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Jean-Pierre Descy
François Darchambeau
Martin Schmid
Editors

Lake Kivu

Limnology and biogeochemistry of a tropical great lake

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Preface

During the first decade of the twenty-first century, a great deal of new knowledge has accumulated on Lake Kivu, in particular thanks to projects run in parallel by Swiss and Belgian research teams. Eawag, in Switzerland, was mainly interested in investigating further the peculiar physical structure and the biogeochemical cycling in Lake Kivu. Their research began with an emergency expedition following the eruption of the volcano Nyiragongo in January 2002. What was the impact of the lava flow that devastated part of the city of Goma and finally entered the lake? Did it disturb the stratification of the lake, and could it trigger a massive eruption of the gases stored in the lake, threatening people and animals all around the lake? Following that volcanic event, studies were conducted for measuring carbon dioxide and methane in the deep waters. Important knowledge gaps were identified concerning the formation of methane in the lake and its link to the nutrient cycling and physical processes. These open questions were tackled in research partnership projects in cooperation with universities in Rwanda and the Democratic Republic of the Congo.

With the objective of assessing Lake Kivu biological resources and their sustainability, and of understanding the mixolimnion ecosystem function, biologists and ecologists also conducted studies in Lake Kivu in the past decades, related to plankton composition and dynamics, following studies which began in the 1980s on the development of the sardine fishery. This sardine, *Limnothrissa miodon*, endemic to Lake Tanganyika, was introduced in the mid 1950 to increase the fishery yield of the lake, as the pelagic zone supported seemingly large amounts of plankton, but no planktivore. The introduction of the *sardine* has been widely considered as a great success and, from the fishery standpoint, is still cited as an example of species introduction with a positive incidence on the livelihood of the poor local population. By contrast, some scientists were less optimistic and, based on observation of a dramatic zooplankton decrease, predicted the collapse of the sardine fishery. If such a collapse did not happen so far, as the annual yield has maintained itself as the fishing methods evolved, the actual sardine production did not meet the expectations, i.e. 35,000 t y^{-1} for the whole lake, estimated by the biogenic capacity of Lake Kivu waters and by comparison with Lake Tanganyika. The research project on the ecosystem of the “biozone”, supported by the Belgian Cooperation to Development, aimed precisely at assessing the ecosystem changes brought about by the sardine introduction, as well as to understand why the sardine fishery had a low yield compared to its original habitat and to other systems where *Limnothrissa* was introduced.

This book has no other objective than gathering the scientific knowledge on Lake Kivu, which may be timely, in the perspective of tapping the lake gas resources for energy production, in a region which needs energy for its development. At the same time, several chapters deal with different aspects of tropical limnology, including elements of comparison with other East African Great Lakes.

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Chapter 1
Lake Kivu: Past and Present

Jean-Pierre Descy, François Darchambeau, and Martin Schmid

Abstract Lake Kivu, located in the Eastern African Rift, in a dramatic volcanic scenery, has fascinated the local people, inspiring legends; the explorers of the nineteenth century, inspiring romantic reports; and the scientists of the twentieth and twenty-first centuries, inspiring limnological and geochemical research. For some, Lake Kivu is a "killer lake", containing vast amounts of carbon dioxide and methane in its deep, anoxic waters, and it has been compared to Lakes Nyos and Monoun, whose eruptions caused massive animal and human death in Cameroon. Fortunately, methane gas exploitation can help to reduce the eruption risk and at the same time supply an important amount of energy for the benefit of local development. However, the management of the lake resources, including methane harvesting and fisheries, is complex, and particular care must be taken during gas exploitation in order to avoid any negative impacts on the ecosystem and the goods and services provided by the lake.

In this chapter, the history of research on Lake Kivu is summarized, and the major findings that resulted from expeditions by British, Belgian, American, and German researchers are presented.

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1.1 The Beauty and the Beast

> … und plötzlich standen wir auf dem felsigen Ufer einer gewaltigen Wasserfläche. Eine frische Seebrise wehte zu uns herüber, und tosende Brandung, wie die des Meeres, rauschte uns entgegen. Der Wasserspiegel erstreckte sich unabsehbar und unbegrenzt für unser Auge weithin nach Süden. Zu den bisher von uns geschauten Wundern dieser herrlichen Länder, zum Kigeri und Kirunga, hatte sich ein drittes gesellt, der Kivu.[1]

Many travellers must have reacted in the same way as Count von Götzen (1895), when their eyes first opened on Lake Kivu. Yet this romantic view is in strong contrast with a local legend about the creation of the lake (Pagès 1920): A farmer was given a bull by the god Imana, but had to promise that he would keep the donation secret. While he was away from his home, his wife betrayed the secret. Imana punished the farmer by inundating his land, and only a few islands jutted out of the vast expanse of water that was now Lake Kivu. It is plausible to assume that this tale relates to the lake's turbulent geological history which is rich in volcanic activity and lake level changes. Indeed, Lake Kivu is both a beauty and a beast, the spectacular landscape and the blue colour of its waters may easily distract from the fact that huge amounts of gases are hidden beneath its surface, with the potential of creating one of the largest natural disasters in the history of humanity.

The catastrophic gas eruptions that occurred in Lake Monoun in 1984 (Sigurdsson et al. 1987) and in Lake Nyos in 1986 (Kling et al. 1987; Sigvaldason 1989) demonstrated the destructive potential of limnic gas eruptions. The deep waters of these lakes are fed by springs containing large concentrations of dissolved carbon dioxide (CO_2). Because of the permanent stratification, the gases cannot escape to the atmosphere, and the lakes are continuously charged with CO_2-rich water until the gas pressure reaches the hydrostatic pressure at some depth (Tietze 1992). At this point, CO_2 bubbles can nucleate and grow and thus lead to a gas eruption from the lake (Zhang and Kling 2006). As the CO_2 released is denser than air, it displaces the air on the lake surface and downstream of the lake, asphyxiating people as well as animals (Kling et al. 1987).

A similar situation is found in Lake Kivu, but on a much larger scale. However, in Lake Kivu, the gas pressure is mainly due to the dissolved methane (CH_4) which is much less soluble than CO_2 (Schmid et al. 2004). A gas eruption from Lake Kivu would therefore be caused primarily by the dissolved CH_4. Still, the erupting gas mixture would be composed mainly of CO_2 that would be stripped from the water by the CH_4 bubbles. Such a gas eruption from Lake Kivu would potentially have much more dramatic consequences as in Lake Nyos or Monoun. However, currently the maximum total gas pressure in the lake, calculated from the gas concentrations (Fig. 10.1) as described by Schmid et al. (2004), reaches only about 55% of saturation.

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[1] English translation: … and suddenly we stood on the rocky shores of a huge expanse of water. A fresh lake breeze blew toward us, and roaring waves like those of the sea, swept towards us. The water surface extended far southward, invisible and infinite for our eyes. To the previous wonders of these marvellous countries, to the Kigeri and the Kirunga, a third one was added: the Kivu.

Schmid et al. (2004) estimated that a large magmatic eruption within the lake would be required to trigger a gas eruption. But a more thorough analysis of this risk still remains to be done, while CH_4 concentrations seem to be increasing in the deep waters of the lake (Schmid et al. 2005; Pasche et al. 2011).

Managing Lake Kivu is therefore a difficult challenge, as the beast needs to be tamed without destroying its beauty. The gases need to be removed from the lake to avert the danger of an eruption. At the same time the goods and services provided by the ecosystem, in particular the fishery, need to be preserved. To complicate matters further, Lake Kivu is also unique in its limnological and geochemical features. A thorough understanding of these complexities is essential as a base for sustainable management of the lake. This book aims at presenting the current knowledge about the physics, biogeochemistry and ecology of Lake Kivu, based on research conducted at Belgian universities (University of Namur, University of Liège, University of Brussels) and at Eawag, Switzerland, in collaboration with the "Institut Supérieur Pédagogique" of Bukavu, DR Congo, and the National University of Rwanda at Butare, in the beginning of this twenty-first century.

1.2 History of Lake Kivu Research

Well hidden in the highlands of East Africa, Lake Kivu for a long time escaped the attention of European explorers, even though it had already been the centre of a local trading system between Rwanda and societies living to the west of the lake (Newbury 1980). It seems that the first account of the existence of Lake Kivu was reported by J. H. Speke (1863), but the first European to see Lake Kivu was Gustav Adolf von Götzen, after his famous crossing of Rwanda with a caravan of 620 people, among which 400 carriers. He left a detailed account of his expedition (von Götzen 1895), which describes the difficulties of exploration at that time, but also conveys his amazement at discovering the marvels of this part of Africa. The scientific interest in the East African Great Lakes further increased with the English expeditions at the beginning of the twentieth century (Cunnington 1920). An inventory of several lakes attracted attention on the poverty of Lake Kivu fish fauna: only 23 species, among which 4 endemic, were recorded at that time. The low fish diversity was attributed to high salinity.

A first analysis of water samples from Lake Kivu as well as from hot springs south of Gisenyi was published by Hundshagen (1909). However, it is only in the 1930s that a Belgian expedition, led by Hubert Damas (Fig. 1.1; Damas 1937), gathered the first comprehensive limnological data from Lake Kivu. Among other things, Damas' publication presents detailed evidence of the meromictic character of the lake and of the presence of large amounts of dissolved gases and nutrients in the deep waters. Damas' work was remarkable in many respects: whereas other scientists involved in research projects on East African lakes at the beginning of the twentieth century were largely motivated by the opportunity of making inventories of the flora and the fauna, Damas – a zoologist from the University of

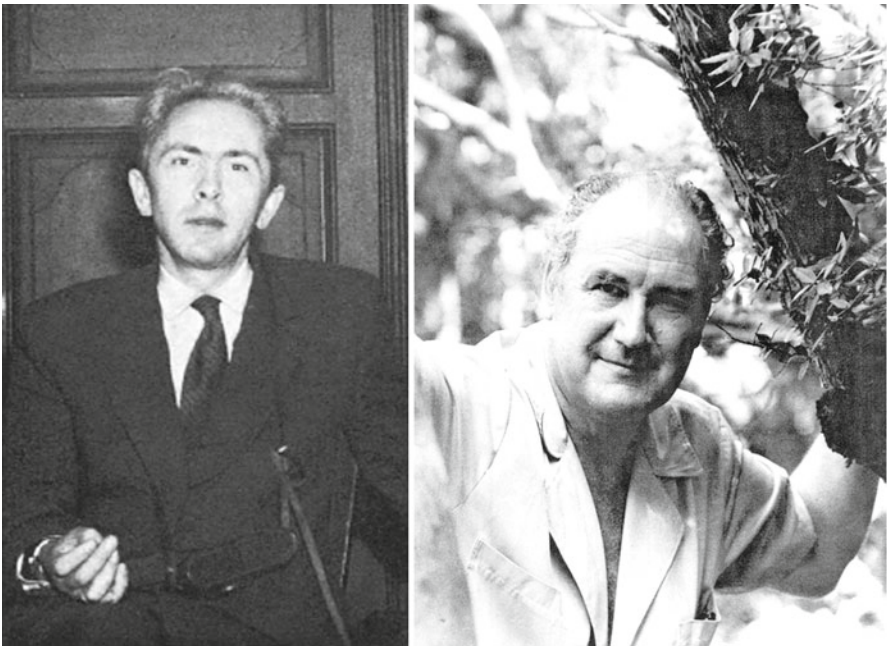

Fig. 1.1 Left: Hubert Damas (1910–1964), professor at University of Liège (Belgium); right: André Capart (1917–1993), director of the Royal Institute of Natural Sciences (Belgium)

Liège, Belgium – was interested in investigating the conditions in which animals lived and developed. In this respect, he was among the leading scientists of that time in tropical limnology, along with Juday, Thienemann, Ruttner, Worthington and Beadle. Although the methods and equipment he used may seem rudimentary compared to the techniques of modern limnology, the publication of the mission conducted in 1935–1936 on Lakes Kivu, Edward and Ndalaga (Damas 1937) remains a model of a limnological study, where the results were presented with precision and interpreted in great detail. Among other things, his observations, combined with geological evidence, contributed to confirm that present Lake Kivu originated from the rise of the Virunga chain in the late Pleistocene. The "old" Lake Kivu was formerly part of the drainage basin of Lake Edward, with which it shares faunal elements, while entire fish families present in Lake Tanganyika are absent from Lake Kivu as well as from Lake Edward (Beadle 1981). Damas understood that the stability of the stratification was due to the increase of salinity below 70 m, but he could not fully explain the increase in temperature. He also noted the horizontal homogeneity in the deep water and observed the main density gradient between 250 and 275 m depth which he speculated to have been caused by a mixing event from the surface during a cold period. Finally, he hypothesized that the gases present at high concentrations in the deep waters were CH_4 or nitrogen, as he excluded CO_2 to be sufficiently concentrated to cause the observed bubbling in deep water samples.

It was Capart and Kufferath (1956) who identified the gases as CO_2 (73.4%) and CH_4 (24.8%), with small amounts of hydrogen sulfide, nitrogen and argon. Schmitz and Kufferath (1955) estimated the total amount of CH_4 to be 57 km^3, and proposed to exploit this enormous source of energy.

Another subsequent Belgian expedition was led by André Capart (Fig. 1.1), then Director of the Royal Institute of Natural Sciences, and reported by Verbeke (1957), on Lakes Kivu, Edward and Albert, often quoted as "mission KEA". For Lake Kivu, this expedition completed the data reported by the Damas' mission, with an emphasis on the littoral flora and fauna, particularly on invertebrates. To date, this study remains the most comprehensive inventory of the biota of the lake shore, stressing for instance the peculiarities of the rocky shores and the absence of *Chaoborus* larvae in the benthos. Capart and others (Capart 1960), besides the purely scientific discoveries, had practical objectives regarding the exploitation of the resources of these large lakes which were at that time part of the Belgian colonies. They first contributed to the development of the pelagic fishery of Lake Tanganyika, and then promoted the introduction of the "Tanganyika sardine" *Stolothrissa tanganicae* or *Ndakala* into Lake Kivu, which supported a substantial zooplankton comprising Copepods and Cladocerans, but no fish (Capart 1959, 1960). The project was, actually, after the introduction of the sardine, to introduce *Lates stappersii*, the most abundant piscivorous fish in Lake Tanganyika. After some failed attempts with adult *Stolothrissa*, which died quickly during the transport between the two lakes, juveniles of the two clupeid species present in Lake Tanganyika (*S. tanganicae* and *Limnothrissa miodon*) were released in Lake Kivu (Collart 1960), and only *Limnothrissa* succeeded in adapting to Lake Kivu (Spliethoff et al. 1983). Another dream of Capart and co-workers was to exploit the CH_4 of the deep waters (Capart and Kufferath 1956), and to increase the productivity of the fishery by releasing the nutrient-rich degassed waters into the surface waters. The advent of the independence of Congo and the decolonization that followed put an end to those projects. Still, the pelagic fishery of Lake Kivu developed later on (Chap. 8), even though its yield was lower than that predicted by the Belgian scientists who envisioned a sardine production as high as 35,000 tons per year.

In the meantime, the exploitation of the CH_4 resource was initiated by the construction of a pilot plant by the Union Chimique Belge at Cap Rubona south of Gisenyi in 1962, which delivered energy to a local brewery. However, despite several studies investigating possibilities for a more extensive exploitation of the CH_4 stored in the lake, it took more than 40 years until the next CH_4 extraction pilot plant was constructed.

In 1971 and 1972, two research expeditions by the Woods Hole Oceanographic Institution, led by Egon T. Degens (Fig. 1.2), focused on the geophysical and biogeochemical properties of the lake. These expeditions provided the most comprehensive compilation of vertical profiles of chemical properties of the lake water in the twentieth century. It was concluded that the deep water of the lake was fed by hydrothermal springs (Degens et al. 1973) and that the CH_4 mainly originated from CO_2 reduction (Deuser et al. 1973). Seismic profiles indicated sediment thicknesses of up to 500 m in the deep part but only a thin sediment layer in the shallower

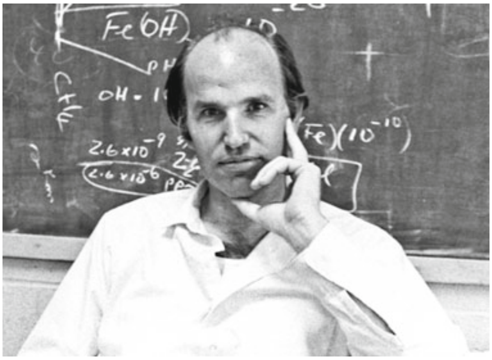

Fig. 1.2 Egon T. Degens (1928–1989), professor at the Woods Hole Oceanographic Institution

parts. The observed variability of sediment thicknesses was attributed to different ages of the different lake basins and lake level fluctuations (Wong and Von Herzen 1974). Several sediment cores were collected which until recently were the only source for paleolimnological information (Chap. 9). These cores were later also used for chemical and biological analyses by other research groups (Haberyan and Hecky 1987; Al-Mutlaq et al. 2008). During the 1972 expedition, Fred C. Newman investigated the fine structure of the temperature profiles in the lake using a recently developed temperature microstructure profiler and thus discovered the unique double-diffusive staircases (Newman 1976; Chap. 2).

In 1974–1975, the German Bundesanstalt für Geowissenschaften und Rohstoffe organized another expedition to the lake which resulted in the PhD thesis of Klaus Tietze (1978). Tietze specifically developed a probe to measure density *in situ* with high precision (Tietze 1981). His work was hitherto the most detailed study on the density stratification, temperature, conductivity and gas concentrations, as well as on the isotopic composition of the CH_4 in the lake. Tietze (Fig. 1.3) estimated the total amount of CH_4 in the lake to 63 km^3 and concluded that it was mostly biogenically produced (Tietze et al. 1980). However, based on a re-analysis of the isotopic data, Schoell et al. (1988) concluded that approximately one-third of the CH_4 was derived from an acetate fermentation process and two-thirds from a CO_2-reducing bacterial process which uses the dissolved CO_2 in the lake water as a carbon source. Following the catastrophic gas eruptions in Lakes Nyos and Monoun, Tietze understood that a similar eruption from Lake Kivu could potentially result in an unimaginable disaster (Tietze 1992). He invested a lot of time and energy in developing strategies for a safe and environmentally sound exploitation of the CH_4 resource (e.g., Tietze 2007 and references therein).

Political instability in the region retarded further research activities on Lake Kivu, until January 2002, when lava from the eruption of the volcano Nyiragongo flowed into the lake. It was feared that this lava flow might trigger a gas eruption from the lake. Subsequently, a dramatic documentary by BBC brought international attention to Lake Kivu, even though the results of an emergency expedition showed that there had been no significant impact by the lava flow on the lake stratification

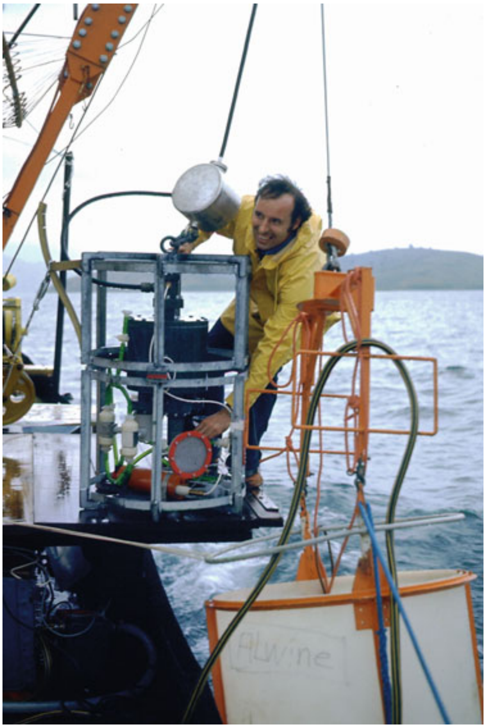

Fig. 1.3 Klaus Tietze during an expedition on Lake Kivu in 1974 (Photo provided by K. Tietze)

(Lorke et al. 2004). Since then, several projects for exploiting the CH_4 gas from the lake have emerged and pilot power plants have been constructed (Fig. 1.4). It is expected that large-scale commercial CH_4 extraction will develop in the next decade and will possibly have important impacts on the density stratification in the lake. The scientific research presented in the following chapters of this book came thus just in time to document the physical, chemical and biological status of the lake before it is entering this new era.

1.3 Outline of the Chapters

The unusual vertical stratification and the physical mixing and transport processes, which are governing internal nutrient cycling in Lake Kivu, are detailed in Chap. 2. The nutrient budget, with estimations of external inputs and internal loading, is treated in Chap. 3, while Chap. 4 deals with partial pressure of CO_2 and CH_4 in the surface waters, mainly driven by the seasonal variation of vertical mixing, and contrasting with the very high concentrations of these gases in the deep waters.

The two following chapters are devoted to the microbial communities, i.e. the prokaryotic and eukaryotic phytoplankton and its ecology in Chap. 5 and the other microbes (bacteria, archaea and microzooplankton) in Chap. 6. Zooplankton and

Fig. 1.4 Gas extraction facility of Kibuye Power 1 (KP1), the first pilot plant for large-scale commercial methane extraction from Lake Kivu that started operating in January 2009 (Photo provided by Kibuye Power Ltd.)

fish diversity, biomass and production are described in Chaps. 7 and 8, respectively. Comparisons are made with other African Great Lakes, highlighting the low diversity and the simplified food web of Lake Kivu, with however a high proportion of endemic fish species.

The historical changes that occurred in Lake Kivu, related to climatic variations over thousands of years, to volcanic events and to very recent changes, are recorded in the sediments (Chap. 9). Finally, Chap. 10 deals with the sources and sinks of the CH_4 present in high concentrations in the deep waters; this chapter also considers different scenarios for sustainable gas exploitation, with the objectives of maintaining the lake stability and ecological integrity, combined with economic viability.

In a final concluding chapter, we synthesize the current knowledge on Lake Kivu and suggest different lines for future investigations of this unique tropical lake.

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Chapter 2
Stratification, Mixing and Transport Processes in Lake Kivu

Martin Schmid and Alfred Wüest

Abstract This chapter summarizes the knowledge on mixing and transport processes in Lake Kivu. Seasonal mixing, which varies in intensity from year to year, influences the top ~65 m. Below, the lake is permanently stratified, with density increasing stepwise from ~998 kg m^{-3} at the surface to ~1,002 kg m^{-3} at the maximum depth of 485 m. The permanently stratified deep water is divided into two distinctly different zones by a main gradient layer. This gradient is maintained by a strong inflow of relatively fresh and cool water entering at ~250 m depth which is the most important of several subaquatic springs affecting the density stratification. The springs drive a slow upwelling of the whole water column with a depth-dependent rate of 0.15–0.9 m $year^{-1}$. This upwelling is the main driver of internal nutrient recycling and upward transport of dissolved gases. Diffusive transport in the deep water is dominated by double-diffusive convection, which manifests in a spectacular staircase of more than 300 steps and mixed layers. Double diffusion allows heat to be removed from the deep zone faster than dissolved substances, supporting the stable stratification and the accumulation of nutrients and gases over hundreds of years. The stratification in the lake seems to be near steady-state conditions, except for a warming trend of ~0.01°C $year^{-1}$.

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2.1 Introduction

The vertical mixing and transport processes in Lake Kivu are different from most other large lakes in the world. This is caused by a combination of the lake's morphometry, the influence of the nearby volcanoes and groundwater inflows. The physics of Lake Kivu is not extraordinarily complex, but its peculiarity can easily lead to misconceptions. Knowledge of physical, geochemical or biological processes gained from other tropical or even temperate lakes should therefore not be applied to Lake Kivu without verifying that it is valid under the special physical characteristics of the lake. Considering their importance, relatively little attention has been paid up to now to the physical processes governing Lake Kivu, and only few relevant publications are available.

This chapter is structured as follows: first the morphometry and the water balance of the lake are reviewed, and an overview of the vertical stratification is given. Then vertical diffusive transport processes, including the unique occurrence of double diffusive convection, and the vertical upwelling of the water column are evaluated. Finally, the observed temporal changes in stratification are discussed. In each of these sections relationships between the physical properties of the lake and the biogeochemical processes described in the following chapters of this book are drawn.

2.2 Morphometry

The morphometric properties of Lake Kivu are given in Table 2.1. The watershed is only about twice as large as the lake surface. More than 100 small tributaries feed the lake. The shores are generally steep, with the exception of the northern shore where the slope gradually steepens towards the volcanoes Nyiragongo and Nyamuragira. The lake consists of the main basin and four smaller sub-basins, the Kabuno Bay, the Ishungu Basin, the Kalehe Basin and the Bukavu Bay (Fig. 2.1).

Kabuno Bay, situated to the northwest of the lake, may almost be considered as an individual lake. Based on the vertical conductivity profiles (Sect. 2.4), the sill separating it from the main basin cannot be deeper than ~11 m. The other sub-basins are much less separated from the main basin. The Kalehe Basin with a maximum depth of ~230 m is connected to the main basin at a depth of ~180 m. The small Ishungu Basin with a maximum depth of ~180 m is connected both to the north to Kalehe Basin (at ~110 m depth) and to the east to the main basin (at ~130 m depth). Bukavu Bay (maximum depth ~100 m) is linked to Ishungu Basin by three channels, the deepest of which reaches a depth of ~50 m. The detailed bottom topography (Lahmeyer and Osae 1998) shows numerous cones that may be ancient volcanoes as well as channels on the lake floor. A detailed investigation of these structures may be a promising option to gain knowledge about the history of the lake.

Table 2.1 Morphometry and hydrology of Lake Kivu (modified from Muvundja et al. (2009))

Parameter	Value
Surface area (excluding islands)	2,370 km^2
Volume	580 km^3
Maximum depth	485 m
Mean depth (volume/lake area)	245 m
Catchment area (excluding lake)	5,100 km^2
Precipitation on lake surface	3.3 (2.9–3.7) km^3 $year^{-1}$
Inflow from surface tributaries	2.0 (1.6–2.4) km^3 $year^{-1}$
Subaquatic inflows	1.3 (1.0–1.5) km^3 $year^{-1}$
Evaporation from lake surface	3.6 (3.0–4.0) km^3 $year^{-1}$
Outflow	3.0 (2.6–3.4) km^3 $year^{-1}$
Flushing time (volume/outflow)	~200 years
Residence time [volume/(precipitation + inflow)]	~100 years

For each component of the water balance, the table contains one value that results in a closed water balance, and in parentheses an estimated uncertainty range based on the information in Sect. 2.3

2.3 Water Balance

The water balance of Lake Kivu has been discussed in detail by Bergonzini (1998) and Muvundja et al. (2009). Nevertheless, the uncertainty of the individual components is still considerable (Table 2.1). Precipitation on the lake surface has been estimated by these authors based on land measurements at 1,400–1,500 mm $year^{-1}$, corresponding to 3.3–3.6 km^3 $year^{-1}$. However, it is unclear whether the observations from land stations are representative for precipitation on the lake surface. Precipitation of nearshore stations is ~1,200 mm on the eastern shore and, with a higher variability, ~1,500 mm on the western shore. The average of the three grid cells covering the lake and most of the watershed in the GPCC Version 5 0.5° gridded data (http://gpcc.dwd.de) for the years 1941–2009 is 1,479 mm.

Evaporation from the lake surface has been estimated by Bultot (1971) at 1,412 mm, probably with an uncertainty on the order of 10–20%. This is the least investigated component of the water balance of the lake. Therefore its value was adjusted to close the water balance in Table 2.1. Large differences between evaporation and precipitation cause a concentration of salts in the surface waters in other East African lakes such as Lake Tanganyika and Lake Malawi (Branchu et al. 2010). In Lake Kivu the difference between these two components is small, and increased salt concentrations are due to inputs by subaquatic springs (Sect. 2.7).

A significant part (~700 km^2) of the watershed, located between the lake and the volcanoes to the north, is not drained by any rivers. Precipitation on this area likely infiltrates and contributes to the groundwater sources feeding the lake. These subaquatic springs are an essential feature of the physics in Lake Kivu, as they drive the nutrient recycling from the permanently stratified deep water. Their total discharge is ~1.3 km^3 $year^{-1}$ (Sect. 2.7).

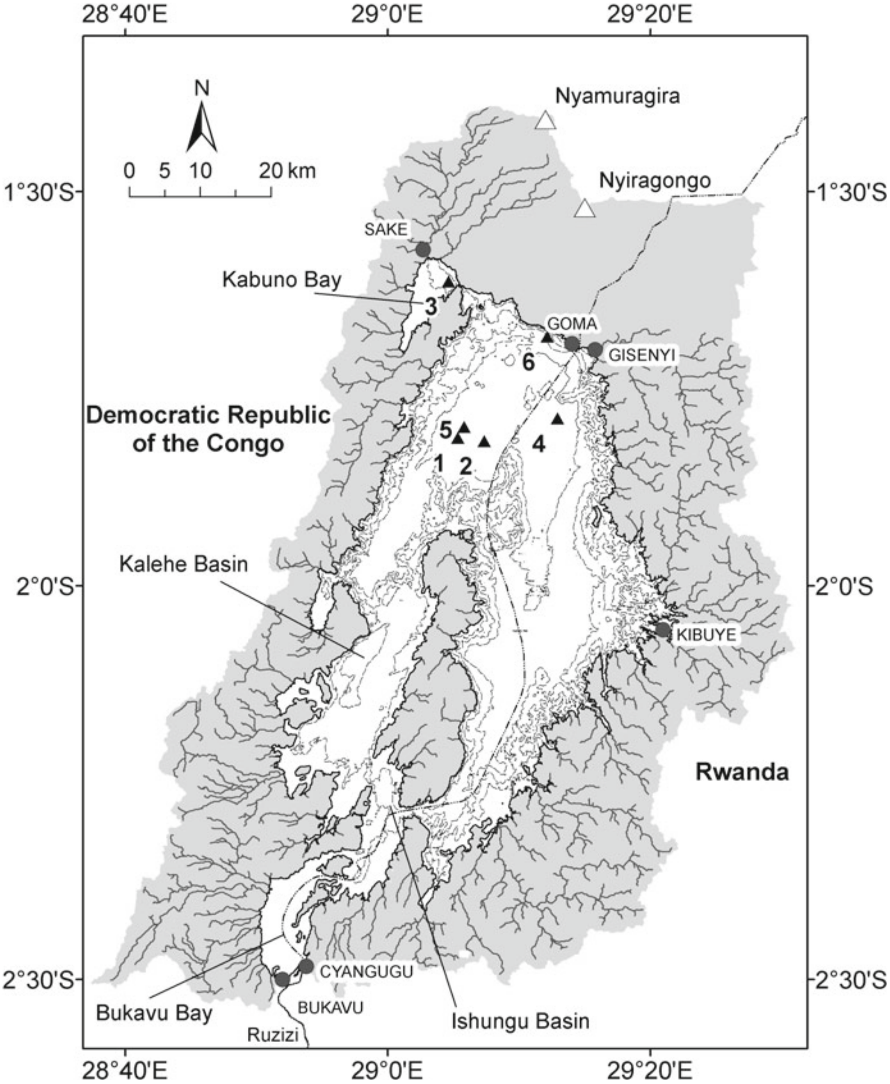


Fig. 2.1 Bathymetric map of Lake Kivu, with depth contours at 100 m intervals, catchment area (shaded in grey), tributaries calculated from a digital elevation model, major cities and volcanoes around the lake, and locations of CTD profiles shown in Figs. 2.2 and 2.6 (numbered triangles; 1: Jan 2002, 2 and 3: Feb 2004, 4: May 2007, 5 and 6: Jan 2010)

The remaining watershed of 4,400 km^2 is drained by more than 100 small rivers (Fig. 2.1). Muvundja et al. (2009) estimated the total riverine inflows at 2.4 km^3 year^{-1} based on discharge estimates for 21 tributaries made during 2 years. This is probably an upper limit, as precipitation was ~10% above average during the measurement period. A simulation with the Soil Water Assessment Tool (SWAT) resulted in total surface inflows of 2.1 km^3 $year^{-1}$ (Rinta 2009). Bergonzini (1998) extrapolated discharge data from one river (Sebeya in Gisenyi) to the whole catchment, resulting in total inflows of only 1.1 km^3 $year^{-1}$. This is certainly an underestimate, as the runoff per area is larger on the Congolese than on the Rwandan side of the lake. In order to close the water balance he estimated the total inflows at 2.6 km^3 $year^{-1}$, but this would have been only 1.3 km^3 $year^{-1}$ if the subaquatic springs had been included in the calculation. In summary, the total surface inflows are probably within the range of 2.0 ± 0.4 km^3 $year^{-1}$.

The only outflow, the Ruzizi River (also spelled Rusizi), leaves the lake at the southern end and is one of the major tributaries of Lake Tanganyika. Its discharge has been determined to 2.8 km^3 $year^{-1}$ for the years 1951–1973 (Bergonzini 1998). Precipitation in these years was almost equal to the long-term average precipitation. Degens et al. (1973) cite a value of 3.2 km^3 $year^{-1}$ based on 10 years of data from the Ruzizi I hydropower station. More recent data from this station for the years 1989–2007 yields an average discharge of 2.6 km^3 $year^{-1}$. This value was calculated from power production and therefore does not include any water released without corresponding production. The 3.6 km^3 $year^{-1}$ given by Muvundja et al. (2009) are likely an overestimate based on an incorrect rating curve. The small size of the catchment compared to the lake volume results in a flushing time on the order of 200 years and a water residence time on the order of 100 years.

2.4 Vertical Stratification

The vertical density stratification in Lake Kivu (Fig. 2.2) is unique for such a large lake with (1) dissolved gases contributing significantly to density, (2) an almost complete decoupling between the deep and the surface waters, and (3) spectacular double-diffusive staircases (Sect. 2.6). The lake is meromictic, i.e., seasonal mixing does not reach its deepest layers. The lake can be divided vertically into three different layers. Stratification in the upper 60 to 65 m is dominated by seasonal mixing similar to that observed in other tropical lakes (Sect. 2.9). This layer is called *mixolimnion*, and has also been called *biozone*, because biological activity is limited to this layer, except for anaerobic microbial processes like methanogenesis (Chap. 10). Below ~65 m depth, the lake is permanently stratified and anoxic. The *permanently stratified deep water* or *monimolimnion* is divided in two sections by a strong density gradient between 255 and 262 m depth. This gradient is maintained by subaquatic springs entering the lake at the top of the gradient (Sect. 2.7). In the following, the upper monimolimnion between the mixolimnion and this main gradient is called *upwelling zone*, because the upwelling created by the subaquatic springs is the most prominent physical property of this layer. The lower monimolimnion below the main gradient is called *deep zone.* This zone has also been called *resource zone*, because it contains most of the methane (CH_4) that can be exploited (Chap. 10).

The temperature structure in the mixolimnion changes seasonally in response to meteorological variations. Temperature reaches a minimum of ~23.0°C at the base

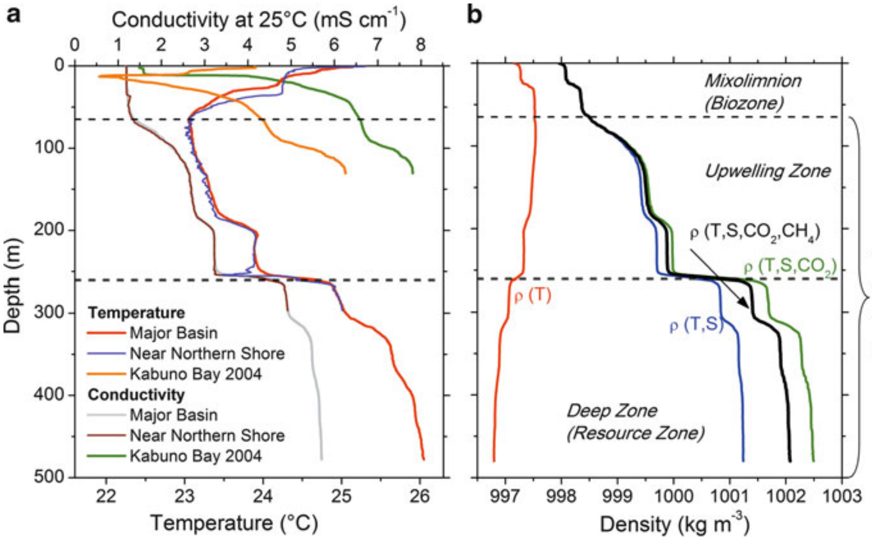


Fig. 2.2 (**a**) Temperature and conductivity κ_{25} (corrected to 25°C) profiles measured in Jan 2010 (Feb 2004 for the profile in Kabuno Bay) at the positions 4, 5 and 6 in Fig. 2.1. (**b**) Contributions of the different components to the average density profile in the main basin (Feb 2004, Schmid et al. 2004b)

of the mixolimnion at ~65 m depth (Fig. 2.2). Below this depth, no seasonality is observed, and temperature increases in an irregular stepwise fashion up to 26°C at the deepest point of the lake. The contribution of temperature to the vertical density gradient in the monimolimnion is thus negative (Fig. 2.2) and the density stratification would be unstable without the contributions of dissolved solids and CO_2. This destabilizing effect is the driving force for the double-diffusive processes described in Sect. 2.6. The density of water in Lake Kivu, excluding the reversible effect of pressure, can be approximated with the following equation (Schmid et al. 2004b):

$$\rho(T,S,CO_2,CH_4) = \rho(T)\cdot(1+\beta\cdot S+\beta_{CO2}\cdot CO_2+\beta_{CH4}\cdot CH_4) \qquad (2.1)$$

Salinity S [g kg^{-1}] is calculated from conductivity at 25°C, κ_{25} [mS cm^{-1}], with a polynomial function that is deduced from the ionic composition (Wüest et al. 1996). As a rule of thumb, for Lake Kivu a difference in κ_{25} of 1 mS cm^{-1} corresponds to a difference in S of ~1 g L^{-1}. The coefficient of haline contraction, β, was estimated at 0.75×10^{-3} kg g^{-1}, based on the measured ionic composition with the method developed for Lake Malawi by Wüest et al. (1996). Its value means that a salinity difference of 1 g L^{-1} results in a density difference of 0.75 g L^{-1}. Finally, the effects of dissolved gases on water density need to be considered, which are opposite for the two main gases in Lake Kivu: CO_2 increases the density of water with a contraction coefficient β_{CO2} of 0.284×10^{-3} kg g^{-1}, while CH_4 decreases density with $\beta_{CH4}=-1.25\times10^{-3}$ kg g^{-1}. The total density is calculated by adding the effects of salinity, CO_2 and CH_4 (Eq. 2.1).

The contributions of temperature, salinity and dissolved gases to the vertical density profile in Lake Kivu (Fig. 2.2b) reveal that the stratification is stable mainly because of the stabilizing salinity gradient. Between 65 and 480 m depth, the density decreases by ~0.7 $g\,L^{-1}$ due to temperature and by ~0.4 $g\,L^{-1}$ due to dissolved CH_4, and increases by ~3.5 $g\,L^{-1}$ due to salinity and by ~1.2 $g\,L^{-1}$ due to dissolved CO_2. Altogether, the stabilizing effect of the dissolved substances is on average 6 times as large as the destabilizing effect of temperature.

2.5 Horizontal Homogeneity

Temperature and conductivity in the monimolimnion are horizontally nearly homogeneous throughout the main basin. Profiles taken at different locations during a cruise typically vary within ±10 $\mu S\,cm^{-1}$ and ±0.01 to ±0.03°C from the basin average. Larger variations are observed at some depths at locations influenced by the overflow of water from Kabuno Bay (Tietze 1978) or by the inflow of subaquatic springs. As an example, one of several profiles measured in Jan 2010 that showed a clear negative temperature peak at 250 m depth near the northern shore is compared to a profile taken in the central part of the main basin in Fig. 2.2a. The profile also shows a weak negative conductivity peak at the same depth, but this can hardly be distinguished on the scale of the figure.

With two notable exceptions, vertical profiles in the sub-basins are also very similar. The density structure in Kabuno Bay differs from that in the main basin so much that the bay can almost be considered a separate lake. It is permanently stratified below the depth of ~11 m of the sill separating it from the main basin, with much higher conductivities (Fig. 2.2a) and CO_2 concentrations (Tietze 1978; Tassi et al. 2009) as well as higher alkalinity and lower pH (Chap. 4). Conversely, Bukavu Bay does not show a significant increase in conductivity below 60 m depth (Sect. 2.3) which indicates that it is regularly completely mixed during the dry season.

The horizontal homogeneity of conductivity and temperature implies that horizontal mixing occurs on a much shorter time scale than vertical transport processes. This has important consequences for the management and monitoring of the lake. It can be assumed that also other constituents, especially gas concentrations, are horizontally homogeneously distributed. Consequently, except for the mixolimnion and for local effects of subaquatic springs or CH_4 extraction facilities, measurements made at one location can be assumed to be valid for the whole main basin. One-dimensional models are appropriate to simulate long-term processes in the lake. Furthermore, it does not matter from which location CH_4 is extracted from the lake. The CH_4 resource can neither be allocated to geographic concession areas nor be exploited independently by the two bordering countries (Expert Working Group 2009). The exact time scale required for horizontal mixing has not been determined, but should be on the order of a few months or at maximum a few years. Observations of reinjection plumes from methane extraction facilities may allow quantifying this more precisely in the future.

2.6 Diffusive Transport

A spectacular staircase of more than 300 double-diffusive steps consisting of mixed layers separated by sharp interfaces has been observed in Lake Kivu. An example of a mixed layer with adjacent interfaces is shown in Fig. 2.3. The physical processes that cause such staircases have been described elsewhere (Turner 1973; Kelley et al. 2003). In short, they are formed due to local instabilities caused by the different molecular diffusivities of heat and dissolved substances.

The occurrence of such a dense layering in lakes is a rare phenomenon, as the requisite preconditions are seldom fulfilled, even less over such a large depth range. It occurs mainly in lakes that are either fed by warm and salty subaquatic springs, such as Lake Kivu or Lake Nyos (Schmid et al. 2004a), or in mining lakes with high concentrations of dissolved solids (von Rohden et al. 2010). Double-diffusive steps in Lake Kivu were first observed by Newman (1976) and analyzed in more detail by Schmid et al. (2010). The staircase in Lake Kivu is the most extensive ever observed in a lake. In the following we focus on the relevance of the double-diffusive staircases for the large-scale physical transport processes in the lake.

Double-diffusive steps were observed in the main basin below ~130 m depth, except for depth ranges that are disturbed by external inflows (Sect. 2.7) and except for strong gradient zones. In the latter, the temperature gradients are so strong that the molecular heat flux is sufficient to remove the excess heat without the need for double-diffusive steps. The presence of these staircases is a strong indicator for the absence of significant small-scale turbulence, which would otherwise destroy these small-scale structures. In most lakes, and above the double-diffusive staircase also in Lake Kivu, vertical diffusive transport is dominated by turbulent diffusion which represents the average transport of constituents due to the random motion of water parcels in turbulent flows. In analogy to molecular diffusion, turbulent diffusion is usually described as a down-gradient flux $F_{C,diff}$ of a constituent that is the product of the gradient of the constituent C and a turbulent diffusion coefficient K. For vertical turbulent diffusion, $F_{C,diff} = -K_Z\, dC/dz$. In contrast to molecular diffusion, the turbulent diffusion coefficient is a property of the flow and as such independent of the constituent.

In a double-diffusive staircase, turbulent mixing is restricted to the mixed layers, whereas the vertical transport through the interfaces is close to molecular. The net vertical flux of a constituent through the staircase can then be described by an "apparent" vertical diffusion coefficient, which is defined as the ratio of the flux of the constituent to its vertical gradient, and which can be estimated from the properties of the double-diffusive staircase.

The apparent vertical diffusion coefficients in the double-diffusive staircase of Lake Kivu have been estimated to be on the order of 1×10^{-6} m^2 s^{-1} for heat and 1×10^{-7} m^2 s^{-1} for dissolved substances (Schmid et al. 2005, 2010). This corresponds to time scales of about 2 or 20 years for vertical mixing over a distance of 5 m, respectively. As a consequence, diffusive transport is relatively unimportant compared to advective transport (Sect. 2.8), especially for dissolved substances. This is

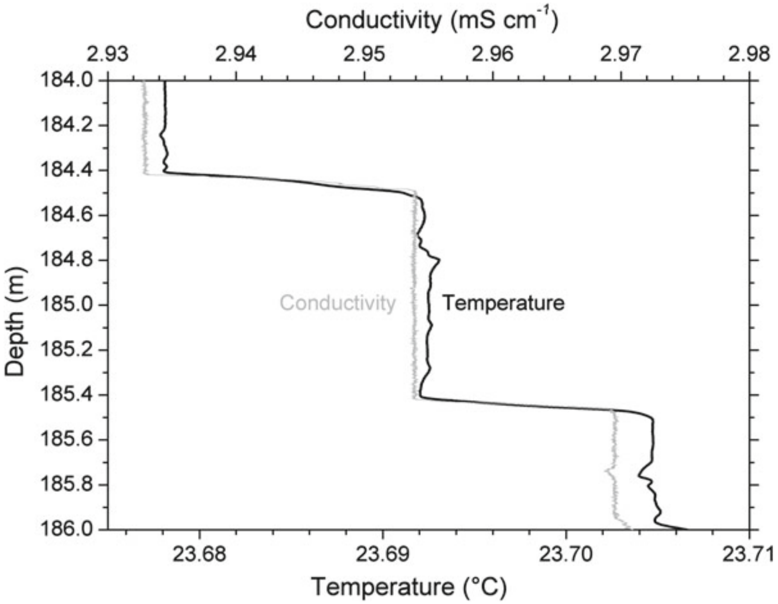


Fig. 2.3 Extract of vertical microstructure profiles of conductivity and temperature in the double-diffusive staircase in Lake Kivu, observed in Apr 2010 (Data provided by T. Sommer, Eawag)

in contrast to other deep African lakes where turbulent diffusive transport is much more important. K_Z has been estimated at ~1×10^{-5} m^2 s^{-1} in the thermocline and ~1×10^{-4} m^2 s^{-1} in the deep water of Lake Tanganyika (Durisch-Kaiser et al. 2010), and at ~3×10^{-5} m^2 s^{-1} below 100 m depth in Lake Malawi (Vollmer 2005). In these lakes, turbulent diffusive transport is not inhibited by such strong density stratification as in Lake Kivu, and they are also exposed to stronger seasonal winds.

There are two reasons why the apparent vertical diffusion coefficients could to some extent underestimate the basin-wide vertical diffusive transport. First, turbulent diffusive transport is usually strongly enhanced within the bottom boundary layer of lakes due to the friction occurring at the sediment (Wüest and Lorke 2003). This boundary-layer mixing can increase basin-scale vertical transport by up to an order of magnitude. However, in the case of Lake Nyos basin-scale vertical heat fluxes within the double-diffusive zone agreed well with those predicted from the properties of the double-diffusive staircase, and there was no indication for a significant enhancement of vertical transport by boundary mixing (Schmid et al. 2004a). To what extent boundary mixing is important for vertical transport in Lake Kivu remains to be investigated. Second, horizontal coherence of most double-diffusive staircases appears to be much smaller than the size of the lake (Schmid et al. 2010). It is therefore possible that horizontal exchange within the staircase may affect the vertical transport of dissolved substances. An investigation of these processes is currently under way.

Since double-diffusion allows a faster upward transport of heat than of dissolved substances, it supports the removal of excess heat supplied by geothermal heat flow or warm subaquatic springs from the deep zone. It thus contributes to maintaining the stable stratification of the lake, as it removes the destabilizing component faster than the stabilizing components. Furthermore, it has been suggested that the different molecular diffusivities of dissolved substances may lead to a differential vertical transport of these substances in double-diffusive staircases (Griffiths 1979).

2.7 Subaquatic Springs and Advective Transport

The vertical density stratification described in Sect. 2.4 is caused by the inflows of subaquatic springs with different properties at various depths. If we assume that there is no significant subaquatic outflow, the water introduced by such subaquatic springs must finally leave the lake at the surface, creating a slow upward advective movement (upwelling) of the whole water column. This upwelling should not be confused with the completely different process also called upwelling that occurs for example in Lake Tanganyika, where prevailing southeast winds during the dry season push the surface waters northward, resulting in upwelling of deep water at the upwind southern shore (Corman et al. 2010).

Based on a one-dimensional model and assuming steady state conditions, the discharge and the depths of the major subaquatic springs in Lake Kivu have been estimated by Schmid et al. (2005). This was done by optimizing the model in order to reproduce the observed vertical profiles of temperature, salinity, and gas concentrations. Two relatively fresh and cool sources were postulated at 180 m depth (~0.7 km^3 year^{-1}) and at 250 m depth (~0.5 km^3 year^{-1}), contributing about 90% to the total discharge of the subaquatic springs. Several smaller, saltier, and warmer springs were assumed to enter the lake below 300 m depth with a total discharge of ~0.15 km^3 year^{-1}. The model was to some extent overparameterized, and other solutions with a similar agreement to the data would have been possible. Nevertheless, the total discharge of the subaquatic springs is relatively well constrained by the whole lake budget of conservative tracers such as sodium or chloride. The average conductivity of the riverine inflows is <1/3 of the lake surface conductivity, while evaporation and precipitation counterbalance each other. Therefore, and because most of the upward transport of these tracers from below 150 m depth is by upwelling rather than diffusion (Sect. 2.8), at least 2/3 of the outflowing tracers must be supplied to the surface layer by upwelling. Concentrations of these tracers at 150 m depth are 1.9 to 2.3 times those in the mixolimnion (Pasche et al. 2009). Consequently, the long-term average of the total source inflows must be at least one third but less than half of the outflow of the lake (Table 2.1). However, it is not clear how variable the discharge of the sources is on time scales of years or decades. An increase of the discharge of these springs and the corresponding supply of nutrients to the surface waters, due to higher precipitation after 1960, may have been the cause for recent changes observed in the sediments of the lake (Chap. 9) and enhanced CH_4 formation (Chap. 10).

The rate of upwelling at any depth is given by the integrated discharge of the sources entering the lake below this depth divided by the cross sectional area of the lake at this depth. The estimated inflows of ~0.15 km^3 year^{-1} into the deep zone result in an upwelling of ~0.15 m year^{-1} through the main density gradient and an average residence time of the water in the deep zone (~120 km^3) of ~800 years. In the upwelling zone, the upwelling rate ranges between 0.5 and 0.9 m year^{-1}, and the water residence time is ~200 years.

The presence of one major source entering the lake at a depth of ~255 m near the northern shore has been confirmed by observations of negative temperature and, to a lesser extent, conductivity peaks at this depth (Fig. 2.2). This source feeds the lake with relatively cool and fresh water. It is the cause for the main density gradient between the deep zone and the upwelling zone. Based on preliminary data, the source at 180 m depth postulated by Schmid et al. (2005) likely consists of a number of smaller sources that are located between 100 and 180 m depth. The sources that supply saltier and CO_2-rich water to the deep zone still need to be located even though some temperature peaks that agreed quite well with the predicted source depths and temperatures have been observed in temperature microstructure profiles (Schmid et al. 2010). Most likely, subaquatic springs are also the cause of the high salinity (Fig. 2.2) and CO_2 concentrations (Tietze 1978) observed below 11 m depth in Kabuno Bay.

Given the importance of these sources for the vertical transport processes in the lake (Sect. 2.9), the current knowledge about them is clearly insufficient. More information is required on the locations, discharge and composition of the inflows as well as their temporal evolution.

2.8 Net Vertical Transport

The total upward transport F_C of a substance C is given by the sum of the advective upwelling transport, $F_{C,adv}$, and the diffusive transport, $F_{C,diff}$:

$$F_C(z) = F_{C,adv} + F_{C,diff} = A(z)\left(w(z) \cdot C(z) - K_Z(z)\frac{dC}{dz} \right) \tag{2.2}$$

Here, z is the vertical coordinate pointing upwards, A is the lake cross-sectional area, w is the upwelling rate, and K_Z is the vertical diffusivity, which corresponds to the apparent diffusivity in the double-diffusive sections, and to the sum of turbulent and molecular diffusivity otherwise.

Figure 2.4 shows the contribution of diffusive transport to the total vertical transport of salt according to the model of Schmid et al. (2005). Advective transport by upwelling is dominant, and diffusive transport (mainly by double-diffusive convection) is negligible below a depth of 120 m except for the transport through the main gradient, where diffusive transport can contribute up to ~20%. The latter number includes a

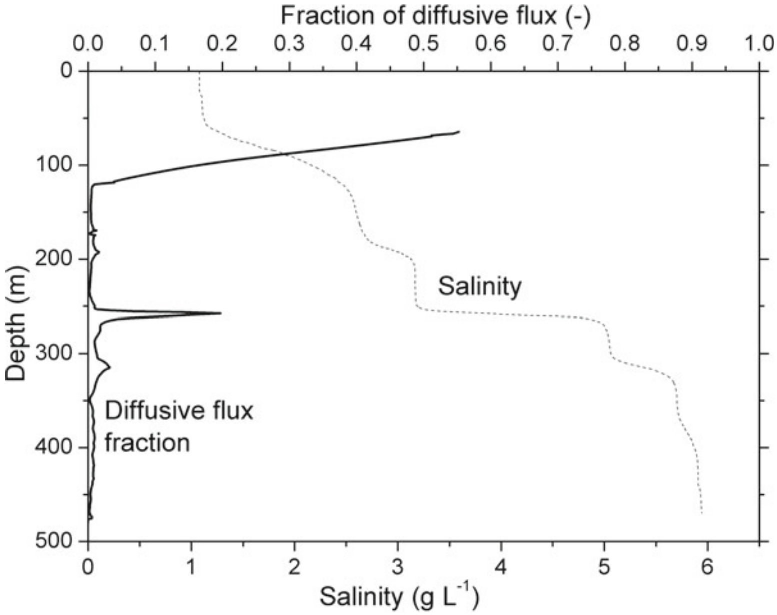


Fig. 2.4 Vertical profile of salinity calculated from observed conductivity and simulated contribution of diffusive transport to the total upward salt transport (based on the model of Schmid et al. (2005))

significant uncertainty, as it is not clear to what extent the diffusion through the gradient is enhanced compared to molecular diffusivity. In the model, the lower level of salt diffusion was set to 10% of the molecular diffusion of heat.

The contributions of diffusion and advection are not necessarily the same for different dissolved substances, because advective transport is proportional to the concentration of a substance, whereas diffusive transport is proportional to its concentration gradient. For example, the contribution of diffusion to total upward transport of H_2S through the major gradient will be much smaller than that of CH_4 or salts, because the H_2S gradient across the main chemocline is relatively weak (Pasche et al. 2009). The contribution of diffusion to the vertical heat fluxes is much more important, because the diffusivity of heat in double-diffusive staircases is typically one order of magnitude larger than that of salts (Schmid et al. 2010).

2.9 Seasonal Mixing

The top 60–65 m of Lake Kivu are influenced by seasonal mixing. In this depth range, conductivity is relatively homogeneous, and mixing and stratification are mainly governed by changes in water temperature. Since the coefficient of thermal expansion is high at the temperatures of tropical lakes, cooling-induced convective

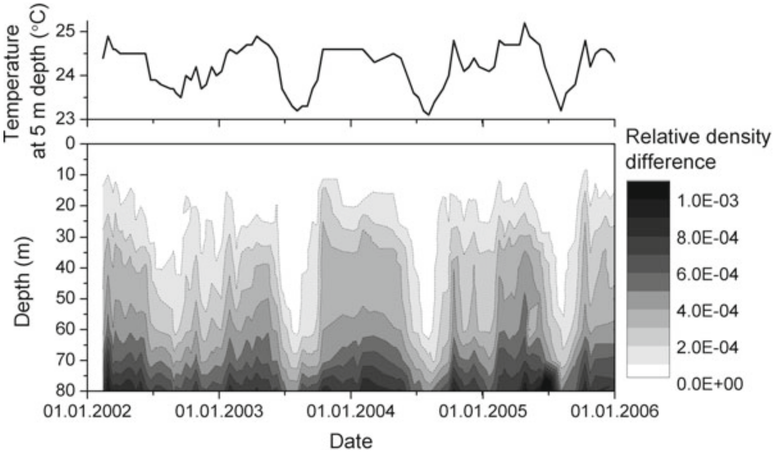


Fig. 2.5 Temperature observed at 5 m depth and relative difference of water density (Δρ/ρ, calculated from temperature and conductivity) to density at 5 m depth at Ishungu Basin. A relative density difference of 10^{-4} corresponds to a temperature difference of ~0.4°C. Temperature and conductivity profiles were provided by the ECOSYKI project (J.-P. Descy, pers. comm.)

mixing is more intense than in temperate lakes (Lewis 1987). Seasonal mixing in Lake Kivu usually occurs during the dry season, mainly in July and August. At this time of the year strong winds and low relative humidity both promote evaporation from the lake. Furthermore, the clear sky reduces incoming long-wave radiation. The increased heat losses more than outweigh the higher input by solar radiation, and the surface heat balance becomes negative, which leads to deepening of the mixed surface layer.

Temperatures observed at 5 m depth over 4 years varied in a small range of only ±1.1°C around an average of 24.2°C. As a consequence, temperature differences of a few tenths of a degree can determine whether convective mixing reaches the base of the mixolimnion or not. The intensity of seasonal mixing therefore depends on the meteorological conditions during the dry season and varies strongly from year to year (Fig. 2.5). This variability has important consequences for the biological processes in the lake. Nutrients are supplied at a probably relatively constant rate to the base of the mixolimnion by the upwelling discussed in Sect. 2.7. However, they are not introduced into the mixolimnion until a mixing event reaches this depth, erodes the top of the gradient at the bottom of the mixolimnion and thus releases the nutrients from the upwelling zone to the mixolimnion. Subsequently, primary production, especially by diatoms, reaches its maximum (Chap. 5), followed in succession by peaks in zooplankton biomass (Chap. 7) and fish production (Chap. 8). In years without sufficiently deep mixing, the density gradient at the bottom of the mixolimnion weakens due to localised turbulent diffusion, preparing the ground for an even higher input of nutrients during the next deeper mixing event. This mechanism leads to interannual variations in primary productivity similar to those occurring in some deep temperate lakes with variable depth of winter time mixing (e.g., Lake

Tahoe; Goldman et al. 1989). The same process probably also governs the irregular calcite precipitation observed in the lake (Pasche et al. 2010). Furthermore, it can be expected that such mixing events may lead to pulses of gas emissions (CO_2 and CH_4) from the lake to the atmosphere (Chap. 4).

During the rest of the year, i.e. from September to June, stable density stratification is usually observed within the mixolimnion, with varying depths of the surface mixed layer of typically around 15–30 m. During this time, nutrient supply for primary production is scarce.

2.10 Temporal Changes of Stratification

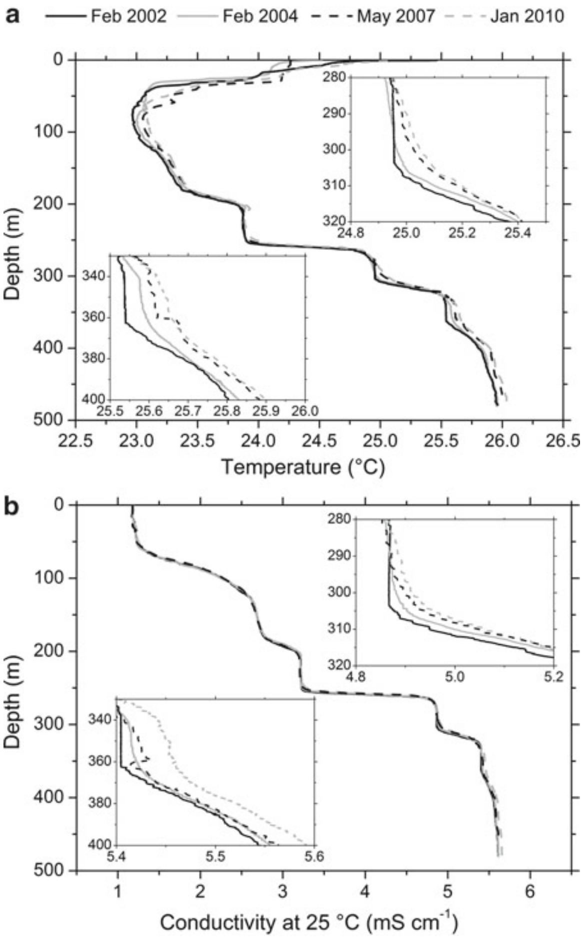
Historical observations of temperature profiles from Lake Kivu are scarce. However, the few available data indicate significant deviations from steady-state conditions, despite the long residence times of the water in the upwelling zone and especially in the deep zone. The data from the CTD profiles measured by Tietze (1978) or the microstructure profiles measured by Newman (1976) are not publicly available except for the figures displayed in their publications. However, both these data sets show significant differences in the stratification compared to recent profiles (Schmid et al. 2010). The two gradients at 260 and 315 m depth both became steeper, mainly due to a lifting of their lower limits, whereas their upper limits remained almost at the same depths. This may suggest an increased advective upward flow caused by increased discharge of the subaquatic springs. The fact that the upper limits did not rise indicates that these steps are indeed maintained by inflows entering the lake at these depths, even though this has recently been disputed (Hirslund 2012).

Temperatures in Lake Kivu have been significantly increasing since the observations of Tietze (1978) in 1975. Lorke et al. (2004) reported a distinct warming of the upwelling zone ranging between 0.2°C and 0.5°C (on average ~0.01°C year^{-1}) for the time between 1975 and 2002, but no significant warming in the deep zone.

A comparison of recent vertical profiles of temperature and conductivity from 2002 to 2010 (Fig. 2.6) confirmed the trend for the upwelling zone and revealed a more recent increasing temperature trend in the deep zone. Temperature in the whole permanently stratified layer increased at an average rate of ~0.010°C year^{-1}. The highest increase was observed in the layer between 80 and 120 m depth (~0.014°C year^{-1}). This warming was driven by heat inputs from both the surface and the deep. The surface warming caused a lowering of the depth of minimum temperature between 2002 and 2007 from 75 to 90 m depth. It is interesting to note that the depth of minimum temperature during this time was far below the depth of seasonal mixing as a result of faster warming from the top than from below. A mixing event in 2008 led to a cooling of the top of the permanently stratified layer, and the depth of minimum temperature was lifted back to 65 m depth.

In the layer just above the main gradient, temperature was nearly constant between 2002 and 2007, while the profile from 2010 seems to indicate a slight

Fig. 2.6 Vertical profiles of temperature and conductivity (normalized to 25°C) measured in Feb 2002 (Lorke et al. 2004), Feb 2004, May 2007 and Jan 2010 at the positions shown in Fig. 2.1. The profiles from 2002 to 2007 were all measured with a Sea-Bird SBE 19 profiler, the one from 2010 with a RBR XR-620



increase. The layer between 280 and 305 m depth seemed to have been convectively mixed shortly before the measurements in 2002. A new temperature gradient has been slowly building up in this range since then. Temperature below 340 m depth has been increasing at a rate of ~0.011°C year^{-1} (insets in Fig. 2.6). The reason for the warming of the deep water is unclear. Potential causes could be a warming of the deep water springs, an increase in the heat flow, or a decrease of the upward heat flux by double diffusion (Schmid et al. 2010).

All reported temperature trends are clearly significant compared to the spatial variability observed in the main basin during the measurement campaigns in 2002, 2004 and 2010. Similar warming trends have been observed in other tropical and temperate lakes, e.g., Lake Tanganyika (Verburg and Hecky 2009) or Lake Malawi (Vollmer 2005).

Conductivity remained constant (typically within 1% or less, i.e., within the uncertainty of the measurements) throughout the lake. The measurements seem to indicate a slight increase between 2007 and 2010, but it should be noted that these measurements were made with different instruments. The constancy of conductivity is especially surprising for the surface layer which would be expected to be influenced to some extent by interannual variation in precipitation, evaporation and seasonal mixing (Fig. 2.5). Altogether, the measurements indicate that, besides a slight warming trend, Lake Kivu is near to steady-state conditions.

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Chapter 3
Nutrient Cycling in Lake Kivu

Natacha Pasche, Fabrice A. Muvundja, Martin Schmid, Alfred Wüest, and Beat Müller

Abstract This chapter investigates phosphorus (P), nitrogen (N), and silica (Si) cycling in tropical Lake Kivu. Its deep water is characterised by high concentrations of nutrients, which are slowly released to the surface mixed layer by an upward advective transport. The nutrient inputs (rivers, internal recycling and subaquatic springs) and outputs (outflow, sedimentation) are quantified to determine each nutrient cycle. Our analyses revealed that N and P cycles are dominated by internal processes, which are internal recycling and burial. P and N external inputs supply only about

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15% (P) to 20% (N) of the total inputs to the epilimnion. In contrast, riverine inflows and internal recycling contribute equally to Si inputs.

3.1 Introduction

This chapter provides an overview of the chemical composition causing permanent stratification of surface and deep waters, and how it influences the cycling of nutrients in Lake Kivu. We focus specifically on the cycles of N, P and Si, which are the main drivers for primary production. The quantification of the lake's nutrient cycles is indispensable to understand (1) the sources and sinks of nutrients, (2) the special role of the subaquatic springs and (3) the lake-internal nutrient fluxes, as well as to estimate the lake's response to any nutrient management actions or alterations of nutrient loads.

Different aspects of the Lake Kivu nutrient cycle have been quantified in separate specific publications. First, Muvundja et al. (2009) estimated the external input loads by measuring nutrients in 21 tributaries as well as in rain and dry deposition samples. The annual loads were then extrapolated to the whole catchment. Second, upward fluxes of nutrients from the permanently stratified zone to the surface mixed layer (Pasche et al. 2009) were determined based on concentration profiles and estimated vertical advective and diffusive transport processes. This analysis also permitted the estimation of nutrient inputs by the major subaquatic spring at a depth of 250 m. Finally, sedimentation was investigated using sediment traps deployed at four different depths and dated sediment cores (Pasche et al. 2010). Gross sedimentation showed a seasonal variation following the primary production pattern. In the following chapter, we present the vertical distribution pattern of major ions in the water column and an overview of the entire nutrient cycle of Lake Kivu, and quantify the essential processes affecting primary production.

3.2 Chemical Composition of the Permanently Stratified Deep Water

The chemical composition of the deep waters of Lake Kivu has been described in detail by Pasche et al. (2009). The major ions and nutrients were measured in five profiles taken at three different locations during three field trips in the years 2004, 2006 and 2007. Below ~65 m, concentration profiles of most components (Fig. 3.1) were characterized by a similar gradual increase with depth and an abrupt change at the major chemocline at 255–262 m. Chemical profiles were remarkably similar regardless of location and sampling time, which is consistent with the long residence time in the stratified layers (Chap. 2). The horizontal homogeneity was confirmed by vertical salinity profiles from different locations in Lake Kivu's basins, except Kabuno Bay and Bukavu Bay. Concentration profiles in the permanently stratified zone remain almost constant over time scales of decades.

Profiles of major ions reveal biogeochemical processes within the lake. Na^+ and Mg^{2+} are the most abundant cations in Lake Kivu, followed by K^+ and Ca^{2+} (Fig. 3.1). Non-biogenic, conservative elements like Cl^- and Na^+ are excellent tracers of

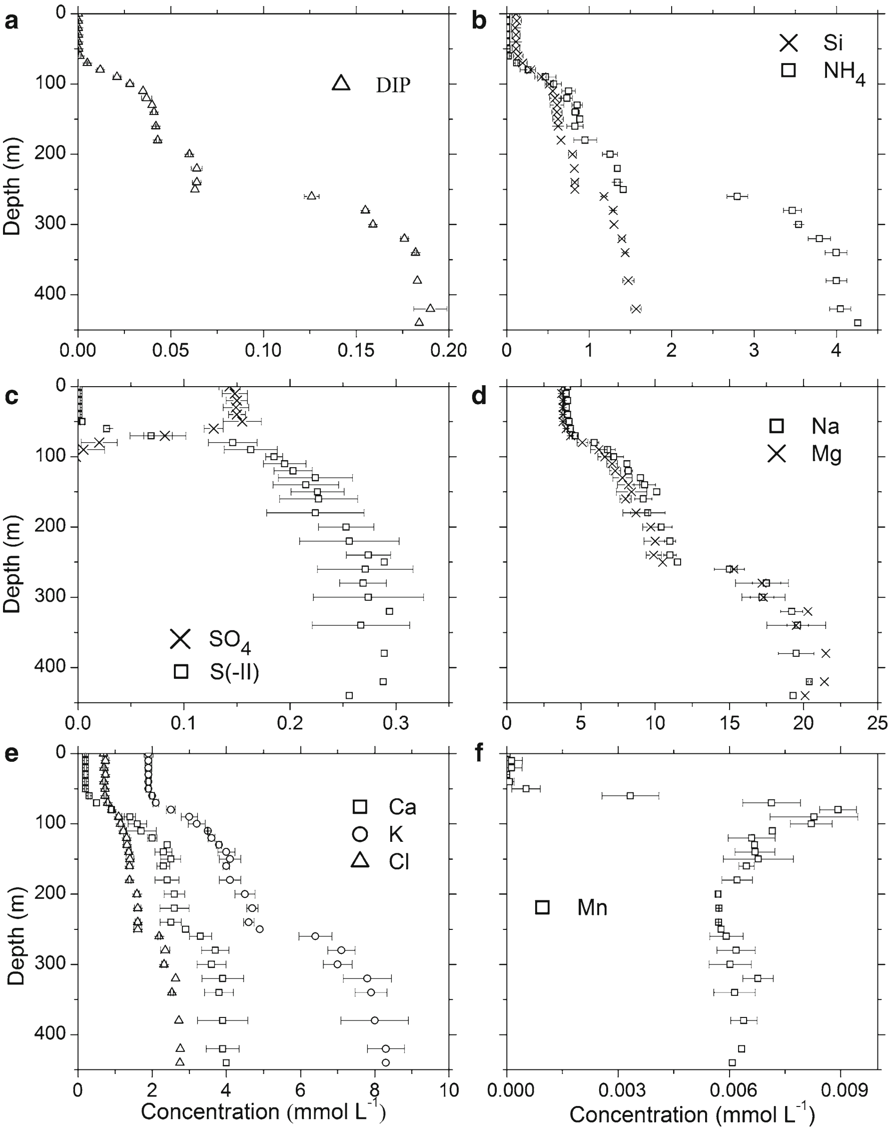

Fig. 3.1 Profiles of nutrients and majors elements (in mmol L^{-1}) averaged for the five sampling sites. Error bars represent standard deviations of those five measurements. (**a**) Dissolved inorganic phosphorus (DIP), (**b**) Si and NH_4^+, (**c**) SO_4^{2-} and S(-II), (**d**) Na^+ and Mg^{2+}, (**e**) Ca^{2+}, K^+, and Cl^- and (**f**) Mn^{2+}

physical mixing. Their comparison with Ca^{2+} and Mg^{2+} profiles revealed that biogenic precipitation and re-dissolution of carbonaceous particles causes a transfer of Ca^{2+} and Mg^{2+} from the surface mixed layer to the deep-water. The alkalinity profile (data not shown) followed the pattern of base cations and reached a maximum level of 72.6 mmol L^{-1} at maximum depth.

Nutrient concentrations also increased in a stepwise pattern and changed abruptly at the major chemocline. Dissolved inorganic phosphorus (DIP) and ammonium (NH_4^+) concentrations were strongly enriched in the deep zone (0.19 mmol PL^{-1} and 4.26 mmol NL^{-1}; Fig. 3.1). By comparison, SiO_2 showed a less pronounced maximum (1.57 mmol L^{-1}). The long residence time of ~800 years allows an estimation of the nutrient enrichment in the deep zone of the lake. Deep waters carry the signature of the long-term stoichiometry of the sinking organic material and sediment mineralization, with N:Si:P ratios of 22:6.5:1. The high N:P ratio indicates P limitation.

By contrast, S(-II) and Mn^{2+} distributions differed completely from other elements. The Mn^{2+} profile was characterized by a distinct peak at the oxycline due to the reductive dissolution of manganese oxides (Fig. 3.1). Below 160 m, Mn^{2+} concentrations were constant at around 6.3 μmol L^{-1}. SO_4^{2-} concentrations in the mixolimnion (0.15 mmol L^{-1}) were four to five times as high as in Lakes Tanganyika and Malawi. Below the oxycline, SO_4^{2-} decreased with a sharp gradient and dropped below the detection limit (0.05 mmol L^{-1}) at 90 m. In contrast, S(-II) that was absent above the oxycline, increased sharply between 50 and 150 m depth, and was homogeneous at ~0.27 mmol L^{-1} below 150 m depth.

3.3 Chemical Composition and Dynamics of Surface Water

A chemocline between ~65 and ~130 m limits the annual convective mixing from the surface to a maximum depth of ~65 m (Chap. 2). Down to this depth, in the mixolimnion, the chemical composition and especially nutrient concentrations vary seasonally. This variability depends on the seasonal evolution of the thickness of the epilimnion due to cooling-induced convection and wind forcing (Sarmento et al. 2006). As a consequence of the seasonal convective mixing, the oxycline varies between ~30 m during the rainy season (October to April) to a maximum of ~65 m during the dry season (June to September).

Nutrient concentrations in the epilimnion are low all year round. However, during the stratified period the supply is more limited than during the cooling period. During the dry season, an annual deep mixing entrains nutrients from the nutrient-rich deeper water. The maximum depth of this mixing is determined by the extent of cooling (the epilimnion temperature) and by the density gradient in this chemocline. During our measurements in the stratified period, the oxycline was situated at ~40 m. The nitrate (NO_3^-) profile was characterized by a temporary peak of only 6 μmol L^{-1} at the oxycline. DIP and NH_4^+ concentrations were below the detection limit (<0.2 and 0.1 μmol L^{-1} respectively) in the surface mixed layer, while Si concentrations were at a level (~0.11 mmol L^{-1}) that is not limiting for diatom growth.

The surface water has a rather high salinity of 1.1 gL^{-1}. Major cations are therefore present in significant concentrations (Na^+ 4.1 mmol L^{-1}, Mg^{2+} 3.8 mmol L^{-1}, K^+ 1.9 mmol L^{-1}, Ca^{2+} 0.18 mmol L^{-1}). Alkalinity was as high as 13.3 mmol L^{-1}, while Cl^- was 0.72 mmol L^{-1}.

3.4 Internal Nutrient Recycling

Two physical processes contribute to the internal recycling of nutrients from the permanently stratified deep water to the mixolimnion: turbulent diffusion, and vertical advection (upwelling) caused by the inflow of subaquatic springs to the deep water (Chap. 2). The total upward fluxes from the permanently stratified zone to the surface mixed layer, F_{total}, resulting from these two processes were calculated by Pasche et al. (2009) using Eq. 3.1:

$$F_{total} = -D_{turbulent}\overline{\frac{\Delta C}{\Delta z}} + \overline{C \times Adv} \tag{3.1}$$

where $D_{turbulent}$ is the turbulent diffusion coefficient ($m^2\ s^{-1}$), $\overline{\frac{\Delta C}{\Delta z}}$ refers to the vertical concentration gradient of the nutrient ($mol\ m^{-4}$), Adv denotes the upwelling velocity ($m\ s^{-1}$), and C stands for the nutrient concentration at the given depth ($mol\ m^{-3}$). The overlying bars indicate an averaging over the whole depth range. The diffusive fluxes were determined in four selected depth sections. Concentration gradients were estimated from nutrient profiles by fitting a linear regression to the concentrations observed in the chosen depth interval. This analysis revealed that the slow advective upwelling caused by the subaquatic inflows dominated upward fluxes, while fluxes caused by turbulent diffusion were negligible.

One major subaquatic spring was indicated at 250 m depth by a diffusive-advective model for CH_4 and salinity (Schmid et al. 2005) and has been observed in temperature profiles (Chap. 2). Our analysis allowed the estimation of the inputs from this major subaquatic spring, as the upward flux of major ions was much stronger above 200 m than below 255 m depth. The concentrations calculated for the inflowing water were smaller than for the lake water at 250 m. This dilution effect in combination with a slow upwelling due to springs entering into the deep zone probably sustained the major chemocline between 255 and 262 m observed in all chemical profiles.

The upward fluxes of NH_4^+ (1.80 mmol $m^{-2}\,day^{-1}$) and DIP (0.082 mmol $m^{-2}\,day^{-1}$) were homogeneous throughout the water column. Considering the increasing area of the lake, homogeneous inputs from the sediment are needed in order to maintain homogeneous fluxes per area throughout the whole water column. By contrast, the upward flux of Si above 200 m (1.41 mmol $m^{-2}\,day^{-1}$) was twice as high as below 255 m (0.62 mmol $m^{-2}\,day^{-1}$). These two distinct fluxes suggest that the subaquatic inflows are enriched in SiO_2, probably through weathering of volcanic rocks.

In summary, NH_4^+ and DIP have a strong sink above 90 m and a source from the sediment, caused by assimilation in the photic zone, sedimentation, and mineralization in the deep water and sediment. Contrary to major ions, there is no additional N and P input from the subaquatic spring at 250 m. In contrast, SiO_2 is not limiting for the production of diatoms and has a point source at 250 m depth (0.8 mmol $m^{-2} day^{-1}$). SiO_2 inputs in the deep water from mineralization appear to be more limited than for N and P, probably due to a weaker degradation of diatom frustules.

3.5 Assessing the Nutrient Cycle

The nutrient cycle within the lake can be viewed as a conveyor belt with external inputs and outputs. N and P are essential nutrients for phytoplankton growth, and silica (SiO_2) is necessary for the diatom frustules. Autochthonous carbon then passes through the food web (Chaps. 6, 7, and 8). Dead organic matter is partly mineralized and recycled in the surface mixed layer, and the rest is exported from the surface mixed layer by settling particles. On its way through the water column and at the sediment water interface, organic matter is largely mineralized and nutrients are released back into the water. Some of these nutrients are then transported back to the surface mixed layer closing the cycle (Fig. 3.2). The external inputs, that drive this cycle, consist of (1) atmospheric deposition, (2) rivers, and (3) subaquatic springs, while the outputs are (1) organic matter stored in the sediment and (2) the loss of nutrients via the Ruzizi outflow.

Muvundja et al. (2009) quantified the external inputs via atmospheric deposition (In_a) and rivers (In_r), and the output via the Ruzizi outflow (Out; Fig. 3.2). Because they had used a slightly different water budget, we scaled their fluxes to agree with the total inflows and the outflow presented in Table 2.1. Pasche et al. (2009) calculated the upward fluxes of nutrients within the lake above (Up_{bio}) and below (Up_{deep}) the major subaquatic spring (250 m depth). We consider the difference ($Up_{bio} - Up_{deep}$) as the input from the subaquatic springs (In_s). The sedimentation (Pasche et al. 2010) was differentiated between export sedimentation (Sed_{exp}) measured in the trap at 50 m; gross sedimentation (Sed_g) averaged from the traps at 90, 130 and 170 m; and net sedimentation (Sed_n) measured in the dated sediment core situated at the same location as the sediment traps (Ishungu Basin).

Here we consider the nutrient cycle individually for the whole lake (Eq. 3.2), as well as for the surface mixed layer (top 50 m; Eq. 3.3). Assuming a steady-state situation where the total inputs are equal to the total outputs, we balance the nutrient fluxes according to Fig. 3.2:

$$V_{Lake} \times dC_{Lake} / dt = In_r + In_a + In_s - Out - Sed_n = 0 \tag{3.2}$$

$$V_{mix} \times dC_{mix} / dt = In_r + In_a + Up_{bio} - Out - Sed_{exp} - 0.12\ Sed_n = 0 \tag{3.3}$$

Here, V_{Lake} and V_{mix} are the volumes of the lake and the surface mixed layer, respectively, C_{Lake} and C_{mix} are the volume averaged concentrations, and the factor 0.12 is the ratio of the sediment surface area in the top 50 m to the total sediment area of the lake.

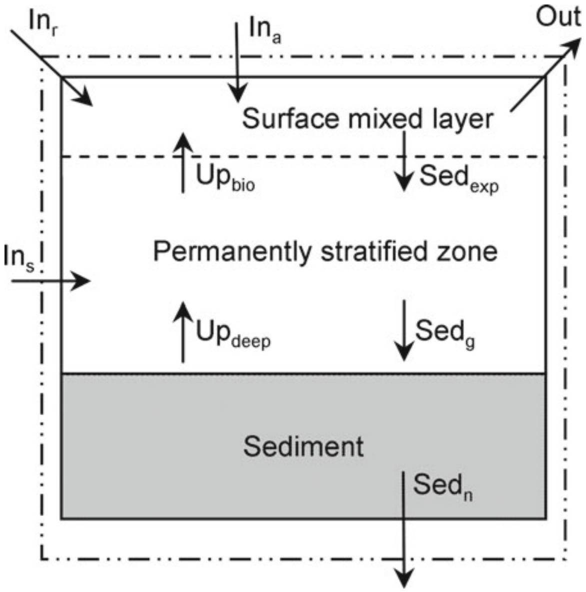

Fig. 3.2 Schematic of the nutrient fluxes in Lake Kivu including the surface mixed layer (0–50 m), the permanently stratified zone (50–485 m) and the sediment. The different inputs consist of riverine inflow (In_r), atmospheric deposition (In_a) and the 250 m subaquatic spring (In_s). The outputs are the outflow (Out) and the net sedimentation (Sed_n). Lake internal processes are the export from the surface mixed layer (Sed_{exp}), gross sedimentation above the sediment (Sed_g), and upward fluxes below (Up_{deep}) and above 250 m depth (Up_{bio})

During the deployment of sediment traps (2 years), primary productivity was unusually low (Chap. 5). Therefore, gross sedimentation was clearly underestimated. Instead of using trap data we estimated the long-term average gross sedimentation from the sum of net sedimentation and upward fluxes of nutrients:

$$\mathrm{Sed}_{\mathrm{g\_corr}} = \mathrm{Up}_{\mathrm{deep}} + \mathrm{Sed}_{\mathrm{n}} \quad (3.4)$$

Gross sedimentation was similar in the three traps at various anoxic depths, indicating that organic matter mineralization during the descent through the anoxic water column was only minor. In contrast, lower fluxes were observed at 50 m depth. These probably resulted either from a more intense mineralization within the trap, which was seasonally exposed to oxic conditions, or because sediment laden river plumes were transported horizontally at some depth below 50 m. We therefore assumed that the export sedimentation equals the gross sedimentation:

$$\mathrm{Sed}_{\mathrm{exp\_corr}} = \mathrm{Sed}_{\mathrm{g\_corr}} \quad (3.5)$$

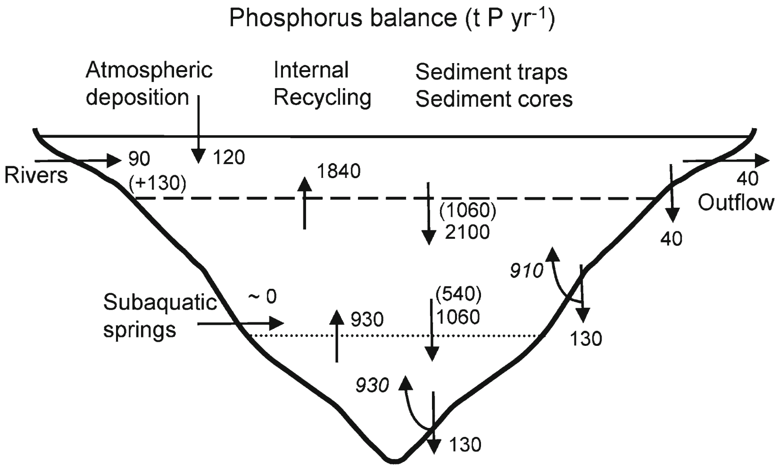

Fig. 3.3 P (dissolved inorganic P, particulate P for sediment) balance in Lake Kivu with fluxes in t year^{-1}. The dashed line separates the epilimnion from the upper monimolimnion (50 m, 2078 km^2). The dotted line separates the upper and lower monimolimnion (260 m, 1053 km^2). Regular numbers are based on analytical measurements and numbers in italics indicate fluxes calculated as the difference between observed fluxes. For sediment traps, the upper numbers (in parentheses) label the measured fluxes and the numbers below were corrected using Eqs. 3.3 and 3.4. The additional inflow of 130 t year^{-1} in parentheses is the fraction of the TP load that needs to become bio-available to close the budget

3.5.1 Phosphorus and Nitrogen Cycles

3.5.1.1 Essential Nutrients

In Lake Kivu, the relatively high C:P (256) and N:P (27) ratios of the seston indicate a severe P limitation and a moderate N limitation for phytoplankton (Sarmento et al. 2009). The P supply of the surface mixed layer thus controls primary production. N is co-limiting mainly during the rainy season (Chap. 5).

Internal recycling dominates P and N supply to the surface mixed layer. The remaining external inputs (Muvundja et al. 2009) represent only ~15% of the total inputs of dissolved P (Fig. 3.3) and ~20% of dissolved N (Fig. 3.4). The internal recycling is driven by subaquatic inflows, which push the lake water upwards, delivering nutrients to the epilimnion. In other tropical lakes, such as Malawi and Tanganyika, upward fluxes are also the main inputs to the epilimnion (Hecky et al. 1996; Hamblin et al. 2003). However, in these lakes, these fluxes are driven by large-scale vertical displacements of the water column during weak stratification periods, which release more nutrients in the southern than in the northern parts of the lakes. The strong stratification of Lake Kivu prevents such vertical dislocations and primary production is thus more homogeneous throughout the lake (Kneubühler et al. 2007).

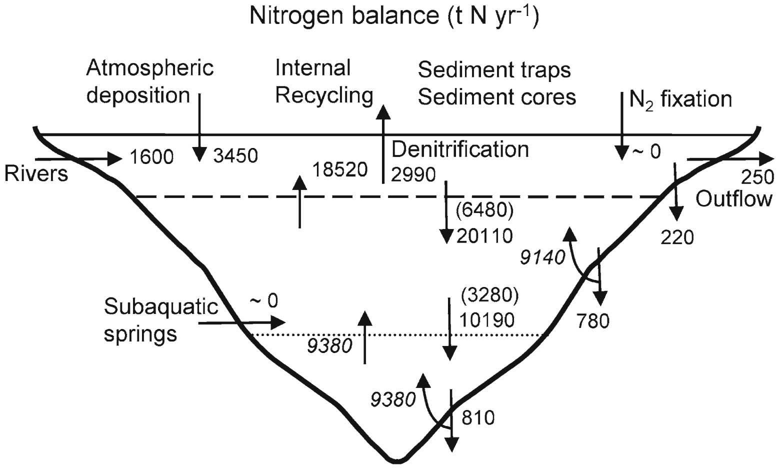

Fig. 3.4 N balance in Lake Kivu with fluxes in t year^{-1}. The dashed and dotted lines are as defined in Fig. 3.3. Regular, italics and in parenthesis numbers are as defined in Fig. 3.3

In Lake Kivu, the long-term average nutrient recycling is determined by the discharge of the subaquatic springs. On short time scales, however, the nutrient supply to the surface mixed layer is driven by fluctuations in the dynamics of the surface layer mixing and therefore primary production is subject to large seasonal and inter-annual variability. During the rainy season, the epilimnion is only 30 m deep and nutrient availability becomes critical. During the dry season (June to September), strong winds, lower temperatures and low humidity drive an annual deep mixing (down to ~65 m depth), which entrains nutrients from the nutrient-rich deeper water. The maximal depth of this annual mixing, and thus the amount of nutrients entrained to the epilimnion, is determined by the intensity of convective mixing and the density gradient in the chemocline. In our simplified cycles, the upward fluxes at 50 m depth represent the average input to the epilimnion over several years, levelling seasonal and annual variations.

3.5.1.2 Minor Importance of External Inputs

More than 127 rivers enter Lake Kivu and their P and N loads represent about half of the total external inputs. Despite the intense land use and the high population density, the nutrient input from rivers estimated by Muvundja et al. (2009) is low, which reflects the limited use of fertilizers in Lake Kivu's catchment. The annual P area-specific load (22 kg P km^{-2} year^{-1}) is even lower than that estimated for two tributaries of Lake Malawi (55 kg P km^{-2} year^{-1}, Hecky et al. 2003). Riverine nutrient inputs to the pelagic zone may be further reduced by the uptake of nutrients by macrophytes in the littoral zone.

In our budget, P inputs to the lake are lower than P outputs. This effect may be caused by a change in P speciation since we measured DIP input from filtered samples, while the major load from tributaries is in the form of soil derived erosional material and mineral particles from weathering (TP load = 1,380 t P year^{-1}; rescaled from Muvundja et al. 2009). A major fraction of these suspended particles are deposited in river deltas but some of the organic TP may become bio-available after decomposition in the lake. To account for the missing DIP (130 t P year^{-1}) of the surface mixed layer P budget, 9% of the TP load needs to become available. This fraction seems realistic, as previously demonstrated in well-investigated Lake Sempach (7%; Moosmann et al. 2006).

Nutrient inputs by atmospheric deposition were generally equal (P) or even larger (N) than riverine inputs. Wet deposition is more important than dry deposition, except for the high particle-related deposition of TP. Rain probably washes out dust and other airborne particulate matter more efficiently. The importance of direct atmospheric deposition is also due to the small ratio of the catchment area to the lake area, which is only about 2:1 for Lake Kivu, whereas it is about 6:1 for Tanganyika and about 3:1 for Malawi. In Lake Tanganyika, wet deposition was also the most important external input and was attributed to the intense biomass burning in the region (Langenberg et al. 2003). In comparison, atmospheric deposition accounted for 33% of new P and 72% of new N input into Lake Malawi (Bootsma et al. 1996). Although biomass burning is forbidden in Rwanda, biomass fuels are widely used for cooking. Particles might also be transported to the lake from the DR Congo and other neighbouring countries. Recent studies of global N deposition (Dentener et al. 2006; Reay et al. 2008) indicated higher values ranging from 1 to 2 g m^{-2} year^{-1} in East Africa than in most other parts of Africa. This agrees well with our estimate of 1.2 g m^{-2} year^{-1} (Muvundja et al. 2009). Our measured rates for P deposition seem higher than those from global model simulations (Mahowald et al. 2008), which might be influenced by TP-containing compounds in volcanic aerosols and dust from non-asphalted road network.

The potential recent increase of N and P external inputs could not lead to eutrophication, as their contributions remain currently low. However, they have probably been enhanced by the fast-growing population in the catchment. In Lake Malawi, external inputs have increased by 50% due to agricultural development and growing population (Hecky et al. 2003). Human activities already have significant effects on some rivers in the catchment of Lake Kivu. Of the riverine inputs in the densely populated region of Bukavu, approximately 1.0 kg P and 0.8 kg N per person and per year could be ascribed to anthropogenic waste (Muvundja et al. 2009). Nevertheless, the current external inputs of Lake Kivu remain too low compared to the internal recycling to induce eutrophication within a timescale of a few decades. However, internal cycles are ultimately driven by external loads, as net production in the lake has to rely on external inputs. So in the long term, it is still important to consider the potential effects of increased nutrient loads from rivers and the atmosphere.

3.5.1.3 High Nutrient Regeneration

N and P are recycled in the surface mixed layer. Dead organic matter is directly mineralized by bacteria, which release nutrients for new production (Chap. 6). In Lake Kivu, N and P uptake by phytoplankton are approximately four times higher than the total inputs to the surface mixed layer (Pasche et al. 2009).

In the permanently stratified deep water, mineralization of the organic matter seems of minor importance. Analyses of sediment trap material revealed a homogeneous flux of particles throughout the water column with no significant degradation, which was also observed in Lake Malawi (Pilskaln 2004). In contrast, approximately 30% of P and 50% of N were recycled within the long but oxic and much colder water column of Lake Baikal (Müller et al. 2005). These differences can be explained by the stronger potential of O_2 to degrade organic matter. The permanently stratified zone of Lake Kivu is completely anoxic. Even SO_4^{2-} disappears at 90 m leaving only CO_2 as electron acceptor.

N and P are mainly regenerated at the sediment-water interface. At this interface, 92% of N and 88% of P are mineralized and released back into the water column. Only 8% of N and 12% of P gross sedimentation are buried in the sediment. These recycled nutrients accumulate in the deep water, and become available for primary production via upwelling.

3.5.1.4 Additional Processes for Nitrogen: N_2 Fixation and Denitrification

Direct N_2 fixation supplies additional nitrogen into the epilimnion. As N_2 fixation requires a large amount of energy, it can be expected to take place only at times of low availability of NO_3^- or NH_4^+. In Lake Kivu, such conditions prevail only during the stratified period, when N becomes co-limiting for phytoplankton growth. During this period, cyanobacteria become dominant but efficient N-fixers are not well represented (Sarmento et al. 2007). In Lakes Malawi and Tanganyika, nitrogen fixation has been estimated to be the major N input (Hecky et al. 1996), *Anabaena sp.* being the main taxon responsible for N_2 fixation in these lakes. However, a more recent study (Gondwe et al. 2008) suggests that nitrogen fixation by *Anabaena sp.* in Lake Malawi represents only 3–4% of the total N input to the epilimnion. As such, we neglect N_2 fixation in the N budget of Lake Kivu, assuming that it is of minor importance.

Denitrification is a process transforming NO_3^- into N_2 and represents an additional sink for N. In Lake Kivu, mineralization in the anoxic sediment releases NH_4^+. Higher up, when NH_4^+ diffuses through the oxycline, it is oxidized into NO_3^- via NO_2^-. Only when the produced NO_3^- diffuses back into the anoxic zone, denitrification can take place. In Lake Kivu, denitrification can therefore reduce NH_4^+ upwelling at the oxycline. Denitrification could further explain why the lake external N inputs (23,570 t year^{-1}) are higher than N outputs (20,580 t year^{-1}). The denitrification rate could therefore be interpreted as the difference between the inputs and outputs (because N_2 fixation set to ~0), and yields a loss of 2,990 t N year^{-1}.

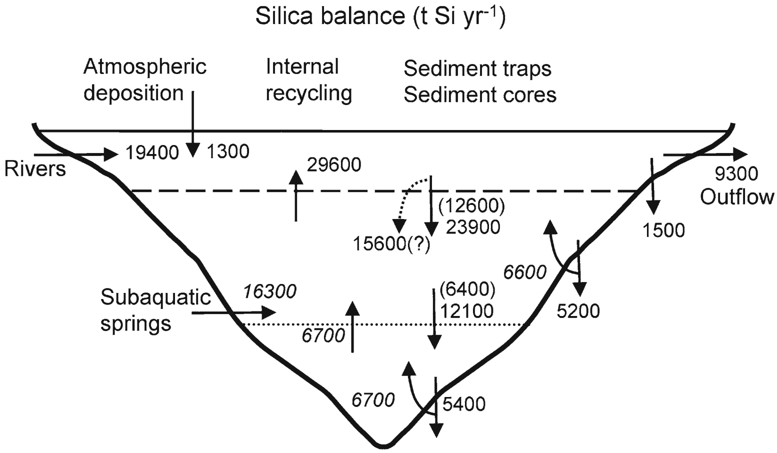

Fig. 3.5 Si balance in Lake Kivu with fluxes in t year^{-1}. The dashed and dotted lines are as defined in Fig. 3.3. Regular, italics and in parenthesis numbers are as defined in Fig. 3.3. The dotted arrow and the number with question mark indicate the annual increase of the Si content in the lake required to close the budget

3.5.2 Contrasting Silica Cycle

3.5.2.1 Non-limiting Nutrient

The high amount of SiO_2 delivered through multiple inputs explains why non-limiting concentrations of SiO_2 prevail in the surface mixed layer (0.10 mmol L^{-1}). SiO_2 inputs to the surface mixed layer (Fig. 3.5) originate to 59% from upwelling and 39% from tributaries, whereas atmospheric deposition is negligible (2.6%). This high riverine load results from weathering of the abundant silicate (volcanic) rocks in the volcanic catchment (Di Figlia et al. 2007). This physical process explains why river concentrations remain constant throughout the year (0.36 mmol L^{-1}; 4.5 t Si km^{-2} year^{-1}). Similar specific loads were determined for Lake Malawi (6.3 t Si km^{-2} year^{-1}; Bootsma et al. 2003).

SiO_2 is the only nutrient present at important concentrations in the subaquatic springs. The subaquatic input at 250 m depth more than doubles the SiO_2 upwelling flux in the deep water. We think that these springs originate from the volcanic region to the north of the lake where rivers are absent. Rain water percolates through the porous volcanic rocks and takes up salts and SiO_2 before entering the lake. This formation process would both explain the high estimated concentration of SiO_2 (0.66 mmol L^{-1}) and the fact that no N and P are present in the springs. In conclusion, Si multiple inputs contrast with N and P inputs dominated by internal recycling.

3.5.2.2 Substantial SiO_2 Export

SiO_2 outputs are divided in two equal parts between the Ruzizi outflow and the net sedimentation. Biogenic silica was measured in sediment using the single-step wet-alkaline leach method of Ohlendorf and Sturm (2008), while the outflow is based on the reactive dissolved SiO_2 of the lake surface water. The surface mixed layer SiO_2 budget reveals that the inputs (50,300 t Si year^{-1}) are 45% higher than the outputs (34,700 t Si year^{-1}). We can explain this difference by either: (1) an overestimation of the riverine input, (2) an underestimation of the outflow, or (3) an underestimated gross sedimentation. Dissolved reactive Si concentrations in inflowing rivers stay remarkably constant throughout the year, thus the extrapolated Si load is probably well estimated. The riverine inflow of biogenic silica (BSi) is probably low due to turbid water and short residence times and was therefore ignored. BSi in the euphotic zone at the lake surface waters was neglected for the outflow flux. We can estimate the BSi outflow loss using the molar C:BSi of sediment traps (7.5) and the average carbon concentration of the seston (30 μmol L^{-1}). The BSi concentration in the surface water is approximately 4 μmol L^{-1}, resulting in 340 t Si year^{-1} in the outflow. The underestimation of the outflow is therefore minimal. This leaves an underestimated gross sedimentation as the most probable explanation for the difference in the budget. The correction of the gross sedimentation (Eq. 3.4) supposes a steady-state; however, Si concentrations in the deep zone have increased since the measurements of Degens et al. (1973). Currently, SiO_2 in the monimolimnion has a total mass of ~7,100 kt Si and an increase of 0.2% per year would be sufficient to balance the budget. This increase probably results from the dissolution of diatom frustules during their descent in the water column.

The fraction of SiO_2 mineralized at the sediment-water interface is much lower than for N and P. SiO_2 recycling is only 55% of gross sedimentation and as much as 45% is buried in the sediment. SiO_2 is principally dissolved from diatom frustules (Müller et al. 2005), while N and P is bound in organic molecules and mineralisation is accelerated by enzymes generated by microbial decomposition (Hecky et al. 1996). The dissolution reaction of SiO_2 depends on the diatom surface area and the bulk SiO_2 concentration. In Lake Kivu, dissolution will be relatively rapid in the surface water but will cease in the deep zone, where the water is saturated with respect to biogenic Si (1.2 mmol L^{-1}). Above 260 m, interstitial water in the top of the sediment is undersaturated and diatom frustules may dissolve. At greater depths saturation is reached and frustules are buried in the sediment without further dissolution. The Kibuye sediment collected at 190 m revealed an excellent preservation of diatom frustules (>90%). High preservation was also observed in Lakes Malawi and Tanganyika. In conclusion, Si losses via the outflow are equally important as Si burial in the sediment. As Si recycling is less efficient, both Si export pathways are more important compared to the internal recycling than it is the case for N and P.

3.6 Conclusion

The composition of surface water varies due to seasonal deep mixing, while the composition of the deep water remains constant. Contrary to holomictic lakes where seasonal deep mixing homogenizes the whole water column periodically, nutrient recycling in Lake Kivu occurs mainly through upward advective transport of nutrient-rich deep waters to the surface mixed layer. The long residence time of ~800 years in the deep zone results in an unusually strong nutrient enrichment.

N and P cycling are dominated by internal fluxes, while Si has a contrasting cycle with higher inputs and less efficient recycling by the biomass. N and P inputs to the surface mixed layer are mainly due to internal recycling, while N and P buried in the sediment constitute the main losses. Loads from rivers and internal recycling supply Si in equal parts to the surface mixed layer. Si losses via the Ruzizi River are as important as Si burial in the sediment. At the sediment water interface, the driving force for the remobilisation of Si is mainly dissolution of biogenic silica of the diatom frustules, which is less efficient than the microbially-driven decomposition of N and P.

The nutrient cycling in Lake Kivu showed the importance of the internal loading of nutrients for primary production. In contrast, the external inputs seem to be of minor importance. These external inputs might have changed as much as in other African lakes, but it takes a few hundred to thousand years for them to have a large impact on the lake. Lake Kivu is therefore probably more resilient to adverse impacts of increased external nutrient inputs to surface water quality.

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Chapter 4
Variability of Carbon Dioxide and Methane in the Epilimnion of Lake Kivu

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Abstract We report a dataset of the partial pressure of CO_2 (pCO_2) and methane concentrations (CH_4) in the surface waters of Lake Kivu obtained during four cruises covering the two main seasons (rainy and dry). Spatial gradients of surface pCO_2 and CH_4 concentrations were modest in the main basin. In Kabuno Bay, pCO_2 and CH_4 concentrations in surface waters were higher, owing to the stronger influence of subaquatic springs from depth. Seasonal variations of pCO_2 and CH_4 in the main basin of Lake Kivu were strongly driven by deepening of the epilimnion and the resulting entrainment of water characterized by higher pCO_2 and CH_4 concentrations. Physical and chemical vertical patterns in Kabuno Bay were seasonally stable, owing to a stronger stratification and smaller surface area inducing fetch limitation

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of wind driven turbulence. A global and regional cross-system comparison of pCO_2 and CH_4 concentrations in surface waters of lakes highlights the peculiarity of Kabuno Bay in terms of pCO_2 values in surface waters. In terms of surface CH_4 concentrations, both Kabuno Bay and the main basin of Lake Kivu are at the lower end of values in lakes globally, despite the huge amounts of CH_4 and CO_2 in the deeper layers of the lake.

4.1 Introduction

Freshwater environments are important components of the global carbon (C) cycle, as they fix carbon dioxide (CO_2) into organic matter and transport organic and inorganic C from the terrestrial biosphere to the oceans. This transport of C is not passive and freshwater ecosystems transform, store and exchange C with the atmosphere (Cole et al. 2007; Battin et al. 2008; Marotta et al. 2009; Tranvik et al. 2009). Freshwater ecosystems are considered to be frequently net heterotrophic, whereby the consumption of organic C is higher than the autochthonous production of organic C, and excess organic C consumption is maintained by inputs of allochthonous organic C (Cole and Caraco 2001). Net heterotrophy in freshwater ecosystems promotes the emission of CO_2 to the atmosphere, with the global emission from continental waters estimated at ~0.75 Pg C year^{-1} (Cole et al. 2007; 0.11 Pg C year^{-1} from lakes, 0.28 Pg C year^{-1} from reservoirs, 0.23 Pg C year^{-1} from rivers, 0.12 Pg C year^{-1} from estuaries, and 0.01 Pg C year^{-1} from ground waters). Such an emission of CO_2 from continental waters is comparable to the sink of C by terrestrial vegetation and soils of ~1.3 Pg C year^{-1} (Cole et al. 2007) and the sink of CO_2 in open oceans of ~1.4 Pg C year^{-1} (Takahashi et al. 2009). Part of the degradation of organic C that occurs in freshwater ecosystems is mediated by anaerobic processes, among which methanogenesis, which leads to the emission of methane (CH_4) to the atmosphere. The global emission of CH_4 to the atmosphere from freshwater ecosystems has been recently re-evaluated by Bastviken et al. (2011) to 103 Tg CH_4 year^{-1} (72 Tg CH_4 year^{-1} from lakes) which is significant when compared

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to other natural (168 Tg CH_4 year^{-1}) and anthropogenic (428 Tg CH_4 year^{-1}) CH_4 emissions (Chen and Prinn 2006).

Our present understanding of the role of lakes on C emissions could be biased because most observations were obtained in temperate and boreal systems, and in general in medium to small sized lakes, while much less observations are available from large tropical lakes. Tropical freshwater environments are indeed under-sampled compared to temperate and boreal systems in terms of C dynamics in general, and specifically in terms of CO_2 and CH_4 dynamics. Yet, about 50% of freshwater and an equivalent fraction of organic C is delivered by rivers to the oceans at these latitudes (Ludwig et al. 1996). Tropical lakes represent about 16% of the total surface of lakes (Lehner and Döll 2004), and Lakes Victoria, Tanganyika and Malawi belong to the seven largest lakes by area in the world.

We report the seasonal and spatial variability of CO_2 and CH_4 in the epilimnion of Lake Kivu, the smallest of the East African Rift lakes (2,370 km^2). It is a deep (maximum depth of 485 m), meromictic and oligotrophic lake (Chap. 5), characterized by a relatively simple pelagic foodweb (Chap. 8), with physical processes (vertical mixing and transport processes) that are different from most other lakes in the world (Chap. 2). Subaquatic springs provide heat, dissolved salts and CO_2 to the bottom waters of the lake (Chap. 2). A prominent feature of Lake Kivu is the huge amounts of CO_2 and CH_4 (300 and 60 km^3, respectively, at 0°C and 1 atm, Schmid et al. 2005) that are dissolved in its deep waters. While CO_2 is mainly of magmatic origin, CH_4 originates for two thirds from anoxic bacterial reduction of CO_2 and for one third from anaerobic degradation of settling organic material (Schoell et al. 1988).

Seasonality of the physical and chemical vertical structure (Chap. 2) and biological activity (Chaps. 5, 6, 7) in surface waters of Lake Kivu is driven by the oscillation between the dry season (June–September) and the rainy season (October–May), the former characterized by dryer winds and a deepening of the surface mixed layer.

4.2 Material and Methods

In order to capture the seasonal variation of the studied quantities, four cruises were carried out in Lake Kivu on 15/03–29/03/2007 (mid rainy season), 28/08–10/09/2007 (late dry season), 21/06–03/07/2008 (early dry season) and 21/04–05/05/2009 (late rainy season). Sampling was carried out at 15 stations distributed over the whole lake (Fig. 4.1).

Vertical profiles of temperature, conductivity, oxygen and pH were obtained with a Yellow Springs Instrument (YSI) 6600 V2 probe. Calibration of sensors was carried out prior to the cruises and regularly checked during the cruises. The conductivity cell was calibrated with a 1,000 μS cm^{-1} (25°C) YSI standard. The pH electrode was calibrated with pH 4.00 (25°C) and pH 7.00 (25°C) National Institute of Standards and Technology (YSI) buffers. The oxygen membrane probe was calibrated with humidity saturated ambient air. Salinity was computed from specific conductivity according to Chap. 2.

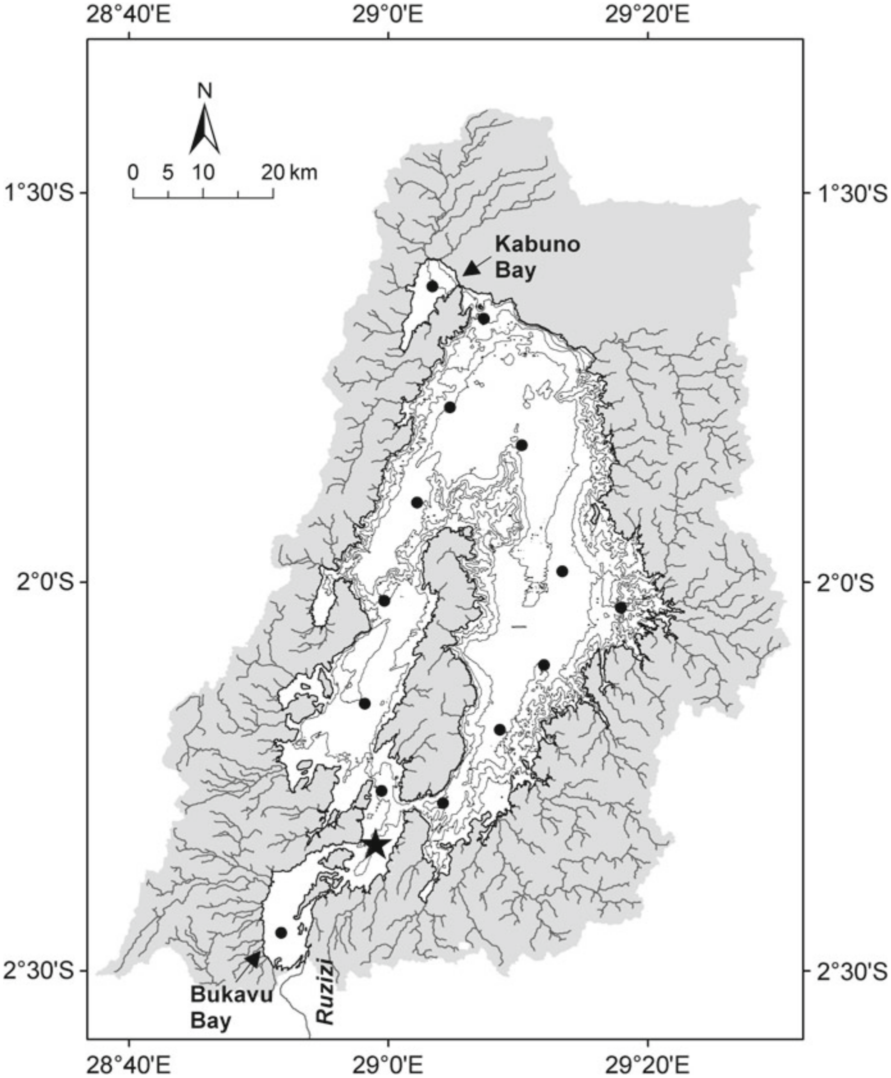

Fig. 4.1 Map of Lake Kivu, showing bathymetry (isobaths at 100 m intervals), catchment area (shaded in grey), tributaries (courtesy of Martin Schmid), and sampling stations. The station identified with a star corresponds to the site of 24 h measurement cycle carried out in March 2007

Sampling for the partial pressure of CO_2 (pCO_2) was carried out at 10 m, with the exception of a 24 h cycle in March 2007 for which data at 1 and 5 m are also presented. Measurements of pCO_2 were carried out with a non-dispersive infrared (NDIR) analyzer coupled to an equilibrator (Frankignoulle et al. 2001) through which water was pumped with a peristaltic pump (Masterflex E/S portable sampler). The sampling depth was determined with a DIMED S.A. Electronic Engineering PDCR 1730 pressure transducer. *In situ* temperature and temperature at the outlet of the equilibrator were determined with Li-Cor 1000-15 probes. The NDIR analyzer (Li-Cor, Li-820) was calibrated with pure nitrogen, and four gas standards with a CO_2 molar fraction of 363, 819, 3,997 and 8,170 ppm (Air Liquide Belgium).

Water for the determination of pH, CH_4 concentrations, $\delta^{13}C$ of dissolved inorganic carbon (DIC), total alkalinity (TA) and total organic carbon (TOC) concentrations was sampled with a 5 L Niskin bottle (Hydro-Bios). Samples were collected every 10 m from 10 to 60–80 m depending on the cruise and station, except for CH_4 which was only sampled at 10 m. Additional samples for pH, $\delta^{13}C_{DIC}$ and TA were collected at 5 m in Kabuno Bay. Water for CH_4 analysis was collected in glass serum bottles from the Niskin bottle with tubing, left to overflow, poisoned with 100 µL of saturated $HgCl_2$ and sealed with butyl stoppers and aluminium caps. Water samples for the analysis of $\delta^{13}C_{DIC}$ were taken from the same Niskin bottle by gently overfilling 12 mL glass headspace vials, poisoning with 20 µL of a saturated $HgCl_2$ solution, and gas-tight capped. A water volume of 50 mL was filtered through a 0.2 µm pore size polysulfone filter and was stored at ambient temperature in polyethylene bottles for the determination of TA. Unfiltered water samples (20 mL) were preserved with NaN_3 (0.05% final concentration) for the determination of TOC.

Measurements of pH in water sampled from the Niskin bottle were carried out with a Metrohm (6.0253.100) combined electrode calibrated with US National Bureau of Standards buffers of pH 4.002 (25°C) and pH 6.881 (25°C) prepared according to Frankignoulle and Borges (2001). Measurements of TA were carried out by open-cell titration with HCl 0.1 M according to Gran (1952) on 50 mL water samples, and data were quality checked with Certified Reference Material acquired from Andrew Dickson (Scripps Institution of Oceanography, University of California, San Diego). DIC was computed from pH and TA measurements using the carbonic acid dissociation constants of Millero et al. (2006). For the analysis of $\delta^{13}C_{DIC}$, a He headspace was created in 12 mL glass vials, and ~300 µL of H_3PO_4 was added to convert all inorganic carbon species to CO_2. After overnight equilibration, part of the headspace was injected into the He stream of an elemental analyser – isotope ratio mass spectrometer (ThermoFinnigan Flash1112 and ThermoFinnigan Delta+XL, or Thermo FlashEA/HT coupled to Thermo Delta V) for $\delta^{13}C$ measurements. The obtained $\delta^{13}C$ data were corrected for the isotopic equilibration between gaseous and dissolved CO_2 using an algorithm similar to that presented by Miyajima et al. (1995), and calibrated with LSVEC and NBS-19 certified standards or internal standards calibrated with the former. TOC was determined using a Dohrman Apollo 2000 TOC analyzer. As in surface waters of Lake Kivu particulate organic carbon contributes to ~20% of TOC (not shown), we refer to dissolved organic carbon (DOC) for the purpose of the cross-lake pCO_2 comparison (hereafter). Concentrations of CH_4 were determined by gas chromatography (GC) with flame ionization detection (GC-FID, Hewlett Packard HP 5890A), after creating a 12 mL headspace with N_2 in 40 mL glass serum bottles, as described by Abril and Iversen (2002). After creating the N_2 headspace, samples were vigorously shaken during 1 min, were placed in a thermostated bath overnight (~16 h) after which samples were again vigorously shaken during 1 min before starting the GC analysis. Certified CH_4:N_2 mixtures (Air Liquide France) of 10 and 500 ppm CH_4 were used as standards. For the March 2009 cruise, CH_4 measurements were carried out with the same procedures but using 30 mL headspace with N_2 in 70 mL serum bottles, and a SRI 8610C GC-FID calibrated with CH_4:CO_2:N_2 mixtures (Air Liquide Belgium) of 1 and 10 ppm CH_4. The concentrations were computed using the CH_4 solubility coefficient given by Yamamoto et al. (1976).

Diffusive air–water CO_2 and CH_4 fluxes (F) were computed according to:

$$F = k\Delta[C]$$

where k is the gas transfer velocity and Δ[C] is the air–water gradient of CO_2 or CH_4, using an atmospheric pCO_2 value ranging from ~372 to ~376 ppm (depending on the cruise) and an atmospheric CH_4 partial pressure of 1.8 ppm.

k was computed from wind speed using the parameterization of Cole and Caraco (1998) and the Schmidt number of CO_2 or CH_4 in fresh water according to the algorithms given by Wanninkhof (1992). Wind speed data were acquired with a Davis Instruments meteorological station in Bukavu (2.51°S 28.86°E). F was computed with daily wind speed averages for a time period of one month centred on the date of the middle of each field cruise. Such an approach allows to account for the day-to-day variability of wind speed, and to provide F values that are seasonally representative.

4.3 Results and Discussion

4.3.1 Spatial Variability of pCO_2 and CH_4

In the surface waters (10 m depth) of the main basin of Lake Kivu (excluding Kabuno Bay but including Bukavu Bay), pCO_2 values were systematically above atmospheric equilibrium (~372 to ~376 ppm depending on the cruise), and varied within narrow ranges of 537–603 ppm in March 2007, 702–775 ppm in September 2007, 597–640 ppm in June 2008, and 581–711 ppm in April 2009 (Fig. 4.2). The coefficient of variation of pCO_2 in surface waters of the main basin ranged for each cruise between 3% and 6%, below the range reported by Kelly et al. (2001) in five large boreal lakes (range 5–40%).

The most prominent feature of the spatial variation was the much higher pCO_2 values in Kabuno Bay ranging between 13,158 and 14,793 ppm (between 18 and 26 times higher than in the main basin). Compared to the main basin, surface and deep waters of Kabuno Bay were characterized by higher salinity, DIC and TA values (Figs. 4.3 and 4.4) and by lower pH and $\delta^{13}C_{DIC}$ values (Figs. 4.3 and 4.4). Comparison of DIC and TA profiles (Fig. 4.4) shows that the relative contribution of CO_2 to DIC is more important in Kabuno Bay than in the main lake, since TA is

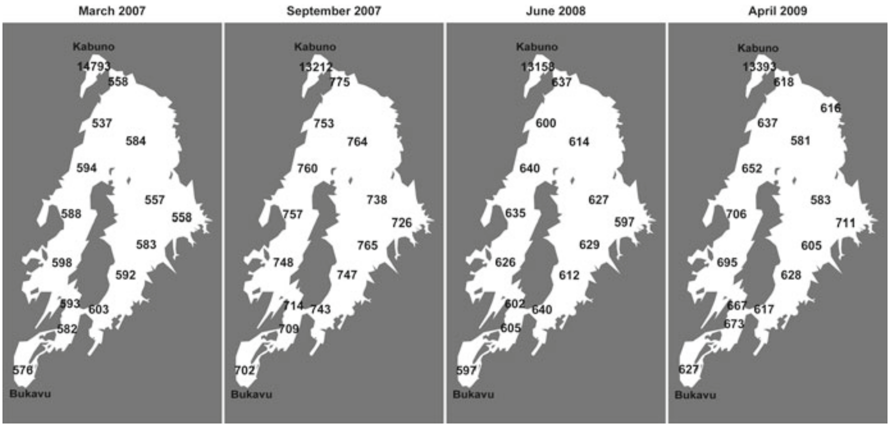

Fig. 4.2 Spatial distribution of the partial pressure of CO_2 (pCO_2, ppm) in the surface waters of Lake Kivu (10 m depth) in March 2007, September 2007, June 2008 and April 2009

mainly as HCO_3^-, and if the CO_2 contribution to DIC is low, then DIC and TA should be numerically close. At 60 m depth, CO_2 contributes ~30% to DIC in Kabuno Bay, and ~1% in the main basin. Kabuno Bay was also characterized by a very stable chemocline (salinity, pH) and oxycline at ~11 m irrespective of the sampling period (Fig. 4.3). In the main basin of Lake Kivu, the oxycline varied seasonally between ~35 m in March and September 2007 and ~60 m in June 2008 (Fig. 4.3). Overall, these vertical patterns indicate that there is a much larger contribution of subaquatic springs to the whole water column including surface waters in Kabuno Bay than in the main basin of Lake Kivu. This is related to the different geomorphology, since Kabuno Bay is shallower than the main basin (maximum depth of 110 m vs. 485 m) and exchanges little water with the main basin (narrow connection ~10 m deep). Also, Kabuno Bay is smaller (~48 km^2) than the main basin (~2,322 km^2). Hence, there is a stronger fetch limitation of wind induced turbulence that also contributes to the stability of the water column vertical structure in Kabuno Bay whatever the season.

Part of the observed horizontal gradients of pCO_2 in the main basin of Lake Kivu could be related to diel variations, since measurements were carried out irrespective of the time of the day (mostly from dawn to dusk, but sometimes at night). We investigated the diel cycle of pCO_2 during a 24 h cycle on 23/03–24/03/2007 (Fig. 4.5). The amplitudes of the daily variations of pCO_2 at the three depths were similar (~30 ppm), but pCO_2 during day-time was up to ~30 ppm higher at 1 m than at 5 m and 10 m depth. This was related to shallow stratification during day-time, with temperatures at 1 m depth up to 1.05°C and 1.15°C higher than at 5 and 10 m depth, respectively. At the end of the night the top 10 m water column became isothermal, due to heat loss to the atmosphere and convection of surface waters. In order to remove the effect of temperature change on the CO_2 solubility coefficient,

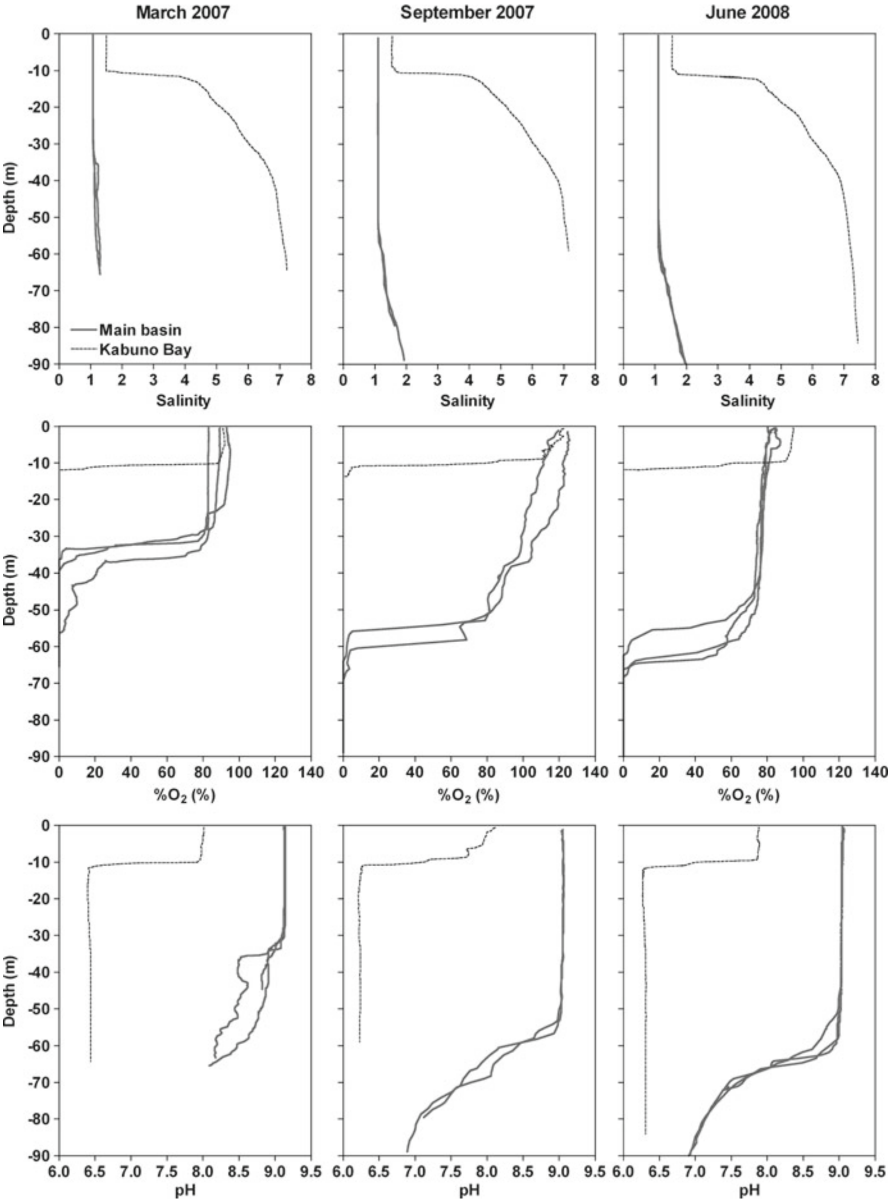

Fig. 4.3 Vertical profiles of salinity, oxygen saturation level (%O_2, %) and pH in Kabuno Bay and in the three northernmost stations of the main basin of Lake Kivu, in March 2007, September 2007 and June 2008 (vertical profiles were not acquired in April 2009)

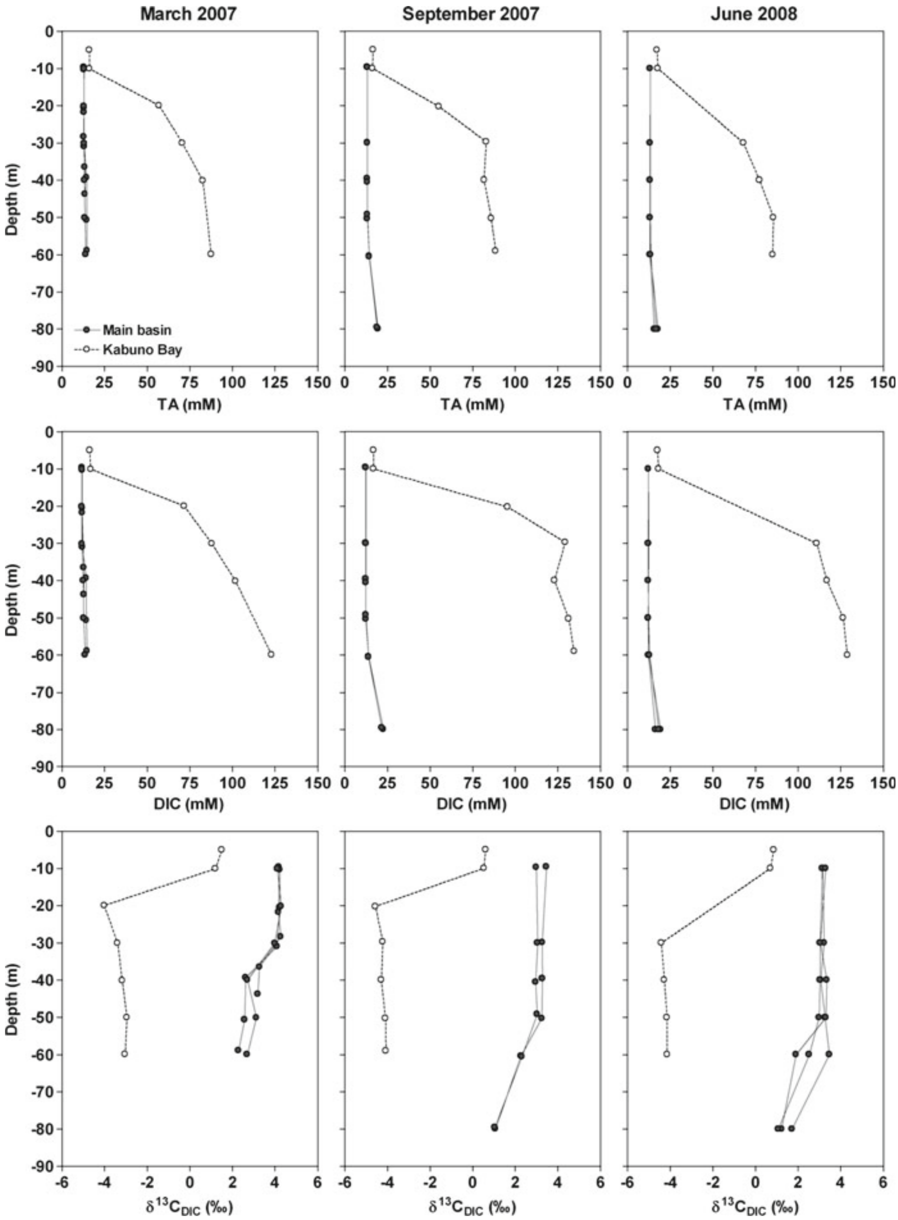

Fig. 4.4 Vertical profiles of total alkalinity (TA, mM), dissolved inorganic carbon (DIC, mM) and $\delta^{13}C_{DIC}$ (‰) in Kabuno Bay and in the three northernmost stations of the main basin of Lake Kivu, in March 2007, September 2007 and June 2008 (vertical profiles were not acquired in April 2009)

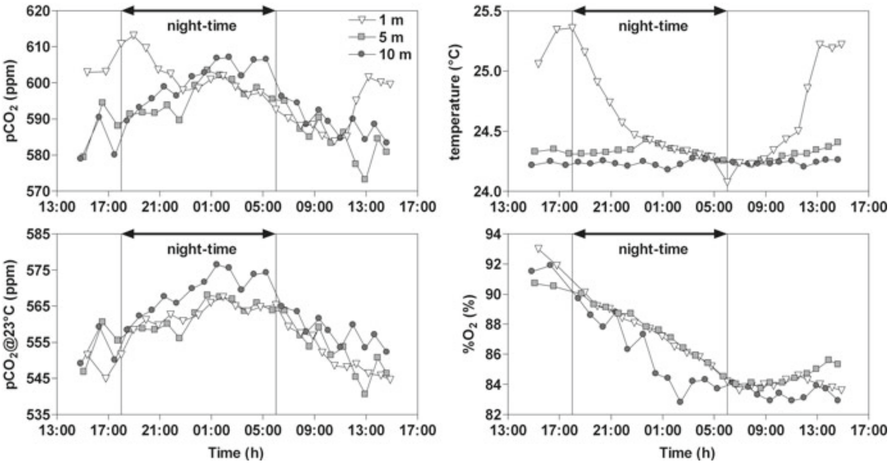

Fig. 4.5 Time series of the partial pressure of CO_2 (pCO_2, ppm), temperature (°C), pCO_2 normalized to a temperature of 23°C (pCO_2@23°C, ppm) and oxygen saturation level (%O_2, %) at 1, 5 and 10 m depth at the station indicated by a star in Fig. 4.1 from 23/03/2007 (13:00) to 24/03/2007 (14:00)

pCO_2 values were normalized to a temperature of 23°C (pCO_2@23°C). At 1, 5 and 10 m depth, pCO_2@23°C values increased during night-time and decreased during day-time, as expected from the dominance of community respiration during night-time and occurrence of primary production during day-time. This was consistent with the %O_2 variations that roughly mirrored those of pCO_2. The daily variations of pCO_2@23°C at all depths were very consistent, and pCO_2@23°C values were lower at 1 m than at 10 m, as expected from higher biological activity in relation to lower light attenuation in surface waters, and possibly also the loss of CO_2 to the atmosphere. Daily variability of pCO_2 in March 2007 was similar to the spatial horizontal gradients in surface waters in the main basin of Lake Kivu observed during that cruise.

CH_4 concentrations in the surface waters of the main basin were systematically above atmospheric equilibrium (~2 nM), and varied within relatively narrow ranges of 30–75 nM in March 2007, 54–197 nM in September 2007, 30–120 nM in June 2008, and 18–83 nM in April 2009 (Fig. 4.6). In September 2007, CH_4 concentrations in Kabuno Bay were within the range of values in the main basin, but they were ~6 times higher in April 2009, and ~8 times higher in both March 2007 and June 2008. CH_4 concentrations in surface waters of lakes result from the balance of inputs from depth or laterally from the littoral zone, and of loss terms (bacterial oxidation and evasion to the atmosphere) (Bastviken et al. 2004). Tietze et al. (1980) showed that CH_4 concentrations in deep waters of Kabuno Bay are similar to the ones for similar depths in the main basin of Lake Kivu. The likely higher relative contribution of deepwater springs in Kabuno Bay than in the main basin increases the upward flux of solutes and might explain the higher CH_4 concentrations observed

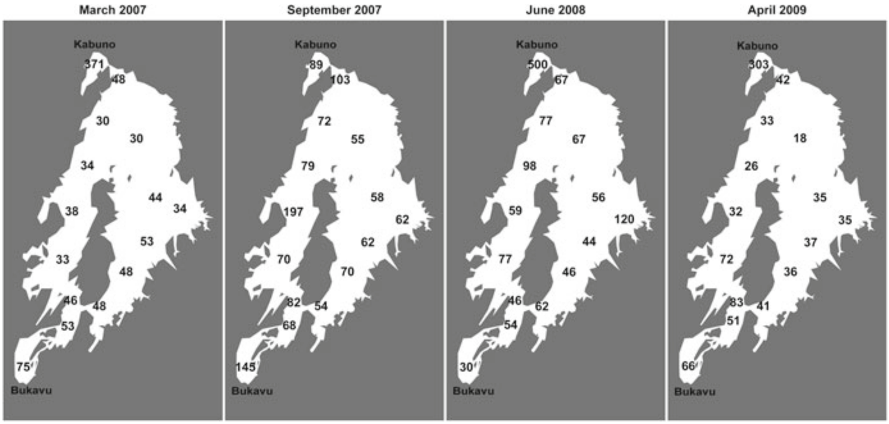

Fig. 4.6 Spatial distribution of the CH_4 concentration (nM) in the surface waters of Lake Kivu (10 m depth) in March 2007, September 2007, June 2008 and April 2009 (Borges et al. 2011)

in Kabuno Bay than in the main basin. The shallower oxycline in Kabuno Bay could also promote less removal of CH_4 by aerobic bacterial oxidation.

4.3.2 *Seasonal Variations of pCO_2 and CH_4 and Diffusive Air–Water Fluxes*

The average pCO_2 in surface waters of each of the four cruises in the main basin of Lake Kivu was positively related to the mixed layer depth and CH_4 concentrations, and negatively related to $\delta^{13}C_{DIC}$ (Fig. 4.7). This suggests than the deepening of the mixed layer and entrainment of deeper waters to the surface mixed layer is a major driver of seasonal variability of pCO_2 and CH_4 concentrations in surface waters of the main basin of Lake Kivu. Indeed, deeper waters are richer in pCO_2 and DIC (Fig. 4.4; Tietze et al. 1980; Schmid et al. 2005) and CH_4 (Tietze et al. 1980; Schmid et al. 2005) than surface waters, and the DIC in deeper waters is more ^{13}C-depleted than that in surface waters (Fig. 4.4; Tassi et al. 2009).

Seasonal variations of wind speed were rather modest (coefficient of variation of 13%), ranging between $1.2 \pm 0.4\ m\,s^{-1}$ in September 2007 and $1.6 \pm 0.2\ m\,s^{-1}$ in June 2008. Hence, seasonal variations of diffusive air–water fluxes of CH_4 and CO_2 closely tracked those of CH_4 concentrations and pCO_2. Emissions of CH_4 from surface waters in the main basin ranged between 26 $\mu mol\ m^{-2}\ day^{-1}$ in March 2007 and April 2009 and 50 $\mu mol\ m^{-2}\ day^{-1}$ in September 2007. Emissions of CH_4 from surface waters in Kabuno Bay ranged between 53 $\mu mol\ m^{-2}\ day^{-1}$ in September 2007 and 185 $\mu mol\ m^{-2}\ day^{-1}$ in April 2009. Emissions of CO_2 from surface waters in the main basin ranged between 4 $mmol\ m^{-2}\ day^{-1}$ in March 2007 and 8 $mmol\ m^{-2}\ day^{-1}$ in September 2007. Emissions of CO_2 from surface waters

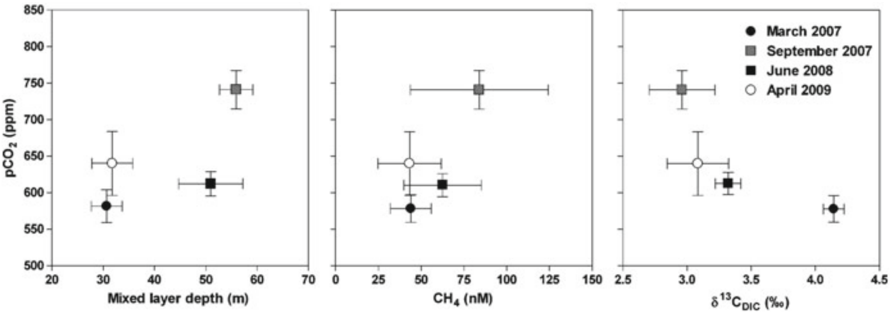

Fig. 4.7 Mean values of the partial pressure of CO_2 (pCO_2, ppm) in the surface waters (10 m) versus mixed layer depth (m), versus CH_4 concentration in surface waters (10 m, nM) and versus $\delta^{13}C_{DIC}$ (‰) in surface waters (10 m) in the main basin of Lake Kivu in March 2007, September 2007, June 2008 and April 2009. Error bars correspond to standard deviations on the mean

in Kabuno Bay ranged between 270 mmol m^{-2} day^{-1} in September 2007 and 307 mmol m^{-2} day^{-1} in March 2007.

4.3.3 Global and Regional Comparison with Other Lakes

When compared to other lakes globally (Bastviken et al. 2004; Sobek et al. 2005), the main basin of Lake Kivu ranks 3,629th in terms of pCO_2 in surface waters (out of 4,904 lakes) and 47th in terms of CH_4 concentration in surface waters (out of 49 lakes) (Fig. 4.8). Kabuno Bay ranks 7th in terms of pCO_2 and 30th in terms of CH_4 concentrations in surface waters.

The comparison of pCO_2 and DOC has been frequently used in limnology for cross-system analysis of pCO_2 data (del Giorgio et al. 1999; Riera et al. 1999; Kelly et al. 2001; Sobek et al. 2003, 2005; Roehm et al. 2009; Teodoru et al. 2009). There is in general a positive relationship between pCO_2 and DOC that can be indicative of terrestrial organic matter inputs (as traced by DOC) sustaining net heterotrophy in freshwater ecosystems (as indicated by pCO_2). Alternatively and not incompatibly, this positive relationship can also be indicative of lateral inputs of both DOC and CO_2 from soils by ground-waters and surface run-off. Values in the main basin of Lake Kivu compare surprisingly well to the relationship of pCO_2 and DOC established from a global compilation of lakes across all climatic zones (Fig. 4.9), yet at the lower end of values in agreement with the oligotrophic nature of Lake Kivu. Values in Kabuno Bay stand clearly above the relationship of pCO_2 and DOC in lakes globally, testifying the role of large contribution of CO_2 from subaquatic springs.

$\delta^{13}C_{DIC}$ signatures for surface waters in Lake Kivu range between +2.6‰ and +3.5‰ for the main basin and between +0.3‰ and +1.5‰ for Kabuno Bay, which is in the higher range of that reported earlier for lakes (Fig. 4.10). $\delta^{13}C_{DIC}$ signatures

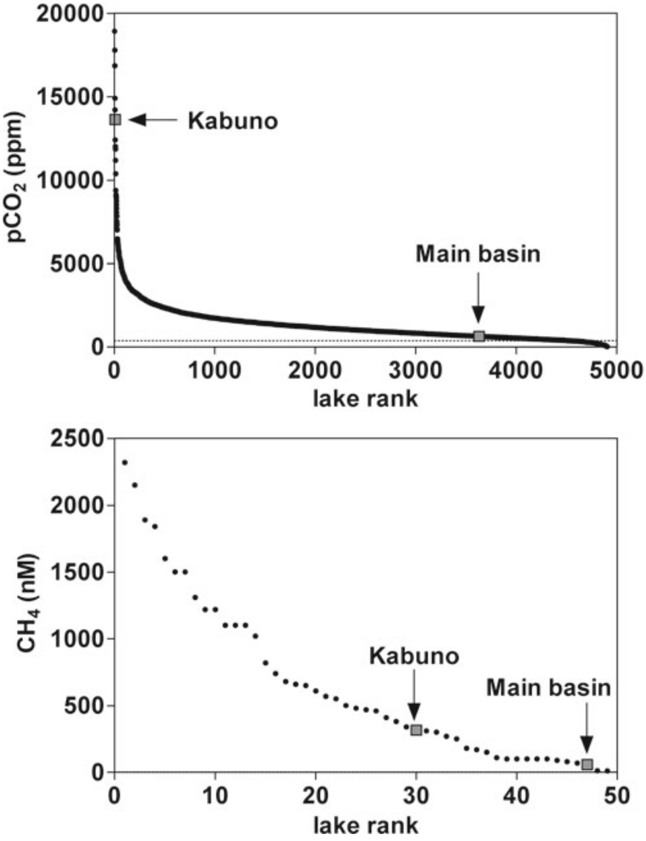

Fig. 4.8 Comparison by rank of the partial pressure of CO_2 (pCO_2, ppm) and of CH_4 concentration (nM) in surface waters of the main basin of Lake Kivu and Kabuno Bay (average of the four cruises at 10 m) with global compilations in lakes by Sobek et al. (2005) and Bastviken et al. (2004), respectively

in lakes are to a large extent determined by the geochemistry of the watershed, but are further influenced by biological processes including respiration (which adds ^{13}C-depleted CO_2), photosynthesis (which preferentially removes $^{12}CO_2$, and subsequently leads to higher $\delta^{13}C_{DIC}$), and methane oxidation (which adds highly ^{13}C-depleted CO_2). In Lake Kivu, the majority of DIC is thought to be of magmatic origin (Schoell et al. 1988), with typically rather ^{13}C-enriched signatures between $^{-}$7‰ and −4‰ (Tietze et al. 1980). $\delta^{13}C_{DIC}$ in surface waters of Lake Kivu are slightly higher and DIC concentrations are consistently higher in Lake Kivu than in Lakes Tanganyika and Malawi (Table 4.1), where the contribution of subaquatic springs is thought to be significantly lower (Table 4.2). Given the very high DIC concentrations in Lake Kivu, the magmatic inputs likely provide the dominant imprint on $\delta^{13}C_{DIC}$ signatures, although seasonal and depth variations (Figs. 4.4 and 4.7) clearly hold information on the mixing regime and biological processes which

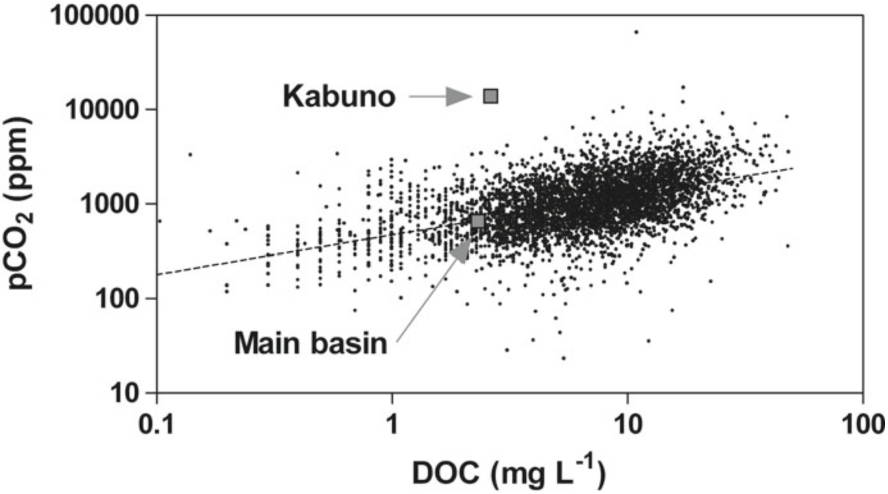

Fig. 4.9 Relationship between partial pressure of CO_2 (pCO_2, ppm) and dissolved organic carbon (DOC, mg L^{-1}) in lakes reported by Sobek et al. (2005; $\log(pCO_2) = 2.67 + 0.414\log(DOC)$; $r^2 = 0.26$) and values in the main basin of Lake Kivu and Kabuno Bay (average of the four cruises at 10 m)

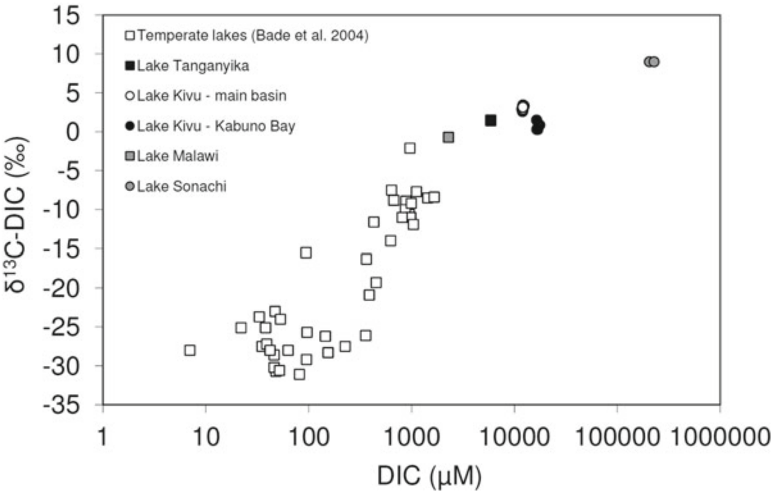

Fig. 4.10 Comparison of dissolved inorganic carbon (DIC, µM) concentrations and $\delta^{13}C_{DIC}$ (‰) across a range of lakes: Lake Kivu (surface waters from main basin and Kabuno Bay, this study), Lake Tanganyika (Craig 1974), Lake Malawi (Hecky and Hesslein 1995), Lake Sonachi (Kenya, own unpublished data), and from a survey in a range of temperate lakes (Bade et al. 2004)

need to be examined in more detail. Interestingly, data from Lake Sonachi, a small crater lake adjacent to Lake Naivasha, Kenya (see e.g. Verschuren 1999) show even more extreme DIC concentrations (200–230 mM) and $\delta^{13}C_{DIC}$ signatures of +9‰ (Fig. 4.10) which is among the highest recorded so far in any lake system. The latter

Table 4.1 Comparison of salinity, total alkalinity (TA, mM), dissolved inorganic carbon (DIC, mM) and the partial pressure of CO_2 (pCO_2, ppm) from surface waters of Lake Malawi (Hecky and Hesslein 1995; Branchu et al. 2010), Lake Tanganyika (Craig 1974), the main basin of Lake Kivu and Kabuno Bay (this study)

	Salinity	TA (mM)	DIC (mM)	pCO_2 (ppm)
Lake Malawi	0.2	2.33	2.3	N/A
Lake Tanganyika	0.7	6.54	5.9	280
Main basin of Lake Kivu	1.2	13.00	12.0	640
Kabuno Bay	1.6	16.90	17.3	13,640

pCO_2 data in Lake Tanganyika were computed from original DIC and TA data reported by Craig (1974) using the carbonic acid dissociation constants of Millero et al. (2006), and adjusted to 2008 by accounting for the increase of atmospheric CO_2

Table 4.2 Morphometry and hydrology of Lakes Kivu (Chap. 2), Tanganyika and Malawi (Branchu 2001)

	Lake Kivu	Lake Tanganyika	Lake Malawi
Surface (km^2)	2,370	32,600	28,800
Volume (km^3)	580	18,880	8,400
Precipitation (km^3 $year^{-1}$)	3.3	32.6	44.1
Evaporation (km^3 $year^{-1}$)	3.6	55.3	59.6
Surface inflows (km^3 $year^{-1}$)	2.0	29.0	28.8
Outflow (km^3 $year^{-1}$)	3.0	6.3	12.1
Flow from subaquatic springs (km^3 $year^{-1}$)	1.3	?	1.3
Flushing time (years)[a]	193	2,997	697
Residence time (years)[b]	88	306	113

[a] Volume/outflow

[b] Volume/(precipitation + inflow)

values would be consistent with high primary production and predominantly mantle-derived CO_2 inputs in this enclosed system.

In Table 4.1, salinity, TA, DIC and pCO_2 values from surface waters of Lake Kivu are compared to limited data-sets from Lakes Malawi and Tanganyika. The higher salinity and TA values in Lake Tanganyika than in Lake Malawi are probably related to the higher residence time, flushing time and ratio of evaporation to precipitation in Lake Tanganyika (Table 4.2). The higher salinity, TA, DIC and pCO_2 values in Lake Kivu than Lake Tanganyika cannot be explained in terms of higher residence time and flushing time. This would suggest that higher values of these quantities in Lake Kivu are due to subaquatic springs that are undocumented in Lake Tanganyika. Subaquatic springs in Lake Kivu are similar in terms of flow to those in Lake Malawi but the volume of Lake Kivu is more than 14 times smaller, leading to a more intense impact on the chemistry of Lake Kivu. Based on available data, Lake Tanganyika behaves as a sink for atmospheric CO_2, while the present data shows that Lake Kivu is a source of CO_2 to the atmosphere throughout the annual cycle. The sink of CO_2 in Lake Tanganyika should be sustained by an export

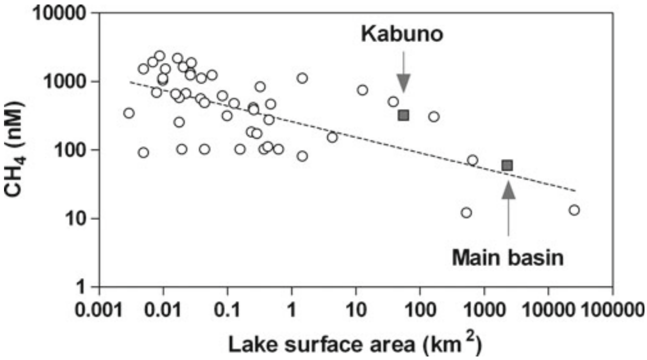

Fig. 4.11 Relationship between CH_4 concentration (nM) and lake surface area (km^2) in the main basin of Lake Kivu and Kabuno Bay (average of the four cruises at 10 m) and from the compilation by Bastviken et al. (2004). Relationship between CH_4 concentration and lake surface area ($\log(CH_4) = 2.42 - 0.229 \log(\text{lake surface area})$; $r^2 = 0.40$; $p < 0.0001$; $n = 47$) was not originally reported by Bastviken et al. (2004) but is based on the same data-set. Note the higher number of observations of CH_4 in lakes smaller than 10 km^2 (adapted from Borges et al. 2011)

of organic carbon from surface to depth. There is no reason to believe that Lake Kivu should behave otherwise in the terms of export of organic C to depth. This would imply that the source of CO_2 to atmosphere in Lake Kivu is mainly sustained from inputs to surface waters of DIC from depth (subaquatic springs).

The CH_4 concentrations in surface waters of Lake Kivu were surprisingly low compared to lakes globally, considering the huge amounts of CH_4 contained in the deep layer of the lake, i.e. concentrations up to 10^6 higher than in surface waters (Schmid et al. 2005). Cross-system comparison of CH_4 in surface waters of lakes was carried out as a function of lake surface area (Fig. 4.11). Both Kabuno Bay and the main basin of Lake Kivu fall on the negative relationship between CH_4 and lake surface area. There is probably not a unique explanation of the negative relationship between CH_4 concentrations and lake surface area, but rather a combination of several factors. In smaller systems there is a higher supply of allochthonous inputs (from catchment and littoral zone) of nutrients and organic C relative to volume of lake (i.e., large ratio of catchment area to lake surface area). This will sustain high levels of degradation in sediments of organic C of allochthonous and autochthonous nature (the former sustained by allochthonous nutrient inputs) (Schindler 1971), and promotes a higher flux of CH_4 from sediments to the water column in smaller systems. As a first approximation, we can also assume that smaller systems are shallower than larger ones. In shallow systems there will be a higher probability of sediment re-suspension coupled to a lower removal of CH_4 by bacterial oxidation, due to a shorter distance between sediments and the air-water interface. Finally, in larger systems, there will be a lower fetch limitation of wind induced turbulence and gas transfer velocity (Wanninkhof 1992; Fee et al. 1996) leading to a higher loss of CH_4 by emission to the atmosphere (for an identical air-water gradient of CH_4). The lower fetch limitation of wind induced turbulence in larger systems will also promote deeper oxygenated mixed layers, promoting CH_4 loss by bacterial aerobic CH_4 oxidation.

4.4 Conclusions

There are several lines of evidence (see Chaps. 5 and 6) that suggest that the epilimnion of Lake Kivu is net autotrophic, whereby gross primary production exceeds community respiration. This is consistent with the fact that the watershed of Lake Kivu is only about twice as large as the lake surface (Chap. 2), and a very narrow littoral zone due to steep shores, whereby the contribution of allochthonous organic C inputs to the overall organic C fluxes in the lake is expected to be minor. We then conclude that the over-saturation of surface waters with respect to atmospheric CO_2 and emission of CO_2 to the atmosphere (on average for the four cruises: 6 and 289 mmol m^{-2} day^{-1}, in the main basin and Kabuno Bay, respectively) are sustained by inputs of CO_2 from depth derived from subaquatic springs and the degradation of organic carbon.

The CH_4 concentrations in surface waters of Lake Kivu were surprisingly low compared to lakes globally, considering the huge amounts of CH_4 contained in the deep layer of the lake, i.e. concentrations up to 10^6 higher than in surface waters (Schmid et al. 2005). This is related to highly stratified conditions of the lake that promote a very strong removal of CH_4 by bacterial oxidation (Jannasch 1975; Pasche et al. 2011) leading to low CH_4 concentrations in surface waters, and a modest emission of CH_4 to the atmosphere (on average for the four cruises: 36 and 106 μmol m^{-2} day^{-1}, in the main basin and Kabuno Bay, respectively).

Kabuno Bay showed distinct pCO_2, CH_4, pH and $\delta^{13}C_{DIC}$ values compared to the main basin of Lake Kivu, which are related to a larger contribution of subaquatic springs inputs as suggested by vertical profiles of all reported variables. A large contribution of CO_2 from subaquatic springs could also explain that Kabuno Bay ranks seventh in terms of pCO_2 in surface waters compared to lakes globally, and that values strongly deviate from the relationship between pCO_2 and DOC in lakes globally.

Acknowledgments We are grateful to Boniface Kaningini and Pascal Isumbisho Mwapu (Institut Supérieur Pédagogique, Bukavu, Democratic Republic of the Congo) and Laetitia Nyina-wamwiza (National University of Rwanda, Butare, Rwanda) and their respective teams for logistic support during the cruises, to Sebastian Sobek for sharing his pCO_2 database and reviewing the previous versions of the manuscript. This work was funded by the Fonds National de la Recherche Scientifique (FNRS) under the CAKI (Cycle du carbone et des nutriments au Lac Kivu) project (contract n° 2.4.598.07), and contributes to the European Research Council starting grant project AFRIVAL (African river basins: catchment-scale carbon fluxes and transformations, 240002) and to the Belgian Federal Science Policy Office EAGLES (East African Great Lake Ecosystem Sensitivity to changes, SD/AR/02A) project. AVB, BD and GL are research associates at the FNRS. FD was a postdoctoral researcher at the FNRS.

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Chapter 5
Phytoplankton of Lake Kivu

Hugo Sarmento, François Darchambeau, and Jean-Pierre Descy

Abstract This chapter reviews taxonomic composition, biomass, production and nutrient limitation of the phytoplankton of Lake Kivu. Present Lake Kivu phytoplankton is dominated by cyanobacteria – mainly *Synechococcus* spp. and thin filaments of *Planktolyngbya limnetica* – and by pennate diatoms, among which *Nitzschia bacata* and *Fragilaria danica* are dominant. Seasonal shifts occur, with cyanobacteria developing more in the rainy season, and the diatoms in the dry season. Other groups present are cryptophytes, chrysophytes, chlorophytes and dinoflagellates. According to a survey conducted in the period 2002–2008, the composition of the phytoplankton assemblage was quasi homogeneous among lake basins. The mean euphotic depth varied between 17 and 20 m, and the increase in the ratio between mixed layer depth and euphotic depth to about 2 in the dry season may have selected for diatoms and cryptophytes, which tended to present their maximal development in this season, when cyanobacteria slightly decreased. Mean chlorophyll *a* concentration was 2.16 mg m^{-3}, and the mean daily primary production was 0.62 gC m^{-2} day^{-1} (range, 0.14–1.92), i.e. in the same range as in other large oligotrophic East African Rift lakes. Seston elemental

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ratios indicated a moderate P-deficiency during the dry, mixed season and a severe P limitation during part of the rainy, stratified season; the C:N ratio indicated a moderate N limitation throughout the year. Nutrient addition assays pointed to a direct N-limitation and co-limitation by P during rainy seasons and P or N limitation during dry seasons depending on the year. Thus, phytoplankton ecology in Lake Kivu does not differ from that of other Rift lakes, where seasonal variations result in a trade-off between low light with high nutrient supply and high light with low nutrient supply. Phytoplankton production in Lake Kivu is also similar to that of other Rift lakes, and nutrient limitation of phytoplankton growth may occur as a result of variable availability of N and P, as in Lakes Tanganyika and Malawi, even though the extent of P limitation seems greater in Lake Kivu.

5.1 Introduction

Because of its large size, substantial depth and consequently reduced littoral zone, the ecological functioning of the mixolimnion of Lake Kivu is dominated by pelagic processes, among which phytoplankton photosynthesis supplies the bulk of the organic carbon available for the food web. In this way, the pelagic ecosystem of Lake Kivu is not different from that of the other oligotrophic African Rift lakes, where strong seasonal changes occur, imposing contrasting constraints on phytoplankton growth, resulting in substantial shifts of the composition and biomass of the planktonic assemblages (Hecky and Kling 1987). Since the earlier studies carried out in the first half of the twentieth century, it was suspected that large variations of phytoplankton abundance occurred in Lake Kivu, but, besides taxonomic lists, few data were available (Beadle 1981). Despite the perception of its oligotrophic status by Damas (1937), Lake Kivu was described as more productive than Lake Tanganyika, based on few data on net plankton abundance (Hecky and Kling 1987). Indeed, subsequent studies confirmed that, in recent years, chlorophyll *a* concentration in the pelagic waters of Lake Kivu was two to three times as high as in Lake Tanganyika and Malawi (Sarmento et al. 2009). But is Lake Kivu “more eutrophic” than Lake Tanganyika (Sarvala et al. 1999)? Is its primary productivity higher than that of the other deep Rift lakes?

Here we review the literature on the autotrophic plankton of Lake Kivu: its taxonomic composition, abundance, production and ecology. Additionally, we summarise the results of the most complete limnological and planktological survey ever realised in Africa, and probably in a tropical lake. The first aim of this review is to establish a well-documented and updated picture of the pelagic phytoplankton of Lake Kivu, which can be used as a reference for the future generations of researchers and naturalists, as well as a baseline for the lake monitoring to evaluate potential effects of the ongoing gas extraction (Chap. 10).

5.2 Light Conditions

Light is an essential factor determining primary productivity and phytoplankton assemblages in aquatic systems (Reynolds 2006). Contrarily to the common sense, light limitation in tropical aquatic systems is relatively common: numerous shallow polymictic lakes receive large amounts of suspended matter due to erosion (e.g. Mukankomeje et al. 1993); in others, like Lake Victoria, phytoplankton is light-limited due to high biomass after eutrophication producing a self-shading effect (Mugidde 1993; Kling et al. 2001). In deep lakes light can equally become a limiting factor as soon as the depth of the upper mixed layer (Zm) reaches or exceeds the depth of the euphotic zone (Zeu), depth at which the light intensity drops to 1% of the surface incident light. In such periods, the Zm:Zeu ratio is larger than 1 and light harvesting by primary producers becomes a selective factor shaping phytoplankton composition (Sarmento et al. 2006).

In Lake Kivu, the Zm:Zeu ratio is often larger than 1, especially during the deep mixing periods, more frequent in the dry season (Fig. 5.1), when Zm often exceeds 50 m (typically occurring between June and September). Although water transparency is higher, on average, during the dry season (mean Zeu = 19.8 m) than during the rainy season (17.1 m), it is during that period that phytoplankton experiences the lowest light conditions, and this is reflected in shifts in the phytoplankton composition (discussed below).

The water transparency co-varies seasonally in a similar range in both the main basin and Ishungu basin (Fig. 5.1). However, the dry season winds may disproportionally affect the main basin, which is more exposed to wind than the Ishungu basin, resulting in more intense vertical mixing in the main basin (Fig. 5.1).

5.3 Taxonomic Composition

The first relevant scientific information concerning the plankton of Lake Kivu is from the mid 1930s, when H. Damas carried out an expedition to the "Parc National Albert" (Damas 1935–1936, 1937). The 55 net samples collected from Lake Kivu were studied by several phycologists and the results were published in two issues of the publication of the Institut of National Parks of Belgian Congo devoted to the Mission H. Damas: fasc. 8 "Süsswasser-Diatomeen" by Hustedt (1949) for the diatoms, and fasc. 19 "Algues et Flagellates" by Frémy et al. (1949) for several other groups of algae, namely Cyanobacteria (P. Frémy), Chrysophyta, Pyrrhophyta, Euglenophyta, Volvocales (A. Pascher), Heterokontae, Protococcales, Siphonocladales (W. Conrad). In the samples from Lake Kivu, 157 species and intraspecific taxa of diatoms were found (including benthic and epiphytic samples); 12 were described as new species. The most common diatoms in the main basin were *Nitzschia confinis* Hust., *N. lancettula* O. Müller, *N. tropica* Hust., *N. gracilis* Hantzsch and *Synedra* (now *Fragilaria*) *ulna* (Nitzsch) Ehrenb. Among the

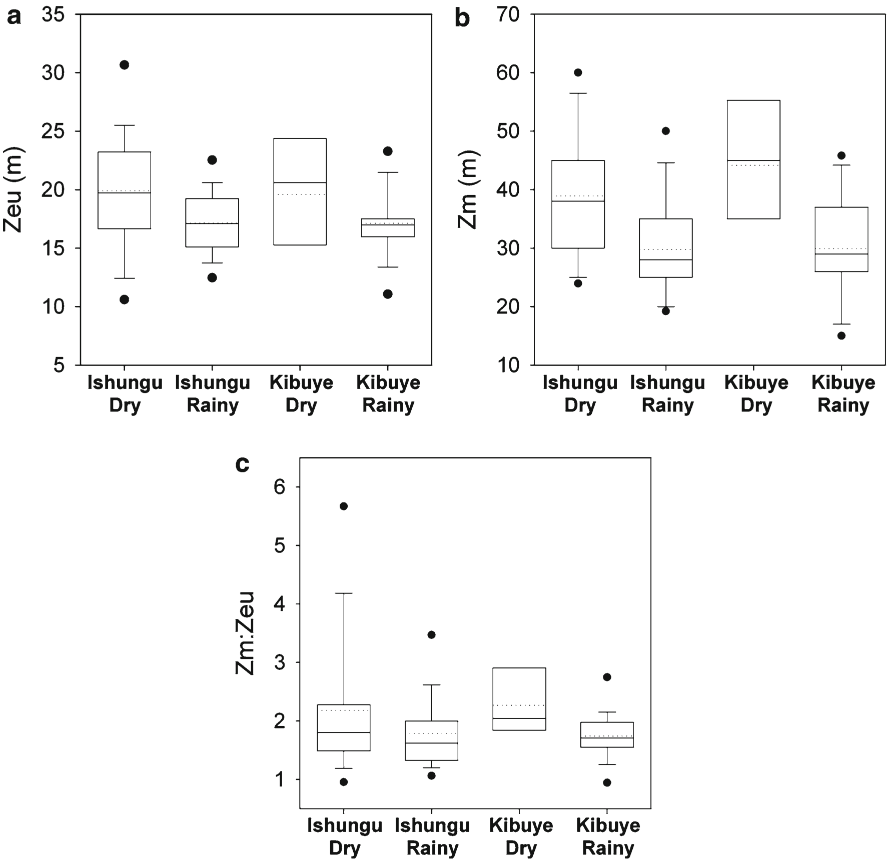

Fig. 5.1 Box plots of (**a**) the euphotic layer depth (Zeu), (**b**) the mixed layer depth (Zm) and (**c**) the Zm:Zeu ratios. Data from two sampling stations (located in Ishungu basin and in the main basin off Kibuye, see Fig. 2.1) and two seasons (rainy vs. dry) are compared. The central full line indicates the median value, the middle dotted line indicates the arithmetic mean values, the box indicates the lower and upper quartiles, the error bars indicate the 10th and 90th percentiles, and the dots correspond to the 5th and 95th percentiles

cyanobacteria, *Microcystis flos-aquae* (Wittrock) Kirchner was the most frequent, together with other *Microcystis* species, such as *M. aeruginosa* (Kütz.) Kütz. and *M. ichthyoblabe* Kütz., and a few planktonic *Lyngbya* (especially *L. circumcreta* West and *L. contorta* Lemm.). Among the other groups, *Botryococcus braunii* Kütz. and *Chlorella vulgaris* Beijerinck were rather abundant, together with several species of *Pediastrum* and *Scenedesmus*. Two new green algae were described from Lake Kivu: *Cosmarium kivuense* Conrad and *Scenedesmus cristatus* Conrad ex Duvigneaud. The data from the Damas' expedition were used by Van Meel (1954) in his book on the phytoplankton of East African great lakes, but without any new addition to the knowledge of the algal flora of Lake Kivu.

Later, in diatom physiology studies, Kilham et al. (1986) and Kilham and Kilham (1990) discussed the *Nitzschia – Stephanodiscus* dominance gradient in the sediments of the lake in the different basins, following a Si:P gradient, and Haberyan and Hecky (1987), in a paleoclimatological study, reported several diatoms and scales of *Paraphysomonas vestita* Stokes (Chrysophyceae) in sediments cores. Drastic changes were recorded around 5,000 years BP in the fauna and flora of the lake, in particular the disappearance of *Stephanodiscus astraea* var. *minutula* (Kütz.) Grunow (an uncertain taxon, see Spamer and Theriot 1997), and the replacement by several needle-like *Nitzschia*. The authors suggested that the cause of this shift may have been the hydrothermal input of CO_2 into the lake due to high volcanic activity in the region, which would have caused lake turnover and consequent disappearance of the plankton by anoxia, extremely low pH or toxic gases.

In a comparative study of the composition and abundance of phytoplankton from several East African lakes, Hecky and Kling (1987) reported for Lake Kivu an algal assemblage dominated by cyanobacteria and chlorophytes, with higher biomass than in Lake Tanganyika. These authors reported *Lyngbya circumcreta* West, *Cylindrospermopsis*, *Anabaenopsis* and *Rhaphidiopsis* as the dominant algae found in settled samples collected in March 1972. Among the green algae, *Cosmarium laeve* Rab. was the most common species. In the northern basin, *Peridinium inconspicuum* Lemm., *Gymnodinium pulvisculus* Klebs and *Gymnodinium* sp. were considerably abundant, whereas diatoms *Nitzschia* and *Synedra* (now included in *Fragilaria*) were abundant only in the isolated Kabuno Bay.

The pelagic flora of Lake Kivu was recently updated with new samples from a long term monitoring survey (Sarmento et al. 2007), in which the most common species (Fig. 5.2) were the pennate diatoms *Nitzschia bacata* Hust. and *Fragilaria danica* (Kütz.) Lange Bert., and the cyanobacteria *Planktolyngbya limnetica* (Lemm.) Komárková-Legnerová and Cronberg. Additionally, the picocyanobacterium *Synechococcus* sp. was shown to constitute a major compartment of the autotrophic plankton in Lake Kivu, with persistently high abundances (~10^5 cells mL^{-1}) throughout the year (Sarmento et al. 2008).

Another important missed (or not reported) aspect in past studies were the high abundances of the centric diatom *Urosolenia* sp. and the cyanobacterium *Microcystis* sp. near the surface under diel stratification conditions (Sarmento et al. 2007). Typical deep epilimnion/metalimnion populations with species such as *Cryptaulax* sp., *Cryptomonas* sp., *Rhodomonas* sp. and *Merismopedia trolleri* Bach were also described. Vertical stratification at different time scales, from day to season, creates a range of different growing conditions that remain stable long enough to allow the development of these segregated phytoplankton populations in specific layers of the water column. This constitutes an important factor of diversification in Lake Kivu.

5.4 Biomass and Production

Historical data on limnology and planktology parameters of Lake Kivu are scarce, and no long-term surveys had been conducted before the year 2002. Hecky and Kling (1987) reported phytoplankton fresh weight biomass from 550 up to 2,100 mg m^{-3} for March 1972 surface samples. Similar to other East African large

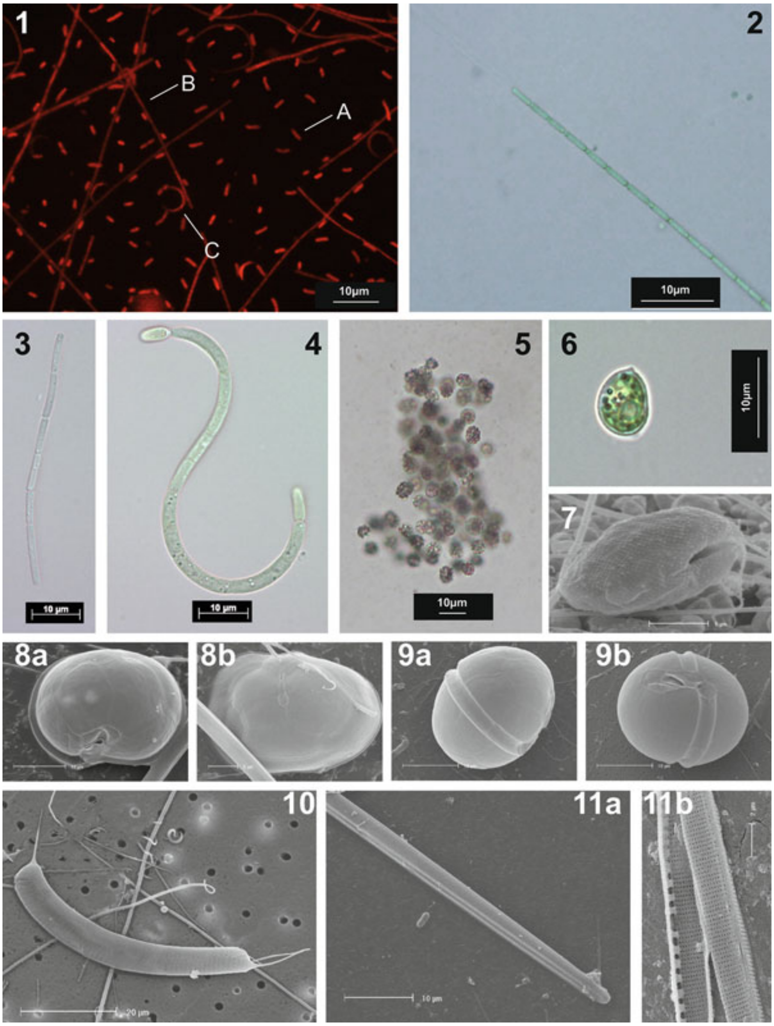

Fig. 5.2 Main phytoplankton taxa present in Lake Kivu. 1. A – *Synechococcus* spp., B – *Planktolyngbya limnetica* (Lemm.) Komárková-Legnerová and Cronberg, C – *Monoraphidium contortum* (Thur.) Kom.-Legn. (epifluorescence microscope); 2. *Planktolyngbya limnetica* (Lemm.) Kom.-Legn. and Cronberg; 3. *Pseudanabaena moniliformis* Kom. and Kling; 4. *Cylindrospermopsis af. curvispora* Wat.; 5. *Microcystis* sp.; 6. *Tetraëdron minimum* (A. Braun) Hansg.; 7. *Cryptomonas* sp.; 8a, b. *Peridinium umbonatum* Stein; 9a, b. *Peridinium* sp.; 10. *Urosolenia* sp.; 11a. *Nitzschia bacata* Hust. (11b. detail of fibulae median interruption). Each scale bar is 10 µm

lakes, the planktonic assemblage of Lake Kivu at that time appeared to be dominated to 70–90% by chlorophytes and cyanobacteria, with diatoms at lower abundances (Hecky and Kling 1987). Another trait of Lake Kivu revealed in that study was its higher algal biomass than in the larger Lakes Malawi and Tanganyika, and a slightly higher primary production: 1.44 g C m^{-2} day^{-1} reported by Beadle (1981), which is an estimate based on few measurements carried out in the 1970s by geochemists (Degens et al. 1973; Jannasch 1975).

In a more complete limnological survey carried out in 2002–2004 (Isumbisho 2006; Isumbisho et al. 2006; Sarmento 2006; Sarmento et al. 2006) phytoplankton biomass and composition were assessed combining diverse complementary techniques such as HPLC analysis of marker pigments and CHEMTAX processing, flow cytometry, and epifluorescence and electron microscopy. Annual average chlorophyll *a* (Chl *a*) in the mixed layer was 2.16 mg m^{-3} and the nutrient levels in the euphotic zone were low, placing Lake Kivu clearly in the oligotrophic range. Seasonal variations of algal biomass and composition were related to variability of wind pattern and water column stability. Contrary to earlier reports, diatoms were the dominant group, particularly during the dry season episodes of deep mixing. During the rainy season, the stratified water column, with high light and lower nutrient availability, favoured dominance of filamentous, diazotrophic cyanobacteria and of picocyanobacteria.

Additional data collected in the framework of a cooperation project (ECOSYKI, 2004–2009) extended the record to the year 2008, thus providing a long-term survey (2002–2008) of Lake Kivu phytoplankton (Fig. 5.3). The first striking aspect is the amplitude of the inter-annual variability of phytoplankton biomass peaks. Apparently, phytoplankton usually peaked during the dry season, but not systematically every year. In Ishungu basin, a phytoplankton bloom with a biomass higher than 100 mg Chl *a* m^{-2} was observed at the end of the dry season (July–August) in 2003, in 2004 and more spectacularly in 2008. A lower dry season peak was observed in 2006 and in 2007, but not in 2002 and in 2005. The variable intensity of the dry season mixing (see Chap. 2) may explain this variation in the phytoplankton biomass peaks.

Grouping the data by station and by season (dry season arbitrarily defined as the period comprised between 1st of June and 30th of September), we can estimate the degree of variance of the total phytoplankton biomass (Chl *a*) and the principal algal groups: diatoms, cyanobacteria and cryptophytes (Fig. 5.4). The dry season Chl *a* values are distributed in a more scattered way than the rainy season values, indicating that extreme and more variable events usually occurred during the dry season. Mean seasonal total biomass was higher during the dry season than during the rainy season in both the main basin and Ishungu basin (Table 5.1, Fig. 5.4). A closer analysis of the phytoplankton community structure indicates a clear seasonal signal: diatoms and cryptophytes were more abundant during the dry season, with a scattered distribution in the box plots, indicating the formation of high biomass peaks during short periods of time, while cyanobacteria showed a more even distribution with slightly lower values during the dry season (Table 5.1, Fig. 5.4). There were no significant differences in the total biomass between the sampling stations, but diatoms and cryptophytes were more abundant in Ishungu basin, while cyanobacteria represented a higher proportion of the biomass in the main basin (Table 5.1, Fig. 5.4).

The vertical distribution of Chl *a* and the major groups of phytoplankton show the typical dominance of cyanobacteria during the stratified conditions of the

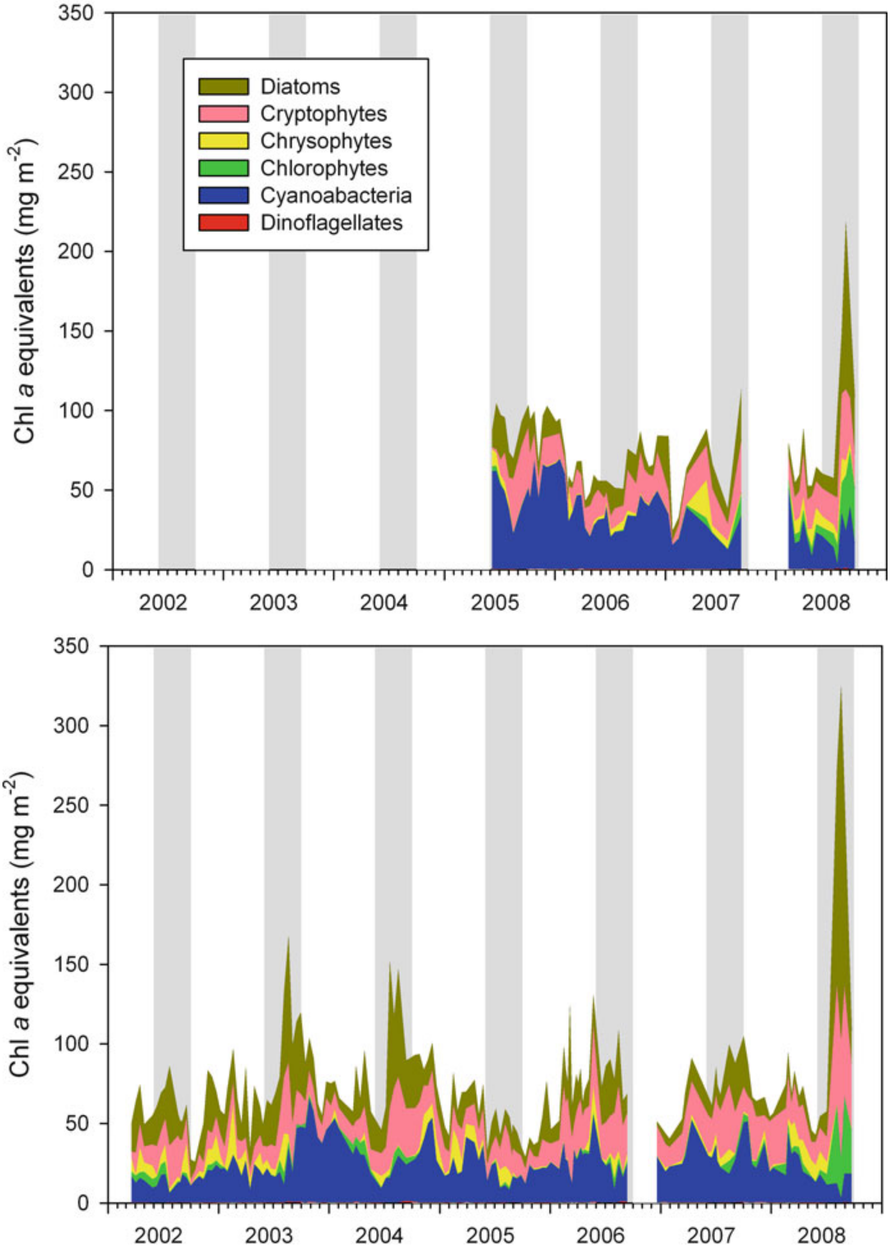

Fig. 5.3 Phytoplankton biomass (chlorophyll *a*, mg m^{-2}) and composition from pigment analysis in Lake Kivu integrated in the upper 70 m layer (2002–2008 period in Ishungu basin; 2005–2008 period in the main basin off Kibuye). Grey areas indicate the annual dry season (from June to September)

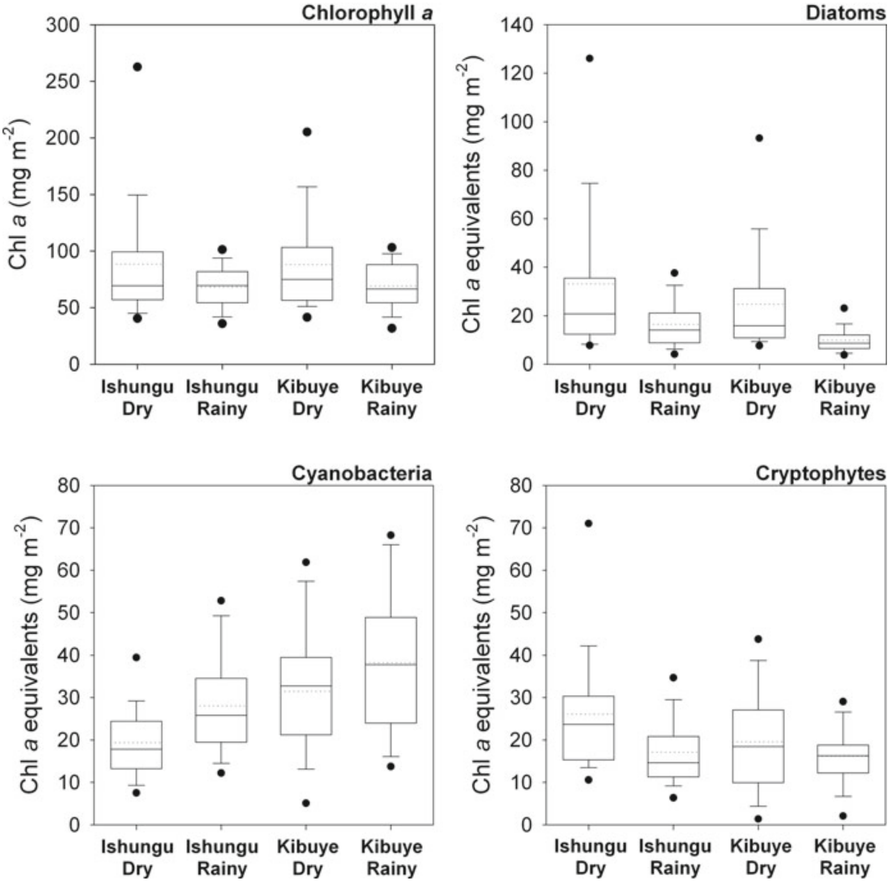

Fig. 5.4 Box plots of the total biomass (chlorophyll *a*, mg m^{-2}) and the major groups of phytoplankton in Lake Kivu. Data from two sampling stations (located in Ishungu basin and in the main basin off Kibuye) and two seasons (rainy vs. dry) are compared. The central full line indicates the median value, the middle dotted line indicates the arithmetic mean value, the box indicates the lower and upper quartiles, the error bars indicate the 10th and 90th percentiles, and the dots represent the 5th and 95th percentiles

Table 5.1 Statistical significance (*p* values of full factorial ANOVA tests with log-transformed data) of the comparison between basins (main vs. Ishungu) and seasons (rainy vs. dry) of the biomass (integrated values over the upper 70 m) of the main phytoplankton groups in Lake Kivu estimated from pigments

Effect	Chlorophyll *a*	Diatoms	Cyanobacteria	Cryptophytes
Basin	0.641	**0.003**	**<0.001**	**0.006**
Season	**0.002**	**<0.001**	**<0.001**	**0.008**
Basin × Season	0.796	0.192	0.321	0.082

Significant values at the 0.05 confidence level are highlighted

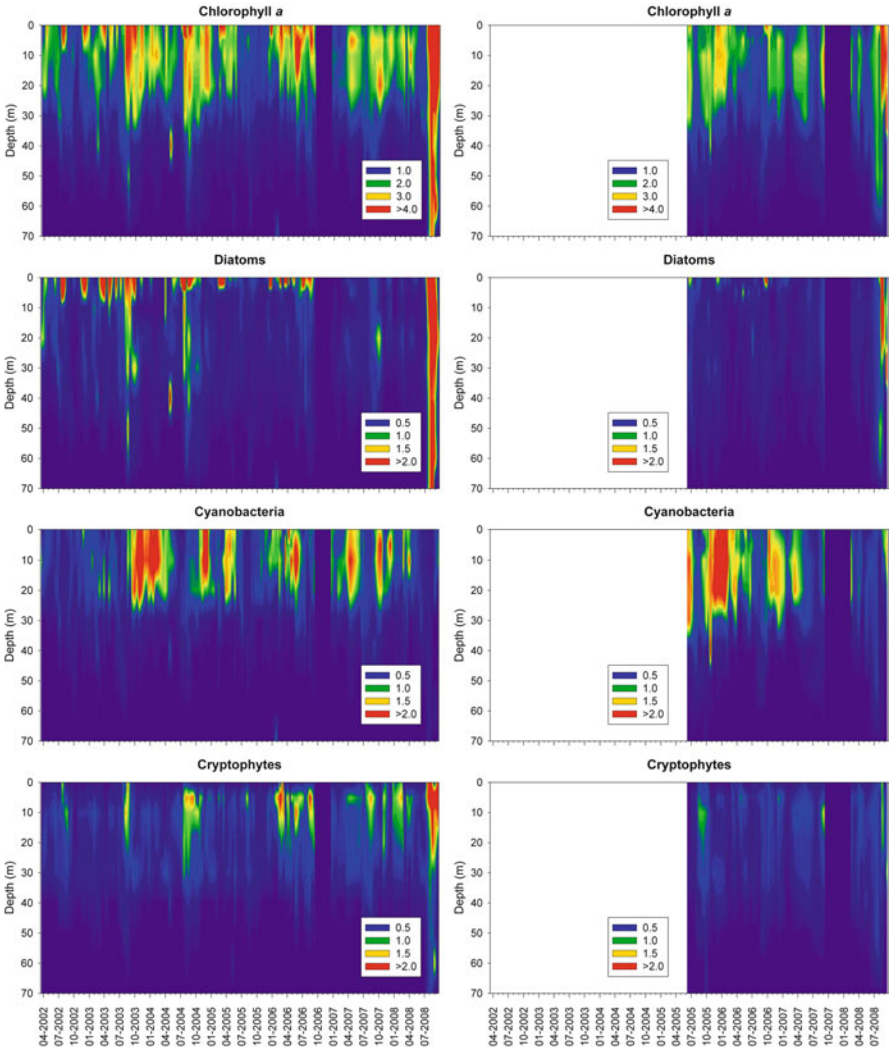

Fig. 5.5 Vertical distribution of the total biomass (chlorophyll *a* , mg m^{-3}) and the major groups of phytoplankton in Ishungu basin during the 2002–2008 period (left column) and the main basin off Kibuye during the 2005–2008 period (right column) in Lake Kivu. Clear areas correspond to missing data

rainy season on the top 20–30 m of the water column (Fig. 5.5). Regularly, during the dry season, lower air temperature (notably night cooling) induced deep mixing, which brought up additional nutrients into the euphotic layer, enhancing phytoplankton and especially diatom growth (Sarmento et al. 2006). The persistence and intensity of these seasonal mixing events may determine the productivity of the lake for the whole year, and most likely affect consumer production and ultimately fisheries yield.

The recent analysis of 96 field photosynthesis-irradiance incubations carried out over the 6 year survey allowed a completion of the planktonic primary production data set of Sarmento et al. (2009), and to design a model for prediction of phytoplankton photosynthesis parameters. The irradiance at the onset of light saturation (Ik) ranged between 91 and 752 $\mu E\ m^{-2}\ s^{-1}$ (mean, 318) and was linearly correlated with the mean irradiance in the mixed layer. The maximum photosynthetic rate (Pmax) ranged between 1.15 and 7.21 $gC\ g\ Chl\ a^{-1}\ h^{-1}$ (mean, 3.57). The mean observed daily primary production was equal to 0.62 $gC\ m^{-2}\ day^{-1}$ (range, 0.14–1.92), and annual primary production, calculated using modeled values of photosynthetic parameters, varied between 138 $g\ C\ m^{-2}\ year^{-1}$ in 2005 and 258 $g\ C\ m^{-2}\ year^{-1}$ in 2003. The mean annual primary production from 2002 to 2008 was 211 $g\ C\ m^{-2}\ year^{-1}$. These data clearly show that the inter-annual variation of phytoplankton production in Lake Kivu was important. This large range of variation and the few historic observations, 1.03–1.44 $gC\ m^{-2}\ day^{-1}$ by Degens et al. (1973), 0.66–1.03 $g\ C\ m^{-2}\ day^{-1}$ by Jannasch (1975) and 0.33 $g\ C\ m^{-2}\ day^{-1}$ by Descy (1990), preclude to detect any significant changes of planktonic primary production during the last 30 years.

A comparison of phytoplankton production data from East African Great Lakes (Table 5.2) shows that primary production in Lake Kivu is not greater than that in Lakes Tanganyika or Malawi, taking into account the differences in methodologies, as well as spatial heterogeneity as revealed by analysis of satellite images (Bergamino et al. 2010). This contrasts with expectations from Chl *a* concentration: mean Chl *a* in the euphotic zone of Lake Kivu (2.16 $mg\ m^{-3}$) is at least twice as high as in Lake Tanganyika – 1.07 $mg\ m^{-3}$ (2003) – and in Lake Malawi – 0.86 $mg\ m^{-3}$ (Guildford and Hecky 2000). This observation holds even when taking into account the great interannual variation, with a minimum mean annual Chl *a* of 1.59 $mg\ m^{-3}$ in the least productive year (2005) and a maximum of 2.94 $mg\ m^{-3}$ in the most productive year (2008).

5.5 Nutrient Limitation

The seston elemental ratios in the mixolimnion of Lake Kivu always remain well above the Redfield ratio and follow a clear seasonal pattern (Fig. 5.6). Significantly lower mean values of C:N, C:P and N:P ratios were observed during the dry season (arbitrarily defined as the period comprised between 1st of June and 30th of September) than during the rainy season ($p < 0.05$). Following elemental thresholds defined by Healey and Hendzel (1980) to estimate nutrient deficiency of phytoplankton in lakes (a C:N ratio between 8.3–14.6 indicates a moderate N-deficiency while a C:N ratio > 14.6 indicates an extreme N-deficiency; a C:P ratio between 129–258 or >258 indicates, respectively, a moderate or an extreme P-deficiency), the C:P ratios of seston in Lake Kivu indicated a moderate P-deficiency during the dry, mixing season and a severe P limitation during part of

Table 5.2 Chlorophyll *a* concentration (Chl *a*, average in the euphotic zone, standard deviation in parentheses) and mean annual phytoplankton production (PP) in the East African Great Lakes

	Chl *a* (mg m^{-3})	Chl *a* (mg m^{-2})	PP (g C m^{-2} $year^{-1}$)
L. Kivu (Ishungu basin)			
2002	1.78 (0.63)	59 (17)	223
2003	2.32 (0.78)	80 (30)	258
2004	2.54 (0.77)	86 (28)	241
2005	1.67 (0.63)	53 (15)	138
2006	2.58 (0.70)	79 (21)	223
2007	2.05 (0.44)	71 (18)	144
2008	2.95 (2.09)	112 (92)	252
Mean 2002–2008	2.24 (0.99)	75 (39)	211
L. Kivu (main basin)			
2005	2.11 (0.49)	91 (13)	
2006	1.94 (0.42)	63 (16)	
2007	2.03 (1.04)	65 (25)	
2008	2.10 (1.20)	88 (48)	
Mean 2005–2008	2.03 (0.78)	77 (32)	
L. Tanganyika (2002–2003)[a]			
Off Kigoma – 2002		23.4	123
Off Kigoma – 2003		25.0	130
Off Mpulungu – 2002		21.7	175
Off Mpulungu – 2003		29.9	205
L. Tanganyika (2003)[b]			
Whole-lake, from remote sensing	1.07	42.9	236
L. Malawi (1990s)[c]			
Pelagic (south)	0.86 (0.31)	34.4	169
L. Victoria (2001/2002)			
Lake-wide averages[d]			1061
Three inshore bays[e]	49.53	149.1	2333
Pilkington bay[f]	46.7		
Offshore (Bugaia)	24.5		

[a] Descy et al. (2005), Stenuite et al. (2007)
[b] Bergamino et al. (2010)
[c] Guildford et al. (2007)
[d] Silsbe (2004)
[e] Recalculated from Silsbe et al. (2006)
[f] Mugidde (1993)

the rainy, stratified season. The C:N ratios indicated however a moderate N limitation throughout the year, except at some dates during the dry, mixing season where no N-limitation occurred. A comparison of mean values (Table 5.3) from other East African large lakes suggests a stronger nutrient limitation in Lakes Kivu and Malawi than in Lakes Tanganyika and Victoria. The relatively high C:N and C:P ratios point to co-limitation of the phytoplankton community by N and P in Lake Kivu.

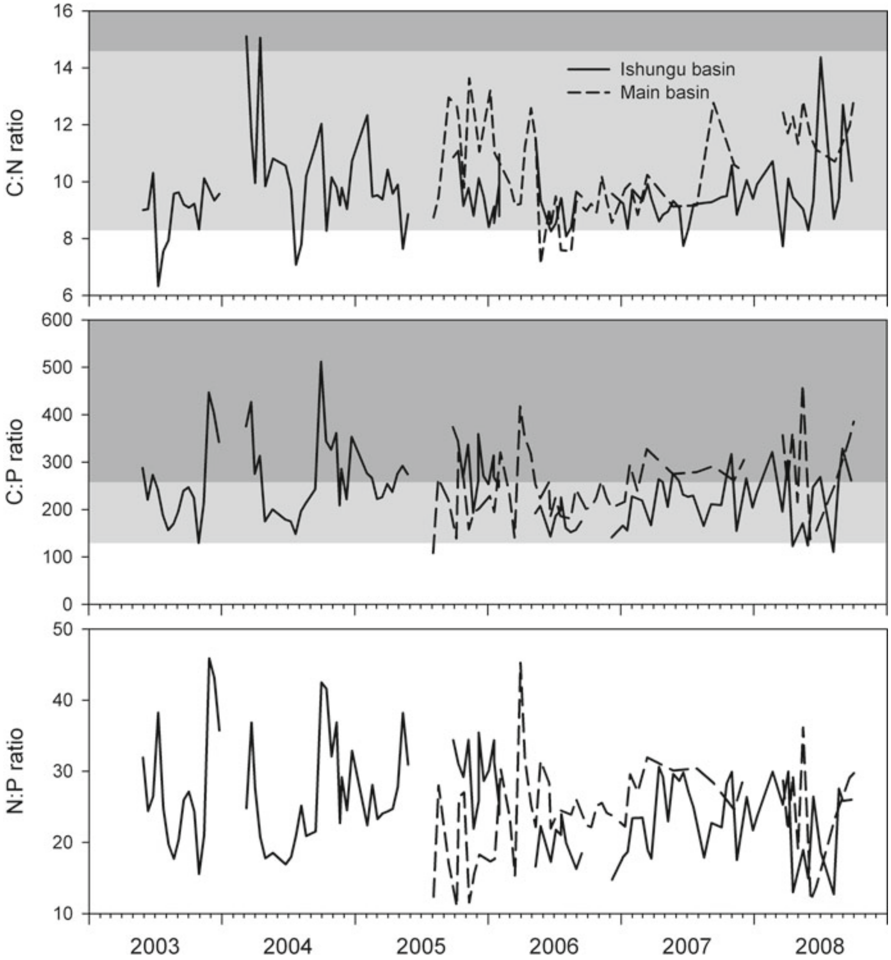

Fig. 5.6 C:N:P elemental ratios (atomic values) of epilimnetic seston in both the main basin and Ishungu basin of Lake Kivu from 2003 to 2008. The light and dark grey areas highlight values indicative of moderate and extreme nutrient limitation, respectively, following Healey and Hendzel (1980)

Table 5.3 C:N:P ratios (elemental values) and chlorophyll *a* (Chl *a*, mg m^{-3}) in the East African Great Lakes (average and standard deviation in the euphotic zone)

	C:P	C:N	N:P	Chl *a* (mg m^{-3})
L. Kivu (Ishungu basin)	243.8 (±73.6)	9.6 (±1.4)	25.4 (±6.8)	2.24 (±0.99)
L. Kivu (main basin)	251.4 (±75.1)	10.5 (±1.7)	24.3 (±6.7)	2.02 (±0.78)
L. Tanganyika[a]	170.8 (±43.3)	8.1 (±1.1)	21.2 (±5.3)	0.67 (±0.25)
L. Malawi[b]	244.3 (±154.4)	12.5 (±3.6)	19.4 (±8.8)	1.40 (±2.00)
L. Victoria[b]	148.5 (±76.4)	8.2 (±1.7)	18.3 (±7.6)	26.50 (±15.90)

[a] Stenuite et al. (2007)

[b] Guildford and Hecky (2000)

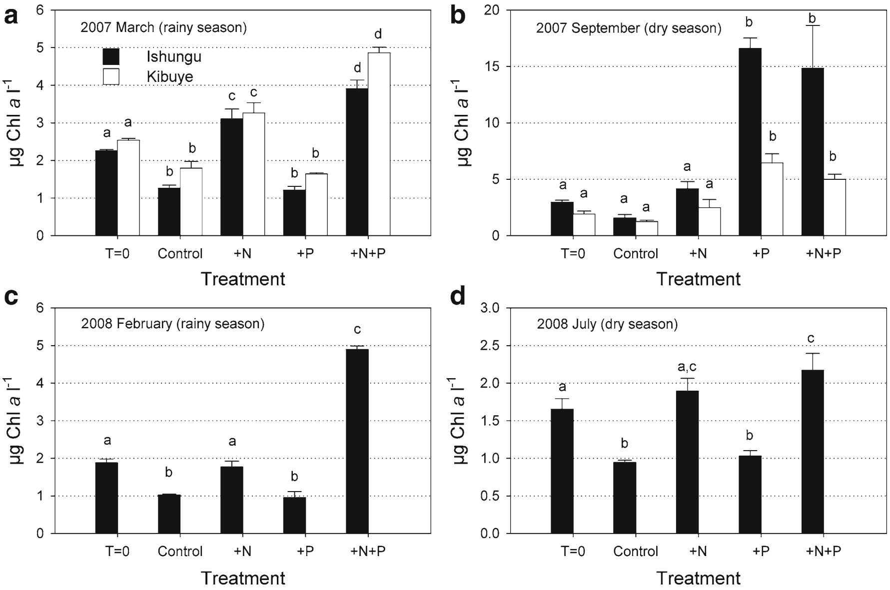

Fig. 5.7 Phytoplankton biomass (chlorophyll *a*, µg Chl *a* l^{-1}) after 4–5 days of incubation at lake temperature in six nutrient addition bioassay experiments carried out during rainy (**a** and **c**) and dry (**b** and **d**) seasons in Lake Kivu. The +N treatment received additional 15 µM NH_4Cl (final concentration), the +P treatment received 5 µM KH_2PO_4 (final concentration), while both N and P supplements were added in the +N+P treatment. All treatments were performed in triplicates. Note the different biomass scales. Identical small letters indicate treatments with no significant difference between biomass at the 0.05 confidence level (Scheffé test)

Nutrient addition assays carried out during rainy and dry seasons in 2007 and 2008 indicated a direct N-limitation and co-limitation by P during rainy seasons (Fig. 5.7a, c) and P or N limitation during dry seasons depending on the year (Fig. 5.7b, d).

5.6 Conclusions

Present Lake Kivu phytoplankton is dominated by diatoms, cyanobacteria and cryptophytes, with substantial seasonal shifts related to variations in depth of the mixed layer, driving contrasting light exposure, and nutrient availability. In this regard, phytoplankton ecology in Lake Kivu does not differ from that of other Rift lakes, where, despite constant irradiance and temperature of the tropical climate, seasonal variations occur and result in a trade-off between low light with high nutrient supply and high light with low nutrient supply. With regard to phytoplankton production, Lake Kivu is also similar to other Rift lakes, despite its greater mean Chl *a* concentration. Phytoplankton growth can be N or P limited, or co-limited by N and P.

Again, such limitations have been shown in Lakes Tanganyika and Malawi, even though the extent of P limitation seems greater in Lake Kivu, giving some indication of less nutrient recycling in the mixolimnion.

However, some features make Lake Kivu different from the other deep East African lakes: a closer look at the phytoplankton composition reveals a peculiar assemblage, with few chlorophytes, but long and slender *Nitzschia* and *Fragilaria* species, thin filamentous cyanobacteria (e.g., *Planktolyngbya limnetica*), picocyanobacteria, and several cryptophytes. In the surface waters, relatively large biomass of *Urosolenia* sp. can be detected at times, and colonies of *Microcystis* make vertical migration, sometimes becoming visible at the lake surface. Therefore, phytoplankton composition suggests affinities with more productive East African Lakes, such as Lakes Edward and Victoria, from a functional group perspective as discussed in Sarmento et al. (2006). As for the higher chlorophyll *a* concentration in Lake Kivu, it may have resulted from the Tanganyika sardine introduction, through a trophic cascade effect: indeed, metazooplankton abundance decreased by a factor of ~3 after the introduction of *Limnothrissa miodon* (see Chap. 7), likely resulting in a proportional decline of the grazing pressure on phytoplankton. This trophic cascade effect, as well as the interaction of phytoplankton with other organisms of the food web, is discussed in Chap. 11. Finally, a key feature of Lake Kivu is the dry season peak of diatoms and cryptophytes, which may determine the productivity for the whole year. However these peaks may vary by a factor of 2 between years, and this variation may determine the productivity of the lake for the whole year, most likely affecting consumer production and ultimately fisheries yield.

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Chapter 6
Microbial Ecology of Lake Kivu

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Abstract We review available data on archaea, bacteria and small eukaryotes in an attempt to provide a general picture of microbial diversity, abundances and microbe-driven processes in Lake Kivu surface and intermediate waters (ca. 0–100 m). The various water layers present contrasting physical and chemical properties and harbour very different microbial communities supported by the vertical redox structure. For instance, we found a clear vertical segregation of archaeal and bacterial assemblages between the oxic and the anoxic zone of the surface waters. The presence of specific bacterial (e.g. Green Sulfur Bacteria) and archaeal (e.g. ammonia-oxidising archaea) communities and the prevailing physico-chemical conditions point towards the redoxcline as the most active and metabolically diverse water layer. The archaeal assemblage in the surface and intermediate water column layers was mainly composed by the phylum *Crenarchaeota*, by the recently defined phylum *Thaumarchaeota* and by the phylum *Euryarchaeota*. In turn, the bacterial assemblage comprised mainly ubiquitous members of planktonic assemblages of freshwater environments (*Actinobacteria*, *Bacteroidetes* and *Betaproteobacteria*

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among others) and other less commonly retrieved phyla (e.g. *Chlorobi*, *Clostridium* and *Deltaproteobacteria*). The community of small eukaryotes (<5 μm) mainly comprised *Stramenopiles*, *Alveolata*, *Cryptophyta*, *Chytridiomycota*, *Kinetoplastea* and *Choanoflagellida*, by decreasing order of richness. The total prokaryotic abundance ranged between 0.5×10^6 and 2.0×10^6 cells mL^{-1}, with maxima located in the 0–20 m layer, while phycoerythrin-rich *Synechococcus*-like picocyanobacteria populations were comprised between 0.5×10^5 and 2.0×10^5 cells mL^{-1} in the same surface layer. Brown-coloured species of Green Sulfur Bacteria permanently developed at 11m depth in Kabuno Bay and sporadically in the anoxic waters of the lower mixolimnion of the main basin. The mean bacterial production was estimated to 336 mg C m^{-2} day^{-1}. First estimates of the re-assimilation by bacterioplankton of dissolved organic matter excreted by phytoplankton showed high values of dissolved primary production (ca. 50% of total production). The bacterial carbon demand can totally be fuelled by phytoplankton production. Overall, recent studies have revealed a high microbial diversity in Lake Kivu, and point towards a central role of microbes in the biogeochemical and ecological functioning of the surface layers, comprising the mixolimnion and the upper chemocline.

6.1 Introduction

Microbes include all organisms smaller than about 100 μm, which can be seen and/or analysed with a microscope (Kirchman 2008). These organisms include viruses, bacteria, archaea, and single-celled eukaryotes (protists). They are present in almost every environment on Earth spanning from the upper layers of the atmosphere to several kilometres below Earth's surface carrying out different types of metabolisms and consequently being involved in nearly all biogeochemical cycles (Kirchman 2008). According to their ubiquity, activity and large numbers, microbes are central players in nutrient cycling (Lindeman 1942; Cotner and Biddanda 2002).

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However, very few studies to date have addressed the diversity and function of microbes in large tropical lakes (Descy and Sarmento 2008). This under-sampling has prevented progress on topics such as microbial biogeography and comparative studies of lake microbial assemblages along latitudinal gradients or between temperate and tropical surface waters. The situation is similar when addressing the roles of microbes in ecosystem functioning and productivity in tropical lakes. Therefore, recently conducted research on the microorganisms of Lake Kivu is highly valuable and will be of use for future cross-system comparisons. The purpose of this chapter is to summarize the existing data on microbial assemblages in Lake Kivu and to provide a framework to interpret the microbial diversity present in this lake. We also discuss the implications of microbes in the major biogeochemical processes operating in the water column, and give currently available numbers of abundance and production.

The ecology of microorganisms from nanoplankton (i.e., with a median size from 2 to 20 μm) and microplankton (20–200 μm) is detailed in Chap. 5. In this chapter, we focus only on picoplankton, i.e. the planktonic organisms with a mean size <2 μm, and on single-celled eukaryotes smaller than 5 μm.

6.2 Lake Kivu and Potential Microbial Processes in Upper and Intermediate Water Layers

The vertical structure of the water column of Lake Kivu is peculiar and complex (more details on general physical and chemical characteristics are given in Chaps. 2, 3 and 4). In short, the surface waters alternate between deep mixing, down to ~65 m, during the dry season and a comparatively long stratification period during the rainy season. This surface layer, the mixolimnion, is separated from the deep waters, the monimolimnion, by a permanent chemocline located at ~65 m. Waters from the monimolimnion are always anoxic and rich in carbon dioxide, methane (CH_4), salts and nutrients (ammonium, NH_4^+, and phosphates) (Chaps. 3 and 10). By contrast, the surface waters are oxygenated and have very low nutrient concentrations. This illustrates the oxidation-reduction (redox) biogeochemical structure within the vertical profile, which sustains various microbial activities and communities.

Observations of the dynamics of the reduced forms of carbon (C), nitrogen (N) and sulfur (S) may help to identify the main microbial processes taking place in these upper layers of Lake Kivu water column. During the dry, windy season, the upper 60–65 m of the water column is well ventilated and mixed. This layer, called the mixolimnion, then contains oxygen with concentrations near the saturation, whereas deeper waters are anoxic and contain reduced forms of N (NH_4^+), C (CH_4) and S (hydrogen sulfide ion, HS^-) (Degens et al. 1973; Pasche et al. 2009). Most chemolithotrophic microbes typically grow at redox interfaces where anoxic water containing reduced substances come into contact with O_2 via water flow or molecular diffusion (Burgin et al. 2011). In Lake Kivu, O_2-driven CH_4 oxidation by aerobic methanotrophs is the major process reducing CH_4 concentrations in surface waters

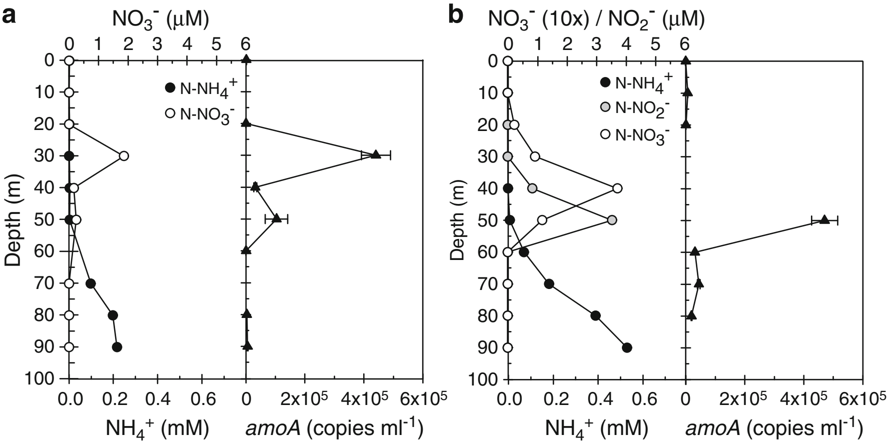

Fig. 6.1 Vertical depth profiles of nitrogen species (left panels) and archaeal ammonia monooxygenase subunit A (*amoA*) gene copy numbers (right panels) in the water column off Kibuye (**a**) and in the Ishungu basin (**b**) in March 2007 (Data extracted from Llirós et al. 2010)

(Pasche et al. 2011; Borges et al. 2011). Methanotrophy may also be performed anaerobically by archaea that oxidize CH_4 to obtain energy using sulfate (SO_4^{2-}) as the electron acceptor (Boetius et al. 2000; Orphan et al. 2001). In Lake Kivu, the inverse profiles of CH_4 and SO_4^{2-} in the intermediate zone from 60 to 90 m (Pasche et al. 2011) suggest the relevance of this process. Nevertheless, the sulfate flux budget indicates that only 3% of the CH_4 would be oxidized with SO_4^{2-} (Pasche et al. 2009, 2011). This estimate is a maximum because sulfate reducers can also use organic matter as an electron donor, pursuing anaerobically the heterotrophic decomposition of settling phytoplankton. The input fluxes of other potential electron acceptors for anaerobic CH_4 oxidation, i.e. nitrate, and oxidized iron and manganese ions, are too low in Lake Kivu to significantly oxidize CH_4 (Pasche et al. 2011).

Inputs of nutrients to surface waters by vertical mixing during the dry season favour phytoplankton growth (Chap. 5). The thermal stratification starts in October-November. An immediate decrease of oxygen concentrations is then observed in the lower mixolimnion (from ~25–30 m to ~65 m) due to the decay of settling organic matter combined to oxidation of reduced species (CH_4, HS^-, NH_4^+) diffusing from the anoxic layer. Therefore, during the major part of the rainy season, a gradient from oxic to anoxic conditions is present in the mixolimnion. The temperature in the lower depths of the mixolimnion is typically ~23°C throughout the year. The low solubility of oxygen coupled with intense microbial metabolic rates at these temperatures justify why these waters become very rapidly anoxic (Lewis 2010). During the second half of the rainy season (February to May), a nitrogenous zone characterized by the accumulation of nitrite (NO_2^-) and nitrate (NO_3^-) is often observed in the lower layer of the mixolimnion (Fig. 6.1). It results from nitrification of ammonium released by decaying organic matter (Wimba 2008; Llirós et al. 2010). Consequently nitrification may substantially contribute to oxygen depletion in the lower mixolimnion. Besides, denitrification and/or anammox might take place under anoxic conditions, with NO_3^-, NO_2^- and/or nitrous oxide (N_2O) diffusing from the nitrogenous zone and, for anammox, NH_4^+ diffusing from the monimolimnion. It is worth noting that the nutrient profiles in Lake Kivu resemble those from Lake Tanganyika, where a tight coupling of NH_4^+ liberation during denitrification-based mineralization and further NH_4^+ oxidation by anammox bacteria was demonstrated (Schubert et al. 2006).

In the intermediate 60–90 m zone, the upward (diffusing and advective) fluxes of HS^- are greater than the downward fluxes of SO_4^{2-} (Pasche et al. 2009). The inverse profiles of HS^- and SO_4^{2-} observed in this zone are mainly explained by O_2-driven sulfide oxidation. When the nitrogenous zone is present, SO_4^{2-} production might also be performed by microbes that use NO_3^- as electron acceptors (Burgin and Hamilton 2008). This microbial process has recently been observed in the chemocline of a permanently stratified temperate fjord (Jensen et al. 2009), along the West-African continental shelf (Lavik et al. 2009) and in the oxygen-minimum zone of the eastern tropical Pacific ocean (Canfield et al. 2010). Finally, we can also predict high rates of aerobic sulfide oxidation during mixing conditions, when anoxic waters enriched with sulfide are mixed with oxygenated waters from the surface. These events must be accompanied by substantial O_2 consumption.

From previous observations, several dissimilatory transformations of oxidation-reduction substances appear in the surface and intermediate water layers of Lake Kivu, leading to an original microbial energy economy (Burgin et al. 2011), which still should be clarified. Major and putative microbially driven biogeochemical processes are summarized in Table 6.1, with references to studies that have so far explored the microbial actors, processes and/or rates. At least two processes should further be explored as they potentially directly couple several elemental cycles in Lake Kivu: anaerobic CH_4 oxidation and NO_3^--driven SO_4^{2-} production.

6.3 Archaeal and Bacterial Assemblages

As the anoxic deep waters of Lake Kivu contain huge amounts of CH_4 (Schmitz and Kufferath 1955; Degens et al. 1973), early microbiology studies focused on microbes involved in the CH_4 cycle, reporting evidence of the presence and activity of CH_4-oxidizing bacteria (Deuser et al. 1973; Jannasch 1975; Schoell et al. 1988). Very recently, Pasche et al. (2011) studied the phylogenetic diversity of the microbial assemblage involved in the CH_4 cycle in Lake Kivu. They used sequences of the particulate CH_4 monooxygenase (*pmoA*) and methyl coenzyme M reductase (*mcrA*) functional genes as molecular markers for, respectively, aerobic methanotrophic bacteria and methanogenic or anaerobic methanotrophic archaea. All *pmoA* sequences were most closely related to *Methylococcus*. In turn, *mcrA* gene sequences were absent from surface samples but the retrieved clones from deeper samples belonged to three main clusters, related to the *Methanomicrobiales* and the archaeal anaerobic methanotrophic ANME-1 clade (Hallam et al. 2003).

Table 6.1 Synthesis of microbially mediated biogeochemical processes known or potentially present in the first 0–100 m water column of Lake Kivu with references to studies when available

Processes	Source of energy	Final electron acceptor	Involved elements	References	Main research
Known processes					
Oxygenic photosynthesis (algae and cyanobacteria)	Light[a]	$NADP^+$	C	Sarmento et al. (2006, 2007, 2008, 2009), Chap. 5	Biodiversity, C incorporation rates
Anoxygenic photosynthesis (Green Sulfur Bacteria)	Light[b]	$NADP^+$	C	This study	Abundance
Aerobic degradation of organic matter	Organic matter	O_2	C, N, P, S, etc	Pasche et al. (2010)	Sedimentation and settling rates
Aerobic CH_4 oxidation	CH_4	O_2	C	Jannasch (1975), Pasche et al. (2011)	CH_4 oxidation measurements, *pmoA* phylogenetic tree
Anaerobic CH_4 oxidation	CH_4	SO_4^{2-}	C, S	Llirós et al. (2010), Pasche et al. (2011)	*mcrA* and 16S rRNA phylogenetic tree
Nitrification	NH_4^+	O_2	N	Llirós et al. (2010)	*amoA* and 16S rRNA phylogenetic tree
Potential processes					
Anaerobic degradation of organic matter	Organic matter	SO_4^{2-}	C, S	Pasche et al. (2011)	Mineralization rates
Denitrification	Organic matter	NO_3^-, NO_2^-, N_2O	N	None	
Dissimilatory nitrate reduction to ammonium (DNRA)	CH_2O, H^+	NO_3^-, NO_2^-	C, N	None	
Anammox	NH_4^+	NO_2^-	N	None	
Sulfur oxidation	H_2S, S^0	O_2	S	None	
NO_3^--driven SO_4^{2-} production	H_2S, S^0	NO_3^-	N, S	None	

$NADP^+$ Nicotinamide adenine dinucleotide phosphate

[a] Uses H_2O as electron donor

[b] Uses H_2S as electron donor

Table 6.2 Relative abundances of bacteria and archaea quantified by CARD-FISH[a] in February 2007 in Lake Kivu. Data are expressed in percentages of total cells enumerated after DAPI staining (data from Llirós et al. 2010)

Basin	Depth (m)	*Bacteria* (%)	*Archaea* (%)
Goma/Gisenyi			
	10	94.8 ± 0.4	0.5 ± 0.1
	30	59.4 ± 9.4	2.5 ± 1.4
	40	87.6 ± 8.5	4.3 ± 2.0
	60	58.1 ± 2.7	0.3 ± 0.1
	85	46.2 ± 3.8	3.3 ± 1.8
Bukavu Bay			
	10	62.5 ± 6.4	0.6 ± 0.1
	30	93.5 ± 5.1	1.1 ± 0.5
	40	79.4 ± 2.9	4.6 ± 1.0
	50	93.2 ± 2.4	2.7 ± 0.4
	85	83.1 ± 8.9	2.5 ± 0.5

[a] CARD-FISH counts using specific probes (EUBI-II-III for *bacteria* and ARC915 for *archaea*)

The sharp oxycline and the oligotrophic nature of the lake's mixolimnion offer an optimal niche for the development of autotrophic nitrifying archaeal populations (Martens-Habbena et al. 2009). Llirós et al. (2010) reported the recovery in Lake Kivu of a large set of sequences affiliated to *Marine Crenarchaeota Group 1.1a* and assigned to a unique OTU (operational taxonomic unit) related to *Nitrosopumilus maritimus*, indicating the presence of active archaeal nitrifiers in the lake water column. Furthermore, the detection of archaeal ammonia monooxygenase subunit A (*amoA*) genes at the depths where maxima of nitrate and nitrite were observed in two basins of the lake (Fig. 6.1) points to the involvement of planktonic archaea in nitrification processes in the oxycline (Llirós et al. 2010). Although confirmation by *in situ* activity measurements is still needed, available data suggest an active contribution of ammonia-oxidizing archaea (AOA) in the N cycle of Lake Kivu.

During the rainy season of 2007, CARD-FISH (Catalyzed Reporter Deposition Fluorescence *in situ* Hybridization) analyses revealed a marked dominance of bacteria over archaea throughout the first 100 m of the water column with values ranging from 46% to 95% of total DAPI stained cells for bacteria and from 0.3% to 4.6% for archaea (Llirós et al. 2010, Table 6.2). The small contribution of archaea to the planktonic microbial community is a common trait for freshwater environments (Casamayor and Borrego 2009). In this regard, values below 10% of total prokaryotes have usually been reported for different freshwater lakes (Pernthaler et al. 1998; Jürgens et al. 2000; Llirós et al. 2011), although higher archaeal abundances have been reported (>20% of total cells) in some oligotrophic (Urbach et al. 2007; Auguet and Casamayor 2008) or oligomesotrophic (Callieri et al. 2009) freshwater lakes.

In spite of their general modest contribution to the microbial assemblage of lakes, archaea are microbes of interest due to their recently documented widespread distribution and contribution to global energy cycles (Schleper et al. 2005). In Lake Kivu, the

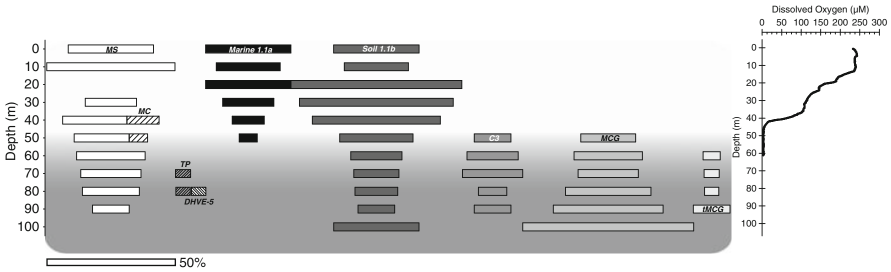

Fig. 6.2 Overview of the archaeal phylogenetic diversity of Lake Kivu water samples (extracted from Llirós et al. 2010). The width of the bar indicates, at each depth, the percentage of OTUs related to the indicated phylogenetic group. The oxygen gradient is plotted on the right. MS, *Methanosaeta*; MC, *Methanocella*; TP, *Thermoplasmata*; DHVE-5, Deep Hydrothermal Vent Euryarchaeota Group 5; Marine 1.1a, Marine Crenarchaeota Group 1.1a; Soil 1.1b, Soil Crenarchaeota Group 1.1b; C3, Crenarchaeota Group 1.2 or C3; MCG, Miscellaneous Crenarchaeotic Group or Crenarchaeota Group 1.3; tMCG, terrestrial Miscellaneous Crenarchaeotic Group

archaeal community in the surface and intermediate water column layers (ca. 0–100 m) during the rainy season 2007 was composed of phylotypes affiliated to the phylum *Crenarchaeota* (32% of the assigned OTUs), to the recently defined phylum *Thaumarchaeota* (43% of the assigned OTUs) and to the phylum *Euryarchaeota* (the remaining 25% of the assigned OTUs) (modified from Llirós et al. 2010). Within this latter phylum, most of the OTUs affiliated to methanogenic lineages, either acetoclastic (*Methanosaeta* spp.) or hydrogenotrophic ones (*Methanocellula* spp.), agreeing with the suggested biological origin of methane in the lake (Schoell et al. 1988; Pasche et al. 2011) and common methanogenic phylotypes present in stratified lakes (Lehours et al. 2007). Concerning *Thaumarchaeota* and *Crenarchaeota*, the phylotype richness showed a vertical structure of microbes related to the oxygen gradient. For the former, OTUs retrieved from the oxic water compartment mainly affiliated to *Marine Group 1.1a* (one single OTU with 95% sequence similarity to *N. maritimus*, a marine ammonia-oxidising archaea, Könneke et al. 2005) and to *Soil Group 1.1b* (some OTUs with high similarities to environmental sequences putatively involved in ammonia-oxidation, *e.g.* fosmid soil clone 54d9; Treusch et al. 2005), which are two lineages of the newly proposed phylum *Thaumarchaeota* containing all ammonia-oxidizing representatives known to date (Brochier-Armanet et al. 2008; Spang et al. 2010; Pester et al. 2011). All retrieved OTUs affiliated to the *Crenarchaeota* were retrieved from the anoxic water compartment with most of the sequences affiliated to lineages *Crenarchaeota Group 1.2* or C3 (DeLong and Pace 2001), the *Group 1.3* or *Miscellaneous Crenarchaeotic Group* (MCG, Inagaki et al. 2003) and the *terrestrial MCG* (tMCG, Takai et al. 2001), with yet unknown community role (Fig. 6.2).

In contrast with the studies of the archaeal assemblage, analyses on bacterial diversity are still scarce and the only available information comes from three recent studies (Libert 2010; Pasche et al. 2011; Schmitz 2011). Using denaturing gradient gel electrophoresis (DGGE) and 16S rRNA sequencing, Schmitz (2011) found a band distribution pattern coherent with the different water layers (Fig. 6.3, Table 6.3),

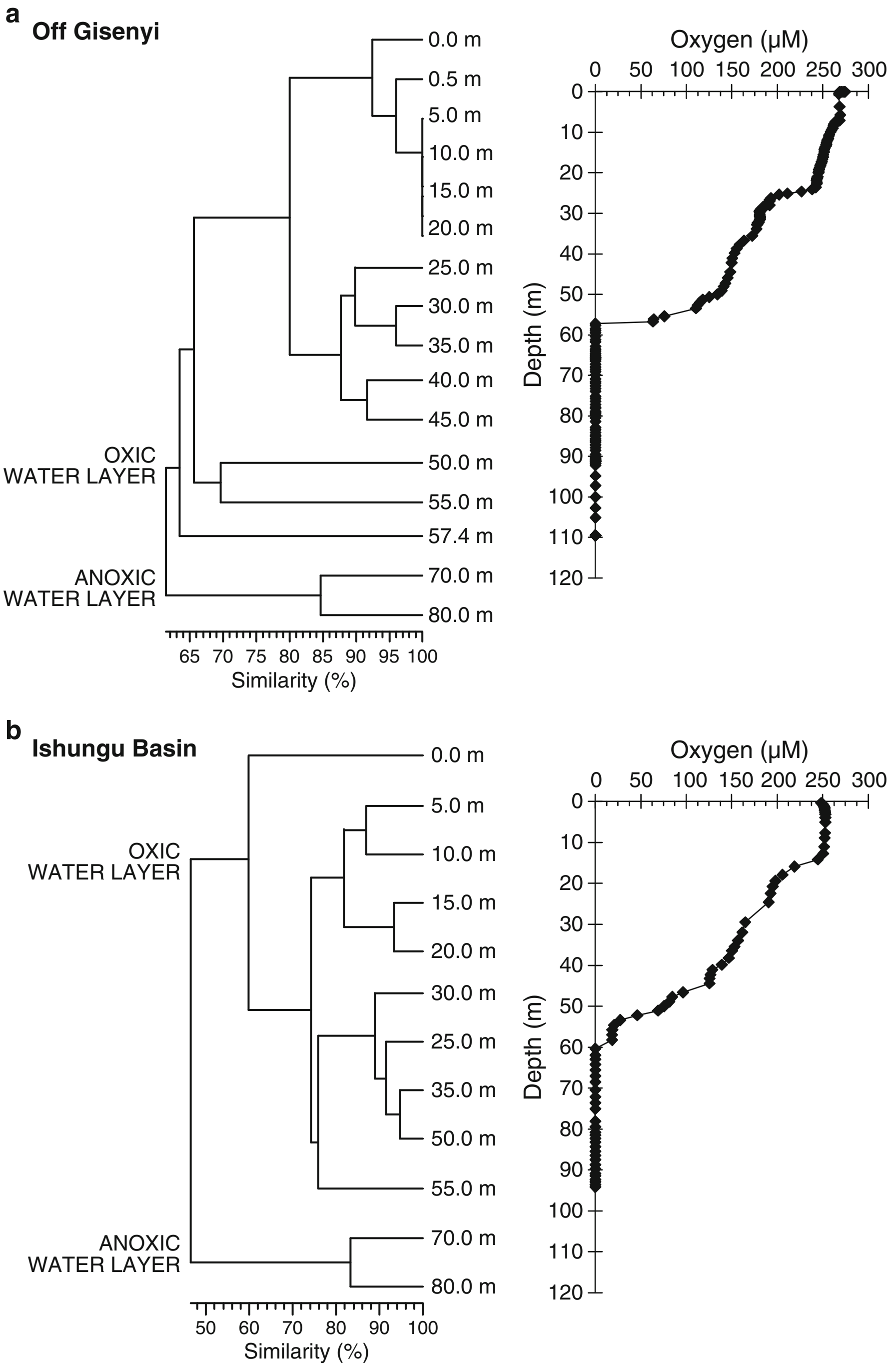

Fig. 6.3 Dendrograms based on Euclidean distances and unweighted pair-group method with arithmetic mean obtained from absence/presence matrices of bands extracted from bacterial 16S rRNA gene DGGE fingerprints from Lake Kivu water samples of October 2010 (rainy season) (from Schmitz 2011). Dissolved oxygen was measured during sampling

Table 6.3 Bacterial and archaeal operational taxonomic units (OTUs) retrieved after DGGE analysis of Lake Kivu water samples and general distribution across the different water layers (bacterial data from Schmitz 2011 and archaeal data from Llirós et al. 2010)

Phylogenetic group	Num.OTUs	Oxic layer[b] (0–30 m)	Oxic-anoxic transition	Anoxic layer (50–100 m)
Bacteria				
Actinobacteria	1	+	+	+
Bacteroidetes	3	+	+	–
Betaproteobacteria	2	+	+	+
Firmicutes/Clostridium	2	+	–	+
Nitrospira	1	+	+	–
Deltaproteobacteria	1	–	–	+
Mollicutes	1	–	–	+
Chlorobi	1	–	–	+
Archaea[a]				
Euryarchaeota				
Methanosaeta	4	+	+	+
Methanocella	1	–	+	–
Thermoplasmata	1	–	–	+
DHVE-5	1	–	–	+
Thaumarchaeota				
Marine 1.1a	1	+	+	–
Soil 1.1b	11	+	+	+
Crenarchaeota				
C3	2	–	+	+
MCG	6	–	+	+
tMCG	1	–	–	+

[a] *DHVE-5* Deep Hydrothermal Vent Euryarchaeota Group 5, *Marine 1.1a* Marine Crenarchaeota Group 1.1a, *Soil 1.1b* Soil Crenarchaeota Group 1.1b, *C3* Crenarchaeota Group 1.2 or C3, *MCG* Miscellaneous Crenarchaeotic Group or Crenarchaeota Group 1.3, *tMCG* Terrestrial Miscellaneous Crenarchaeotic Group

[b] +, presence; –, absence

as also evidenced for the archaeal assemblage (Llirós et al. 2010). Some phylogenetic groups were commonly retrieved over the whole water column, i.e. *Actinobacteria* and *Betaproteobacteria*, whereas some other groups were exclusively retrieved from the oxic water layer, i.e. *Bacteroidetes*, *Nitrospira* and one *Firmicutes/Clostridium* related sequence, or exclusively detected in anoxic waters, i.e. *Deltaproteobacteria*, *Mollicutes* and *Chlorobi*. Whereas most of the recovered bacterial phylotypes are ubiquitous members of planktonic communities of freshwater environments (*Actinobacteria*, *Bacteroidetes* and *Betaproteobacteria* among others), other phyla (e.g. *Chlorobi*, *Clostridium* and *Deltaproteobacteria*) have been less commonly retrieved in lakes (Newton et al. 2011). It is worth noting that no *Alphaproteobacteria* or *Verrucomicrobia* phylotypes were recovered despite the oligotrophic nature of the lake (Newton et al. 2011). Among the retrieved bacterial OTUs, it is important to notice the detection of *Nitrospira* and *Chlorobi* related sequences. The detection after DGGE band sequencing of one OTU related to *Nitrospira*, a nitrite-oxidizing bacterium, added putative new players to the N cycle in Lake Kivu. In turn, sequences affiliated to *Chlorobi* and mainly related to *Chlorobium limicola*, a Green Sulfur Bacterium (GSB), were recovered in the main basin from those depths where light reaches anoxic waters and reduced-sulfur compounds were present, but also where bacteriochlorophyll peaks were detected (see Sect. 6.4 below).

6.4 Prokaryotic Cell Abundances, Biomass and Production

To date, only few studies reported abundance and production of picoplankton in East African Great lakes (Pirlot et al. 2005; Sarmento et al. 2008; Stenuite et al. 2009a, b). Sarmento et al. (2008) reported the first data on bacterial abundances in Lake Kivu. Since then, complementary data have been collected covering bacterial abundances and biomass (Malherbe 2008; Nzavuga Izere 2008), heterotrophic bacteria production and bacterial carbon demand (Nzavuga Izere 2008), and finally extracellular release of organic matter by phytoplankton and bacterial re-assimilation (Morana 2009).

During these studies, abundances of prokaryotic cells were measured by flow cytometry. Typical cytograms from Lake Kivu mixolimnion exhibited two main heterotrophic bacteria subpopulations (Fig. 6.4): high nucleic-acid bacteria (HNA) and low nucleic-acid bacteria (LNA). These subpopulations are often present in various aquatic systems (see e.g. Bouvier et al. 2007). The general pattern that emerges from the literature is that HNA cells appear to be not only larger cells but also more active cells, with high specific metabolism and growth, and that changes in total bacterial abundance are often linked to changes in this fraction (Lebaron et al. 2001, but see Jochem et al. 2004; Bouvier et al. 2007 for other possible scenarios on this topic).

HNA were typically more abundant than LNA in the euphotic layer of Lake Kivu, whereas the proportion of LNA increased with depth. The total abundance of prokaryotic cells was between 0.5×10^6 and 2.0×10^6 cells mL^{-1}, with depth maxima located at the 0–20 m layer (Fig. 6.5). HNA abundance in the euphotic layer was positively correlated to chlorophyll *a* concentration, agreeing with a similar pattern reported by Sarmento et al. (2008).

Several subpopulations of heterotrophic bacteria, other than the HNA and LNA, were also observed in cytograms from anoxic waters. They presented different light side scatter and fluorescence (nucleic acid staining) than LNA and HNA subpopulations from surface waters (Fig. 6.4). Further investigations coupling cell sorting and molecular analyses (e.g. Zubkov et al. 2001; Schattenhofer et al. 2011) would be required to identify these microorganisms.

Photosynthetic picoplankton cells were also commonly observed using flow cytometry (Fig. 6.4). In surface samples, the abundance of phycoerythrin-rich picocyanobacteria, identified as *Synechococcus* spp. (Sarmento et al. 2007), ranged between 0.5×10^5 and 2.0×10^5 cells mL^{-1} (Sarmento et al. 2008) and were similar to those observed in Lake Tanganyika (Stenuite et al. 2009a). Vertical depth profiles

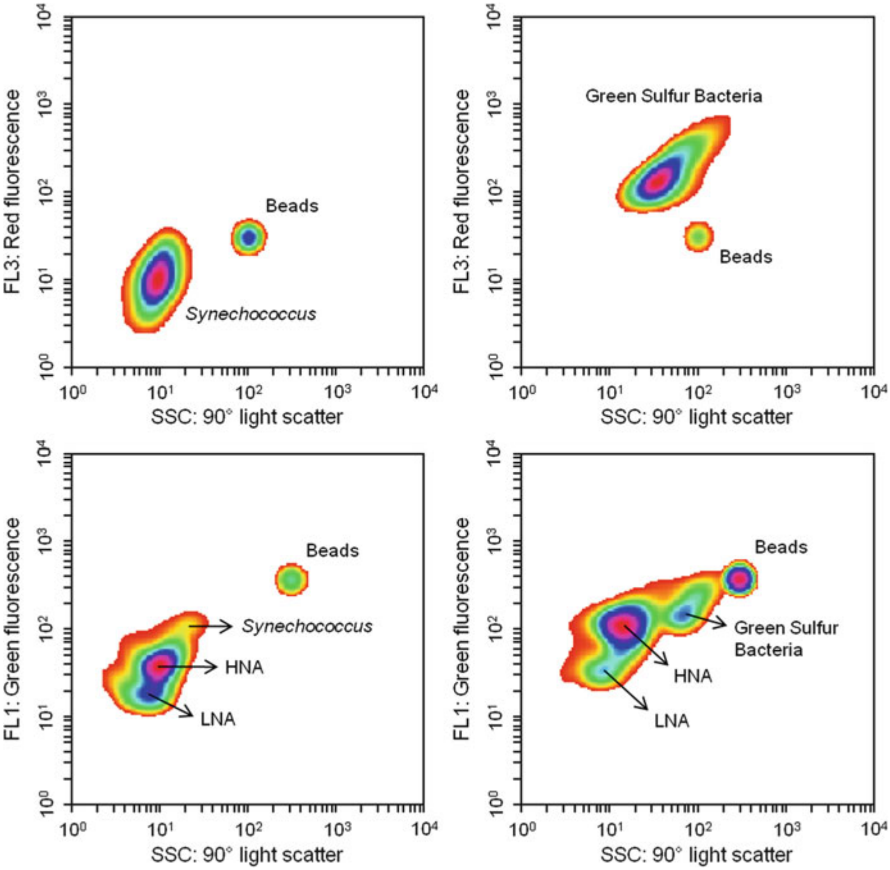

Fig. 6.4 Example of cytograms showing picoplankton cells with natural fluorescence (upper panels) and cells stained with a nucleic acid marker (bottom panels) from Lake Kivu surface waters (5 m depth, left panels) and anoxic waters of the mixolimnion (35 m depth, right panels). The red fluorescence (FL3) is produced by chlorophyll-containing cells. Green Sulfur Bacteria can be distinguished from *Synechococcus* cells because they present a higher red fluorescence signal per cell basis. The nucleic acid stain used (SYBRgreen) develops a green fluorescence (FL1). HNA: bacteria with high nucleic-acid content; LNA: bacteria with low nucleic-acid content

of picoplankton abundances revealed higher values in the euphotic zone than in the deeper mixolimnion, with a sharp decrease at around 30 m depth.

Using *in situ* fluorometry, a permanent chlorophyll peak was detected just below the oxycline (ca. 11 m depth) in Kabuno Bay (Fig. 6.6). A less important chlorophyll peak was also sporadically observed during the rainy season in the upper anoxic layer of the mixolimnion of the main basin (Fig. 6.6). High-performance liquid chromatography pigment analyses of samples collected at the chlorophyll peak allowed the identification of Bacteriochlorophyll *e* (BChl *e*) and isorenieratene, the representative biomarkers for brown-coloured taxa of GSB. No carotenoids from

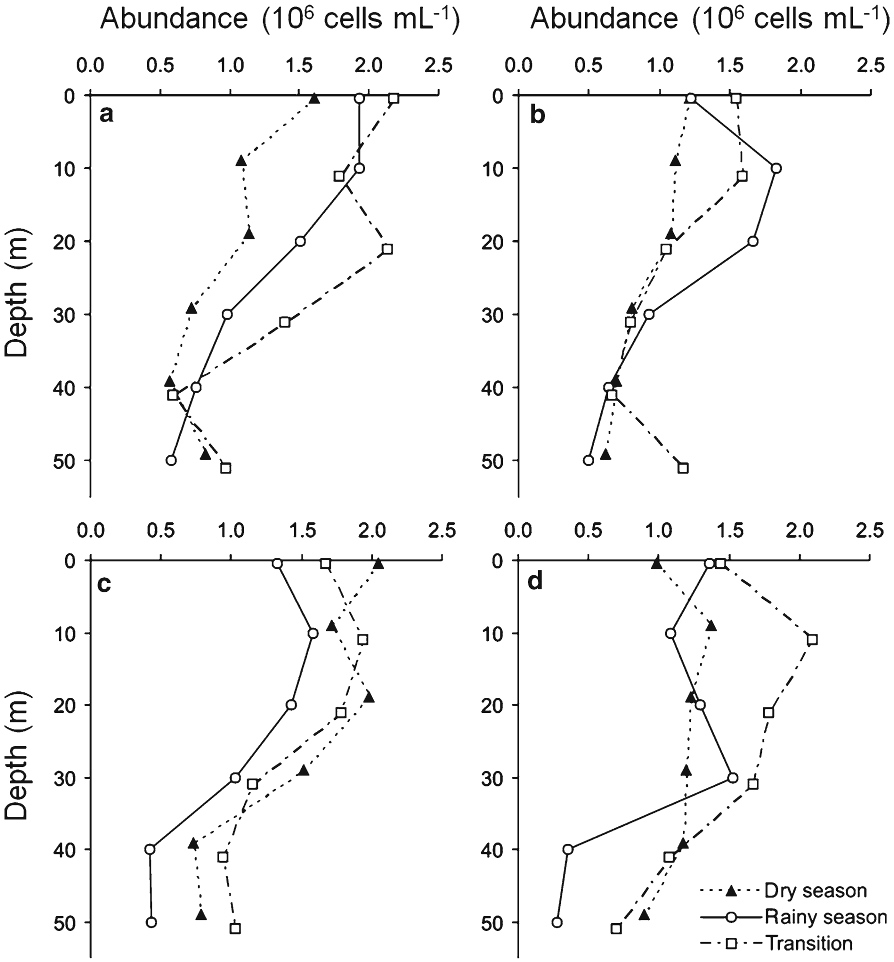

Fig. 6.5 Vertical depth profiles of total abundance of prokaryotic cells observed by flow cytometry, at different seasons, in the Ishungu basin (**a**), in the Kalehe basin (**b**), in the main basin off Kibuye (**c**) and in the main basin off Goma (**d**) of Lake Kivu (modified from Sarmento et al. 2008)

Purple Sulfur Bacteria were detected. These chlorophyll-containing microorganisms were also identified by flow cytometry (Fig. 6.4). GSB are obligatory anaerobic photoautotrophic bacteria, using H_2S, hydrogen or Fe^{2+} as an electron donor (Overmann 2006; Imhoff and Thiel 2010; Table 6.1). They are known to be adapted to extreme low-light conditions (Overmann et al. 1992), such as those prevailing in the lower mixolimnion of the main basin and in Kabuno Bay. In fact, the composition of the main farnesyl-esterified BChl *e* homologs from the population thriving in Lake Kivu suggests a severe *in situ* light limitation (Borrego and García-Gil 1995; Borrego et al. 1997) which deserves further investigation.

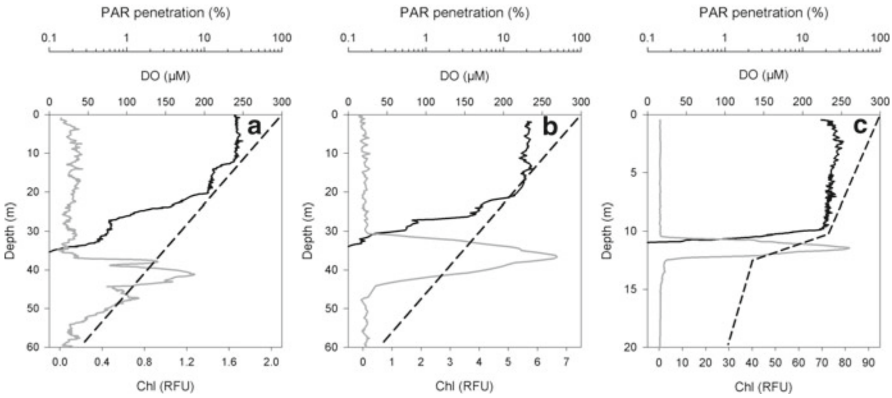

Fig. 6.6 Vertical depth profiles of dissolved oxygen (DO, µM, black line), *in situ* chlorophyll fluorescence (Chl, Relative Fluorescence Unit – RFU, grey line) and photosynthetically active radiation penetration (PAR, %, dashed line) in Lake Kivu, in the Ishungu Basin (**a**), off Gisenyi (**b**) and in Kabuno Bay (**c**) on May 2009

6.5 Bacterial Production and the Phytoplankton-Bacterioplankton Coupling

Several estimates of planktonic bacterial production (BP) were recently performed using ^{3}H-thymidine uptake (Fuhrman and Azam 1980) following the protocol and conversion factors of Stenuite et al. (2009b) described for Lake Tanganyika. Some results are shown in Fig. 6.7. In 2008, the mean BP in the mixed layer off Kibuye was 336 mg C m^{-2} day^{-1} and ranged between 34 and 902 mg C m^{-2} day^{-1} ($n = 10$, Nzavuga Izere 2008). This range was similar to that of Lake Tanganyika (Stenuite et al. 2009b). In Lake Kivu, BP was relatively low during the dry season, when the mixed layer was deep (Fig. 6.7d, e and f). The highest BP was observed at the beginning of the rainy season, when the mixolimnion started to re-stratify and when the mixed layer was shallow (Fig. 6.7g and h). This dynamics followed that of phytoplankton biomass (Nzavuga Izere 2008).

Considering a bacterial growth efficiency (BGE) of 0.3 (del Giorgio and Cole 1998), the mean bacterial carbon demand (BCD) is expected to be ca. 1120 mg C m^{-2} day^{-1}. The particulate phytoplankton production (PPP) in Lake Kivu is estimated to be around 500–600 mg C m^{-2} day^{-1} (Chap. 5) and is thus lower than the mean BCD. Nevertheless in planktonic systems a variable fraction of total phytoplankton production (TPP) is actually released and directly re-assimilated by bacteria (Baines and Pace 1991; Nagata 2000). This fraction, called the dissolved primary production (DPP), was not taken into account in the initial ^{14}C-incorporation experiments conducted in Lake Kivu and is therefore not accounted for in the PP estimation (Chap. 5). Consequently, additional experiments were conducted for evaluating the percentage of extracellular release (PER) of dissolved organic carbon

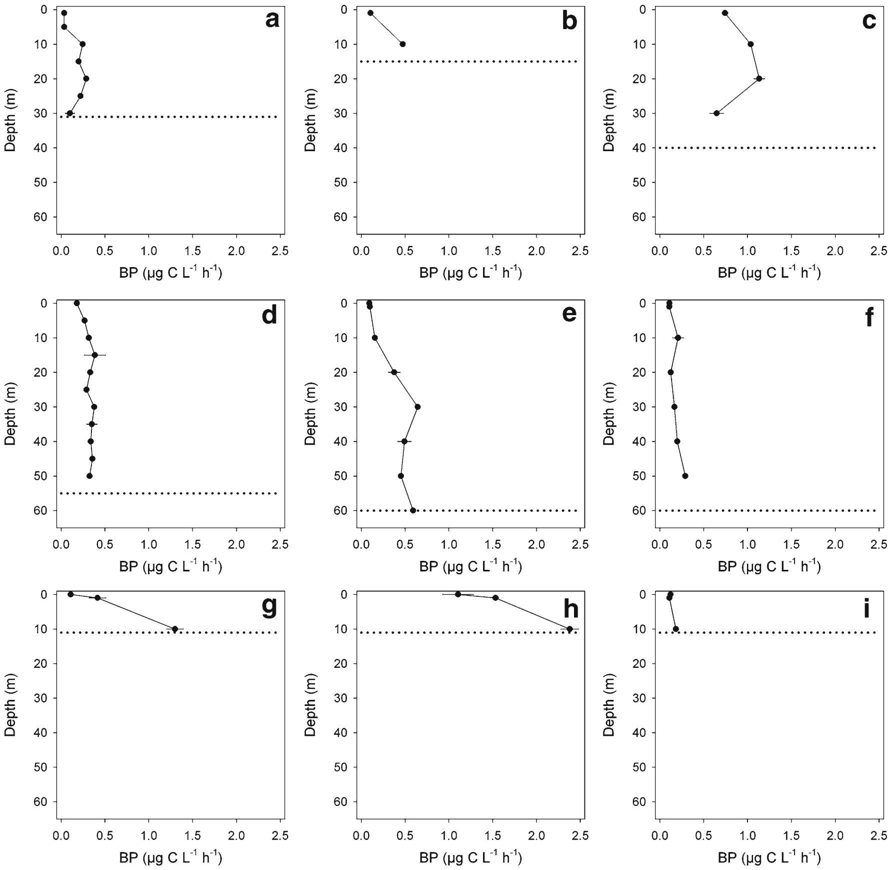

Fig. 6.7 Examples of vertical depth profiles of bacterial production (BP, µg C L^{-1} h^{-1}) off Kibuye in 2008 (**a**, February 14th; **b**, April 29th; **c**, June 3rd; **d**, July 11th; **e**, July 22th; **f**, August 5th; **g**, August 19th; **h**, September 2nd; **i**, September 18th). The dotted lines indicate the lower end of the mixed layer. (data from Nzavuga Izere 2008)

by phytoplankton, i.e. the contribution of DPP to TPP. These experiments, which used a protocol based on ^{14}C uptake kinetics (Morán et al. 2001), were conducted in the Ishungu basin, off Kibuye (main basin) and in Kabuno Bay in May 2009 (Morana 2009). PER was near 50% of total primary production, providing evidence that a substantial fraction of phytoplankton production was excreted. These estimates are in the upper end of the range of commonly observed values for other environments (Baines and Pace 1991; Nagata 2000) but consistent with the high temperature, irradiance and nutrient conditions of this tropical oligotrophic lake (Zlotnik and Dubinsky 1989; Myklestadt 2000; Hansell and Carlson 2002). So, the mean TPP (sum of PPP and DPP) is estimated around 1000–1200 mg C m^{-2} day^{-1} and is in good agreement with the observed BCD, allowing to envision a direct and important transfer of organic matter from phytoplankton to bacterioplankton in Lake Kivu.

6.6 The Assemblage of Small Eukaryotes

The protistan assemblage of Lake Kivu, with the exception of the photosynthetic organisms treated in Chap. 5, is poorly known. For instance, no reliable data on the abundance of phagotrophic protists have been collected so far, whereas a substantial contribution of these microorganisms to the pelagic food web could be envisaged (Tarbe et al. 2011). A recent biodiversity study of the small eukaryotes (0.2–5 μm size fraction) in the surface waters of Lake Kivu, using 18S rRNA fingerprinting, provided data for comparison of the small eukaryotes assemblage with that of Lake Tanganyika (Tarbe 2010).

Two clone libraries were constructed from two different epilimnetic water layers sampled during the rainy season of 2008 (Tarbe 2010). Clone sequences revealed that various phylogenetic groups composed the small eukaryote assemblage in Lake Kivu, including heterotrophs but also photosynthetic microorganisms. Overall, six classes dominated the diversity and represented 78.6% of the retrieved diversity (87.3% of the clones) in the two pooled samples: *Stramenopiles* (21.4%), *Alveolata* (21.4%), *Cryptophyta* (14.3%), *Chytridiomycota* (8.9%), *Kinetoplastea* (7.1%) and *Choanoflagellida* (5.4%). No clones affiliated to *Chlorophyta*, a group poorly developed in Lake Kivu (Chap. 5), were detected from the two Lake Kivu libraries. With closest cultured match rather distant from Lake Kivu sequences, except for some *Chrysophyceae* and *Ciliophora* sequences, the small-eukaryote diversity of Lake Kivu appeared to be poorly represented in culture collections. For instance, Lake Kivu *Kinetoplastea* and *Choanoflagellida* chiefly consisted of new sequences. Moreover, the small eukaryotes assemblage present in Lake Kivu was rather specific, since less than 11% of retrieved sequences were also retrieved in Lake Tanganyika (Tarbe 2010).

6.7 Synthesis and Perspectives

The current data on the microbial community structure in the water column of Lake Kivu are scarce and only based upon very few snapshot studies. Because of the extremely complex vertical structure of this system, which creates totally different ecological niches sometimes within a few centimetres, the microbial diversity is potentially high. High-throughput sequencing technologies will certainly provide a way to access this biodiversity in the near future.

A central role of microbes in the functioning of the Lake Kivu ecosystem can already be envisaged from the available data. The strong temporal coupling between phytoplankton biomass and bacterial abundance and the fact that bacterial carbon demand can be sustained by phytoplankton primary production suggest a preferential transfer of organic matter through the microbial food web in Lake Kivu (Descy and Sarmento 2008). The pivotal role of the microbial food web was recently demonstrated in Lake Tanganyika (Tarbe et al. 2011), where photosynthetic picoplankton dominated autotrophic biomass and production (Stenuite et al. 2009a, b). Picophytoplankton production and transfer to upper trophic levels should nevertheless be evaluated in Lake Kivu.

Microbial communities developing in the anoxic water compartment carry out different microbial processes from those functioning in the oxic water layers. The production of chemolithotrophs and anoxygenic photoautotrophs (GSB) should be evaluated and compared with the production of oxygenic photoautotrophs (Casamayor et al. 2008). The importance of methanotrophy as a source of energy and carbon for the pelagic food web of Lake Kivu should also be investigated (Jones and Grey 2011).

A promising field of future investigation remains the assessment of the relative role of bacterial and archaeal planktonic assemblages in some important biogeochemical processes, such as nitrification, denitrification and anaerobic methane oxidation. GSB, which are regularly found in the upper anoxic water layers of the lake, also deserve attention, not only as producers but also as sulfide detoxifiers. In this regard, the presence and activity of other bacterial groups involved in sulfur and sulfide oxidation (e.g. *Gamma*- and *Epsilonproteobacteria*, Glaubitz et al. 2009) in oxic/anoxic interfaces of stratified aquatic environments might constitute an interesting topic to be addressed to clarify the contribution of these communities to carbon fixation in sulfide-rich environments.

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Chapter 7
Zooplankton of Lake Kivu

François Darchambeau, Mwapu Isumbisho, and Jean-Pierre Descy

Abstract The dominant species of the crustacean plankton in Lake Kivu are the cyclopoid copepods *Thermocyclops consimilis* and *Mesocyclops aequatorialis* and the cladoceran *Diaphanosoma excisum*. Mean crustacean biomass over the period 2003–2004 was 0.99 g C m^{-2}. The seasonal dynamics closely followed variations of chlorophyll *a* concentration and responded well to the dry season phytoplankton peak. The mean annual crustacean production rate was 23 g C m^{-2} $year^{-1}$. The mean trophic transfer efficiency between phytoplankton and herbivorous zooplankton was equal to 6.8%, indicating a coupling between both trophic levels similar to that in other East African Great lakes. These observations suggest a predominant bottom-up control of plankton dynamics and biomass in Lake Kivu. Whereas the present biomass of crustacean plankton in Lake Kivu is comparable to that of other African Rift lakes, the zooplankton biomass before *Limnothrissa* introduction was 2.6 g C m^{-2}, based on estimation from available historical data. So, if the sardine introduction in the middle of the last century led to a threefold decrease of zooplankton biomass, it did not affect zooplankton production to a level which would lead to the collapse of the food web and of the fishery.

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7.1 Introduction

In all pelagic systems, metazooplankton is a key link between primary producers and consumers. In this regard, however, Lake Kivu was exceptional, as pelagic fishes were completely missing before the introduction of the “Tanganyika sardine”, *Limnothrissa miodon* (see Chap. 8). In fact, the introduction of the sardine was one of the largest biomanipulations ever, comparable to the introduction of the Nile perch in Lake Victoria. It is hardly surprising that the impact of the sardine introduction has attracted the attention of scientists, who stressed the highly detrimental effect of introducing an efficient predator of zooplankton in a system where there was no zooplanktivorous fish before.

Dumont (1986) described the sardine introduction as an ecological disaster, which caused the disappearance of a major grazer, the cladoceran *Daphnia curvirostris* Eylmann 1887, and a decrease in size and abundance of the remaining crustaceans. However, zooplankton records of Lake Kivu, on which Dumont’s conclusions were based, are somewhat contradictory. In the earliest records of cladocerans of the “Parc National Albert” (Brehm 1939), there is no mention of a *Daphnia* species in the zooplankton of Lake Kivu, but of two *Ceriodaphnia* species, of *Moina dubia*, of three *Alona* species, and of *Chydorus sphaericus*. From samples collected in 1953 by Verbeke (1957), *Daphnia pulex* is mentioned, along with *Moina dubia* and *Ceriodaphnia rigaudi*. But a later re-examination by Reyntjens (1982) of Verbeke’s samples conserved at the Institute of Natural Sciences in Brussels identified the *Daphnia* species as *D. curvirostris*. Monthly samplings in 1953 showed a peak of cladocerans in the dry season (July–August). In the subsequent literature (e.g. Lehman 1996), the crustacean community of Lake Kivu has been reported as comprising three species of cyclopoid copepods, no calanoid, and four species of cladocerans, with *Daphnia* missing. According to Dumont (1986), this large cladoceran vanished from Lake Kivu following the sardine introduction; on the other hand, such large *Daphnia* are so conspicuous that one may question whether it is possible that they were not observed in the samples from the Parc National Albert mission of 1936–1937 (Damas 1937; Brehm 1939). Dumont (1986) also noted an important decrease of copepod mean body size and zooplankton biomass since the introduction of *Limnothrissa* and predicted the collapse of the fishery.

In this chapter, we report the present taxonomic composition of Lake Kivu metazooplankton, its abundance, biomass and production, and how they are influenced by seasonality. Furthermore, we present some data about diel vertical migration of the most important species, and comment about spatial variations at the scale of the whole lake. Diversity and abundance results are from Isumbisho (2006), completed by subsequent new estimates of biomass and productions. We also reanalyze all available historical data in order to reassess the effects of *Limnothrissa* introduction on the zooplankton community.

7.2 Diversity of Lake Kivu Metazooplankton

The three common groups of freshwater metazooplankton are represented in Lake Kivu: copepods, cladocerans and rotifers. The copepod and cladoceran species found in the lake are common in the tropics or with worldwide distribution. By contrast, the presence of rotifers in the plankton of the pelagic zone is rather surprising, as they are totally absent from the pelagic waters of the other oligotrophic Rift lakes, Lake Malawi and Lake Tanganyika. Actually, rotifers are the most diverse metazooplankton group in Lake Kivu, with 12 taxa (among which Bdelloids, with unknown diversity).

7.2.1 Copepods

As in temperate waters, three suborders of copepods inhabit freshwater in the tropics: calanoids, cyclopoids and harpacticoids. The latter comprises exclusively meiobenthic species that are very rarely found in plankton samples (Alekseev 2002). Calanoids are exclusively planktonic and, while they are present in the other oligotrophic Rift lakes, they are absent from Lake Kivu. Therefore, cyclopoids are the sole copepods in the pelagic metazooplankton of Lake Kivu, with only three species: *Mesocyclops aequatorialis* Kiefer 1929, *Thermocyclops consimilis* Kiefer 1934 and *Tropocyclops confinis* (Kiefer 1930).

The genus *Mesocyclops* Sars 1914 occurs worldwide. It is successful in the tropics and subtropics and marginal in temperate and arctic regions (Van de Velde 1984) and is one of the largest genera of the family Cyclopidae. At present, it consists of about 66 species (Ueda and Reid 2003). Distinctive features of *M. aequatorialis* were described in several studies (e.g. Dussart 1967a, b, 1982; Kiefer 1978; Ueda and Reid 2003; Hołyńska et al. 2003) and even revised (e.g. Van de Velde 1984). The most easily recognizable traits during microscopic observations are the following:

- Body slender (Fig. 7.1a–c), female antennule 17-segmented reaching the third thoracic segment;
- Fifth pair of paws (P5) two-segmented, first segment bearing lateral seta, second segment with slender apical and spiniform medial setae, latter seta implanted about mid-length of segment (Fig. 7.1d–e);
- More easily visible is the shape of the furca (Fu): internal median furcal seta of about four times as long as Fu and externally oriented (Fig. 7.1a–c).

With an average body size of about 0.725 mm at adult stage, *M. aequatorialis* is the largest copepod species in Lake Kivu. It is also present in Lake Malawi (Irvine 1995), where it reaches a similar size. Actually it is a common species in the tropics.

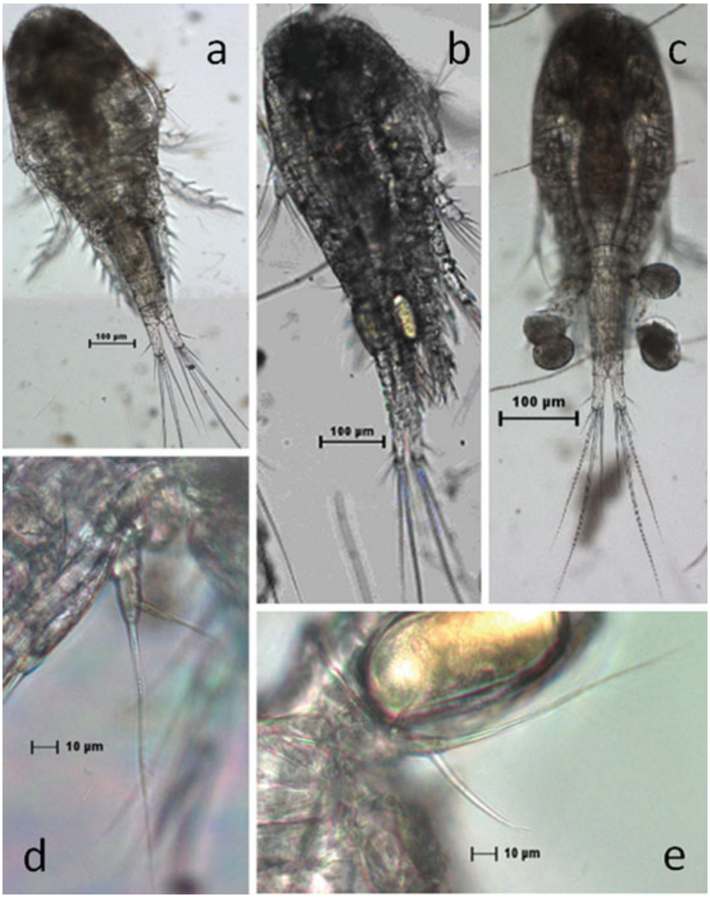

Fig. 7.1 *Mesocyclops aequatorialis*: Adult female without eggs (**a**), adult male (**b**), egg-bearing female (**c**), fifth paw of adult female (**d**) and male (**e**). The scale bars indicate 100 µm (**a**, **b**, **c**) and 10 µm (**d**, **e**), respectively

The genus *Thermocyclops* Kiefer 1929 is found all over the world and comprises about 50 species and subspecies. It differs from the genus *Mesocyclops* by several characteristics (Fig. 7.2a–c) but the most easily visible are the shape of:

- P5: terminal segment with internal spine and external seta both implanted ± apical in *Thermocyclops* (Fig. 7.2d) while implanted on a different level in *Mesocyclops*;
- Fu: internal median furcal seta of about two times as long as Fu and internally oriented (Fig. 7.2e).

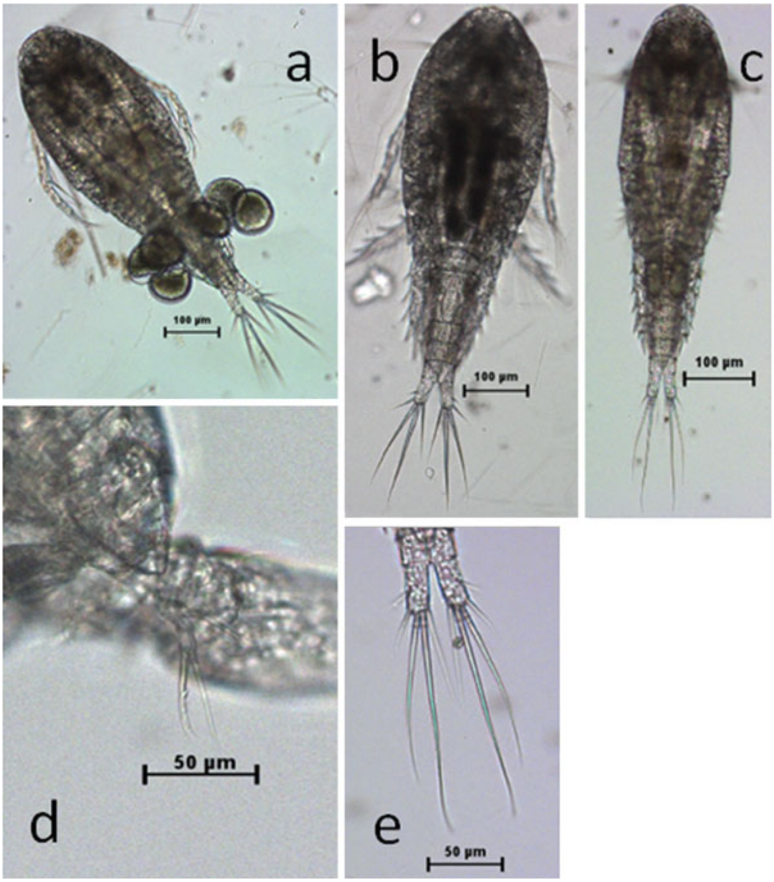

Fig. 7.2 *Thermocyclops consimilis*: egg-bearing female (**a**), female without eggs (**b**), adult male (**c**), fifth paw (**d**) and the furca (**e**). The scale bars indicate 100 μm (**a**, **b**, **c**) and 50 μm (**d**, **e**), respectively

In Lake Kivu, the genus is represented by *T. consimilis*, a very common species, with an adult average body size of 0.534 mm.

The genus *Tropocyclops* Kiefer 1927 comprises 15 species and 15 subspecies in the tropics (Alekseev 2002) but only *Tropocyclops confinis* occurs in Lake Kivu. It is easily distinguished from both *Thermocyclops* and *Mesocyclops* by:

- Its small size (Fig. 7.3a–b) which is on average 0.417 mm at adult stage;
- The shape of Fu with a very reduced internal furcal seta (Fig. 7.3c).

In addition, the antennules carried by adult females are 12-segmented.

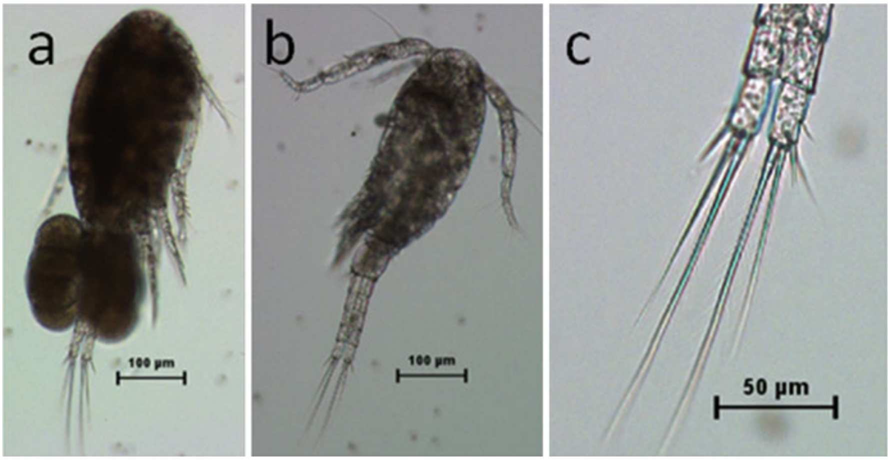

Fig. 7.3 *Tropocyclops confinis*: egg-bearing female (**a**), adult male (**b**) and the furca (**c**). The scale bars indicate 100 μm (**a**, **b**) and 50 μm (**c**), respectively

7.2.2 Cladocera

Cladocera are represented in Lake Kivu by four species belonging to four different families: *Diaphanosoma excisum* Sars 1885 (Sididae), *Moina micrura* Kurz 1875 (Moinidae), *Ceriodaphnia cornuta* Sars 1885 (Daphniidae) and *Coronatella (Alona) rectangula* (Sars 1861) (Chydoridae).

D. excisum (Fig. 7.4a) is one of the most common species of the genus in the tropics and subtropics. It is characterized by a large head, rectangular, with well-developed dorsal part, ventral fold of carapace and two spines near posterior carapace margin (Kořínek 2002). In Lake Kivu samples, it is easily recognized and distinguished from the other cladoceran species by its second biramous antenna with the exopodite presenting two articles. *D. excisum* is a common species in Lake Kivu with a small body size (0.488 mm), smaller than in Lake Malawi (Irvine 1995).

Normally littoral and benthic, *C. rectangula* (Fig. 7.4b) is present also in the pelagic zone of Lake Kivu. With a small body size (0.275 mm), it is recognized and easily distinguished from other cladocerans by the general shape of its body with a visible carapace with two valves.

C. cornuta (Fig. 7.4c) is very rare in Lake Kivu but easily recognized by its small rounded head with small pointed projection. The rostrum is also pointed. In addition, the tip of the caudal side of its carapace is characteristic.

M. micrura (Fig. 7.4d) seems rare in Lake Kivu. Like *D. excisum*, it is recognized by its biramous second antenna but with a four-segmented exopodite. Its average body size in the lake is 0.449 mm. According to Kořínek (2002), *M. micrura* is a species living in all types of water bodies, in pelagic as well as in littoral weedy areas. Originally described in Australia, this species is distributed in the tropics and subtropics of all continents.

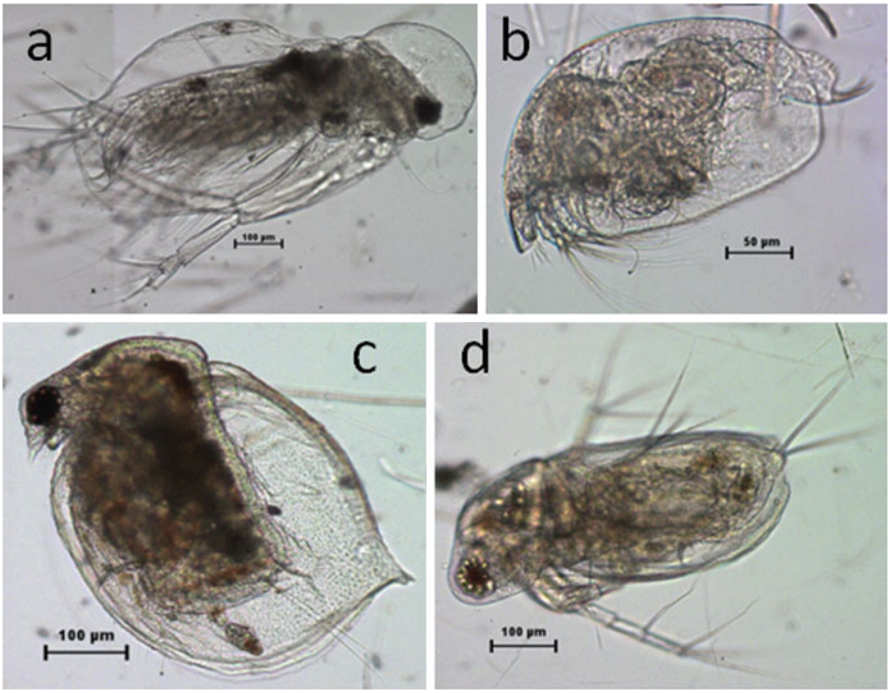

Fig. 7.4 Cladocerans of Lake Kivu: *Diaphanosoma excisum* (**a**), *Coronatella rectangula* (**b**), *Ceriodaphnia cornuta* (**c**) and *Moina micrura* (**d**). The scale bars indicate 100 µm (**a**, **c**, **d**) and 50 µm (**b**), respectively

7.2.3 Rotifera

Rotifera (Fig. 7.5) constitute the most diverse group of Lake Kivu pelagic metazooplankton, with 12 taxa: *Anuraeopsis fissa* Gosse 1851, *Brachionus calyciflorus* Pallas 1766, *Brachionus caudatus* Barrois and Daday 1894, *Brachionus falcatus* Zacharias 1898, *Brachionus quadridentatus* Hermann 1783, *Colurella* sp., *Keratella tropica* (Apstein 1907), *Lecane* sp., *Trichocerca* sp., *Polyarthra* sp., *Hexarthra* sp. and unidentified Bdelloids. Among these taxa, the most common are the Bdelloids, *K. tropica*, *Lecane* sp., *Brachionus* spp. and *A. fissa*.

7.3 Abundance, Biomass and Production

Zooplankton was sampled fortnightly in three subsequent years (2003–2005) in the mixolimnion of the Ishungu Basin (see Fig. 2.1), using a 75-cm diameter, 55-µm mesh closing net in three different strata (0–20, 20–40, 40–60 m). The abundance of

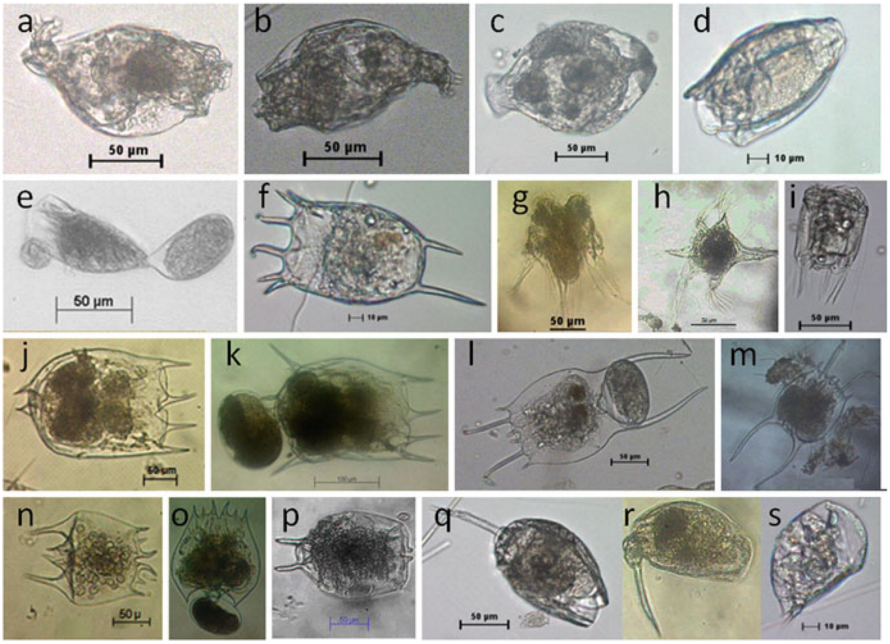

Fig. 7.5 Rotifers of Lake Kivu: Bdelloids (**a**–**c**), *Anuraeopsis fissa* (**d**–**e**), *Keratella tropica* (**f**), *Hexarthra* sp. (**g**–**h**), *Polyarthra* sp. (**i**), *Brachionus calyciflorus* (**j**–**k**), *Brachionus falcatus* (**l**–**m**), *Brachionus quadridentatus* (**n**–**o**), *Brachionus caudatus* (**p**), *Lecane* sp. (**q**–**r**), *Colurella* sp. (**s**). The scale bars indicate 100 µm (**k**), 50 µm (**a**, **b**, **c**, **e**, **g**, **h**, **i**, **j**, **l**, **n**, **p**, **q**) and 10 µm (**d**, **f**, **s**), respectively

rotifers and crustacean zooplankton was estimated under an inverted microscope. Rotifers, cladocerans and post-naupliar copepods were identified to species, separating copepodids from adults. Nauplii were grouped together. Comparative tests with the 55-µm plankton net and a 20-L Schindler trap mounted with a 37-µm plankton net showed that net hauls systematically underestimated abundance of copepodids and copepods at adult stage by a factor of 1.5, nauplii and rotifers by a factor of 3 and cladocerans by a factor of 1.2 for the 0–20-m layer, and by a factor of 5 and 7, respectively for copepodids and copepods at adult stage, and for nauplii, rotifers and cladocerans, for deeper strata (i.e., 20–40 and 40–60 m). This resulted from rapid net clogging. Consequently, abundance results for each species/stage were multiplied by the respective factor for the considered strata before adding results of each stratum for obtaining areal estimates of abundance.

From each sample, at least 50 individuals, unless rare, of each of the main crustacean species were measured using a calibrated eye-piece graticule. Copepod body length was measured from the top of the head to the base of the furci rami. Cladocerans were measured from the top of the head to the tip of the abdomen excluding spines and projections. Biomass was estimated using length-weight relations from Irvine and Waya (1999) for *D. excisum* and for copepodid and adult stages of *M. aequatorialis* and *Thermocyclops*, from Dumont et al. (1975) for

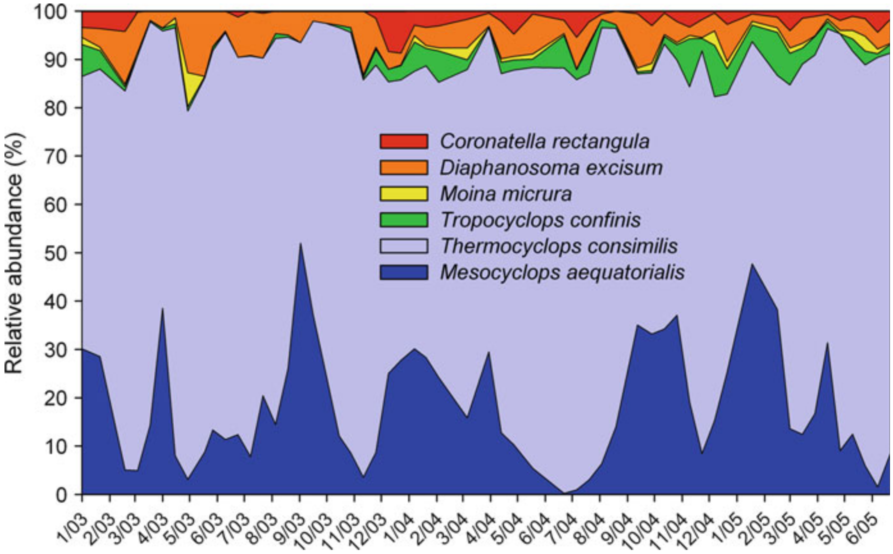

Fig. 7.6 Relative abundance of the six main crustacean species in the mixolimnion of Lake Kivu (Ishungu Basin) from January 2003 to June 2005

nauplii and the other cladoceran species, and using weight data from Sarvala et al. (1999) for *Tropocyclops*. Copepod production was estimated following Irvine and Waya (1999) for production of zooplankton in Lake Malawi. Briefly, we used the Growth Increment Summation Method or the mathematically similar Instantaneous Growth Method which takes into account the development rates of each distinct life-stage or group of life-stages (i.e. nauplii). The production rate of the cyclopoid copepods *M. aequatorialis* and *T. confinis* was calculated assuming linear growth rates within size-classes (Equation 3 in Irvine and Waya 1999) while an exponential growth rate was assumed for *T. consimilis* (Equation 4 in Irvine and Waya 1999). Partitioning of nauplii into the three cyclopoid species was done on the assumption that the proportion of nauplii approximated that of post-naupliar animals. Development times were obtained from Irvine and Waya (1999) for *M. aequatorialis* and from Mavuti (1994) for *Thermocyclops* and *Tropocyclops*.

Production of cladocerans, which generally constituted a low proportion of the zooplankton abundance, was estimated from published production/biomass ratio estimates (Amarasinghe et al. 2008). Production estimates of each crustacean species were calculated for each sampling date. Dry weight biomass and production were converted into C using a C:dry weight ratio of 0.5.

Numerically, copepods dominated other groups (Figs. 7.6 and 7.7), with >90% of crustacean numbers in the dry seasons. They were significantly less abundant in the rainy season, when cladocerans increased up to 20% of total crustacean abundance. Rotifers and cladocerans were always present in lower numbers than copepods with a mean abundance of, respectively for rotifers and cladocerans, 3.6×10^5 ind. m^{-2} and 2.5×10^5 ind. m^{-2} (Fig. 7.7c). Their respective abundance and dynamics were apparently not linked to seasonal events. Rotifers were dominated by Bdelloids,

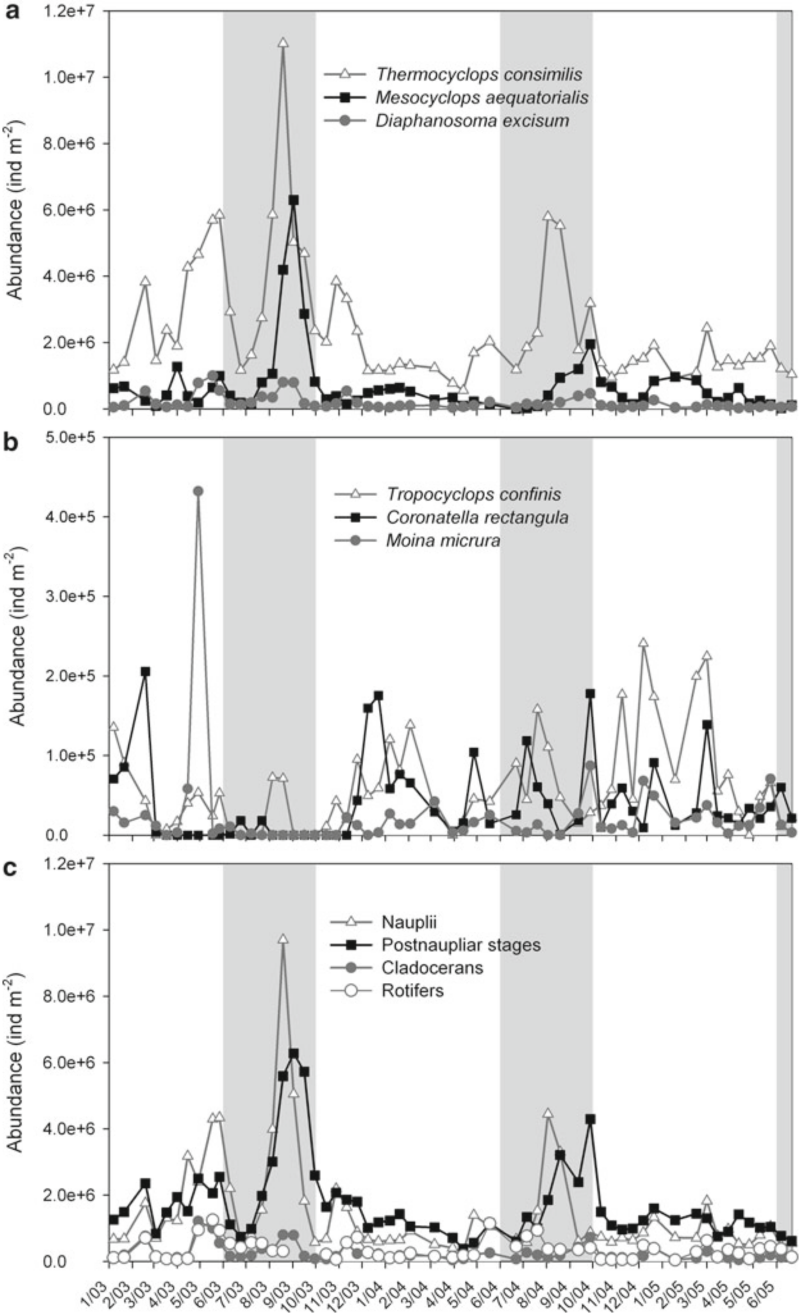

Fig. 7.7 Variation of metazooplankton abundance in the 0–60 m water column of Lake Kivu (Ishungu basin) from January 2003 to June 2005. Note the different scales on the Y-axis for **a**, **b** and **c**. The light grey boxes indicate the dry season periods

with an average of 76% of rotifer individuals, followed in decreasing order by *K. tropica*, *Lecane* sp., *B. calyciflorus*, *B. quadridentatus* and *Anuraeopsis fissa*. Owing to their low number and biomass, rotifers probably play a minor role in the Lake Kivu food web.

The dominant crustacean species were *T. consimilis*, *M. aequatorialis* and *D. excisum*. Total zooplankton abundance may reach 12 × 10^6 individuals m^{-2}, with conspicuous maxima occurring in the second half of the dry season, around August–September. Contrasting dynamics occurred among species (Fig. 7.7), but the three main taxa showed well-correlated maxima during the dry season (Fig. 7.7a). Nauplii and post-naupliar stages followed the same dynamics, with distinct peaks in the late dry season (Fig. 7.7c). *C. rectangula*, *T. confinis* and *M. micrura* showed a distinct pattern, with higher abundances during the rainy season.

Interannual variability was high, with lower zooplankton numbers but higher diversity in 2004 than in 2003. Seasonal sampling in different lake basins did not show large contrast among lake regions, suggesting homogeneity of zooplankton distribution throughout the lake (Isumbisho et al. 2006).

Crustacean biomass closely followed the abundance pattern. Although maximal metazooplankton biomass could reach up to 3.8 gC m^{-2}, mean biomass over the period 2003–2004 was 0.99 gC m^{-2}. For the whole sampling period (2003–2005), *T. consimilis* contributed about 61% to crustacean biomass, while *M. aequatorialis* and cladocerans accounted for, respectively, 27% and 11% of annual crustacean biomass. Total crustacean biomass was about 14% of phytoplankton biomass (assuming a mass C:chlorophyll *a* ratio of 92.8, according to Isumbisho et al. 2006), and closely followed variations of chlorophyll *a* concentration (Fig. 7.8).

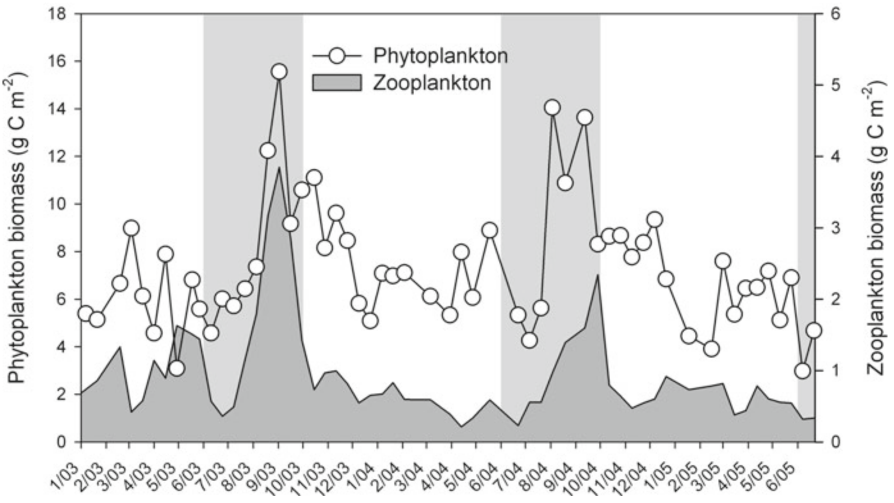

Fig. 7.8 Biomass of phytoplankton and zooplankton integrated in the mixolimnion (0–60 m) from January 2003 to June 2005 in Lake Kivu. Phytoplankton biomass data are from Sarmento et al. (Chap. 5) and converted into C using a C:chlorophyll *a* ratio of 92.8. The light grey boxes indicate the dry season periods

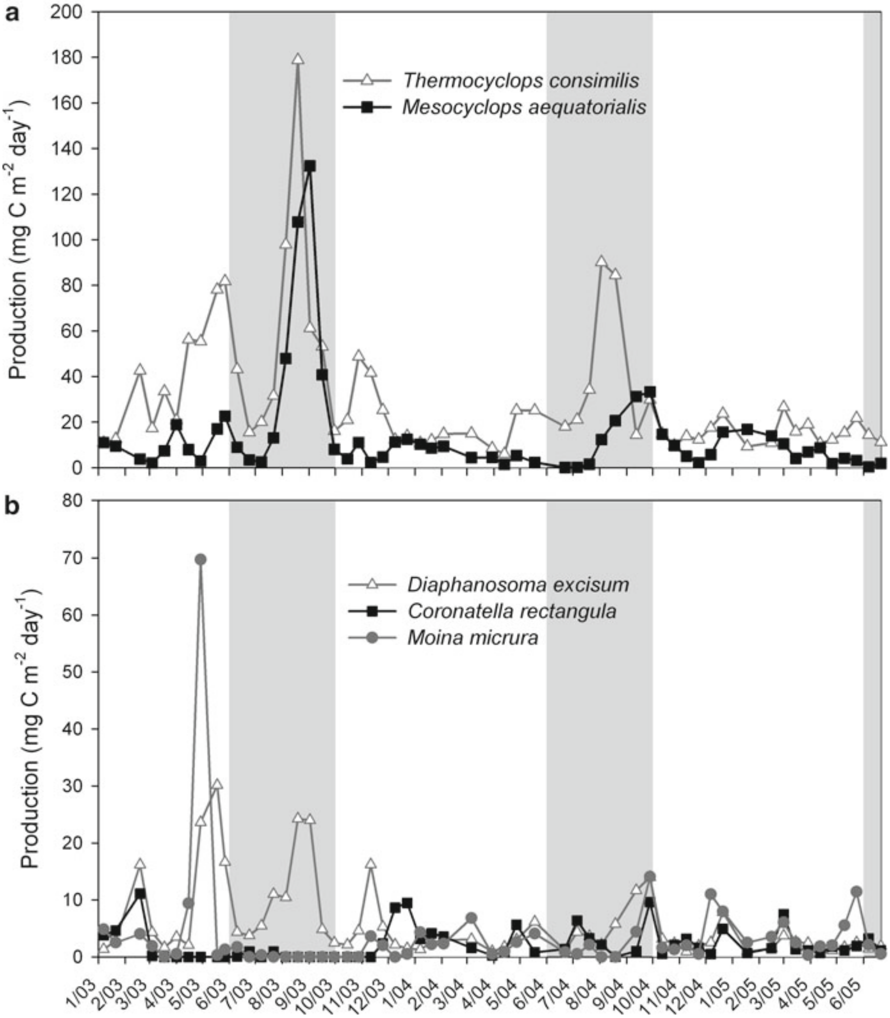

Fig. 7.9 Copepod (**a**) and cladoceran (**b**) production of the main crustacean species from January 2003 to June 2005 in Lake Kivu (Ishungu Basin). The light grey boxes indicate the dry season periods

Estimates of production for the five main crustacean species are presented in Fig. 7.9. Copepods accounted on average for 77% of the total crustacean production, with contributions > 95% during dry season blooms. *T. consimilis* was the most productive species (on average, 55% of the total crustacean production), followed by *M. aequatorialis* (22%) and *D. excisum* (10%). Maximum total copepod production occurred at the end of the dry season, in August 2003 (~311 mg C m^{-2} day^{-1}) and August 2004 (~111 mg C m^{-2} day^{-1}), and was generally much lower in the rainy season. Annual crustacean production rates estimated for the 2 years were 29 g C m^{-2} year^{-1} in 2003 and 16 g C m^{-2} year^{-1} in 2004.

Table 7.1 Total and herbivorous plankton crustacean biomass, production, production:biomass (P:B) ratio and trophic transfer efficiency between phytoplankton and herbivorous zooplankton in the East African Rift large lakes

	Total crustacean zooplankton			Herbivorous crustacean zooplankton			
Lake	Mean annual biomass (g C m^{-2})	Mean annual production (g C m^{-2} year^{-1})	Mean P:B (year^{-1})	Mean annual biomass (g C m^{-2})	Mean annual production (g C m^{-2} year^{-1})	Mean P:B (year^{-1})	Trophic transfer efficiency
Tanganyika[a]	1.00	25.2	25	0.81	23.0	29	3.5–5.4%
Malawi[b]	0.80	29.1	36	0.70	26.4	38	5–8%
Kivu[c]	0.99	22.5	22	0.68	17.0	25	8.3% in 2003 5.2% in 2004

Data from [a]Sarvala et al. (1999), [b]Irvine and Waya (1999), [c]This study

Considering all crustacean species as herbivorous except *M. aequatorialis*, which is raptorial preying mainly on young *T. consimilis*, and based upon a mean annual primary production of 258 and 241 g C m^{-2} $year^{-1}$, respectively, in 2003 and 2004 (Chap. 5), the estimated trophic transfer efficiency between primary producers and herbivorous zooplankton was 8.3% and 5.2%, respectively, in 2003 and 2004 (Table 7.1). These values are in good correspondence with the ones calculated for Lakes Tanganyika and Malawi (Table 7.1). Moreover they are in the middle range of energy transfer efficiencies reported by Pauly and Christensen (1995) for 48 aquatic communities; they indicate a tight coupling between both trophic levels.

7.4 Effects of *Limnothrissa* on Zooplankton Biomass and Body Size

Numerous studies in the limnological literature have documented the effects of a planktivore introduction on lacustrine metazooplankton (e.g. Gliwicz 1985): typical consequences are a shift in zooplankton body size and a decrease of total biomass, as a result of increased predation pressure. Large cladocerans, in particular, are under increased risk of extinction, since they are more visible for a predator than copepods.

The most ancient historical data on zooplankton biomass in Lake Kivu were given by Verbeke (1957) who indicated monthly biovolumes during 1952–1953. For comparison with recent data, Verbeke's biovolumes can be converted to biomass using a density of 1 g fresh weight cm^{-3}, a water percentage of 83% and a C:dry mass ratio of 0.5. Results are presented in Fig. 7.10. The mean yearly calculated biomass was 2.6 g C m^{-2} which is close to the biomass (3.8 g C m^{-2}) calculated from abundance counting and body size measurements of Verbeke's samples made by Reyntjens (1982, in Dumont 1986). Based on three samples collected in July–September 1981 by Reyntjens (1982) and one sample in April 1983, Dumont (1986) observed an important decrease of crustacean biomass, in parallel with the disappearance of the main historical grazer, *D. curvirostris*, and concluded that this dramatic decline would lead to future collapse of the sardine fishery. The more comprehensive survey made by Isumbisho et al. (2006) allows us to calculate in this study a mean annual biomass of 0.99 g C m^{-2}. While we might not exclude a recovery of the zooplankton community during the last two decades, it appears that the predicted collapse may have been overstated (Fig. 7.10). We estimate that the zooplankton biomass decreased by a factor of 3 after the *Limnothrissa* introduction, reaching at present a level comparable to other great lakes of the East African Rift (Table 7.1).

Effects of *Limnothrissa* on zooplankton may also be investigated from historical data on body size of main zooplankton species. To assess a possible impact of predation by the introduced sardine, the body size of the three dominant zooplankton species was examined. *M. aequatorialis* is the largest zooplankton species in Lake Kivu.

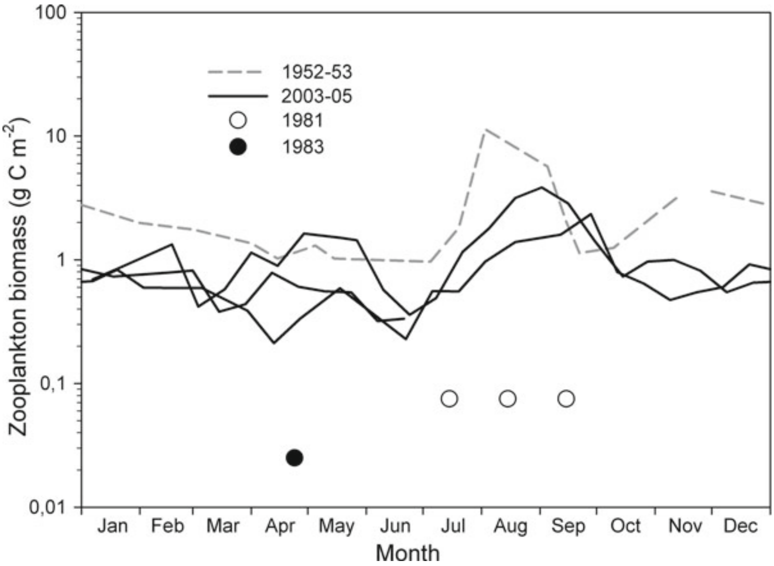

Fig. 7.10 Estimates of zooplankton biomass in Lake Kivu: 1952–1953 data from Verbeke (1957), 1981 data from Reyntjens (1982), 1983 data from Dumont (1986) and 2003–2005 data from the present study. Note the logarithmic Y-scale. See explanations on the calculations in the text

Its adult size was on average 0.725±0.082 mm (mean±SD; range 0.54–1.0 mm) throughout 2003 and 0.740±0.09 mm (range 0.51–1.1 mm) in May–June 1990 (Fourniret 1992). The data available from earlier publications are less precise: Dumont (1986) cited an average body length of 0.54 mm and a range of 0.24–0.71 mm, all three copepods species and all stages considered. Dumont (1986) gave a range from Verbeke's samples (Verbeke 1957) of 0.23–1.05 mm in 1953, again for all copepod species and all stages, and Damas (1937) gave a range of 0.9–1.05 mm for adult *M. aequatorialis*. Given the heterogeneity of the data, no conclusion can be drawn, except for the maximal size of copepods, as *M. aequatorialis* is the largest species found in Lake Kivu. *M. aequatorialis* in the recent zooplankton of Lake Kivu still reached the maximal size recorded before the sardine introduction, suggesting that there was no change in body length of the largest copepod species of the lake.

Isumbisho (2006) mentioned a decreasing trend for the size of the cladoceran *D. excisum*, based on a comparison between his and historical data, but again a closer look shows a large heterogeneity in the data. No or little change in maximal body length of this species occurred since 1981, without available data before the sardine introduction. For the other cladocerans, the data present similar uncertainties, with some differences which might be related to sampling strategy, sample size and consideration of different stages (only adults vs. all stages, including the smallest instars). Therefore, no conclusion can be drawn on a potential decrease of crustacean zooplankton body size as a consequence of the *Limnothrissa* introduction.

7.5 Diel Vertical Migration

The diel vertical migration (DVM) of the three copepod species and of *D. excisum* – the largest prey items among the metazooplankton – was investigated by Isumbisho (2006) in the pelagic zone of Lake Kivu. Vertical migration of zooplankters is generally considered as a predator avoidance behavior, with a trade-off between reducing mortality losses at daytime and the energy costs of moving vertically in a deep water column. According to Gliwicz and Pijanowska (1988), the typical behavior of vertical migration (descent at dawn and ascent at dusk) should only be expected when both following conditions are fulfilled: (1) the risk of mortality due to predation is significantly higher in the upper than in the lower strata during the day, and (2) the gain associated with migration is significantly higher than the energy investment for migration. The first condition is never fulfilled when no visual predator is present; it would also be unfulfilled in the presence of visual predators when predation by invertebrate predators is equally important but restricted to the lower strata. Both conditions for triggering a typical DVM in larger zooplankters are clearly at present fulfilled in the pelagic zone of Lake Kivu, with the presence of an efficient planktivorous fish, without any invertebrate predator.

Isumbisho (2006) calculated the mean residence depth (MRD; Frost and Bollens 1992) from sampling 12 different 5-m deep strata and determining abundance of the following categories: the cladoceran *D. excisum* and several stages (ovigerous females, adult females without eggs, adult males and copepodids) of the three copepod species (*T. consimilis*, *M. aequatorialis* and *T. confinis*). The different species exhibited different survival strategies depending on their feeding habits, life stages and adult body sizes (Fig. 7.11). The relatively small *T. confinis* was permanently present in the euphotic layer while the largest copepod species, *T. consimilis* and *M. aequatorialis*, exhibited a clear DVM behaviour, with some differences among life stages. Egg-bearing females of *T. consimilis* remained permanently in the aphotic zone while *M. aequatorialis* ovigerous females migrated to the top 20 m during the night. *D. excisum* occupied mostly the intermediate layer except at midday.

This suggests that vertical migration at daytime to the aphotic zone may provide the largest copepods with adequate protection against fish predation, and that the cladocerans, which exhibit a smaller range of downward migration, may be more vulnerable.

7.6 Conclusions

The diversity of the Lake Kivu metazooplankton community, with seven species of crustaceans, does not seem that low when compared with other Rift lakes (see e.g. Lehman 1996). Currently, a total of 19 taxa have been identified in samples collected from 2002 to 2009: 3 copepods, 4 cladocerans and 12 rotifers (among which unidentified Bdelloids). Bdelloids were not reported before, whereas

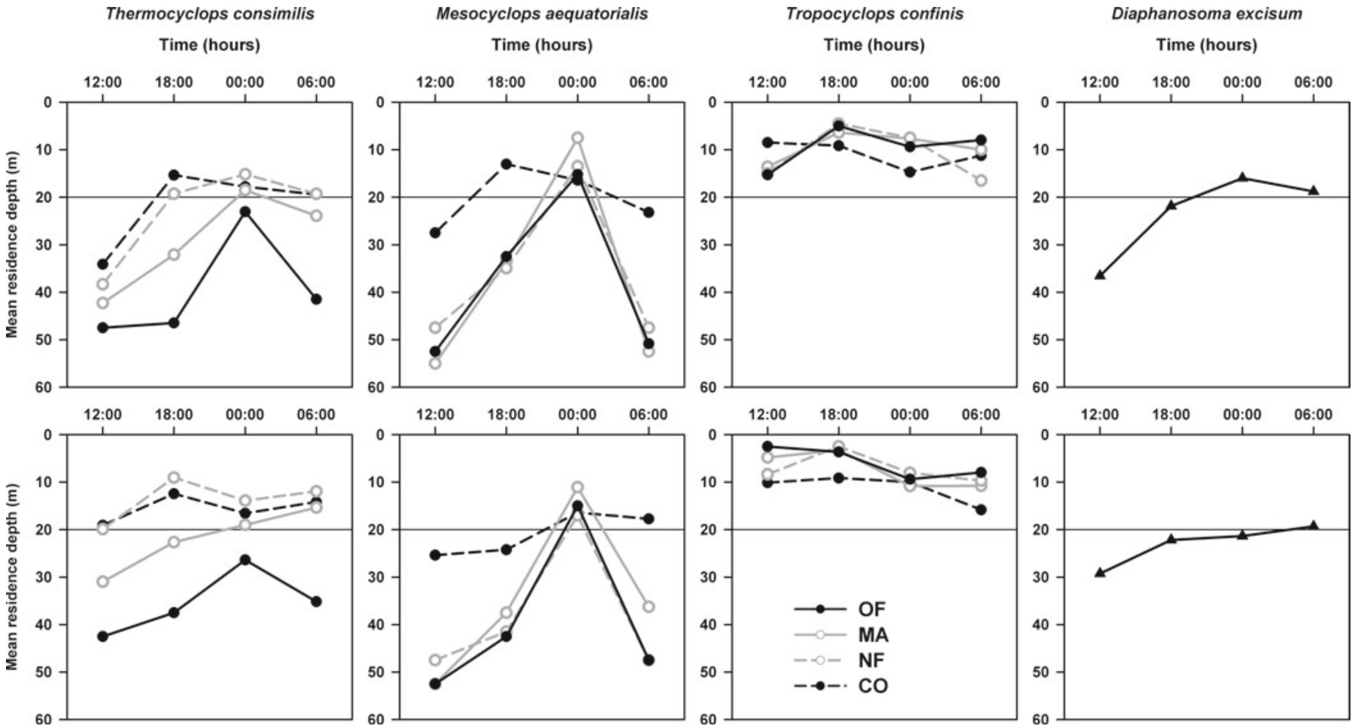

Fig. 7.11 Diel vertical migration of the four main species of crustaceans in Lake Kivu; MRD: mean residence depth; OF: ovigerous females; NF: adult females without eggs; MA: males; CO: copepodids. The horizontal lines indicate the limit of the euphotic zone. Upper panel: 5–6 August 2005, lower panel: 19–20 August 2005 (modified from Isumbisho 2006)

they have a worldwide distribution; in Africa alone, a total of 104 Bdelloid species are known, of which 24 are endemic (Ricci 1987). Also, *Keratella tropica*, another common rotifer in the pelagic Lake Kivu, was not observed before Isumbisho (2006). The reason for the abundance of rotifers in the pelagic waters of Lake Kivu, whereas they are scarce in other oligotrophic Rift lakes, might be the low invertebrate predation, in contrast to other East African great lakes where the dipterans *Chaoborus* (Lake Malawi) or open water shrimps (Lake Tanganyika) are present (Lehman 1996).

The effect of *Limnothrissa miodon* introduction in Lake Kivu, devoid of any pelagic fish in the 1950s, is a key question, but definite, reliable and precise quantitative data are missing to estimate this effect. In particular, the earlier records have many gaps as far as zooplankton abundance and diversity are concerned: even the presence of a *Daphnia* species in the lake before the introduction is not verified according to the earliest plankton record. In the study that directly addressed the effect on metazooplankton, Dumont (1986) based his assessment of the extent of the changes on few samples, collected in a short period of time, whereas the system presents a large seasonal and interannual variability in plankton abundance. Presumably the capture efficiency of his net was also low and abundance data were not corrected. By contrast, estimates based on recent and long-term observations, and comparison with Verbeke's (1957) data, revealed a probable decline of total crustacean biomass by a factor of 3, whereas a change in zooplankton size cannot be asserted on the basis of available data. Yet, the pelagic food web of Lake Kivu when a pelagic planktivorous fish was missing was atypical, with a very large average zooplankton biomass of ~2.6 g C m^{-2}, while comparable Rift lakes have a mean annual biomass of 0.8–1.0 g C m^{-2} (Table 7.1). The appearance of an important top-down control since the *Limnothrissa* introduction reduced the zooplankton biomass and production and the trophic transfer efficiency to levels similar to those of other Rift lakes (Table 7.1). The observed tight coupling between phytoplankton and zooplankton dynamics and the trophic transfer efficiency at the algae-grazer interface suggest that plankton dynamics and biomass in this oligotrophic, large tropical lake are at present predominantly controlled by bottom-up processes, i.e. seasonal mixing and nutrient availability, as already found for Lakes Malawi (Irvine et al. 2000; Guildford et al. 2003) and Tanganyika (Naithani et al. 2007).

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Chapter 8
Fishes in Lake Kivu: Diversity and Fisheries

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Laetitia Nyina-wamwiza, and Jean Guillard

Abstract This contribution reviews the knowledge on fish diversity and fisheries in Lake Kivu, with an emphasis on the biology and stock assessment of the introduced Tanganyika sardine, *Limnothrissa miodon*. Lake Kivu is famous, compared to the other African great lakes, for its poor fish fauna, with 29 species comprising a.o. 15 endemic haplochromines and a few non-native species. In a first part devoted to diversity and biogeography, all species are briefly described, with some details on their biology and ecology in the lake. A second part of this chapter focuses on the non-native *Limnothrissa miodon*, with a review on its biology, on its past and present abundance, and on available data on the production of the pelagic fishery of this species. The main conclusion is that the fishery yield is relatively low, amounting ~10,000 t year^{-1}. A recent concern is the arrival of a possible competitor, *Lamprichthys tanganicanus*, an endemic fish to Lake Tanganyika. Future studies should be conducted on the food web of the littoral zone, where most endemic cichlids are located. More detailed fisheries surveys are also needed, in order to estimate the pressure on the different species.

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To the biologist the main interest of Lake Kivu is the relative poverty of the fauna and its ecological immaturity (Beadle 1981)

8.1 Introduction

With only 29 species of fish described, among which several were introduced, the fish diversity of Lake Kivu is very low compared to its great neighbours. This low diversity is inherently linked to the geological history of the lake. The waters in Lake Kivu area have been at high altitude for maybe as long as the mid-Miocene East African uplifting. This fact in itself might account for part of the poor fish diversity of the current lake. However, the lake also went through some catastrophic events. After the uplifting, the area used to be part of a drainage system encompassing the current Lake Edward region, and a proto-lake even existed, from the mid-Pleistocene (Haberyan and Hecky 1987) or even much longer (Degens et al. 1973), that was connected to Lake Edward, but then got blocked by the Virunga volcanoes. As such, the lake was probably endorheic until it found its current outlet towards the south via the Rusizi river. In the meantime the lake did not escape the large drought that affected the whole area about 18,000–15,000 years ago (Elmer et al. 2009). Though the lake did not dry out completely, most probably it went to one or more stages of higher salinity, affecting the fish fauna. Equally, the lake went through some hydrothermal events that had severe effects on its ecosystem and hence on the fish fauna (Haberyan and Hecky 1987). All of these events must have affected the lake fishes to a certain extent.

Before the introduction of *Limnothrissa miodon* – the "Tanganyika sardine" (called *isambaza* or *sambaza* by the local fishermen, *lumpu* in the Tanganyika region) – the fishery in Lake Kivu was poorly developed (Kaningini et al. 1999). Artisanal fishing took place in the littoral areas and was based on small native cichlids (*Haplochromis* spp.), and on few other species (*Oreochromis niloticus*, two species of *Clarias*), with a maximal annual production of barely 1,500 t. Therefore, several attempts were made for introducing the *Ndakala* (*Stolothrissa tanganyikae*), with the hope of increasing the annual fish production up to 35,000 t (Capart 1959; Collart 1960). The outcome was that *Limnothrissa miodon*, not *Stolothrissa*, colonised Lake Kivu, allowing the progressive development, during the 1970s, of a productive pelagic fishery. The fishery grew rapidly from 1979 to 1991, particularly at the end of this period, due to the promotion of fishing techniques by a PNUD/FAO project, which operated mainly in the Rwandan part of the lake. The fishery grew in parallel in DR Congo, partly thanks to an impulse given by scientists located in Bukavu, who promoted a technique using gill nets (Kaningini et al. 1999), instead of the "trimarans" operating at night with a crew of several fishermen. For most specialists of fisheries, the story of the *sambaza* in Lake Kivu has widely been described as a success (Spliethoff et al. 1983; Roest 1999, Gozlan 2008), with an estimated annual yield of ca. 13,500 t for the whole lake (Spliethoff et al. 1983).

In this chapter we review the most recent results regarding fish diversity, the biology of *Limnothrissa miodon*, fisheries and stock of pelagic fish in Lake Kivu. A recent concern is the appearance in the lake and in the catches of another species introduced from Lake Tanganyika, which may compete with the sardine for the lake's scant planktonic resources.

8.2 Species Diversity

Lake Kivu has traditionally been regarded as a species-poor lake (Snoeks 1994). At present 29 fish species are known from the lake, five of which, however, are introduced (Table 8.1). Of the remaining 24 native species, the majority (16) belongs to one family, the Cichlidae.

Table 8.1 Fish species composition for Lake Kivu

Clupeidae	
Limnothrissa miodon (Boulenger 1906)	Introduced from Lake Tanganyika
Cyprinidae	
Raiamas moorii (Boulenger 1900)	Lake Kivu, Rusizi, Lake Tanganyika, Malagarasi, Lake Rukwa and associated river systems
'*Barbus*' *kerstenii* Peters 1868	Distribution still under discussion. Currently cited from Lakes Victoria, Edward-George and Kivu basins, coastal rivers in Kenya and Tanzania, Okavango, Cunene, Zambezi system, Save, possibly Aswa river in Upper Nile
'*Barbus*' *pellegrini* Poll 1939	Lakes Edward-George, Kivu, Tanganyika and Rukwa drainages, including Rusizi and Malagarasi
'*Barbus*' *apleurogramma* Boulenger 1911	Lakes Victoria, Edward-George, Kivu, Tanganyika and Rukwa basins, including Rusizi and Malagarasi; possibly Lukuga system, coastal rivers in Kenya and Tanzania, possibly Aswa river in Upper Nile system and Aoué in Chad
Labeobarbus altianalis (Boulenger 1900)	Lakes Victoria, Kyoga, Edward-George and Kivu basins, Rusizi and northern part of Lake Tanganyika
Amphiliidae	
Amphilius cf. uranoscopus (Pfeffer 1889)	Distribution still under discussion; coastal rivers in east and south-east Africa, Okavango, Zambezi system, affluents of Lakes Victoria, Kivu and Tanganyika, Upper Zaire system
Clariidae	
Clarias liocephalus Boulenger 1898	Lakes Victoria, Edward-George, Kivu, Tanganyika and their associated river systems including Rusizi and Malagarasi, Bangweulu-Mweru system, Lake Rukwa, Cunene, Okavango, Zambezi system and Lake Malawi catchment

(continued)

Table 8.1 (continued)

Clarias gariepinus (Burchell 1822)	Almost pan-African
Poeciliidae	
Lamprichthys tanganicanus (Boulenger 1898)	Introduced from Lake Tanganyika
Cichlidae	
Oreochromis niloticus (Linnaeus 1758)	Senegal, Gambia, Niger, Benue, Volta, Chad system, Jebel Marra, Nile, Yarkon river (Israel), Lake Turkana system, Lakes Albert, Edward-George, Kivu and Tanganyika basins, Lake Tana, Lake Baringo, Suguta river, Ethiopian rift valley lakes from Lake Zwai to Lake Stefani, Omo system, Awash system [populations from the latter three regarded as *O. cancellatus* (Nichols 1923) by Seyoum and Kornfield]. The Lake Kivu population is part of the subspecies *O. niloticus eduardianus*
Oreochromis macrochir (Boulenger 1912)	Introduced (escaped from fish ponds)
Oreochromis leucostictus (Trewavas 1933)	Introduced (escaped from fish ponds?)
Tilapia rendalli (Boulenger 1897)	Introduced (escaped from fish ponds)
Haplochromis spp. (15 species)	All endemic to the lake

For autochthonous species, the currently known natural distribution is indicated (Based on Snoeks et al. 1997; additional data from Snoeks 2004; Muderhwa and Matabaro 2010). Following current taxonomic practice, the genus for the small '*Barbus*' species is put between single quotes

8.2.1 The Non-Cichlid Taxa

Limnothrissa miodon (Fig. 8.1a) is a freshwater clupeid originally endemic to Lake Tanganyika. Confusion about its possible presence in Lake Mweru is due to an erroneous locality record of *Microthrissa stappersii* Poll 1948, a synonym of *L. miodon* (Gourène and Teugels 1993). The species has been introduced in 1959 in a sample of juveniles mixed with *Stolothrissa tanganicae* Regan 1917, which was the Tanganyika sardine actually targeted for introduction in Lake Kivu (Collart 1960). In addition, *L. miodon* has successfully been introduced in Lake Kariba, from which it invaded Lake Cahora Bassa downstream (Marshall 1991). Both lakes are man-made reservoirs on the Zambezi system. In these areas as well as in Lake Kivu, *L. miodon* has become an important food fish (see Sect. 8.5 on fisheries below).

The family Cyprinidae is represented by five species. *Raiamas moorii* (Fig. 8.1b), a predatory powerful swimmer, may well be the only species that has colonized Lake Kivu from Lake Tanganyika (Robben and Thys van den Audenaerde 1984). Conversely, *Labeobarbus altianalis* (Fig. 8.1f) may have colonized the extreme northern part of Lake Tanganyika by descending the Rusizi from Lake Kivu (Snoeks et al. 1997). The species is also present in the drainage systems of Lakes Edward and Victoria. While the Kivu population had been allocated in the past to the subspecies *L. altianalis altianalis*, De Vos and Thys van den Audenaerde (1990a) did not find enough evidence to justify the use of subspecies and applied the specific name to all known populations.

Three small '*Barbus*' occur in the lake. '*Barbus*' *kerstenii* (Fig. 8.1c) is the most common in the lake. Most of the confusion surrounding the taxonomy of these species has been clarified by De Vos and Thys van den Audenaerde (1990b) and their distribution has been reviewed by Snoeks et al. (1997). However, some confusion remains within the taxa '*B.*' *kerstenii* and '*B.*' *pellegrini* (Fig. 8.1d). The correct separation of the latter species and '*B.*' *neumayeri* in some Ugandese waters remains problematic (Snoeks pers. obs.).

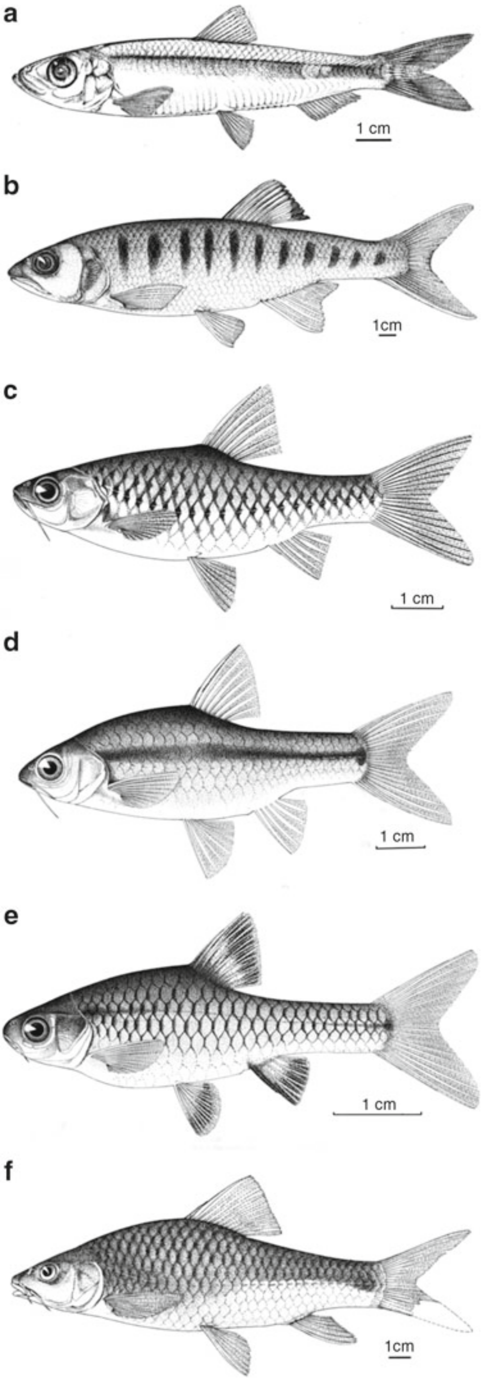
The catfishes of the Kivu basin are represented by two widespread *Clarias* and one *Amphilius* species. The latter is not living in the lake itself but in its affluent rivers. It has been named *A. cf. uranoscopus* (Fig. 8.2a) by Snoeks et al. 1997 and *A. uranoscopus* by De Vos et al. (2001). *Amphilius uranoscopus* is a widespread species of East and Central Africa (Skelton 1984). Its status in the Kivu drainage system is in need of review.

Recently, a new taxon has been added to the list of Kivu species, i.e. *Lamprichthys tanganicanus* (Fig. 8.2b). This fish is an endemic to Lake Tanganyika. How exactly it arrived in Lake Kivu is unclear. It is excluded that this small Cyprinodontiform species could have migrated up the Rusizi to Lake Kivu. The species is not adapted to the riverine environment and is not capable of mounting the rapids and cascades, an opinion shared by Muderhwa and Matabaro (2010). These authors advanced two hypotheses explaining the presence of *Lamprichthys* in Lake Kivu. The first one implies a recent introduction, probably by an aquarist. While this hypothesis cannot be ruled out, Muderhwa and Matabaro (2010) did not find any indication that such an aquarist has been active in the region. They postulated that juveniles of *Lamprichthys* might have been introduced in 1959 together with those of *Limnothrissa miodon*. Because of its much lower fecundity compared to that of *Limnothrissa* and the possible stronger predation on its fry, it has taken a long time for this species to become abundant (Muderhwa and Matabaro 2010). Assuming the latter scenario, it nevertheless remains strange that it would have taken almost 50 years after its possible introduction before the species was discovered in the lake. Most likely, *Lamprichthys tanganicanus* has been recently introduced in Lake Kivu. It is a pelagic dweller, living in coastal areas and is one of the most abundant fishes in these areas in Lake Tanganyika (Snoeks pers. obs.).

During reproduction, *L. tanganicanus* deposits eggs in cracks and holes between rocks (Wildekamp 2004). While there are abundant rocky areas in Lake Kivu, the abundance of crevices and cracks is much less than in Tanganyika, because of the rocks being "cemented" together by a calcareous precipitate (Beadle 1981). Apparently, since the species is now very abundant, the lack of suitable places is at present no major impediment for its reproduction in Lake Kivu.

Not only is the lake generally species poor; also quite a number of families and genera present in the surrounding areas are lacking. There are no Protopteridae,

Fig. 8.1 (**a**) *Limnothrissa miodon*; (**b**) *Raiamas moorii*; (**c**) '*Barbus*' *kerstenii*; (**d**) '*Barbus*' *pellegrini*; (**e**) '*Barbus*' *apleurogramma*; (**f**) *Labeobarbus altianalis.* (**a**, **b**) Unpublished; (**c**, **d**, **e**, **f**) (From De Vos and Thys van den Audenaerde (1990a, b). Copyright RMCA, Tervuren, Belgium)



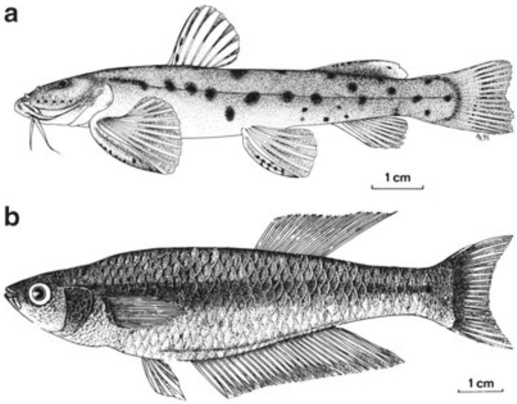


Fig. 8.2 (**a**) *Amphilius cf uranoscopus*; (**b**) *Lamprichthys tanganicanus*. Unpublished. Copyright RMCA, Tervuren, Belgium

Mormyridae, Alestidae, Anabantidae or Mastacembelidae present, to name the most obvious ones. Within the Cyprinidae, perhaps most striking is the lack of a species of the genus *Labeo*. Similarly, the obvious missing catfish taxon in Lake Kivu is *Synodontis*. No fossil data are available like for Lake Edward for which families now absent are known to have existed in the past (Greenwood 1983).

Records of *Gnathonemus petersii* (Günther 1862), *Bryconaethiops microstoma* Günther 1873 and *Hydrocynus vittatus* (Castelnau 1861) from the lake are erroneous (De Vos et al. 2001).

8.2.2 The Cichlids

Currently 19 species of cichlids are known from the lake, four of which are tilapiines and 15 endemic haplochromines (Table 8.1). These tilapiines include three introduced tilapias and the native *Oreochromis niloticus* (De Vos et al. 2001). The Kivu population of the latter species belongs to *O. niloticus eduardianus*, a subspecies also present in the basins of Lakes Albert, Edward-George and Tanganyika.

Lake Kivu haplochromines are notoriously difficult to identify. For most species, a reliable identification can only been done after a check of its most important characteristics under a dissecting microscope. Adult males can have a species-specific colour pattern and can be distinguished by an experienced person, though similar patterns do exist. Except for some species that have a distinctive habitus, the females of most species are very similar and all brown greyish coloured. Because of the large interspecific overlap, a simple dichotomous identification key cannot be compiled. Hence Snoeks (1994) produced a number of identification guidelines that can be used as a first approach, the results of which should be checked against the more elaborate differential diagnoses and species descriptions. Haplochromines are essentially located in the littoral zone of the lake, although some species can be present in the pelagic zone.

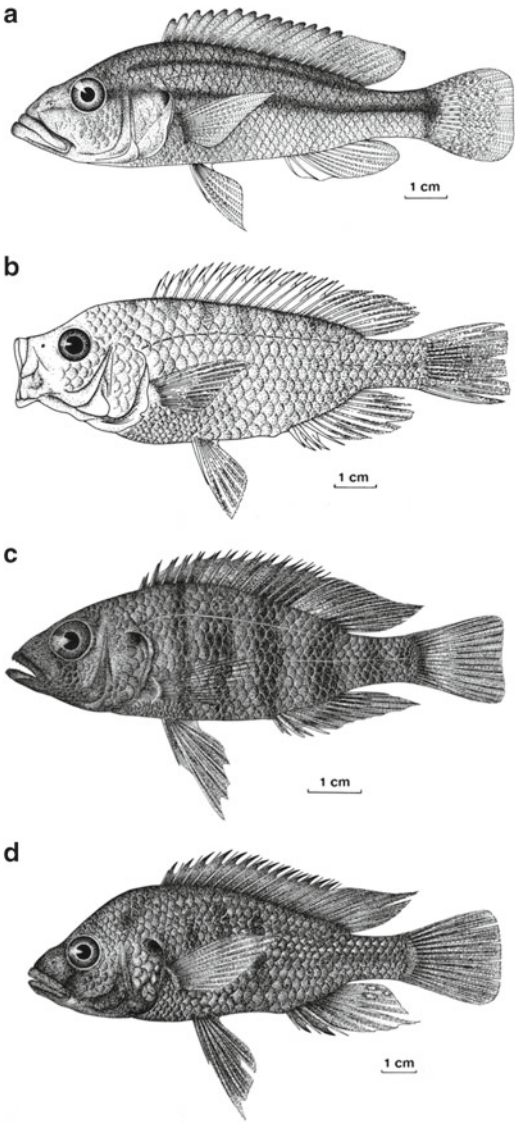


Fig. 8.3 (**a**) *Haplochromis vittatus*; (**b**) *Haplochromis paucidens*; (**c**) *Haplochromis gracilior*; (**d**) *Haplochromis adolphifrederici* (From Snoeks (1994). Copyright RMCA, Tervuren, Belgium)

Haplochromis vittatus (Fig. 8.3a) was the first haplochromine species to be described from the lake. It is the largest species (up to 191.0 mm standard length) and the only large piscivorous predator.

Haplochromis adolphifrederici (Fig. 8.3d) can be distinguished by its molariform pharyngeal dentition. The amount of enlargement of the pharyngeal jaws and the degree of molarization of the teeth is very variable (Snoeks 1986) and the intra-specific variability is larger than in any other known haplochromine species in the region. Such a pharyngeal dentition is typical for mollusc crushers. However, all data currently available indicate that the species is rather entomophagous and only in a few specimens have mollusc shell fragments been found (Ulyel et al. 1990; Snoeks 1994). This observation was tentatively linked to the rarity of molluscs within the lake.

Haplochromis paucidens (Fig. 8.3b) is a common species with a relatively small mouth with relatively few teeth and thick lips. The species has been described three times, with *H. schoutedeni* (Poll 1932) and *H. wittei* (Poll 1939) as synonyms (Snoeks 1988). Part of this confusion has to do with the species being polymorphic, comprising three morphs with different colour patterns (see below).

In *Haplochromis gracilior* (Fig. 8.3c), almost no vivid colour components are present except for the obvious yellow egg spots in adult males. Territorial males are uniformly dark brown to black while non-territorial males are yellowish-brown. In this species a sexual dimorphism has been discovered in the dentition. The change from bicuspid teeth in the outer rows and from tricuspid teeth in the inner rows towards unicuspid teeth happens at a smaller size in males than in females. This may be linked to a change in feeding behaviour, but no further data are available (Snoeks 1994).

The habitus of *Haplochromis graueri* (Fig. 8.4a), is similar to that of *H. adolphi-frederici* and both species have a "heavy head" look. Although the pharyngeal teeth are not enlarged in *H. graueri*, both species have been mixed in the past.

Haplochromis astatodon (Fig. 8.4b) is the only species with a closely-set outer dentition of fine and slender teeth, moveably attached to the jaw and with a large obliquely truncated crown. This type of dentition is typical for epiphytic algae scrapers. However, the species was found to be mainly detritivorous (Ulyel et al. 1990). While most of its capture localities might have been close to submerged or coastal vegetation, the species was captured on rocky habitats as well (Snoeks 1994).

Haplochromis nigroides (Fig. 8.4c) is a problematic species. Described first as a variety of *H. astatodon*, the holotype is clearly different and represents another species. Few of the specimens allocated to *H. nigroides* by subsequent authors actually belong to the species. At this moment, only adult males are included in the re-description of the species (Snoeks 1994). It is very difficult to separate from *H. scheffersi* as all meristics and measurements overlap to a large extent.

Haplochromis kamiranzovu (Fig. 8.4d) is an elongate species. It is the most pelagic-living haplochromine species in Lake Kivu but it has been found near the coast at river mouths as well. It is the most common species in the catches of the local sardine fishermen. *Haplochromis kamiranzovu* has been reported as a microphytophage by Ulyel et al. (1990), though morphologically it is similar to the zooplanktivores from Lake Victoria as described by Witte and van Oijen (1990).

Haplochromis scheffersi (Fig. 8.4e). As for *H. nigroides*, the identification of females of this species remains problematic. Little is known of its ecology though its morphology is quite generalized.

Haplochromis occultidens (Fig. 8.5a) is a rare species, many specimens of which have been identified in the past as *H. paucidens*. Interestingly and in contrast to all other Kivu haplochromines in the lake, the number of teeth in the outer rows of the oral jaws diminishes with size. This is undoubtedly linked to the ecological niche of

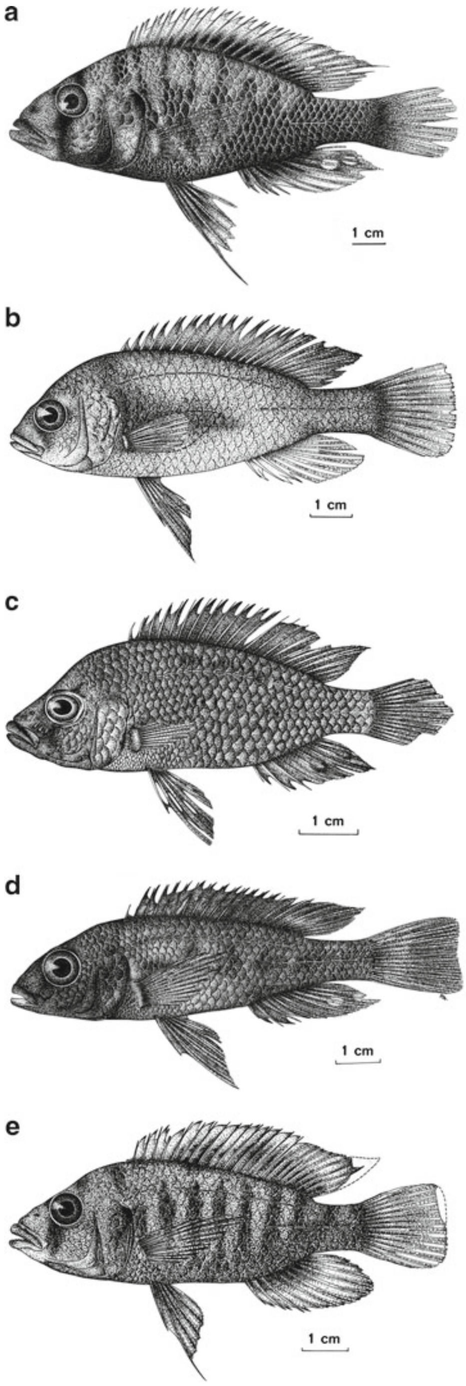


Fig. 8.4 (**a**) *Haplochromis graueri*; (**b**) *Haplochromis astatodon*; (**c**) *Haplochromis nigroides*; (**d**) *Haplochromis kamiranzovu*; (**e**) *Haplochromis scheffersi* (From Snoeks (1994). Copyright RMCA, Tervuren, Belgium)

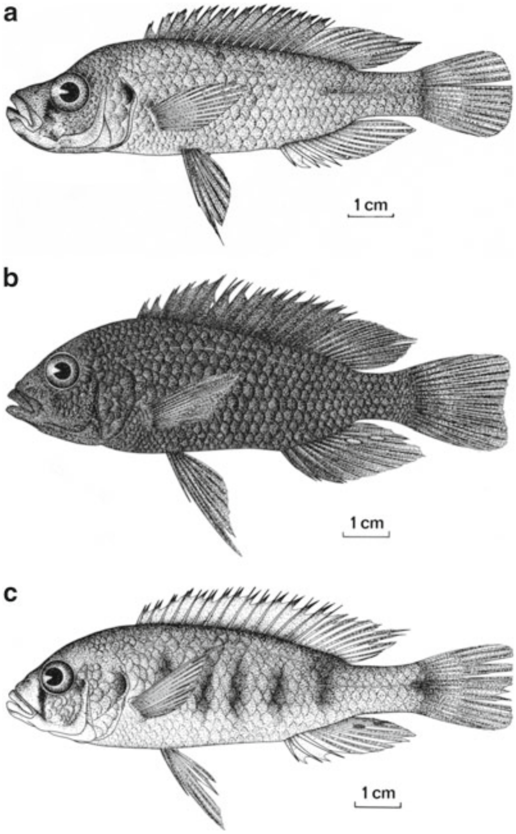


Fig. 8.5 (**a**) *Haplochromis occultidens*; (**b**) *Haplochromis olivaceus*; (**c**) *Haplochromis crebridens* (From Snoeks 1994. Copyright RMCA, Tervuren, Belgium)

the species. Indeed the diet is composed of young fish and eggs. Its feeding habits have not been observed on live specimens, but it is likely that the species is a paedophage of the snout-engulfing type. The thick oral mucosa with only few teeth hidden, probably forms an effective instrument to engulf the snout of mouth-brooding females (Snoeks 1994).

Haplochromis olivaceus (Fig. 8.5b) and *Haplochromis crebridens* (Fig. 8.5c) form a species pair, at least from a morphological point of view. Again, this represents an example where non-territorial males and females of both species are difficult to distinguish. Both are epilithic algae scrapers, which corresponds well to their dentition with numerous rows of densely set teeth with large cusps (Snoeks et al. 1990). Both species may be ecologically segregated to a certain extent as *H. crebridens* has been found relatively more often in floating gill nets both during the day and at night (Snoeks 1994).

Haplochromis microchrysomelas (Fig. 8.6a) is one of the smaller species in the lake, characterized by a low number of vertical bars on the body. It has relatively few teeth, but more so than *H. occultidens* and *H. paucidens*. Virtually nothing is known about its ecology as the species has been mixed with *H. scheffersi* in the past.

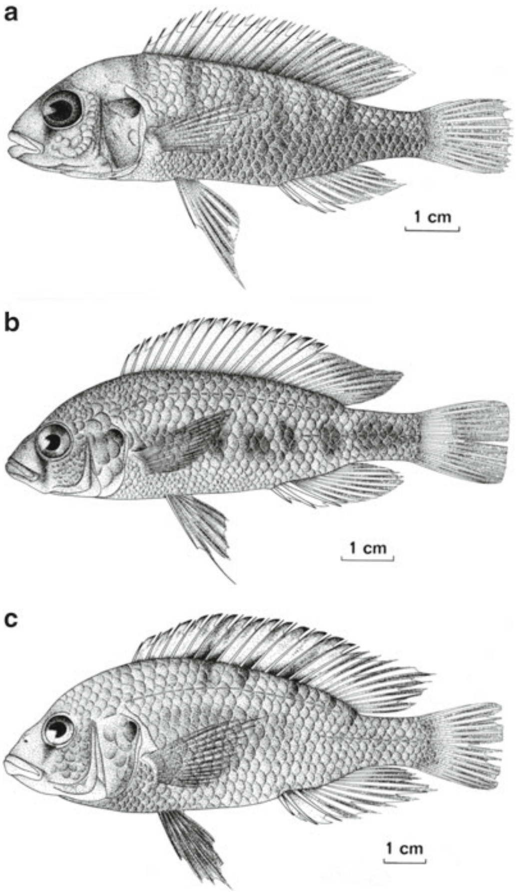


Fig. 8.6 (**a**) *Haplochromis microchrysomelas*; (**b**) *Haplochromis insidiae*; (**c**) *Haplochromis rubescens* (From Snoeks (1994). Copyright RMCA, Tervuren, Belgium)

Haplochromis insidiae (Fig. 8.6b) represents a combination of morphological characters that puts it midway between *H. astatodon* and *H. kamiranzovu*. Indeed the species is elongated but less so than *H. kamiranzovu* and has protracted teeth but less pronounced than in *H. astatodon*. Most adult males were found in muddy or sandy areas but some non territorial specimens were found amongst the catches of sardines in pelagic waters.

Of *Haplochromis rubescens* (Fig. 8.6c) only seven adult males have been positively identified in the collections. These are characterized by a red colour on the body, which is more pronounced than in *H. graueri*. Nothing is known about its ecology, but its dentition, though less specialized than in *H. crebridens* and *H. olivaceus*, is typical for an epilithic algae grazer.

Some taxonomic issues are not completely solved. There is still a lack of specimens of certain haplochromine species such as *H. nigroides* and *H. rubescens*. Hence it is difficult to delineate these species. Especially, the differential diagnosis between the former and *H. scheffersi* is not well developed.

The endemic haplochromines belong to the superflock of East African haplochromines present in the drainage systems of Lakes Victoria-Kyoga, Edward-George and Albert (Snoeks 1994). The relationships between the taxa have been a matter of discussion for a long time. Greenwood (1979, 1980) did a remarkable attempt to apply a cladistic approach that resulted in the hundreds of species known at that moment, being classified in 25 resurrected or newly described genera whose distributions cut across the boundaries of the various drainage systems (Snoeks 2000; Fryer 2004). Snoeks (1994) tried to apply Greenwood's classification scheme on the Lake Kivu haplochromines, but with moderate success. He preferred using the gender name *Haplochromis*, as was done by the Dutch Hest group for the species from Lake Victoria (e.g. Hoogerhoud 1984; van Oijen 1996; Witte et al. 2009). The use of the generic name *Haplochromis* in a broad geographic context has been supported by recent molecular results (Verheyen et al 2003; Elmer et al. 2009), clearly demonstrating that even when using a fast evolving fragment of mtDNA or a large array of microsatellites, species cannot be distinguished. No signal of genus structuring is present in these results as genetic differentiation for the whole flock is extremely low (Elmer et al. 2009). The global picture as far as relationships are observed is one of Lake Kivu haplochromines mixed with those of the other regions without clear species-specific boundaries except for *H. gracilior* (Verheyen et al. 2003) or Lake Kivu being basal to the remaining parts of the superflock (Elmer et al. 2009). A special feature observed in Lake Kivu haplochromines is the large amount of polychromatism. This is limited to the so-called piebald or bicolor specimens showing an irregular blotched pattern of brown-black pigment on a whitish-yellowish background. Orange blotched specimens (dark blotches on an orange background), such as in some Lake Victoria species (Maan et al. 2008), have never been observed in Lake Kivu. The presence of piebald or bicolor specimens has been observed in four of the fifteen species (*H. vittatus, H. occultidens, H. adolphifrederici, H. paucidens*). In the latter species, a grey, peppered form has been discovered as well, albeit in small numbers and only in females (Snoeks 1994). In *H. adolphifrederici* and *H. paucidens*, for which large samples were available, about half of the females were found to be of the piebald morph. No morphological differences were found between the normal and the piebald specimens (Snoeks 1994). Piebald males are very rare (Snoeks 1995). Another type of polychromatism, found in the normal or plain coloured morph in some Lake Victoria species (Maan et al. 2006) has, up to now, not been found in Lake Kivu. The range of colour variation reported for the latter type of polychromatism is indeed present in Lake Kivu haplochromines, but appears to be confined to intra-individual variability.

8.3 Origin and Ichthyogeography

Lake Kivu currently belongs to the Congo basin through its connection with Lake Tanganyika via the Rusizi. Traditionally, the lake has been included in the Congo region, or if a smaller scale categorization was made, in the same ichthyogeographic region as Lake Tanganyika (Snoeks et al. 1997). The Rusizi connection is however very recent in geological terms (see above). In 1997, Snoeks et al. discussed the ichthyogeographic position of Lake Kivu and concluded that, with respect to the non-cichlids of the lake, the lake had more affinities with the area to which it was connected before the origin of its current outlet, than with Tanganyika and the Congo basin. After an analysis of the distribution patterns of the fish fauna of the lake, they concluded that, similarly to the classification of Lakes Edward and George into the East Coast province, suggested by Greenwood (1983), the ichthyofauna of Lake Kivu had most affinities with the East Coast province.

This hypothesis, mainly based on non-cichlids, in the opinion of Snoeks et al. (1997) matched the observation that the endemic Kivu haplochromines were part of a larger super species flock comprising the haplochromines from Lakes Victoria, Kyoga, Edward, George, Kivu and affluent river systems. The latter was confirmed by Verheyen et al. (2003), based on a large review of sequencing data of the mitochondrial control region DNA of 290 haplochromine specimens from the region, resulting in 122 different haplotypes. At no level, Kivu, Edward and Victoria haplochromine species could be distinguished from each other. Individual species had multiple haplotypes and haplotypes were shared by different species. One exception proved to be three small specimens identified as *Haplochromis gracilior*, which were found to represent the sister taxon to all other haplochromines of the super species flock. As such, the evolutionary history of the super species flock was traced back to Lake Kivu. These results, but especially the biological refutation of the Lake Victoria desiccation scenario, came as a surprise to those involved in faunal studies of the area and is still a matter of debate (Fryer 2004; Stager and Johnson 2008) with a yet unresolved conflict between the interpretation of geophysical and palaeo-ecological data on the one hand and molecular data on the other hand. However, the scenario outlined was confirmed in a later paper (Elmer et al. 2009) in which 12 nuclear microsatellite loci were analyzed and in which Lake Kivu specimens came out as the ancestral lineage to the Lake Victoria Region haplochromines. Surprisingly, the Kivu haplochromines were found to contain more interspecific genetic differentiation than the more derived and younger, but much larger group of Victoria haplochromines.

In addition, some evolutionary questions are left open. Did the Lake Kivu area also act as the central point of dispersal toward Lakes Edward and Victoria for some of the non-cichlid taxa? Which molecular markers can be used for species recognition in haplochromines?

8.4 The Biology of *Limnothrissa miodon* in Lake Kivu

The growth of *L. miodon* is similar in Lake Tanganyika and Lake Kivu (Kaningini 1995). In both lakes, *L. miodon* grows rapidly, with a mean monthly growth rate of more than 10 mm during its early life (5–6 months), reaching approximately 10 cm after 1 year. Its life expectancy is short, approximately 1 year. In both lakes, *L. miodon* is essentially zooplanktivorous in its early life but becomes omnivorous at the adult stage, feeding on diverse prey: zooplankton, insect larvae and adults, other small fishes, including their larval and juvenile stages (Isumbisho et al. 2004). However, the habitat preference of *L. miodon* appears to differ between lakes. In Lake Kivu, the larvae of *L. miodon* live along the littoral zone and migrate progressively further offshore during growth (Spliethoff et al. 1983). However, the oldest specimens are found inshore. In contrast, in Lake Tanganyika, *L. miodon* lives essentially in the littoral zone during most of its life; only the oldest specimens migrate offshore, where they live in shoals of *Stolothrissa tanganicae* (Coulter 1991).

Marshall (1993) noted that, despite considerable differences among the lakes in which *Limnothrissa miodon* became established (Lake Kivu, Lake Kariba and Lake Cahora Bassa), the biology of *Limnothrissa* was similar in many respects in all of them. Similarities included its feeding and breeding biology, whilst its populations fluctuate, on both an annual and a seasonal basis, in relation to environmental changes. The major differences between the lakes concerned the size to which *Limnothrissa* grows. Marshall (1993) observed that the size of *Limnothrissa* in Lake Kivu (up to 169 mm) was similar to that in Lake Tanganyika (up to 200 mm), whereas it had about half the length in the artificial lakes. Marshall explained this by the cannibalistic behaviour of *Limnothrissa* in the two natural lakes and by the fact that *Limnothrissa* can maintain a high biomass and productivity in the face of intense predation. In Lake Kivu, where no piscivorous fish exist in the pelagic zone, predation is replaced by the intense fishing effort.

Limnothrissa was until recently the only species in the pelagic zone of Lake Kivu, with no competitor and no predator, but this has changed since *Lamprichthys* turned up in the lake. Nowadays, *Lamprichthys* has colonized the littoral and the pelagic zone and it is still increasing in the pelagic catches. This recent invader feeds mainly on mesozooplankton offshore, whatever its body size (Fig. 8.7), which results in substantial niche overlap with the sardine. Although the niche overlap appears to be somewhat reduced inshore, the expansion of *Lamprichthys* raises concern about the future of the sardine fishery.

Limnothrissa larvae and juveniles partition their living space: juveniles migrate in an intermediate zone to feed on large zooplankton while larvae remain in the littoral zone and show little or no size selectivity towards copepods (Isumbisho et al. 2004). Adult *Limnothrissa* colonize all the areas of the lake. *Limnothrissa* exhibits this opportunistic foraging in Lake Kivu as well as in other lakes (Poll 1953; Coulter 1991; Mandima 1999, 2000). In Lake Kivu, as in the artificial lakes (Mandima 1999), *Limnothrissa* appears to feed on zooplankton in the middle of the day (Masilya et al. 2005; Masilya 2011), whereas in early morning and late afternoon, it consumes terrestrial insects, small fishes and mesozooplankton in the littoral zone (Masilya 2011).

8.5 Whole-lake Assessment of *Limnothrissa miodon* Abundance

A whole-lake fish stock survey using hydroacoustics was conducted by Lamboeuf (1991), in the framework of the PNUD/FAO/Rwa/87/012 project for the development of the fishery in Lake Kivu. This survey comprised seven hydroacoustics surveys

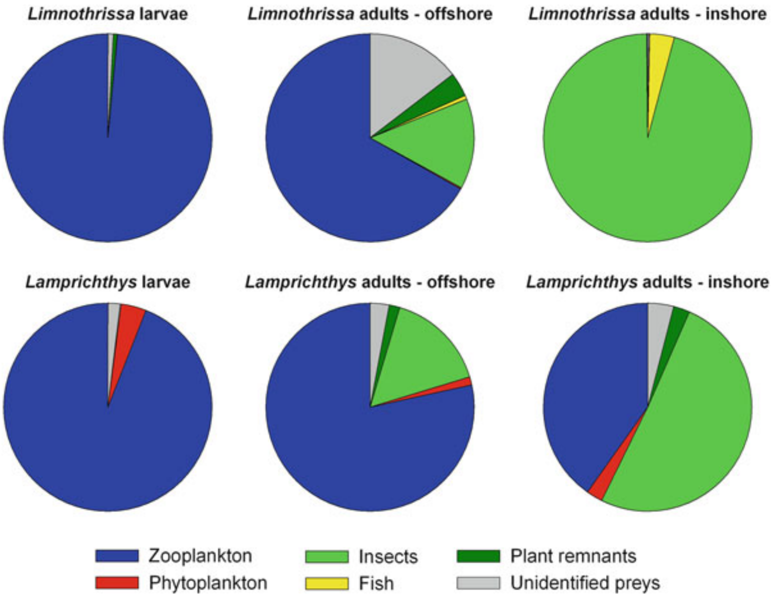


Fig. 8.7 Diet of juveniles and adults (Lauzanne's index espressed as %) of *Limnothrissa miodon* and *Lamprichthys tanganicanus* in Lake Kivu (modified from Masilya et al. 2011)

covering the whole lake, between April 1989 and May 1990. Total abundance of pelagic fish varied little between campaigns and provided a mean stock of 4,460 t. All class sizes were represented in all lake regions, and fishes were distributed down to 50–60 m depth, i.e. all over the mixolimnion, but their vertical distribution was restricted to the oxygenated layers.

In order to update this fish stock assessment, two new surveys were carried out in 2008 (Guillard et al. 2012), during the rainy season (14–22 February), and in the dry season (1–11 July 2008). The lake was divided into 4 large basins (Table 8.2), and Kabuno Bay was not included in our surveys (Fig. 8.8). The layers were similar to those sampled by Lamboeuf (1991), i.e. from surface to 15 m, 15 to 30 m, 30 to 45 m, and 45 to 60 m, then merged to calculate total biomass. The sampling protocol and all methods for data processing were as close as possible to those of Lamboeuf (1989, 1991).

Daily observations carried out *in situ* showed several types of structure, and the absence of targets in layers lower than 60 m, due to the lack of oxygen; furthermore no fish were detected in layers close to the surface (Fig. 8.9). Very dense schools (Fig. 8.9a) were mainly observed close to the shores, with depths <40–50 m or near areas of shallows in pelagic areas. The night survey (Fig. 8.9c) showed fish dispersion at dusk, in conformity with previous descriptions (Kaningini et al. 1999).

The fish densities (Fig. 8.10) were heterogeneous, according to localizations and seasons. In February, the strongest densities were detected in the south and the east basins, whereas in July the distributions among basins appeared more homogeneous.

Table 8.2 Characteristics of the basins, used for calculations for the hydroacoustic survey

Basin	North	East	West	South	Littoral area depth < 50 m
Surface (km^2)	900[a]	900[a]	320	97	50[a]
Depth max (m)	485	400	225	105	50

[a]Estimated

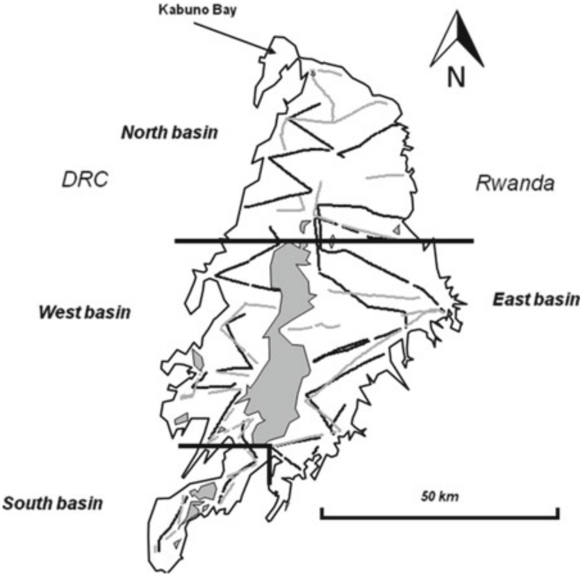


Fig. 8.8 Transects of the hydroacoustic survey carried out in February (grey lines) and July (black lines) 2008 in Lake Kivu

The densities detected inshore were much higher (by a factor 5–7) than those in the pelagic area. The vertical structures were also different according to the season, the fish being more abundant in the upper layers in July. In the deepest layers (45–60 m), average values were always low: furthermore in 80–100% of the Elementary Sampling Distance Units (ESDU) no detection was recorded, except during July in the west and south basins where a few fishes were detected in these deepest layers. When this deepest layer was not taken into account, the percentage of units without fish detections was very low, and over the entire water column there were very few areas without any detection. The fractions in the major size class (>ca. 6 cm, <12–13 cm), were constant in number, around 50%, whatever the season and the basin (Table 8.3). The number of fish per area, and the total tonnage by basin was obtained by multiplying the average areal biomass by the estimated surface area of each basin (Fig. 8.10).

Behaviour such as dispersion at dusk (Fréon et al. 1996) and schooling during day time (Fréon and Misund 1999), described as anti-predatory mechanisms by many authors (Parrish et al. 2002), were observed in Lake Kivu (Fig. 8.9), despite

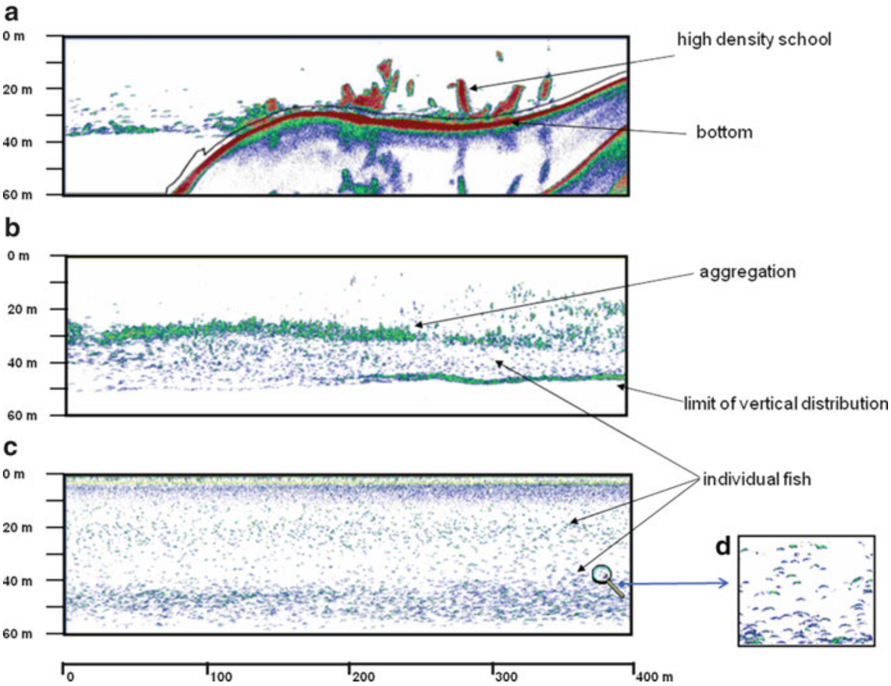


Fig. 8.9 Echograms recorded in Lake Kivu during daylight in the inshore area (**a**) and in the pelagic area (**b**), and at night in the pelagic area (**c**), with a zoom on individual fish (**d**). The horizontal scale is an approximate of the distance covered

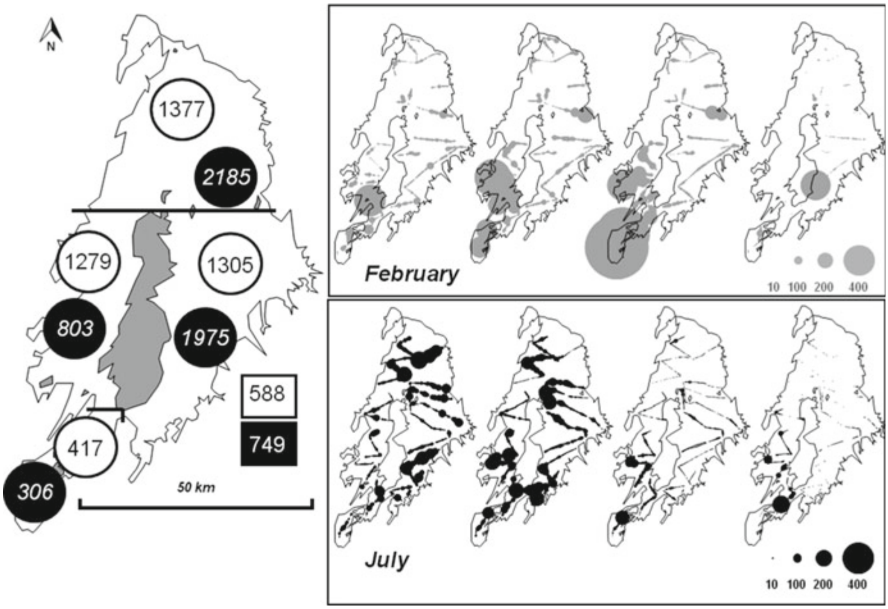


Fig. 8.10 Tonnage by basin for the two surveys (February, white circles; July, black circles) and for littoral areas (February, white square; July, black square). Maps of fish densities for the four layers (3–15, 15–30, 30–45, 45–60 respectively from left to right), during February (grey) and July (black) 2008: the values are in “Sa” (m^2 ha^{-1}) × 100, i.e. acoustic energy reflected per unit area

Table 8.3 Size classes of fish detected by basin for the two surveys

	North			East			West			South			Littoral depth < 50 m		
	<6 cm		>12–13 cm	<6 cm		>12–13 cm	<6 cm		>12–13 cm	<6 cm		>12–13 cm	<6 cm		>12–13 cm
February															
%	35	56	9	35	53	12	28	53	18	34	57	10	28	51	21
July															
%	27	49	24	30	51	19	21	62	16	39	46	15	7	70	22

the absence of predators in the pelagic zone. This agrees with previous observations of fish distribution in the lake (Kaningini et al. 1999). Shallow areas are not well sampled by hydroacoustic surveys, and this affects the whole-lake estimate of fish abundance in most lakes (Brehmer et al. 2006); in Lake Kivu, as the shallow areas make less than 10% of the lake area, this kind of bias is reduced. Furthermore, due to the homogeneous distribution during daytime and the absence of fish close to the surface, which are usually not detected by hydroacoustic, one can be confident that the acoustic surveys were reliable (Simmonds and MacLennan 2005).

Even though high amounts of fish were recorded in the north and east basins in the dry season (July), the densities per unit area were always higher in the west and south basins, whatever the season. The densities in these two basins were higher in the rainy season. In the same way, Marshall (1991) had noted that the catch per unit effort (CPUE) was higher in the south in February and in the north in July, connecting this phenomenon to a south to north migration, related to the morphology of the south basin which presents more coastal zones, favorable to reproduction. The vertical structures were heterogeneous according to areas, but the limit of the vertical distribution was very clear.

The adult fish percentage did not vary according to region and season and was around 50%, the juveniles, greater than ~1–2 cm, accounted for about 30–35% of the total number and the largest fish 15%. The whole-lake sardine stock, from these two recent acoustic surveys, was estimated to 5,000–6,000 t. This estimate is of the same order as for the survey carried out by Lamboeuf (1991) at the end of the 1980s (4,460 t). Average surface densities observed were also similar to those given by Lamboeuf (1991), i.e. 15–40 kg ha^{-1}. Considering a P/B ratio of 1.6 for *Limnothrissa* (Roest 1999), the annual production would be 8,000–9,600 t $year^{-1}$.

8.6 The Status of the Fishery

The stability of the pelagic fish stock over some 20 years, as shown by the hydroacoustic surveys, offers compelling evidence that, although the fishing effort has probably increased since the end of the 1980s, the *Limnothrissa* population of Lake Kivu has remained remarkably stable.

By contrast, recent direct estimates of the total annual sardine catch have hardly been available, due to the absence of reliable fish statistics from systematic surveys. At the end of the PNUD/FAO project, the estimate of the total number of fishing units over the whole lake (Kaningini et al. 1999) was 227 fishing units, using 400 m^2 lift nets, with a mean CPUE of ~50 kg day^{-1}. Catches varied strongly depending on season. Data from Bukavu Bay, where a fishing unit was followed for 1.5 years, provided an average daily catch of ~40 kg, with lowest values (15–20 kg day^{-1}) in the May-July period and highest (50–100 kg day^{-1}) in the November-January period. The total *Limnothrissa* catch around 1990 was ~3,200 t $year^{-1}$, whereas *Haplochromis* catches amounted to 1,460 t $year^{-1}$. The use of gill nets, promoted by the EC project

ONG/219/92/Zaïre (Kaningini et al. 1999) may have further increased the annual *Limnothrissa* catches by 280 t. A study of population dynamics (Kaningini 1995) demonstrated that natural mortality and mortality from the fishery were nearly equal, suggesting an optimal exploitation rate.

Since then, no update on the fisheries yield in Lake Kivu has been available, with the exception of recent records from the MINAGRI (Ministry of Agriculture of Rwanda, in charge of fisheries and aquaculture), which has recorded data on total catch in the lake. The data available for the years 2007 and 2008 indicate a total fish catch between 5,742 and 6,692 t. Assuming that the sardine represented 85% of the catches (Kaningini et al. 1999), the average sardine catch for the Rwandese waters would be about 5,300 t, which represents ~60% of the annual *Limnothrissa* production. Although no comprehensive catch data are available for the Congolese part of the lake, it may be safe to assume that they were similar to those in the Rwandese waters. This suggests that the total sardine catch in recent years was close to the estimated annual production of ~9,000 t, so that, at lake-wide scale, the *Sambaza* may not have been overexploited since the fishery has developed. However, the fishing pressure is not distributed evenly: some areas may present greater than average sardine production, offer better catches, and hence be subjected to high fishing pressure. This is the case of the Bukavu Bay, where the number of fishing units is greater than elsewhere, resulting in heavy pressure on the sardine stock. In recent years, as the mean fish size was declining, the fishery has been regularly closed for several months in DR Congo (Kaningini pers. comm.). Another concern for the fishery is the catch of sardine larvae and juveniles in the littoral areas, which is a common practice all over the lake shores: the impact of this practice on the pelagic fishery has not been assessed yet, but it remains a serious concern.

8.7 The Food Web Structure

The food web of Lake Kivu was described by Villanueva et al. (2008), using the ECOPATH modeling approach. This model included several fish species and identified phytoplankton and detritus as the major sources of carbon for the food web. However, this study failed to separate the pelagic and the littoral food webs, which are largely uncoupled in Lake Kivu, due to the reduced proportion of the lake area being in the littoral zone. In fact, the pelagic zone is essentially occupied by *Limnothrissa miodon* and by *Lamprichthys tanganicanus*, with only few species of *Haplochromis* (see 8.1) found in the pelagic waters. Moreover, Villanueva et al. (2008), in addition to general assumptions of their modeling approach, used essentially gut content analyses and general knowledge on the biology and the diet of the fish species for describing trophic relationships in the lake. Recent studies based on stable isotopes measurements and on fatty acid analyses may provide a better view of the food web structure of Lake Kivu, although the littoral food web has remained understudied so far. The results of these recent studies (Masilya 2011) showed some separation of pelagic and littoral food webs based on stable isotopes signatures of the organisms (Fig. 8.11).

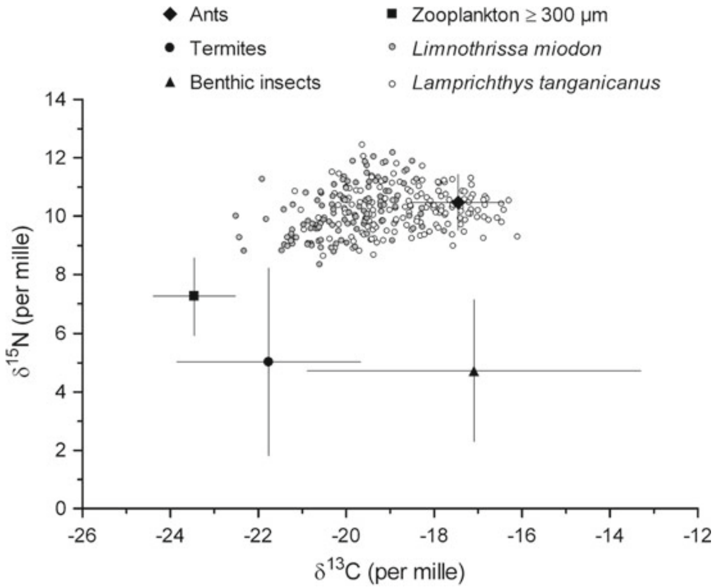


Fig. 8.11 Stable isotopes of C and N in various components of the food web in Lake Kivu (from Masilya 2011)

This analysis (Masilya 2011) shows that *Limnothrissa* and *Lamprichthys* have a similar trophic position, with the sardine being more dependent on the planktonic resources than *Lamprichthys*, which seems to depend also on littoral resources. The study of fatty acids in the seston, the zooplankton and the fishes reveals that the mesozooplankton diet relies on diatoms, cryptophytes and chrysophytes, whereas cyanobacteria are not or less consumed (Masilya 2011). Moreover, bacterial fatty acids found in the picoplankton fraction (seston 0.7–2 µm) were also found in the largest mesozooplankton specimens. This indicates a probable contribution of the microbial loop to the functioning of the pelagic food web in Lake Kivu.

8.8 Conclusion

The ichthyofauna of Lake Kivu is unique because of its fifteen endemic haplochromine species that seem to have played a pivotal role in the evolutionary history of the haplochromine fauna in the region, being in a basal position to the other haplochromines of the Albert-Edward Victoria flock. Identification remains difficult and problems persist in the delineation of certain species such as *H. nigroides* and *H. rubescens*. The non-cichlid fauna is very poor, reflecting the lake's intense geological history. It includes eight native and five introduced species, with some taxonomic confusion remaining in '*Barbus*' *pellegrini* and *Amphilius uranoscopus* living in the affluent rivers. Major fish families present in other basins in the region are absent from Lake Kivu.

Species diversity is concentrated in the littoral area. However detailed ecological studies on these cichlids and non-cichlids are lacking.

The studies in the field of fish biology and fisheries of the two last decades have been mostly devoted to *Limnothrissa miodon*, and largely used for fisheries management, notably for promoting alternative, size-selective, fishing techniques, aiming at catching the largest size classes of the sardines and allowing the smallest specimens to grow further. The use of hydro-acoustic surveys is particularly adapted to Lake Kivu, where the sole pelagic fish is the sardine, although catches of the recently introduced *Lamprichthys* have been reported by the fishermen. Therefore, in future stock assessment surveys, hydroacoustic records should be complemented by experimental catches, in order to verify the presence of *Lamprichthys* in significant numbers offshore. Indeed, this species, a potential competitor of *Limnothrissa* for zooplankton and other food resources, seems to be preferentially located close to the shore, as in its original habitat. Still, monitoring both species by experimental catches and fisheries statistics remains important to follow the possible expansion of the invader in the fragile pelagic ecosystem of Lake Kivu.

Compared to Lake Tanganyika, the sardine production in Lake Kivu is low. This may be due to several reasons, the most obvious being the low amount and diversity of planktonic resources in the pelagic zone, which is the most extended (>90% of the lake area). Although other preys are found in the adult sardine guts, *Limnothrissa* essentially depends on plankton production, and alternative prey does not compensate for the paucity and variability of zooplankton biomass during most of the year. We may speculate that this dependence on a variable resource may affect the survival of the *Limnothrissa* juveniles, which can only develop to the adult stage when resources are sufficient, i.e. at the end of the dry season. Otherwise, the studies conducted on fatty acids in the seston and in the zooplankton clearly show that the food quality in Lake Kivu is adequate for meeting the planktivore's requirements. Therefore future studies should focus on the survival of *Limnothrissa* juveniles, and explore other less known areas, such as the food web structure and function in the littoral zone, where several endemic and specialized haplochromines are found. There may actually be an issue of species conservation here, as fishing in the littoral zone is commonly practiced, seemingly without regulation. This stresses the need for detailed fishery surveys, which should be conducted in order to be able to assess the pressure on different fish populations, and for a proper management of this lake's resource of vital importance for the local human population.

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Chapter 9
Paleolimnology of Lake Kivu: Past Climate and Recent Environmental Changes

Natacha Pasche

Abstract This chapter reviews the sedimentation history of Lake Kivu back to 14,000 years before present (BP). Similar to other African lakes, the water level of Lake Kivu was lower during the dry period before 12,000 years BP. Maximum lake levels due to a more humid climate were recorded between 10,000 and 8,000 years BP. The Lake Kivu basin was probably closed between 8,000 and 6,800 years BP. The sediment record of Lake Kivu revealed dramatic changes around 5,000 years BP. The more recent past sedimentation (~200 years) is investigated with a short core from the main basin. The sediment core revealed an abrupt change ~50 years ago, when carbonates started to precipitate. Since the 1960s, the sedimentation fluxes of nutrient and soil minerals have increased considerably, while diatom frustules have decreased. These modifications are probably underlain by three non-mutually exclusive processes, namely: (1) the reduced top-down control over phytoplankton following the introduction of the non-native Tanganyika sardine, (2) bottom-up effects due to increased external nutrient inputs caused by the fast-growing population, and/or (3) increased rainfall leading to higher discharge of the subaquatic springs and thus enhanced upwelling of nutrient-rich deep water. These alterations might have induced a higher productivity in the lake, leading to increased sedimentation and to the onset of carbonate precipitation.

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9.1 Introduction

Sediments are excellent archives to reconstruct the history of lake internal processes and past inputs to the lake. Sediments are mainly composed of dead organic matter, diatom frustules, as well as minerals precipitating in the lake or supplied by inflows. For a sensible reconstruction of history, both catchment and lake processes should be taken into account. The evolution of a lake over time, and the resulting signals observed in sediment cores, can be influenced by many different factors, both natural (climate, catchment geology, vegetation) and anthropogenic (land-use, settlements, lake management, global warming). One of the major challenges of paleolimnology is to distinguish natural from anthropogenic factors (Lotter 2001).

Diatom frustules are well preserved in most lake sediments. As each diatom species has its own ecological preferences, diatom frustules can give information on past water column conditions, including pH, salinity, and trophic status (Battarbee et al. 2001). For instance, Kilham et al. (1986) proposed a ranking of African planktonic diatoms according to their preferences for the Si:P and light:Si ratios in the surface waters. They found that long and slender *Fragilaria* spp. (formerly *Synedra*) tend to dominate at high Si:P, as they have high Si requirements and low P requirements for growth. *Nitzschia* spp. are intermediate, while *Stephanodiscus* spp. grow best at low Si:P ratios.

In reconstructing climatic changes during the Pleistocene and Holocene in Africa, Nicholson and Flohn (1980) pointed out a period of aridity between 20,000 and 12,000 years before present (BP), and two moist, lacustrine periods from 10,000 to 8,000 years BP and from 6,500 to 4,500 years BP. Sediment cores from the Great African Lakes have confirmed this reconstruction of the past climate (Talbot and Laerdal 2000). The level of Lake Victoria was shallowest at ~11,200 years BP after the period of extreme aridity (Stager et al. 1997). Then, it rapidly rose and seems to have peaked at ~7,300 years BP. For Lake Malawi, low levels were inferred between 23,000 and 15,700 years BP (Johnson et al. 2002). Similar to other East African lakes, Lakes Tanganyika and Kivu also had lower water levels between 14,000 and 13,000 years BP (Haberyan and Hecky 1987). Rising water levels were recorded from 12,000 to 10,000 years BP, when the climate became more humid. Maximum lake levels were maintained at least from 10,000 to 8,000 years BP. The basins of Lakes Tanganyika and Kivu were probably closed from 8,000 to 6,800 years BP, due to the more arid conditions (Felton et al. 2007). Another century-scale drought occurred in East Africa from 4,100 to 3,300 years BP (Stager et al. 2009).

Lake Kivu contains between 300 and 500 m of sediment accumulated in its deep basin (Wong and Von Herzen 1974). With such a large accumulation, this ancient lake was estimated to date back to the mid-Pleistocene (between about 1 and 5 million years). In the late Pleistocene, its original outflow toward Lake Edwards was blocked by the Virunga volcanoes in the north (Degens et al. 1973). The opening of Lake Kivu through its southern outflow toward Lake Tanganyika was dated back between 10,600 (Felton et al. 2007) and 9,500 years BP (Stoffers and Hecky 1978).

In this chapter, we first review the existing literature about the sediments of Lake Kivu. In the second part, the analysis of a short sediment core reveals abrupt changes in the 1960s. We will also give possible causes for the ecosystem modifications suggested by these observations.

9.2 Learning from the Past

9.2.1 Geophysical Properties of the Sediment

Centered on the rift escarpments of the Western East African Rift system, the Lake Kivu Basin is dominated by a regional active fault (Wong and Von Herzen 1974). Major tectonic fractures align approximately north-south from the Nyiragongo volcano into the northern basin of Lake Kivu.

Seismic reflection studies have revealed that the unconsolidated sediments are thicker in the main basin in the north (Wong and Von Herzen 1974). Differences in sediment thickness across the lake reflect the difference in age of the basins, the amount of deposition and erosion, as well as fluctuations in lake levels. In particular, sediment thickness is limited above 300 m depth, probably because the lake has been shallower than this depth throughout most of its history (Degens and Kulbicki 1973). Within the unconsolidated sediment, thin layers with high acoustic contrast are probably indicative of tuffaceous material, beach conglomerates or gas trapped within the sediment. Finally, the basement material of unknown thickness had a high velocity, probably the signature of granite or metamorphic rock.

9.2.2 Biogeochemistry of Sediment Cores

Sediment cores up to 8 m long were taken by Degens et al. (1973) in the main basin, containing the last 14,000 years of Lake Kivu history. Core dating was based on radiocarbon of internally produced organic matter. However, radiocarbon is influenced to an unknown extent by the assimilation of old carbon of magmatic CO_2 by phytoplankton. This dating is therefore unreliable in absolute terms.

Haberyan and Hecky (1987) divided these cores into three different zones. In zone A, extending from 14,000 to 9,400 years BP, Lake Kivu was shallower with a high sedimentation rate and elevated organic content. These shallower lake levels, possibly caused by a more arid climate, were further supported by dating beach deposits recovered at 310 m depth (Haberyan and Hecky 1987). The alkalinity in the lake was moderately high. The dominance of *Stephanodiscus astraea* var. *minutula*[1] indicated low Si:P ratios. This zone was separated from zone B by a massive ash layer probably from a sublacustrine eruption, as the ash dispersion was restricted laterally.

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[1] This uncertain taxon is presently assigned to *Stephanodiscus rotula* Kützing, renamed *Stephanodiscus neoastraea* Håkansson & Hickel.

In zone B from 9,400 to 5,000 years BP, Lake Kivu became a deeper more diluted lake, resulting in lower sedimentation rates. This rise of lake level is believed to have led to the overflow at the Ruzizi outlet (Stoffers and Hecky 1978). Carbo-nates ($CaCO_3$) accumulated in the sediment, probably because the non-corrosive deepwater did not dissolve the precipitating $CaCO_3$. Higher water column stability favoured both blue-green algae and the diatom *Nitzschia fonticola.*[2] The Si:P ratio increased during this period, due to P limitation. Fine laminations were observed: dark layers rich in non-diatom algae were separated by light layers composed of nearly pure diatomite.

The transition to zone C at about 5,000 years BP revealed dramatic changes in the history of Lake Kivu. Carbonate precipitation abruptly ceased, while organic carbon and total nitrogen sharply increased. Simultaneously Ti:Si increased reflecting an input of volcanic ashes. Diatom assemblages were completely modified in a short time, and new species became dominant. These dramatic changes were attributed to volcanism and hydrothermal activities. Haberyan and Hecky (1987) proposed that a lake eruption similar to that of Lakes Nyos (Kling et al. 1987) and Monoun might have happened. Restricted oxygen during such an event might have killed most fishes, which could explain the present impoverished fish fauna in Lake Kivu. Indeed, nowadays only 24 native and 5 introduced fish species are living in Lake Kivu (Chap. 8), which contrasts to the extremely high biodiversity of Lake Tanganyika.

Analysis of zone C shows that from 5,000 years BP to present, the lake became strongly stratified due to a cooler, drier climate (Haberyan and Hecky 1987). Reduced inflows increased the lake surface salinity. The diatom assemblage became dominated by needle-like *Nitzschia* taxa and *Chaetoceros* sp., indicating strong P limitation and increased water column stability. *Chaetoceros* provides the first evidence of relatively saline conditions in Lake Kivu. Beginning 1,200 years BP, Lake Kivu became meromictic due to the warmer and wetter climate, similar to that found today (Stoffers and Hecky 1978). The present stratification currently observed in the lake dates back to this time (Degens and Kulbicki 1973).

In conclusion, the analysis of long sediment cores has revealed changes linked to climate variability. Volcanic ashes (at 3.5–3.9 m depth, ~12,000 years BP) indicate the large influence of volcanic eruptions. Further, a gas outburst might have occurred at around 5,000 years BP which could have partially destroyed the fish fauna.

9.3 Recent Changes in Sedimentation

9.3.1 Main Characteristics of the Kibuye Short Sediment Core

In total, three short sediment cores were taken in Lake Kivu in 2006 and 2007. The analysis of these cores has been presented in detail by Pasche et al. (2010).

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[2] Another uncertain taxon, usually referred to *Nitzschia fonticola* Grunow.

As all three cores showed the same characteristics, we will, in this chapter, only focus on the Kibuye core. This core was taken in May 2006 in the deep basin near Kibuye (2°02.886′S, 29°18.307′E) at a depth of 190 m. Unfortunately, intact sediment cores could not be taken below 200 m depth due to violent outgassing. The Kibuye core was therefore retrieved from a location relatively close to the shore.

The core was dated using ^{210}Pb and ^{137}Cs activities measured by γ-counting in a well-type Ge-Li borehole detector. The core was sectioned at intervals of 0.5 to 1 cm, and samples were analyzed for total carbon (TC), total inorganic carbon (TIC), total nitrogen (TN), total phosphorus (TP), as well as major and trace elements, biogenic silica (BSi) and diatom frustules (Fig. 9.1). The detailed methods have been described by Pasche et al. (2010).

An abrupt visual change from non-laminated dark to white laminae was observed in the upper part of the sediment core. At the depth of this transition, the mass accumulation rates, calculated with the constant rate of supply model (Appleby and Oldfield 1978), increased from 62 $\mathrm{g\,m^{-2}\,year^{-1}}$ in the deeper part to 212 $\mathrm{g\,m^{-2}\,year^{-1}}$ in the upper part (Table 9.1). The transition occurred, within dating uncertainties, in the early 1960s.

9.3.2 Major Changes in Sedimentation During the Last 50 Years

The visual characteristics and the sedimentation rates both revealed major changes in the sedimentation beginning ~50 years ago. Most fluxes of the core constituents clearly increased after ~1960 (Fig 9.1). From these core constituents, a mass balance was established (Fig. 9.2) for the four different fractions, which are $CaCO_3$, organic matter (OM), diatom frustules (BSi), and minerals. Since ~1960, this mass balance demonstrates a massive increase of $CaCO_3$, and a large increase of minerals. While OM also increased, diatoms slightly decreased (Table 9.1).

The most sudden change in the sediment record is the onset of carbonate precipitation in the early 1960s. Calcite was nearly absent in the sediment previously, and its accumulation suddenly increased by a factor of 16 (Table 9.1, Fig. 9.1). In Lake Kivu, the water above 60 m depth is oversaturated with respect to calcite and the saturated deep water prevents re-dissolution (Pasche et al. 2009). Even if the water is oversaturated, carbonate precipitation is often initiated by phytoplankton photosynthetic uptake of carbon dioxide and bicarbonate (Stabel 1986; Dittrich and Obst 2004). The sudden onset of carbonates deposition might therefore have been induced by higher primary productivity.

In the last 50 years, OM fluxes appear to have increased by 50%. More precisely, fluxes increased for TOC (40%) and TN (80%) but nearly tripled for TP (Table 9.1). These higher net sedimentation fluxes indicate a higher gross sedimentation. Surprisingly, TP increased far more than TN and TOC. This larger increase might be explained by enhanced TP loads from rivers (Muvundja et al. 2009), which might have influenced the coring site.

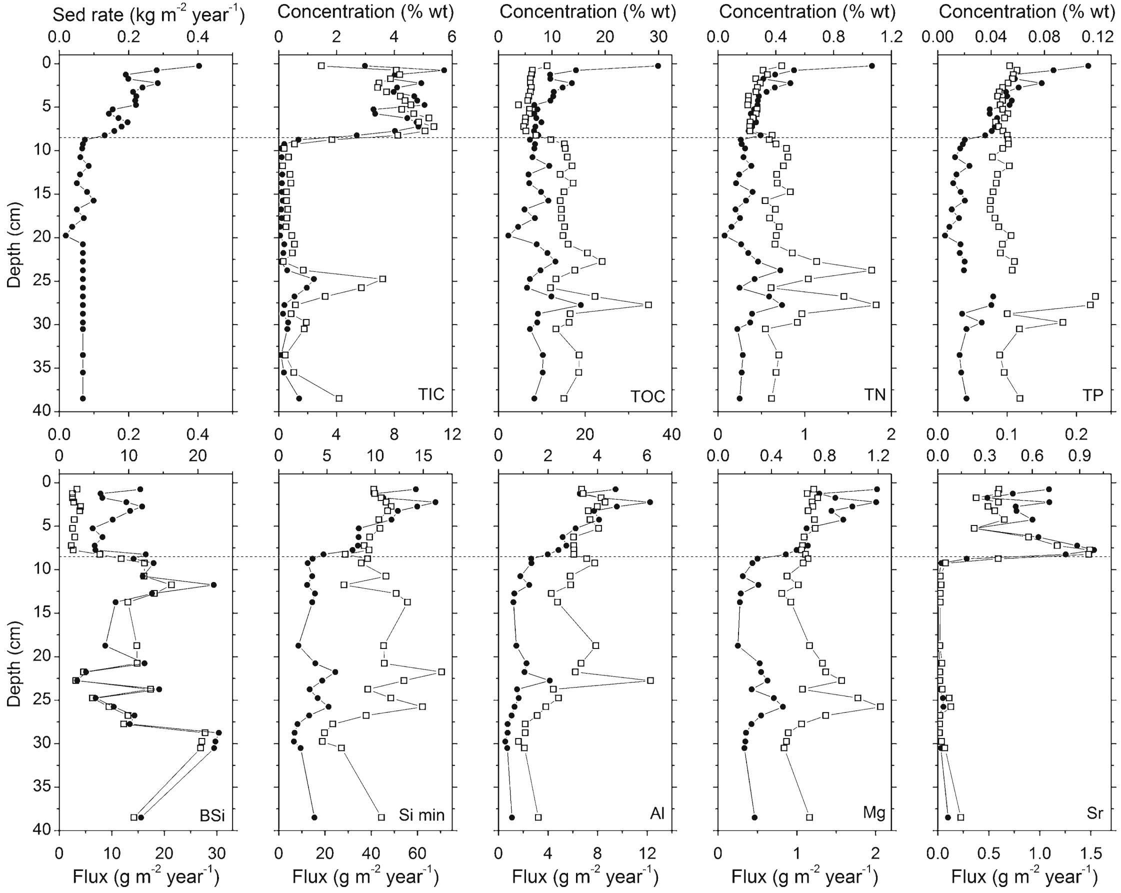

Fig. 9.1 Sedimentation rates (kg m^{-2} year^{-1}), and concentrations (upper x axis, open rectangles, % wt) and fluxes (lower x axis, black dots, g m^{-2} year^{-1}) of total inorganic carbon (TIC), total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), biogenic silica (BSi), silica in minerals (Si min; difference between total silica and BSi), and of different elements measured by X-ray fluorescence for the Kibuye sediment core

Table 9.1 Fluxes of sediment components for the Kibuye core

Kibuye core	Sedimentation rate	TIC	TOC	TN	TP	$CaCO_3$	OM	BSi	Minerals
Depth range cm	Fluxes in g m^{-2} $year^{-1}$								
White 0–8.5	212	8.41	12.8	0.60	0.108	74	34	11	79
Brown 8.5–39	65	0.53	9.0	0.33	0.037	5	23	16	22
Ratio white/brown	3.3	15.9	1.4	1.8	2.9	14.5	1.5	0.7	3.5

The first layer contained the white laminae of carbonates (white layer), which were absent from the second unit (brown layer). The four last columns are the components used in the mass balance (Fig. 9.2). TIC, total inorganic carbon; TOC, total organic carbon; TN, total nitrogen; TP, total phosphorus; OM, organic matter; BSi, biogenic silica

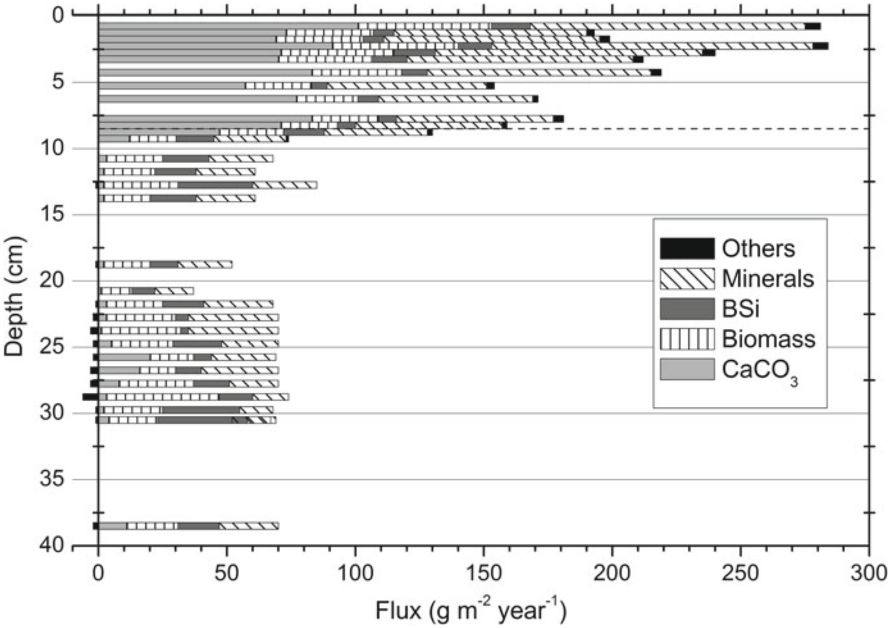

Fig. 9.2 Composition of the Kibuye core partitioned between carbonates, biomass, biogenic silica and minerals. The horizontal dashed line represents the lower limit of the layer containing white laminae (8.5 cm). The fraction "others" corresponds to the difference between the sedimentation rate and the four fractions mentioned above

Total mineral accumulation increased by a factor of 3.5. Similar positive trends (Fig. 9.1) were observed for soil tracers (Al, Si) and elements co-precipitating with carbonates (Mg, Sr). The increased proportions of soil particles in the sediment reflect the higher erosion occurring in the watershed, as a result of human activities (deforestation, agriculture and mining).

In contrast to the other fractions, BSi fluxes have reduced by 30% in the last 50 years. In Lake Kivu, diatoms are the major phytoplankton group (Chap. 5) and their frustules preserve well in sediment. The last 50 years were dominated by the planktonic, freshwater *Nitzschia fonticola*[3] and *Nitzschia lancettula* (Pasche et al. 2010). Further, a large increase in testate amoebae scales is indicative of increased catchment inwash. Between 1970 and 2006, a substantial peak in *Chaetoceros* probably indicated lower Si:P and a salinity increase. Lowering surface Si:P ratios may have been induced by recent nutrient inputs from the catchment, and increased upwelling of more saline, low Si:P deep waters.

In conclusion, the strong increase of the sedimentation rate since the 1960s was caused by a sudden onset of carbonate accumulation in combination with increased deposition of external minerals from catchment erosion.

9.4 Possible Environmental Changes

The major modifications in the last 50 years might be explained by one or a combination of three environmental changes: food web modifications due to the introduction of *Limnothrissa miodon*, increased nutrient inputs due to the fast-growing population, and increased upwelling due to higher rainfall. Theses three hypotheses are described in more detail below.

9.4.1 Introduction of Limnothrissa miodon

In 1959, *Limnothrissa miodon*, a clupeid endemic to Lake Tanganyika, was introduced into Lake Kivu (Chap. 8) in order to exploit the empty pelagic niche and provide proteins for the local population. The planktivorous "Tanganyika sardine" may have led to the extinction of the cladoceran *Daphnia curvirostris*, an efficient grazer and nutrient recycler (Dumont 1986), which was presumably present in the lake in the 1950s. The current zooplankton is dominated by copepods, which are less efficient grazers (Chap. 7). Further, predation by the sardine has led to a reduction of zooplankton biomass, which has reduced the top-down control over phytoplankton (Chap. 7). These food web alterations may have substantially influenced nutrient cycling in the mixolimnion, resulting in a larger gross sedimentation of carbon, nutrients, and $CaCO_3$ precipitation. Unfortunately, the quality of historical data is not sufficient to confirm the hypothesis of increased primary production due to the fish introduction (Chap. 5).

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[3] *Nitzschia bacata* and *Nitzschia tropica* are the dominant diatoms in the present mixolimnion. However, the separation between *N. bacata* and *N. lancettula* is not clear, the same is true for *N. fonticola* versus *N. tropica*.

9.4.2 Increased Nutrient Inputs

In the Lake Kivu catchment area, the population dramatically rose to a current density of ~400 inhabitants km^{-2}. For example, Goma had 14,000 inhabitants in 1959 but 200,000 inhabitants in 2000. In order to feed this growing population, the catchment was deforested and turned into agricultural subsistence. Erosion on the steep hills might have led to the observed increase in soil minerals and terrestrial testate amoebae. Erosion might also have supplied abundant nucleation sites for $CaCO_3$ precipitation. Further, P sedimentation could have been amplified via the flux of P-rich soil particles.

The population might have increased the nutrient inputs to the lake, due to agricultural fertilizers, untreated sewage discharge and biomass burning for cooking and cultivating. However, the external nutrient inputs currently account only for 10–20% of the total inputs to the surface layer, which are largely dominated by upwelling (Chap. 3). In conclusion, only a modification of the internal transport might lead to a significantly increased nutrient availability, which can sustain a higher primary production. The major increase of the external inputs only dates back to the last few decades whereas the residence time of the nutrients in the monimolimnion is several hundred years. Thus, the increasing inputs could not yet have had a large impact on the nutrient concentrations below the mixolimnion, and consequently on the internal recycling of nutrients.

9.4.3 Hydrological Changes

The lake level, recorded at the Ruzizi hydropower dam, increased by 44 cm between 1940/1960 and 1965/1993 (Fig. 9.3). These two periods were separated by extreme rainfall events recorded in 1961 and 1967 over East Africa (Nicholson and Yin 2001). Annual rainfall from meteorological stations in the Lake Kivu catchment increased by about 100 mm year^{-1} between 1932/1961 and 1962/1990 (data from the Rwanda Meteorological Service). Unfortunately, it is not entirely clear whether the lake levels were influenced by the construction of the Ruzizi I dam in 1958.

On the flanks of the Nyiragongo volcano in the north of the lake, the absence of rivers might indicate that rainfall directly percolates in the porous volcanic rocks, and enters the lake as subsurface inputs. These subaquatic springs (Chap. 2) cause a slow upwelling in the lake, responsible for the internal loading of nutrient into the surface water. The hypothesis is therefore that the increased precipitation has increased the inflow of subaquatic springs, leading to increased upwelling of nutrients. As more nutrients were delivered to the surface layer, a higher primary production could be sustained, which, combined with higher sedimentation, explains the higher accumulation of TOC, TN, TP and carbonate precipitation.

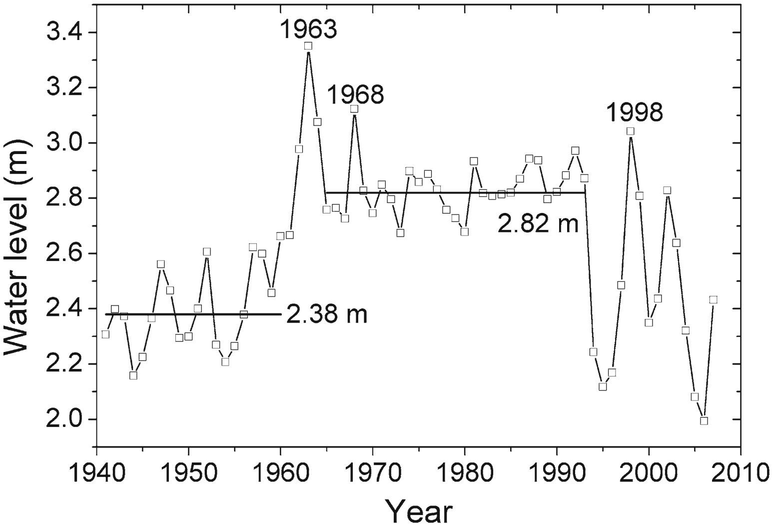

Fig. 9.3 Lake level recorded by Ruzizi I Hydropower Plant (m above 1460 m a.s.l.). The averaged lake level between 1941 and 1959 was 1462.38 m, while it was 1462.82 m between 1965 and 1993

9.5 Conclusion

The analyses of the Kibuye sediment core revealed an onset of $CaCO_3$ accumulation ~50 years ago, accompanied by nutrient increases, and a shift towards more halophilic diatoms with lower Si:P requirements. These changes probably resulted from the following ecosystem modifications occurring around 1960: introduction of *Limnothrissa miodon*, and/or increased external nutrient inputs and/or hydrological changes. Unfortunately, quantifying the effects of these environmental modifications is currently not possible. It is therefore difficult to state whether the observed changes in the sediment result from one or a combination of these three ecosystem modifications.

Acknowledgments This work was supported by the Swiss National Science Foundation and the Swiss Agency for Development and Cooperation under grant 207021-109710 (Nutrient cycling and methane production in Lake Kivu).

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Chapter 10
Methane Formation and Future Extraction in Lake Kivu

Alfred Wüest, Lucas Jarc, Helmut Bürgmann, Natacha Pasche, and Martin Schmid

Abstract This chapter summarises the current knowledge on the vertical distribution of methane (CH_4) and its formation in Lake Kivu. Additionally, we review the objectives and restrictions under consideration for sustainable extraction (safe, environmentally acceptable, and economically effective) of the enormous amount of CH_4 from the lake. The harvested CH_4 will be used to produce electricity which is desperately needed in both neighbouring countries: the Democratic Republic of the Congo and Rwanda.

From a system-analysis point of view, the following processes need to be included as the minimum for adequately evaluating the vertical and temporal development of the lake CH_4 during extraction: (1) *in situ* CH_4 formation occurring in the permanently stratified, anoxic deep-water, (2) CH_4 oxidation in the oxic surface water, (3) natural lake-water upwelling caused by subaquatic springs, (4) artificial

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lake-water up- and downwelling due to extraction- and reinjection-related flows, and (5) upward diffusion caused by double diffusive convection and weak turbulence. Water density is parameterised as a function of temperature, salinity, and the two gases carbon dioxide and CH_4. For the sake of clarity of the presentation, we use a simplified 4-box analysis and are neglecting the diffusion process (5). This allows for the essence of the CH_4 extraction challenge to be conveyed while avoiding excessive complexities.

The system analysis for different CH_4 extraction concepts clearly reveals that the depth of reinjection of the CH_4-depleted deep-water is critical for the sustainability of the extraction and an optimal CH_4 harvesting plan. Here, the suitability of different reinjection scenarios is compared by evaluating each of them in terms of the objectives "safety" (water column stability), "lake ecological integrity" (nutrient upward fluxes), and "economic viability" (amount of harvestable CH_4). Comparison of model simulations, run over 50 years, revealed that (1) using lake surface (dilution) water for adjusting the density of the reinjection water and (2) reinjecting the nutrient-rich deep-water in the top 190 m are both unacceptable in terms of sustainability.

10.1 Introduction

Lake Kivu is among the most extraordinary lakes in the world. With a maximum depth of ~485 m, the "classical" lake-water constituents, such as temperature, salinity (Schmid et al. 2010), nutrients (phosphate, ammonium, and silica) as well as the gases carbon dioxide (CO_2) and methane (CH_4) all increase with depth. This peculiarity is caused by the inflow of warm, ion- and CO_2-rich water from deep subaquatic springs (Chap. 2). The high density of the intruding water leads to an unusually strong stratification which suppresses turbulence and reduces diffusion of dissolved substances (such as nutrients and gases) out of the permanently anoxic deep-water. This sealing effect of the stratification, combined with the high rate of CH_4 formation (Pasche et al. 2011), has resulted in the accumulation of ~65 km^3 of CH_4 (Fig. 10.1) and ~300 km^3 of CO_2 (at 0°C and 1.013 bar; Schmid et al. 2005; Tietze 1978).

The CH_4 in Lake Kivu is a boon and a bane. On one hand, this enormous amount of CH_4 provides a unique opportunity for making use of the CH_4 such as for producing electricity with a total commercial value of 10–40 billion dollars (Jones 2003; Expert Working Group 2009). On the other hand, a potential limnic gas eruption, as has occurred in Lakes Monoun and Nyos (Sigurdsson et al. 1987; Kling et al. 1987; Tietze 1992), is a threat to the ~2 million people living close to the lakeshore, especially in view of the continuous increase of the CH_4 content in the last decades (Schmid et al. 2005; Pasche et al. 2011). Removing the gases in the upcoming decades, particularly the less-soluble CH_4, is therefore critical for preventing a catastrophic outgassing. Although the basic concept of CH_4 extraction is straightforward (Fig. 10.1), many scientists and engineers have struggled over the details of this unprecedented challenge (Data Environnement 2003; Tietze 2007; Wüest et al. 2009).

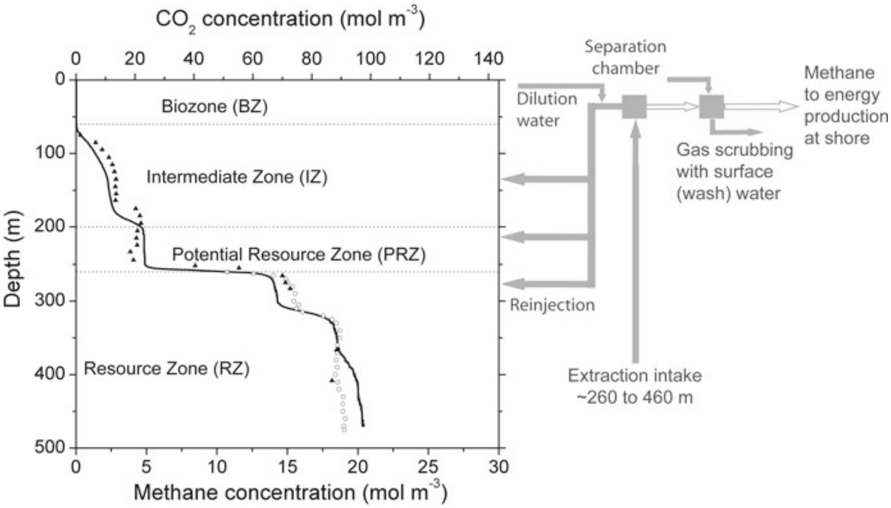

Fig. 10.1 Left: Measured profiles of CH_4 (open and black symbols indicate two different measurement methods) and CO_2 (black line), according to Schmid et al. (2005). In addition, the black line also indicates the CH_4 profile assumed to be proportional to CO_2 (as used in model calculations). The four lake zones are defined by the CH_4 content and its formation rates (details in Table 10.1): *Biozone* (BZ, negligible CH_4 and CO_2), *Intermediate Zone* (IZ, low CH_4 concentrations), *Potential Resource Zone* (PRZ, not yet harvestable CH_4 concentrations) and *Resource Zone* (RZ, harvestable CH_4 concentrations). Right: Schematic of CH_4 extraction from the deep-water of the RZ. After lifting, the CH_4-rich water is degassed in the separation chamber. While the CH_4-depleted deep-water is reinjected into the lake (to the left), CO_2 and hydrogen sulphide (H_2S) are washed from the stripped gases (to the right) and finally the cleaned CH_4 is piped to the shore. Full and empty arrows represent flows of water and gases, respectively

Besides reducing the risk of a limnic eruption, the extraction needs to account for maintaining the ecological integrity of the lake. Finally, the extraction has to be economically viable and should aim at maximising CH_4 harvest. By considering these objectives together, the extraction has a well-defined perspective. The goal is (1) to harvest as much CH_4 as possible, while (2) maintaining the overall lake stratification and (3) restricting nutrient fluxes to the surface within reasonable limits relative to natural conditions. In this chapter, we present four reinjection scenarios and evaluate their pros and cons with respect to these objectives after 50 years of extraction. We use a simple 4-box model which allows for discussing the essential impacts of different scenarios while avoiding complexity. A more comprehensive analysis, based on one-dimensional modelling and including additional processes and variables, has recently been published (Wüest et al. 2009).

This chapter is structured as follows: first, the CH_4 concentrations in the lake as well as the sources and sinks of CH_4 are reviewed and the resulting CH_4 accumulation without extraction is quantified. Then, reinjection scenarios are defined and their consequences are quantified and assessed. The chapter ends with conclusions relevant for the planning of the reinjection scheme.

10.2 Methane Concentrations

Methane is known to accumulate in permanently stratified and anoxic water bodies. For examples, concentrations of up to 1.4 mol m^{-3} were observed in Lake Matano (Crowe et al. 2011), up to 4.4 mol m^{-3} in Lake Pavin (Assayag et al. 2008) and 3 mol m^{-3} in Sakinaw Lake (Vagle et al. 2010). Although concentrations in Lake Kivu do not reach the maximum of 21.8 mol m^{-3} observed in permanently ice-covered Lake Untersee (Wand et al. 2006), they are by far the highest globally in large lakes.

Concentrations in Lake Kivu, increasing stepwise with depth (Fig. 10.1), can qualitatively be interpreted as a quasi-steady-state profile resulting from three processes: (1) the different CH_4 formation rates below and above 260 m depth (Sect. 10.3), (2) the subaquatic intrusions of CH_4-free spring water in the top 260 m (Table 10.1) creating steep gradients (such as the chemocline in 255–262 m depth; Chap. 2) and diluting the upwelling water, and (3) the oxidation of CH_4 when it approaches the oxygen-containing surface layer (Sect. 10.3).

Currently, the layer below 260 m, here called *Resource Zone* (RZ), is economically viable for CH_4 extraction (45 km^3 at 17 mol m^{-3}). The total gas pressure is in favourable support of an extraction as gas bubbles are generated at a depth of 150–200 m due to pressure decrease as deep-water is lifted in a tube (Fig. 10.1). The layer between 200 and 260 m depth, the so-called *Potential Resource Zone* (PRZ), shows average CH_4 concentrations of 5.4 mol m^{-3} (Table 10.1). This CH_4 is currently difficult to exploit, but may become so, if concentrations increase further or if more efficient CH_4 harvesting techniques are developed in the future. The *Biozone* (BZ; top 60 m) contains hardly any CH_4, as the surface layer is convectively mixed annually during the dry season, and subsequently the BZ is, at least partly, oxic for most of the time (Chap. 4; Borges et al. 2011). Therefore the BZ is also called mixolimnion in other chapters of the book (Chap. 2). The zone underneath, the so-called *Intermediate Zone* (IZ; 12 km^3 at 2.3 mol m^{-3}) will probably never become of economic interest, even though there is also CH_4 formed (Fig. 10.2). Dilution by subaquatic springs and high upwelling rates limit CH_4 from accumulating to an extractable concentration level. The CH_4 in the lake is distributed horizontally to about equal shares between the Democratic Republic of the Congo and Rwanda (Fig. 2.1 in Chap. 2). The definition of the four zones is shown in Fig. 10.1 and details of the zones' properties are provided in Table 10.1.

CO_2 concentrations in the deep water of the lake are almost five times as high as CH_4 concentrations (Fig. 10.1). However, because CO_2 is much more soluble, its contribution to the total gas pressure is only about 1/4 of that of CH_4 (Schmid et al. 2004).

10.3 Formation and Accumulation of Methane in Lake Kivu

Whereas CO_2 is of geogenic origin (subaquatic springs), CH_4 is most probably formed by biogenic processes (Deuser et al. 1973; Tietze 1978; Tietze et al. 1980; Schoell et al. 1988; Pasche et al. 2011). Fermentation of sedimentary organic matter

Table 10.1 Physical and geochemical characteristics as well as CH_4 formation and accumulation over the next 50 years in the four zones of Lake Kivu

Zone properties	BZ	IZ	PRZ	RZ	Total
Depth range, m	0–60	60–200	200–260	260–485	0–485
Zone volume, km^3	132	229	70	118	549
Area of upper boundary, km^2	2,368	2,019	1,282	1,053	2,368
Zone sediment area, km^2	349	737	229	1,053	2,368
Salt content, 10^6 t	145	521	228	640	1,534
Mean salinity, kg m^{-3}	1.1	2.3	3.3	5.4	2.8
CO_2 content (2004), km^3	0.1	42	38	214	294
Phosphate, 10^3 t P	1	227	161	620	1,010
Mean phosphate concentration, g P m^{-3}	0.01	1.0	2.3	5.2	1.8
CH_4 content (2004), km^3	0	11.9	8.5	44.7	65.1
Mean CH_4 concentration (2004), mol m^{-3}	0	2.3	5.4	16.9	5.3
CH_4 formation rate, g C m^{-2} $year^{-1}$ (km^3 $year^{-1}$)	0	49 (0.067)	49 (0.021)	93 (0.18)	72 (0.27)
CH_4 formation during 50 years, km^3	0	3.4	1.0	9.1	13.6
CH_4 net storage during 50 years, km^3	0	~0.6[a]	0.2	6.2	~7.0[a]
Subaquatic spring water flow, km^3 $year^{-1}$	0	0.69	0.47	0.14	1.3
Upwelling at lower boundary, m $year^{-1}$	0.65	0.48	0.14	0	
Upwelling at upper boundary, m $year^{-1}$		0.65	0.48	0.14	
Water residence time in zone, years	44[b]	180	110	840	183[b]

The zones BZ, IZ, PRZ, and RZ are explained in the text of Sect. 10.2

[a] The overall storage rate of CH_4 is about half of the formation rate, as ~35 g C m^{-2} $year^{-1}$ is lost to the BZ (Pasche et al. 2011). The change in the IZ cannot be modelled adequately by this box model, as about half of the loss to the BZ is by upward diffusion

[b] The water residence time in the BZ is determined not only by the upwelling as in the other zones, but by the lake total outflow of ~3.0 km^3 $year^{-1}$ (Table 2.1 in Chap. 2) equivalent to ~1.3 m $year^{-1}$

and methanogenesis occur throughout the entire deep-water (below 60 m depth; mostly at the sediment surface). During the degradation of organic matter, CH_4 is formed by two processes (Conrad 1999): at least 2/3 of the CH_4 is formed by

1. acetoclastic methanogenesis: $CH_3COOH \rightarrow CO_2 + CH_4$,

and up to 1/3 by

2. CO_2 reduction: $CO_2 + 4H_2 \rightarrow 2H_2O + CH_4$.

Observed concentrations and isotopic compositions in the PRZ and IZ can be explained using these fractions (Pasche et al. 2011).

Conversely, in the RZ, different relative contributions to the CH_4 formation have been estimated (Schoell et al. 1988; Pasche et al. 2011):

1. 30–40% (~1/3) by acetoclastic methanogenesis, and
2. 60–70% (~2/3) by CO_2 reduction.

The observation that in the RZ only ~1/3 CH_4 is formed by acetoclastic methanogenesis – different to the PRZ/IZ – implies that a maximum of 50% of the CH_4 stems from fermentation of organic matter, and therefore an additional source of CH_4 must exist. This could be either (1) due to the reduction of geogenic CO_2, with mostly geogenic H_2 or (2) by direct inflows of geogenic CH_4, or a combination of both.

According to Pasche et al. (2011) the CH_4 formation rate – expressed as carbon per horizontal (sediment) area and per unit time – is ~49 g C m^{-2} $year^{-1}$ to a depth of 260 m and ~93 g C m^{-2} $year^{-1}$ below. Horizontally integrated over the entire anoxic sediment surface (below 60 m depth) and over the entire lake volume, the two CH_4 sources yield a total rate of CH_4 formation of ~72 g C m^{-2} $year^{-1}$ or 0.27 km^3 $year^{-1}$, respectively (Table 10.1).

Due to the subaquatic inflows, CH_4-rich water is pushed upwards and subsequently reaches shallower sulphate- and oxygen-containing layers (Chap. 3). The CH_4-oxidising consortia of archaea and sulphate-reducing bacteria eliminate a small fraction of CH_4 between 60 and 90 m depth. The large bulk of CH_4 is oxidised to CO_2 by aerobic methanotrophic bacteria in the oxic surface layer (top 60 m). The total oxidation rate (Jannasch 1975; Pasche et al. 2011) is ~35 g C m^{-2} $year^{-1}$, which is about half of the formation rate given above. The release to the atmosphere is negligible (~0.2 g C m^{-2} $year^{-1}$; Borges et al. 2011; Chap. 4).

Comparing rates of formation and oxidation indicates that ~50% of the newly formed CH_4 is accumulating within the lake. This storage rate corresponds to 0.14 km^3 $year^{-1}$, or 0.2% $year^{-1}$ if compared to the total CH_4 content (Table 10.1). The measurements by Schmid et al. (2005) indicated that CH_4 concentrations had increased by up to ~15% since the measurements of Tietze (1978), corresponding to a rate of increase of ~0.5% $year^{-1}$. Therefore we expect that the current formation exceeds the steady-state. However, so far we could not determine with certainty, whether more geogenic H_2 or CH_4 has entered into the deepest layers, or whether the amount of CH_4 produced from degrading organic material has increased. There are indications in support of the latter hypothesis: The ^{14}C and ^{13}C contents of CH_4 have changed since the 1970s (Tietze 1978; Pasche et al. 2011) suggesting more CH_4 being formed from recent organic material. We consider this as realistic in view of several processes which may potentially have increased the sedimentation of *in situ* produced organic matter (Isumbisho et al. 2006; Muvundja et al. 2009; Sarmento et al. 2009; Pasche et al. 2010; Chap. 9). Based on this CH_4 formation excess, we can expect an increase of the lake CH_4 content from currently 65 to 72 km^3 over the next 50 years (Table 10.1), if CH_4 would not be harvested.

The upward flux of CH_4 relative to the total amount in the lake (standing crop) reveals the average residence time of CH_4 in the lake of several hundred years. Using the current upward flux (Table 10.1) as the long-term steady-state rate of CH_4 formation, the calculated residence time is ~400 to ~500 years.

10.4 Methane Extraction: Approach and Scenarios

The basic extraction principle is summarised schematically in Fig. 10.1. While CH_4-rich deep-water is lifted in a tube, the *in situ* hydrostatic pressure in the upward moving water decreases until the total gas pressure exceeds the *in situ* pressure and causes supersaturation (Wüest et al. 2009). Above this critical depth, bubbles are generated in the tube at a depth of 150–200 m, and the gases CO_2 (largest gas fraction), H_2S (smallest gas fraction), and CH_4 are stripped off the water. The evolving gas-water mixture in the tube is strongly buoyant and drives the flow up to the surface. In the separation chamber (Fig. 10.1), the deep-water is diverted from the stripped gases, which are subsequently washed by gas-free near-surface water. Thanks to the high solubilities of CO_2 and H_2S, these two gases are almost quantitatively removed. The washed gas flow, now concentrated in CH_4 but still containing some CO_2 (and traces of the other gases H_2S, N_2, O_2, and water vapour), is piped to the shore and converted to electricity. The H_2S-containing wash-water can be released into the top of the IZ (~70 m depth), where the absence of oxygen should assure that fishes are not present and hence not harmed. As long as wash-water is discharged into the stratification, horizontal mixing is diluting the poisonous H_2S before upwelling entrains it into the oxic BZ. There H_2S could become detrimental to zooplankton and other aerobic organisms. For large-scale extraction, the natural H_2S flux into the BZ (Pasche et al. 2009) would be significantly increased and its impacts on oxygen depletion and on oxygen-dependent organisms need to be carefully monitored. The CH_4-depleted deep-water is returned deep into the lake (Fig. 10.1). As shown in the following discussion, the depth of reinjection is the most critical design parameter in regard to all three objectives of the extraction. Therefore, in the following, we concentrate specifically on the selection of the depth ranges for the release of the CH_4-depleted deep-water and provide an evaluation for four different reinjection scenarios.

From a purely economic point of view, releasing the CH_4-depleted water at the lake surface would be most beneficial. As compensation for the upward flow in the tube, the layers of the lake-water would be drawn down, and in consequence, CH_4 from the IZ would no longer reach the surface and the CH_4 oxidation would almost come to a halt (some upward diffusion would continue). This implies that the entire newly formed CH_4 of 0.27 km^3 $year^{-1}$ would stay in the lake and could eventually become available for harvesting in the future. For two reasons, however, this most simple approach is unfortunately not feasible: First, the deep-water holds enormous amounts of nutrients, such as phosphate, ammonium, silica, and trace-elements (Chap. 3). Injecting deep-water into the BZ would severely increase the naturally occurring upward flux of those nutrients (Table 10.2), and the reduced substances, especially ammonium, would create large oxygen depletion. Possible consequences would be anoxic conditions in large parts of the BZ, as well as a drastic growth of phytoplankton (eutrophication), including potentially harmful cyanobacteria. Second, the salinity would increase in the BZ, and decrease in the RZ and thereby weaken the lake stratification (Table 10.2). It is, however, important to maintain

Table 10.2 Comparison of deep-water reinjection scenarios (explained in the text) projected over 50 years

	RZ-INJ	PRZ-INJ	IZ-INJ	BZ-INJ
Reinjection depth, m	260	200	60–200	0–60
Extraction = reinjection/dilution water flow, km^3 year^{-1}	2.4/0			
Phosphate upward flux over 50 years, t P year^{-1}	1,300	1,300[a]	3,400	12,400[b]
Salinity difference over entire depth after 50 years, kg m^{-3}	5.5–1.1	4.6–1.1	3.5–1.4	3.3–2.7
CH_4 extracted/harvested over 50 years, km^3	44.7/40.3[c]			
CH_4 oxidation, over 50 years, g C m^{-2} year^{-1} (km^3 year^{-1})	35 (0.13)	33[d] (0.12)	32 (0.12)	>24[e] (0.09)
Stock of CH_4 in RZ + PRZ after 50 years, km^3	13.4 + 6.5	22.0[d]	18.9 + 3.6	18.9 + 3.5
CH_4 concentration in RZ after 50 years, mol m^{-3}	5.0	5.2[d]	7.1	7.1
Evaluation summary[f]	RZ-INJ	PRZ-INJ	IZ-INJ	BZ-INJ
Safety (stratification)	++	+ to ++	–	– –
Lake ecology (nutrients)	++	+ to ++	– –	– –
Economy (harvestable CH_4)	0	+	++	++
Total assessment	+4	+4	–1	–2

[a] No change of nutrient upward fluxes during 50 years of extraction. In the following ~100 years, the nutrient upward fluxes would increase to a not-well-known level. However, such an increase is expected to occur even when the CH_4 is not harvested (Wüest et al. 2009)

[b] 12,400 t P year^{-1} is the initial phosphate input by the reinjected deep-water. This would later approach a steady-state value of 6,800 t P year^{-1}

[c] We assume that the RZ volume is replaced during the 50 years of extraction. The input by new CH_4 formation is added to the CH_4 stock for easier comparison; the extracted CH_4 volumes are therefore in reality slightly different

[d] For scenario *PRZ-INJ* the RZ and PRZ will become mixed (one box) after 50 years (Fig. 10.3). If it is possible to remove almost all CO_2, then a slight gradient in the RZ + PRZ volume may be maintained with slightly larger concentrations in the RZ. For the CH_4 budgets we assume that CH_4 can be extracted from the RZ before mixing occurs

[e] Oxidation in the BZ for *BZ-INJ* is equal to the reinjected CH_4 (10% of extracted CH_4 from deep-water = 24 g C m^{-2} year^{-1}) plus upward turbulent diffusion. Therefore, at the beginning of extraction the oxidation rate would be significantly higher (~40 g C m^{-2} year^{-1}) but continuously decline to 24 g C m^{-2} year^{-1} over time

[f] Evaluation marks: very favourable (++); suitable (+); neutral (0); not suitable (–); not acceptable (– –)

the strong density stratification, in order to ensure that newly formed CH_4 and CO_2 as well as intruding geogenic CH_4 and CO_2 remain trapped in the deep-water. There, theses gases can accumulate without migrating upwards, whereas in shallow depth large amounts of gases could cause a limnic gas eruption under low-enough pressure.

From a purely ecological point of view, releasing the CH_4-depleted water into the layer of its origin would be ideal, as this approach would maintain entirely the physical structure of the lake, prevent any changes in stratification and avoid any additional fluxes of nutrients or salt within the lake.

In summary, the dialectics becomes obvious: Whereas the first ("surface") reinjection scenario would stimulate unnatural phytoplankton growth and destroy the stratification, the second ("deep") reinjection scenario could potentially dilute the CH_4 resources and jeopardise the economic viability of the long-term extraction. Due to these opposing effects, it is necessary to develop a systematic comparison in order to find an optimal approach. In other more general terms, the challenge of an optimised extraction concept is to fulfil simultaneously the following three objectives:

1. Maintaining strong density stratification and avoiding critical gas concentrations in order to reduce the risk of a limnic gas eruption (**safety**);
2. Maintaining the lake ecological integrity by restricting the extraction-induced nutrient fluxes into the surface layer (BZ) in order to avoid eutrophication (**lake ecology**); and
3. Maximising the harvestable CH_4 (amount of CH_4 stored at high concentration, suitable for extraction) by minimising the losses of CH_4 to the IZ, BZ, and the atmosphere (**economy**).

For comparing the effects of different reinjection depths, we need quantities in order to scale and evaluate how well these scenarios fulfil the three objectives formulated above. As proxies to measure the three objectives' fulfilment, we use the following indicators:

1. *Measure for risk of limnic eruption*: The salinity difference between maximum depth and surface is a reliable indicator for the overall density difference over the entire vertical water column and is thereby an ideal measure for the overall strength of the density stratification. In the more detailed analysis by Wüest et al. (2009), we included also the total gas pressure as an evaluation criterion, which turned out to be strongly correlated to the overall vertical density difference. For extraction from the RZ the gas saturations do not develop to critical levels (Wüest et al. 2009) and we therefore do not discuss the total gas pressure in detail here.
2. *Measure for lake ecological integrity*: The flux of phosphate into the BZ is a representative measure of the lake-internal nutrient fluxes into the BZ and is thereby also a measure of the change relative to the current (near-natural) primary production.

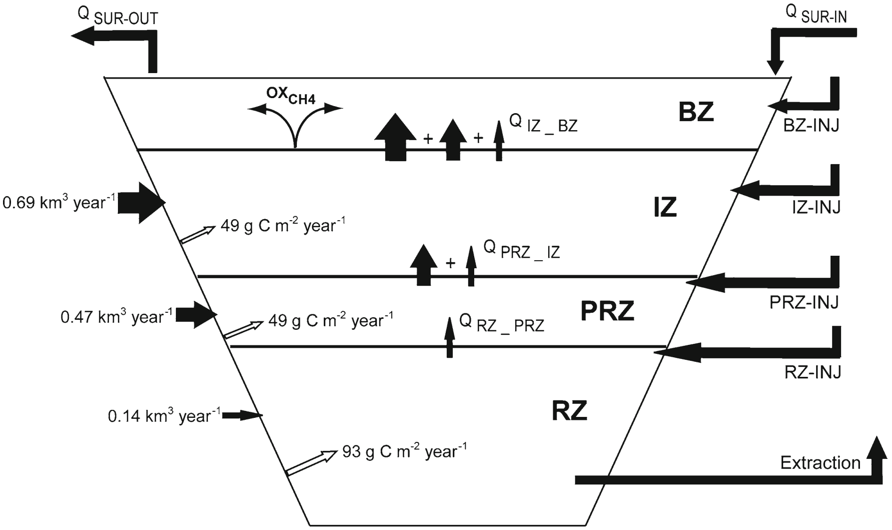

Fig. 10.2 4-box model of the water flows and CH_4 fluxes in Lake Kivu. The formations of CH_4 in the RZ, PRZ and IZ are given by the areal rates (open arrows from left) times the respective sediment areas and are 0.18, 0.021 and 0.067 km^3 $year^{-1}$, respectively (Table 10.1). The natural water inflows from the subaquatic springs into the three zones (black horizontal arrows from left) are based on the analysis by Schmid et al. (2005). These subaquatic water inflows cause upwelling of the lake-water layers of the same flow as indicated by the black vertical arrows. Shown are the water upwelling from RZ to PRZ ($Q_{RZ\text{-}PRZ}$, one arrow), from PRZ to IZ ($Q_{PRZ\text{-}IZ}$, two arrows) and from IZ to BZ ($Q_{IZ\text{-}BZ}$, three arrows). CH_4 transported to the BZ is oxidized (OX_{CH4}). The CH_4 extraction scenarios modify this natural upwelling depending on the depth and flows of the extraction (arrow to right) and the reinjection (*BZ-INJ* to *RZ-INJ*, arrows from right), respectively. The surface flow, $Q_{SUR\text{-}IN}$, refers to the net water surface inflow (rivers, precipitation and evaporation; Chap. 2), whereas $Q_{SUR\text{-}OUT}$, indicates the lake outflow via Ruzizi river (Chap. 2)

3. *Measure for the economic viability*: The amount of harvestable CH_4 (harvested plus left in RZ + PRZ) is a quantitative measure of how much of the lake CH_4 resource is extractable and can be made available for use. We have to be aware that this purely-physical measure does not represent an economic quantity, as the commercial value of CH_4 is a function of time, and the effort to extract CH_4 varies with its concentration and the CO_2/CH_4 ratio. Those two factors influencing the commercial value of CH_4 are evidently not accounted for in the amount of harvestable CH_4.

In the next section, we test the following scenarios for the reinjection of the CH_4-depleted water (Fig. 10.2):

- ***BZ-INJ***: injection into the BZ (0–60 m depth)
- ***IZ-INJ***: injection into the IZ (60–200 m depth)
- ***PRZ-INJ***: injection into the upper end of PRZ (200 m depth)
- ***RZ-INJ***: injection into the upper end of RZ (260 m depth).

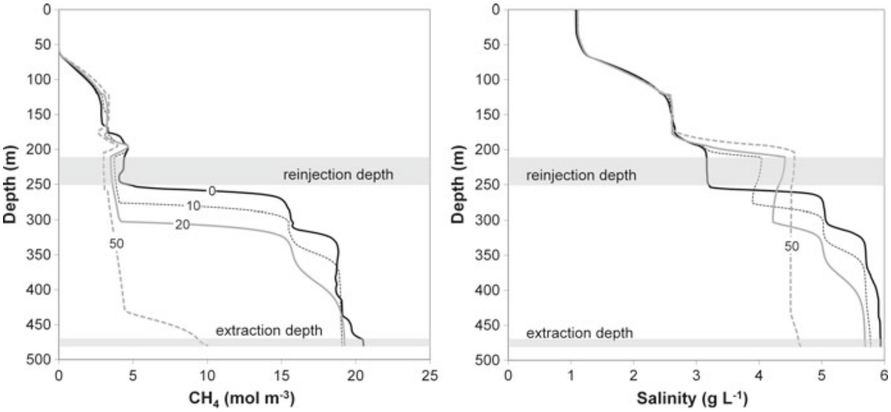

Fig. 10.3 Vertical profiles of CH_4 concentrations (left) and salinity (right) for 50 years of simulation with the model of Wüest et al. (2009) for the *PRZ-INJ* scenario with the indicated extraction and reinjection depths (grey shaded). Additional assumptions are: extraction flow of 75 $m^3\ s^{-1}$, gas removal of 90% (CH_4) and 20% (CO_2), and CH_4 formation rates as described in Table 10.1 and Fig. 10.2. Numbers on the profiles indicate the years of simulation. The effect of the drawdown – due to the extraction flow – is apparent from the downwelling of the salinity and the CH_4 profiles

For all four scenarios, the following assumptions are identical (Table 10.2): The extraction of the entire RZ volume (Table 10.1) is equally distributed over 50 years, causing a water flow of 2.4 $km^3\ year^{-1}$ (=118 km^3/50 years = 75 $m^3\ s^{-1}$). Further we assume 90% extraction efficiency for CH_4 and 20% removal efficiency for CO_2. 10% of CH_4 is assumed to be returned to the lake at the indicated reinjection depth. Dilution water flow (Fig. 10.1) has been set to zero (Table 10.2). Upwelling and drawdown cause fluxes in and out of the four boxes. We assume that the stratifications within the boxes remain during the 50 years. An exception represents the *PRZ-INJ* scenario (Fig. 10.2), where the high density of the reinjected water causes mixing of the PRZ and RZ (Fig. 10.3). For this *PRZ-INJ* scenario, we treat therefore RZ + PRZ as one box (Table 10.2). The internal loading of CH_4 from the IZ to the BZ (= CH_4 oxidation) is set to 35 g C $m^{-2}\ year^{-1}$ for the current CH_4 content in IZ (see above) and assumed to be proportional to the future IZ content.

10.5 Comparison of the Methane Extraction Scenarios

In Table 10.2 the results for the four scenarios (Fig. 10.2) are summarised. In the following each of the scenarios is explained and evaluated regarding the three objectives introduced.

BZ-INJ: For this scenario the deep-water is extracted from the RZ and reinjected into the BZ (Fig. 10.2). As indicated above, this scenario would cause a drastic increase of nutrients and salinity in the surface layer, as the deep-water carries high nutrient concentrations (phosphate: 5.2 gP m^{-3}) and salinity of 5.4 kg m^{-3} (Table 10.1). The extraction-related salt flux would progressively increase salinity in the BZ and decrease salinity in the RZ until the entire lake would be almost homogeneous. After several hundred years, the salinity would approach the current surface value of 1.1 kg m^{-3} throughout the entire water column.

A most conservative option for this scenario would be to extract only the amount of newly-formed CH_4 (0.27 km^3 $year^{-1}$, Table 10.1), and operate the extraction as steady-state into the future. To maximise the CH_4 harvest, the extraction water flow could be identical to the subaquatic spring-water flow (~1.3 km^3 $year^{-1}$, Table 10.1) such that almost no CH_4 would be lost to CH_4 oxidation (some loss due to turbulent diffusion would remain). The stability would be substantially reduced, as surface salinity would increase to 2.7 kg m^{-3} after 50 years. The steady-state deep-water CH_4 concentration of 9.3 mol m^{-3} and the fact that CO_2 would be removed during extraction from the deep-water to the atmosphere would not cause any safety concerns.

However the ecological effects would be drastic for the first several decades: The BZ would expand in depth as the surface salinity, rising to ~2.7 kg m^{-3} in the future, would become higher than the current salinity in the upper IZ and therefore seasonal mixing of the BZ would deepen. The phosphate flux into the surface layer would increase from the current 1,300 t P $year^{-1}$ (Pasche et al. 2009) to 6,800 t P $year^{-1}$, causing massive changes to ecosystem processes – potentially including harmful effects like toxic cyanobacteria blooms (Paerl et al. 2011). Furthermore the upward flux of reduced substances to the BZ would be similarly increased, with a high risk of creating anoxic conditions in the lower part of the BZ during the first decades.

Although the described negative effects would relax in the long-term, during the first decades the lake ecological integrity would be massively deteriorated. Therefore, this simple approach is unfortunately not acceptable (Table 10.2).

IZ-INJ: The deep-water is extracted from the RZ and reinjected into the IZ (Fig. 10.2). Generally, the same arguments hold as for *BZ-INJ* (above), although to a lesser extent. The release of the CH_4-depleted deep-water would increase nutrients and salinity in the IZ. These two properties are then carried by the natural upwelling (subaquatic springs; ~0.65 m $year^{-1}$; Table 10.1; Fig. 10.2) into the BZ. As a result, the salinity would increase in the BZ to 1.4 kg m^{-3} and decrease in the RZ to 3.5 kg m^{-3}. After 50 years the vertical salinity gradient over the entire depth range would be only about half of today. This could probably be acceptable, as the gases CH_4 and CO_2 would be massively reduced by then. However the phosphate flux would be 2.6-fold of today (3,400 t P $year^{-1}$), with similar negative ecological consequences for eutrophication as those described above for the *BZ-INJ* scenario.

The *IZ-INJ* scenario highlights another important practical aspect – the use of dilution water (Fig. 10.1) to adjust the density of the reinjection water. The important disadvantage is the additional compensatory flow due to the dilution water from the surface. For reasons of continuity, the same amount of lake-water is lifted to the surface and thereby enhancing the natural upwelling and therefore the nutrient fluxes into the BZ. Hence, the use of dilution water is strictly discouraged (Expert Working Group 2009; Wüest et al. 2009).

The advantage of this *IZ-INJ* scenario is the large amount of 18.9 km^3 of CH_4 left in the RZ after 50 years. When water from the PRZ, which contains already high CH_4 concentrations, is drawn down into the RZ, where CH_4 is formed at a higher rate, then CH_4 is further accumulated in the long-term and remains available for future use. After 50 years, the deep-water concentrations would reach ~7.1 mol m^{-3} and approach economically harvestable levels. In total 22.5 km^3 would remain in the RZ + PRZ volume combined (Table 10.2).

PRZ-INJ: For this scenario the deep-water is extracted from the RZ and released at 200 m depth (Fig. 10.2), at the upper end of the PRZ. Here, the problematic arguments from above do not apply anymore. As shown in Table 10.2, during the 50 years of extraction, the phosphate flux would not increase. Although the nutrient concentrations in the PRZ will eventually increase, it takes longer than 50 years for the upwelling of PRZ water up to the BZ. In the long-term, however, the phosphate released into the PRZ would reach the BZ, although diluted by the subaquatic spring inflows between the PRZ and the BZ. Most probably also under purely natural conditions the nutrient upward flux will increase (non-steady-state argument in Sect. 10.2) to a not-well-defined level (variabilities of subaquatic springs over centuries). The salinity in the RZ would decrease from 5.4 to 4.6 kg m^{-3} and therefore the salinity gradient over the entire lake depth would decrease from 4.3 to 3.5 kg m^{-3}, which is certainly still acceptable (Table 10.2).

The disadvantage of this approach is that the RZ and the PRZ would become entirely homogenous in salinity (Fig. 10.3 right) and therefore the two zones would be almost mixed (Wüest et al. 2009). The total remaining CH_4 in the combined volume of RZ + PRZ would be 22 km^3, which corresponds to a concentration of 5.2 mol m^{-3} (Table 10.2). This implies that for further extraction, one would need to wait for several decades until CH_4 would again reach economically interesting concentrations (Fig. 10.3 *left*). For this scenario, also the one-dimensional model of Wüest et al. (2009) was run as an exemplary case. The results (Fig. 10.3) confirm well the CH_4 budgets but also demonstrate some remaining vertical structures of the water constituents after 50 years of extraction. The input of those constituents occurs mainly in the RZ while higher in the water column subaquatic inflows are diluting the concentration profiles (Fig. 10.3).

RZ-INJ: For this scenario the deep-water is extracted from the RZ and reinjected at the top of the RZ at 260 m (Fig. 10.2). The vertical density structure, the stability of the density stratification, and the nutrient flux to the BZ all remain practically unaffected. After 50 years of extraction, the total remaining CH_4 in the RZ and PRZ together amounts to 19.9 km^3 with almost the same concentration, 5.0 mol m^{-3}, as for the *PRZ-INJ* scenario.

More detailed one-dimensional calculations, which take the density-driven mixing and the vertical diffusion into account, are needed as the difference between *RZ-INJ* and *PRZ-INJ* is small (Table 10.2). For example it should be checked whether with more removal of CO_2 the *PRZ-INJ* scenario could be run without homogenising the entire volume of RZ + PRZ. Another important aspect is the evaluation to what extent the different temporal evolution of CH_4 concentrations of those scenarios would affect the economic efficiency of gas extraction.

10.6 Conclusions for Methane Extraction Approaches

The presented results for the four different reinjection scenarios, by using a 4-box model, and the evaluation of the advantages and disadvantages (Table 10.2) yield the following conclusions:

1. Reinjection into the *Biozone* is not at all acceptable, as it would destroy the natural vertical structure of the lake. In particular it would remove the stable density stratification and extend the seasonal thickness of the *Biozone*, lead to substantial increase in phytoplankton growth (eutrophication), increase the oxygen depletion due to the reduced substances input and therefore change the physical, chemical and biological character of the lake entirely.
2. Reinjection into the *Intermediate Zone* is also not acceptable, as the nutrient and reduced substances fluxes into the *Biozone* would still substantially increase. Even though the nutrients and the reduced substances are not directly released at the surface, the natural upwelling caused by the subaquatic springs transports those injected substances to the *Biozone*, where they contribute to oxygen depletion and to primary production in the *Biozone.* Although the effects would be less drastic compared to (1), releasing the nutrient-rich, high-salinity, and reduced substances-charged deep-water into the upwelling-driven IZ, would still substantially modify the biogeochemical structure and ecological integrity of Lake Kivu.
3. Following the argument of (2), any extraction-related artificial flows, bringing water from the surface to deep layers, cause compensatory upwelling of the lake-water. Using surface water for density adjustment of the reinjection water (dilution) on a large scale is therefore not acceptable. This conclusion is not relevant for the wash-water which can be released right below the *Biozone*: This volume flow is comparably small and is recycling low-nutrient surface water within the *Biozone*. The proper management (release depth and dilution) of the poisonous H_2S is, however, important.
4. Both injections into the *Potential Resource Zone* and into the *Resource Zone* maintain strong and sufficient density stratification, avoid enhanced nutrient fluxes within the time scale (50–100 years) of the extraction, and yield similar amounts of harvestable (extracted plus to-be-extracted) CH_4. The injection into the *Potential Resource Zone* – at least initially – avoids dilution of the *Resource Zone*, but has some impact on density stratification. The management prescriptions for gas extraction from Lake Kivu (Expert Working Group 2009) only allow the *Resource Zone* injection method, in order to avoid any significant changes in the density stratification.

More detailed simulations and analyses such as those made by Wüest et al. (2009) are required in order to predict the safety – in particular the density stratification and the vertical distribution of the gases – and the ecological impacts as well as the economic efficiency of the *Potential Resource Zone* and the *Resource Zone* injection scenarios. It is important to check the sensitivity of the results versus not-well-known model parameters such as the CH_4 formation rate and the location and discharge of the subaquatic springs. We also expect that CH_4 fluxes out of the sediment will increase while CH_4 is removed from PRZ and RZ. Also the option of varying the removal rate of CO_2 and thereby influencing the density of the reinjected water needs to be further evaluated. Finally, for the discussion of the economic aspects of the different scenarios, it will be important to estimate the economic value of the CH_4 resource as a function of CO_2/CH_4 concentrations at the intake depth and the varying technological costs for the sustainable scenarios.

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Chapter 11
Lake Kivu Research: Conclusions and Perspectives

Jean-Pierre Descy, François Darchambeau, and Martin Schmid

Abstract In this chapter the knowledge gained from the interdisciplinary research on Lake Kivu presented in the previous chapters is synthesized. The importance of the sublacustrine springs as a driving force for physical and biogeochemical processes is highlighted, the special properties of the lake's food web structure are discussed, and the consequences and impacts of both the introduction of a new fish species and methane extraction are evaluated. Finally, a list of open research questions illustrates that Lake Kivu has by far not yet revealed all of its secrets.

11.1 Conclusions

11.1.1 The Dynamics of the System: The Importance of the Subaquatic Springs

Observations of vertical profiles of temperature, conductivity and solutes in Lake Kivu show a remarkable horizontal homogeneity and temporal constancy. At first sight, these observations may suggest that Lake Kivu is a relatively simple, near-steady-state

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system, where no significant changes are expected to occur within time scales of years or even decades. In contrast, biological activity in the surface waters varies strongly from year to year (Chaps. 5 and 7), observations from sediment cores indicate a sudden change that occurred in the 1960s (Chap. 9), and methane concentrations seem to have increased significantly within only a few decades (Chap. 10).

The results presented in this book highlight the relative importance of the subaquatic springs in the lake for governing these processes and their time scales. The subaquatic springs were previously mainly considered as suppliers of the carbon dioxide and minerals dissolved in the deep waters, but not as the driving forces for the vertical structure of density stratification and the nutrient supply to the mixolimnion by upwelling. In fact, the deepest water layers, below the main density gradient, are almost decoupled from the rest of the lake. They are fed by subaquatic springs which are enriched in dissolved salts and carbon dioxide. The discharge of these springs is relatively weak, and residence times of nutrients and gases in the deep zone are on the order of several hundred to one thousand years. At 250 m depth, one or several springs with a much higher discharge introduce less saline, nutrient-poor and cooler water into the lake. These springs create the main density gradient and, together with further springs at shallower depths, are the driving forces for the upwelling of nutrient-rich water towards the lake surface.

The upwelling is the major source for the mixolimnion of the nutrients limiting phytoplankton growth, i.e. nitrogen and phosphorus (Chaps. 3 and 5). However, on short time scales, the access of primary producers to these continuously upwelling nutrients is modified by the mixing dynamics in the surface layer. As a consequence of temporary stratification of the mixolimnion during the rainy season, severe nutrient limitation occurs, both by N and P, which remain trapped in the monimolimnion. This contrasts with the situation in the dry season, when vertical mixing (caused by higher wind velocity and lower surface temperature) increases nutrient supply to the euphotic zone, promoting phytoplankton growth and the subsequent mesozooplankton peak (Chaps. 5 and 7). The fish yield also responds, with some delay, as shown by the increased catches of sardine occurring in the November-January period (Chap. 8).

Because of the dominance of the upwelling and the comparatively low importance of external inputs for nutrient supply to the surface layer, the ecosystem is not expected to react sensitively to increased external nutrient inputs on short time scales (Chap. 3). However, it should be kept in mind that a large fraction of additional external nutrient inputs will be transferred by settling particles to the monimolimnion where they will be mineralized and may accumulate over hundreds of years. The effective and then irreversible impacts of increased external nutrient inputs may thus only become visible after centuries.

The sudden increase in net sedimentation, especially of inorganic carbon, but also of nutrients, observed in sediment cores and dated to the 1960s, must be a result of a sudden change that occurred at this time in the surface layer of the lake (Chap. 9). Whether this was caused by an increased upwelling in connection with higher regional rainfall or by changes in the food web structure due to the introduction of *Limnothrissa miodon*, still remains unclear, as both these changes occurred at almost the same time. However, it seems probable that the same process led to an increase in methane concentrations in the deep water (Chap. 10).

11.1.2 The Food Web Structure

The structure of the pelagic food web of Lake Kivu has usually been perceived as rather simple: a linear food chain involving a phytoplankton dominated by few taxa of cyanobacteria, diatoms and cryptophytes, a mesozooplankton with two main copepod species and one cladoceran, and the sardine, *Limnothrissa miodon*, at the top, without a piscivorous predator. A more detailed analysis of the available data reveals that the food web is actually more complex, in particular because it comprises a previously neglected microbial food web, fuelled by autochthonous organic matter provided by phytoplankton DOM (dissolved organic matter) excretion (Chap. 6). The microbial food web of Lake Kivu seems to contribute significantly to consumer productivity: microbes are diverse and abundant in the mixolimnion and the redoxcline, and production of heterotrophic bacteria is high when compared to phytoplankton production (Chap. 6). Still, phytoplankton composition matters, as it determines to a large extent the fate of primary production: the large diatoms dominating in the dry season tend to settle, while cyanobacteria, dominating in the rainy season, seem not to be consumed by mesozooplankton, as revealed by analysis of fatty acid markers (Masilya 2011). Therefore, a substantial part of the primary production contributes to a downward nutrient and carbon flux (Chap. 9) rather than to the pelagic productivity. Moreover, recycling of sedimenting organic matter may be relatively limited due to the shallow oxic layer, which varies seasonally with a maximum depth of 60 m. In contrast, in Lake Tanganyika, most of the sedimenting organic matter is decomposed and recycled in the 120–200 m of oxygenated waters (Descy et al. 2005).

Figure 11.1 presents a synthesis of the available data on production rates and carbon flows between the main ecosystem compartments of the pelagic zone of Lake Kivu. A first look at the annual production rate of producers (phytoplankton) and consumers (mesozooplankton and fish), shows that primary and secondary productions of Lake Kivu are typical of a tropical oligotrophic lake, and compare well with those of Lakes Malawi and Tanganyika, which are also deep and oligotrophic (Chaps. 5 and 7). Worth noting in particular is that mesozooplankton production is remarkably similar to that of those other great lakes, despite the grim predictions made about the consequences of the sardine introduction (Chaps. 7 and 8). It also appears that the trophic transfer efficiency at the phytoplankton/mesozooplankton interface is quite good (up to 8.3% in 2003), and again in a range found in other great lakes of the same trophic status (Chap. 7). However, this estimate can be misleading, as not all the primary production is edible to mesozooplankton: most likely, copepods cannot ingest the large diatoms, and they cannot feed directly on the smallest plankton. Therefore, it is likely that planktonic crustacean production is sustained partly by microzooplankton (unknown rate 9 in Fig. 11.1): thus, grazing by ciliates and flagellates on bacteria (bacterivory, 7) and on photosynthetic picoplankton (herbivory, 8) is just another pathway to channel pelagic photosynthetic production to consumers, as in Lake Tanganyika (Tarbe et al. 2011), where herbivory dominates the microbial food web. Some contribution of autotrophic bacteria and archaea - methanotrophs, Green Sulfur Bacteria and nitrifiers - is also expected, although the C flux involved might be an order of magnitude lower than that transiting through heterotrophic bacteria.

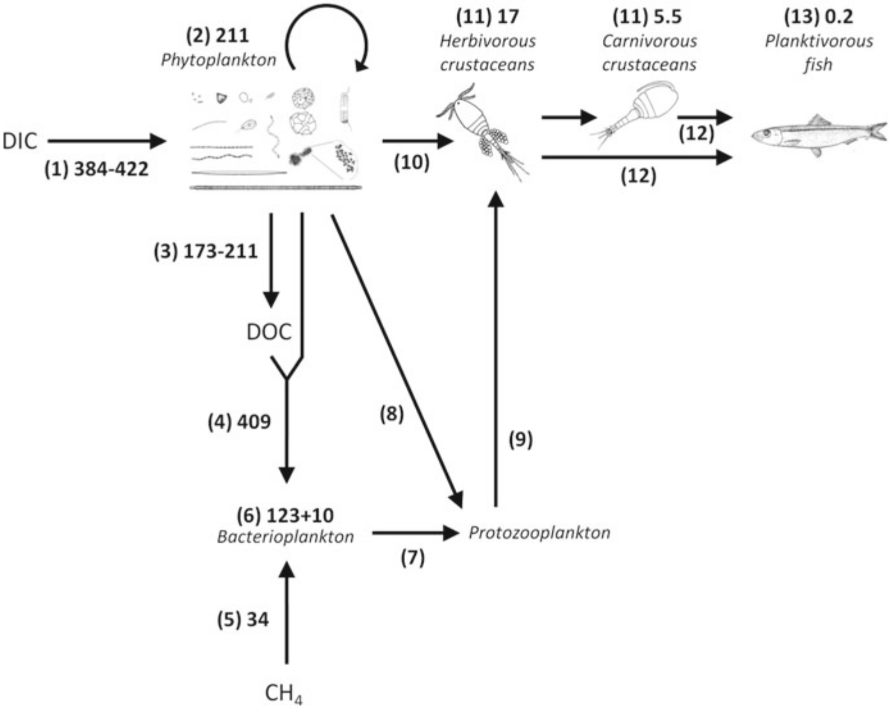

Fig. 11.1 Synthesis of the trophic carbon flows in the pelagic ecosystem of Lake Kivu. Rates are in g C m^{-2} $year^{-1}$. Phytoplankton and zooplankton respiration rates are not taken into account (i.e., rates are net). DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; CH_4, methane. 1: total primary production of phytoplankton (Chap. 6); 2: particulate primary production of phytoplankton (Chap. 5); 3: dissolved primary production of phytoplankton (Chap. 6); 4: bacterioplankton carbon demand (Chap. 6), 5: aerobic and anaerobic methane oxidation by methanotrophs (Pasche et al. 2010); 6: biomass production of heterotrophic (Chap. 6) and methanotrophic bacterioplankton; 7: bacterivory of protozooplankton; 8: herbivory of protozooplankton; 9: mesozooplankton grazing on protozooplankton; 10: crustacean zooplankton grazing on phytoplankton; 11: biomass production of herbivorous and carnivorous crustacean zooplankton (Chap. 7); 12: predation of planktivorous fish on mesozooplankton; 13: planktivorous fish production (Chap. 8)

A second look at the data summarized in Fig. 11.1 allows suspecting that the transfer of crustacean production to fish is lower than the mean trophic transfer efficiency of 10% commonly observed in pelagic food chains (Pauly and Christensen 1995). We recall here that the pelagic fishery yield in Lake Kivu did not meet the historical expectations (Chaps. 1 and 8): *Limnothrissa* production (~9,000 t $year^{-1}$ or ~38 kg ha^{-1} $year^{-1}$, Chap. 8) is lower than sardine production in Lake Tanganyika (~210 kg ha^{-1} $year^{-1}$ considering an estimated mean sardine biomass of 60 kg ha^{-1}, Szczucka 1998, and a conservative production:biomass ratio of 3.5 $year^{-1}$, Coulter 1981). We believe that this estimate of sardine production in Lake Kivu is robust - other authors have obtained similar figures (Chap. 8). Then, it seems that there is a major bottleneck here, which might have several explanations. As total phytoplankton and zooplankton productions are comparable in both lakes (Chaps. 5 and 7), productivity effects do not explain the difference in *Limnothrissa* production. Other hypotheses must be considered.

First, the predation rate of *Limnothrissa* on mesozooplankton may greatly depend on zooplankton availability, abundance and size. *Mesocyclops aequatorialis*, the largest copepod species in Lake Kivu, is abundant solely during a few weeks, at the end of the dry season (Chap. 6). During the rest of the year, zooplankton is far less abundant and composed of smaller species (e.g., *Thermocyclops consimilis*, *Tropocyclops confinis*, *Coronatella rectangula*). *Limnothrissa* may therefore suffer from a lack of dietary resources during a major part of the year. This hypothesis is supported by observations of the fish ingestion rate: Masilya (2011) found that *Limnothrissa* ingested daily three times more copepods in the dry season than in the rainy season. In contrast, the mesozooplankton communities of both Lakes Malawi and Tanganyika comprise a large-bodied calanoid copepod, which is an efficient grazer. For instance, in Lake Malawi, the lowest encountered biomass of the calanoid copepod *Tropodiaptomus cunningtoni* during the 1992–1993 surveys was 511 mg dry weight (DW) m^{-2} (Irvine and Waya 1999) while in Lake Kivu long periods with biomass of *M. aequatorialis* below 100 mg DW m^{-2} have been observed (for example from April to July 2004; Isumbisho 2006). Also, in the other Great Rift lakes, other resources than planktonic crustaceans are available to the planktivorous fish, such as shrimps (Lake Tanganyika) and *Chaoborus* larvae (Lake Malawi).

Another process that can reduce predation efficiency on crustaceans in the rainy season is the copepod vertical migration down to the aphotic layer (Chap. 7). Such a refuge below the euphotic layer is deeper in Lake Tanganyika, where light penetrates to deeper layers (mean euphotic depth = ~35 m, Stenuite et al. 2007) than in Lake Kivu (mean euphotic depth = 20 m, Chap. 5). Sardines, like all zooplanktivorous fish, are visual predators. The predation efficiency should then be reduced by the relatively weak light penetration in Lake Kivu: thus, a shallow oxycline in the wet season and relatively low water transparency may explain why pelagic fish are mostly located in the 0–45 m layer (Chap. 8).

Finally, variations of recruitment and larvae survival play a significant role in clupeid stock fluctuations (Mölsä et al. 2002; Kimirei and Mgaya 2007). In Lake Kivu, the growth of *Limnothrissa* larvae and juveniles takes place in the inshore zone, which is spatially reduced and where fishermen often use inappropriate fishing techniques for catching the young fish. This activity, coupled with the incidence of predation by *Limnothrissa* adults and other fish species in inshore areas (De Iongh et al. 1983; Masilya et al. 2011), might significantly reduce larvae survival. Likewise, little access to benthic resources, which are significant food items for *Limnothrissa* in both Lake Kivu (De Iongh et al. 1983; Masilya 2011; Masilya et al. 2011) and in Lake Tanganyika (Matthes 1968), may not allow feeding the spawning stock and fry during the rainy season, when planktonic resources are low (Chap. 7).

A conclusion ensuing from these reflections is that an increase of the nutrient supply to the mixolimnion would increase primary production, but may not necessarily result in a proportional increase of fish yield (Sect. 11.1.4).

11.1.3 Consequences of the Sardine Introduction on Biogeochemical Processes and Ecosystem Structure and Function

As discussed in Chap. 7, the effect of *Limnothrissa miodon* introduction in Lake Kivu, which was devoid of any pelagic fish until the 1950s, is a key issue, primarily because alien species introductions have often produced adverse effects on ecosystems. In the case of Lake Kivu, Dumont (1986), from observations of a decrease of zooplankton abundance, along with the disappearance of a major grazer, predicted that the fishery would collapse.

What we see in Lake Kivu decades later is quite different: it seems that the pelagic fish stock has remained similar to that at the end of the 1980s, the fishery is thriving (even though it doesn't reach the same yield as the sardine fishery of Lake Tanganyika) and zooplankton biomass is remarkably similar to that of other Rift lakes. A comprehensive assessment of changes in ecosystem structure is difficult because of the lack of precise quantitative historic data and the long time series required in order to representatively sample the high seasonal and interannual variability. Nevertheless, a trophic cascade effect can be detected in Lake Kivu. For instance, we were able to estimate that total crustacean biomass has declined by two-third since the 1950s, based on the zooplankton biomass data of Verbeke (1957), as a result of the planktivore introduction (Chap. 7). A substantial release of the grazing pressure on phytoplankton may have resulted from the mesozooplankton decline. As a result, phytoplankton biomass might have increased, reaching values twice as high as in the northern part of Lake Tanganyika where trophic status and primary productivity are similar to those of Lake Kivu (Chap. 5).

However, the change in zooplankton biomass does not completely explain the relatively high chlorophyll *a* concentration in Lake Kivu, as zooplankton biomass is now roughly the same in the two lakes. Part of the explanation may lie in phytoplankton edibility for herbivorous cyclopoids. Indeed, Lake Kivu phytoplankton comprises a large proportion of grazing-resistant forms, such as very long diatoms (*Nitzschia* and *Fragilaria*) or very small cyanobacteria (*Synechococcus*), both out of the typical size range (5–50 μm) of the copepod preys. Accordingly, the mesozooplankton diet consists of diatoms, chrysophytes and cryptophytes, plus some bacterivorous microzooplankton, but almost no cyanobacteria, as indicated by recent data based on fatty acid analysis in components of the pelagic food web (Masilya 2011).

However, these hypotheses involving changes in grazing pressure and in phytoplankton biomass and composition cannot be validated, as we miss data on phytoplankton structure before the sardine introduction: only sediment studies can reveal the changes that occurred in Lake Kivu after the 1950s. First analyses of short sediment cores confirmed that significant changes must have occurred in the lake around 1960 (Chap. 9). The sedimentation flux of carbonates suddenly increased by an order of magnitude, while net sedimentation of organic matter increased by ~50%; both changes may be indicative of increased primary production. In contrast, fluxes of biogenic silica seem to have reduced by 30%, which may have been caused by a change in the diatom assemblage or a reduced contribution of diatoms to primary production. An evaluation of how exactly these changes observed in the sediments relate to changes in the food web requires more detailed palaeolimnological studies, using different proxies, such as fossil pigments, fossil diatoms and stable isotopes of C, N and Si.

11.1.4 Potential Ecological Impacts of Methane Extraction

Recent studies have provided additional evidence that methane concentrations have indeed been increasing in the past few decades, even though probably at a lower rate than has previously been feared (Pasche et al. 2011; Chap. 10). The enormous potential impact of a gas eruption from the lake and the tectonic and volcanic activity in the region clearly call for the methane being removed from the lake. Nevertheless, this must be done with utmost care, in order not to artificially create a dangerous situation or to irreversibly damage the ecosystem. The possible impacts of different methane exploitation scenarios have been discussed in Chap. 10. The most important consequence of these analyses is that the water from the deep zone must be returned below 200 m depth.

In case of shallower re-injection, the nutrient upward flux would increase, driving higher primary and secondary production. At first sight, this might be beneficial to the fishery as a sardine stock increase would be expected. However, two elements must be taken into account. First, as the rainy season stratification takes place, the lower mixolimnion becomes quickly oxygen-depleted from the decay of particulate and dissolved organic matter. Increased primary production in combination with the additional supply of reduced substances would likely result in more severe and quicker oxygen depletion, reducing the thickness of the water layer accessible to fish (see Chap. 8 for the fish distribution in the mixolimnion). Second, it seems, according to the available productivity estimates at the different trophic levels, that there is a bottleneck at the mesozooplankton-fish interface, so that an increase in planktonic production may not necessarily result in a proportional increase of fish production. Then, the likely consequence of a higher nutrient upward flux would be a degradation of water quality, with negative effects on the fisheries, rather than a benefit.

11.2 Outlook

Many bookshelves would undoubtedly have been filled with scientific publications on Lake Kivu, if it were located in Europe or North America. A search for “Lake Kivu” in scientific publication databases at the time of writing of this book yielded ~100 publications. About the same number were found for a single publication year on each of the North American Great Lakes. The studies presented in this book filled some of the knowledge gaps, but many more questions remain open than have been answered. In the following we outline some of the relevant issues that need to be addressed in future research on Lake Kivu.

The physical and geochemical processes in the lake still need to be investigated further. What is the provenance and the composition of the water that feeds the subaquatic springs? Is there a geogenic source of hydrogen (H_2) that may be used to reduce CO_2 into CH_4? And if yes, what is its past and present importance compared to the H_2 produced during the anaerobic degradatation of organic matter? Do the springs introduce substances such as sulfate that could be used to oxidise methane and thus affect the methane cycling in the lake? What is the discharge and composition of the subaquatic springs in Kabuno Bay, and how is it hydrologically linked to the main basin?

In order to study the physics of the mixolimnion in more detail, it would be important to collect meteorological data on the lake. Because of the steep shores, stations located on the shore cannot be expected to be representative for the conditions on the lake. This is especially true for wind speed, precipitation and radiation. Data from the lake itself could help to better constrain the water balance and could be used to drive models of the mixing processes in the surface layer.

The sediments of Lake Kivu certainly contain much more information than what we have learnt from them up to now. Can the history of the lake be reconstructed in more detail and with more confidence? Can we gain information on the past nutrient cycle, phytoplankton, zooplankton and fish communities? Is there a way to confirm or reject the hypothesis that gas eruptions from the lake did occur in the past? Can we derive more information on past fluctuations in lake levels, salinity or temperature? Model predictions for the impacts of methane extraction currently assume near steady-state of the hydrological conditions (Chap. 10). A better knowledge of the lake history would be important to understand how its present state evolved and to derive scenarios for its future development.

The microbiology of the lake has hardly been touched. Microbially-mediated processes are of utmost importance for the biogeochemistry of the lake. The water column of Lake Kivu provides a huge natural laboratory with a sequence of different redox conditions, and large volumes of water with nearly constant properties over long time scales, where all kinds of microbially-mediated processes could be studied. We currently do not know which organisms are supporting which processes in this system, and even less do we know about their physiological constraints. The subaquatic springs could also be hot spots for microbial diversity and activity.

During the last decade, a continuous set of limnological and phytoplankton data has been collected in Lake Kivu. This dataset is unique for an African lake. It highlights important inter-annual variations of the duration and the magnitude of the seasonal mixing and the phytoplankton bloom. What are the main climatic drivers of this mixing? And how may these inter-annual variations be explained? Connections with climate fluctuations at regional and global scales must be investigated. Another key issue is to examine the link between annual phytoplankton and fish productivity. Are the years with high phytoplankton blooms characterized with high *Limnothrissa* production? If so, can we predict the annual fish yield based upon some regional or global climate indexes? These issues are of great importance for local populations which depend on fish resources.

Despite the low fish biodiversity, much knowledge still needs to be acquired, in particular on the ecology of the fish species. For instance, the endemic cichlids inhabiting the littoral zone have been exploited by local fishermen for a long time and very little is known about their biology and ecology. The same is true for the littoral food web, which plays a role in the maintenance of the pelagic *Sambaza* population: it is there that the *Limnothrissa* larvae grow, but what are the respective contributions of allochtonous, littoral and pelagic prey to *Limnothrissa* growth, maintenance, and reproduction at their different life stages? Abundance and production of benthic resources (algae, macrophytes and invertebrates) have never been investigated in Lake Kivu. Are they different from those in Lakes Tanganyika and Malawi? We may suspect that the important calcareous incrustations of submerged substrates in Lake Kivu reduce significantly habitat diversity, but does it influence invertebrate abundance and production? Harvesting *Sambaza* larvae with mosquito nets is a common practice in some parts of the lake, and has always been a concern for fish biologists. The larvae are also submitted to predation by the adult *Limnothrissa*, and the impact of cannibalism has never been assessed: is it harmful or beneficial for the *Sambaza* population? A recent cause for concern is the arrival of *Lamprichthys tanganicanus*: does this invader add to the lake biodiversity, increasing fish productivity? What is its impact on littoral and pelagic species? These issues have only been partially addressed so far, revealing the possibility of interspecific competition between *Limnothrissa* and *Lamprichthys* from exploitation of the same planktonic and benthic preys (Masilya 2011; Masilya et al. 2011), calling for monitoring of the recent invader.

Concerning the hazard assessment, no thorough studies have been performed up to now. We know that lava inflows at the lake surface of the size of those during the Nyiragongo eruption in 2002 are harmless (Lorke et al. 2004). But what if there would be a magmatic eruption inside the lake? What is the probability of such an event? How much magma could be released, and would it be sufficient to trigger a gas eruption? And what about an internal tsunami caused by the failure of an unstable slope? How much sediment has accumulated in delta areas? Is there a significant risk of large slope failures? What would be the size of the resulting internal waves? And could such an event be sufficient to trigger a gas eruption?

Finally, the impacts of the upcoming industrial methane exploitation need to be carefully investigated. Because of the long time scales involved, wrong decisions made today may affect the lake irreversibly for several centuries. In order to be able to early identify potentially harmful alterations, it will be important to monitor the development of the lake stratification, but also geochemical processes as well as the biology in the lake with great accuracy. Observations need to be compared with model predictions, and in case of significant discrepancies, the predictive models need to be improved. This will require high-level monitoring efforts, and an open-minded and critical scientific attitude to gain a further understanding of the relevant processes. Although this book has summarized our current knowledge on Lake Kivu, it is clear that there is still a lot to be learned from this fascinating lake.

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