

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/299423330>

# Limnothrissa miodon (Boulenger, 1906) in Lake Kariba: daily ration and population food consumption estimates, and potential application to predict the fish stock biomass from prey...

Article in *Hydrobiologia* · October 2016

DOI: 10.1007/s10750-016-2732-8

CITATIONS

3

READS

542

3 authors:



**Jimmiel Mandima**

International Fund for Animal Welfare (IFAW)

16 PUBLICATIONS 58 CITATIONS

SEE PROFILE



**Raine Kortet**

University of Eastern Finland

160 PUBLICATIONS 5,226 CITATIONS

SEE PROFILE



**Jouko Sarvala**

University of Turku

162 PUBLICATIONS 4,418 CITATIONS

SEE PROFILE

*Limnothrissa miodon* (Boulenger, 1906) in Lake Kariba: daily ration and population food consumption estimates, and potential application to predict the fish stock biomass from prey abundance

**Jimmiel Mandima, Raine Kortet & Jouko Sarvala**

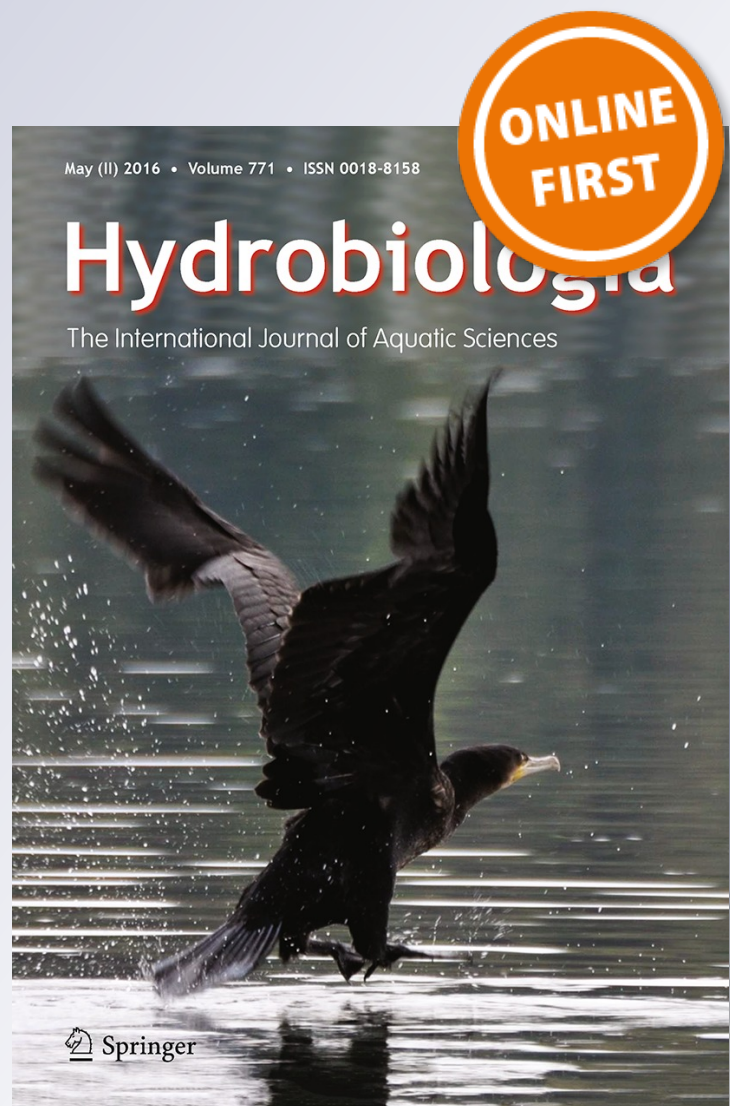
**Hydrobiologia**

The International Journal of Aquatic Sciences

ISSN 0018-8158

Hydrobiologia

DOI 10.1007/s10750-016-2732-8



**Your article is protected by copyright and all rights are held exclusively by Springer International Publishing Switzerland. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at [link.springer.com](http://link.springer.com)".**

# *Limnothrissa miodon* (Boulenger, 1906) in Lake Kariba: daily ration and population food consumption estimates, and potential application to predict the fish stock biomass from prey abundance

Jimmiel Mandima · Raine Kortet · Jouko Sarvala

Received: 16 December 2015 / Revised: 1 March 2016 / Accepted: 5 March 2016  
© Springer International Publishing Switzerland 2016

**Abstract** The offshore pelagic niche in Lake Kariba is mainly occupied by the Tanganyika sardine, *Limnothrissa miodon*, commonly called ‘kapenta’, which is a mainly zooplanktivorous clupeid fish. The population dynamics of kapenta fluctuate seasonally in synchrony with the physical processes that shape the trophic status of the lake. Diel feeding periodicity and mean stomach fullness of *L. miodon* were used to estimate the daily ration and food consumption rates of the population. The daily ration ( $R_d$ ) was estimated from mean stomach contents and evacuation rates calculated using the modified Bajkov (Trans Am Fish Soc 65:288–289, 1935) formula. Data on stomach contents present at different time intervals over

continuous feeding cycles under experimental conditions were analysed. The results show a daily ration of 8.8–9.9% of fresh body weight day<sup>-1</sup>. The estimated whole population food consumption rate suggests very efficient grazing. The present data enable estimations of the potential standing biomass of *L. miodon* sustained by the lake under known zooplankton biomass regimes. This basis can be utilised further in future work focusing on spatial and temporal dynamics and climate change scenarios to provide a realistic food consumption estimate for the *L. miodon* population in Lake Kariba and similar artificial reservoirs.

**Keywords** Lake Kariba · *Limnothrissa miodon* · Daily ration · Population food consumption · MAXIMS Model

Guest editors: Paula Kankaala, Tiina Nöges, Martti Rask, Dietmar Straile & Arkady Yu. Terzhevik / European Large Lakes IV. Ecosystem Services and Management in a Changing World

J. Mandima (✉)  
African Wildlife Foundation, 1400 16th Street NW,  
Washington, DC 20036, USA  
e-mail: jmandima@awf.org

J. Mandima · R. Kortet  
Department of Environmental and Biological Sciences,  
University of Eastern Finland, P.O. Box 111,  
80101 Joensuu, Finland

J. Sarvala  
Department of Biology, University of Turku,  
20014 Turku, Finland

## Introduction

The quantitative assessment of fish stock productivity and the understanding of species and community dynamics require accurate estimates of daily rates of food consumption (Jobling, 1981). Contemporary ecological studies use trophic modelling for multi-species ecosystems as a common tool where ‘food consumption rate’ is an essential input parameter (Allison et al., 1995). Predator–prey interactions, in general, are important determinants of yield to fisheries. The knowledge on the nature and magnitude

of species interactions helps us to understand the concept of multispecies management of renewable resources. To achieve this, it is necessary to assess the food habits and daily food intake rations of major predators in the ecosystem (Olson & Mullen, 1986).

In Lake Kariba, a major reservoir on the Zambezi River, the pelagic fish community is dominated by the introduced Lake Tanganyika clupeid, *Limnothrissa miodon* (Boulenger, 1906) commonly called 'kapenta', which, despite showing opportunistic feeding tendencies, is in Kariba mainly zooplanktivorous (Mandima, 1999, 2000). The population dynamics of this freshwater sardine shows remarkable seasonal fluctuations that are directly related to physical processes that influence the trophic status of the lake, and hence also to productivity.

The largely zooplanktivorous nature of the diet of *L. miodon* implies that the sustainability of the pelagic kapenta fishery is likely largely dependent on the lake's zooplankton productivity. This suggestion is indeed corroborated by Begg's (1974) observations that there is a delicate balance between the standing biomass of *L. miodon* and availability and abundance of zooplankton in Lake Kariba. However, this early observation of the predator–prey relationship has not been quantified and hence its corroboration was one of the objectives for the present study. Comparable *L. miodon*–prey relationships have been observed in Lakes Tanganyika and Kivu (Rufi & Chapman, 1976 cited in de Iongh et al., 1983; Hecky, 1991; Sarvala et al., 2002; Masilya et al., 2011).

There is a plethora of studies that confirm the strong relationship between the dynamics of zooplankton abundance and fish biomass, and their respective production dynamics (e.g. Ploskey & Jenkins, 1982). On the basis of this established trend in lower and higher level consumer interactions in reservoir fisheries worldwide, it is consistent to expect that fish production can be estimated on the basis of known food abundance dynamics and a known rate of consumption by the predatory fish. In general, the evaluation of fish communities through assessment of zooplankton populations and measurement of lake productivity has been proposed as a potential tool for the future management of warm water fish populations (Downing et al., 1990).

The subject of food consumption rates in fishes has been intensively studied using mostly fish species from temperate zone. Various models have been

proposed for the calculation of daily ration and population food consumption rates (Bajkov, 1935; Elliott & Persson, 1978; Tseitlin, 1980; Jobling, 1981, 1986; Persson, 1984, 1986; Pennington, 1985; Sainsbury, 1986; Palomares & Pauly, 1989). It is now generally accepted that the change in stomach content is a function of both feeding rate and evacuation rate (Elliott & Persson, 1978; Sainsbury, 1986; Jarre et al., 1991; Bromley, 1994). The assessment of gastric evacuation rates (GERs) is commonly used to estimate feeding rates of natural fish populations in order to quantify the extent of predator–prey interactions. Gastric evacuation is the process by which individual fish empties its stomach after a full meal through digestive processes entirely or reaching a residual stomach content level. This enables the construction of quantitative descriptions of food webs and provides means of enhancing the accurate management of fish stocks (Bromley, 1994).

The accuracy of daily food consumption estimates critically depends on the appropriateness of the selected model from amongst the numerous feeding and evacuation models used by different authors (Sainsbury, 1986). Feeding models that are commonly used interchangeably include the linear model (Bajkov, 1935; Bromley, 1987), the square root model (Jobling, 1981), and the exponential model (Thorpe, 1977; Elliott & Persson, 1978; Eggers, 1979). It has, however, been observed that exponential patterns of feeding and evacuation are more applicable to fish with small- and medium-sized stomachs that feed on small prey at frequent intervals (Bromley, 1994). This applies also to the feeding pattern of *L. miodon*, the study species of the present paper.

The main objective of this study was to use data on the diel feeding periodicity and mean stomach fullness of *L. miodon* to estimate the daily ration and population food consumption rates in Lake Kariba. We hypothesised that the daily ration and food consumption rate in *L. miodon* would show similar patterns that have been detected in other tropical fishes. A second objective was to correlate the population food consumption rates of *L. miodon* to the estimated zooplankton production in Kariba and use that as a basis to predict *L. miodon* stock strength. However, we note the complex and often unpredictable patterns that occur in the wild so the validity of this relationship remains to be tested in future studies.

**Materials and methods**

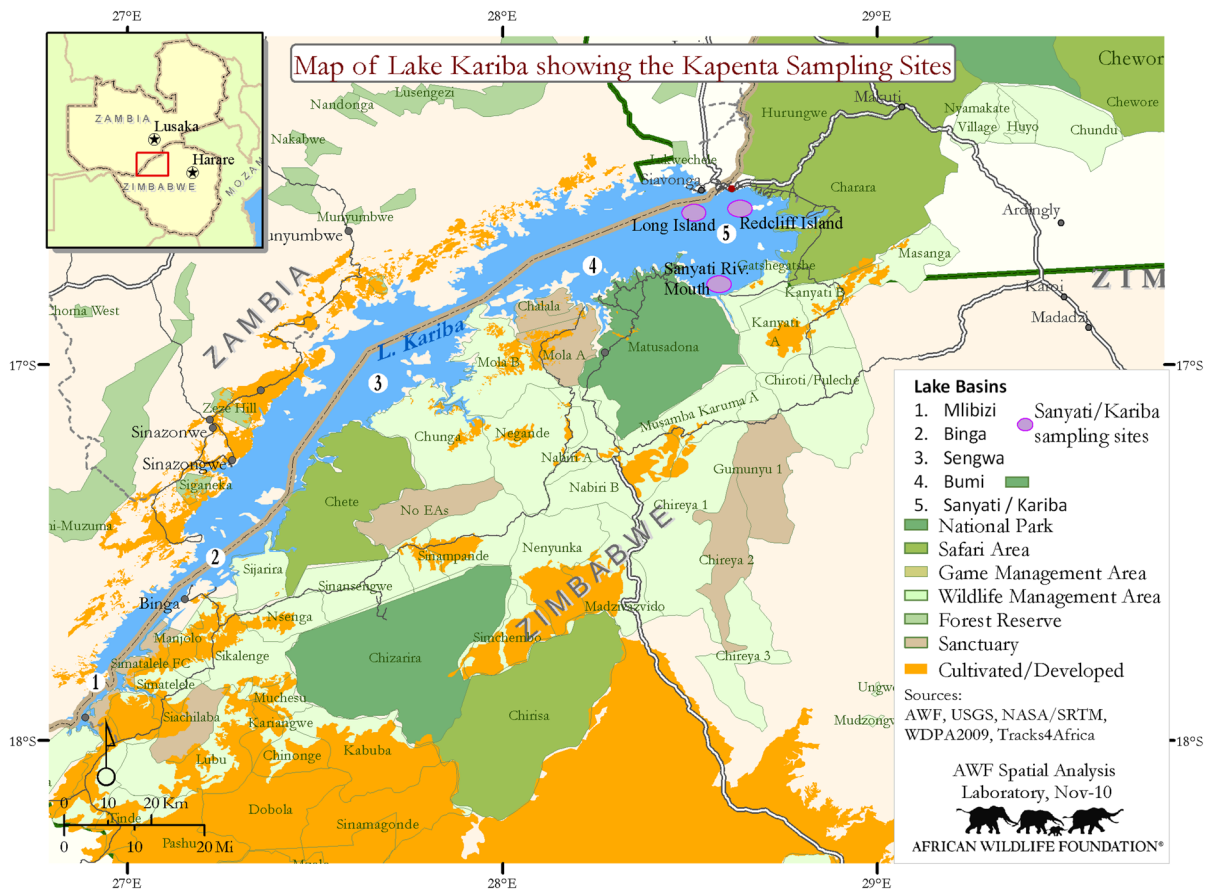
**Study site**

Lake Kariba's location stretches from the confluence of the Deka and Zambezi Rivers at the western end (18°04'S, 26°42'E) to the Kariba Gorge (16°31'S, 28°45'E) in the North-East, forming the natural border between Zambia and Zimbabwe (Fig. 1). The reservoir is about 280 km long and 40 km at its widest point with maximum and mean depths of 120 and 29 m, respectively (Balon & Coche, 1974). This reservoir, created in 1958, has a storage capacity of 185 billion m<sup>3</sup> of water and a surface area of 5580 km<sup>2</sup> making it the second largest dam in the world by volume.

The first attempt to introduce *L. miodon* was conducted in 1963 with limited success, and subsequent follow-up airlifts were conducted in 1967 and

1968, which resulted in a successful translocation (Balon & Coche, 1974). After these introductions, the first documented evidence of *L. miodon* in Lake Kariba was in the form of juvenile and adult clupeids that were found in the stomach contents of the African tigerfish *Hydrocynus vittatus* caught on 25 July 1969 at Sinazongwe, Zambia. By 1973, *L. miodon* occurred over the whole lake and commercial exploitation commenced in 1974, barely 5 years after its introduction (Balon & Coche, 1974).

The fish used in the study were sampled from the Sanyati Basin of Lake Kariba (Fig. 1) mainly using a small dip net that is a prototype of the large commercial dip nets used in Lake Kariba. The gear is a conical net attached to a circular hoop with a diameter of 2 m at the mouth end. The net had a depth of 7 m made of 8 mm mesh nylon and the lower 2 m cod end was lined with mosquito netting to retain very small fish. The net was lowered into the water column



**Fig. 1** Map of Lake Kariba showing the geographical context of the study sites

and hauled using a manual winch with a rope passing through an A-frame gantry mounted at the stern of the University Lake Kariba Research Station's research vessel. An alternative method used a 2-m-long conical plankton net with a 50-cm-diameter mouth opening, which was lowered to the substrate in the littoral zone, left static at the bottom (with mouth open) until the water calmed and shoals of juvenile kapenta appeared swimming in the area. The net was then pulled horizontally by hand to scoop targeted juvenile kapenta shoals and subsequently hauled vertically to the surface capturing juvenile kapenta that were unable to escape. In both methods, the fish were quickly transferred to large buckets that were pre-filled with lake water and aerated with electronic bubble aerators. The fish were transferred by speed boat to the station where they were transferred to the experimental tanks using fine mesh scoops and left to acclimatise before experiments commenced.

#### Daily food intake ration analyses

The daily ration ( $R_d$ ) was estimated from mean stomach contents and evacuation rate using the Bajkov (1935) formula as modified by Eggers (1979). In this method, daily ration is equated to the product of an instantaneous evacuation rate ( $E$ ) and mean stomach contents [ $\text{avg}(S_t)$ ] over a 24-h period as shown in the equation:

$$R_d = \text{avg}(S_t) \times E \times 24 \text{ h (modified Bajkov formula).}$$

The method assumes feeding and evacuation rates that follow a simple exponential model as recommended by Jobling (1981) for estimation of food consumption rates for species that feed on relatively small prey (Sainsbury, 1986; Jarre et al., 1991; Jarre-Teichmann, 1992). This assumption is considered to hold for *L. miodon*.

The parameters for input to the equation were determined separately. Average stomach contents [ $\text{avg}(S_t)$ ] were calculated on the basis of *L. miodon* stomach content variations measured during three 24-h feeding cycles in aquaria under experimental conditions. Temperature conditions in the aquaria during the experiments were kept in the range of 22.5–25°C. A total of 137 individual fish were processed during the three experiments. Individual fish mean length was in the range of 21–28 mm and

the mean weight was in the range of 0.07–0.28 g. The standard length and wet weight of each individual fish were measured in the laboratory to the nearest millimetre and 0.01 g, respectively, using a standard ruler and a sensitive microbalance. Thereafter, the fish were dissected to separate the stomach from the rest of the body. The stomach was blotted to remove any external moisture and subsequently weighed to get the full stomach weight ( $F_{\text{stomach weight}}$ ). All weight measurements were on a wet weight basis.

Each stomach was opened up and its contents were emptied into a glass Petri dish and the stomach was subsequently weighed to get the empty stomach weight ( $E_{\text{stomach weight}}$ ). The weight of stomach contents for each fish was then taken as the difference between the  $F_{\text{stomach weight}}$  and the  $E_{\text{stomach weight}}$  (Getachew, 1989; De Silva et al., 1996) as in the relationship:

$$S_{\text{content(mg)}} = F_{\text{stomach (mg)}} - E_{\text{stomach (mg)}}.$$

The determinations were made on the basis of diel feeding cycles monitored for *L. miodon* in experimental aquaria from which fish were serially sampled at 2-h intervals during a 24-h cycle, an interval selected to be consistent with an earlier one-off study on Lake Kariba by Paulsen (1994). This short-time interval also made it easier to satisfy the assumption of constant feeding over a time (Cochran & Adelman, 1982). In order to reduce the effect of fish size differences on the data (since daily ration is size specific), stomach content weights were expressed as a ratio to the fish weight, i.e. as milligrams per gram body weight ( $\text{mg g bw}^{-1}$ ) (Jenkins & Green, 1977; Palomares & Pauly, 1989; Allison et al., 1995). The fish bw was the fish wet weight [ $F_{\text{wet wt (mg)}}$ ] minus the weight of stomach contents [ $S_{\text{content wt (mg)}}$ ].

The instantaneous evacuation rate ( $E$ ) was calculated on the basis of gastric evacuation experiments conducted under laboratory conditions. The data obtained were analysed using the MAXIMS software, a computer programme for estimating the food consumption of fishes from daily stomach contents data and population parameters (Jarre et al., 1991; Richter et al., 1999).

#### Design of aquarium experiments to monitor feeding and gastric evacuation

To establish the average stomach contents of kapenta, two feeding experiments were conducted over two

consecutive years, the first in May 1999, and the second in February 2000. The timing was based on availability of large enough samples of 'live' kapenta after successful capture from the lake, and repetition was done to ascertain the general diel feeding pattern.

The first feeding experiment was carried out in five small glass tanks of the same size and capacity with dimensions of 49 cm long, 29 cm wide and 39 cm deep. The tanks were placed on a table surface in the laboratory approximately 1 m above ground and arranged in a row 10 cm from each other. The tanks were filled with water from the lake to a volume of 38.2 l and the water was subsequently inoculated with concentrated samples of 'live' planktonic organisms collected from the lake. Twelve specimens of *L. miodon* were stocked in each one of the tanks and left to acclimatise for a period of 7 days. The water in the tanks was continuously aerated using electronic bubble aerators. The medium was continuously recharged with planktonic organisms to guarantee fish feeding to satiation. Water temperature in the aquaria was monitored throughout the period (from the time of acclimatisation and during the experiment) and maintained in the range of 23–23.5°C. A total of 60 fish were processed.

The second feeding experiment was conducted in one asbestos tank with 30 individual fish. This tank was 118 cm long, 61 cm wide and 87 cm deep, and was filled with lake water to a volume of 205.3 l. The tank was continuously inoculated with concentrated samples of planktonic organisms from the lake. Water temperature was monitored throughout and maintained between 22.5 and 25°C.

There was no pre-treatment of fish prior to the commencement of both 24-h feeding experiments. The experiments were conducted on the assumption that the density of planktonic organisms was adequate for *L. miodon* to feed to satiation.

The third aquarium experiment was carried out to determine the GER of kapenta so that the food consumption rate could be estimated. Acclimatised fish were starved for more than 18 h before the tank was inoculated with planktonic food organisms. Concentrated planktonic food was administered into the tank at 1300 h. The fish were then left to feed to satiation for a period of 2 h after which the water with food organisms was drained from the tank and replaced with fresh, filtered lake water that contained no food. At 1500 h, a sub-sample of five fish was taken out for stomach content analysis using the method

described earlier. Similar sub-samples of fish were serially taken at 2-h intervals until empty stomachs started to be encountered (Olson & Mullen, 1986). A total of 47 specimens were processed.

#### Analysis of aquarium experiments

##### *Feeding experiments*

The data on stomach contents at different time intervals monitored over a continuous feeding cycle (i.e. the period during which both ingestion and evacuation alternate) under experimental conditions were analysed using the MAXIMS Model for estimating daily ration and food consumption rates for *L. miodon*. While this model incorporates the estimation of daily ration in three possible ways, only the approach of daily ration estimation from mean stomach contents and evacuation rate was used according to the modified Bajkov equation. This approach uses Model A of the software that assumes that there is one feeding period and a constant ingestion rate (Jarre et al., 1991). For the gastric evacuation experimental data, one feeding period was also assumed, but the partial model of MAXIMS was used that simultaneously estimates the daily ration and evacuation rate.

##### *Gastric evacuation experiment*

The weight of stomach contents measured at the different time intervals was plotted against time after feeding and the slope of the relationship was taken as the measure of the GER. The time taken to empty a full meal entirely or to reach the residual stomach content level ( $S_r$ ) was taken as the gastric evacuation time. The graphical plot for the determination of gastric evacuation was made using relative values of stomach content weight, i.e. expressed as a ratio to the fish weight ( $\text{mg g bw}^{-1}$ ). The slope of the regression of the logarithm of stomach contents plotted against time after feeding was taken as a measure of the evacuation rate (Elliott, 1972), and expressed as an absolute measure in units of  $\text{mg h}^{-1}$ .

#### Population food consumption versus zooplankton production

The population food consumption was estimated on the basis of reference abundance estimates for *L.*



*miodon* and zooplankton in Lake Kariba close to the time of the study (Masundire, 1991; Ngalande, 1995). The *L. miodon* abundance and biomass data used were from the results of hydroacoustic surveys conducted in January 1992, November 1993, January 1994 and July 1994 (Ngalande, 1995). These data are based on whole lake survey mean density (number of fish ha<sup>-1</sup>) and mean biomass per transect (kg ha<sup>-1</sup>) converted into overall mean biomass (Table 1). The population food consumption was then estimated as the product of the calculated daily ration and the biomass of *L. miodon*. Zooplankton production data were obtained from Masundire (1991).

## Results

### Food consumption pattern from the feeding experiments

In the first feeding experiment carried out in May 1999, the amount of stomach contents at different times during a 24-h cycle fluctuated, with alternating feeding and non-feeding intervals. The relative amount of stomach contents was ~33 mg g bw<sup>-1</sup> after the first 2-h feeding interval at dawn. The contents subsequently decreased sharply by 0800 h to ~6 mg g bw<sup>-1</sup>, signifying a fast evacuation rate. Thereafter, another feeding cycle commenced that culminated in a stomach content peak of ~30 mg g bw<sup>-1</sup> at 1200 h. This was followed by a non-feeding period when contents decreased to ~14 mg g bw<sup>-1</sup> by

1600 h. A new feeding cycle started resulting in a peak of ~33 mg g bw<sup>-1</sup> by 2000 h. From 2000 h, a non-feeding period followed and stomach contents decreased to a low of about 10 mg g bw<sup>-1</sup> by 0000 h (midnight) when a fourth feeding period started that resulted in a peak of ~42 mg g bw<sup>-1</sup> by dawn the following morning. The mean stomach contents throughout the 24-h experiment period was 23.05 ± 11.25 mg g bw<sup>-1</sup>.

Analysis of these data using Model A of MAXIMS resulted in an evacuation rate of 0.159 and a daily ration of 88.09 mg g bw<sup>-1</sup> and when this evacuation rate was used in the modified Bajkov formula, it yielded a daily ration of 87.95 mg g bw<sup>-1</sup> (Table 2).

In the second feeding experiment carried out in February 2000, fish with fully distended stomachs had nearly 30 mg of food in the beginning of the serial sampling at 1000 h. After 4 h, the contents decreased to ~5 mg and remained more or less constant until 2000 h. This was followed by a slight decrease in contents to just below 1 mg in the early hours of the morning (0200 h) and this subsequently increased to between 1 and 2 mg before dawn (Fig. 2). An exponential plot of the relative stomach contents (calculated as a ratio to fish weight) showed a decrease from a maximum of ~60 mg g bw<sup>-1</sup> at the beginning when fish stomachs were full to ~5 mg g bw<sup>-1</sup> at 0600 h the following morning (Fig. 3).

Based on this feeding pattern, a GER of 0.167 and a daily ration of 95.57 mg g bw<sup>-1</sup> was found using Model A of MAXIMS. When this evacuation rate was

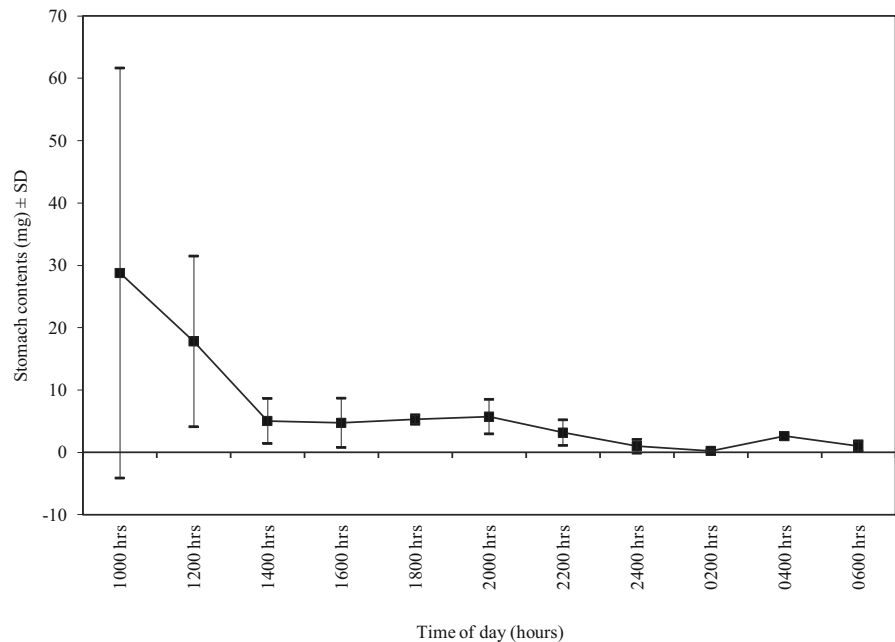
**Table 1** Data on *L. miodon* mean density and mean biomass in Lake Kariba

Transects	Mean density (fish ha <sup>-1</sup> )	Mean indiv. fish wt (g)	Mean biomass (kg ha <sup>-1</sup> )
1	35,815	1.00	35.8
2	50,347	0.52	26.2
3	49,057	0.99	48.6
4	56,527	0.59	33.4
5	58,180	0.99	57.6
6	51,667	0.97	50.1
7	63,203	0.76	48
8	44,097	0.62	27.3
9	28,292	1.14	32.3
10	46,062	1.20	55.3
11	20,990	1.04	21.8
12	25,162	0.99	24.9
Mean	44,117 ± 13,663	0.90 ± 0.22	38.4 ± 12.7

Adopted and modified from Ngalande (1995)

**Table 2** Summary of daily ration for *L. miodon* determined under different times and experimental conditions

Parameters	Food consumption in first experiment	Food consumption in second experiment	Gastric evacuation experiment
Evacuation	0.159	0.167	0.176
Start time (h)	1800	1200	1500
End time (h)	2400	0200	2300
Daily ration	88.01	95.57	99.00
Bajkov output	87.95	95.83	98.81
Daily ration			

**Fig. 2** Changes in the weight of stomach contents in *L. miodon* during a diurnal feeding cycle under experimental conditions ( $N = 30$ )

used in the modified Bajkov formula, it gave a daily ration of  $95.83 \text{ mg g bw}^{-1}$  (Table 2).

#### Gastric evacuation pattern

Fish fed to satiation had  $\sim 62 \text{ mg g bw}^{-1}$  in the beginning of the serial sampling when all the food in the aquarium had been removed (Fig. 4). Stomach contents decreased to  $\sim 23 \text{ mg g bw}^{-1}$  within the first hour of starvation. Thereafter, the contents decreased at a much slower rate to about  $11 \text{ mg g bw}^{-1}$  after a further 3 h. After a further 4 h, the contents decreased to  $\sim 2\text{--}3 \text{ mg g bw}^{-1}$  (Fig. 4). At this point, the stomachs were generally empty, and this level was considered to be the *residual stomach content* that is

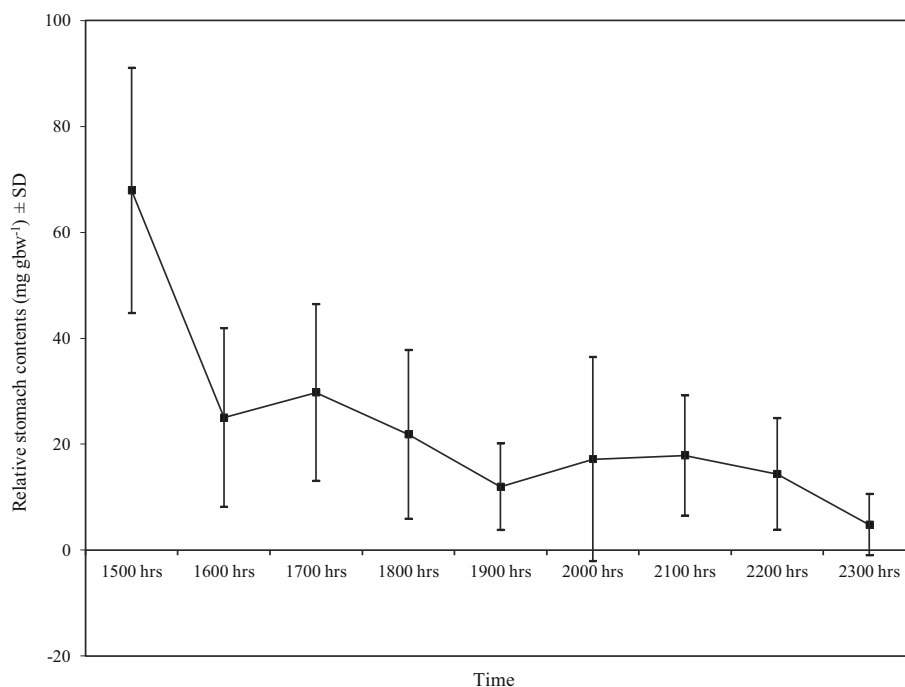
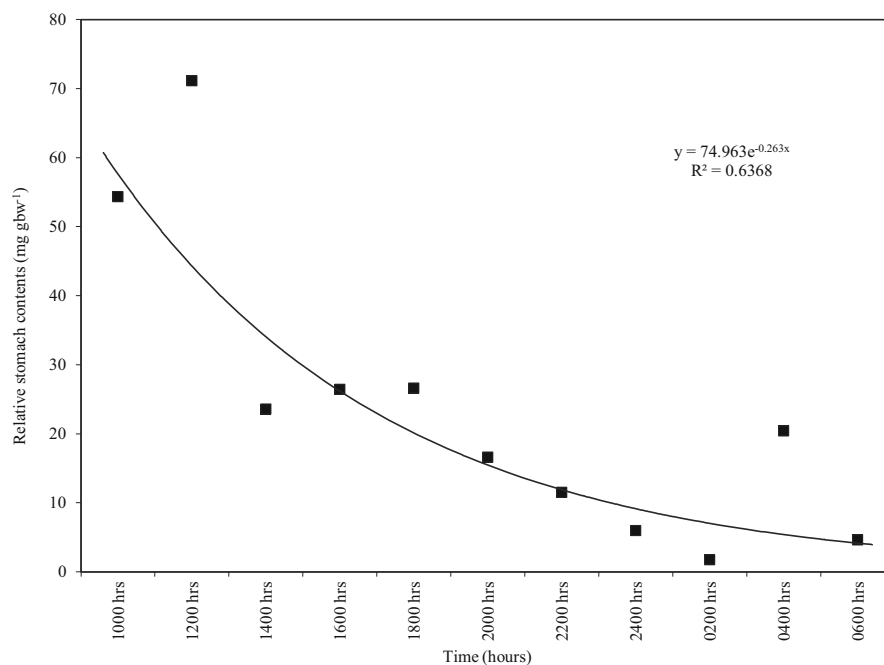
always present in the stomachs. The same data presented as an exponential plot of the relative stomach contents and the respective log-transformed data are shown in Fig. 5.

When the data were analysed using the partial model of MAXIMS, an evacuation rate of 0.176 and daily ration of  $99.00 \text{ mg g bw}^{-1}$  was found. This evacuation rate gave a daily ration of  $98.81 \text{ mg g bw}^{-1}$  when used in the Bajkov equation (Table 2).

#### Estimation of population food consumption

The food consumption rate for *L. miodon* in Lake Kariba was calculated on the basis of the average reservoir area at the time of the study and the mean

**Fig. 3** Changes in the relative amount of stomach contents ( $\text{mg g bw}^{-1}$ ) of *L. miodon* under experimental conditions

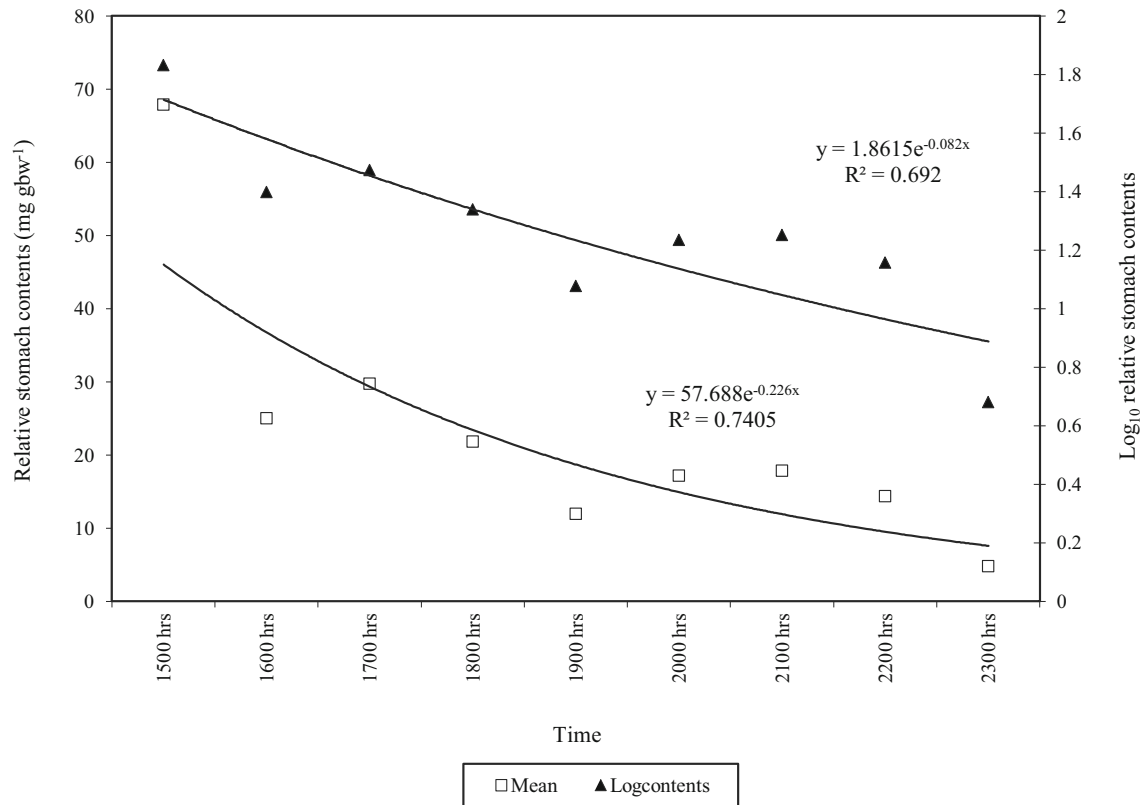


**Fig. 4** Gastric evacuation pattern shown by *L. miodon* under experimental conditions in aquaria ( $N = 47$ )

biomass of *L. miodon* from hydroacoustic surveys (Table 1). The calculated total standing biomass for *L. miodon* in the whole lake during the study period was 20,181 metric tonnes, which still remains comparable

to the September 2014 estimated average standing biomass of  $16,277 \pm 9,730$  tonnes (Mafuca, 2014).

The daily ration determined in aquarium feeding experiments was in the range of  $88.0\text{--}99.0 \text{ mg g bw}^{-1}$ .



**Fig. 5** Exponential plot of gastric evacuation rate and log-transformed gastric evacuation rate for *L. miodon* under experimental conditions

These values were used to calculate the population food consumption rate. The product of the *L. miodon* biomass and daily ration yielded a population food consumption estimate in the range of 1,776–1,998 tonnes day<sup>-1</sup>.

### Zooplankton production

Historical zooplankton production estimates were used and these approximated zooplankton production to be 3 mg dry weight m<sup>-3</sup> day<sup>-1</sup> (Masundire, 1991). Based on the literature (Post & Lee, 1996), this dry weight value was assumed to be 20% of wet weight, and using a lake mean depth of 29 m and approximate surface area of 5,250 km<sup>2</sup> at the time of the study, the approximate total zooplankton production was 2,284 tonnes day<sup>-1</sup>. When this production value is compared to the estimated average food consumption of *L. miodon* of 1,887 tonnes day<sup>-1</sup>, it is evident that *L. miodon* are extremely efficient grazers as they

consume up to 83% of the zooplankton produced in a day. This relationship though is only roughly approximate, and more long-term studies are needed to assess feeding among a wider range of kapenta age and size classes, as size is a key factor in determining food consumption.

### Discussion

Only one previous study on the food consumption rates of *L. miodon* has been carried out on Lake Kariba (Paulsen, 1994), and a few others such as Sarvala et al. (2002) and de Iongh et al. (1983) in the other natural lakes and reservoirs it occurs. Paulsen (1994) estimated the food consumption of *L. miodon in situ* in Lake Kariba on the basis of samples collected in the winter of 1992/1993 and found it to be in the range from 5.8 to 8.7% of fresh kapenta bw day<sup>-1</sup>. The results obtained with different methods were encouragingly consistent as in the current study daily ration

estimated under experimental conditions was 8.8–9.9% of fresh bw day<sup>-1</sup>. The slight difference from Paulsen's estimates is most probably a result of the converse relationship between daily ration and increasing fish size since specimens used in his study were larger than those used in this study. The daily ration is further likely influenced by temporal variations and methods used. In general, if the parameters vary, it is unlikely to get similar results from different food consumption studies (Talbot et al., 1984). Food consumption rate is affected by numerous factors, predator size, prey type and temperature accounting for most of the variance (Temming & Anderson, 1992; Bromley, 1994).

The difference between the present results and earlier data can be attributed to the variation between the experimental and in situ settings for data gathering, seasonality, and variation in size between fish specimens used in the experiment and those sampled from the field. Fish used in this study had lengths in the range of 19–33 mm and those used by Paulsen were larger, in the range of 39–98 mm. The difference in daily ration could be because as fish grow, the weight of food they consume relative to their bw decreases although the absolute weight consumed increases (Pauly, 1989; Wootton, 1990).

Comparable studies have been conducted in Lake Kariba on the cichlids *Tilapia rendalli* (Boulenger, 1897) and *Sargochromis codringtonii* (Boulenger, 1908) under comparable temperature regimes (Caulton, 1977; Moyo, 1994). *T. rendalli* during summer consumed an average of 16.4% of its dry weight day<sup>-1</sup> (Caulton, 1977) while *S. codringtonii* consumed 13.96% of its dry weight day<sup>-1</sup> (Moyo, 1994). These consumption rates, together with that of *L. miodon* found in this study, are in the range of 4.1–36% of bw day<sup>-1</sup> known for tropical fishes (Pandian & Vivekanandan, 1985). This is, in general, more than consumption rates of temperate fishes which are in the range of 1.8–17.3% of bw day<sup>-1</sup>. Lake Kariba is in a subtropical climatic zone, hence the consumption rates are realistic when compared to previous data on other teleost fishes in the same temperature zones.

The evacuation rate obtained in this study is lower than the 0.59–0.96 h<sup>-1</sup> rate obtained in 1992/1993 from field sampling by Paulsen (1994), an expected outcome due to the high incidence of empty stomachs in most of Paulsen's field samples. In contrast, during this study, the fish in aquaria were fed to satiation and

none of the fish had empty stomachs except those that maintained a certain residual stomach content. The evacuation rate range of 0.15–0.18 h<sup>-1</sup> is comparable to other species living under similar sub-tropical and tropical environments. For instance, *Rhamphochromis longiceps* (Günther, 1864) in Lake Malawi, though not a clupeid, had evacuation rates of 0.18–0.22 h<sup>-1</sup> in August 1993, and this tended to be much higher during October when the temperatures are warmer (Allison et al., 1995). This temporal change in evacuation rate for the same species agrees with the observation that estimates of the rate of consumption made over a single period of 24 h should be treated with caution since there are considerable day-to-day variations in the rate (Smagula & Adelman, 1982). It is thus desirable for consumption rate determinations to be based on relatively long-term sampling. The influence of seasonality renders it inevitable that comparisons of studies done at different times usually show differences (Weliange et al., 2006). The magnitude of these differences depends on the variability of other abiotic factors in the ecosystem that have a bearing on the biotic factors that affect feeding rate.

Results by Allison et al. (1995) from *R. longiceps* in Lake Malawi probably demonstrate the influence of water temperature on changes in rate of consumption. While similar influence holds for most natural populations, the causal effect of temperature may still be confounded with the other abiotic factors and especially changes in availability of food (Worobec, 1984). The influence of other abiotic factors and food availability is likely to be the cause for differences between the two investigations on *L. miodon* in Lake Kariba. This is corroborated, for example, by studies on the walleye, *Stizostedion vitreum vitreum*, where the consumption rate increased from 1% in June, to 2% in July and 3% in August and September (Swenson & Smith, 1973) and yellow perch, *Perca flavescens*, where daily ration variation was attributed to interacting effects of temperature, food availability and gonad development (Nakashima & Leggett, 1978). A study on the Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758) from Lake Awasa in Ethiopia showed a daily ration of 14.3% of bw (Getachew, 1989), but the temperature conditions were not specified.

The population food consumption rate estimated from experimentally determined daily ration for *L. miodon* compares well to that estimated by Paulsen

(1994). This is so regardless of differences in the input parameter of population standing biomass and additional differences for other input variables like lake surface area. The maximum possible consumption of 1,998 tonnes out of a daily plankton production of 2,284 tonnes (87.5% of production) points to seemingly unsustainably efficient grazing on zooplankton by *L. miodon*. However, this grazing rate compares very well with earlier assessments by Paulsen (1994) that estimated *L. miodon* to consume 2,100 tonnes out of a daily plankton production of 2,400 tonnes. The fact that the experimental results of daily ration are comparable to earlier findings from field sampling gives credence to the results, notwithstanding the known day-to-day variability in consumption rate (Smagula & Adelman, 1982). We caution that this high food consumption is likely exaggerated by the relatively smaller specimens of fish that were used in the feeding experiment that have a higher consumption rate which, when applied to the lake wide *L. miodon* population, will overestimate the population food consumption. A more accurate and realistic estimate would require creating a regression between food consumption rate and fish size, and applying this to the size distribution of the population with a result likely to show a lower, more realistic utilisation rate of zooplankton production by *L. miodon*. Thus, although the grazing rates determined in this study should only be considered as the first rough approximations, they still allow us to confidently conclude that the predation on zooplankton by *L. miodon* seems to be very efficient in Kariba, in contrast to at least Lake Tanganyika where *L. miodon* is not the major planktivore, and perhaps also Lake Kivu. As such, this is a good starting point to estimate the total population food consumption in the lake.

The calculations of daily ration and total population food consumption in Lake Kariba were based on values from earlier studies on zooplankton biomass estimates. Moreover, because of the relatively reliable estimated values for lake surface area and depth, we feel that the findings provide a useful guide to the food consumption rate of *L. miodon* in Lake Kariba. If the grazing rate of about 83% is used as a guideline, it should be possible to estimate the potential standing biomass of *L. miodon* that the lake can sustain under a known zooplankton standing biomass regime. Considering that Lake Kariba is an artificial reservoir, the day to day and seasonal variability of these input

parameters will always be very high. The future research should transcend spatial and temporal differences and thus produce a realistic seasonal food consumption estimate for the *L. miodon* population in Lake Kariba, which would provide an accurate tool for adaptive fisheries management.

**Acknowledgments** The corresponding author would like to thank the University of Zimbabwe and technical staff at the Lake Kariba Research Station for the assistance in the field and experimental laboratory work during this study. It is also gratefully acknowledged that Jimmiel Mandima's participation in the 4th European Large Lakes Symposium was sponsored by his employer, the African Wildlife Foundation, and Jouko Sarvala's participation was supported by the Pyhäjärvi Protection Fund.

## References

- Allison, E. H., A. B. Thompson, B. P. Ngatunga & K. Irvine, 1995. The diet and food consumption rates of the offshore fish. In Menz, A. (ed.). The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa. Scientific Report of the UK/SADC Pelagic Fish Resources Assessment Project, Natural Resources Institutes. Overseas Development Administration: 233–278.
- Bajkov, A. D., 1935. How to estimate the daily food consumption of fish under natural conditions. Transactions of the American Fisheries Society 65: 288–289.
- Balon, E. K. & A. G. Coche, 1974. Lake Kariba: a tropical man-made ecosystem in Central Africa. Monograph of Biology 24: 1–767.
- Begg, G. W., 1974. Investigations into the Biology and Status of the Tanganyika Sardine, *Limnothrissa miodon*, Boulenger in Lake Kariba, Rhodesia. L.K.F.R.I. Project Report 17, 151 pp.
- Bromley, P. J., 1987. The effects of food type, meal size and body weight on digestion and gastric evacuation in turbot, *Scophthalmus maximus* L. Journal of Fish Biology 30: 501–512.
- Bromley, P. J., 1994. The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. Reviews in Fish Biology and Fisheries 4: 36–66.
- Caulton, M. S., 1977. A quantitative assessment of the daily ingestion of *Panicum repens* L. by *Tilapia rendalli* Boulenger (Cichlidae) in Lake Kariba. Transactions of Rhodesian Scientific Association 58(6): 38–42.
- Cochran, P. A. & I. R. Adelman, 1982. Seasonal aspects of daily ration and diet of largemouth bass, *Micropterus salmoides*, with an evaluation of gastric evacuation rates. Environmental Biology of Fishes 7: 265–275.
- 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.
- De Silva, S. S., U. S. Amarasinghe & N. D. N. S. Wijegoonawardena, 1996. Diel feeding patterns and daily ration of cyprinid species in the wild determined using an iterative

- method, MAXIMS. *Journal of Fish Biology* 49: 1153–1162.
- Downing, J. A., C. Plante & S. Lalonde, 1990. Fish production correlated with primary productivity, not the morphoedaphic index. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 1929–1936.
- Eggers, D. M., 1979. Comments on some recent methods for estimating food consumption by fish. *Journal of the Fisheries Research Board of Canada* 36: 1020.
- Elliott, J. M., 1972. Rates of gastric evacuation in brown trout, *Salmo trutta*. *Freshwater Biology* 2: 1–18.
- Elliott, J. M. & L. Persson, 1978. The estimation of daily rates of food consumption for fish. *Journal of Animal Ecology* 47: 977–991.
- Getachew, T., 1989. Stomach pH, feeding rhythm and ingestion rate in *Oreochromis niloticus* L. (Pisces: Cichlidae) in Lake Awasa, Ethiopia. *Hydrobiologia* 174: 43–48.
- Hecky, R. E., 1991. The pelagic ecosystem. In Coulter, G. W. (ed.), *Lake Tanganyika and Its Life*. Oxford University Press, Oxford: 90–110.
- Jarre-Teichmann, A., 1992. MAXIMS – A Computer Program for Estimating the Food Consumption of Fish. International Council for the Exploration of the Sea.
- Jarre, A., M. C. Palomares, M. L. Soriano, V. C. Sambilay (Jr) & D. Pauly, 1991. Some new analytical and comparative methods for estimating the food consumption of fish. ICES Marine Science Symposium 193: 99–108.
- Jenkins, B. W. & J. M. Green, 1977. A critique of field methodology for determining fish feeding periodicity. *Environmental Biology of Fishes* 1: 209–214.
- Jobling, M., 1981. Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. *Journal of Fish Biology* 19: 245–257.
- Jobling, M., 1986. Mythical models of gastric emptying and implications for food consumption studies. *Environmental Biology of Fishes* 16: 35–50.
- Mafuca, J. M., 2014. Preliminary Results of the Hydroacoustic Survey Conducted on Lake Kariba. Report/Rapport: SF-FAO/2014/33. September 2014. FAO-SmartFish Programme of the Indian Ocean Commission. Ebene.
- Mandima, J. J., 1999. The food and feeding behaviour of kapenta, *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, M. P., F. Darchambeau, M. Isumbusho & J. P. Descy, 2011. Diet overlap between the newly introduced *Lamprichthys tanganicus* and the Tanganyika sardine in Lake Kivu, Eastern Africa. *Hydrobiologia* 675: 75–86.
- Masundire, H. M., 1991. Bionomics and production of zooplankton and its relevance to the pelagic fishery in Lake Kariba. D.Phil. Thesis, University of Zimbabwe, 281 p.
- Moyo, N. A. G., 1994. The biology of *Sargochromis codringtonii* in Lake Kariba, Zimbabwe. PhD Thesis, University of Waterloo, Canada, 262 pp.
- Nakashima, B. S. & W. C. Leggett, 1978. Daily ration of yellow perch (*Perca flavescens*) from Lake Memphremagog, Quebec–Vermont, with a comparison of methods for in situ determinations. *Journal of the Fisheries Research Board of Canada* 35: 1597–1603.
- Ngalande, P., 1995. Assessment of the Tanganyika clupeid, *Limnothrissa miodon*, in Lake Kariba by hydroacoustics. M.Phil. Thesis, University of Bergen, Norway, 60 p.
- Olson, R. J. & A. J. Mullen, 1986. Recent developments for making gastric evacuation and daily ration determinations. *Environmental Biology of Fishes* 16: 183–191.
- Palomares, M. L. & D. Pauly, 1989. A multiple regression model for predicting the food consumption of marine fish populations. *Australian Journal of Marine Freshwater Research* 40: 259–273.
- Pandian, T. J. & E. Vivekanandan, 1985. Energetics of feeding and digestion. In Tyler, P. & P. Calow (eds), *Fish Energetics*. Croom Helm, London: 99–124.
- Paulsen, H., 1994. The Feeding Habits of Kapenta, *Limnothrissa miodon* in Lake Kariba. Zambia/Zimbabwe SADC Fisheries Project Report No. 30.
- Pauly, D., 1989. Food consumption by tropical and temperate fish populations: some generalisations. *Journal of Fish Biology* 35(Suppl. A): 11–120.
- Pennington, M., 1985. Estimating the average food consumption by fish in the field from stomach contents data. *Dana* 5: 81–86.
- Persson, L., 1984. Food evacuation and models for multiple meals in fishes. *Environmental Biology of Fishes* 10: 305–309.
- Persson, L., 1986. Patterns of food evacuation in fishes: a critical review. *Environmental Biology of Fishes* 16: 51–58.
- Ploskey, G. R. & R. M. Jenkins, 1982. Biomass model of reservoir fish and fish–food interactions, with implications for management. *North American Journal of Fisheries Management* 2: 195–221.
- Post, J. R. & J. A. Lee, 1996. Metabolic ontogeny of teleost fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 910–923.
- Richter, H., U. Focken & B. Klaus, 1999. A review of the fish feeding model MAXIMS. *Ecological Modelling* 120: 47–64.
- Ruffi, H. & D. W. Chapman, 1976. Preliminary Analysis of Zooplankton Sampling and Estimates of Fish Abundance in Lake Tanganyika in October 1975. United Nations Food and Agriculture Organisation Report. FI: DP/URT/71/012/31, 14 p.
- Sainsbury, K. J., 1986. Estimation of food consumption from field observations of fish feeding cycles. *Journal of Fish Biology* 29: 23–36.
- Sarvala, J., M. Tarvainen, K. Salonen & H. Mölsä, 2002. Pelagic food web as the basis of fisheries in Lake Tanganyika: a bioenergetic modeling analysis. *Aquatic Ecosystem Health and Management* 5: 283–292.
- Smagula, C. M. & I. R. Adelman, 1982. Day to day variation in food consumption by largemouth bass. *Transactions of the American Fisheries Society* 111: 543–548.
- Swenson, W. A. & L. L. Smith Jr., 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada* 30: 1327–1336.
- Talbot, C., P. J. Higgins & A. M. Shanks, 1984. Effects of pre- and prandial starvation on meal size and evacuation rate of juvenile Atlantic salmon, *Salmo salar*. *Journal of Fish Biology* 25: 551–560.

- Temming, A. & N. G. Anderson, 1992. Modelling Gastric Evacuation in Cod. ICES CM 1992/G 61, 7 pp.
- Thorpe, J. E., 1977. Daily ration of adult perch, *Perca fluviatilis*, during summer in Loch Leven, Scotland. *Journal of Fish Biology* 11: 55–68.
- Tseitlin, V. B., 1980. Duration of gastric digestion in fishes. *Marine Ecology Program Series* 2: 277–280.
- Weliange, W. S., U. S. Amarasinghe, J. Moreau & M. C. Villanueva, 2006. Diel feeding periodicity, daily ration and relative food consumption in some fish populations in three reservoirs of Sri Lanka. *Aquatic Living Resources* 19: 229–237.
- Wootton, R. J., 1990. *Ecology of Teleost Fishes*. Chapman and Hall, London: 404 pp.
- Worobec, M. N., 1984. Field estimates of the daily ration of winter flounder *Pseudopleuronectes americanus* (Walbaum) in a southern New England salt marsh. *Journal of Experimental Marine Biology and Ecology* 77: 183–196.