

# Chapter 11

## Lake Kivu Research: Conclusions and Perspectives

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**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).

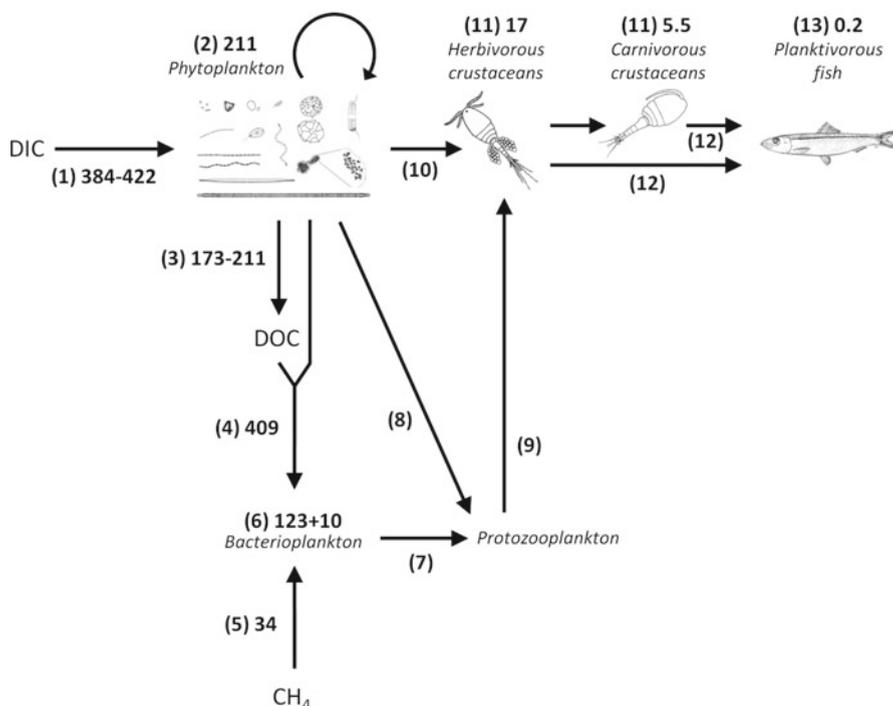
Because of the dominance of the upwelling and the comparatively low importance of external inputs for nutrient supply to the surface layer, the ecosystem is not expected to react sensitively to increased external nutrient inputs on short time scales (Chap. 3). However, it should be kept in mind that 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  $\text{g C m}^{-2} \text{ year}^{-1}$ . Phytoplankton and zooplankton respiration rates are not taken into account (i.e., rates are net). DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; CH<sub>4</sub>, 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 ( $\sim 9,000 \text{ t year}^{-1}$  or  $\sim 38 \text{ kg ha}^{-1} \text{ year}^{-1}$ , Chap. 8) is lower than sardine production in Lake Tanganyika ( $\sim 210 \text{ kg ha}^{-1} \text{ year}^{-1}$  considering an estimated mean sardine biomass of  $60 \text{ kg ha}^{-1}$ , Szcucka 1998, and a conservative production:biomass ratio of  $3.5 \text{ year}^{-1}$ , 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<sup>-2</sup> (Irvine and Waya 1999) while in Lake Kivu long periods with biomass of *M. aequatorialis* below 100 mg DW m<sup>-2</sup> have been observed (for example from April to July 2004; Isumbiso 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  $\mu\text{m}$ ) 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 degradation 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 allochthonous, 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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