



Plankton abundance and resource exploitation by the endemic sprat *Nannothrissa stewarti* (Poll & Roberts, 1976) in a large blackwater lake of the middle Congo River basin, Lake Mai-Ndombe

Mwapu Isumbisho^{1,2} , Jean-Pierre Descy^{3,*} , Steven Bouillon⁴,
Jean Jacques Bowanga wa Litute¹, Likoko Kashala^{1,5} and Jos Snoeks⁶

¹Laboratoire d'Etude de Milieux Aquatiques (LEMA), Département de Biologie et Techniques Appliquées, Institut Supérieur Pédagogique de la Gombe (ISP-Gombe), Avenue Père BOKA N°2 Kinshasa, DR Congo

²École Régionale postuniversitaire d'Aménagement et de Gestion Intégrés des Forêts tropicales et Territoires tropicaux (ERAIFT), Campus UNIKIN - BP 15373 - Kinshasa, DR Congo

³Chemical Oceanography Unit, FOCUS, University of Liège, Quartier Agora, allée du six Août 11, 4000 Liège 1, Belgium

⁴Department of Earth and Environmental Sciences, KU Leuven, Celestijnenlaan 200E B-3001 Leuven-Heverlee, Belgium

⁵Département de Géographie et Gestion de l'Environnement, Institut Supérieur Pédagogique de la Gombe (ISP-Gombe), Avenue Père BOKA N°2 Kinshasa, DR Congo

⁶Department of Biology, Fish Diversity and Conservation, KU Leuven, Charles Deberiotstraat 32 - box 2439 3000 Leuven, Belgium

*Corresponding author: jpdescy@uliege.be

Corresponding editor: Beatrix Beisner

ABSTRACT

Lake Mai-Ndombe is a large natural shallow lake of the Congo River basin. We investigated the composition and abundance of plankton and the diet of *Nannothrissa stewarti* that is at the basis of an important fishery. The lake is not stratified, phytoplankton being well developed during low water (LW) conditions with higher biomass (average value $\sim 2.5 \pm 1.1 \mu\text{g}$ chlorophyll a L^{-1}) than in high water (HW) conditions ($0.14 \pm 0.1 \mu\text{g}$ chlorophyll a L^{-1}). It is oligotrophic but with an autochthonous algal primary production, in contrast to earlier reports. The metazooplankton comprises 15 species (excluding bdelloid rotifers), among which the dipteran *Chaoborus* sp. Its biomass is low ($\sim 0.20 \pm 0.1 \text{ g C m}^{-2}$ in LW vs $0.130 \pm 0.02 \text{ g C m}^{-2}$ in HW). Based on gut contents analysis, *Nannothrissa* is a highly selective feeder in Lake Mai-Ndombe, feeding mostly on Cladocera despite their relatively low abundance. This suggests that only part of the metazooplankton production is being exploited by the sprat. However, stable carbon and nitrogen isotope data are inconsistent with the dominance of zooplankton in stomach contents, and further work should elucidate which ^{13}C -depleted sources further support the diet of this key consumer in Lake Mai-Ndombe.

KEYWORDS: Congo River basin; trophic transfer efficiency; prey selectivity

INTRODUCTION

Throughout the world, the importance of shallow lakes is well established, as they play important socio-economic roles and are vital for the protection or conservation of biodiversity (e.g. Golterman and De Groot, 1994; Hillbricht-Ilkowska, 1999; Kanangire *et al.*, 1999; Chillasse *et al.*, 2001; Coops and Hoesper, 2002; Bocaniov *et al.*, 2019).

Central African shallow lakes, in particularly those from the Congo Basin, have attracted little scientific interest in comparison to those from the Amazon Basin (e.g. Arcifa *et al.*, 1992; Cardoso and Marques, 2004; Sendacz *et al.*, 2006). Although they support subsistence fisheries important for the local human populations, the lack of data on their biodiversity and

productivity hampers the protection of these water bodies, and the sustainable exploitation of their resources is compromised by various anthropogenic impacts.

Lake Mai-Ndombe, literally meaning “black waters” in local language, is located in the “Cuvette Centrale” of the Democratic Republic of the Congo. With a surface area of 2300 km^2 , it is the largest natural shallow lake of the Congo Basin. Its waters have a very low mineral content (specific conductivity is typically less than $50 \mu\text{S cm}^{-1}$) and are acidic ($\text{pH} \sim 4$) and dark brown colored (Burgis and Symoens, 1987) due to a high dissolved organic matter concentration, which originates from the drainage of flooded forest areas (Borges *et al.*, 2022). The lake level (mean depth $\sim 5 \text{ m}$), and thus the surface area, undergo

Received: July 10, 2025. Revised: November 12, 2025. Accepted: December 2, 2025

© The Author(s) 2026. Published by Oxford University Press. All rights reserved. For commercial re-use, please contact reprints@oup.com for reprints and translation rights for reprints. All other permissions can be obtained through our RightsLink service via the Permissions link on the article page on our site—for further information please contact journals.permissions@oup.com.

large seasonal variations (Bongeba and Micha, 2013; Luhusu and Micha, 2013), related to rainfall pattern, inputs from tributaries and runoff from the flooded forest.

Apart from the description of some fish species (e.g. Stewart and Robert, 1984; Schliewen and Stiassny, 2006; Hardman and Stiassny 2008; Delling *et al.*, 2024), little has been published on the lake's aquatic biodiversity (Micha *et al.*, 2018). Seventy-nine fish species have been reported from the lake and its affluents (unpublished data, FishBase team of the Royal Museum of Central Africa, Belgium), among which eight endemics, including the Mai-Ndombe dwarf sprat, *Nannothrissa stewarti*. The fishery of Lake Mai-Ndombe is practiced by at least 65 000 fishermen (Luhusu and Micha, 2013) and seems to be flourishing, representing an important resource for local populations, which face serious problems of poverty and demographic growth. At the end of the 1970s, the potential yield of the fishery, mainly based on *N. stewarti* (Micha *et al.*, 2018), was evaluated at about 10 000 tons (Compère and Symoens, 1987).

The food web supporting this important fish production has not been investigated so far. Compère and Symoens (1987) mentioned that nothing is known on Lake Mai-Ndombe phytoplankton, except that its concentration and production was very low, assuming that exogenous inputs from the rainforest should be much more important than endogenous inputs from phytoplankton. Recent data (2015) based on two samples (Willén, pers. comm.) indicate a low phytoplankton biomass (0.3–0.4 mg/L) and a composition dominated by chrysophytes, diatoms and green algae. This indicates that fish production may partially or even mainly be sustained by terrestrial organic matter, fueling a heterotrophic microbial production, which in turn supports metazooplankton production. The metazooplankton of Lake Mai-Ndombe has not yet been thoroughly studied but it appears to be poorly diversified according to a preliminary survey reported in Micha *et al.* (2018). So far, data on zooplankton abundance and biomass are poorly documented: only the dominance of calanoid copepods, which represented ~81% of the crustacean numbers, was mentioned by Micha *et al.* (2018). The small-species fishery, based on the Mai-Ndombe dwarf sprat, seems, unfortunately, already suffering of overexploitation (Micha *et al.*, 2018). This is a persisting problem also elsewhere in the Democratic Republic of the Congo (Mbadu *et al.*, 2010; Bongeba and Micha, 2013; Luhusu and Micha, 2013; Van der Knaap *et al.*, 2014; Mushagalusa *et al.*, 2015; Micha, 2019), notably because of the use of inappropriate fishing techniques, such as the use of mosquito nets with too fine mesh sizes, which leads to the elimination of larvae and juveniles. However, throughout the African continent, small-species fisheries are of vital importance, providing proteins and micronutrients that support the health of local populations (Kolding *et al.*, 2019). The small fish species exploited in subsistence fisheries have conventionally been regarded by fisheries managers as resources with “low economic value” and have been assigned low priority with respect to research and monitoring (Kolding *et al.*, 2019). The biology and ecology of many of these small fishes are often poorly known. They have a high biological turnover, are mostly planktivorous (Turner, 1982; van Zwieten *et al.*, 1996; Bos *et al.*, 2006; Welcomme, 1972; Villanueva *et al.*, 2008) and make up an important biomass at intermediate levels of the food web (Cury

et al., 2000; Palomera *et al.*, 2007). Connecting the lower and higher trophic levels (Cury *et al.*, 2000), their populations can exert a substantial pressure on zooplankton, inducing changes in community size distribution, and, at the same time, they are the main prey for predator species (e.g. Costalago *et al.*, 2012).

In the context of Lake Mai-Ndombe, where limnological studies have been very limited so far, data acquisition on plankton composition and abundance, as well as on the feeding biology of the sprat, appears essential from the perspective of the management of the lake's fishery. It is expected that *N. stewarti*, similarly to other small clupeid species, feeds essentially on metazooplankton (e.g. Cochrane, 1984; Phiri, 1991; Mandima, 1999; Isumbisho *et al.*, 2004; Zanga *et al.*, 2022).

Here, we report recent data on limnology, physical and chemical characteristics of the lake water, phytoplankton biomass, with a focus on zooplankton composition and abundance, and on the diet of the main species supporting the fishery of Lake Mai-Ndombe, *N. stewarti*. We used different approaches (plankton composition analysis, plankton biomass assessment, fish stomach content and stable C and N isotopes analyses), with the aim of assessing planktonic resources availability and their exploitation by the Mai-Ndombe dwarf sprat. Our expectation was that, given the zooplankton composition reported in previous studies, *Nannothrissa* would feed equally on the most abundant crustacean groups in Lake Mai-Ndombe, i.e. copepods and cladocerans.

METHODS

Study area

The lake catchment area characteristics

Situated in the “Cuvette Centrale Congolaise” (an enormous depression of flooded wet tropical forest whose catchment area covers about 800 000 km²) between 1°30'S and 2°45'S and 18°00' E and 18°40'E (Fig. 1) at about 300 m asl, Lake Mai-Ndombe is the largest shallow lake of the Congo River basin forest floodplain. Compère and Symoens (1987) reported its characteristics as follows: a surface area of about 2300 km² (total length ~140 km, mean width ~14 km), varying significantly with season, a total water volume varying seasonally from 4.10⁹ m³ to 10.10⁹ m³, a mean depth of about 5 m (maximum ~10 m) and a catchment area of about 67 680 km². The age of Lake Mai-Ndombe is unknown but the beds of the eastern and the southwestern parts of the lake are of Pleistocene, or even of Pliocene age, dating from the time when the entire depression was flooded. In the northwestern part, however, the lake beds are very recent (Hughes and Hughes, 1992).

The lake is supplied by many tributaries, the most important being: the Lobeke, Lokoro, Mbalenzala, Mpata-mbalu, Bolongoosongo, Bolongoolule, Bolongomboo, Bowola, Botswana, Podote, Monopoli, Nkolé and the Nzalenkanda (Bongeba and Micha, 2013). Lake Mai-Ndombe drains to the Congo River via the Fimi, a tributary of the Kasai river.

Climatic conditions at the sampling sites

To characterize the climate at the sampling site, we collected data from the National Aeronautics and Space Administration website (<https://power.larc.nasa.gov>): the data correspond to the

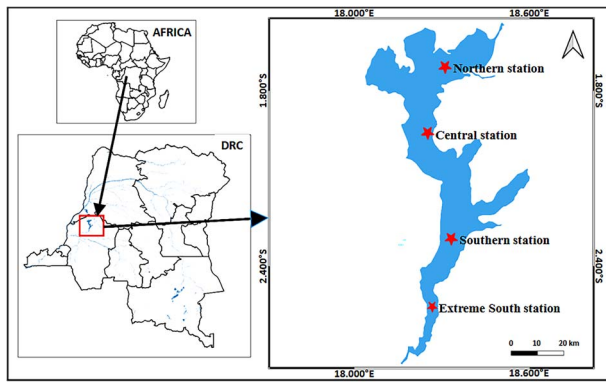


Fig. 1. Geographical location of Lake Mai-Ndombe (Star = sampling station).

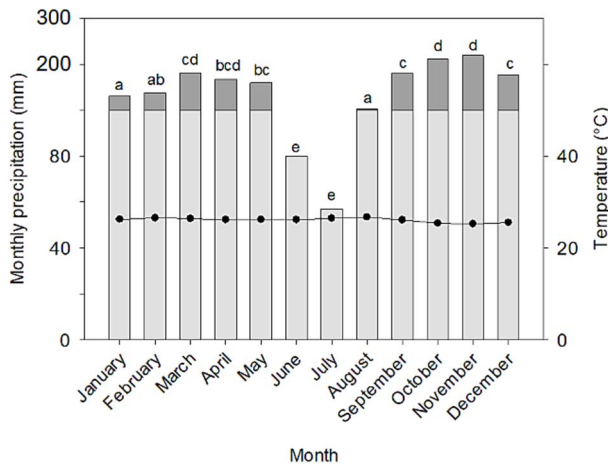


Fig. 2. Umbrothermal diagram of Lake Mai-Ndombe region (1981-2022): precipitations of more than 100 mm are presented in a darker colour and different letters on bar charts indicate significant difference in monthly rainfall ($p < 0.05$).

point situated at $1^{\circ}93' S$ and $18^{\circ}29' E$) for 42 years (1981–2022). Their analysis indicates that the climate of this part of the Lake Mai-Ndombe is of the equatorial type with high precipitation (monthly average of 150.2 ± 50.3 mm) and temperature (monthly average of $26.1 \pm 0.4^{\circ}C$). As expected, the umbrothermal diagram (Fig. 2) from the four last decades does not show a marked dry season, indicating a typical equatorial climate characterized by abundant precipitation and high humidity throughout the year (Mpounza and Samba-Kimbata, 1990).

However, there is a significant difference between monthly precipitations ($P < 0.05$, Mann-Whitney test): the heaviest rainfall occurs in October–November and the lowest in June–July. In terms of rainfall abundance, four periods are clearly observed: (i) June–July when precipitation is lower than 100 mm; (ii) January, February and August with rainfall values between 100 mm and 150 mm (150 mm = the periodic annual average); (iii) March, April, May, September and December with rainfall values between 150 mm and 200 mm, and (iv) October–November when precipitation is the most intense (over 200 mm). This rainfall distribution over the year determines the lake water level. According to Compère and Symoens (1987),

the water level passes by a minimum in August–September with high waters occurring from January to April. Thus, in the present publication, we adopted the denomination of low water (LW) and high water (HW) instead of dry and wet seasons.

Sampling program and fieldwork

For logistical reasons, fish samples were collected only at Inongo in the central basin of the Lake (Fig. 1), on 29 August 2018 during LW and on 24 February 2019 during HW, at day time (10–13 hours local time). They were collected by fishermen who used a beach seine that integrates a mosquito net in the pocket (see Micha *et al.*, 2018). The fishing activity took place for 2–3 hours. The technique was carried out by four fishermen and consisted in deploying the net in the pelagic zone in a circular way. Larvae, juvenile and adult specimens of *Nannothrissa* were collected from the catches and preserved in a formalin solution (4%).

Other environmental parameters were measured at the fish sampling site. Physical and chemical parameters (Dissolved oxygen, temperature, conductivity at *in situ* temperature and pH) were measured at different depths from surface to bottom, using a Hydrolab DS4a multiprobe (Loveland, USA) that also measured the depth of the water column, while water transparency was measured using a Secchi disk. Vertical profiles of temperature and dissolved oxygen were measured at different times of the day (at 18:00 on 23 February 2019 and at 00:00, 06:00 and 12:00 on 24 February 2019). Zooplankton were collected using a 20 cm diameter, 60- μ m mesh open plankton net for vertical net hauls in the water column, from bottom to surface. Five vertical net hauls were carried out to obtain sufficient zooplankton material. The five subsamples were mixed to obtain a unique sample that was preserved in 4% formalin, according to the method of Haney and Hall (1973). For the phytoplankton study, one-liter samples were collected at 1 m depth intervals at four pelagic sites (two in the northern part, two in the central part of the lake), from surface to bottom, using a 5 L Van Dorn vertical water sampler. Water samples from each depth were filtered on Macherey–Nägel (Düren, Germany) 47 mm GF5 filters (nominal pore size 0.7 μ m) that were kept in the dark and frozen for further analysis in the laboratory. Eight water samples were also collected in the littoral zone during fish sampling to measure chlorophyll a concentration, after mixing subsamples from different depths.

Two additional plankton sampling series were conducted in February 2020 and August 2021 to document further abundance and composition of phytoplankton and zooplankton, and their seasonal variation. During these two campaigns, samples were collected in the three main parts of the lake (Fig. 1): at the Northern Station ($01^{\circ}72.10'S$, $18^{\circ}28.43'E$), at the Central Station ($01^{\circ}95.67'S$, $18^{\circ}17.31'E$) and at the Southern Station ($02^{\circ}32.88'S$, $18^{\circ}18.40'E$). For phytoplankton, however, samples were also collected at the Extreme Southern Station (near the outlet) ($02^{\circ}72.96'S$, $18^{\circ}12.86'E$); it was impossible to collect zooplankton samples at this last station. Water samples for the analyses of stable C and N ratios of suspended matter were taken ~ 0.5 m below the surface, and a known volume was filtered on precombusted ($450^{\circ}C$, 5 hours) 25 mm GFF filters (nominal pore size 0.7 μ m). These filters were air-dried in the field and kept in the dark until their analysis in the laboratory.

Laboratory analyses

Phytoplankton pigment extraction was performed in 90% HPLC-grade acetone, using two 15 min sonication steps in melting ice, separated by an overnight at 4°C in the dark, as in Sarmiento *et al.* (2006). Extracts were kept in portable freezers until further analysis. Phytoplankton biomass and composition were assessed throughout the study by the determination of chlorophyll a (Chla) and marker pigments by high performance liquid chromatography (HPLC) coupled with the processing of the pigment concentrations using the CHEMTAX software, as in Deirmendjian *et al.* (2021). Chlorophyll degradation products (chlorophyllide a, phaeophorbide a and phaeophytin a and b) were also quantified. When samples from different depths were available for a site, pigment concentrations were averaged, considering that the water column was fully mixed. Samples for microscopic examination were collected (250 mL) at the four main parts of the lake in the LW period and fixed in formalin; they were concentrated by settling up to 25 mL. The identification of the dominant taxa was carried out using the relevant phycological literature, as in Descy *et al.* (2017).

The contribution of phytoplankton classes to Chla was calculated using CHEMTAX (Mackey *et al.* 1996), with input ratio matrices including phytoplankton groups identified by microscopic examination, which allowed to verify the presence of diatoms, green algae, cyanobacteria, cryptophytes, chrysophytes, dinoflagellates and raphidophytes. The presence of raphidophytes, typical of humic lakes and peatbogs (Ott *et al.*, 2015) was assumed from the phytoplankton composition reported by Willén (in Micha *et al.*, 2018).

The main markers used for assessing the biomass of the phytoplankton classes were peridinin (dinoflagellates), fucoxanthin (diatoms and chrysophytes), lutein and chlorophyll b (green algae), alloxanthin (cryptophytes) and zeaxanthin (cyanobacteria and green algae). Secondary marker pigments were also used, including violaxanthin (green algae and chrysophytes), diadinoxanthin and diatoxanthin (diatoms, dinoflagellates and raphidophytes), and chlorophyll c1–c2 (diatoms, dinoflagellates, cryptophytes and raphidophytes).

Zooplankton samples were concentrated by settling for 48 hours in the laboratory and the final volume was standardized to 50 mL. From each sample, three subsamples of 2 mL were taken after homogenization and completely examined under an inverted microscope. Each zooplankton individual was counted and identified to the lowest possible taxonomic level (genus or species) using relevant literature resources (Dussart, 1967a, 1967b, 1982; Harding and Smith, 1974; Pontin, 1978; Dumont, 1981; Amoros, 1984; Dussart *et al.*, 1984; Kořinek, 1999). We estimated zooplankton biomass from dry weight obtained using length-weight relations from studies undertaken in subtropical waterbodies for the same taxon and the same development stages (e.g. Dumont *et al.*, 1975; Downing and Rigler, 1984; Culver *et al.*, 1985; Irvine and Waya, 1999; Sendacz *et al.*, 2006; Castilho-Noll and Arcifa, 2007; González *et al.*, 2008) for copepods and cladocerans. The body length of at least 50 individuals was measured for each taxon using a graduated eyepiece under an inverted microscope. For rotifers and *Chaoborus* larvae, we used mean dry weight from the references listed above.



Fig. 3. Young life stages of Lake Mai-Ndombe *Nannothrissa stewarti*: larva with its straight gut (a) and juvenile with well-developed stomach (b).

Fish samples were sorted and measured (total length TL, mm) in the laboratory. After measurements, specimens were dissected in a Petri dish and their digestive tracts isolated and opened under a dissecting microscope (magnification 40 X). Given that the ontogenetic development of the digestive tract of *Nannothrissa* relatively to its body size was not known, we started by examining the digestive tract content of the smallest specimens available in preserved samples (12 mm). We observed that the stomach bulb appears generally in specimens of 14 mm of total length (TL) while sexual differentiation of the gonads appears in fish of a TL of 20 mm.

Since it is well known that at the time when a fully or almost fully developed stomach bulb appears, fish develop new digestive enzymes and might change their feeding habits (e.g. Dabrowski, 1981, 1984; Stroband and Dabrowski, 1981; Mähr *et al.*, 1983; Lauff and Hofer, 1984), we considered *N. stewarti* with a straight gut as larvae, those with a well-developed stomach bulb but without any sign of sexual maturity, as juveniles (Fig. 3), and those with a well-developed stomach bulb and sexually differentiated gonads, as adults. Thus, for the present study, we considered as larvae fishes smaller than 15 mm TL, juveniles those with a TL between 15 mm and 20 mm, and adults those with a TL greater than 20 mm.

A total of 935 digestive tract contents of *N. stewarti* were examined under the dissecting microscope, followed by observation at high magnification under inverted microscope: 243 larvae (146 from the LW and 97 from the HW), 314 juveniles (137 from the LW and 177 from the HW) and 378 adults of which 155 males (90 from the LW and 65 from the HW) and 223 females (87 from the LW and 136 from the HW). Prey items were sorted, identified to the lowest possible taxonomic level according to different identification keys (see zooplankton identification), and counted whenever possible. Given the size of the smallest digestive tract content, the volume of each prey item was determined by the points method (Hynes, 1950).

For carbon and nitrogen stable isotope ratios, faunal samples (fish and zooplankton collected at the same time), were sorted from previous samples, preserved in formalin, and later oven

dried (50°C) and homogenized with a mortar and pestle. Subsamples were weighed in Ag cups, acidified with dilute HCl to remove possible carbonates, and analyzed by elemental analyzer-isotope ratio mass spectrometry (Thermo EA1110 and Delta V Advantage IRMS). Data were calibrated using certified and in-house standards (IAEA-600, leucine, and tuna muscle tissue); reproducibility was typically better than 0.15‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. GFF filters for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses were acidified in HCl fumes to remove potential carbonates, dried overnight at 50°C and then packed in Ag cups. They were analyzed as described above for faunal samples. Given that preservation of faunal samples on formalin can lead to a shift in stable isotope data, zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were corrected by -0.2 and $+0.25$ ‰, respectively (based on Rennie *et al.*, 2012), and fish $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were corrected by -0.94 and $+0.33$ ‰, respectively (based on González-Bergonzoni *et al.*, 2015).

Dietary data analysis

For each prey item, the frequency of occurrence (O_i), percentage by number (N_i), and percentage by volume (V_i) (Hyslop, 1980) were determined. Using these percentages, three indices were calculated:

(1): Lauzanne's Alimentary Index (IA_i) (Lauzanne, 1976), which combines total volume (%) and frequency of occurrence (%) of each item (Kawakami and Vazzoler, 1980) as:

$$IA_i = (O_i \times V_i) / 100$$

where IA_i is the alimentary index, O_i is the percentage frequency of occurrence, i.e. the percentage of non-empty gut in which a certain prey item occurred and V_i the percentage by volume, i.e. the percentage contribution to the volume of all dietary items present in each non-empty gut (Hyslop, 1980). This index corresponds to the index of preponderance (Natarajan and Jhingran, 1961) and allows a ranking of prey items according to their importance. IA_i was standardized to 100% by calculating the percentage of the total IA_i contributed by each prey type (% IA_i) as:

$$\%IA_i = \frac{IA_i}{\sum_{i=0}^n IA_i} \times 100$$

with n the number of different prey categories (i);

(2): Ivlev diet selectivity index (Krebs, 1989) was calculated as:

$$E_i = \frac{r_i - p_i}{r_i + p_i}$$

where r_i is the proportion of prey item i in the diet and p_i is the proportion of prey item i available in the lake. This index can range between -1 and $+1$, with negative values indicating avoidance or inaccessibility of the prey item, zero indicating random selection from the environment, and positive values indicating active selection;

(3): Pianka's niche overlap index was calculated to evaluate the niche overlap between different development stages. This index is based on the classical Pianka index (Pianka, 1974), derived from the composition of the diet (percentages) of the

different development stages and calculated as:

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where O_{jk} is the Pianka index of niche overlap between stages j and k ; p_{ij} , the proportion of the i resource in the diet of the stage j ; p_{ik} , the proportion of the i resource in the diet of the stage k ; and n , the total number of items. The index values range from 1 (complete overlap) to 0 (no overlap), and diet overlap is usually considered significant when O_{jk} exceeds 0.6 (Wallace, 1981).

Statistical analyses

Differences in monthly rainfall as well as in physical and chemical parameters within water level phases were tested by one-way ANOVA test followed by the non-parametric Mann-Whitney U pairwise multiple test. Analyses were performed with the PAST software (v.3.25: Hammer *et al.*, 2001) and statistical significance was set at the $P < 0.05$ level.

RESULTS

Environmental variables in the water column at the sampling station

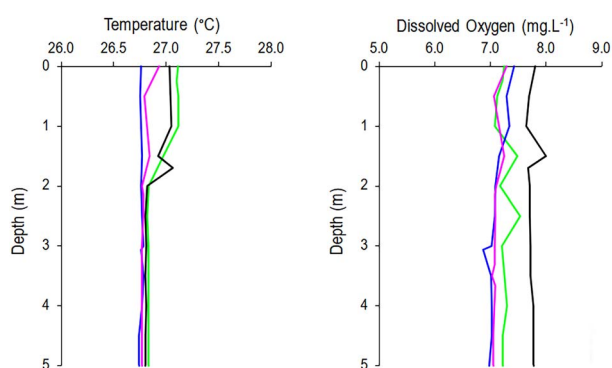
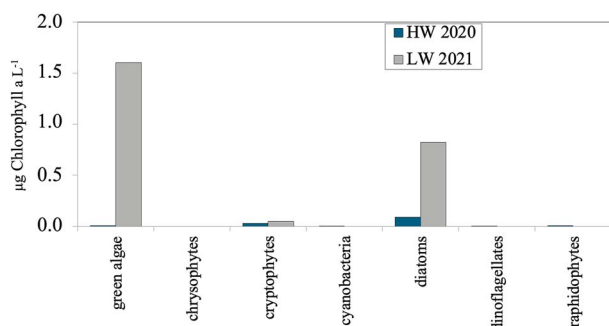
The average values of physical and chemical parameters measured in the water column at different depths during the sampling period are presented in Table I. The mean temperature in the water column was high, $28.5 \pm 0.5^\circ\text{C}$ during HW, and $29.0 \pm 0.5^\circ\text{C}$ during LW. Dissolved oxygen concentration was below saturation at all times, ($70.7 \pm 3.8\%$; 5.0 ± 0.5 mg/L at HW vs $60.7 \pm 2.8\%$; 6.3 ± 0.3 mg/L at LW) while water conductivity at *in situ* temperature was low (43.4 ± 0.9 $\mu\text{S}/\text{Cm}$ during HW vs 43.4 ± 0.6 $\mu\text{S}/\text{Cm}$ at LW) as well as the pH (3.8 ± 0.1 during HW and 4.2 ± 0.2 during LW). The Secchi disk depth was also low (63.0 cm during HW and 73.0 cm at LW) and the water depth varied greatly with water phase (6.1 m at HW and 3.5 m at LW). Statistically, there was a significant difference ($F = 5.787$; $P < 0.05$) between the HW and LW physical and chemical conditions. This difference is well marked for the temperature ($Z = 2.78$; $P < 0.05$), dissolved oxygen concentration ($Z = 1.93$; $P < 0.05$) and pH ($Z = 3.08$; $P < 0.05$). However, there was no significant difference between the two periods for water conductivity ($Z = 0.35$; $P = 0.72$) and dissolved oxygen water saturation ($Z = 0.45$; $P = 0.64$) The vertical profiles of temperature and dissolved oxygen concentration presented in Fig. 4 indicate that the lake waters were fully mixed at all times.

Phytoplankton biomass and composition

The HW data collected in 2019, i.e. when the fishes were collected, show an average Chl-a concentration of 1.77 ± 1.55 μg Chl-a L^{-1} for the pelagic sites ($n = 4$), with a large coefficient of variation (87%), close to the value in the littoral sites ($1.41 \mu\text{g} \pm 1.13$ Chl-a L^{-1} , $n = 8$). A single value of 1.7 Chl-a L^{-1} is available for the LW conditions in 2018, thus not allowing a comparison between periods. The contrast between HW and LW conditions is more evident in the data from 2020 and 2021.

Table I: Mean with standard deviation and minimum-maximum (in brackets) of principal physical and chemical parameters at the Central Station water column during LWs and HWs in lake Mai-Ndombe; different letters on the mean value for a variable indicate significant difference at $P < 0.05$

		HW	LW
Temperature ($^{\circ}\text{C}$)	Mean \pm SD (min–max)	28.5 ^a \pm 0.5 (28.3–30.0)	29.0 ^b \pm 0.4 (28.4–29.3)
Dissolved oxygen (%)	Mean \pm SD (min–max)	70.7 ^a \pm 3.8 (65.6–79.5)	60.7 ^a \pm 2.8 (57.6–64.6)
Dissolved oxygen (mg L^{-1})	Mean \pm SD (min–max)	5.0 ^a \pm 0.2 (4.6–5.2)	6.3 ^b \pm 0.3 (6.0–6.7)
Conductivity ($\mu\text{S/cm}$)	Mean \pm SD (min–max)	43.4 ^a \pm 0.9 (42.7–46.2)	43.4 ^a \pm 0.6 (42.7–46.2)
pH	Mean \pm SD (min–max)	3.8 ^a \pm 0.1 (3.7–4.1)	4.2 ^b \pm 0.2 (3.9–4.3)
Secchi depth (cm)	–	62.0	68.0
Depth (m)	–	6.1	3.5

**Fig. 4.** Vertical profiles of temperature and dissolved oxygen in the water column at the Central Station of Lake Mai-Ndombe, at different times of the day (23–24 February 2019).**Fig. 5.** Average biomass, expressed as chlorophyll a concentration, of the phytoplankton classes in the pelagic zone of Lake Mai-Ndombe, in high water conditions (HW: February 2020) and low water conditions (LW: August 2021).

In all four regions of the lake, Chla concentration in the pelagic zone was larger in the LW phase (average $2.47 \pm 1.06 \mu\text{g Chla L}^{-1}$) than in the HW conditions ($0.14 \pm 0.07 \mu\text{g Chla L}^{-1}$) (Fig. 5).

Remarkably, the degree of Chla degradation was greater in HW than in LW, as shown by the average proportion of

phaeophytin a (the major degradation product of Chla in the lake) to total Chla: 70.4% in HW vs 30.3% in LW. A similar difference between periods was observed for phaeophytin b, the major degradation product of chlorophyll b. Marker pigment data show a dominance of the phytoplankton assemblage by green algae and diatoms, with a low contribution of the other phytoplankton groups. Diatom diversity was low, with a dominance of *Aulacoseira herzogii* (Lemmermann) Simonsen; *Stenopterobia* sp. (cf. *Stenopterobia pseudodelicatissima* Siver and Hamilton) was also abundant, and several species of *Eunotia* were present in much lower numbers.

Zooplankton composition and abundance

A total of 16 metazooplankton taxa (15 identified up to species or genus level and one group of unidentified Bdelloid rotifers) were observed in samples collected at the three sampling stations: six rotifer taxa, five cladocerans, four copepods and one insect (Table II). Larvae of the dipteran *Chaoborus* sp. were observed only in samples collected during the HW period in the central basin, the rotifer *Brachionus quadridentatus* only in the southern basin, while the copepods *Mesocyclops* sp. and the rotifer *Hexarthra* sp. were absent from the northern basin of the lake. Copepods clearly dominated zooplankton numbers in the three basins (75.4%, 65.3% and 50.0%, respectively in the south, the center and the north of the lake, during HW period, and 80.0%, 60.6% and 91.1%, respectively at LW). They also dominated the total biomass (Fig. 6a) with at least 50%, except in February 2020 (HW) in the central basin where the *Chaoborus* sp. larvae (Diptera) clearly dominated (66.1%) despite its lower relative abundance (2.8%).

Figure 7 presents the total metazooplankton biomass in the three sampling stations during the two contrasted waters levels. The mean total biomass was 2.7 times higher in the LW period ($61.7 \text{ mg C.m}^{-3} \pm 24.7 = 187.3 \text{ mg C.m}^{-2} \pm 106.6$) than in HW ($22.6 \text{ mg C.m}^{-3} \pm 3.1 = 131.7 \text{ mg C.m}^{-2} \pm 24.6$) with a more important contrast in the southern basin ($25.3 \text{ mg C.m}^{-3} = 154.6 \text{ mg C.m}^{-2}$ during HW vs $88.5 \text{ mg C.m}^{-3} = 309.8 \text{ mg C.m}^{-2}$ during LW).

Table II: Faunistic list of metazooplankton of Lake Mai-Ndombe during HWs and LWs

	Southern Basin		Central Basin				Northern Basin		
	HW 2020	LW 2021	LW 2018	HW 2019	LW 2019	HW 2020	LW 2021	HW 2020	LW 2021
Rotifera									
<i>Keratella</i> sp	X	X	X	X	X	X	X	X	X
<i>Lecane</i> sp	X		X	X		X		X	X
<i>Polyarthra vulgaris</i> CARLIN 1943	X		X	X	X	X		X	
<i>Hexarthra</i> sp	X					X	X		
<i>Brachionus quadridentatus</i> HERMANN 1783	X	X							
Bdelloids	X	X	X	X	X	X	X	X	X
Cladocera									
<i>Diaphanosoma brachyurum</i> LIEVIN 1848	X	X	X	X	X	X	X	X	X
<i>Moina micrura</i> KURZ 1874	X			X	X	X		X	
<i>Alona rustica</i> SCOTT 1895	X							X	X
<i>Bosmina longirostris</i> MUELLER 1776	X	X	X	X	X	X	X	X	X
<i>Bosminopsis deitersi</i> RICHARD 1895	X	X	X	X	X	X	X	X	X
Copepoda									
<i>Tropodiptomus</i> spp	X	X	X	X	X	X	X	X	X
<i>Mesocyclops</i> spp	X		X	X	X	X			
<i>Thermocyclops</i> spp	X	X	X	X	X	X	X	X	
<i>Tropocyclops</i> spp	X	X	X	X	X	X	X	X	X
Insects									
<i>Chaoborus</i> sp						X			

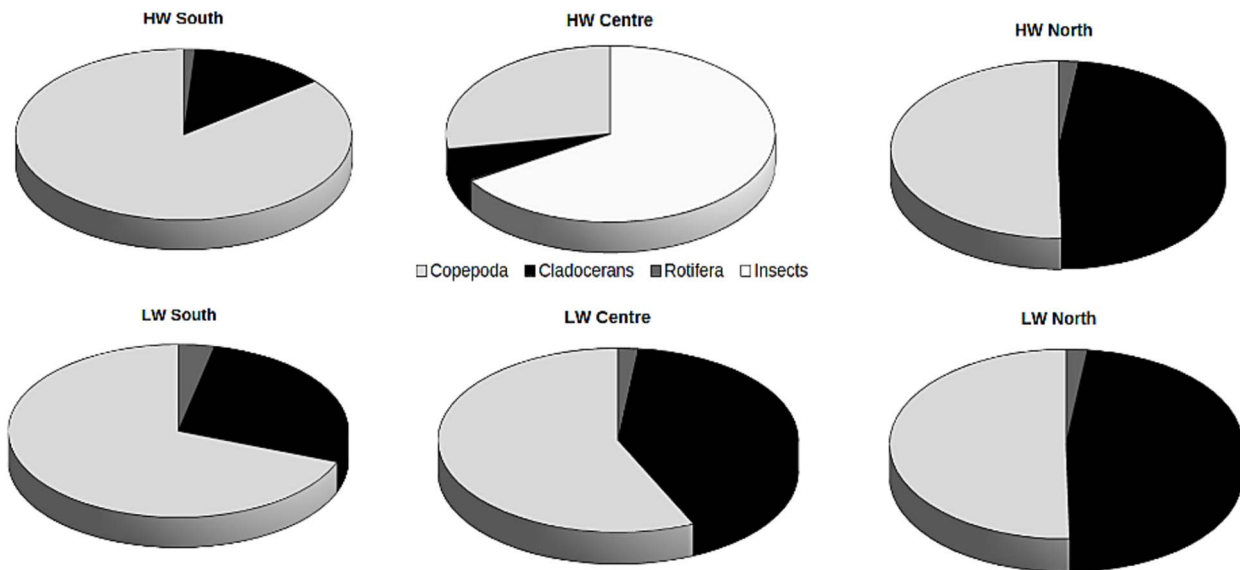


Fig. 6. Contribution of the main metazooplankton groups to the total biomass in the pelagic zone of three regions of Lake Mai-Ndombe in high water conditions (HW: February 2020) and low water conditions (LW: August 2021).

Feeding habits of the sprat

Diet composition and prey preference

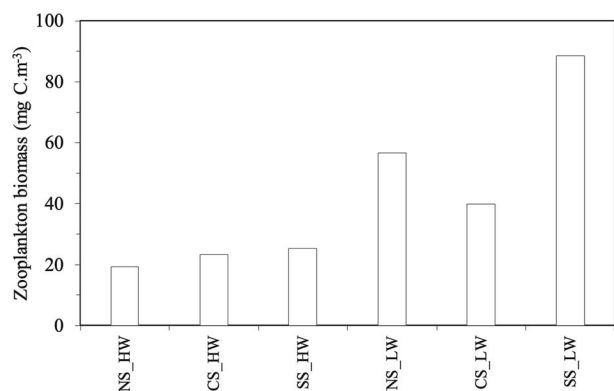
The average body length (TL) of the larvae, juveniles, males and females of *N. stewarti* collected and analyzed was respectively 13.3 ± 0.7 mm, 16.9 ± 1.6 mm, 38.8 ± 7.3 mm and 39.8 ± 9.8 mm. In the diet of *Nannothrissa*, zooplankton was the dominant/preferential food item (% IA > 50) for both young and adult individuals during both LW and HW periods (Table III). Some differences appear only when supplementary preys are considered: detritus for larvae during the two sampling

periods; insect fragments and detritus during the two periods and sand in HW for juvenile individuals. For adult males, algae, small unidentified eggs, insect fragments and detritus were recorded during LW and insect fragments in HW while for adult females insect fragments, small unidentified eggs and algae were present during both HW and LW periods. Among zooplankton, cladocerans constituted the dominant prey of *Nannothrissa* regardless of age class or water levels.

At the lowest taxonomic level, the Index of Relative Importance indicates the prey preference of *Nannothrissa* at its different

Table III: Lauzanne's Alimentary Index evaluating the importance of prey items in the Mai-Ndombe sprat diet (LW = Low Waters; HW = High Waters)

Food Items	Lauzanne index (% IA)							
	Larvae		Juveniles		Males		Females	
	LW	HW	LW	HW	LW	HW	LW	HW
Zooplankton	98.51	96.29	99.52	95.01	98.15	99.93	77.58	99.60
Copepods	24.04	4.35	48.65	40.33	4.85	11.52	26.46	7.14
<i>Tropodiatomus sp</i>	12.31	1.41	42.03	6.44	5.24	11.90	26.72	7.50
Nauplii	13.49	1.54	5.40	30.44	0.03	0.00	0.00	0.00
Cladocerans	75.69	95.65	51.35	59.66	91.50	86.24	50.70	79.54
<i>Bosmina longirostris</i>	21.25	34.13	21.36	36.60	22.78	10.47	20.57	1.51
<i>Bosminopsis deitersi</i>	25.51	16.06	17.81	1.70	45.19	66.02	18.89	75.75
<i>Diaphanosoma brachyurum</i>	0.78	0.00	0.00	0.00	0.57	0.00	0.22	0.00
Rotifera	0.59	0.00	0.003	0.00	1.26	0.00	1.57	0.00
<i>Keratella cochlearis</i>	0.59	0.00	0.003	0.00	1.26	0.00	1.57	0.00
Zooplankton fragments	0.00	0.00	0.00	0.00	3.21	2.30	21.77	13.98
Algae	0.00	0.00	0.00	0.00	0.78	0.00	0.39	0.10
Insect fragments	0.00	0.00	0.37	0.72	0.33	0.07	21.24	0.10
Small eggs	0.00	0.00	0.00	0.00	0.69	0.00	0.79	0.10
Detritus	1.49	3.71	0.11	4.14	0.05	0.00	0.00	0.00
Sand	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00

**Fig. 7.** Average zooplankton biomass in the pelagic zone of three regions of Lake Mai-Ndombe (NS=Northern Station; CS=Central Station; SS= Southern Station) in high water conditions (HW) and low water conditions (LW).

development stages. Larvae consumed primarily the cladoceran *Bosminopsis deitersi* (% IA =25.5), *Bosmina longirostris* being a non-negligible prey (% IA =25.5) during the LW period while during HW, they preferred *B. longirostris*. Juveniles consumed primarily the copepod *Tropodiatomus sp.* during LW while in HW, they primarily fed on nauplii larvae and *B. longirostris* during HW. Adult females fed primarily on *Tropodiatomus sp.* during LW, *B. deitersi* being their dominant prey (% IA =75.8) in HW while for males *B. deitersi* was their dominant prey in LW and HW.

Prey selection and niche overlap between the different development stages

According to Ivlev's diet index (Table IV), *B. longirostris* was actively selected by *Nannothrissa* at all its developmental stages during the two water level periods. *Bosminopsis deitersi*

underwent the same selective pressure by adults while larvae selected it only during LW period; juveniles showed no interest in this cladoceran prey. *Nannothrissa* seems to have avoided *Diaphanosoma brachyurum* except during the LW period when it was selected by larvae and adults. On the other hand, the calanoid *Tropodiatomus sp.* was moderately selected only by juveniles at LW, while the rotifer *Keratella* as well as copepod larvae (nauplii) were almost completely avoided by the sprat.

Pianka's index revealed a significant diet overlap between each development stage ($O_{ij} > 0.94$); during the LW period. However, during the HW period, niche overlap was only observed between larvae and juveniles ($O_{ij} = 0.89$) and between females and males ($O_{ij} = 0.97$).

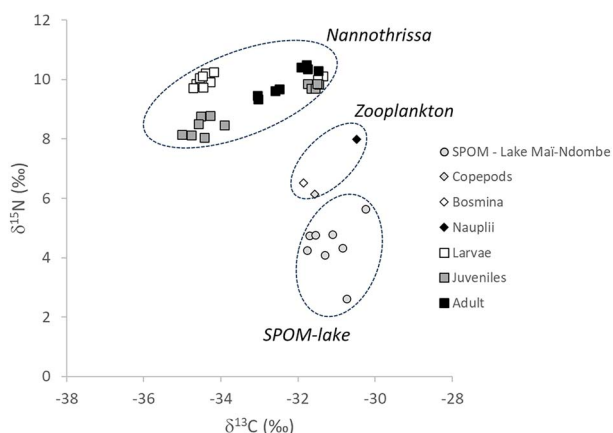
Stable isotope data

The suspended particulate of organic matter (SPOM) pool showed $\delta^{13}\text{C}$ values between -31.8 and -30.0‰ , and $\delta^{15}\text{N}$ values between 2.6 and 5.7‰, with no differences between LW and HW ($\delta^{13}\text{C}$ values of -30.8 ± 0.5 and $-31.5 \pm 0.4\text{‰}$ during HW and LW, respectively; $\delta^{15}\text{N}$ values of 4.3 ± 1.3 and $4.5 \pm 0.3\text{‰}$ during HW and LW, respectively; data are pooled in Fig. 8). Combined with C/N ratios (mass basis) of 11.7 ± 1.0 and the low Chla concentrations relative to POC concentrations ($1.55 \pm 0.67 \text{ mg POC L}^{-1}$), this points towards predominantly C3-derived terrestrial contributions to the POC pool.

Data on zooplankton are available for copepods ($\delta^{13}\text{C}$ -31.6‰ , $\delta^{15}\text{N}$: 6.1‰), *Bosmina* ($\delta^{13}\text{C}$ -31.9‰ , $\delta^{15}\text{N}$: 6.5‰), and nauplii ($\delta^{13}\text{C}$ -30.5‰ , $\delta^{15}\text{N}$: 8.0‰; Fig. 8). For *Nannothrissa*, $\delta^{13}\text{C}$ values show a relatively wide variation (-35.0 to -31.4‰), and values are consistently lower than those observed in SPOM and zooplankton (Fig. 8). $\delta^{15}\text{N}$ values for *Nannothrissa* ranged between 8.0 and 10.5‰, substantially higher than observed in SPOM or zooplankton (Fig. 8). No clear seasonal differences were observed in *Nannothrissa* stable

Table IV: Ivlev index evaluating prey selectivity by *Nannothrissa* in Lake Mai-Ndombe (LW = Low Waters; HW = High Waters)

Food Items	Ivlev diet selectivity index							
	Larvae		Juveniles		Males		Females	
	LW	HW	LW	HW	LW	HW	LW	HW
Copepods								
<i>Tropodiptomus</i> sp.	0.3	-0.2	0.6	0.0	0.1	0.1	0.2	0.1
Nauplii	-0.5	-0.3	-0.4	0.0	-1	-1	-1	-1
Cladocerans								
<i>Bosmina longirostris</i>	0.9	0.9	0.8	0.7	0.9	0.9	0.9	0.8
<i>Bosminopsis deitersi</i>	0.7	0.5	0.3	0.2	0.8	0.9	0.6	0.9
<i>Diaphanosoma brachyurum</i>	0.9	-1	-1	-1	0.7	-1	0.8	-1
Rotifera								
<i>Keratella cochlearis</i>	-0.7	-1	-1	-1	-0.3	-1	-0.2	-1

**Fig. 8.** $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for suspended particulate organic matter (SPOM) from Lake Mai-Ndombe and rivers, zooplankton (nauplii, the cladoceran *Bosmina*, and copepods) and larvae, juveniles and adult *Nannothrissa*.

isotope data ($\delta^{13}\text{C}$ values of -32.7 ± 1.4 and $-33.7 \pm 1.2\text{‰}$ during HW and LW, respectively; $\delta^{15}\text{N}$ values of 9.7 ± 0.5 and $9.5 \pm 0.9\text{‰}$ during HW and LW, respectively), and there was partial overlap between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between the different age classes (Fig. 8). In particular, data on juveniles and adults both showed a similar relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, yet larvae stand out with somewhat higher $\delta^{15}\text{N}$ values (Fig. 8).

DISCUSSION

Values of physical and chemical parameters in the water column of Lake Mai-Ndombe are similar to those reported by Compère and Symoens (1987) nearly half a century ago, as well as those from more recent studies, including Micha (2019) and Borges et al. (2022). The water column is probably entirely oxygenated constantly as is typical for shallow lakes (e.g. Reynolds et al., 2002; Padišák and Reynolds, 2003; Viviane et al., 2012). The water conductivity in Lake Mai-Ndombe is very low ($41.1\text{--}45.5 \mu\text{S cm}^{-1}$) in relation to low concentrations of dissolved salts (Compère and Symoens, 1987; Micha et al., 2018), with low pH values (3.7–4.3) due to a high concentration

in humic acids from the flooded forest in the lake's watershed that turn waters black and reduce water transparency (Secchi depth: 62.0–68.0 cm).

Chla concentrations, used as a proxy of phytoplankton biomass, were low on average ($1.8 \mu\text{g L}^{-1}$ based on LW values), even though they were slightly higher during the more productive LW period in 2020. This indicates the oligotrophic character of the lake. With a mean depth of ~ 5 m, one can estimate an areal Chla content of $\sim 9 \text{ mg m}^{-2}$, which is much lower than that of other African large lakes (see e.g. Descy et al., 2012 Table 5.2). A rough estimate of phytoplankton biomass in terms of carbon would give $\sim 0.45 \text{ g C m}^{-2}$, based on the mean Chla value, and on a putative C:Chla ratio of 50. Our data indicate that light availability can be a major limiting factor for primary production, along with low nutrient supply typical of blackwater ecosystems (e.g. Edwards and Meyer, 1987; Lewis, 1988). Nevertheless, there is clear evidence of significant phytoplankton production in the lake in LW conditions, contrary to earlier assumptions based on observations by Compère and Symoens (1987). Based on the mean Secchi depth (SD) values, the euphotic zone depth (m) can be estimated by $\text{SD} \times 2.7$ (Koenings & Edmunson, 1991). Then the average total depth: euphotic depth ratio would be ~ 3.6 at HW and ~ 1.8 at LW, meaning that, assuming full mixing of the water column, net photosynthetic production could take place in the water column only at LW whereas it was likely light-limited at HW. The phytoplankton assemblage appears well developed in LW conditions, with Chla reaching $3 \mu\text{g L}^{-1}$ and more, with a high relative abundance of green algae and diatoms. The diatom assemblage was clearly dominated by acidophilic taxa, such as the meroplanktonic *Aulacoseira* spp. and several benthic species belonging to the genera *Eunotia* and *Stenopterobia*. This suggests that the phytoplankton community may in fact be composed of an assemblage of meroplanktonic and benthic taxa, resuspended into the water column by frequent mixing in the shallow lake, where stratification is virtually absent. However, a more comprehensive sampling effort and detailed study of the algal assemblage, coupled with measurements of key variables such as nutrient concentrations, are necessary to further investigate the phytoplankton ecology of Lake Mai-Ndombe.

It is clear that, compared to many subtropical shallow lakes throughout the world (e.g. Eskinazi-Sant'Anna, 2000; Cardoso and Marques, 2004; Claps *et al.*, 2004; Sendacz *et al.*, 2006; Xin-Li *et al.*, 2011; de Paggi *et al.*, 2012), Lake Mai-Ndombe's metazooplankton is poorly diversified. Only two copepod and three cladoceran species have been reported from this lake (Micha *et al.*, 2018). In the present study we report 15 species (excluding Bdelloidea) including the dipteran *Chaoborus* sp. Extreme conditions of low pH and conductivity may favor a few adapted species and thus reduce taxonomic diversity. The low diversity of metazooplankton in Lake Mai-Ndombe appears comparable only to that observed in certain subtropical, saline, shallow lakes (e.g. D'Ambrosio *et al.*, 2016) and large deep lakes of central eastern Africa (e.g. Isumbisho *et al.*, 2006). This suggests that, with a surface area of about 2300 km², Lake Mai-Ndombe's pelagic zone has a low habitat diversity. This contrasts with the theory of island biogeography (MacArthur and Wilson, 1967), which posits that larger lake and catchment areas should support greater ecosystem richness. The presence of *Chaoborus* larvae in the metazooplankton community of Lake Mai-Ndombe is not unexpected, as these dipterans are commonly found in the zooplankton communities of many subtropical shallow lakes (Arcifa *et al.*, 1992), as well as in some large and deep lakes (e.g. Lake Malawi, Irvine, 1997).

The mean biomass of metazooplankton in the lake was low, with higher values recorded during LW conditions (0.20 ± 0.1 g C m⁻²) than during HW conditions (0.13 ± 0.02 g C m⁻²), and remained lower than values reported from other subtropical shallow lakes in the region [(e.g. Lake George (0.49 g C m⁻²: Burgis *et al.*, 1973; Burgis, 1978), Lake Awasa (0.45 g C m⁻²: Mengestou and Fernando, 1991)]. In addition, the periodical variation in metazooplankton biomass in Lake Mai-Ndombe is pronounced, aligning with the typical seasonal zooplankton dynamics observed in shallow tropical lakes, such as lakes Awasa (Mengestou and Fernando, 1991) and Kariba (Masundire, 1992, 1994, 1997). More important, however, is the fact that average metazooplankton biomass in Lake Mai Ndombe (~ 0.2 g C m⁻²) cannot be derived only from grazing of the very low phytoplankton biomass (~ 0.5 g C m⁻²). Based on a 10% trophic transfer efficiency (e.g. Lindeman, 1942; Pauly and Christensen, 1995; Schulz *et al.*, 2004; Fetahi *et al.*, 2011; Lischke *et al.*, 2017), phytoplankton would account for roughly only a quarter of the zooplankton biomass. This supports the conclusion that metazooplankton production in the lake is largely sustained by allochthonous carbon and nutrient inputs from the surrounding flooded forest, as indicated by the carbon and nitrogen isotope data. Indeed, it is likely that these allochthonous inputs also support heterotrophic microbial production, providing an additional trophic resource for the metazooplankton.

Nannothrissa stewarti is, according to Micha *et al.* (2018), a major contributor to the Lake Mai-Ndombe fishery. In this study, we investigated its feeding habits at different ontogenetic stages, as a first attempt to understand how this primarily planktivorous fish copes with the reduced food resources in this natural ecosystem. The focus on young stages is important since their survival is the key of the recruitment success (Copp *et al.*, 2005; Lomartire

et al., 2021) and because they are especially sensitive to changes in environment (Govoni, 2005; Costalago *et al.*, 2011).

In Lake Mai-Ndombe, the stomach bulb appears well-developed in the digestive tract when the sprat reaches ~ 14 mm TL, (Whitehead, 1985). Recently, Zanga *et al.* (2022) reported the composition of the *Nannothrissa*'s diet in Lake Mai-Ndombe, unfortunately with errors in identifying zooplankton prey and therefore their relative abundance. For example, these authors consider that *Daphnia* (which does not exist in LMN) is not a cladoceran. Similar errors are found in the identification of the phytoplankton. Thus, the conclusions of this work should be considered with caution with regard to the diet of the sprat. Our results confirm that, similar to other small clupeids (e.g. Gliwicz, 1986, 1994; Isumbisho *et al.*, 2004), *N. stewarti* is a zooplanktivorous species that prefers and actively selects cladocerans, despite their lower abundance relative to copepods. This raises questions related to optimal foraging theory, which has been proposed to explain prey selection in fishes, emphasizing the importance of prey abundance and size as key determinants (Stephens *et al.*, 2007). For example, copepods, that are the dominant group of zooplankton in Lake Kivu (Isumbisho *et al.*, 2006; Darchambeau *et al.*, 2012), constitute the basis of the diet of the introduced sardine, *Limnothrissa miodon*, even though this fish also feeds on cladocerans when they become sufficiently abundant (Isumbisho *et al.*, 2004). By contrast, *Nannothrissa* in Lake Mai-Ndombe exhibits limited plasticity in its feeding behavior, consistently preferring cladocerans over the more abundant copepods across all seasons.

We observed that *Bosmina longirostris*, which was preferred and highly selected by both young and adult sprats during both HW and LW periods, was the least abundant among cladoceran species. This suggests that prey abundance is not the primary factor influencing prey selectivity by *Nannothrissa* in Lake Mai-Ndombe, contrary to expectations based on conventional foraging theory (e.g. Schoener, 1970, 1971, 1986; Werner and Hall, 1974; Svanbäck and Bolnick, 2005). For instance, *D. brachyurum*, which was much more abundant than *Bosmina*, was completely avoided by juvenile sprats and was selected only during the LW period by larvae and adults. The differences in prey preference and selectivity exhibited by *Nannothrissa* may reflect a strategy to optimize food resource exploitation while minimizing intraspecific competition.

Prey size, which generally plays an important role in fish predator-prey relationships (e.g. Scharf *et al.*, 2000; Gliwicz *et al.*, 2004; Cachera *et al.*, 2017), does not seem to affect the sprat's feeding habits, since *B. longirostris* is smaller than the dominant copepod *Tropodiptomus* sp. One plausible explanation is the influence of reduced water transparency on prey visibility, which is particularly relevant for this visually oriented predator. Indeed, when light and water transparency are reduced, small preys become less obvious to visual predators, thereby alleviating predation pressure (e.g. Gliwicz, 1986). According to Zaret and Kerfoot (1975), the pigmentation in *B. longirostris* that is concentrated in the large, black, compound eye of these transparent animals, is the key factor of their selection by planktivorous fish, their body size being of secondary importance.

Furthermore, our observations reveal a significant diet overlap among development stages during the LW period. However, when the water level was high, the diet overlap was significant only between the young stages (larvae vs juveniles), and also between adult females vs males. As observed in Lake Kivu for *L. miodon* (Isumbisho *et al.*, 2004), this may be a strategy for habitat structuration and utilization of feeding resources. Based on the above observations, we suggest that during HW conditions, adult and juvenile *Nannothrissa* tend to feed on different prey items whenever possible (e.g. Isumbisho *et al.*, 2004; Costalago *et al.*, 2012), likely as a strategy to reduce intraspecific competition.

The stable isotope data collected here on SPOM, selected zooplankton and three age classes of *Nannothrissa* paint a highly complementary picture of the food web in Lake Mai-Ndombe. Despite the numerical and volumetric dominance of zooplankton to the diet of *Nannothrissa* based on the gut content analyses (Table III), the stable isotope data are inconsistent with a dominant reliance on zooplankton or general SPOM, given that *Nannothrissa* $\delta^{13}\text{C}$ values are consistently lower by up to 4‰ (Fig. 8), while a small enrichment in ^{13}C is expected (e.g. Caut *et al.*, 2009). Thus, the isotope data indicate that our sampling did not capture all relevant possible food sources, and that a ^{13}C -depleted food source is missing, which provides an important C input to the diet of *Nannothrissa*. Several hypotheses can be proposed to explain this inconsistency. First, only a limited number of zooplankton samples were analyzed for stable isotopes, and we may not have captured the full temporal and taxonomic variability in their stable isotope ratios, given their shorter turnover time than that of *Nannothrissa*, we may have missed ^{13}C -depleted zooplankton. Zooplankton with lower $\delta^{13}\text{C}$ values can be expected in case they feed selectively on either phytoplankton (expected to show low $\delta^{13}\text{C}$ values due to the ^{13}C -depletion in the inorganic C pool), or on methanotrophic bacteria. Indeed, some streams in the central Congo Basin have been shown to have very low $\delta^{13}\text{C}$ -POC values indicative of a strong methanotroph community (Borges *et al.*, 2019), and zooplankton with $\delta^{13}\text{C}$ values as low as -43.3‰ have been measured in some of these streams (P. Isumbisho, unpublished data). Secondly, direct selective feeding on either of these two potential ^{13}C -depleted C sources (phytoplankton, methanotrophic bacteria) by *Nannothrissa*, would also be consistent with the isotope data recorded in the latter; whereby it is plausible that these would not be clearly distinguishable in the gut contents. The diet overlap between different age classes of *Nannothrissa* discussed above is consistent with the overlap in stable isotope data from the three age classes (Fig. 8). *Nannothrissa* larvae presented somewhat higher $\delta^{15}\text{N}$ values than juveniles or adults within the same $\delta^{13}\text{C}$ range (Fig. 8); this difference is not readily explained by patterns in the stomach content analyses (Table III, IV) and more data would be needed to evaluate whether this isotopic separation is robust and what the underlying mechanism may be.

In aquatic ecosystems, small fish play an important role by connecting the lower and the upper trophic levels and hence are crucial for a flourishing fishery. Their abundant populations exert a great predation on zooplankton while being the main food for larger predators (Cury *et al.*, 2000). In Lake Mai-Ndombe, *Nannothrissa* is primarily zooplanktivorous and a highly selective feeder. It feeds on the least abundant zooplankton group, which

suggests a low efficiency of the trophic transfer with only a small portion of the metazooplankton production being exploited by the sprat. Furthermore, our study indicates a low phytoplankton biomass that cannot support the observed zooplanktonic secondary biomass, which depends more on allochthonous inputs coupled to a possibly important internal microbial production. Therefore, the role of the microbial loop in the lake's food web needs to be investigated. In addition, the fishery yield of the lake, which has been evaluated at about 10 000 tons at the end of 1970th (Compère and Symoens, 1987), should be re-assessed. More in-depth studies of the biogeochemistry and ecology of Lake Mai-Ndombe ecology are still needed to understand its food web function, likely depending on the inputs from the flooded forest and on the variation of the water level (and related variables) inducing large differences in autochthonous production between water phases.

CONCLUSION

We investigated plankton (composition and abundance) and the diet of *N. stewarti*, aiming to provide basic information related to the understanding of ecological functioning of the shallow black water Lake Mai-Ndombe. Our results highlight that the lake is never stratified, with significant autochthonous primary production occurring during LW periods, allowing the development of a phytoplankton biomass that remains characteristic of an oligotrophic lake. The metazooplankton community of Lake Mai-Ndombe is poorly diversified and characterized by low biomass. Notably, it includes a *Chaoborus* species (diptera), which makes a significant contribution to the total metazooplankton biomass during HW periods.

Gut content analysis indicates that *Nannothrissa* is a highly selective feeder in Lake Mai-Ndombe, primarily consuming cladocera despite their low relative abundance and small size compared to the larger and more abundant copepods. However, carbon and nitrogen stable isotope data suggest that this small fish exploits additional food sources that warrant further investigation.

ACKNOWLEDGEMENTS

We thank Héritier Lofongola Litoi and the whole fishermen team from Kinkole (Kinshasa) and Inongo (Mai), Gracien Mpeti and the fishermen from the FPMA (Fédération des Pêcheurs du lac Mai-Ndombe et ses Affluents) for their assistance during the field work. We are grateful to Yannick Stroobandt (KU Leuven) for his help in the stable isotope analyses.

FUNDING

This work was supported by the Department of Earth and Environmental Sciences and the Department of Biology (Fish Diversity and Conservation) of the KU Leuven, the Unit of Chemical Oceanography, University of Liège (Professor Alberto Borges, Research Director at the FNRS), the Institut Supérieur Pédagogique de la Gombe (DR Congo), a Global Minds Short term Research Stay (BE2017GMUKULA101) and the VLIR-UOS Short Initiative project (CD2022SIN337A101), at the KU Leuven.

REFERENCES

- Amoros, C. (1984) Introduction pratique à la systématique des organismes des eaux continentales françaises. *Crustacés Cladocères. Bull. Soc. limn. Lyon*, **53**, 72–107.
- Arcifa, M. S., Gomes, E. A. T. and Meschiatti, A. J. (1992) Composition and fluctuations of the zooplankton of a tropical Brazilian reservoir. *Arch. Hydrobiol.*, **123**, 479–495. <https://doi.org/10.1127/archiv-hydrobiol/123/1992/479>.
- Bocaniov, S. A., Van Cappellen, P. and Scavia, D. (2019) On the role of a large shallow lake (Lake St. Clair, USA-Canada) in modulating phosphorus loads to Lake Erie. *Water Resour. Res.*, **55**, 10548–10564. <https://doi.org/10.1029/2019WR025019>.
- Bongeba, C. and Micha, J.-C. (2013) Etat de la pêche au Sud du lac Mai-Ndombe. *Revue Scientifique et Technique Forêt et Environnement du Bassin du Congo*, **1**, 46–55.
- Borges, A. V., Darchambeau, F., Lambert, T., Morana, C., Allen, G. H., Tambwe, E., Toengaho, S. A., Mambo, T. *et al.* (2019) Variations in dissolved greenhouse gases (CO₂, CH₄, N₂O) in the Congo River network overwhelmingly driven by fluvial-wetland connectivity. *Biogeosciences*, **16**, 3801–3834. <https://doi.org/10.5194/bg-16-3801-2019>.
- Borges, A. V., Deirmendjian, L., Bouillon, S., Okello, W., Lambert, T., Roland, A. E. F., Razanamahandry, F. V., Voarintsoa, G. R. N. *et al.* (2022) Greenhouse gas emissions from African lakes are no longer a blind spot. *Sci. Adv.*, **8**, 1–17.
- Bos, A. R., Kapasa, C. K. and van Zwieten, P. A. M. (2006) Update on the bathymetry of Lake Mweru (Zambia), with notes on water level fluctuations. *Afr. J. Aquat. Sci.*, **31**, 145–150. <https://doi.org/10.2989/16085910609503882>.
- Burgis, M. J. (1978) Case studies of lake ecosystems at different latitudes: the tropics. The Lake George ecosystem. *Int. Ver. Theor. Angew. Limnol.*, **20**, 1139–1152.
- Burgis, M. J., Darlington, J. P. E. C., Dunn, I. G., Ganf, G. G., Gwahaba, J. J. and McGowan, L. M. (1973) The biomass and distribution of organisms in Lake George. *Uganda. Proc. R. Soc. Lond.*, **184**, 271–298.
- Burgis, M. J. and Symoens, J. J. (1987) African wetlands and shallow water bodies/ zones humides et Lacs peu profonds d'Afrique. Editions de L'ORSTOM. Coll. Travaux et Documents, **211**, 654 p.
- Cachera, M., Ernande, B., Villanueva, M. C. and Lefebvre, S. (2017) Individual diet variation in a marine fish assemblage: optimal foraging theory, niche variation hypothesis and functional identity. *J. Sea Res.*, **120**, 60–71. <https://doi.org/10.1016/j.seares.2016.08.004>.
- Cardoso, L. and Marques, D. (2004) Structure of the zooplankton community in a subtropical shallow lake (Itapeva Lake - south of Brazil) and its relationship to hydrodynamic aspects. *Hydrobiologia*, **518**, 123–134. <https://doi.org/10.1023/B:HYDR.0000025062.08366.1b>.
- Castilho-Noll, M. S. M. and Arcifa, M. S. (2007) Length-weight relationships for zooplanktonic species of a tropical Brazilian lake: Lake Monte Alegre. *Acta Limnol. Bras.*, **19**, 93–100.
- Caut, S., Angulo, E. and Courchamp, F. (2009) Variation in discrimination factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): the effect of diet isotopic values and applications for diet reconstruction. *J. Appl. Ecol.*, **46**, 443–453. <https://doi.org/10.1111/j.1365-2664.2009.01620.x>.
- Chillasse, L., Dakki, M. and Abbassi, M. (2001) Valeurs et fonctions écologiques des zones humides du Moyen atlas (Maroc). *Humedales Méditerranéens*, **1**, 139–146.
- Claps, M. C., Gabellone, N. A. and Benítez, H. H. (2004) Zooplankton biomass in an eutrophic shallow lake (Buenos Aires, Argentina): spatio-temporal variations. *Ann. Limnol. Int. J. Limnol.*, **40**, 201–210. <https://doi.org/10.1051/limn/2004018>.
- Cochrane, K. L. (1984) The influence of food availability, breeding seasons and growth on commercial catches of *Limnotherissa miodon* (Boulenger) in Lake Kariba. *J. Fish Biol.*, **24**, 623–635. <https://doi.org/10.1111/j.1095-8649.1984.tb04833.x>.
- Compère, P. and Symoens, J. J. (1987) Le bassin du Congo. In Burgis, M. J. and Symoens, J. J. (eds.), *Zones Humides et Lacs Peu Profonds d'Afrique*, ORSTOM, Paris, pp. 401–456.
- Coops, H. and Hosper, H. S. (2002) Water-level Management as a tool for the restoration of Shallow Lakes in the Netherlands. *Lake and Reservoir Management*, **18**, 293–298. <https://doi.org/10.1080/07438140209353935>.
- Copp, G. H., Vranovský, M., Černý, J. and Kováč, V. (2005) Dynamics of young fishes and zooplankton in a lentic side-channel of the river Danube over a 24-hour cycle in late summer. *Biologia, Bratislava*, **60**, 179–188.
- Costalago, D., Tecchio, S., Palomera, I., Alvarez-Calleja, I., Ospina-Alvarez, A. and Raicevich, S. (2011) Ecological understanding for fishery management: condition and growth of anchovy late larvae during different seasons in the northwestern Mediterranean. *Estuar. Coast. Shelf Sci.*, **93**, 350–358. <https://doi.org/10.1016/j.ecss.2011.05.005>.
- Costalago, D., Tecchio, S., Palomera, I., Alvarez-Calleja, I., Ospina-Alvarez, A. and Raicevich, S. (2012) Ontogenetic and seasonal changes in the feeding habits and trophic levels of two small pelagic fish species. *Mar. Ecol. Prog. Ser.*, **460**, 169–181. <https://doi.org/10.3354/meps09751>.
- Culver, D. A., Boucherle, M. M., Bean, D. J. and Fletcher, J. W. (1985) Biomass of freshwater crustacean zooplankton from length-weight regressions. *Can. J. Fish. Aquat. Sci.*, **42**, 1380–1390. <https://doi.org/10.1139/f85-173>.
- Curry, P., Bakun, A., Crawford, R. J. M., Jarre-Teichmann, A., Quinones, R., Shannon, L. J. and Verheye, H. M. (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in 'wasp-waist' ecosystems. *ICES J. Mar. Sci.*, **57**, 603–618. <https://doi.org/10.1006/jmsc.2000.0712>.
- D'Ambrosio, D. S., García, A. and Claps, M. C. (2016) Zooplankton diversity of a protected and vulnerable wetland system in southern South America (Llancanelo area, Argentina). *Int. Aquat. Res.*, **8**, 65–80. <https://doi.org/10.1007/s40071-016-0125-2>.
- Dabrowski, K. (1981) The spawning and early life history of the pollan (*Coregonus pollan* Thompson) in lough Neagh. *Northern Ireland. Int. Rev. ges. Hydrobiol.*, **66**, 299–326. <https://doi.org/10.1002/iroh.19810660303>.
- Dabrowski, K. (1984) The feeding of fish larvae: present « state of the art » and perspectives. *Reprod. Nutr. Dev.*, **24**, 807–833. <https://doi.org/10.1051/rnd:19840701>.
- Darchambeau, F., Isumbisho, M. and Descy, J.-P. (2012) Zooplankton of Lake Kivu. In Descy, J.-P., Darchambeau, F. and Schmid, M. (eds.), *Lake Kivu: Limnology and Biogeochemistry of a Tropical Great Lake, Aquatic Ecology Series*, Springer, Dordrecht, pp. 107–126.
- de Paggi, S. B. J., Muñoz, S., Frau, D., Paggi, J. C., Scarabotti, P., Devercelli, M. and Meerhoff, M. (2012) Horizontal distribution of rotifers in a subtropical shallow lake (Paraná floodplain, Argentina). *Fundam. Appl. Limnol.*, **180**, 321–333. <https://doi.org/10.1127/1863-9135/2012/0245>.
- Deirmendjian, L., Descy, J. P., Morana, C., Okello, W., Stoyneva-Gärtner, M. P., Bouillon, S. and Borges, A. V. (2021) Limnological changes in Lake Victoria since the mid-20th century. *Freshw. Biol.*, **66**, 1630–1647. <https://doi.org/10.1111/fwb.13780>.
- Delling, B., Zanga, L. N. and Norén, M. (2024) New data on the clupeoids of lakes Mai-Ndombe and Tumba, western Democratic Republic of the Congo, using an integrated approach combining morphology and barcoding. *Afr. Zool.*, **59**, 1–9. <https://doi.org/10.1080/15627020.2023.2294749>.
- Descy, J.-P., Darchambeau, F., Lambert, T., Stoyneva-Gaertner, P. P., Bouillon, S. and Borges, A. V. (2017) Phytoplankton dynamics in the Congo River. *Freshw. Biol.*, **62**, 87–101. <https://doi.org/10.1111/fwb.12851>.
- Descy J.-P., Darchambeau, F. and Schmid M. (2012) Lake Kivu: Limnology and Biogeochemistry of a tropical great lake. *Aquatic Ecology Series*, Springer, Dordrecht, 190 p, <https://doi.org/10.1007/978-94-007-4243-7>.

- Downing, J. A. and Rigler, F. H. (1984) *A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters Tanganyika*, Oxford University Press, London, p. 501.
- Dumont, H. J. (1981) Cladocera and free-living Copepoda from the Fouta Djallon and adjacent mountain areas in West Africa. *Hydrobiologia*, **85**, 97–115. <https://doi.org/10.1007/BF00006620>.
- Dumont, H. J., Van de Velde, I. and Dumont, S. (1975) The dry weight estimate of biomass in a selection of cladocera, copepoda and rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia*, **19**, 75–97. <https://doi.org/10.1007/BF00377592>.
- Dussart, B. (1967a) Les copépodes des eaux continentales d'Europe occidentale. I. *Calanoïdes et Harpacticoïdes*. Boubée et Cie, Paris, p. 500.
- Dussart, B. (1967b) Les copépodes des eaux continentales d'Europe occidentale. In II. *Cyclopoïdes et Biologie*. Boubée et Cie, Paris, p. 292.
- Dussart, B. (1982) *Faune de Madagascar: crustacés copépodes Des Eaux intérieures*, ORSTOM-CNRS, Paris, p. 146.
- Dussart, B. H., Fernando, C. H., Matsumura-Tundisi, T. and Shiel, R. J. (1984) A review of systematics, distribution and ecology of tropical freshwater zooplankton. *Hydrobiologia*, **113**, 77–91. <https://doi.org/10.1007/BF00026594>.
- Edwards, R. T. and Meyer, J. L. (1987) Metabolism of a sub tropical low gradient Blackwater river. *Freshw. Biol.*, **17**, 251–263. <https://doi.org/10.1111/j.1365-2427.1987.tb01046.x>.
- Eskinazi-Sant'Anna, E. M. (2000) Zooplankton abundance and biomass in a tropical estuary (Pina estuary-Northeast Brazil). *Trab. Oceanog. Univ Fed. PE, Recife*, **28**, 21–34.
- Fetahi, T., Chagerlb, M., Mengistou, S. and Libralato, S. (2011) Food web-structure and trophic interactions of the tropical highland Lake Hayq, Ethiopia. *Ecol. Model.*, **222**, 804–813. <https://doi.org/10.1016/j.ecoimodel.2010.09.038>.
- Gliwicz, Z. M. (1986) A lunar cycle in zooplankton. *Ecology*, **67**, 883–897. <https://doi.org/10.2307/1939811>.
- Gliwicz, Z. M. (1994) Relative significance of direct and indirect effects of predation by planktivorous fish on zooplankton. *Hydrobiologia*, **272**, 201–210. <https://doi.org/10.1007/BF00006521>.
- Gliwicz, Z. M., Jawiński, A. and Pawłowicz, M. (2004) Cladoceran densities, day-to-day variability in food selection by smelt, and the birth-rate-compensation hypothesis. *Hydrobiologia*, **526**, 171–186. <https://doi.org/10.1023/B:HYDR.0000041605.72338.22>.
- Golterman, H. L. and De Groot, C. J. (1994) Nouvelles connaissances des formes du phosphate: conséquences Sur le cycle du phosphate dans les sédiments des eaux douces peu profondes. *Ann. Limnol.*, **30**, 221–232. <https://doi.org/10.1051/limn/1994017>.
- González, E. J., Matsumura-Tundisi, T. and Tundisi, J. G. (2008) Size and dry weight of main zooplankton species in Bariri reservoir (SP, Brazil). *Braz. J. Biol.*, **68**, 69–75. <https://doi.org/10.1590/S1519-69842008000100010>.
- González-Bergonzoni, I., Vidal, N., Wang, B., Ning, D., Liu, Z., Jeppesen, E. and Meerhoff, M. (2015) General validation of formalin-preserved fish samples in food web studies using stable isotopes. *Methods Ecol. Evol.*, **6**, 307–314. <https://doi.org/10.1111/2041-210X.12313>.
- Govoni, J. J. (2005) Fisheries oceanography and the ecology of the early life histories of fishes: a perspective over fifty years. *Sci. Mar.*, **69**, 125–137. <https://doi.org/10.3989/scimar.2005.69s1125>.
- Hammer, Ø., Harper, D. A. T. and Ryan, P. D. (2001) PAST: paleontological statistics software package for education and data analysis. *Palaeontol. Electron.*, **4**, 9.
- Haney, J. F. and Hall, D. J. (1973) Sugar-coated daphnia: a preservation technique for Cladocera. *Limnol. Oceanogr.*, **18**, 331–333. <https://doi.org/10.4319/lo.1973.18.2.0331>.
- Harding, J. P. and Smith, W. A. (1974) A key to the British freshwater cyclopoid and calanoid copepods with ecological notes. *Freshwater Biological Association*, **18**, 54.
- Hardman, M. and Stiassny, M. L. J. (2008) A sexually dimorphic species of Chrysichthys (Siluriformes: Claroteidae) from lac Mai-Ndombe, Democratic Republic of Congo. *Ichthyol. Explor. Freshwaters*, **19**, 175–184.
- Hillbricht-Ilkowska, A. (1999). Shallow lakes in lowland river systems: Role in transport and transformations of nutrients and in biological diversity. *Hydrobiologia* **408**, 349–358. https://doi.org/10.1007/978-94-017-2986-4_39.
- Hughes, R. H. and Hughes, J. S. (1992) A directory of African wetlands. IUCN, Gland, Switzerland and Cambridge, UK. XXXIV, 557–558.
- Hynes, H. B. N. (1950) The food of the freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in studies of the food of fishes. *J. Anim. Ecol.*, **19**, 36–58. <https://doi.org/10.2307/1570>.
- Hyslop, E. J. (1980) Stomach contents analysis—a review of methods and their application. *J. Fish Biol.*, **17**, 1–429.
- Irvine, K. (1997) Food selectivity and diel vertical distribution of *Chaoborus edulis* (Diptera, Chaoboridae) in Lake Malawi. *Freshw. Biol.*, **37**, 605–620. <https://doi.org/10.1046/j.1365-2427.1997.00187.x>.
- Irvine, K. and Waya, R. (1999) Spatial and temporal patterns of zooplankton standing biomass and production in Lake Malawi. *Hydrobiologia*, **407**, 191–205. <https://doi.org/10.1023/A:1003711306243>.
- Isumbisho, M., Kaningini, M., Descy, J.-P. and Baras, E. (2004) Seasonal and diel variations in diet of the young stages of *Limnothrissa miodon* in Lake Kivu, eastern Africa. *J. Trop. Ecol.*, **20**, 73–83. <https://doi.org/10.1017/S0266467403001056>.
- Isumbisho, M., Sarmiento, H., Kaningini, B., Micha, J.-C. and Descy, J. P. (2006) Zooplankton of Lake Kivu, East Africa: half a century after the Tanganyika sardine introduction. *J. Plankton Res.*, **28**, 971–989. <https://doi.org/10.1093/plankt/fbl032>.
- Kanangire, C. K., Depiereux, E. and Micha, J.-C. (1999) Essai de caractérisation de quelques Lacs rwandais par leur peuplement piscicole. *Ann. Limnol.*, **35**, 141–150. <https://doi.org/10.1051/limn/1999019>.
- Kawakami, E. and Vazzoler, G. (1980) Método gráfico e estimativa de índice alimentar aplicado no estudo de alimentação de peixes. *Bol Inst Oceanogr.*, **29**, 205–207. <https://doi.org/10.1590/S0373-55241980000200043>.
- Koenings, J. P. and Edmundson, J. A. (1991) Secchi disk and photometer estimates of light regimes in Alaskan lakes: effects of yellow color and turbidity. *Limnol. Oceanogr.*, **36**, 91–105. <https://doi.org/10.4319/lo.1991.36.1.0091>.
- Kolding, J., van Zwieten, P., Marttin, F., Funge-Smith, S. and Poulain, F. (2019) Freshwater small pelagic fish and fisheries in major African lakes and reservoirs in relation to food security and nutrition. FAO Fisheries and Aquaculture Technical Papers No. 642. FAO, Rome, 122 p.
- Kořínek, V. (1999) *A Guide to Limnetic Species of Cladocera of African Inland Waters (Crustacea, Branchiopoda) (Using the Morphology of Parthenogenetic Females)*. International Association of Theoretical and Applied Limnology, Vol. N° 1, Occasional Publication, Geneva, p. 57.
- Krebs, C. J. (1989) *Ecological Methodology*, Harper Collins Publishers, New York, NY, p. 654.
- Lauff, M. and Hofer, R. (1984) Development of proteolytic enzymes in fish and the importance of dietary enzymes. *Aquaculture*, **37**, 335–346. [https://doi.org/10.1016/0044-8486\(84\)90298-9](https://doi.org/10.1016/0044-8486(84)90298-9).
- Lauzanne, L. (1976) Régimes alimentaires et relations trophiques des poissons du lac Tchad. *Cahiers Orstom, Série Hydrobiologie*, **10**, 267–310.
- Lewis, W. M. (1988) Primary production in the Orinoco River. *Ecology*, **69**, 679–692. <https://doi.org/10.2307/1941016>.
- Lindeman, R. L. (1942) The trophic-dynamic aspect of ecology. *Ecology*, **23**, 399–417. <https://doi.org/10.2307/1930126>.
- Lischke, B., Mehner, T., Hilt, S., Attermeyer, K., Brauns, M., Brothers, S., Grossart, H. P., Köhler, J., et al. (2017) Benthic carbon is inefficiently transferred in the food webs of two eutrophic shallow lakes. *Freshw. Biol.*, **62**, 1693–1706. <https://doi.org/10.1111/fwb.12979>.
- Lomartire, S., Marques, C. J. and Gonçalves, M. M. A. (2021) The key role of zooplankton in ecosystem services: a perspective of interaction

- between zooplankton and fish recruitment. *Ecol. Indic.*, **129**, 107867. <https://doi.org/10.1016/j.ecolind.2021.107867>.
- Luhusu, K. F. and Micha, J.-C. (2013) Analyse des modes d'exploitation des ressources halieutiques du lac Mai-Ndombe en République Démocratique du Congo. *Geo-Eco-Trop.*, **37**, 273–284.
- MacArthur, R. H. and Wilson, E. O. (1967) *The Theory of Island Biogeography*, Princeton University Press, Princeton.
- Mackey, M. D., Mackey, D. J., Higgins, H. W., Wright, S. W. (1996). CHEMTAX - a program for estimating class abundances from chemical markers: application to HPLC measurements of phytoplankton. *Mar. Ecol. Progr. Ser.* **144**, 265–283.
- Mähr, K., Grabner, M., Hofer, R. and Moser, H. (1983) Histological and physiological development of the stomach in *Coregonus* sp. *Arch. Hydrobiol.*, **98**, 344–353.
- Mandima, J. J. (1999) The food and feeding behaviour of *Limnoithrissa miodon* (Boulenger, 1906) in Lake Kariba, Zimbabwe. *Hydrobiologia*, **407**, 175–182. <https://doi.org/10.1023/A:1003752423082>.
- Masundire, H. M. (1992) Population dynamics of *Bosmina longirostris* (Crustacea: Cladocera) in Lake Kariba, Zimbabwe. *Hydrobiologia*, **243–244**, 167–173. <https://doi.org/10.1007/BF00007032>.
- Masundire, H. M. (1994) Seasonal trends in zooplankton densities in Sanyati Basin, Lake Kariba: multivariate analysis. *Hydrobiologia*, **272**, 211–230. <https://doi.org/10.1007/BF00006522>.
- Masundire, H. M. (1997) Spatial and temporal variations in the composition and density of crustacean plankton in the five basins of Lake Kariba, Zambia Zimbabwe. *J. Plankton Res.*, **19**, 43–62. <https://doi.org/10.1093/plankt/19.1.43>.
- Mbadu, Z. V., Micha, J.-C., Moreau, J. and Mbomba, N. B. (2010) Age and growth of *Distichodus antonii* (Schilthuis, 1891) (Pisces, Teleostei, Distichodontidae) in pool Malebo, Congo River. *Afr. J. Environ. Sci. Technol.*, **4**, 279–283.
- Mengestou, S. and Fernando, C. H. (1991) Biomass and production of the major dominant crustacean zooplankton in a tropical Rift Valley lake, Awasa. *Ethiopia. J. Plankton Res.*, **13**, 831–851. <https://doi.org/10.1093/plankt/13.4.831>.
- Micha, J.-C. (2019) Inland fisheries suffering from malaria in Central Africa. *Tropicicultura*, **37**, 2295–8010.
- Micha, J.-C., Bangulu, B.-L. N., Ibofa, R., Mumba, F., Mutambwe, S., Zanga, N., Willem, E., Svennsson, J.-E. et al. (2018) Une ressource surexploitée, *Nannothrissa stewarti*, sardine endémique du lac Mai-Ndombe (RD Congo), résultat inattendu du programme national de Lutte contre le Paludisme. *Bull. Séanc. Acad. R. Sci. Outre-Mer*, **64**, 61–91.
- Mpounza, M. and Samba-Kimbata, M. J. (1990) Aperçu sur le climat de l'Afrique centrale occidentale. In Lanfranchi, R. and Schwartz, D. (eds.), *Paysages Quaternaires de L'Afrique Centrale Atlantique*, ORSTOM, Paris, p. 535.
- Mushagalusa, C. D., Micha, J.-C., Ntakimazi, G. and Nshombo, M. (2015) Brief evaluation of the current state of fish stocks landed by artisanal fishing units from the extreme northwest part of Lake Tanganyika. *International Journal of Fisheries and Aquatic Studies*, **2**, 41–48.
- Natarajan, A. V. and Jhingran, A. C. (1961) Index of preponderance—a method of grading the food elements in the stomach analysis of fishes. *Indian J. Fish.*, **8**, 54–59.
- Ott, D.W., Oldham-Ott, C.K., Rybalka, N., Friedl, T., 2015. Chapter 11 - Xanthophyte, Eustigmatophyte, and Raphidophyte Algae, in: Wehr, J.D., Sheath, R.G., Kocielek, J.P. (Eds.), *Freshwater Algae of North America* (Second Edition). Academic Press, Boston, pp. 485–536. <https://doi.org/10.1016/B978-0-12-385876-4.00011-6>
- Padisák, J. and Reynolds, C. S. (2003) Shallow lakes: the absolute, the relative, the functional and the pragmatic. *Hydrobiologia*, **506**, 1–11.
- Palomera, I., Olivar, M. P., Salat, J., Sabates, A., Coll, M., Garcia, A. and Morales-Nin, B. (2007) Small pelagic fish in the NW Mediterranean Sea: an ecological review. *Prog. Oceanogr.*, **74**, 377–396. <https://doi.org/10.1016/j.pocean.2007.04.012>.
- Pauly, D. and Christensen, V. (1995) Primary production required to sustain global fisheries. *Nature*, **374**, 255–257. <https://doi.org/10.1038/374255a0>.
- Phiri, H. (1991) Preliminary report on the food of Lake Tanganyika clupeids. In Kawanabe, H. and Nagoshi, M. (eds.), *Ecological and Limnological Study on Lake Tanganyika and its Adjacent Regions*, 7, Kyoto University, Kyoto, Japan.
- Pianka, E. R. (1974) Niche overlap and diffuse competition (desert lizards/resource partitioning/community structure/species diversity). *Proc. Natl. Acad. Sci.*, **71**, 2141–2145. <https://doi.org/10.1073/pnas.71.5.2141>.
- Pinkas, L., Oliphant, M. S. and Iverson, I. L. K. (1971) Food habits of albacore, bluefin tuna, and bonito in California waters. *Fish. Bull. Calif.*, **152**, 1–105.
- Pontin, R. M. (1978) *A Key to British Freshwater Planktonic Rotifera. Scientific Publications 38, Freshwater Biological Association*, Titus Wilson & Son Ltd, Kendal, p. 178.
- Rennie, M. D., Ozersky, T. and Evans, D. O. (2012) Effects of formalin preservation on invertebrate stable isotope values over decadal time scales. *Can. J. Zool.*, **90**, 1320–1327. <https://doi.org/10.1139/z2012-101>.
- Reynolds, C. S., Huszar, V., Kruk, C., Naselli-Flores, L. and Melo, S. (2002) Towards a functional classification of the freshwater phytoplankton. *J. Plankton Res.*, **24**, 417–428. <https://doi.org/10.1093/plankt/24.5.417>.
- Sarmiento, H., Isumbisho, M. and Descy, J.-P. (2006) Phytoplankton ecology of Lake Kivu (eastern Africa). *J. Plankton Res.*, **28**, 815–829. <https://doi.org/10.1093/plankt/fbl017>.
- Scharf, F. S., Juanes, F. and Rountree, R. A. (2000) Predator size- prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar. Ecol. Progr. Ser.*, **208**, 229–248. <https://doi.org/10.3354/meps208229>.
- Schliwien, U. K. and Stiassny, M. L. J. (2006) A new species of Nanochromis (Teleostei: Cichlidae) from Lake Mai Ndombe, Central Congo Basin, Democratic Republic of Congo. *Zootaxa*, **1169**, 33–46. <https://doi.org/10.11646/zootaxa.1169.1.2>.
- Schoener, T. W. (1970) Non synchronous spatial overlap of lizards in patchy habitats. *Ecol.*, **51**, 408–418. <https://doi.org/10.2307/1935376>.
- Schoener, T. W. (1971) Theory of feeding strategies. *Annu. Rev. Ecol. Syst.*, **2**, 369–404. <https://doi.org/10.1146/annurev.es.02.110171.002101>.
- Schoener, T. W. (1986) Resource partitioning. In Kikkawa, J. and Anderson, D. J. (eds.), *Community Ecology-Pattern and Process*, Blackwell Scientific, London.
- Schulz, M., Koschel, R., Reese, C. and Mehner, T. (2004) Pelagic trophic transfer efficiency in an oligotrophic, dimictic deep lake (Lake Stechlin, Germany) and its relation to fisheries yield. *Limnologia*, **34**, 264–273. [https://doi.org/10.1016/S0075-9511\(04\)80050-1](https://doi.org/10.1016/S0075-9511(04)80050-1).
- Sendacz, S., Caleffi, S. and Santos-Soares, J. (2006) Zooplankton biomass of reservoirs in different trophic conditions in the state of Sao Paulo. *Brazil. Braz. J. Biol.*, **66**, 337–350. <https://doi.org/10.1590/S1519-69842006000200016>.
- Stephens, D. W., Brown, J. S. and Ydenberg, R. C. (2007) *Foraging: Behavior and Ecology*. Chicago, University of Chicago Press, Chicago & London, p. 576.
- Stewart, D. J. and Robert, T. R. (1984) A new species of dwarf cichlid fish with reversed sexual Dichromatism from lac Mai-ndombe, Zaire. *Copeia*, **1**, 82–86.
- Stroband, H. W. J. and Dabrowski, K. (1981) Morphological and physiological aspects of the digestive system and feeding in fresh-water fish larvae. In Fontaine, M. (ed.), *Nutrition Des Poissons*, C.N.R.S, Paris.
- Svanbäck, R. and Bolnick, D. I. (2005) Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. *Evol. Ecol. Res.*, **7**, 993–1012.
- Turner, J. L. (1982) Analysis of the catch and effort data of a purse seine fishery for *Engraulicypris sardella* at the southern end of Lake Malawi. In *Biological Studies on the Pelagic Ecosystem of Lake Malawi. FAO Technical Report*, FAO, Rome, 109–115.
- Van der Knaap, M., Katonda, K. I. and De Graaf, G. J. (2014) Lake Tanganyika fisheries frame survey analysis: assessment of the options for management of the fisheries of Lake Tanganyika.

- Aquat. Ecosyst. Health Manage.*, **17**, 4–13. <https://doi.org/10.1080/14634988.2014.882733>.
- van Zwieten, P. A. M., Aarnink, B. H. M., Kapasa, C. K. and Ngalande, P. (1996) The biology, fishery and trade of chisense from Mweru-Luapula. Status of present knowledge. Department of Fisheries, Zambia. DoF/ML/1996/report No. 31. p.115.
- Villanueva, M. C. S., Isumbisho, M., Kaningini, B., Moreau, J. and Micha, J.-C. (2008) Modeling trophic interactions in Lake Kivu: what roles do exotics play? *Ecol. Model.*, **212**, 422–438. <https://doi.org/10.1016/j.ecolmodel.2007.10.047>.
- Viviane, L. S. A., Maria Da Graça, G. M. and Ariadne, N. M. (2012) Plankton diversity and limnological characterization in two shallow tropical urban reservoirs of Pernambuco state. *Brazil. An Acad Bras Cienc.*, **84**, 537–550.
- Wallace, R. K. (1981) An assessment of diet-overlap indexes. *Trans. Am. Fish. Soc.*, **110**, 72–76. [https://doi.org/10.1577/1548-8659\(1981\)110<x003C;72:AAODI&x003E;2.0.CO;2](https://doi.org/10.1577/1548-8659(1981)110<x003C;72:AAODI&x003E;2.0.CO;2).
- Welcomme, R. L. (1972) The inland waters of Africa. CIFA (Committee for Inland Fisheries of Africa). Technical paper No. 1. FAO, Rome, p.117.
- Werner, E. E. and Hall, D. J. (1974) Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology*, **55**, 1042–1052. <https://doi.org/10.2307/1940354>.
- Whitehead, P. J. P. (1985) FAO species catalogue. Vol. 7. Clupeoid fishes of the world (suborder Clupeoidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. *FAO Fish. Synop.*, **125**, 1–303 Rome: FAO.
- Xin-Li, W., Yi-Long, X. and Fang-Ping, Q. (2011) Comparative analysis of rotifer community structure in five subtropical shallow lakes in East China: role of physical and chemical conditions. *Hydrobiologia*, **661**, 303–316. <https://doi.org/10.1007/s10750-010-0539-6>.
- Zanga, L. N., Pwema, K. V., Mboma, B. N., Mutambwe, S. and Micha, J.-C. (2022) Diet study of *Nannothrissa stewarti* (Poll & Roberts, 1976) Clupeidae in Lake Mai-Ndombe, Democratic Republic of Congo. *Afr. J. Environ. Sci. Technol.*, **16**, 252–263. <https://doi.org/10.5897/AJE-ST2022.3120>.
- Zaret, T. M. and Kerfoot, C. W. (1975) Fish predation on *Bosmina longirostris*: body-size selection versus visibility selection. *Ecology*, **56**, 232–237. <https://doi.org/10.2307/1935317>.