

Zooplankton of Lake Kivu, East Africa, half a century after the Tanganyika sardine introduction

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*The introduction into Lake Kivu of the planktivorous fish *Limnothrissa miodon* at the end of the 1950s raised major concern about the fate of mesozooplankton, but few data were available to assess the impact of predation. In this study, we followed zooplankton variations in Lake Kivu for 3.5 years. Present Lake Kivu mesozooplankton is dominated by cyclopoid copepods (*Thermocyclops conSIMILIS*, *Mesocyclops aequatorialis* and *Tropocyclops confinis*), but cladocerans and rotifers are also present. Each year, total crustacean abundance in the plankton increased to a distinct seasonal maximum following a rise of phytoplankton production associated with a deep epilimnetic mixing in the dry season (August–September). This dependence on phytoplankton resource suggests that mesozooplankton dynamics in Lake Kivu is mainly bottom-up controlled, contrary to expectations from the food web structure. However, measurements of body size indicate that sardine predation affects the cladoceran *Diaphanosoma excisum*, whereas the larger copepods may efficiently escape predation by migration in the deep mixolimnion at daytime. Total biomass of mesozooplankton in Lake Kivu is lower than in lakes Tanganyika and Malawi. This may be related to the disappearance of a large grazer that existed before the sardine introduction, whereas the large lakes of the same region have a more complex pelagic food web, with piscivorous fish, and with calanoid copepods, which can more efficiently exploit phytoplankton production.*

INTRODUCTION

Lake Kivu, the smallest of the Great Rift lakes of Eastern Africa, is well known for its peculiar geochemical and limnological features: its deep, anoxic waters contain large amounts of methane and CO₂ (Tietze *et al.*, 1980). It is also the only natural lake in which *Limnothrissa miodon* Boulenger, an endemic sardine from Lake Tanganyika, was introduced (Collart, 1954) to fill an apparent empty niche of a pelagic zooplanktivore, so as to enhance fishery potential. Indeed, before the introduction, no planktivorous fish was present in the pelagic waters of Lake Kivu. Since its introduction, the sardine has become of great economic and nutritional importance to the riparian human population (De Iongh *et al.*, 1983; Spliethoff *et al.*, 1983; Marshall, 1991, 1995; Roest,

1999). However, the Tanganyika sardine induced a large change in zooplankton structure (Dumont, 1986), notably in the disappearance of a large grazer, *Daphnia curvirostris* Eylmann. Whether the sardine fishery was sustainable led to a Food and Agriculture Organization project (Lamboeuf, 1989, 1991; Lamboeuf *et al.*, 1989) that included fish stock estimates and some plankton studies (Marshall, 1991; Roest, 1999).

Because high temperature and light throughout the year allow for primary production to occur all year round in tropical lakes (Talling, 1965a, 1965b; Lewis, 1974; Hecky and Fee, 1981), it was long reported that tropical plankton populations remain relatively constant over time. Indeed, contrary to temperate zooplankton (Burgis, 1971; Burgis and Walker, 1972), tropical

zooplankton can breed continuously (Hart, 1981) so that there would be little seasonal variation in production, biomass and species. However, as stressed by Twombly (Twombly, 1983a), when the population dynamics are examined in detail, this assumption of little seasonal variations in tropical plankton proves false. In particular, there is an important body of data which documents seasonal variations in the abundance of zooplankton in large lakes of the African Rift Valley as Lake Tanganyika (Narita *et al.*, 1986; Mulimbwa and Bwebwa, 1987; Mulimbwa, 1991; Kurki *et al.*, 1999) and Lake Malawi (Irvine and Waya, 1999), as well as in smaller, shallow tropical lakes (Mengestou and Fernando, 1991). These temporal variations may depend on changes in the availability of edible phytoplankton and microzooplankton, which often vary depending on physical processes that drive nutrient availability and depth of the mixed layer, which are known to be key factors determining primary production in tropical lakes (Beadle, 1981; Hecky and Fee, 1981; Hecky and Kling, 1987; Sarmiento *et al.*, 2006).

Seasonal variation of resources and top-down control by predators affect zooplankton structure and biomass (Gliwicz and Pijanowska, 1988; Carpenter and Kitchell, 1993). In particular, the effects of *L. miodon* introduction on zooplankton have been thoroughly studied in two tropical reservoirs, Lake Cahora Bassa and Lake Kariba (Gliwicz, 1984, 1991). In that context, Lake Kivu presents a unique example of *Limnothrissa* introduction in a natural lake, without any assessment of the consequences on the food web structure and on ecosystem functioning (Dumont, 1986).

The primary purpose of our study was to examine variations of zooplankton composition, abundance and the possible impact of the sardine introduction in Lake Kivu. Studies on zooplankton in this lake have very limited data, with conclusions often drawn from a few samples, collected with different methods. Only total zooplankton numbers and a taxonomic list are available for the period preceding the sardine introduction (Verbeke, 1957; Kiss, 1959), and the subsequently published studies that reported changes in zooplankton composition and biomass were based on relatively few samples (Reyntjens, 1982; Dumont, 1986) or were conducted only in the Bukavu Bay (Kanigini *et al.*, 2003), where limnological conditions are different from those of the open lake (Sarmiento *et al.*, 2006). Thus, if the main change in zooplankton composition following *Limnothrissa* introduction is indisputable [i.e. the disappearance of *D. curvirostris*, probably the main phytoplankton grazer, reported by Dumont (Dumont, 1986)], a comprehensive study of zooplankton dynamics as influenced by resource availability (bottom-up control) or by predation by the sardine (top-down control) was missing.

Here, we report patterns of abundance, over a period of 3.5 years, of zooplankton in Lake Kivu. We present seasonal changes of zooplankton abundance and community composition, as well as more irregular variations in population size, with the backdrop of limnological conditions and variations of phytoplankton biomass. We analysed the response of zooplankton to these factors, estimated total biomass and measured body size of the main species, with a comparison to other African great lakes. Indeed, quantitative estimates of the sardine predation rate on zooplankton are still missing, and the only way to show a possible top-down control by the planktivorous fish is to examine body size distribution of the prey, because *Limnothrissa* is a visual predator.

METHOD

Study area

Situated in the western Rift Valley between Rwanda and the Democratic Republic of Congo (Fig. 1), Lake Kivu is the smallest of the East African Great Lakes, with a surface of 2370 km² and a volume of 650 km³ (Beadle, 1981). It is a deep (maximum 489 m), meromictic, high-elevation lake (1463 m above sea level), with an oxic mixolimnion of ~60 m and a deep monimolimnion rich in dissolved gases, particularly methane (Tietze *et al.*, 1980) whose production within the sediment has seemingly increased during the last three decades (Schmid *et al.*, 2005).

Biological diversity in Lake Kivu is low, with only 26 fish species of which 15 are endemic haplochromines (Snoeks *et al.*, 1997). Paleolimnological studies have established that the lake was subject to volcanic and hydrothermal events some 5000 years BP (Hecky, 1978; Haberyan and Hecky, 1987), which are responsible for the impoverished fish fauna. Presently, the ichthyofauna is dominated by a planktivorous fish, the introduced sardine *L. miodon*. Lake Kivu combines a relatively shallow euphotic layer, usually smaller than its mixed layer, with relatively low nutrient content and unstable thermal stratification of the surface waters (Hecky and Kling, 1987; Sarmiento *et al.*, 2006). In 1987, Hecky and Kling reported phytoplankton fresh-weight biomass from 550 to 2100 mg m⁻³ from March 1972 surface samples, with cyanobacteria and green algae accounting for 70–90% of total biomass. Recent data (Sarmiento *et al.*, 2006) report an annual average chlorophyll *a* (Chl *a*) in the mixed layer of 2.2 mg m⁻³. In addition, different diatom taxa were reported from the north and the south of the lake and related to differences in Si : P dissolved ratio (Kilham *et al.*, 1986). Lake Kivu has phytoplankton biomass concentration higher than that

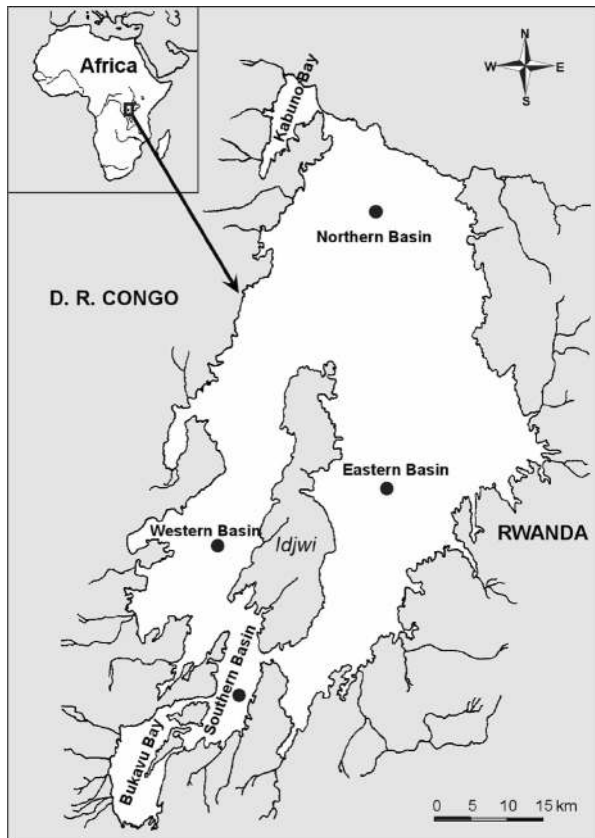


Fig. 1. Geographic situation of Lake Kivu. Black dots are the sampling sites.

of the largest Rift lakes, Lake Malawi and Lake Tanganyika (Sarmiento *et al.*, 2006), and has slightly higher mean daily primary production, $1.44 \text{ g C m}^{-2} \text{ day}^{-1}$, reported by Beadle (Beadle, 1981).

Field sampling and measurement of limnological variables and Chl *a*

Regular samples were collected every 2 weeks from February 2002 to June 2005 in the Southern basin (Ishungu basin) of Lake Kivu ($02^{\circ}33.94' \text{ S}$, $28^{\circ}97.65' \text{ E}$) (Fig. 1), located in the open lake. Water column samples were collected with a 6-L Van Dorn bottle (Kahlsico, USA) every 10 m from the surface down to 90 m. In addition, four cruises took place: two during the rainy season (27–31 January 2003 and 23 February to 6 March 2004) and two in the dry season (26 August to 2 September 2003 and 9–12 September 2004). Cruises' sampling points (Fig. 1) were distributed across the lake, in the northern basin ($01^{\circ}68.08' \text{ S}$, $29^{\circ}15.69' \text{ E}$), the eastern basin ($01^{\circ}96.17' \text{ S}$, $29^{\circ}12.26' \text{ E}$), the western basin ($02^{\circ}22.79' \text{ S}$, $28^{\circ}97.35' \text{ E}$) and the southern

basin. The sampling protocol and equipment were identical to those used at the Ishungu station.

Limnological variables [dissolved oxygen (DO), temperature, conductivity and pH] were measured using separate instruments (a YSI Model 55 DO probe, a Cyberscan CON 410 conductivity probe and a WTW 330/SET-1 pH meter) or a Hydrolab DS4a multiprobe (Loveland, USA). Transparency measurements were carried out with a Secchi disk, and the euphotic depth (Zeu, depth at which light is 1% of subsurface light) was derived from estimates of the vertical light attenuation coefficient from Secchi depth using a coefficient ($k = 1.34/\text{Secchi disk depth}$) obtained by calibration with measurement of light downward attenuation with LI-COR quantum sensors at each sampling site ($n = 16$). The depth of the mixed layer (Zm) was estimated from the depth of the top of the thermocline, as shown by the temperature and oxygen vertical profiles.

Samples for high-performance liquid chromatography (HPLC) analysis of Chl *a* were obtained from filtration of 3 L on Macherey-Nägel GF5 filters, of $0.7 \mu\text{m}$ nominal pore size. The subsequent procedure for pigment extraction and analysis followed a procedure described by Descy *et al.* (Descy *et al.*, 2000). Extracts in 90% acetone were then stored in 2-mL amber vials at -25°C , usually for several months and transported to Belgium on ice in cooler boxes. The possible loss due to pigment degradation during the long-term freezer storage was checked for Chl *a* against fluorometric measurements taken at ISP-Bukavu with a Turner TD700 instrument immediately after extraction. Chl *a* from HPLC after storage was on average $\sim 14\%$ lower than Chl *a* from immediate measurements. Because degraded pigment forms occurred only infrequently in the chromatograms, it appeared that no significant degradation of Chl *a* occurred during extracts storage. Using a Carlo Erba NA 1500 elemental analyser, parallel measurements of particulate organic carbon (POC) in the total seston were carried out to determine the conversion coefficient from Chl *a* concentration to phytoplankton carbon. A Chl *a* : carbon ratio of 92.8 was estimated from linear regression of Chl *a* against POC and then accounted for non-phytoplankton organic carbon. For comparison with zooplankton biomass, phytoplankton biomass was expressed (in g C m^{-2}) by integrating on the whole mixolimnion, i.e. the top 60 m of the water column.

Zooplankton was sampled with vertical net hauls in the mixolimnion (60–0 m) using a 25-cm diameter, 100- μm mesh net from February to December 2002, but this plankton net did not collect copepod nauplii efficiently. From January 2003 to June 2005, we used a 75-cm diameter, 55- μm mesh closing net to collect all crustaceans' development stages in three different strata (0–20,

20–40 and 40–60 m). We verified that the two nets provided similar samples for post-naupliar copepods, whereas nauplii numbers from the samples with the 100- μm mesh net were significantly lower than in samples collected with the other net [analysis of variance (ANOVA); $F = 336.8$; $P < 0.0001$]. Samples were preserved using formalin with final concentration of 4% as proposed by Haney and Hall (Haney and Hall, 1973). In the laboratory, each sample was concentrated by settling for 48 h and adjusted to a volume of 100 mL.

Zooplankton were identified according to the studies of Dussart (Dussart, 1967a, 1967b, 1982), Harding and Smith (Harding and Smith, 1974), Pontin (Pontin, 1978), Amoros (Amoros, 1984) and Kořínek (Kořínek, 1999) and counted under an inverted microscope. More accurate taxonomic identifications were carried out for the most abundant taxa in the Department of Ecology of the University of Ghent (Belgium). At least 500 individuals were identified and counted for each sample. Zooplankton biomass was estimated using length–weight relations from the studies of Downing and Rigler (Downing and Rigler, 1984) and Irvine and Waya (Irvine and Waya, 1999) for adult and copepodite stages and from the studies of Dumont *et al.* (Dumont *et al.*, 1975) for nauplii. Individual body length was measured using a graduated eyepiece under an inverted microscope, and at least 100 individuals were measured for each taxon from samples collected in 2003.

RESULTS

Limnological variables and Chl *a* in the water column

In all basins of the lake, limnological conditions (Fig. 2) were similar (coefficient of variation 0.06–14.14%) and the seasonal stratification of the mixolimnion during the rainy season was clearly visible, especially from the DO profiles (oxycline at 30–40 m depth). In the rainy season, the average (number \pm SD) surface temperature was 25.04 ± 0.29 and $24.69 \pm 0.5^\circ\text{C}$, respectively, in 2003 and 2004, whereas it decreased only slightly in the dry season ($23.44 \pm 0.02^\circ\text{C}$) in 2003 and ($24.11 \pm 0.29^\circ\text{C}$) in 2004. The vertical temperature gradient was well marked in both rainy seasons, with a seasonal thermocline located between 20 and 30–40 m depth, below which anoxic conditions prevailed. In the dry seasons, as a result of surface cooling, the temperature difference between top and bottom of the mixolimnion decreased, allowing a deeper mixed, oxygenated layer of ~ 60 m.

Conductivity varied very little between years and seasons. Surface water conductivity was $1160 \mu\text{s cm}^{-1}$

at 25°C . It increased slightly at 50–60 m, and depth below this level presented a steep gradient corresponding to the chemocline between mixolimnion and monimolimnion. As shown by the pH values, the surface waters were alkaline, with pH ~ 9 or above (whole-lake average 9.17 ± 0.15). Like conductivity, pH slightly decreased with depth in the mixolimnion and presented a strong decrease in the chemocline, reaching 6.60 ± 0.42 at 100 m.

Chl *a* distribution in the water column varied seasonally (Fig. 2), with maxima in the dry season, depending on the mixing conditions in the mixolimnion. Whole-lake Chl *a* average in the top 60 m was 1.3 mg m^{-3} ($n = 78$), and the observed range was 0.5 and 3.0 mg m^{-3} .

Regular and long-term sampling indicates that the water column structure depended on seasonal changes of meteorological factors. The deep mixing occurred from June to October (Fig. 3b), i.e. during the long dry season. Indeed, during this period, wind speed increases, whereas air temperature decreases (Fig. 4), thereby reducing the density gradient in the mixolimnion and allowing deep mixing of the water column to occur, however not deeper than 60 m depth, where the chemocline is located. The temporal variation of phytoplankton biomass was related to the depth of the mixed layer (Fig. 3a): the marked seasonal peaks occurred in the dry season.

Zooplankton composition and relative abundance of different taxa

Three species of cyclopoid copepods were observed: *Mesocyclops aequatorialis* (Kiefer), *Thermocyclops consimilis* (Kiefer) and *Tropocyclops confinis* (Kiefer). Cladocerans were represented by *Alona rectangula* (Sars), *Ceriodaphnia cornuta* (Sars), *Diaphanosoma excisum* (Sars) and *Moina micrura* (Kurz), whereas rotifers were more diversified and represented by the following taxa: *Anuraeopsis fissa* (Gosse), *Brachionus calyciflorus* (Pallas), *Brachionus caudatus* (Barrois and Daday), *Brachionus falcatus* (Zacharias), *Brachionus quadridentatus* (Hermann), *Cohurella* sp., *Keratella tropica* (Apstein), *Lecane* sp., *Trichocerca* sp., *Polyarthra* sp., *Hexarthra* sp. and unidentified Bdelloids.

The mean total zooplankton abundance in the mixolimnion was 8.36×10^5 individual m^{-2} (2003) and 7.94×10^5 individual m^{-2} (2004) in the rainy season. In the dry season, zooplankton abundance was higher: 14.74×10^5 individual m^{-2} in 2003 and 10.62×10^5 individual m^{-2} in 2004. Numerically, copepods dominated other groups (Fig. 5). They represented 73.6% of total zooplankton numbers during the rainy season against 94.2% during the dry season in 2003. In 2004, they represented 69.0 and 86.2% of total zooplankton numbers, respectively, in the rainy and the dry seasons. Cladocerans comprised 16.4 and 5.5% of zooplankton

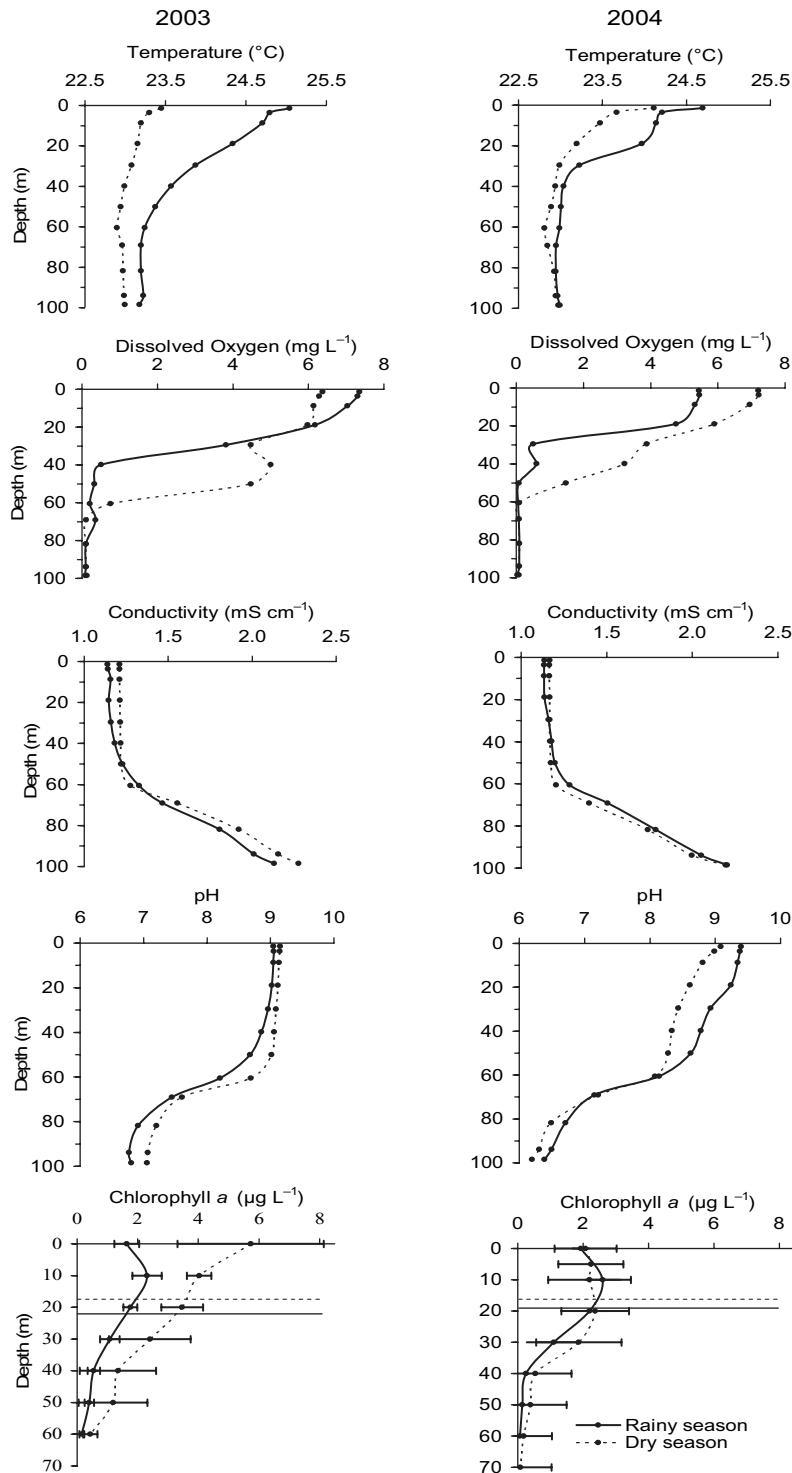


Fig. 2. Limnological profiles in the water column of Lake Kivu during the rainy and the dry seasons in 2003 and 2004. Horizontal lines in the chlorophyll *a* (mean \pm SD) profiles (bottom) are the depth of the euphotic zone (solid line for the rainy season and dashed line the dry season).

abundance, respectively, during the rainy and the dry seasons in 2003, whereas in 2004, there was less seasonal contrast (13.2 versus 11.4%, respectively). Rotifers

represented 10.0 and 0.3% of total zooplankton numbers during the rainy and the dry season in 2003; in 2004, they represented 17.8 and 2.4%, respectively, in the

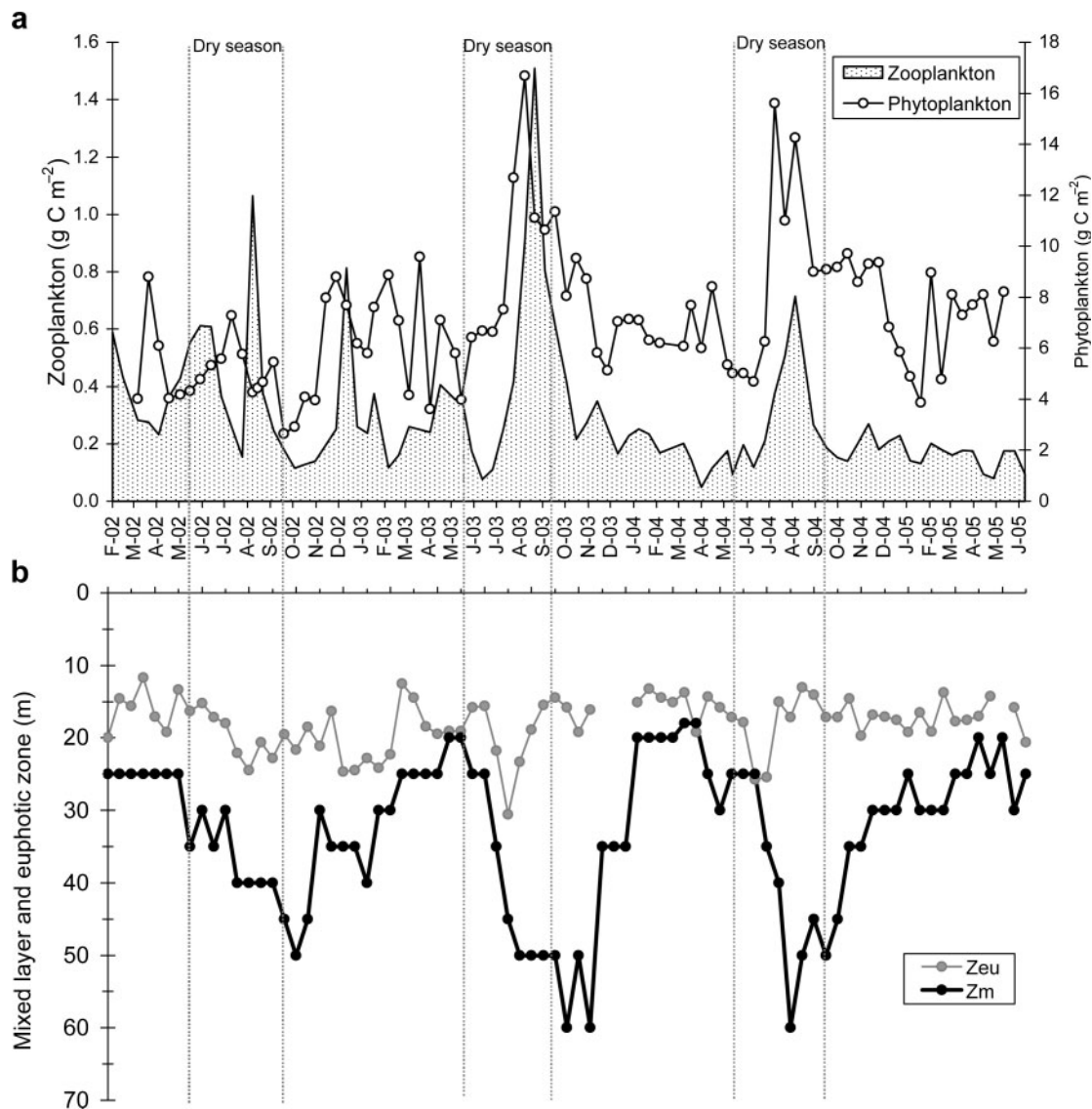


Fig. 3. (a) Biomass of total zooplankton and phytoplankton integrated in the top 60 m; (b) euphotic zone and mixolimnion variation from February 2002 to June 2005 in Lake Kivu (Ishungu basin).

rainy and the dry season. So, copepod relative abundance was significantly more important during the dry season [$P < 0.0001$, Fisher's projected least significant difference (PLSD)], whereas the opposite was observed for cladocerans ($P < 0.05$, Fisher's PLSD) and rotifers ($P < 0.0001$, Fisher's PLSD), which were more abundant at all stations in the rainy season.

Among copepods (copepodites + adults), *T. consimilis* dominated numerically during the rainy season, with 81.2% in 2003 and 83.6% in 2004, whereas *M. aequatorialis* represented 13.8% (in 2003) and 11.4% (in 2004) and *T. confinis* 5.1 and 5.0% of total copepod abundance, respectively, in 2003 and 2004. However, during the dry

season in 2003, *M. aequatorialis* dominated total copepod numbers with a mean percentage of 66.6% over the lake. *Thermocyclops consimilis* and *T. confinis* represented, respectively, 32.9 and 0.5%. During the dry season of 2004, *T. consimilis* dominated numerically at the different sampling stations, but in the eastern and the northern basins, *M. aequatorialis* represented, respectively, 45.5 and 35.4% of copepod abundance, whereas *Tropocyclops* represented <1.0% at each sampling station. Among cladocerans, there were also some variations in the proportion of the different taxa, with greater diversity in the rainy season, particularly in 2004, and marked numerical dominance of *D. excisum* in the dry season. The seasonal variation of

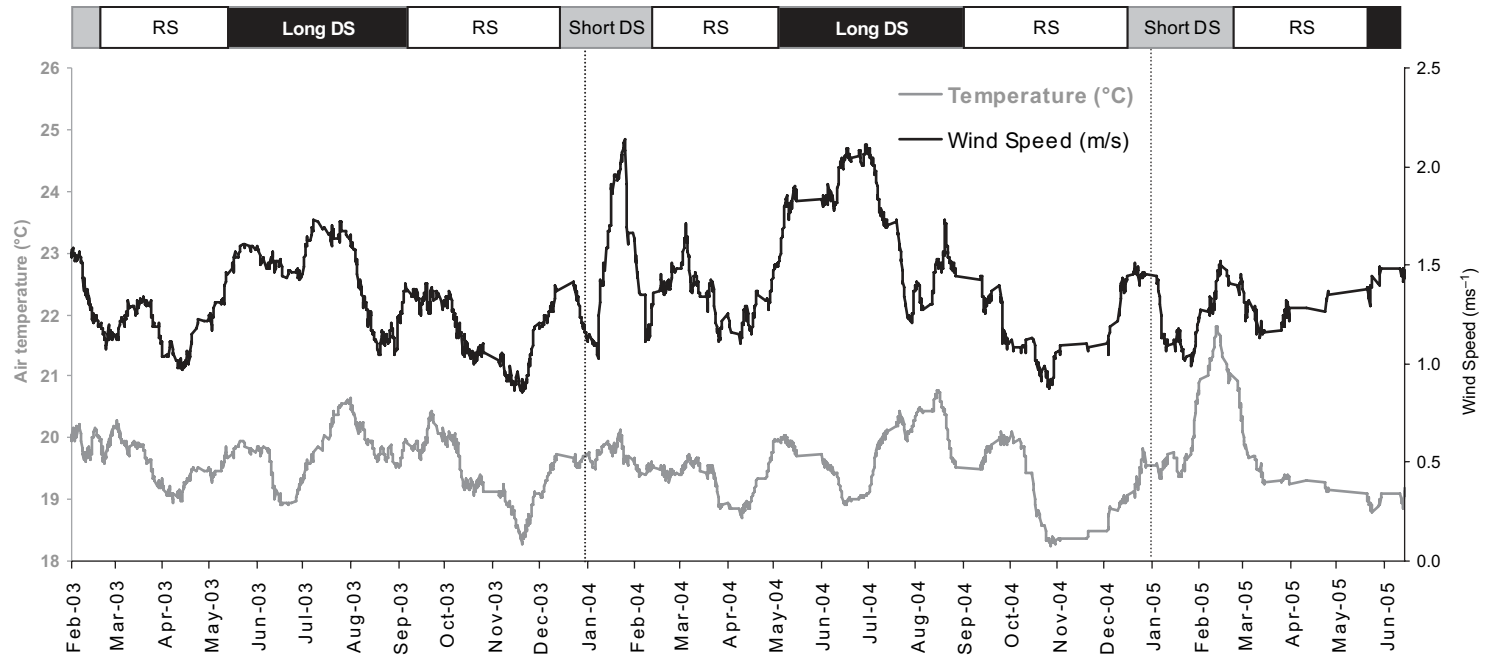


Fig. 4. Wind speed and air temperature in the southern end of Lake Kivu (Bukavu, R. D. Congo) and season delimitation in 2003 and 2004 (from Sarmento *et al.*, 2006).

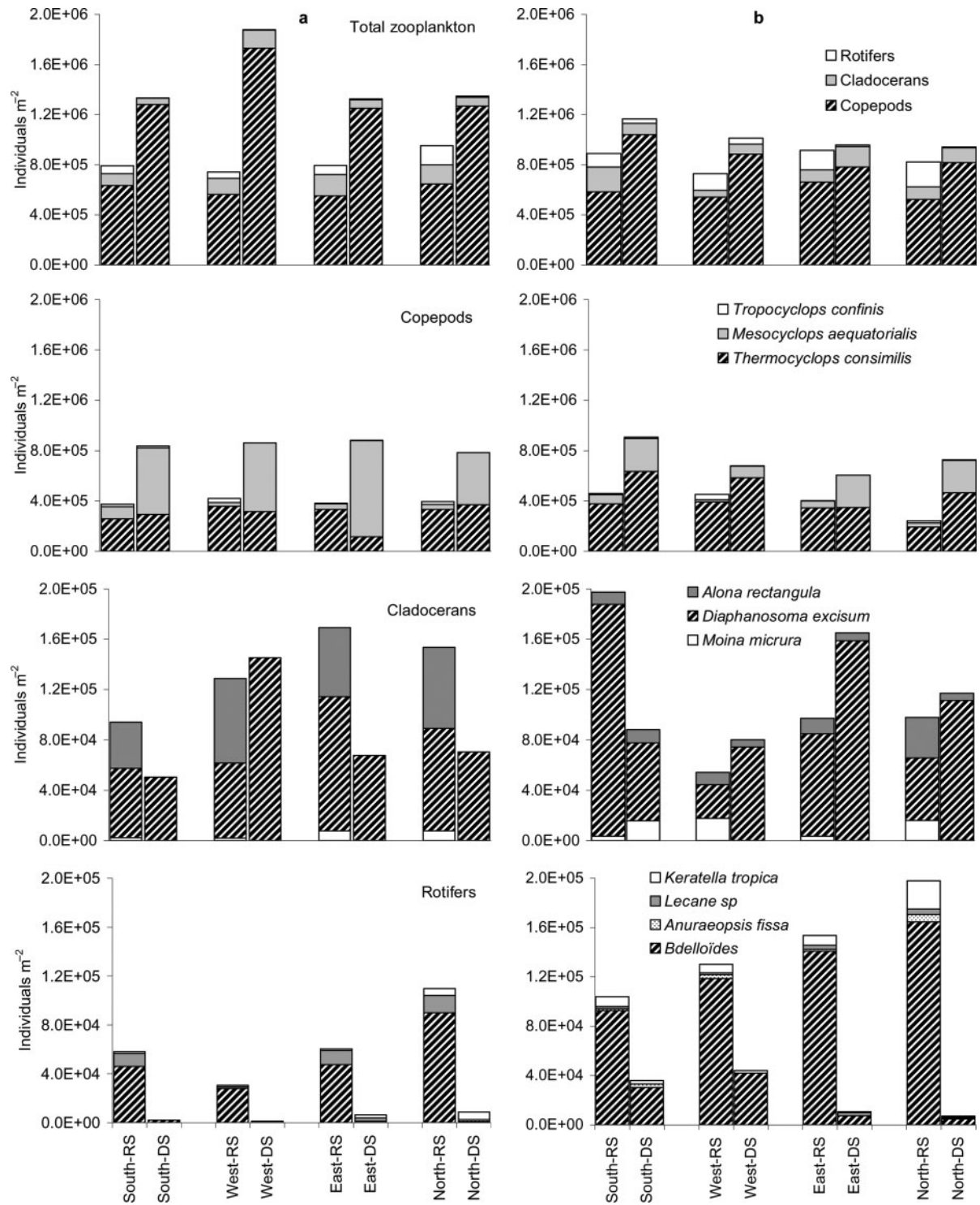


Fig. 5. Abundance of the main mesozooplankton categories during the rainy (RS) and the dry seasons (DS) in the four major basins of Lake Kivu in 2003 (a) and 2004 (b). Note change of scale on the *I*-axis for cladocerans and rotifers.

numerical abundance was even greater in rotifers, with a general tendency of dominance by Bdelloids, which comprise typically benthic taxa.

Temporal pattern of crustacean zooplankton abundance

The proportion of nauplii was examined for samples collected from January 2003 to June 2005. Their relative abundance varied between 7.89 and 59.84% over this period, but throughout the year, their proportion was comparable with that observed for copepodites and adult copepods (~33%) (Fig. 6b).

Of the seven crustaceans of the pelagic zone found in Lake Kivu, *M. aequatorialis*, *T. consimilis* and *D. excisum* were found throughout the year, whereas *T. confinis*, *A. rectangula* and *M. micrura* occurred more intermittently, and *C. cornuta* appeared very sporadically. In addition, there were temporal changes in the relative

contribution of the six common species to the total assemblage (Fig. 6a). *Mesocyclops aequatorialis* showed three periods of high relative abundance throughout the year: January–April, August–September and December. On the contrary, *T. consimilis* contributed more to the total copepod abundance in March, May–July and October–November, whereas the contribution of *D. excisum* to the total zooplankton exhibited an irregular pattern: May–October in 2002, January–February and May–August in 2003 and April–July in 2004.

The analysis of the absolute abundance of individual species in detail provides more information. Total copepod abundance increased to an annual maximum in the dry season, August–September, even though other secondary peaks occurred throughout the year. Some of these secondary peaks were repeated in 2002, 2003 and 2004 and appeared in May–June and November–December, whereas others had an irregular recurrence throughout the years. Seasonal patterns similar to those

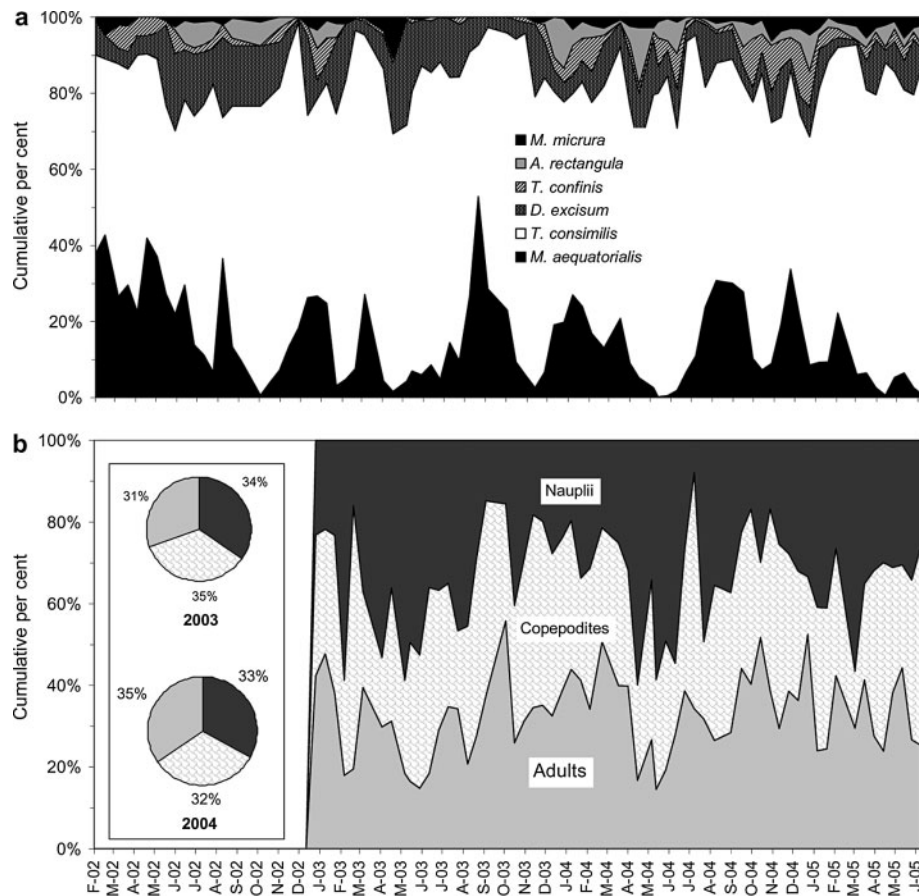


Fig. 6. Percentage contribution of the six most common species to total crustacean zooplankton (nauplii excepted) from February 2002 to June 2005 (a), percentage contribution of nauplii and post-naupliar (copepodites and adults) to total copepods from January 2003 to June 2005 and their mean annual percentage contribution in 2003 and 2004 (b) in Lake Kivu (Ishungu, south basin).

observed in total zooplankton were apparent in the abundance of *T. consimilis*, of *M. aequatorialis* and, to a lesser extent, of *D. excisum*, whereas the temporal variation of *T. confinis*, *M. micrura* and *A. rectangular* was characterized by an irregular pattern (Fig. 7).

The abundance of nauplii exhibited a maximum during the dry season in August, but there were other periods with increasing numbers during the rainy season in May–June and October–November. Those peaks were repeated in 2003 and 2004. Post-naupliar copepods also showed three periods of high abundance, even though the most important peak was observed during the dry season, in August–September, often ~2 weeks after the nauplii peak (Fig. 8).

There was no significant difference in mean biomass between the 3 years. However, there were differences between years in the timing, magnitude and recurrence of population peaks for *T. consimilis*, *M. aequatorialis* and *D. excisum*. The peaks of *T. consimilis* occurred in June, August and December 2002 and were of a comparable magnitude. In 2003 however, these peaks occurred in April–May, August–September and November, whereas in 2004, the peak was marked in July–August. *D. excisum* population presented its peak in June, August and December 2002; in February, May, September and November 2003; and in May, August and November 2004 but with a lower intensity. For the *M. aequatorialis* population, the situation was highly variable among years. The dry season peak occurred in August 2002 and 2004 and in September 2003 (Fig. 7), with a pronounced difference in magnitude. To evaluate the inter-annual variability in the timing of seasonal maxima, we calculated correlations in patterns of abundance between two successive years sampled (Table I). The correlations in patterns of abundance between the 2 years were very low and not significant for nauplii and the three dominant species (*T. consimilis*, *M. aequatorialis* and *D. excisum*), whereas three other crustacean zooplankton species presented a relatively important and statistically significant correlation between the 2 years. Thus, the relatively important correlation in the abundance of *T. confinis*, *M. micrura* and *A. rectangular* between two successive years could indicate seasonal patterns that were probably blurred by certain irregular increases in population size, especially in 2003 and 2004 (Fig. 7).

Seasonal variation of crustacean zooplankton biomass

During the rainy season, the lake-wide mean biomass was 0.108 g C m⁻² in 2003 and 0.121 g C m⁻² in 2004, whereas during the dry season, it reached 0.379 and 0.295 g C m⁻², respectively, in 2003 and 2004. The

relatively small standard deviation (SD) indicates little spatial variation among the main basins. However, variability among sites was greater in both seasons in 2004 (coefficient of variation ~30%) than in 2003 (coefficient of variation ~9%). By contrast, the seasonal variation was large, with average copepod biomass in the dry season increasing by a factor of 2.5–3.5 relative to the rainy season data. Otherwise, when compared with the lakes Tanganyika and Malawi crustacean zooplankton biomass, the biomass in Lake Kivu was about three times as low as in both large lakes in all seasons.

Total crustacean zooplankton biomass in the southern basin (Fig. 3a) showed a pattern comparable with the one observed for numerical abundance, with seasonal maximum in the dry season and presence of smaller peaks in the rainy season.

Zooplankton body size and vertical distribution

To assess a possible impact of predation by the introduced sardine, we examined body size of the three dominant zooplankton species. *Mesocyclops aequatorialis* is the largest zooplankton species in Lake Kivu. Its adult size was on average 0.730 ± 0.051 mm, which is very significantly different from the size of *T. consimilis* adults (0.534 ± 0.024 mm). The cladoceran *D. excisum* was definitely smaller (0.363 ± 0.073 mm). *Mesocyclops aequatorialis* and *D. excisum* as well as *T. neglectus*, a congeneric species of *T. consimilis*, exist in Lake Malawi (Irvine, 1995). The comparison of body size suggests that *M. aequatorialis* is of comparable size in the two lakes. The *T. consimilis* body size is comparable with that of *T. neglectus*, whereas the cladoceran *D. excisum* is about half the size in Lake Kivu as in Lake Malawi. Moreover, *D. excisum* size shows a decreasing trend over time in Lake Kivu since 1984, whereas copepod size did not change.

The daytime vertical distribution of copepods, which may result from a predator-avoidance behaviour, was size structured (Fig. 9). At daytime, the mean zooplankton abundance was greatest in the top 20 m of the water column, with 70–80% of total abundance in that layer. However, there was a size (stage)-structured habitat utilization by copepod populations in the lake, which varied seasonally. Nauplii and copepodites occupied the top 20 m of the water column at all times (~80.0 and 64.0% for nauplii and 87.5 and 81.6% for copepodites, respectively, during the rainy and the dry seasons). *Thermocyclops* adult males and non-ovigerous females had a similar vertical distribution with at least 50% of the population in the surface layer (Fig. 9a). *Mesocyclops* adult males and non-ovigerous females were distributed preferentially in the 20- to 40-m layer in the rainy season

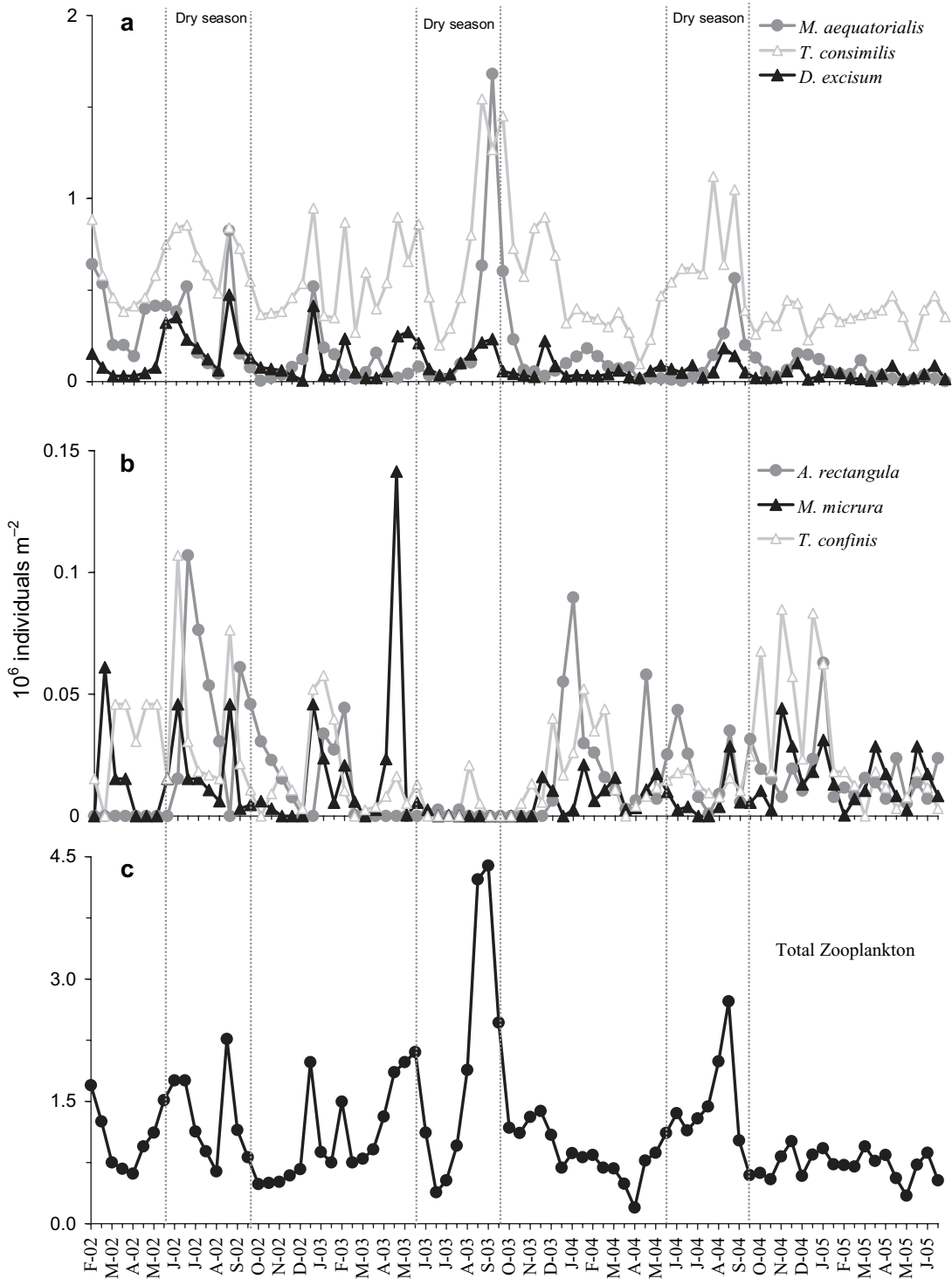


Fig. 7. Abundance variation of the six most common species (**a**, **b**) and of total zooplankton (**c**) in the Lake Kivu (Ishungu, south basin) water column from February 2002 to June 2005. Note the different scales on the Y-axis for **a**, **b** and **c**.

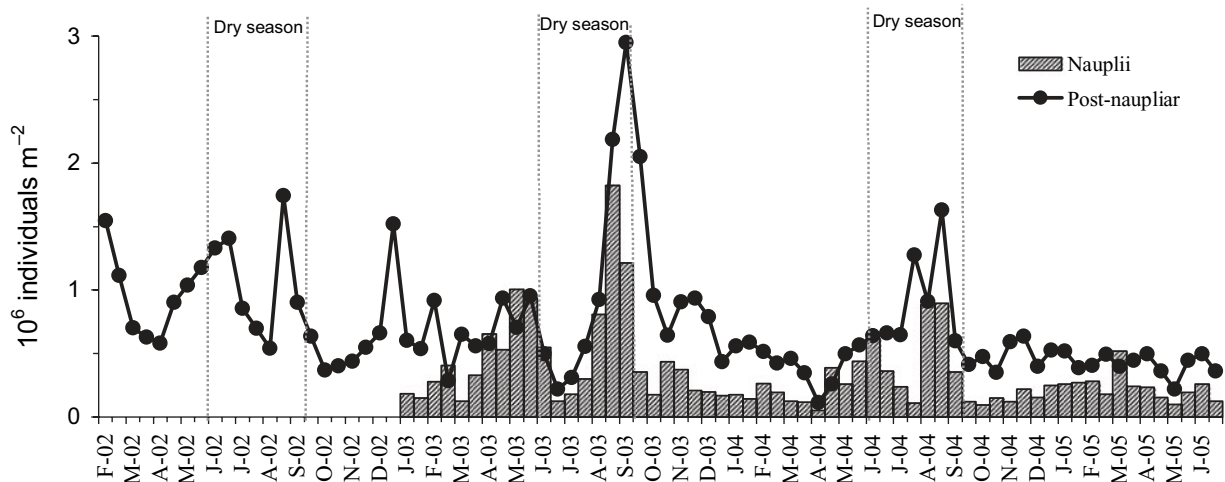


Fig. 8. Abundance of total nauplii (2003–05) and post-naupliar (2002–05) copepods in Lake Kivu water column during the sampling period (Ishungu, south basin).

Table I: Spearman’s rank correlation coefficients (r) for patterns of zooplankton abundance between 2003 and 2004 (1) and between zooplankton abundance and the mixolimnion cycle in 2003 and 2004 (2)

Species or stage	(1) n = 20		(2) n = 40	
	r	P-level	r	P-level
Nauplii	−0.09	0.54	0.42	0.27
<i>Thermocyclops consimilis</i>	−0.14	0.37	0.65	<0.01
<i>Mesocyclops aequatorialis</i>	0.26	0.66	0.59	<0.05
<i>Diaphanosoma excisum</i>	−0.13	0.39	0.33	0.49
<i>Tropocyclops confinis</i>	0.62	<0.05	−0.30	0.05
<i>Moina micrura</i>	0.60	<0.05	−0.50	<0.01
<i>Alona rectangula</i>	0.76	<0.01	−0.35	<0.05

(60.3 and 56.4%, respectively), whereas during the dry season, they were found in greater numbers in the top 20 m of the water column (44.0 and 50.0%). The greatest contrast in distribution was observed for the *Mesocyclops* egg-bearing females (Fig. 9b), which were concentrated in the deeper layers. They were limited in the water layer between 20 and 40 m depth during the rainy season, whereas they were found in greater numbers in the lower layer, 40–60 m (where Chl *a* value is low), during the dry season (77.7%).

DISCUSSION

A remarkable feature of Lake Kivu ecosystem is the ‘incomplete’ pelagic food chain without piscivorous fish, but dominated by an introduced planktivorous fish species,

L. miodon. Clearly, Lake Kivu provides an interesting model system for investigating the effects of fish predation, the survival mechanisms of the prey (Isumbisho *et al.*, 2004) and the impacts at ecosystem level.

The limnological measurements showed homogeneity of conditions in the open lake in the major four basins. The differences were essentially seasonal and resulted from the variation in stability of the water column and depth of the mixed layer within the mixolimnion of the lake, restricted to the top 60 m overlying the large volume of anoxic waters. As in the other Rift lakes, wind velocity increase in the dry season induces cooling of the surface waters, thereby decreasing the temperature–density gradient. Enhanced vertical mixing induces nutrient supply to the euphotic zone and favours algal growth, as shown by the high phytoplankton biomass observed during the dry season (Sarmiento *et al.*, 2006).

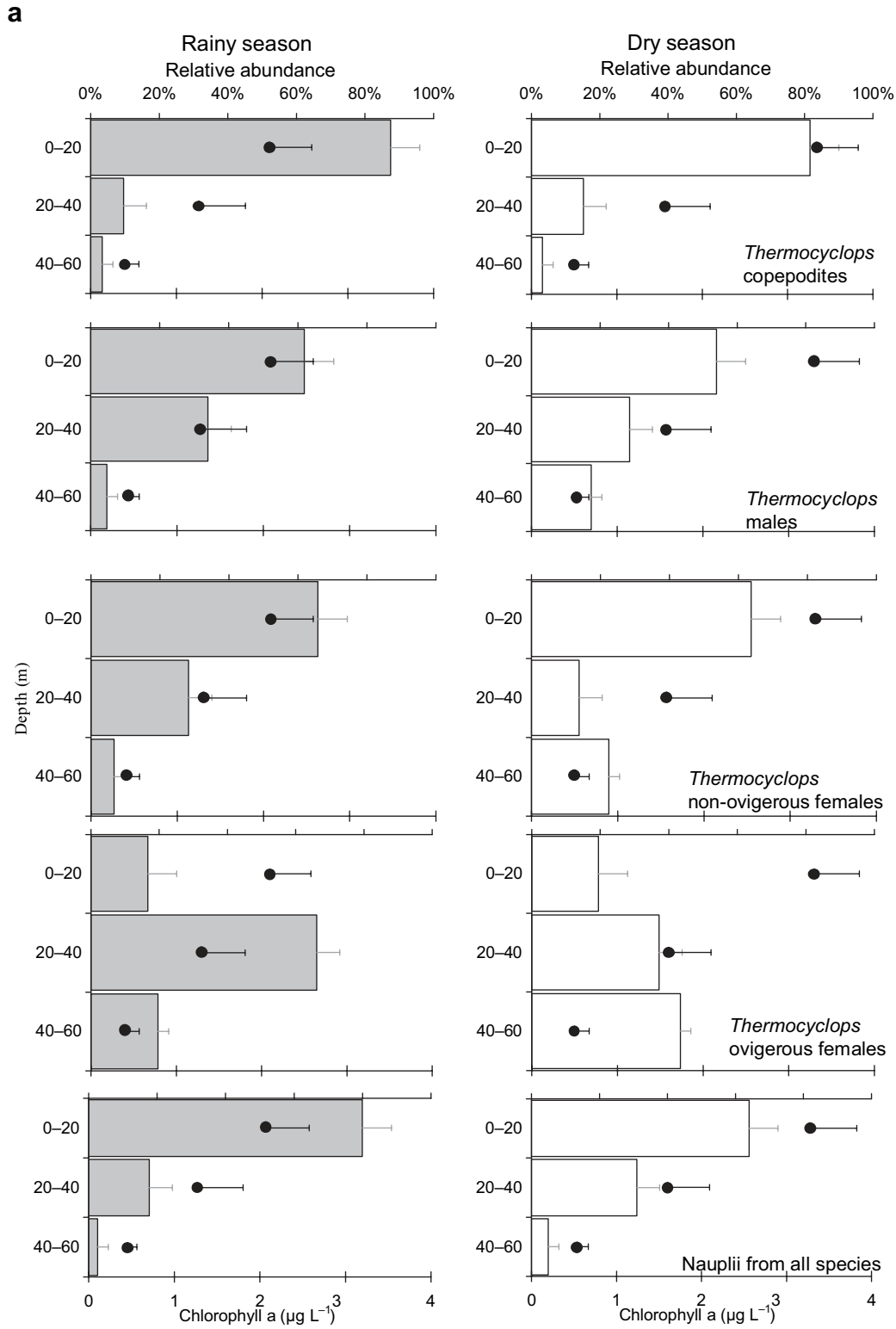


Fig. 9. (a) Vertical distribution (mean percentage of total abundance in the water column) of *Thermocyclops consimilis* and all Nauplii (bars) and chlorophyll *a* (Chl *a*) (dots) profiles in Lake Kivu during the rainy and the dry seasons. (b) Vertical distribution (mean percentage of total abundance in the water column) of *Mesocyclops aequatorialis* (bars) and Chl *a* (dots) profiles in Lake Kivu during the rainy and the dry seasons.

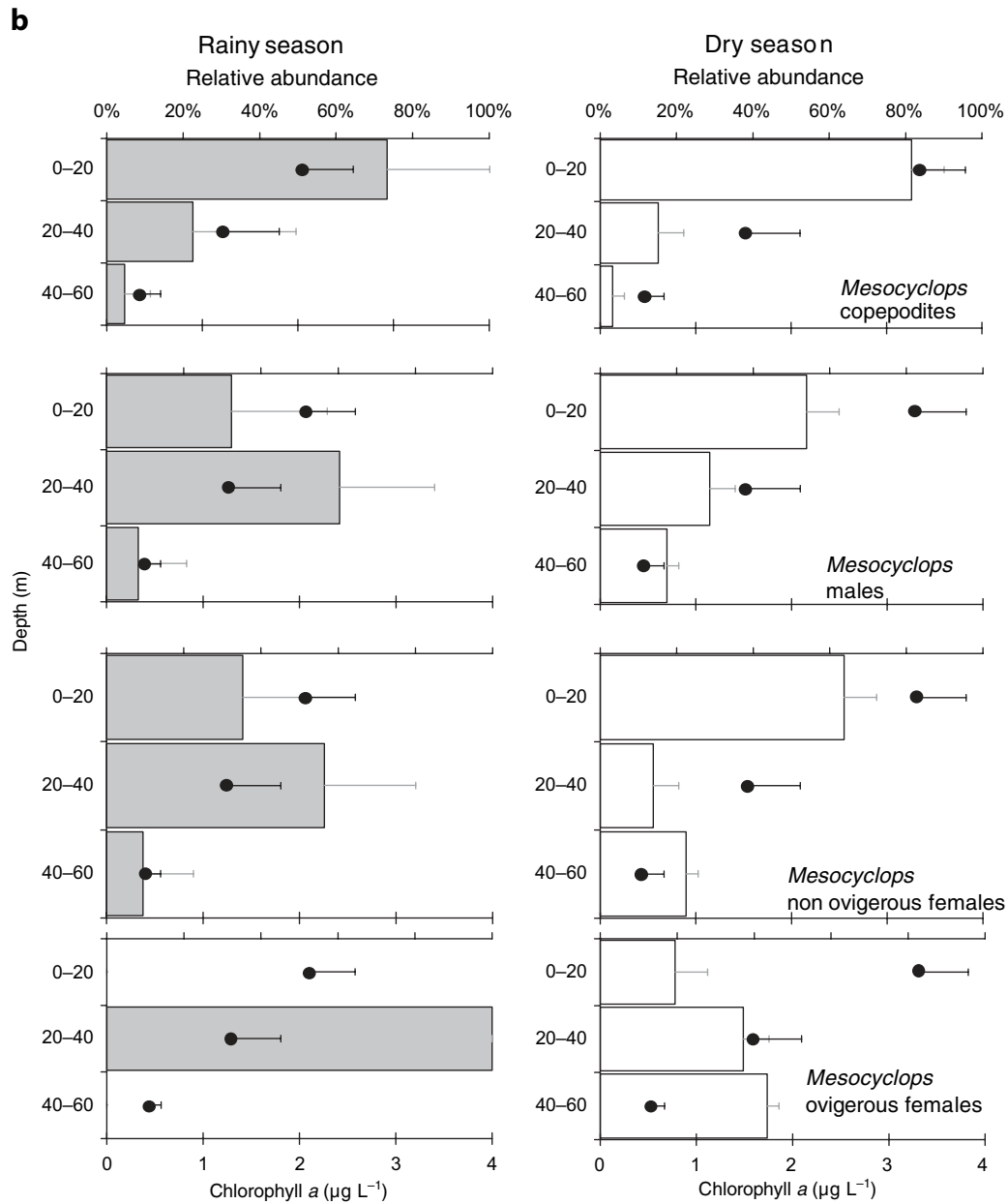


Fig. 9. Continued

For planktonic animals, in addition to change in resource availability, a major consequence of the alteration of stratified conditions in the rainy season and deeper vertical mixing in the dry season is the change of thickness of the oxic layer. When stratification develops in the mixolimnion of the lake, the deeper layers become less accessible to large zooplankton, because of the lack of oxygen and food resources. However, copepods can survive in oxygen-depleted layers inaccessible to fish (Strickle *et al.*, 1989). In the same way, Kizito (Kizito,

1998) reported copepod survival for 8 days at DO concentration as low as 0.50 mg L^{-1} . The vertical distribution we observed suggests that oxygen depletion below 40 m, when the mixolimnion stratifies, may reduce the extent of vertical migration of larger specimens, particularly egg-bearing females. Given the transparency of the lake waters, it can be considered that fish predation on mesozooplankton is the most effective in the top 20 m of the water column. This is in accordance with the daytime distribution of copepods, i.e. the larger proportion, in the

upper layer, of nauplii and copepodite stages of *Mesocyclops* and of all stages of the smaller *Thermocyclops*, with the exception of egg-bearing females. Thus, refuge from fish predation is necessary for the survival of these largest and more visible stages and is probably more effective in the more productive dry season when the whole mixolimnion is oxygenated, even from 40 m depth down to the chemocline. The poorly illuminated but well-oxygenated layer, whose thickness increases during the dry season, may provide adequate refuge from *Limnothrissa*, which is an efficient visual predator (Gliwicz and Pijanowska, 1988). So, limnological conditions may affect the mortality rate and the population dynamics of mesozooplankton, particularly for the largest species of the lake, *M. aequatorialis*. The situation for daytime vertical migration in Lake Kivu is probably very different from that in Lake Tanganyika (Vuorinen *et al.*, 1999), where the oxic zone is much deeper, so that mesozooplankton may escape predation without having to migrate to low-oxygen layers. The case of Lake Kivu is more similar to that of Cahora Bassa reservoir (Gliwicz, 1984, 1986), where the extent of zooplankton vertical migration has been shown to depend on water transparency. In Lake Kivu, it is likely that migration below 20–40 m—thus with a limited energetic cost—provides the largest copepods with an adequate refuge from predation.

Present Lake Kivu's pelagic mesozooplankton differs from that of Lake Tanganyika (Hecky, 1991) and Lake Malawi (Irvine, 1995) by the absence of a calanoid species, which can graze efficiently at low phytoplankton concentration and often dominates the mesozooplankton in these two large oligotrophic lakes. This may explain the fact that the mean zooplankton biomass in Lake Kivu (0.3 g C m^{-2}) is closer to that of the smaller Lake George (0.4 g C m^{-2} ; Burgis, 1978) and Lake Awasa (0.45 g C m^{-2} ; Mengestou and Fernando, 1991) than to the annual average of Lake Malawi (0.89 g C m^{-2} ; Irvine, 1995) and of Lake Tanganyika (1.2 g C m^{-2} ; Kurki *et al.*, 1999), whereas the opposite is observed for phytoplankton biomass (Sarmiento *et al.*, 2006). Besides, the zooplankton species list of Lake Kivu compares favourably with those of the other East African Great lakes, which have also a rather poor taxonomic diversity. A peculiar feature of pelagic Lake Kivu zooplankton is the presence of several rotifers taxa, which makes it apparently closer to the pelagic fauna of smaller African lakes. For other East African lakes, Lehman (Lehman, 1988) reviewed the species list and noted the rarity of rotifers in the largest lakes. He attributed this to the lack of refuge from invertebrate predation in pelagic waters, notably by *Chaoborus* (in Lake Malawi) and possibly by *Mesocyclops* (in Malawi and Tanganyika). It is quite possible that, in Lake Kivu, invertebrate predation

on rotifers is reduced by the control of the largest cyclopoids by *Limnothrissa*.

Compared with the situation before the sardine introduction, Lake Kivu zooplankton pelagic community composition has changed (Reyntjens, 1982; Dumont, 1986; Descy and Fourniret, 1991; Kaningini *et al.*, 2003). It is dominated by copepods, and the diversity is slightly higher now. However, our study did not reveal the catastrophe predicted by Dumont (Dumont, 1986): present zooplankton biomass is much higher than the 0.07 g C m^{-2} (estimated from 0.15 g DW m^{-2}) reported for July–September 1981.

The temporal pattern of zooplankton development in Lake Kivu is characterized by a large seasonal contrast, with low biomass in the rainy season and a dry season increase, closely following the dry season rise of phytoplankton biomass. In the long dry season (July–September), changes in phytoplankton biomass and composition occurred (Sarmiento *et al.*, 2006), which resulted in greater abundance and, possibly, quality of edible resources. Each time the phytoplankton peak was well marked (e.g. in 2003), zooplankton responded by an increase of abundance with a 2-week delay. Differences among years in the timing, magnitude and recurrence of those main zooplankton peaks were observed. Several studies on large, deep, African lakes reported comparable observations. For example, Twombly (Twombly, 1983a) indicated that the overall patterns of zooplankton abundances in Lake Malawi can vary between years, or the same pattern be repeated, but the timing of population increase and decline differs from one year to another. For the same lake, Irvine (Irvine, 1995) reported that the mean biomass of crustaceans in 1993 was significantly greater than that recorded in 1992. Kurki *et al.* (Kurki *et al.*, 1999) also obtained the same result in Lake Tanganyika and estimated that the horizontal migration of the planktivorous clupeids, reported by Ruffi and Chapman (Ruffi and Chapman, 1976) in this lake, may explain the annual changes observed in zooplankton. In Lake Kivu, Marshall (Marshall, 1991) reported that there may be a migration from south to north of the introduced planktivore *L. miodon*. However, our studies (Sarmiento *et al.*, 2006; this article) show that the magnitude of phytoplankton peaks can vary strongly from year to year. This suggests that, in Lake Kivu as in the other Rift lakes (Descy *et al.*, 2005), large climate-driven variation in primary production can directly influence consumer production.

Several studies on other tropical lakes documented fluctuations in zooplankton abundance (Talling, 1969; Lewis, 1978; Kalk, 1979). These studies concerned deep, oligotrophic lakes such as lakes Malawi (Twombly, 1983a, 1983b; Irvine, 1995; Irvine and

Wayu, 1999) and Tanganyika (Mulimbwa, 1988, 1991; Kurki *et al.*, 1999), as well as shallow lakes, namely Awasa (Mengestou and Fernando, 1991), Kariba (Masundire, 1992, 1994, 1997), Nkuruba and Nyahiryia (Kizito, 1998). They showed that the main seasonal trends are frequently interrupted by short-term irregular changes in population size. In Lake Kivu, zooplankton populations, especially *T. confinis*, *M. micrura* and *A. rectangularis*, also exhibited short-term fluctuations in abundance. As discussed by Irvine (Irvine, 1995), excluding variability due to sampling, the mechanisms driving short-term fluctuations in abundance of tropical zooplankton are uncertain, but physical and biological processes may be involved. Physical processes may include the mixing of a weakly stratified water column, increasing nutrient availability and allowing short-term increase of primary production (Lewis, 1973; Twombly, 1983a) or nutrient inputs from tributaries during the ‘calm’ wet season. Because Lake Kivu is surrounded by mountains, local winds and surface cooling at night may disturb water column stratification and influence, aseasonally, primary production and zooplankton abundance. As for the influence of tributaries, no important river discharges into Lake Kivu, so that the impact of rivers’ inputs is presumably minimal. Fish predation may also be a significant factor resulting in aseasonal variation, primarily because there are large fluctuations in *Limnothrissa* adult population (Marshall, 1991; Kaningini, 1995) depending on recruitment and fishery effort. Another factor influencing planktivorous fish predation is the lunar cycle (Gliwicz, 1986, 1994) coupled to variable weather conditions. Therefore, fish predation on zooplankton is expected to exert a major influence when the fish population responds to increase of its food resource (i.e. typically at the end of the year, after the major zooplankton peak), and it is also likely to be affected by natural monthly variations. This may explain the irregular temporal pattern of *D. excisum* (probably the species most affected by predation) population, compared with the regular pattern of the two dominant copepod species.

To summarize, this study demonstrates that, despite sharing many common traits with other great African lakes, showing strong seasonality in plankton production, Lake Kivu has a mean annual total zooplankton biomass which is much lower than that in lakes Malawi and Tanganyika. The explanation of this low zooplankton production despite relatively high phytoplankton production may be in the food web structure: the zooplankton community in Lake Kivu does not include a large calanoid species, which represents a major contribution to mesozooplankton biomass in the two larger lakes and efficiently exploits the phytoplankton by

grazing. Indeed, these lakes have a more complex pelagic food web, including piscivorous fish and calanoid copepods, which can efficiently exploit phytoplankton production. In Lake Kivu, the ‘large grazer’ niche was previously occupied by a *Daphnia* that disappeared following the sardine introduction. Other factors may be involved in this relatively low trophic efficiency, notably a trophic cascade (Carpenter and Kitchell, 1993) that would explain why in Lake Kivu relatively high phytoplankton biomass does not result in high zooplankton biomass. However, no study so far has been devoted to quantitative assessment of zooplankton production and fish predation rates, which could verify this hypothesis. The evidence we provide here is that Lake Kivu zooplankton has a temporal pattern similar to that observed in the larger African Rift lakes. Its abundance and biomass clearly depend on the dry season wind-driven increase of primary production. Besides this main seasonal event, fluctuations occur, which may be dependent on physical disturbances of the water column or on transient effects of predation by the planktivorous fish. Thus, our results suggest that, during our study period (2002–04), zooplankton dynamics in Lake Kivu were essentially bottom-up controlled. This contrasts with the view conveyed by earlier studies (Dumont, 1986) of a strong top-down control of zooplankton by *L. miodon* predation. The sole indication of a significant impact of *L. miodon* predation is the small average body size of the cladoceran *D. excisum*, which is twice as small as in Lake Malawi (Irvine, 1995), whereas the two dominant copepods (*T. consimilis* and *M. aequatorialis*) have a similar body size range as in the other Rift lakes. Furthermore, it is unclear whether the introduction of *L. miodon* has had a very large impact on total copepod biomass. Planktonic copepods can escape a visual predator by migrating below the euphotic zone, which in Lake Kivu never exceeds 25 m. Still, it is quite evident that zooplankton community composition was adversely affected by the sardine introduction, which wiped out the most efficient grazer (Dumont, 1986), and this single change may have affected the lake’s food web efficiency and productivity to a very large extent.

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