text{ km}^3 \text{ yr}^{-1}$ (Schmid and Wüest 2012), but similar to the $1.8 \text{ km}^3 \text{ yr}^{-1}$ proposed by Rinta (2009) from the application of the Soil and Water Assessment Tool (SWAT) model. However the SWAT estimates for evaporation ($2.2 \text{ km}^3 \text{ yr}^{-1}$) and precipitation ($2.8 \text{ km}^3 \text{ yr}^{-1}$) were lower than the estimates found in the literature (Bultot 1971; Bergonzini 1998; Muvundja et al. 2009) probably due to large uncertainties in the data sources and comparably low precipitation during the study period (1998 to 2008) of the SWAT model. Precipitation and its seasonal variability are the same as for the runoff model (Fig. 4), while the river inflows correspond to the sum of the surface runoff and the baseflow. The SGD inflows were estimated in previous studies to close the salt balance of the lake (Schmid et al. 2005).

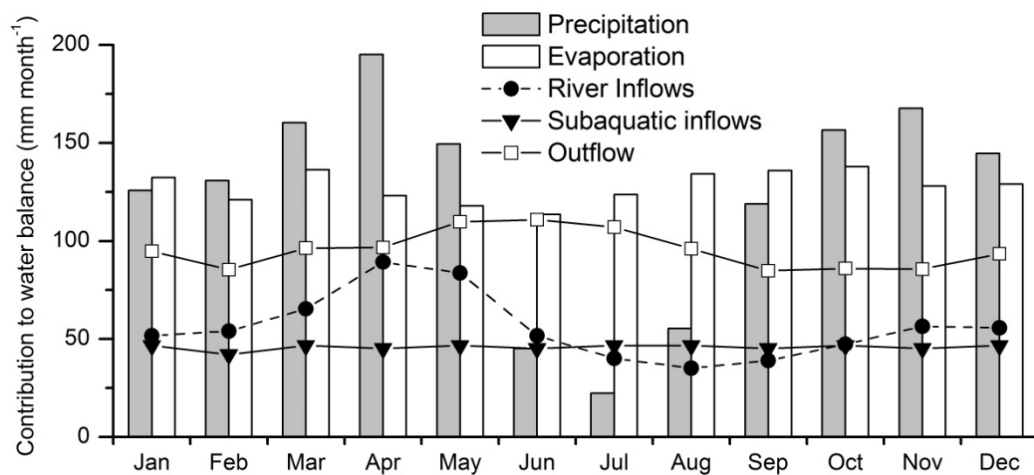


Figure 12. Seasonal contribution of the different inputs and outputs to the lake water balance averaged for the period from 1941 to 1991. Precipitation and evaporation refer to the lake surface precipitation and evaporation, respectively, whereas subaquatic inflows represent the SGD and outflow indicates the lake discharge.

They are assumed to be constant in the model, and their small apparent temporal variability in Fig. 12 is due to the different number of days per month. The seasonal variation of the water balance is mainly due to the variation in precipitation and the resulting seasonality. The total output is almost constant throughout the year, as the seasonal variation of the outflow that results from water level variations is almost exactly compensated by the seasonal variation of evaporation from the lake surface.

2.7. Discussion

The hydro-meteorological features of the Lake Kivu Basin are in accordance with the regional climate (Fig. 4) where the altitude-moderated equatorial climate is bimodal with rainy months (September to May) interrupted by dry months (June to August) because of the twice-annual passage of the Intertropical Convergence Zone (Verschuren et al. 2009). Less seasonal variation is noticed in evaporation and potential evapotranspiration (Figs. 4 and 10) due mostly to low variation in air temperatures near the equator. Evaporation rates of East-African lakes are similar to the precipitation they receive: 1537 mm yr⁻¹ for Lake Victoria (Nicholson and Yin 2002, 2004), and 1695 mm yr⁻¹ for Lake Tanganyika (Bultot 1962, 1971).

This study shows a strong similarity of the dynamics of precipitation and lake levels between the basins of Lakes Kivu and Victoria (Fig. 3). Results in Fig. 12 indicate that the Lake Kivu level takes about two months lag to react from precipitation inputs and one month from catchment runoff. The Lake Victoria Basin experienced drought conditions in the 1930s, 1950s, 1970s and 1980s (Nicholson and Yin 2002; Mbungu et al. 2012). Corresponding low precipitation (Mbungu et al. 2012) was observed in the Lake Kivu Basin (Fig. 2) and led to lake water level low stands (Fig. 6). However the two basins underwent remarkable increasing and decreasing hydrological trends since the 1960s and the 1990s, respectively (Fig. 6), as also reported by Mbungu et al. (2012). The increase in rainfall for the period from 1961 (which was an extreme rainfall year for Lake Victoria; Conway 2002) until 1993 compared to 1941-1960 is very similar in both basins (Fig. 2). These observations are in agreement with those of Hulme et al. (2001) who estimated that there was a wetting trend over the East-African region, as a part of a more coherent zone of wetting across most of the equatorial Africa where some areas experienced increasing rainfall

trends of up to 10% or more per century. Meanwhile, an increasing trend in natural hazards mostly due to hydro-meteorological events from the 1960s has recently been reported by Vandecasteele et al. (2010) for the African Great Lakes region (Kivu, Rwanda and Burundi). IPCC (2007) also forecasts a rainfall increase of ~10 to ~20% for East Africa for the next century, which has been confirmed by a more recent simulation project (Bony et al. 2013).

The low lake levels of East-African lakes during the period of 2005/2006 which were felt as an emergency case by the hydropower companies on Ruzizi River (SNEL and SINELAC 2006), were related to the El-Niño Southern Oscillation cycle and a forcing by the 2006 Indian Ocean dipole (Becker et al. 2010). The response of Lake Kivu to these events was similar to those of Lakes Victoria and Edward (Fig. 5). Bergonzini (2002) discussed the interannual variation of the water balance of Lake Tanganyika and found that its current status is related to precipitation variability. However he argued that the change in runoff conditions due to human activities might also have led to a change in the runoff coefficient relatively to the period before 1960.

The similarity of the agreement before and after dam construction indicates that the dam had no significant influence on the lake level (Figs. 7-10). The correlations for the rainy season are better than those for the dry season indicating that our predictions for runoff (which characterise the rainy season) are better than those for evaporation. This is probably caused by the lack of information on the interannual variation of lake surface evaporation as well as the overall uncertainties of this parameter on the basin scale. Another major source of uncertainty in the lake level model might be the quality of the outflow rating curves.

After 1977, when the hydropower bypass was set up at the Ruzizi outlet together with the Ruzizi channel dredging and widening, the lake level regime seems to have been disturbed considerably as the model is much less successful in predicting the lake levels. Tractionel and RRI (1980) reported that the dam has occasionally operated inadequately during this period causing a slowing down of the river flow. In contrast, the average seasonal variation of the lake level was still perfectly reproduced by the model. The average absolute residuals between the calculated and the observed seasonality were 0.01 m for all periods studied until 1998 (Fig. 11) and only increased to 0.03 m for the period where the TRMM data were used. This confirms that the modification on the Ruzizi outlet did not modify the seasonality of the outflow, but induced

some interannual variability in the outlet rating curve. Possible causes might be that the outlet was further modified by changes in flow conditions after the construction work made in 1977, that the modification of the outlet allowed the dam operations to take some influence on the mean annual water level, e.g. in cases of malfunctioning of the turbines as reported above, or that the outflow of the lake was to some extent managed.

Despite of the uncertainties in the raw data and the model setup, the water balance devised in this study matches well with the ranges provided by previous studies (Schmid and Wüest 2012). The long-term average precipitation estimate used in this study (1470 mm yr^{-1}) is very close to the estimate of 1497 mm yr^{-1} used by Bergonzini (1998), while he used 8% lower lake surface evaporation (1412 mm yr^{-1} from Bultot 1971). However, previous evaporation estimates range from 1060 mm yr^{-1} (Verbeke 1957) to 1690 mm yr^{-1} (UNESCO 1978).

The model estimated average baseflow and surface runoff to 220 mm yr^{-1} and 150 mm yr^{-1} , respectively. Together they yield 370 mm yr^{-1} , which corresponds to a runoff coefficient of 0.25. Similar values have been predicted in several studies for this region (Shahin 2002). The baseflow is estimated to be more important than surface runoff, which may be due to the volcanic soils which retain much water (Driessen et al. 2001; IUSS 2007). The subaquatic groundwater discharge (SGD) is an important component of lake water balance (Schmid et al. 2005; Schmid and Wüest 2012). The inflow by SGD is assumed to be at least partially derived from infiltration in the volcanic soils on the river-free area of 685 km^2 in the North of the lake. However, the estimated SGD of $1.3 \text{ km}^3 \text{ yr}^{-1}$ would correspond to 1900 mm yr^{-1} relative to this sub-catchment area, which is higher than the precipitation received. Further investigations are therefore required to determine the origin of these water masses as well as their residence time. Recent findings revealed that groundwater resources in East Africa are dependent on extreme rainfall rather than average rains (Taylor et al. 2013).

Previous lake discharge estimates of $3.2 \text{ km}^3 \text{ yr}^{-1}$ (Degens et al. 1973) and $3.6 \text{ km}^3 \text{ yr}^{-1}$ (Muvundja et al. 2009) were rather applicable to a certain period of the time series or overestimates. However our estimate of $2.7 \text{ km}^3 \text{ yr}^{-1}$ is close to the value of $2.8 \text{ km}^3 \text{ yr}^{-1}$ suggested by Bergonzini (1998) despite of the difference in the method he used to establish the outflow data for the period of 1951 to 1973. Although Bergonzini (1998) accorded low

confidence to the lake level records up to 1950, our compilation showed only a slight difference of +5% between the lake discharge ($1.9 \text{ km}^3 \text{ yr}^{-1}$) for the period of 1941 to 1950 and that of 1951 to 1959 ($2.0 \text{ km}^3 \text{ yr}^{-1}$). In addition, Bultot (1962) estimated the lake discharge to be $2.1 \text{ km}^3 \text{ yr}^{-1}$ for the period of 1951 to 1973, which is similar to our estimations. From the early 1960s, the lake level (Fig. 8) as well as the discharge significantly increased with the latter rising to $2.9 \text{ km}^3 \text{ yr}^{-1}$ for the period 1961 to 1993 due to an increase in rainfall. Recently, the mean lake level has fallen back to the level before 1961, but with a twice as high interannual variability than before (Fig. 7).

Precipitation and net inflow (runoff + SGD) represent 55% and 45% of the overall inputs (Table 4) in agreement with estimates (54 vs. 46%) of Bergonzini (1998). Evaporation and outflow represented 57 and 43 % (Table 4) of the total water losses, respectively, indicating a high lake level sensitivity to hydro-meteorological changes (Russell and Johnson 2006). By reducing the precipitation values in the model input, we can roughly estimate at which average of long-term precipitation the lake would get closed, assuming that evaporation from the lake surface as well as the SGD remain unchanged. This would be the case if the precipitation in the basin were reduced to ~60% of its current value or $\sim 900 \text{ mm yr}^{-1}$.

The results of the present study and the discussion of the uncertainties involved highlight the necessity to better monitor the hydrology of Lake Kivu and its basin. Continuous time series of quality-assured data of precipitation and other meteorological observations on the lake and in the catchment, as well as of the discharge of selected tributaries to the lake would help to better constrain the water balance of the lake. This will be necessary in order to be able to observe and quantify potential effects of climate change on the water level and the hydrological balance of the lake in the future.

2.8. Acknowledgements

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Chapter 5. General conclusion and perspectives

5.1. General discussion

Lake Kivu lies in a complex geological basin characterized by intense tectonism and volcanism which led to a faulty relief communicating subaquatically with the lake in the northern basin (Ross et al. 2014, 2015a, b). These faults act as conduits for water infiltrating within the river-free catchment area of Goma-Gisenyi (Muvundja et al. 2009, this thesis, chap. 2). These conduits feed at least partially the several subaquatic springs ($1.3 \text{ km}^3 \text{ yr}^{-1}$, i.e., 20% of the total inputs, Schmid et al. 2005), some being warm (hydrothermal) sources and others cold (Ross et al. 2015a,b). The release of salty hydrothermal groundwaters into the lake deep waters has led to a strong and permanent stratification of the lake (Schmid et al. 2005; Schmid and Wüest 2012) characterized by a thermohaline structure consisting of alternating small-scale mixed and high-gradient layers in staircases (Sommer et al. 2013).

The subaquatic groundwater discharge creates a slow uplift of nutrient-rich deep waters towards the surface (Pasche et al. 2009) resulting in an internal nutrient loading (80-85% of the total supply of nitrogen and phosphorus, Pasche et al. 2012) to the mixolimnion by upwelling that contributes 80-85% to the total supply of nitrogen and phosphorus (Pasche et al. 2012). In turn the nutrient availability stimulates the phytoplankton growth as primary production ($1440\text{-}1600 \text{ mg C m}^{-2} \text{ d}^{-1}$, this thesis, chap 3). The primary production estimates in this study were higher than the previously published data for the Southern (Ishungu) basin (Sarmiento et al. 2012; Darchambeau et al. 2014). According to previous studies which covered the period of 2002-2006 (Isumbisho et al. 2006; Darchambeau et al. 2012), a fraction of the primary production is grazed by zooplankton, with a carbon transfer efficiency of 6.8% between the two trophic levels, to sustain the $63 \text{ mg C m}^{-2} \text{ d}^{-1}$ of zooplankton production (Darchambeau et al. 2012). The remaining decaying phytoplankton together with phytoplankton excretion sustain the heterotrophic bacterial production of $336 \text{ mg C m}^{-2} \text{ d}^{-1}$ (data of 2008; Llirós et al. 2012), and hence supply to the high bacterial carbon demand (Morana et al. 2014a). The more refractory POM sinks and settles down on the lake floor where it undergoes further degradation by methanogens and supports ~40% of methane formation in the lake (Schoell et al. 1988; Pasche et al. 2011). Finally the most

refractory material (partially transformed and some intact POM) is buried, archived and finally fossilized within the sedimentary rock.

The main purposes of this study consisted of assessing the recent variability observed in lake water levels as well as tracing the dynamics of particulate organic matter cycling in Lake Kivu, in order to contribute to the knowledge of the functioning of Lake Kivu in particular, and of the African large lakes in general. Under conditions of global warming and anthropogenic pressure on natural ecosystems, it becomes more and more important to evaluate ecosystem sensitivity to environmental changes. However modeling Lake Kivu is not an easy way to go due to long-term data scarcity. Excluding the exploration by naturalists and European travelers, scientific research itself on Lake Kivu started in 1920 (Descy et al. 2012a) with the expedition of Cunnington (1920). Thereafter various other studies were conducted but Lake Kivu remains understudied compared to other Great lakes of the world and even those of East-Africa (Descy et al. 2012b).

Although a considerable effort has been made in knowledge acquisition about Lake Kivu during the last two decades, there are still many gaps regarding the hydrological patterns and the biogeochemical processes governing the lake functioning. The first comprehensive work on the hydrology of Lake Kivu has only been conducted in 1998 by Bergonzini (1998). It is curious that Lake Kivu's hydrology escaped from the attention of scientists for such a while. Nevertheless it is obvious that hydrological studies are long-time data demanding, and this is a serious constraint for this lake hidden in the Kivu highlands where the catchments of the numerous tributaries of the lake are small and poorly developed and consequently remain largely ungauged. The lack of long-time data series makes the hydrological modeling difficult to handle. Bergonzini (1998) was the first author to estimate the water balance of the lake and its sensitivity to local climate but he did not have enough information on the river inflow network nor did he take into account the subaquatic groundwater discharge, or assessed the potential effect on the lake water levels of the Ruzizi I HP dam construction at the outflow.

In this thesis, we collected and analyzed data from various sources covering 70 years of records, and we applied a simple mathematical model to elucidate the importance of each hydrological component to the lake water level dynamics. The examination of the Lake Kivu water level dynamics during the last seven decades allowed concluding that the recent variability of modern

Lake Kivu hydrology was caused by inter-annual variability of meteorological factors (mainly precipitation) rather than the hydropower operation. This was the first hydrological study on Lake Kivu to comprehensively address the lake response to actual and potential changes of any hydrological component linking the lake water levels to the catchment hydrology. No evidence was found about the effect of the hydropower dam construction and operation.

Furthermore this thesis intended to contribute to the knowledge of the biogeochemistry and paleolimnology of Lake Kivu by tracing the sources, the export and the fate of particulate organic matter in Lake Kivu as well as its historical records.

Cycling of OM is an important biogeochemical process because it allows the regeneration of nutrients, and in the case of a permanently stratified lake with an anoxic monimolimnion like Kivu, it is important in feeding methanogenesis (Schoell et al. 1988; Pasche et al. 2011). Chapter 4 aimed to evaluate the distribution and fluxes of particulate organic matter (POM) in different compartments of the water column and surface sediments in order to determine the export regime from oxic to anoxic zones, the degradation within the water column, the sinking rates and the burial of POM.

Lake Kivu organic matter was identified as deriving mostly from autochthonous sources. Large seasonal variations were found in export fluxes of seston and POM into the deep waters depending on the mixing status of the mixolimnion and on phytoplankton community composition. Higher chlorophyll degradation (~ up to 75%) was observed in the water column from 30 m to 60 m depth and in the sediment traps (settling POM) than in the euphotic zone (floating POM) where photooxidation, bacterial degradation and grazing occur. The distribution of phaeophytins a compared to that of phaeophorbide a among the water compartments was an evidence that microbial processes dominate the pigment degradation in Lake Kivu compared to zooplankton grazing. The POC export to the monimolimnion was estimated at 6% of primary production indicating that the largest fraction of primary production becomes available to bacterial production in the water column as dissolved organic matter (Llirós et al. 2010, 2012; Morana et al. 2014a). At an annual scale, the PIC fluxes were occasional and peaks were observed at the culmination of rainy season when the lake mixolimnion reaches the maximum stratification. The exported POM contributes to the enrichment of the deep water nutrient pool

(5.9-7.7 mg N m⁻² d⁻¹ and 0.33-0.5 mg P m⁻² d⁻¹, this thesis, chap 3) and methanogenesis. Some phytoplankton groups such as diatoms + cryptophytes and cyanobacteria are likely to contribute more than other groups to the sinking POM. Thus, given that methane production in the deep waters and the sediment relies also on organic matter availability (Pasche et al. 2011; Wüest et al. 2012), it can be assumed that a change in phytoplankton production and community structure may affect the methane production. Some carotenoid pigments such as alloxanthin and zeaxanthin were found to be more useful as paleolimnological proxies than others like fucoxanthin and diadinoxanthin which were completely lost during their transport to deep waters and/or on sediment surface due to their high vulnerability to degradation.

Previous paleolimnological studies (Pasche et al. 2010; Ross et al. 2014; Votava 2014) reported an alternating carbonate precipitation in the sediments of Lake Kivu but the geochemical process governing it remained unclear. In this chapter we discussed several scenarios based on carbonate concentration in relationship to other geochemical proxies. The outcome was that carbonate precipitation as CaCO₃ has probably been a permanent inter-annual phenomenon in Lake Kivu in the time period covered by the study but high variability in CaCO₃ precipitation may occur on seasonal time scales, depending on phytoplankton biomass, photosynthesis and depth of the mixed layer. Nevertheless, there have been periods of poor preservation of the precipitates in the sediments due to re-dissolution caused by acidic conditions generated by the diagenesis (acetoclastic fermentation) of organic-rich sedimentary material.

Nutrient cycling in Lake Kivu paleolimnology was found to be regularly changing. In modern Lake Kivu, nutrient sources to the productive layers are dominated by internal processes (upwelling, Muvundja et al. 2009; Pasche et al. 2012), and the latter is subject to variation in the mixing regime induced by climatic patterns (Thiery et al. 2014; Katsev et al. 2014) and SGD fluctuations conditioned at least by hydrothermalism and meteoric precipitation (Ross et al. 2014, 2015a). We used nutrient elemental and stable isotope proxies to track the history of nutrient supply and cycling into the productive layers. Episodic changes in nutrient limitation and utilization were recorded in the sediments.

The lake evolved from (N, P) co-limitation conditions to strong P limitation before shifting to N-deficient conditions due to stronger stratification. These nutrient conditions were also

corroborated by phytoplankton pigment markers. During low OM accumulation cyanobacteria (indicated by zeaxanthin, myxoxanthophyll and echinenone) and chlorophytes (indicated by lutein) were among the dominant phytoplankton groups under a weak mixing regime as indicated by the presence of isorenieratene. However during high OM accumulation in the sediment archives, diatom blooms were obvious as evidenced by peaks of biogenic silica, which were related to strong mixing conditions in the mixolimnion. During such events, episodic changes in elemental stoichiometry evidenced by peaks of BSi/TOC, BSi/TN and BSi/TP, were recorded and interpreted as an ephemeral change in diatom community (Kilham et al. 1986).

In the topmost core, a change in the ratio of phaeophorbide *a* to the sum of chlorophyll *a* and derivatives coupled with an increase of phaeophytin *a* may be interpreted as an effect of intense microbial activity taking place at the water/sediment interface and/or the effect of diagenesis. The origin of sedimentary OM was also identified as typically autochthonous as indicated by (C, N) stable isotopes and organic molecular markers. Paleoenvironmental data showed that OM in Lake Kivu is poorly preserved due to relatively high heterotrophic microbial uptake (Morana et al. 2014b) in the water column and intense diagenesis in the sediments. Sedimentary pigment preservation in the sediments of Lake Kivu was assessed and results indicated that specific markers of cyanobacteria, chlorophytes and cryptophytes were preserved in the sedimentary material. However no diatom, chrysophyte or dinoflagellate pigments were detected in the sediments which suggested that the labile diatom pigments were totally degraded. The absence of chrysophyte and dinoflagellate pigments in Lake Kivu sediments can also be related to their weak presence in the mixolimnion (Sarmiento et al. 2012; Darchambeau et al. 2014).

5.2. Perspectives

Lake Kivu is a fascinating ecosystem to study yet to be further explored. It is an interesting natural laboratory for research and education in all field studies of natural sciences. The hydrological features of the subaquatic sources such as the amount of water in the reservoir, its residence time as well as its underground circulation and the infiltration processes are still challenging and should be tackled because some of these hydrothermal springs which may be important as geothermal energy production, are also vital for the stability of the lake.

Organic matter fermentation sustains an important fraction of CH₄ production but nothing is yet known on how much the change in phytoplankton community structure and/or POC export to sediments can affect the methane production. In the present study we focused on pigment geochemistry. Future research could explore the geochemistry of other OM classes such as lipids, carbohydrates amino-acids, and humic substances (Arndt et al. 2013) which would contribute to elucidate the mechanisms governing the POM losses in the water column during the downward fluxes. The use of labile organic molecules in experimental studies with cultured microorganisms from Lake Kivu may help understanding the mechanisms and active organisms responsible of key biogeochemical processes because OM degradation processes result from the combined effort of billions of individual microorganisms (Arndt et al. 2013). Furthermore the application of molecular biology tools to the paleolimnology of Lake Kivu will help tracking the evolution of the microbial community and the history of biogeochemical processes sustaining the lake functioning.

Finally, the expected development of industrial methane exploitation is intended to “kill two birds with one stone” by cutting off the natural hazard of gas eruption threatening the riparian populations and at the same time by producing energy for the development of the riparian countries (Wüest et al. 2012). However cautious and wise measures are required to avoid the disruption of the lake stratification as well as to avoid eutrophication. Given that a zero-risk zero method does not exist, the monitoring of biogeochemical processes (e.g, N-fixation, CH₄, CO₂ concentrations, primary productivity, OM sedimentation rates, etc.) is necessary for early detection of any unexpected change in the lake functioning. Although the reservoir of the methane resource in the water column is well known, there is still a gap about the amounts of methane trapped within the large sediment layers. The catchment hydrology and mass fluxes to the lake should also be monitored as a base for assessing management options to preserve the water quality of the lake.

5.3. References

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