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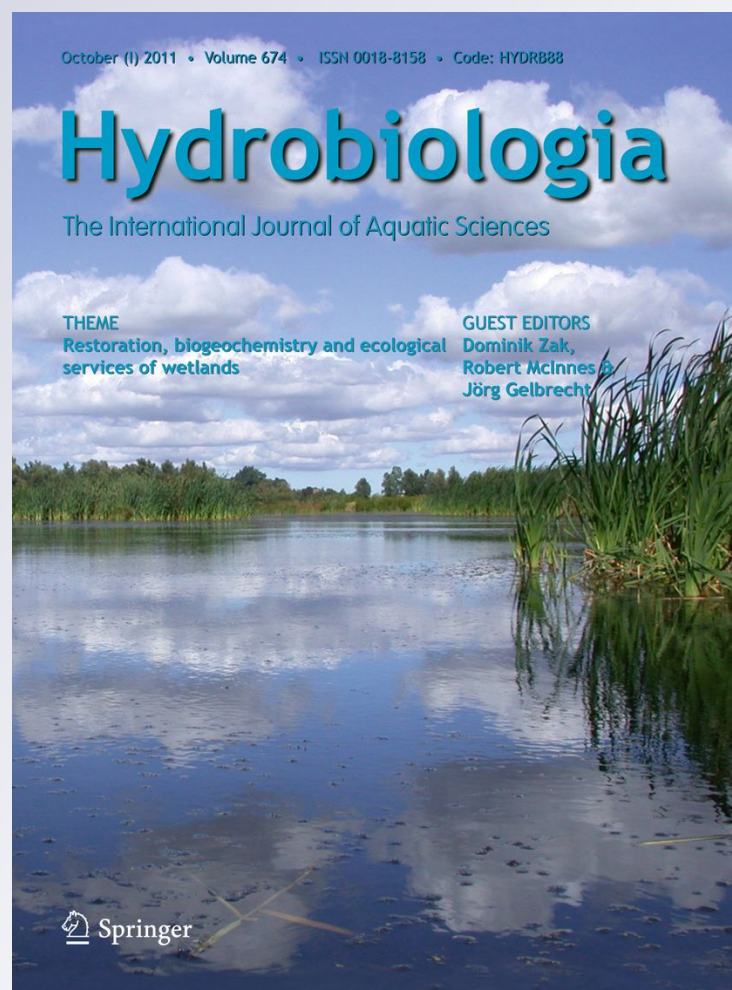
*M. P. Masilya, F. Darchambeau,  
M. Isumbisho & J.-P. Descy*

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# Diet overlap between the newly introduced *Lamprichthys tanganicanus* and the Tanganyika sardine in Lake Kivu, Eastern Africa

M. P. Masilya · F. Darchambeau · M. Isumbisho · J.-P. Descy

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**Abstract** This study evaluates the possible competition for food between *Lamprichthys tanganicanus*, recently introduced in Lake Kivu, and *Limnothrissa miodon*, which has been the basis of the pelagic fishery in this lake for several decades. Since 2006, *L. tanganicanus* has expanded in the lake and its numbers have increased in the captures, raising concern for the sardine fishery. We carried out a 2-year monthly survey, based on experimental captures in littoral and pelagic stations, which demonstrated the invasive dispersal of *L. tanganicanus* in littoral and pelagic waters. The diet of both species was determined on the basis of gut content analyses, taking into account the influence of site and season, and a diet overlap index was calculated. In the pelagic zone, where almost all size classes of both

species were present and essentially fed upon mesozooplankton, the diet overlap was high. This situation stems from the fact that *L. tanganicanus* has colonized the pelagic zone in Lake Kivu, likely in search for more abundant mesozooplankton. Inshore, the diet overlap between the two species was lower, as *L. tanganicanus* consumed a broad range of food, whereas *L. miodon* strongly selected insects and, chiefly for the largest specimens, fishes. These results suggest a likelihood of interspecific competition, particularly offshore, where mesozooplankton is the main available food type, and call for further monitoring of the sardine fishery, to assess a possible impact of the invader.

**Keywords** Exotic species · Resource competition · Large African lake · Fisheries

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M. P. Masilya (✉) · F. Darchambeau · J.-P. Descy  
Laboratory of Freshwater Ecology, URBE, Department of  
Biology, University of Namur, 5000 Namur, Belgium  
e-mail: pascalmasilya@yahoo.fr;  
pascal.masilyamulungula@fundp.ac.be

M. P. Masilya · M. Isumbisho  
Unité d'Enseignement et de Recherche en Hydrobiologie  
Appliquée (UERHA), ISP/Bukavu, B.P. 854, Bukavu,  
Democratic Republic of Congo

F. Darchambeau  
Chemical Oceanography Unit, Université de Liège,  
4000 Liège, Belgium

## Introduction

Accidental and/or deliberate introduction of exogenous species into ecosystems has been a frequent phenomenon (Lodge et al., 1998). In the aquatic ecosystems, direct competition between exotic and native fish species (Lévêque, 1997; Ogutu-Ohwayo et al., 1997; Pardo et al., 2009) may eventually lead to modified fisheries activities (Lévêque, 1997; Ogutu-Ohwayo et al., 1997; Preikshot et al., 1998). Moreover, Gozlan (2008) notes that these introductions will have inevitable implications in the future on the

distribution of native freshwater fish species; so the need to rely on non-native fish may become a growing reality.

Lake Kivu has a very poor fish fauna compared to other large lakes of East-African rift valley (Beadle, 1981). Only 29 species have been described, among which four species were accidentally or voluntarily introduced (Snoeks et al., 1997): 3 cichlids (*Oreochromis macrochir* (Boulenger, 1912); *Oreochromis leucostictus* (Trewavas, 1933) and *Tilapia rendalli* (Boulenger, 1896)) and 1 clupeid (*Limnothrissa miodon* Boulenger, 1906). Among those introduced species, the most famous is the “Tanganyika sardine”, *L. miodon* which was voluntarily introduced in 1959 (Collart, 1960) into Lake Kivu, where no planktivorous fish existed in the pelagic waters. Though this introduction maybe seen as a major disturbance of the pelagic ecosystem (Dumont, 1986; Isumbisho et al., 2006a), it permitted the development of an important fishery with an exploitable stock evaluated at about 6,000 tons (Lamboeuf, 1989, 1991). Despite pessimistic predictions of the future harvestable stock based on observed changes in the mesozooplankton composition and biomass (Dumont, 1986), the stock of *L. miodon* seems to have maintained itself over the years (Guillard, 2009).

In 2006, *Lamprichthys tanganicus* (Boulenger, 1898), an omnivorous Poeciliidae, also endemic to Lake Tanganyika (Coulter, 1991), began to appear in the commercial catches of fishermen from several sites of Lake Kivu (Muderhwa & Matabaro, 2010). Few data exist on the biology and ecology of *L. tanganicus* in its natural ecosystem. The species lives mainly among rocks along the littoral zone and rarely offshore (Coulter, 1991). It feeds upon small zooplankton and insects (adults and larvae). Sometimes fishes' scales were also found in gut contents (Lushombo & Nshombo, 2008). Nothing is known about the biology and the ecology of this fish in Lake Kivu. However, some characteristics of Lake Kivu raise the concern that food competition may develop between *L. tanganicus* and *L. miodon*. Lake Kivu has an extremely reduced littoral zone—the pelagic zone extends up to >90% of the surface area of the lake (Beadle, 1981)—consisting of submerged rocks covered with calcareous precipitates and dense mats of the filamentous green alga *Cladophora* (Verbeke, 1957). In addition, in Lake Kivu, *L. miodon* is

essentially zooplanktivorous in its early life but becomes omnivorous at the adult stage, feeding on diverse preys: zooplankton, insect larvae and adults, other small fishes and their own young stages (de Jongh et al., 1983; Isumbisho et al., 2004; Masilya et al., 2005). So, at first sight, the diet of the two species is rather similar, and their coexistence in a lake where resources are scarce may lead to severe interspecific competition.

This article presents a study of the diet of *L. tanganicus* and *L. miodon* in the pelagic and in the littoral zone of Lake Kivu, based on stomach content analyses. We attempted to evaluate a possible niche overlap between the two species, which would point to potential competition for resources. In addition, we analyzed the ability of invasive dispersal of *L. tanganicus* through experimental catches.

## Materials and methods

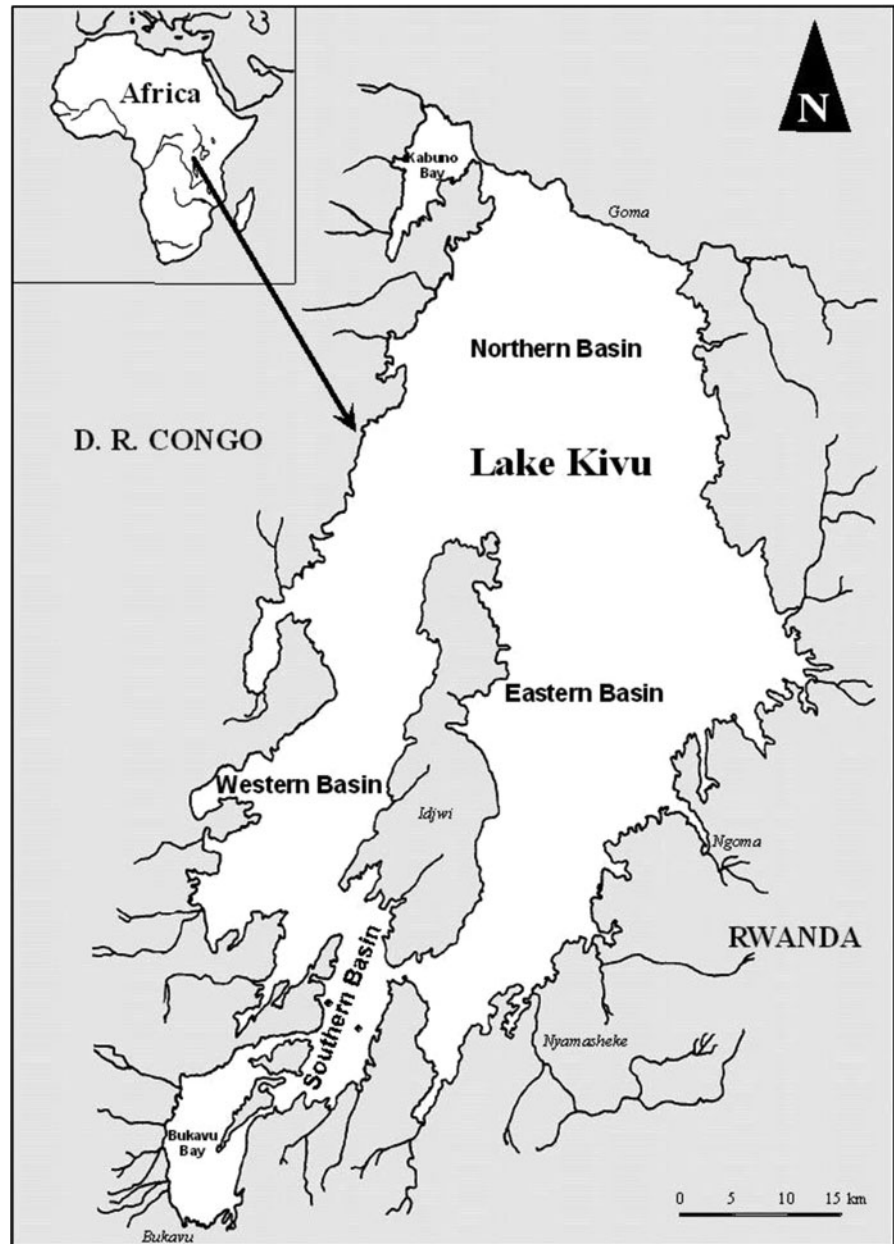
### Study area

Lake Kivu is a large (surface area 2,370 km<sup>2</sup>), deep (max. depth 489 m), oligotrophic lake with a reduced littoral zone (<10% of the lake surface area; Beadle, 1981). The lake is meromictic, with oxygenated waters limited to the upper 60 m and permanently separated from the deep waters by several steep salinity gradients (Degens et al., 1973). The study site is located in the southern (Ishungu) basin (Fig. 1). Two stations were sampled, one located in the pelagic area (02.3394°S, 28.9765°E), where the lake is ~120 m deep, and one located in the littoral zone along the shoreline (02.1969°S, 28.5794°E). The littoral station was ~10 m deep and the substrate mainly constituted of submerged rocks, macrophytes, and sand. Most native fish species in Lake Kivu are confined to the littoral zone (Snoeks et al., 1997) where zooplankton density is 15–50 times lower than in the pelagic zone (Isumbisho et al., 2004, 2006a).

### Fish sampling

Diurnal fishing was carried out monthly at both stations from September 2007 to September 2009. At each station, fishes were passively captured using a 10-mm mesh—size fish net (length: 200 m; height: 9 m), left floating vertically from the water surface

**Fig. 1** Lake Kivu geographic situation and sampling sites location (black dots)



for 1 h around noon. In addition, larvae and juveniles of *L. tanganicus* and *L. miodon* were actively captured in the littoral station using a small seine net (3.5 m × 1.3 m; 300- $\mu$ m mesh size).

In the field, fishes were sorted by species, counted, and measured (nearest 1-mm length, total length, TL) using a graduated board. Fishes were dissected and their sex was noted after observation of their gonads. Their digestive tracts were extracted and preserved in 5% buffered formalin.

#### Fish diet analysis (gut contents)

In the laboratory, the content of digestive tracts was removed, weighed (nearest 0.01 mg), and examined under a dissecting microscope. For *L. miodon*, only the stomach content was examined, while for *L. tanganicus*, which does not have a true pylorus between stomach and intestine (personal observation), the contents of stomach and anterior intestine were examined. For the young stages of *L. tanganicus*



and *L. miodon* which did not have a developed stomach, all the digestive tract (from esophagus to lower intestine) was examined. All items present in the digestive tracts were counted and identified to the lowest possible taxonomic level, using Tachet et al. (1980) for macroinvertebrates, Sarmiento et al. (2007) for phytoplankton, and Isumbisho et al. (2006b) for mesozooplankton.

The fishes' diet was described using three common dietary indices (Hyslop, 1980): the occurrence (%FO), the abundance (%N), and the volume (%V) of each prey category. For volume, as *L. miodon* and *L. tanganicanus* have a small stomach and their preys are small, we employed the point method as recommended by Hyslop (1980): each food category is awarded points proportional to its estimated contribution to stomach volume. The points allocated to a food category were summed up and expressed as a percentage of the total points awarded. Empty guts were not taken into account in abundance and volume calculations.

In order to characterize and compare diets, the contribution of each food category (*i*) to the diet was estimated using the percentage of Lauzanne's index (%IA<sub>*i*</sub>) (Lauzanne, 1976):

$$\%IA_i = \frac{IA_i}{\sum_{i=1}^n IA_i} * 100$$

where IA<sub>*i*</sub> (Lauzanne's index) = (%FO<sub>*i*</sub> \* %V<sub>*i*</sub>)/100, and *n* is the number of the different food categories. Compared to other compound indices used in the study of fish feeding (Rosacchi & Nouazé, 1987), Lauzanne's index allows considering countable and uncountable food type, which is a real advantage when the diets of omnivorous or opportunistic fishes must be compared.

#### Diet overlap

Similarity between diets and dietary overlap between two species indicates their potential for trophic interactions (Qin et al., 2007; Bănaru & Harmelin-Vivien, 2009). In the present study, we calculated the Pianka's index (*O*) (Pianka, 1974):

$$O = \frac{\sum \%V_{iA} \%V_{iB}}{\sqrt{\sum \%V_{iA}^2 \sum \%V_{iB}^2}}$$

where %V<sub>*iA*</sub> is the percentage by volume of food category *i* in the diet of the species A, and %V<sub>*iB*</sub> is the

percentage by volume of the same food category in the diet of the species B. Only the food categories that were identified were considered in this calculation, using the lowest possible taxonomic level: fragments of zooplankters, insects, and fishes were not considered.

Pianka's index varies from 0 (no overlap) to 1 (complete overlap); an overlap was considered significant in several studies (Dolbeth et al., 2008; Corrêa et al., 2009) when values exceeded 0.6.

#### Data analyses

Effects of species, station, and season (the dry season from June to August and the rainy season from September to May) on captures were evaluated using generalized linear models with a quasi-Poisson error distribution (log-linear models). Models were compared using *F* test and the most parsimonious model was retained. All statistical tests were carried out in the R environment (R Development Core Team, 2005).

#### Results

In total, from September 2007 to September 2009, 542 *L. tanganicanus* and 208 *L. miodon* adults were caught in our experimental catches. *L. tanganicanus* represented 52% of the catch in the pelagic station and 81% in the littoral station while *L. miodon* represented 48 and 17% of the catch respectively in the pelagic and the littoral stations. Some *Haplochromis* spp. were also caught with *L. miodon* and *L. tanganicanus* but only in the littoral station where they represented 2% of the total catch. For the littoral station, the mean monthly catch was 3.8 (range 0–25) for *L. miodon* and 16.3 (0–60) for *L. tanganicanus*, while the mean monthly catch was 4.2 (0–23) for *L. miodon* and 4.6 (0–35) for *L. tanganicanus*, in the pelagic station. The simplest generalized linear model of captures is presented in Table 1. It was not significantly different from the full model ( $F_{96,97} = 0.126$ ,  $P = 0.723$ ). There was no effect of season on captures, but there were significant main and interactive effects of species and stations on captures. In other words, *L. tanganicanus* dominated in all captures, especially in the littoral zone.

**Table 1** Results of the most simplified but significant generalized linear model of captures with a quasi-Poisson error distribution

Effects	SS	df	F	P (>F)
Species	154.10	1	10.903	<b>0.001</b>
Station	116.75	1	8.260	<b>0.005</b>
Season	19.70	1	1.394	0.241
Species * station	62.80	1	4.444	<b>0.038</b>
Species * season	10.64	1	0.753	0.388
Station * season	0.19	1	0.013	0.909
Residuals	1370.95	97		

Significant effects at 0.05 level are highlighted (*bold* values in the table)

### Food composition in the gut contents

Six main food categories were identified in the gut contents of both species: terrestrial plant remains, benthic algae (*Cladophora* sp.), phytoplankton, zooplankton, insects, and fishes (Table 2). Fishes were more frequently observed in *L. miodon* stomachs than in *L. tanganicanus*.

Numerically, zooplankton (mainly *Thermocyclops consimilis* Kiefer, 1934; *Diaphanosoma excisum* Sars, 1885; and Bdelloids) was the most abundant food type in the diet of both species. By volume, insects (mainly Formicidae and Culicidae) were the dominant food type in *L. miodon* adults while zooplankton and insects (mainly Formicidae) contributed volumetrically in similar proportions (46.8% vs. 39.3%) to the diet of *L. tanganicanus* adults. The diet of young stages of *L. tanganicanus* and *L. miodon* was, in terms of occurrence and volume, dominated by zooplankton (Table 2).

### Variability in fish diet

The importance of the different food items in the diet of both species varied depending on size and habitat (littoral vs. pelagic) (Figs. 2 and 3). Insects were the dominant food type for *L. miodon* adults caught in the littoral zone but in the biggest *L. miodon*, fishes were most frequently observed (Fig. 2). In the pelagic area, some differences were observed in function of size: fish smaller than 110 mm fed preferentially upon zooplankton, while larger fish fed mainly upon insects (especially ants and mosquito larvae) and fishes (Fig. 2). In comparison, *L. tanganicanus* from the pelagic area fed mainly upon zooplankton, whatever the size (Fig. 3). In contrast, in the littoral area, *L. tanganicanus* shifted their diet to insects (mainly ants) as their size increased (Fig. 3). There

was no clear seasonal variation in the diet of both species. Young stages of both *L. miodon* and *L. tanganicanus* were mainly zooplanktivorous (Fig. 4).

### Diet overlap

Diet overlap estimated by the Pianka's index varied according to habitat and season. It was relatively high (>0.6) between both fish species at the pelagic station but was lower in the littoral zone ( $\leq 0.6$ ). Diet overlap varied between seasons: the index reached 0.73 offshore and 0.54 inshore during the dry season, whereas, in the rainy season, it tended to decrease in both sites (0.68 offshore and 0.37 inshore). Concerning the larvae, their diet overlap was extremely high whatever the season. Their diet overlap index was equal to 0.99 and 0.98 in rainy and dry season respectively.

### Discussion

The present study investigated the invasive dispersal and the feeding ecology of *L. tanganicanus*, an endemic species of Lake Tanganyika recently introduced in Lake Kivu.

The first scientific observation of *L. tanganicanus* presence in Lake Kivu was made in December 2006 (Muderhwa & Matabaro, 2010). The time of its arrival into Lake Kivu is not well established but some evidence points to a recent, likely accidental, introduction, contrary to the opinion that this species was accidentally introduced with *L. miodon* in 1959 (Muderhwa & Matabaro, 2010). Indeed, if the new species had been introduced at the end of the 1950s, it would have been noticed by the fishermen before, since this species is easily distinguished from

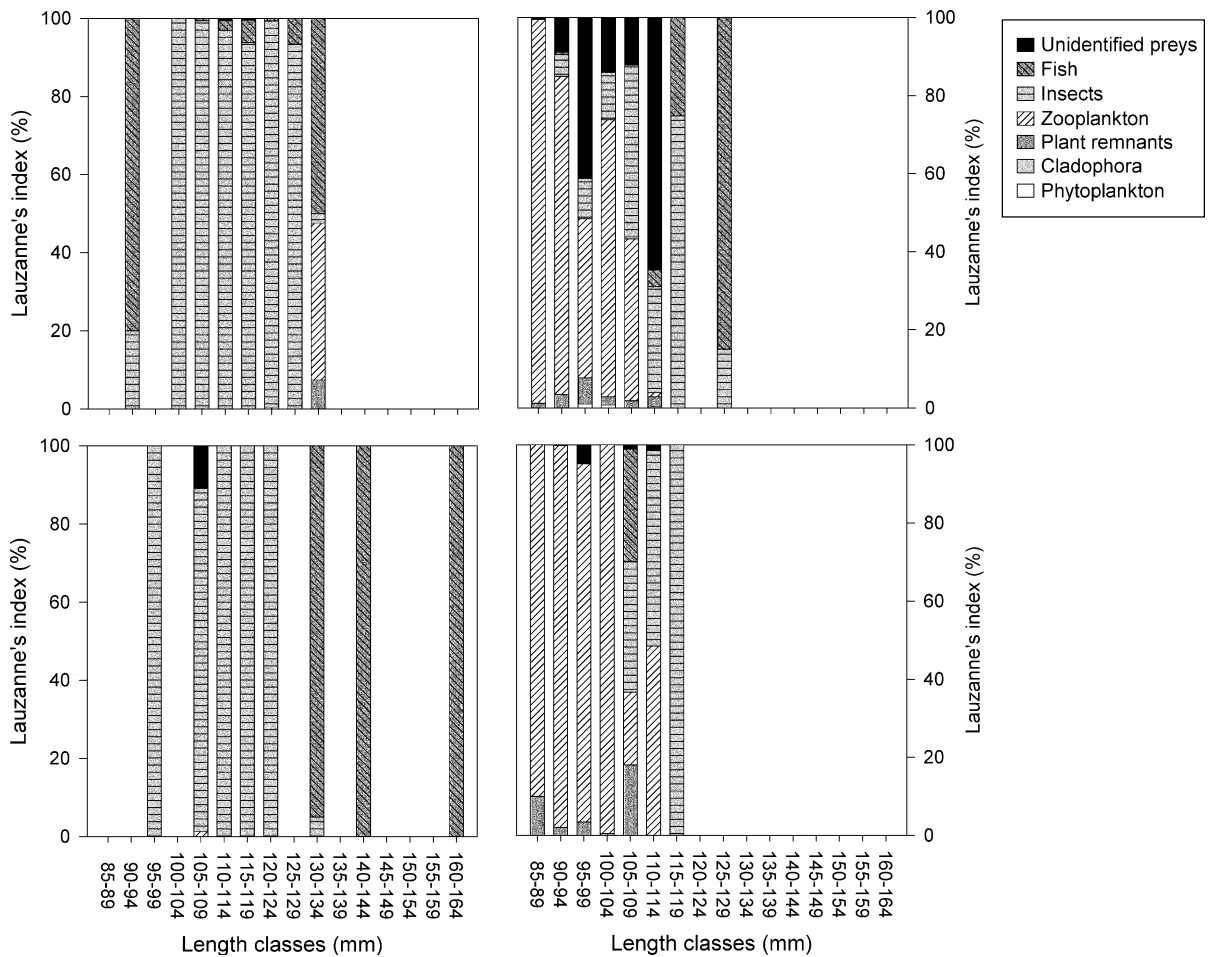
**Table 2** Importance of food types (%FO, occurrence in %; %N, abundance in %; %V, volume in %) in gut contents of *Limnothrissa miodon* and *Lamprichthys tanganicanus* from Lake Kivu

Size range (TL, mm): Food types/indices	<i>Lamprichthys tanganicanus</i>						<i>Limnothrissa miodon</i>					
	Young			Adult			Young			Adult		
	9–36			72–129			11–42			85–164		
	%FO	%N	%V	%FO	%N	%V	%FO	%N	%V	%FO	%N	%V
Plant remnants	8.3	–	0.7	36.6	–	2.8	1.0	–	0.7	21.1	–	2.4
<i>Cladophora</i> sp.	–	–	–	2.7	–	0.1	–	–	–	–	–	–
Phytoplankton	75.8	29.1	4.9	44.4	4.8	3.1	0.1	0.1	<0.1	4.7	<0.1	0.5
Cyanobacteria ( <i>Microcystis</i> sp.)	–	–	–	41.3	–	2.5	0.1	0.1	<0.1	4.7	–	0.5
Diatom ( <i>Nitzschia</i> sp.)	–	–	–	7.6	4.8	0.6	0.1	0.1	<0.1	0.6	<0.1	<0.1
Zooplankton	99.2	70.9	89.9	68.4	92.0	46.8	92.8	99.0	91.0	34.5	94.8	23.2
Copepods	98.0	67.2	85.3	53.3	42.7	6.9	86.9	89.0	82.8	28.1	15.4	2.9
<i>Mesocyclops aequatorialis</i>	–	–	–	6.9	0.3	0.2	–	–	–	2.3	0.1	0.1
<i>Thermocyclops consimilis</i>	–	–	–	52.8	42.3	6.7	–	–	–	28.1	15.3	2.9
<i>Tropocyclops confinis</i>	–	–	–	0.2	0.1	<0.1	–	–	–	–	–	–
Nauplii larvae	–	–	–	–	–	–	–	–	–	0.6	<0.1	<0.1
Cladoceran	51.2	0.8	2.1	43.2	36.8	6.6	10.4	9.9	6.9	17.5	15.9	2.3
<i>Alona rectangula</i>	–	–	–	6.9	0.1	0.1	–	–	–	5.3	0.1	<0.1
<i>Ceriodaphnia cornuta</i>	–	–	–	4.4	0.1	0.1	–	–	–	0.6	<0.1	<0.1
<i>Diaphanosoma excisum</i>	–	–	–	39.8	35.5	6.1	–	–	–	14.6	15.7	2.3
<i>Moina micrura</i>	–	–	–	6.5	1.1	0.4	–	–	–	0.6	<0.1	<0.1
Rotifera	84.9	2.9	2.6	44.4	12.6	1.5	–	–	–	30.4	63.5	2.4
Unidentified Bdelloïds	–	–	–	43.6	12.5	1.5	–	–	–	30.4	63.5	2.4
<i>Brachionus calyciflorus</i>	–	–	–	0.2	<0.1	<0.1	–	–	–	–	–	–
<i>Lecane</i> sp.	–	–	–	1.5	<0.1	<0.1	–	–	–	–	–	–
Zooplankton fragment	–	–	–	66.9	–	31.8	2.1	–	1.3	34.5	–	15.5
Insects	6.7	–	0.9	67.6	3.2	39.3	1.1	0.5	0.5	65.5	4.9	53.4
Imago	–	–	–	26.3	0.8	15.2	–	–	–	31.6	2.0	18.7
<i>Apidae</i>	–	–	–	1.1	<0.1	0.1	–	–	–	0.6	<0.1	<0.1
<i>Coccinellidae</i>	–	–	–	0.8	<0.1	<0.1	–	–	–	1.8	0.1	0.3
<i>Corixidae</i>	–	–	–	–	–	–	–	–	–	1.2	<0.1	0.4
<i>Formicidae</i>	–	–	–	22.7	0.6	13.5	–	–	–	29.2	1.5	16.6
<i>Muscidae</i>	–	–	–	–	–	–	–	–	–	1.8	<0.1	<0.1



Table 2 continued

Size range (TL, mm): Food types/indices	<i>Lamprichthys tanganicus</i>						<i>Limnothrissa miodon</i>					
	Young			Adult			Young			Adult		
	9–36			72–129			11–42			85–164		
	%FO	%N	%V	%FO	%N	%V	%FO	%N	%V	%FO	%N	%V
<i>Termitidae</i>	–	–	–	3.8	0.2	1.5	–	–	–	3.5	0.4	1.3
Larvae	–	–	–	0.4	1.6	<0.1	1.1	0.5	0.5	28.7	2.3	14.1
<i>Chironomidae</i>	–	–	–	0.2	1.6	<0.1	1.1	0.5	0.5	0.6	<0.1	<0.1
<i>Culicidae</i>	–	–	–	0.2	<0.1	<0.1	–	–	–	26.9	2.0	12.7
<i>Leuctridae</i>	–	–	–	–	–	–	–	–	–	7.6	0.3	1.4
Nymph	–	–	–	12.6	0.8	0.6	–	–	–	8.8	0.6	0.8
Insects fragment	6.7	–	0.9	52.8	–	23.5	–	–	–	37.4	–	19.9
Fish	–	–	–	0.6	<0.1	0.1	–	–	–	13.5	0.3	10.8
<i>Limnothrissa miodon</i>	–	–	–	–	–	–	–	–	–	8.2	0.3	5.9
Larvae	–	–	–	–	–	–	–	–	–	5.8	0.3	4.1
Juvenile	–	–	–	–	–	–	–	–	–	2.3	<0.1	1.8
<i>Lamprichthys tanganicus</i>	–	–	–	0.2	<0.1	0.1	–	–	–	–	–	–
Juvenile	–	–	–	0.2	<0.1	0.1	–	–	–	–	–	–
<i>Haplochromis</i> spp.	–	–	–	–	–	–	–	–	–	1.8	<0.1	1.3
Juvenile	–	–	–	–	–	–	–	–	–	1.8	<0.1	1.3
Fish fragments	–	–	–	0.6	–	<0.1	–	–	–	8.2	–	3.6
Unidentified prey	51.6	–	3.5	39.8	<0.1	7.7	9.3	0.5	7.8	22.2	<0.1	9.6
Number of non empty stomach analyzed	252			475			962			171		
Number of stomach analyzed	252			542			962			208		

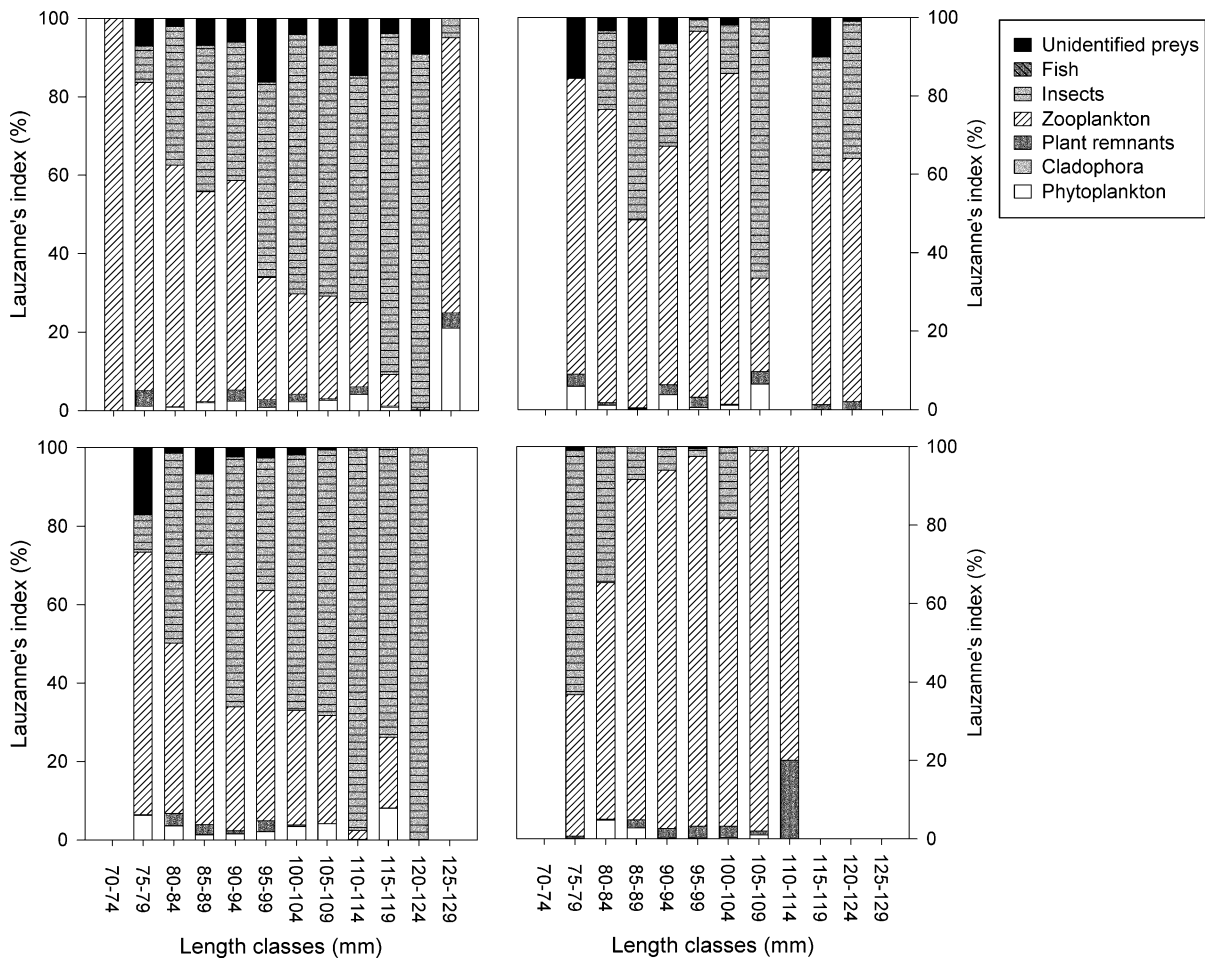


**Fig. 2** Percentage of Lauzanne's index of broad taxonomic groups for different length classes of adults *Limnothrissa miodon* from the littoral (left panels) and pelagic (right panels) stations of Lake Kivu during rainy (upper panels) and dry season (lower panels)

*L. miodon*. Moreover, several scientific studies on *L. miodon* were conducted in the past decades (e.g., Lamboeuf, 1989, 1991; Kaningini, 1995) and none ever mentioned the presence of *L. tanganicus*. Presently, as shown by our experimental captures, the species, which retains its original preference for the littoral areas, has invaded the pelagic zone of Lake Kivu.

The occupation of pelagic waters by *L. tanganicus* in Lake Kivu is a behavior not observed in Lake Tanganyika, where the species is mainly present in the rocky shore but rarely in the pelagic area (Coulter, 1991). The occupation of the pelagic niche in Lake Tanganyika is probably prevented by biotic interactions, i.e., competition and/or predation, with native species. The recent Lake Kivu dates from Late

Pleistocene (25,000–20,000 years BP according to Beadle, 1981; 14,000–11,000 years BP according to Pouclet, 1978) while Lake Tanganyika communities have evolved for at least 9–12 million years (Cohen et al., 1993). In Lake Tanganyika, pelagic piscivorous fishes (e.g., *Lates stappersii* (Boulenger, 1914); *Lates microlepis* Boulenger, 1898) are present and feed upon *L. miodon* and *Stolothrissa tanganicae* Regan, 1917 shoals (Coulter, 1991). The absence of large predators in Lake Kivu most probably allowed *L. tanganicus* to successfully colonize new habitats, including the pelagic area where it found fewer competitors (most of native fish in Lake Kivu are confined to the littoral zone; Snoeks et al., 1997) and more abundant mesozooplankton (Isumbisho et al., 2004; Isumbisho et al., 2006a).



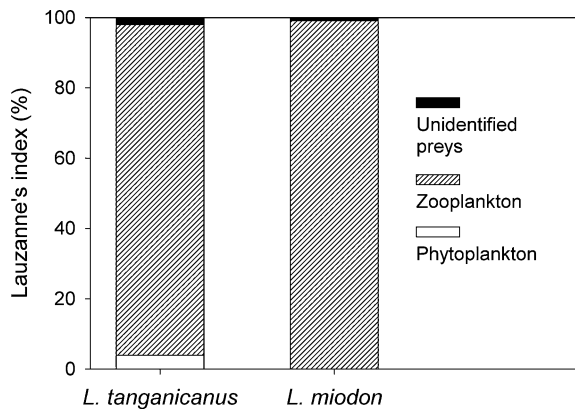
**Fig. 3** Percentage of Lauzanne's index of broad taxonomic groups for different length classes of adults *Lamprichthys tanganicanus* from the littoral (left panels) and pelagic (right

panels) stations of Lake Kivu during rainy (upper panels) and dry season (lower panels)

Our results show that *L. miodon*, despite being primarily a zooplanktivore, feeds on diverse prey in Lake Kivu, including phytoplankton, insects, and fishes, as previously reported by other authors (de Iongh et al., 1983; Isumbisho et al., 2004; Masilya et al., 2005). This ability to feed on various resources was already mentioned by those who studied *L. miodon* in the other lakes where the species was also introduced, i.e., lakes Kariba and Cahora Bassa (Mandima, 1999, 2000). The diet of *L. miodon* varies with habitat and size (de Iongh et al., 1983; Mandima, 2000): small fish essentially present in pelagic waters ingest mainly zooplankton, while larger fish tend to move inshore, where the contribution of floating insects increases in their diet. By contrast, most size classes of *L. tanganicanus* consumed mesozooplankton, even though for

littoral specimens the share of mesozooplankton in the guts decreased with size and was replaced by insects. The presence of copepods in the gut contents of *L. tanganicanus* from Lake Kivu were reported also by Lushombo & Nshombo (2008). Its important to note that food types as terrestrial plant remnants and benthic algae seemed to have been incidentally ingested.

The analysis of gut contents from both species suggests their opportunistic feeding in Lake Kivu. This behavior may be related to the scarce resources in the lake (Isumbisho et al., 2006a; Sarmiento et al., 2009). Evidence of opportunistic feeding in both species is provided by the high contribution of insects, when they are present, in the diet of the largest specimen along the littoral zone (see Figs. 2 and 3) as well as by the high diet overlap index in dry



**Fig. 4** Percentage of Lauzanne's index of broad taxonomic groups for larvae of *Limnothrissa miodon* and *Lamprichthys tanganicanus* of Lake Kivu

season when bigger zooplankton are abundant and zooplankton biomass high than in rainy season (Isumbisho et al., 2006a). Opportunistic feeding on large prey is a common behavior in freshwater fishes (Lazzaro, 1987) and is explained by the optimal foraging theory (Persson, 1985; Lazzaro et al., 2009).

The high diet overlap observed at all times in the pelagic zone suggests a significant niche overlap between *L. miodon* and *L. tanganicanus*. Several authors used Pianka's index or other indexes for estimating diet overlap between fish species (Qin et al., 2007; Corrêa et al., 2009), with contrasting conclusions in terms of interspecific competition. In theory, we may expect low or absence of food competition, whatever the degree of diet overlap observed, between species which have coexisted in the same environment for a long time (Sale, 1974; Genner et al., 1999) or which live in productive systems where resources are abundant (Dolbeth et al., 2008; Macneale et al., 2010). Pianka as well as Sale discussed this point, insisting that high diet overlap between two species may indicate competition only where and when available food resources are limited (Pianka, 1974; Sale, 1974). Accordingly, Sampson et al. (2009) and Museth et al. (2010) concluded from their studies of interactions between introduced fish species in various systems that high diet overlap did not necessarily point to effective competition. Moreover, resource use and habitat occupation by an introduced species may change with time (e.g., Museth et al., 2010), depending on the interactions with the species already present in the system. The

same situation can also be observed with a native species after an introduction of an exotic species (Qin et al., 2007).

Lake Kivu is a low-productivity lake, as a result of low nutrient concentration, limiting primary production (Sarmiento et al., 2009). Moreover, a large fraction of the phytoplankton biomass is lost by sedimentation to the anoxic deep waters (Pasche, 2009). Another significant fraction is composed of picoplankton (Sarmiento et al., 2008), on which mesozooplankton cannot feed directly (Hansen et al., 1994). The mesozooplankton diversity is low, with four main crustacean species which present large variations over an annual cycle, and an efficient grazer is missing (Isumbisho et al., 2006a). Actually, the pelagic zone of Lake Kivu harbors a low zooplankton biomass most of the time, except for the relatively short-lived increase of primary production of the dry season (June–August), on which mesozooplankton and fish production heavily depend (Isumbisho et al., 2006a). In this context, it is very likely that competition for food resources between *L. tanganicanus* and *L. miodon* is strong in the pelagic zone of Lake Kivu, where both species consume essentially mesozooplankton. This likely food competition for resources must still be higher in the littoral zone between the young stages of these species, exclusively zooplanktivorous, as in this zone of lake, zooplankton is less abundant than in pelagic zone (Isumbisho et al., 2004, 2006a). If so, we assume that this could have a negative effect on the survival rates of the young stages of these species and consequently on the future of their populations.

The outcome of interspecific competition is theoretically competitive exclusion of the less efficient species (e.g., Qin et al., 2007), but prediction at this stage remains risky. However, a likely outcome in the years to come is that the pelagic fishery yield, which is relatively low in Lake Kivu (Roest, 1999), is going to be negatively affected by the introduction and the consecutive expansion of *L. tanganicanus*. Therefore, continued monitoring of the stock of the two species is needed, as well as the study of their interactions.

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## References

- Bănar, D. & M. Harmelin-Vivien, 2009. Feeding behaviour of Black Sea bottom fishes: did it change over time? *Acta Oecologica* 35: 769–777.
- Beadle, L. C., 1981. *The Inland Waters of Tropical Africa, an Introduction to Tropical Limnology*, 2nd ed. Longman, London.
- Cohen, A. S., M. J. Soreghan & C. A. Scholz, 1993. Estimating the age of formation of lakes – an example from Lake Tanganyika, East-African rift system. *Geology* 21: 511–514.
- Collart, A., 1960. L'introduction du *Stolothrissa tanganyicae* (Ndagala) au lac Kivu. *Bulletin Agricole du Congo LI*: 975–986.
- Corrêa, C. A., N. S. Hahn & R. L. Delariva, 2009. Extreme trophic segregation between sympatric fish species: the case of small sized body *Aphyocharax* in the Brazilian Pantanal. *Hydrobiologia* 635: 57–65.
- Coulter, G. W., 1991. Pelagic and the benthic fish community. In Coulter, G. W. (ed.), *Lake Tanganyika and Its Life*. Natural History Museum Publications/Oxford University Press, London: 111–138, 151–199.
- de Iongh, H. H., P. C. Spliethoff & V. G. Frank, 1983. Feeding habits of the clupeid *Limnothrissa miodon* (Boulenger), in Lake Kivu. *Hydrobiologia* 102: 113–122.
- Degens, E., R. P. Herzen, H.-K. Wong, W. G. Deuser & H. W. Jannasch, 1973. Lake Kivu: structure, chemistry and biology of an East African rift lake. *Geologische Rundschau* 62: 245–277.
- Dolbeth, M., F. Martinho, R. Leitao, H. Cabral & M. A. Pardal, 2008. Feeding patterns of the dominant benthic and demersal fish community in a temperate estuary. *Journal of Fish Biology* 72: 2500–2517.
- Dumont, H. J., 1986. The Tanganyika sardine in Lake Kivu: another ecodisaster for Africa? *Environmental Conservation* 13: 143–148.
- Genner, M. J., G. F. Turner & S. J. Hawkins, 1999. Foraging of rocky habitat cichlid fishes in Lake Malawi: coexistence through niche partitioning? *Oecologia* 121: 283–292.
- Gozlan, R. E., 2008. Introduction of non-native freshwater fish: is it all bad? *Fish and Fisheries* 9: 106–115.
- Guillard, J., 2009. Estimation de l'abondance du stock de *Limnothrissa miodon* dans le lac Kivu au cours de deux campagnes : février et juillet 2008. Rapport ECOSYKI, Commission Universitaire pour le Développement, Communauté Française de Belgique.
- Hansen, B., P. K. Bjørnsen & P. J. Hansen, 1994. The size ratio between planktonic predators and their prey. *Limnology and Oceanography* 39: 395–403.
- Hyslop, E. J., 1980. Stomach contents analysis – a review of methods and their application. *Journal of Fish Biology* 17: 411–429.
- Isumbiso, M., M. Kaningini, J.-P. Descy & E. Baras, 2004. Seasonal and diel variations in diet of the young stages of *Limnothrissa miodon* in Lake Kivu, Eastern Africa. *Journal of Tropical Ecology* 20: 73–83.
- Isumbiso, M., H. Sarmento, B. Kaningini, J.-C. Micha & J.-P. Descy, 2006a. Zooplankton of Lake Kivu, East Africa, half a century after the Tanganyika sardine introduction. *Journal of Plankton Research* 28: 971–989.
- Isumbiso, M., H. Sarmento & J.-P. Descy, 2006b. Qualitative composition of the pelagic mesozooplankton in Lake Kivu, eastern Africa: impact of *Limnothrissa miodon* introduction. In Isumbiso, M. (ed.), *Zooplankton Ecology of Lake Kivu (Eastern Africa)*. PhD thesis, Presses Universitaires de Namur, Belgium: 39–55.
- Kaningini, M., 1995. Etude de la croissance, de la reproduction et de l'exploitation de *Limnothrissa miodon* au lac Kivu, bassin de Bukavu (Zaïre). Faculté de Sciences, Thèse, Facultés Universitaires Notre Dame de la Paix, Namur, Belgique.
- Lamboeuf, M., 1989. Estimation de l'abondance du stock d'Isambaza (*Limnothrissa miodon*), résultats de la prospection acoustique de septembre 1989. *Projet/RWA/87/012*: 13 pp.
- Lamboeuf, M., 1991. Abondance et répartition du *Limnothrissa miodon* du lac Kivu, résultat des prospections acoustiques d'avril 1989 à juin 1991. *DOC/TR NO. RWA/87/012/DOC/TR/46 (Fr)*. FAO.
- Lauzanne, L., 1976. Régimes alimentaires et relations trophiques des poissons du lac Tchad. *Cahiers Orstom, Série Hydrobiologie* 10: 267–310.
- Lazzaro, X., 1987. A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. *Hydrobiologia* 146: 97–167.
- Lazzaro, X., G. Lacroix, B. Gauzens, J. Gignoux & S. Legendre, 2009. Predator foraging behaviour drives food-web topological structure. *Journal of Animal Ecology* 78: 1307–1317.
- Lévêque, C., 1997. Introductions de nouvelles espèces de poissons dans les eaux douces tropicales : objectifs et conséquences. *Bulletin Française de Pêche et de Pisciculture* 344(345): 79–91.
- Lodge, D. M., R. A. Stein, K. M. Brown, A. R. Covich, C. Brönmark, J. E. Garvey & S. P. Klosiewski, 1998. Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. *Australian Journal of Ecology* 23: 53–67.
- Lushombo, M. & M. Nshombo, 2008. Apparition au lac Kivu du poisson *Lamprichthys tanganyicanus* (Poeciliidae), espèce endémique du lac Tanganyika. *Annales des Sciences de l'Université Officielle de Bukavu* 1: 1–5.
- Macneale, K. H., B. L. Sanderson, J.-Y. P. Courbois & P. M. Kiffney, 2010. Effects of non-native brook trout (*Salvelinus fontinalis*) on threatened juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in an Idaho stream. *Ecology of Freshwater Fish* 19: 139–152.
- Mandima, J. J., 1999. The food and feeding behaviour of *Limnothrissa miodon* (Boulenger, 1906) in Lake Kariba, Zimbabwe. *Hydrobiologia* 407: 175–182.
- Mandima, J. J., 2000. Spatial and temporal variations in the food of the sardine *Limnothrissa miodon* (Boulenger,



- 1906) in Lake Kariba, Zimbabwe. Fisheries Research 48: 197–203.
- Masilya, P., B. Kaningini, P. Isumbisho, J.-C. Micha & G. Ntakimazi, 2005. Food and feeding activity of *Limnothrissa miodon* (Boulenger, 1906) in the southern part of Lake Kivu, Central Africa. In International Conference Africa's Great Rift: Diversity and Unity. Royal Academy for Overseas Sciences Royal Museum for Central Africa, Brussels, 29–30 September, 2005: 83–93.
- Muderhwa, N. & L. Matabaro, 2010. The introduction of the endemic fish species, *Lamprichthys tanganicus* (Poeciliidae), from Lake Tanganyika into Lake Kivu: possible causes and effects. Aquatic Ecosystem Health and Management 13: 203–213.
- Museth, J., R. Borgström & J. E. Brittain, 2010. Diet overlap between introduced European minnow (*Phoxinus phoxinus*) and young brown trout (*Salmo trutta*) in the lake, Øvre Heimdalsvatn: a result of abundant resources or forced niche overlap? Hydrobiologia 642: 93–100.
- Ogutu-Ohwayo, R., R. E. Hecky, A. S. Cohen & L. Kaufman, 1997. Human impacts on the African Great Lakes. Environmental Biology of Fishes 50: 117–131.
- Pardo, R., I. Vila & J. J. Capella, 2009. Competitive interaction between introduced rainbow trout and native silverside in a Chilean stream. Environmental Biology of Fishes 86: 353–359.
- Pasche, N., 2009. Nutrient Cycling and Methane Production in Lake Kivu. Thèse de Doctorat, Swiss Federal Institute of Technology, Zurich.
- Persson, L., 1985. Optimal foraging: the difficulty of exploiting different feeding strategies simultaneously. Oecologia (Berlin) 67: 338–341.
- Pianka, E. R., 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences 71: 2141–2145.
- Poucllet, A., 1978. Les communications entre les grands lacs de l'Afrique centrale. Implications sur la structure du rift occidental. Musée royal d'Afrique centrale, Département de Géologie et Minéralogie. Rapport annuel 1977: 145–155.
- Preikshot, D., E. Nsiku, T. Pitcher & D. Pauly, 1998. An interdisciplinary evaluation of the status and health of African lake fisheries using a rapid appraisal technique. Journal of Fish Biology 53: 381–393.
- Qin, J., J. Xu & P. Xie, 2007. Diet overlap between the endemic fish *Anabarilius grahami* (Cyprinidae) and the exotic noodlefish *Neosalanx taihuensis* (Salangidae) in Lake Fuxian, China. Journal of Freshwater Ecology 22: 365–370.
- R Development Core Team, 2005. R: A Language and Environment for Statistical Computing, Reference Index Version 2.2.1. R Foundation for Statistical Computing, Vienna, Australia. ISBN 3-900051-07-0. <http://www.R-project.org>.
- Roest, F. C., 1999. Introduction of a pelagic fish into a large natural Lake: Lake Kivu, Central Africa. In van Densen, W. L. T. & M. J. Morris (eds), Fish and Fisheries of Lakes and Reservoirs in Southeast Asia and Africa. Westbury Publishing, Otley: 327–338.
- Rosecchi, E. & Y. Nouazé, 1987. Comparaison de cinq indices alimentaires utilisés dans l'analyse des contenus stomacaux. Revue des Travaux de l'Institut des Pêches Maritimes 49: 111–123.
- Sale, F. P., 1974. Overlap in resource use, and interspecific competition. Oecologia (Berlin) 17: 245–256.
- Sampson, S. J., J. H. Chick & M. A. Pegg, 2009. Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. Biological Invasions 11: 483–496.
- Sarmiento, H., M. Leitao, M. Stoyneva, P. Compère, A. Couté, M. Isumbisho & J.-P. Descy, 2007. Species diversity of pelagic algae in Lake Kivu (East Africa). Cryptogamie and Algologie 28: 245–269.
- Sarmiento, H., F. Unrein, I. Mwapu, S. Sténuite, J. M. Gasol & J.-P. Descy, 2008. Abundance and distribution of picoplankton in tropical, oligotrophic Lake Kivu, eastern Africa. Freshwater Biology 53: 756–771.
- Sarmiento, H., M. Isumbisho, S. Sténuite, F. Darchambeau, B. Leporcq & J.-P. Descy, 2009. Phytoplankton ecology of Lake Kivu (eastern Africa): biomass, production and elemental ratios. Verhandlungen des Internationalen Verein Limnologie 30: 709–713.
- Snoeks, J., L. De Vos & D. Thys van den Audenaerde, 1997. The ichthyogeography of Lake Kivu. South African Journal of Science 93: 579–584.
- Tachet, H., M. Bournaud & P. Richoux, 1980. Introduction à l'étude des macroinvertébrés des eaux douces (Systématique élémentaire et aperçu écologique). Association Française de Limnologie, Lyon, France.
- Verbeke, J., 1957. Exploration hydrobiologique des lacs Kivu, Edouard et Albert. Recherches Ecologiques sur la faune des Grands Lacs de l'est du Congo Belge, Vol. III. Institut Royal des Sciences Naturelles de Belgique, Bruxelles.