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.

F. Darchambeau (✉)
Chemical Oceanography Unit, University of Liège, Liège, Belgium
e-mail: francois.darchambeau@ulg.ac.be

M. Isumbisho
Institut Supérieur Pédagogique, Bukavu, D.R. Congo
e-mail: isumbisho@yahoo.fr

J.-P. Descy
Research Unit in Environmental and Evolutionary Biology, University of Namur, Namur, Belgium
e-mail: jpdescy@fundp.ac.be

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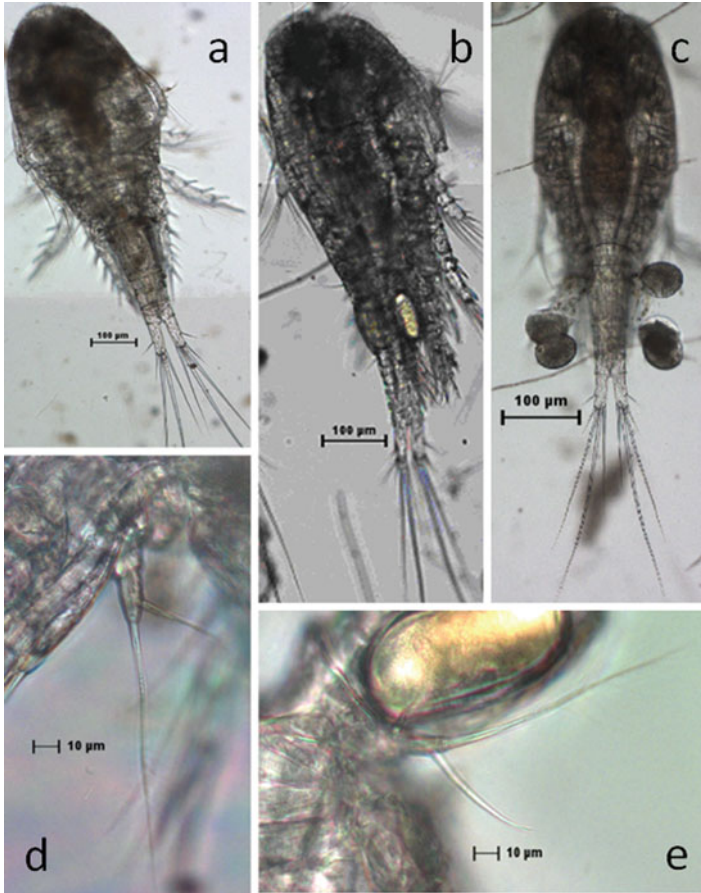
Fig. 7.1 *Mesocyclops aequatorialis*: Adult female without eggs (**a**), adult male (**b**), egg-bearing female (**c**), fifth paw of adult female (**d**) and male (**e**). The scale bars indicate 100 μm (**a**, **b**, **c**) and 10 μm (**d**, **e**), respectively

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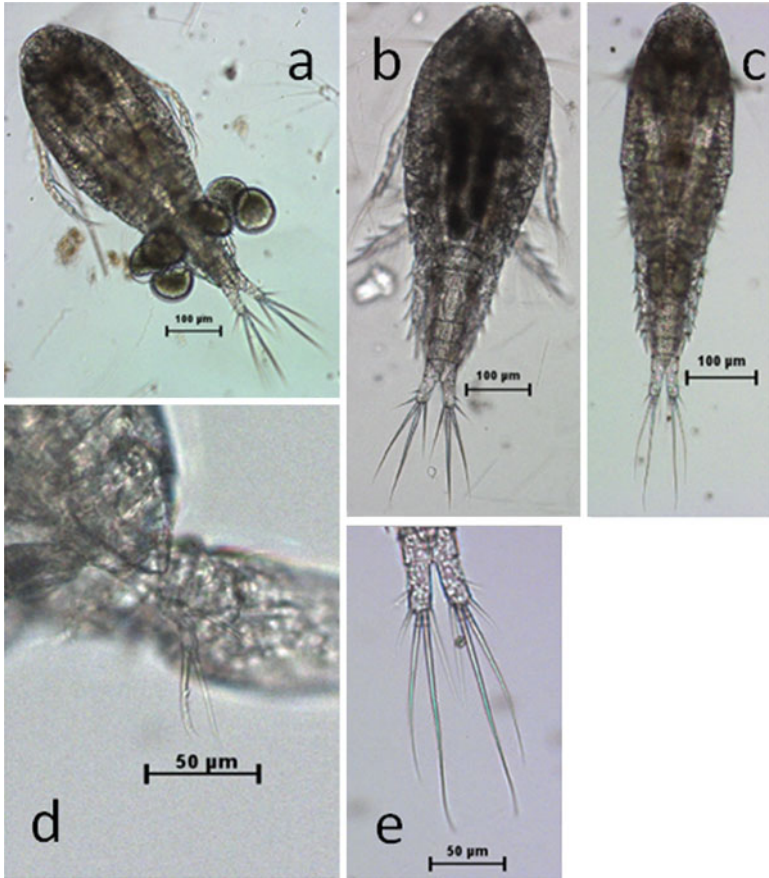
Fig. 7.2 *Thermocyclops consimilis*: egg-bearing female (**a**), female without eggs (**b**), adult male (**c**), fifth paw (**d**) and the furca (**e**). The scale bars indicate 100 μm (**a**, **b**, **c**) and 50 μm (**d**, **e**), respectively

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).

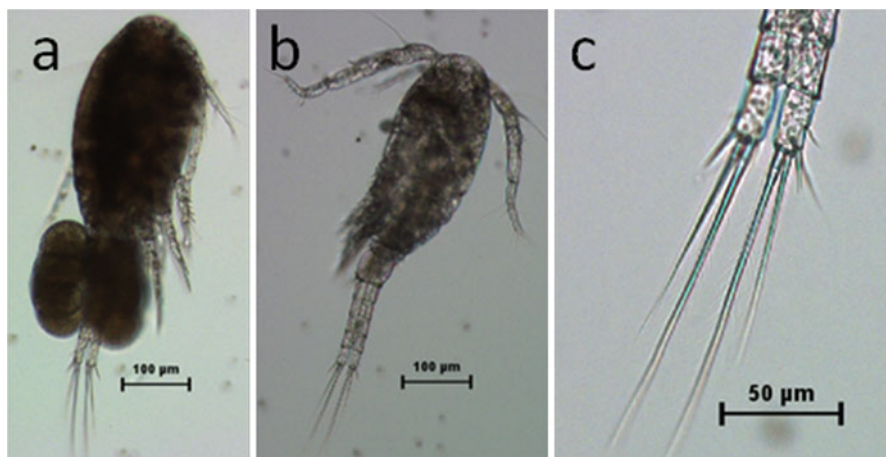In addition, the antennules carried by adult females are 12-segmented.

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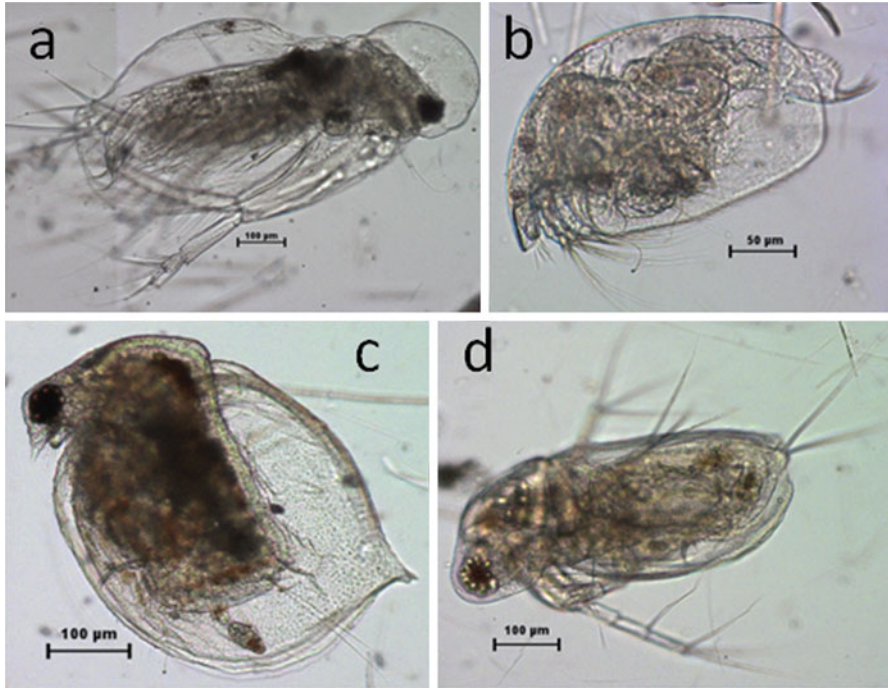
Fig. 7.4 Cladocerans of Lake Kivu: *Diaphanosoma excisum* (**a**), *Coronatella rectangula* (**b**), *Ceriodaphnia cornuta* (**c**) and *Moina micrura* (**d**). The scale bars indicate 100 μm (**a**, **c**, **d**) and 50 μm (**b**), respectively

7.2.3   Rotifera

Rotifera (Fig. 7.5) constitute the most diverse group of Lake Kivu pelagic meta-zooplankton, 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
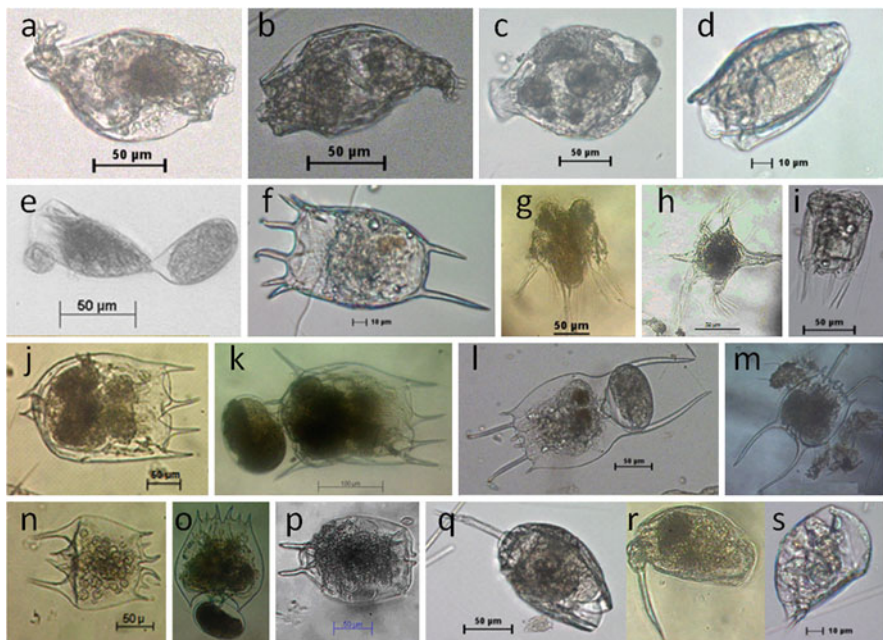
Fig. 7.5 Rotifers of Lake Kivu: Bdelloids (**a–c**), *Anuraeopsis fissa* (**d–e**), *Keratella tropica* (**f**), *Hexarthra* sp. (**g–h**), *Polyarthra* sp. (**i**), *Brachionus calyciflorus* (**j–k**), *Brachionus falcatus* (**l–m**), *Brachionus quadridentatus* (**n–o**), *Brachionus caudatus* (**p**), *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
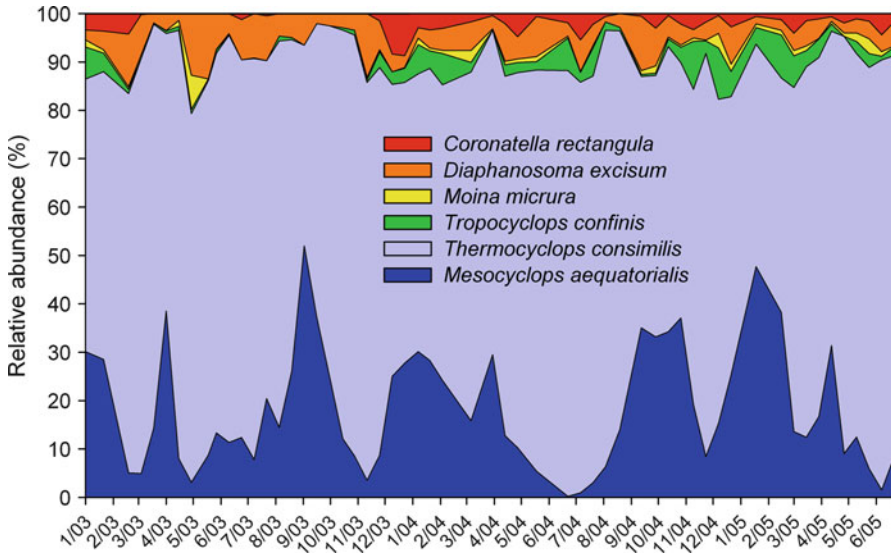
Fig. 7.6 Relative abundance of the six main crustacean species in the mixolimnion of Lake Kivu (Ishungu Basin) from January 2003 to June 2005

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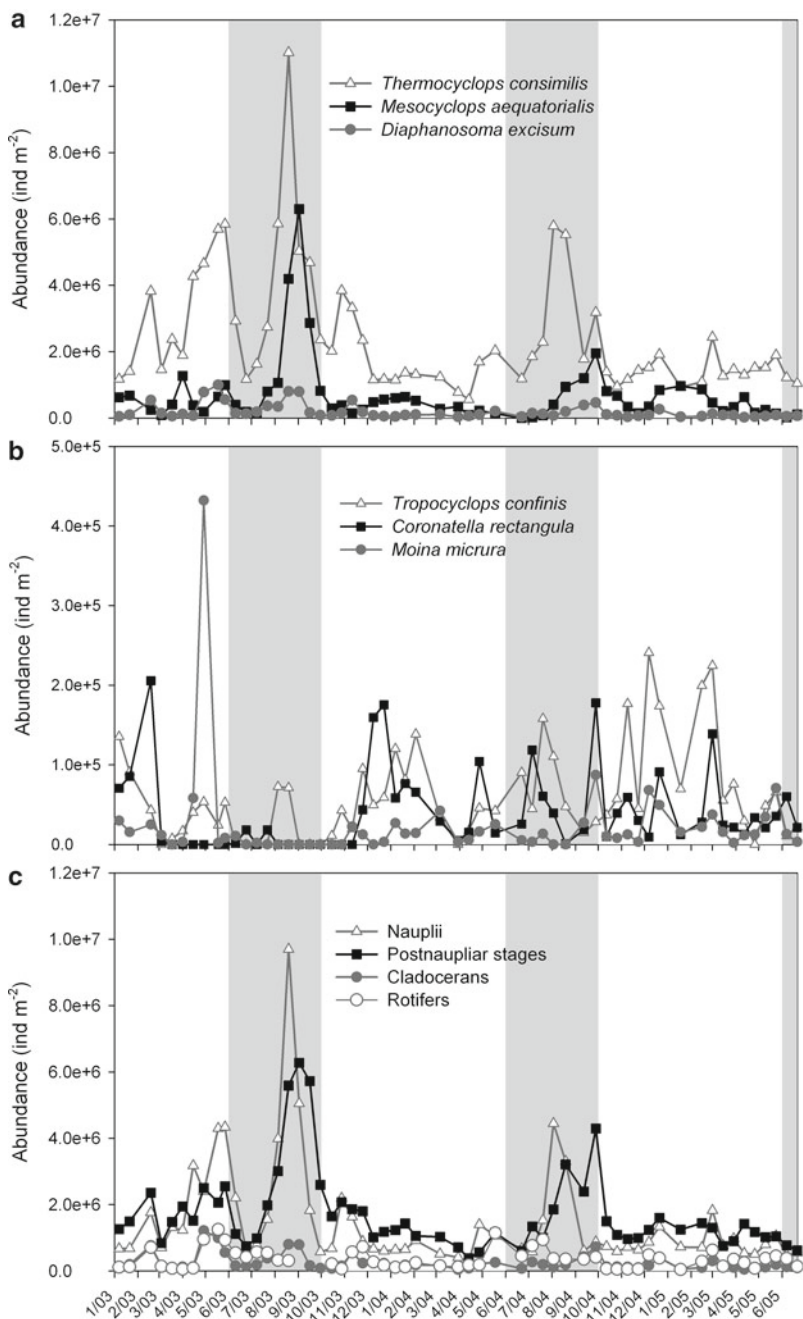
Fig. 7.7 Variation of metazooplankton abundance in the 0–60 m water column of Lake Kivu (Ishungu basin) from January 2003 to June 2005. Note the different scales on the Y-axis for **a**, **b** and **c**. The light grey boxes indicate the dry season periods

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 g C m^{-2}, mean biomass over the
period 2003–2004 was 0.99 g C m^{-2}. For the whole sampling period (2003–2005),
T. consimilis contributed about 61% to crustacean biomass, while *M. aequatoria-
lis* and cladocerans accounted for, respectively, 27% and 11% of annual crusta-
cean 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),
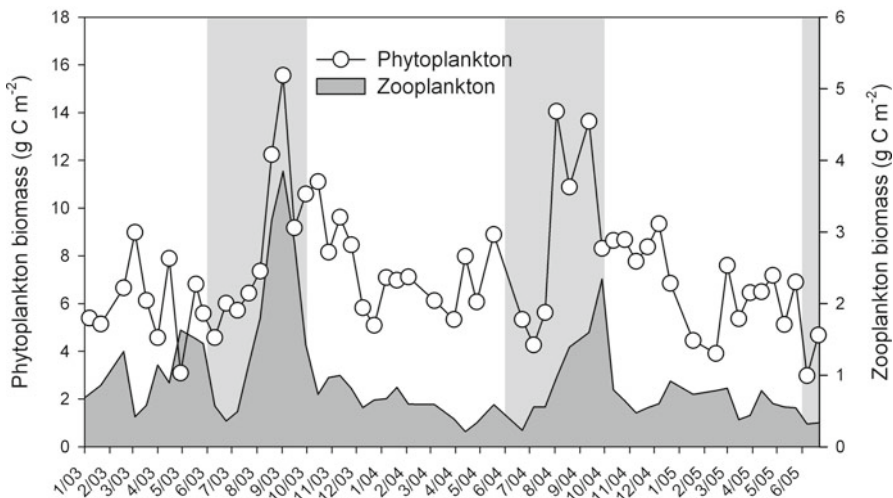and closely followed variations of chlorophyll *a* concentration (Fig. 7.8).

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
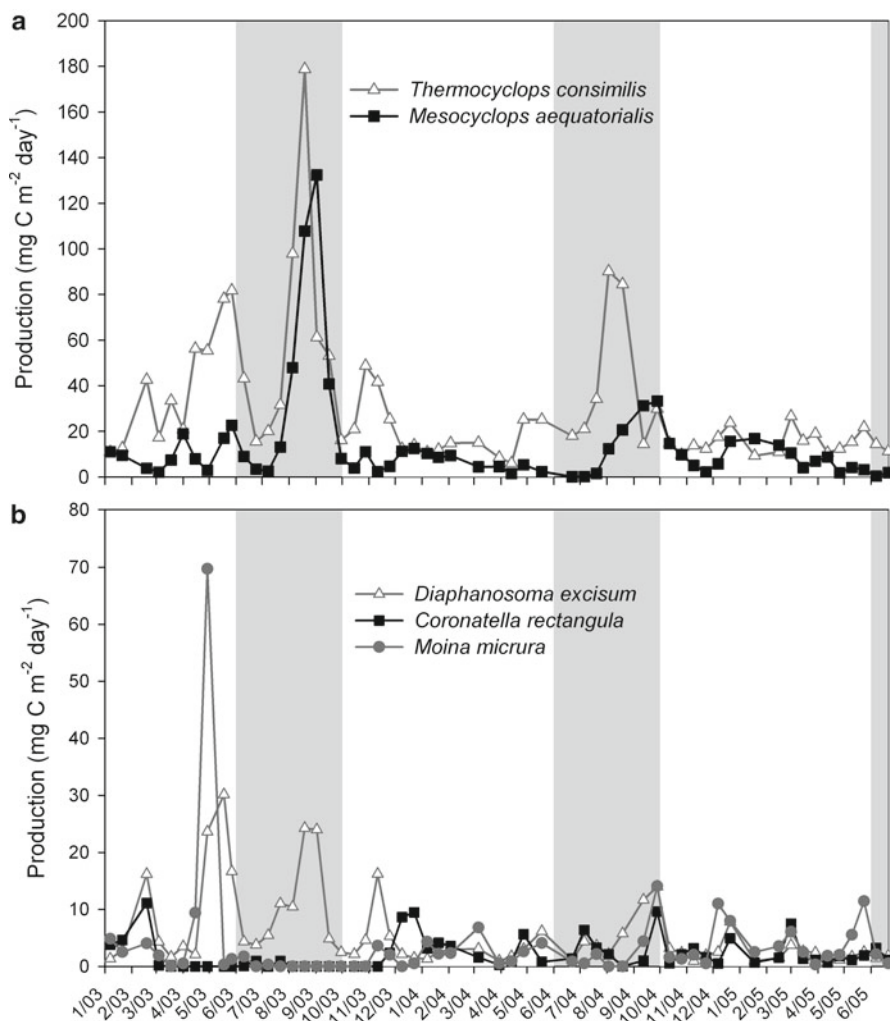periods

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

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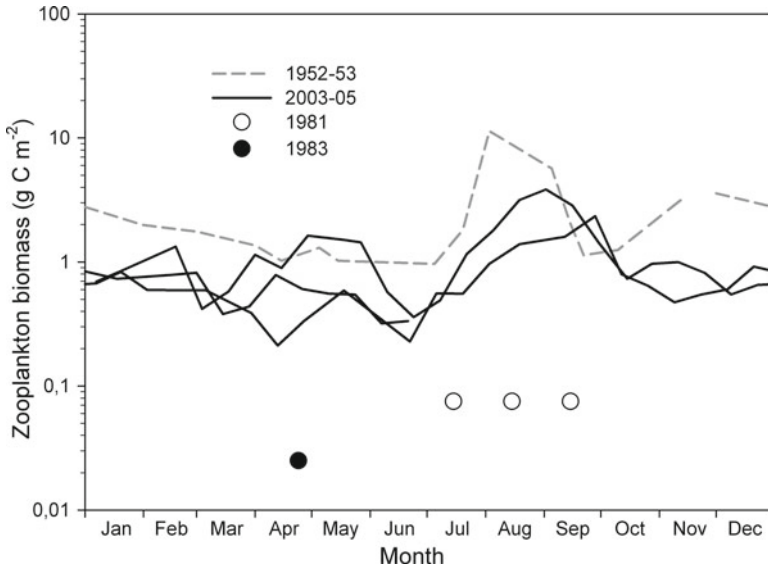
Fig. 7.10 Estimates of zooplankton biomass in Lake Kivu: 1952–1953 data from Verbeke (1957), 1981 data from Reyntjens (1982), 1983 data from Dumont (1986) and 2003–2005 data from the present study. Note the logarithmic Y-scale. See explanations on the calculations in the text

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 zoo-
plankters 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 cope-
pod 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 aph-
otic 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
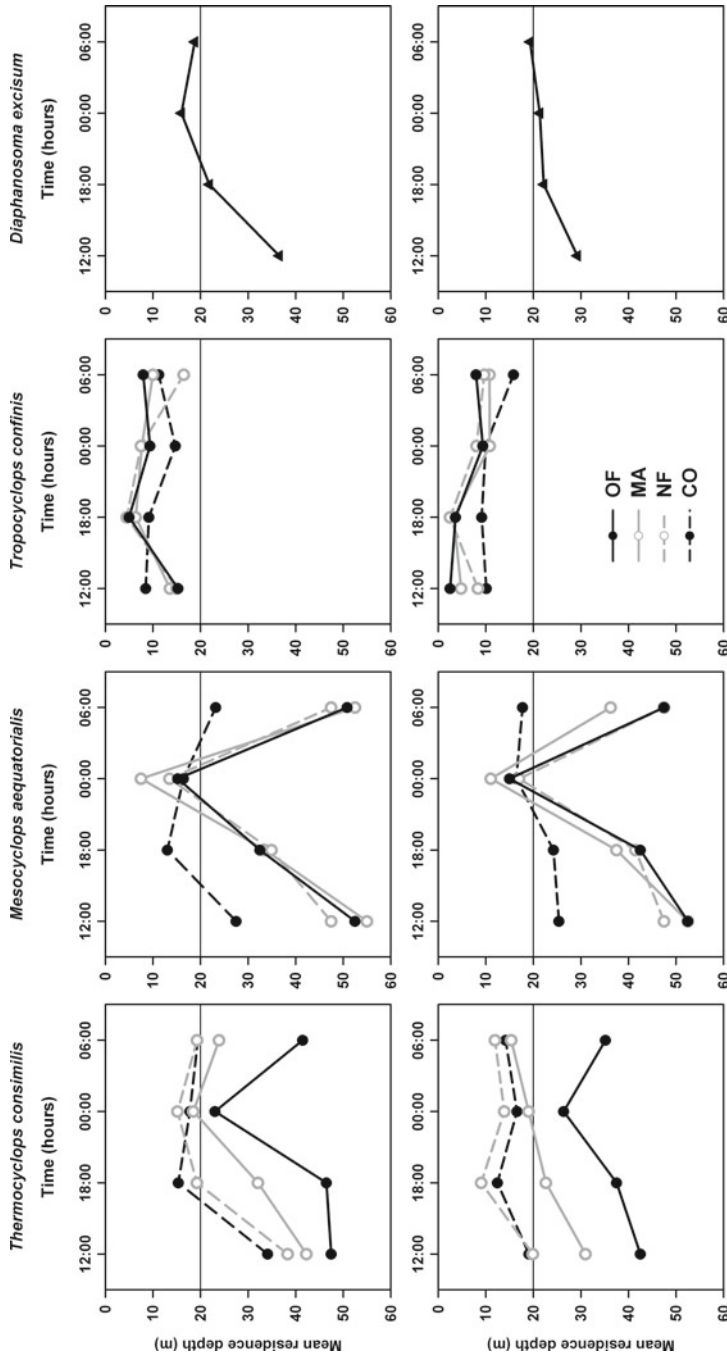
Fig. 7.11 Diel vertical migration of the four main species of crustaceans in Lake Kivu; MRD: mean residence depth; OF: ovigerous females; NF: adult females without eggs; MA: males; CO: copepodids. The horizontal lines indicate the limit of the euphotic zone. Upper panel: 5–6 August 2005, lower panel: 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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