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# PELAGIC FISH STOCKS OF LAKE TANGANYIKA: BIOLOGY AND EXPLOITATION

by

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## PREFACE

The Research for the Management of the Fisheries on Lake Tanganyika Project (Lake Tanganyika Research) became fully operational in January 1992. It is executed by the Food and Agriculture organization of the United Nations (FAO) and funded by the Finnish International Developmental Agency (FINNIDA) and the Arab Gulf Programme for United Nations Development Organizations (AGFUND).

This project aims at the determination of the biological basis for fish production on Lake Tanganyika, in order to permit the formulation of a coherent lake–wide fisheries management policy for the four riparian States (Burundi, Tanzania, Zaïre and Zambia).

Particular attention will be also given to the reinforcement of the skills and physical facilities of the fisheries research units in all four beneficiary countries as well as to the build-up of effective coordination mechanisms to ensure full collaboration between the Governments concerned.

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# 1. INTRODUCTION

This report is based on the compilation and processing of commercial fish catch data collected from July 1993 to December 1995 at various localities around Lake Tanganyika.

In the past, research work on the main commercial pelagic fish was carried out for different time periods and with varied sampling strategies. The results are difficult to compare and there is a lack of data about the biology and exploitation of the major stocks in different areas of the lake. A comprehensive review of the available knowledge of Lake Tanganyika’s ecosystem is given by Coulter (1991)

The aim of the present work is to estimate some of the vital statistics of the most important pelagic commercial species, the clupeids, *Stolothrissa tanganicae* and *Limnothrissa miodon,* and the centropomid, *Lates stappersii.* Differences between lake areas in biology and exploitation rates of the three species were also evaluated.

The results given here need to be compared and combined with further lakewide data (i.e. from lakewide scientific cruises) in order to establish a valid picture of the behaviour of the stocks of these species.

## 2. MATERIAL AND METHODS

### 2.1 Data collection

The collection of fish data from various areas around the lake (Fig. 1) has been carried out following standardized procedures (Aro, 1993; Mannini, 1993). Fish were sampled from commercial fish catches. The gears used target the pelagic fish stocks. Thus in the northern sector of the lake (Bujumbura, Uvira and Karonda) samples came from the artisanal liftnet fishery, and in the Kigoma area from both the industrial (purse seine) and artisanal fishery. In the western sector (Kalemie and Moba), catches from the liftnet fishery were sampled. In the south (Kipili and Mpulungu) the beach seine fishery was included for fish collection as this gear efficiently catches small pelagics during some phases of their life cycle. Fish were also sampled from the industrial purse seine fishery and from the minor liftnet and chiromilla fisheries.

Weekly sampling was carried out during each lunar fishing season. Monthly samples were taken onboard purse seiners in Tanzania and Zambia during the whole of the period of study.

Total length (TL, mm) and stage of sexual maturity (Aro, 1993) were recorded from length stratified subsamples throughout the study. From March 1994 individual body weight (W, g), gonadal weight (g) and, in case of *L. stappersii*, stomach contents were collected. The stomachs were preserved in 10% formalin and later prey were identified as precisely as possible (Mannini, 1994). In addition some stomachs were collected during scientific cruises.

### 2.2 Data analysis

Von Bertalanffy Growth Function (VBGF) coefficients (von Bertalanffy, 1938) have been estimated for all three species from the main study areas. The ELEFAN I method (Pauly and David, 1981; Pauly, 1987) and Shepherd Length Composition Analysis, SLCA, (Shepherd, 1987) were used in coefficient estimator. To facilitate the comparison of growth, phi prime values, Phi', (Pauly and Munro, 1984) were calculated. Not all data sets were used. Some were discarded because they were unsuitable for length-based analysis (i.e. lack of evidence of modal class progression). When necessary length was converted to relative age using the inverse von Bertalanffy growth equation (Sparre and Venema, 1992)

Annual total mortality rates (Z $yr^{-1}$) and natural mortality (M $yr^{-1}$) rates were estimated by using different methods. The value of M obtained from Pauly's equation (Pauly, 1980) was reduced by 20% for both clupeid species following the suggestion of Pauly in the case of small schooling pelagics (Pauly, 1983a) . In addition to the estimation of a constant natural mortality, M values for different life stages were calculated using the size-dependent equation for M developed by Peterson and Wroblewski (1984) . The model is based on the information from size spectra of suspended particles in the sea where M for a given size is predicted to be a power function of the mean wet weight.

One of the most important assumptions of the length converted catch curve (LCCC) analysis (Pauly, 1983b, 1984a and 1984b) to estimate Z is that the sample should, as far as possible, be representative of the stock. Therefore, for each species LCCC was carried out from fish collected during the lakewide combined hydroacoustic and mid-water trawling surveys of June and November 1995 (Aro *et al.,* 1995; Aro, 1996; Mannini and Aro, 1995).

The gonado-somatic index (GSI = gonadal weight/total body weigh x 100) was calculated to determine the seasonal pattern of gonadal development. Mean length at sexual maturity was estimated by fitting a logistic curve to the adjusted proportion (P) of sexually mature individuals by linear regression (King, 1995).

The logistic curve took the form:

$$P = l/(l+\exp[b(TL-L_m)])$$

where $L_m$ (Lm = a/-b) is the mean length at sexual maturity (the length at which 50% of fish are mature) and a and b are constants.

Independent estimates of $L_m$ were also obtained by the optimal $L_m$ model proposed by Roff (1986, 1992) which is based on the von Bertalanffy coefficient, K, and M. For this model, M derived from the Pauly equation (1980, 1983a) was used.

A seasonal recruitment pattern was obtained, assuming the proportion of recruits in monthly samples to be representative of recruitment to the fishing grounds. Further, approximations of recruitment periods were made by backward projection, as defined by the VBGF, onto the relative time axis of L/F samples (Pauly, 1983a, 1987)

Stomach contents, preserved in 10% formalin, were analyzed, for each prey category, by percentage, by weight and number and by frequency of occurrence (Hylsop, 1980)

Liftnet selectivity was estimated by performing covered codend experiments during November 1994 in the Kigoma area. The codend of the liftnet was covered with mosquito netting. Assuming selection was similar to a trawl net, the gear selection ogive and the length at first capture (the length at which a fish has 50% probability of being retained in the net, $L_c$) for *S. tanganicae* were obtained using the method given in Sparre and Venema (1992) . Further, $L_c$ was also estimated from each available L/F distribution by backward extrapolation of the lengthconverted catch curve (Pauly, 1984a, 1987) . It was not possible to obtain gear selection ogives by selectivity experiments for *L. miodon* and *L. stappersii* due to the low occurrence of small individuals in the Kigoma liftnet fishing area. The body shapes of *L. miodon* and *L. stappersii* are very similar to that of *S. tanganicae* and it may be assumed that liftnet selectivity for all three species is the same. However, catch curve analysis was used to estimate $L_c$ values for *L. miodon* and *L. stappersii.*

The following geomorphological terminology, after Tiercelin and Mondeguer (1991), has been used, unless otherwise indicated, throughout this study. Seven sub-basins have been identified by these authors:

1) Bujumbura sub-basin (70km long, 25km wide, 350m max. depth). In the text also referred to as the northern end or north of the lake.

2) Rumonge sub-basin (80km long, 35km wide, 1150m max. depth). In the text also referred to as the Karonda area.

3) Kigoma sub-basin (170km long, 80km wide, 1310m max. depth).

4) Kalemie sub-basin (130km long, 40km wide, 800m max. depth).

5) Moba sub-basin (70km long, 50km wide, 600m max. depth).

6) East-Marungu sub-basin (120km long, 30km wide, 1470m max. depth) . In the text also referred to as the Kipili area.

7) Mpulungu sub-basin (100km long, 25km wide, 800m max depth). In the text also referred to as the southern end or south.

The terms inshore and offshore or pelagic can cause some ambiguity. The continental shelf is very limited in the lake due to the very steep shoreline. Throughout the text coastal areas with <200m bottom depth are referred to as inshore areas, while areas 200m are considered to be offshore, pelagic and open water irrespective of their distance from the coast.

## 3. RESULTS

Results are given by species and by sampled areas. Functional relationships between total length (TL), standard length (SL), fork length (FL) and weight (W) are given in Table 1.

### 3.1 *Stolothrissa tanganicae*

### 3.1.1 Distribution and exploitation

Only the liftnet fishery exploited the *S. tanganicae* stock in northern areas of the lake, but the catch composition differed between the northern end (Bujumbura and Uvira) and Karonda. In the former area immature fish made a greater contribution to the catch. In the Kigoma sub-basin *S. tanganicae* was the main target of liftnets, yet the juveniles were better represented in the purse seine catches (Fig. 2). As the mesh size of liftnets and purse seines were similar (stretched mesh of 8-10mm and 10mm respectively), the appearance of juveniles in the purse seine fishery was probably due to operation of the seine in offshore nursery areas, outside the usual range of the liftnet fishery (5km radius) . These nursery areas were identified during lakewide mid-water trawling surveys with R/V Tanganyika Explorer (Aro *et al.,* in preparation).

In the south of the lake juveniles of *S. tanganicae* were caught by beach seines but not by purse seines (Fig. 2). Comparison with the catch composition of others areas is difficult because of the use of unselective beach seine nets (mosquito netting is used to cover the codend) in the Mpulungu area. Currently S. *tanganicae* is not the main exploited species in the south but a supplementary species whose catches are not constant (Pearce, 1995; Plisnier, 1995)

In Kipili waters the numeric abundance of *S. tanganicae* in the liftnet sampled catch was lower (22% of the total for both species) than that of *L. miodon* and it was negligible (0.9%) in the Mpulungu liftnet catch. In the beach seine catch the numeric abundance of *S. tanganicae* was 28% of the total for both clupeid species at Kipili and only 11% at Mpulungu.

Figure 3 shows the size distribution of the entire (lakewide) *S. tanganicae* population as observed from two surveys. In June 1995 the juveniles, mainly found in offshore water, made up the bulk of the population. By November they had been recruited to the adult stock.

### 3.1.2 Gear selectivity

From covered codend experiments in Kigoma waters, $L_0$ **=** 56mm was estimated (Fig. 4). The liftnet gear used on Lake Tanganyika is similar throughout and therefore the liftnet selection ogive (Fig. 4) can reasonably be regarded as typical for *S. tanganicae* (excluding the northern end where L~ should be smaller, see Bujumbura and Uvira L/F distribution in Fig. 2) . **L~** estimates made from the catch curve of the various L/F distributions are given in Table 2. The mean length at first capture for all areas was the same as that obtained through the selectivity experiments.

### 3.1.3 Growth and mortality

Growth coefficients of *S. tanganicae* estimated from data sets were similar (coefficient of variation, CV, of mean phi' was 0.97) with the exception of those from Mpulungu data (Table 2). Overall, the growth of *S. tanganicae,* during the study period, was the same throughout the lake. Longevity was estimated at 1.5 yr. Total and natural mortality rates derived by different methods are given in Table 2. Mean estimates of Z ranged from 5.0 to 5.8 $yr^{-1}$. Total mortality was also estimated from cruise survey data and a Z value of 4.12 $yr^{-1}$ was obtained (r = 0.98; 95% CI = 3.68-4.56; first length included in the regression, L', i.e. size at which fish are fully vulnerable to the fishing gear, L' = 70mm). The values derived give a broad range for the estimate of Z (Table 2) . However, a Z value for *S. tanganicae* between 4 to 5 $yr^{-1}$ is probably appropriate. Thus 99% of a cohort will die within one year.

As with Z rates, M rates were estimated by different methods (Table 2). Mean values for the whole lake ranged from 1.8 to 2.9 $yr^{-1}$. A overall value of 2.3 $yr^{-1}$ was probably representative of natural mortality for *S. tanganicae* throughout the lake.

Size dependent natural mortality rate estimates (Peterson and Wroblewski, 1984) are given in Figure 5a. The overall M value was 3.7 $yr^{-1}$ and that of adults was 1.9 $yr^{-1}$.

### 3.1.4 Reproduction

During the year, the gonado-somatic index, GSI, of *S. tanganicae* increased at intervals of 3-4 months (Figs. 6, 7 and 8) for females from Bujumbura and Kigoma and males from Kigoma. There were insufficient numbers of males from Bujumbura and of either sex from Mpulungu for analysis.

During the 21 month period covered (March 1994 - December 1995) *S. tanganicae* GSI increased at about March-April, June-July and November-December. No remarkable difference resulted between the northern and Kigoma areas.

The percentage frequency of maturity stages (Fig. 9) showed that at Kigoma the catch consisted mainly of fish at the early stage of sexual maturity. The sexual maturity pattern was unclear. It seemed that the frequency of mature individuals increased every 4 months following a temporal pattern similar to that of the GSI. Data from the north of the lake are not included as they were biased by overestimation of maturity stage II.

No reproductive pattern was apparent at the southern end of the lake (Figure 10). When caught *S. tanganicae* individuals were either entirely juveniles or sexually mature adults and the simultaneous occurrence of both was rare.

Estimates of mean L, for *S. tanganicae* from the different areas (Table 3, Figs. 11, 12, 13 and 14) were in close agreement (overall mean $L_m$ = 78mm TL, CV = 6.57, for females and mean $L_m$= 77mm TL, CV = 3.59, for males), indicating that, around the lake, *S. tanganicae* all reached sexual maturity at the same length which corresponds to an age of 8.5 months. This same length was predicted by the optimal $L_m$ theory (Roff, 1986, 1992). *Stolothrissa tanganicae* enters into the reproductive phase when the most of the somatic growth has been achieved, the overall ratio $L_m/L_\infty$, is 0.73.

### 3.1.5 Recruitment

Recruitment of juveniles < $L_c$ (56mm TL) to the liftnet fishery in the Bujumbura area appeared to be continuous throughout the year. The proportion, for the most of the year, was > 50% (Fig. 15).

The recruitment pattern to the Uvira liftnet fishery was more seasonal (Fig. 15). In a twelve month cycle there are two recruitment periods. Early in the year a first, minor, pulse extended over three months (from February to April) and the main recruitment period lasted from June/July to October/November.

The recruitment of *S. tanganicae* to the Kigoma fishing grounds (Fig. 15) was similar to that of Uvira with respect to the major recruitment period from June to November 1994, but in 1995 it ended in August.
Overall, the principal recruitment season of *S. tanganicae* in the Kigoma area and in the north of the lake took place from June to November i.e. during the dry season.

## 3.2 *Limnothrissa miodon*

### 3.2.1 Distribution and exploitation

Liftnets and beach seines exploited different parts of the *L. miodon* population in the north. The liftnet catch consisted mainly of immature fish whereas mostly adults were caught by the modest beach seine operation (Fig. 16) because of the highly selective 20mm mesh.

Only the adult *L. miodon* population was exploited in Kigoma waters and the largest individuals were caught only in the purse seine fishery operating in more open water. The L. *miodon* size distribution at Kigoma and at the southern end of the lake was different (Fig. 16). At Mpulungu beach seines and liftnets used mosquito netting as codend covers and these gears harvested the inshore stock of young *L. miodon.* As in Kigoma waters, the very large fish occurred almost exclusively offshore and were caught by the purse seines.

The length distribution of liftnets and beach seine catches in the Kipili area was similar because both these gears, when targeting clupeids, operated along the coastal zone (Kihakwi and Challe, 1995; personal observation) . They were often equipped with small mesh codend covers. Length composition from both gears was characterized by a sharp decline to the right. This was not due to mortality but to emigration of large *L. miodon* from the fishing grounds to more open waters.

*Limnothrissa miodon* juveniles were absent in both the June and November cruises catches (Fig. 17) . As there was no trawling in inshore, shallow waters the juveniles may have been missed. Length distributions from survey data were biased towards larger fish which were missing or underrepresented from commercial catches.

### 3.2.2 Growth and mortality

Only the L/F distributions from Bujumbura, Kipili and Mpulungu were suitable for VBGF coefficient estimation (Table 4) . The resulting growth patterns were the same for the three areas (CV of mean phi' was 0.13). Longevity of *L. miodon* was estimated at 2.5 yr.

All Z estimates of *L. miodon* are high considering the longevity of the species (Table 4). Total mortality rates obtained from catch curve analysis range from 5.4 to 6.6 $yr^{-1}$ (mean values from various methods). Total mortality of *L. miodon* should not be expected to be higher than *S. tanganicae* mortality rates (compare longevity) . This probable overestimation, mainly evident from Kipili and Bujumbura, could have been due to emigration from the fishing grounds of fully grown individuals. Where fishing gears were not operated offshore, the right side of the *L. miodon* catch curve shows a sharp decline. This would lead to higher values of the regression slope and thus of Z. Truncated distributions were not encountered from samples collected by offshore nets such as purse seines (see Fig. 16)

Survey data appeared to be more representative of the *L. miodon* adult population. From catch curve analysis, applied to the pooled L/F from both surveys, Z = 3.12 $yr^{-1}$ (r = 0.97; 95% CI = 2.92-3.32; L' = 94mm) which appears more realistic than the Z estimates obtained from the fishery data.

Natural mortality rates calculated as constant values throughout the life (means from each method) ranged from 1.2 to 1.8 $yr^{-1}$. From the Peterson and Wroblewski model (1984) a population mean M = 2.8 $yr^{-1}$ and adult mean = 1.4$yr^{-1}$ were calculated (Fig. 5b).

As Z is certainly overestimated it is not realistic to calculate fishery mortality (F = Z - M)

### 3 .2 .3 Reproduction

From all the study areas the reproductive pattern, as indicated by GSI, of *L. miodon* showed less marked periodicity than did *S. tanganicae.* The reproductive effort of *L. miodon* reflected in gonadal development appeared to be almost constant in the north of the lake while monthly variations were noted in the Kigoma and Mpulungu data (Figs. 18, 19, 20, 21, 22, 23) . As there was high variability and lack of data for some months no pattern could be identified. As stated above, data on *L. miodon* from commercial catches were thought to be poorly representative of the population.

The percentage distribution of maturity stages from the Kigoma samples (Fig. 24) indicate that the maximum number of mature fish were found twice a year (May-July and September-November) . In the south only the period July 1993 to July 1994 could be considered due to the scarcity of adult fish during the rest of the sampling programme (Fig. 25). During this period ripe L. *miodon* occurred for the most of the year with the highest frequency in May and June. Data from Bujumbura and Uvira are not given as maturity stage II was overestimated.

The mean value of $L_m$ for *L. miodon* was 101mm (CV 13.8) for females and 95mm (CV 7.6) for males (Figs. 26, 27, 28 and 29; Table 5) . The optimal $L_m$ theory (Roff, 1986, 1992) would predict = 130mm which is much higher than the lengths obtained from the logistic model. This predicted value is probably not realistic as only a very small fraction of the population would attain it.

On lakewide basis *L. miodon* achieves sexual maturity at 8.6 months and the resulting overall $L_m/L_\infty$ ratio is 0.54.

### 3.2.4 Recruitment

In the north *L. miodon* had a main recruitment period during the 1994 dry season which was not repeated in 1995 (Fig. 30)

Recruitment to the beach seine fishery at the southern end of the lake (at $L_c$ = 15mm corresponding to a relative age of one month) was sustained throughout the year with increased intensity at the onset of the dry season (April/June) and in November/December (Fig. 30).

## 3.3 *Lates stappersii*

### 3.3.1 Distribution and exploitation

Only open water gears exploited *L. stappersii* and virtually no adult fish occurred in catches north of the Rumonge sub-basin. Young individuals were caught in the northern area until they reached a length = 100mm (at c. 6 months of age) . Kigoma catch data showed a classic bimodal length frequency distribution composed of juveniles and adults while the Mpulungu catch consisted mainly of adult fish (Fig. 31). The Mpulungu industrial fishery is now entirely based on this adult fish concentration in the south. As this abundant adult stock exists in the south of the lake for the most of the year, one or several important nursery areas probably occur outside the fishing grounds of the purse seine fishery.

The *L. stappersii* population which was sampled during the two lake wide surveys consisted of at least three identifiable cohorts (Fig. 32). In both months, June and November, length groups which were poorly represented in catches of some fisheries (e.g. Karonda, Kigoma and Kipili) were well represented suggesting a possible size related distribution.

### 3.3.2 Growth and mortality

Growth model coefficients of *L. stappersii* estimated by ELEFAN I and SLCA methods (Table 6) were similar (CV of mean Phi' was 0.50). The major differences were from the Kipili data and this was probably due to the small number of available L/F distributions. The maximum lifespan of *L. stappersii* is about 7 yr but very few specimens live more than 5 yr.

Mean values of mortality rates derived from the different methods ranged from 1.66 to 1.89 $yr^{-1}$ and 0.6 to 0.9 $yr^{-1}$ for Z and M respectively (Table 6). Total mortality was significantly higher in the south of the lake than in the Kigoma area. From survey data Z = 1.79 $yr^{-1}$ (r = 0.97; 9S% CI = 1.60-1.98; L' = 140mm) which lies between the Kigoma and Mpulungu estimates. The estimates of M from the Peterson and Wroblewski model (1984) gave mean M = 1.4 $yr^{-1}$ and an adult mean M = 0.7 $yr^{-1}$ (Fig. 5c)

Despite the inaccuracy in extrapolating F from Z-M and thus the exploitation rate (E = F/Z) it seems evident that the heaviest exploitation is experienced by *L. stappersii* in the south area. Fishing effort, and thus fishing mortality, for this species is the highest in this area of the lake.

### 3.3.3 Reproduction

The changes in the monthly mean values of the GSI of *L. stappersii* differ between Kigoma and Mpulungu (Figs. 33, 34, 35, 36). At Mpulungu the reproductive effort, as shown by the GSI, clearly increased from October to March.

This seasonal pattern was much less evident from the Kigoma data. Common to both the Kigoma and Mpulungu data was the apparent decrease in reproductive output during the second sampling year (March 1995 - March 1996)

The proportion (%) of each sexual maturity stage (Figs. 37 and 38) followed the same the reproductive cycle as indicated by the GSI pattern and showed that while in the Kigoma area both immature and adult *L. stappersii* were equally exploited, in the south the catch consisted entirely of mature fish.

Mean length at maturity ($L_m$) could be estimated only from the Kigoma and Mpulungu samples due to the absence of adult fish in the north of the lake (Figs. 39 and 40). $L_m$ = 278mm for both sexes at Kigoma and $L_m$ = 237mm and $L_m$ = 255mm for females and males respectively at Mpulungu (Table 7). At Mpulungu the $L_m$ estimate for females was affected by the occurrence of large sized individuals which were not fully mature. The mean $L_m$ for both sexes was 16% smaller than $L_m$ = 311mm predicted by the optimal $L_m$ theory (Roff, 1986, 1992)

*Lates stappersii* becomes sexually mature during the second year of life at the age of about 1.7 yr. The overall $l_m/l_\infty$ ratio is 0.51.

### 3.3.4 Recruitment

No adult *L. stappersii* were caught by liftnets in the north of the lake. Within a yearly cycle only one major recruitment pulse took place lasting five months from April to August (Fig. 41).

The recruitment to the Kigoma fishing grounds was similar to that of the north but, unlike it, the single annual recruitment period was later, from July to November (Fig. 41)

As stated earlier, in the south of the lake *L. stappersii* juveniles are never recruited to the purse seine fishery and only the adult stock is exploited (Fig. 41).

Only in Kigoma were juveniles and adults found together in both liftnet and purse seine catches. The highest occurrence of sexually mature individuals (fish of TL $L_m$ from February to April was followed 5-6 months later (August-October) by the appearance of juveniles (recruits) in the catch (Figs. 41C and 41D) . The time lag between the occurrence of adults and juveniles was in agreement with the estimated age of the latter which at a $L_c$ of 90mm was 5.5 months.

### 3.3.5 Feeding ecology

A total of 4195 stomachs (1596 from Mpulungu and 2599 from Kigoma) were examined. No significant difference ($X^2$ **=** 14.42, df **=** 8, p **<** 0.05) was found between the diet of Kigoma male and female *L. stappersii,* so the data were pooled for sex within each area. In each month of the study empty stomachs were never **>** 11% of the total. Stomach fullness was mainly “nearly empty” or “half full” (45% and 25% at Mpulungu and 41% and 32% at Kigoma respectively) . Hauling operations started normally at about midnight and continued during darkness. Feeding activity probably takes place at dusk and is possibly resumed at dawn.

The diet of *L. stappersii* in the south was almost entirely based upon clupeids and shrimps (Fig. 42). The palaemonid shrimps, *Palaemon moorei,* and the atyid *Limnocaridina parvula* were the commonest prey for the most of the year. Around Kigoma *L. stappersii* displayed a more heterogeneous food spectrum including mesozooplankton (copepods) and *S.* tanganicae larvae (Fig. 43)

*Stolothrissa tanganicae* was the commonest fish prey at Kigoma, its frequency in the stomachs was the highest from July up to January when the catch of this species in the fisheries was also highest. *S. tanganicae* larvae were important in the diet especially from May to July. From July larvae abundance decreased and *L. stappersii* fed on juveniles and adults. The timing of maximum occurrence of *S. tanganicae* larvae and adults in the predator stomachs reflected the reproductive phase of the prey. It took place in May and was followed by a recruitment period. The appearance of copepods in the diet of *L. stappersii* from September to January was due to large number of young *L. stappersii* in the sample. These fish are planktivorous feeders. Shrimps were common prey throughout the year.

As far as identification of gut contents would allow, *L. miodon* was the commonest fish prey at Mpulungu. No significant quantity of clupeid larvae was found in the stomach contents of fish from this part of the lake. *Limnothrissa miodon* probably spends its early life in inshore waters which are not feeding grounds for *L. stappersii* and may be *S. tanganicae* abundance is too low to make it an important prey item, either as larvae or adults. Therefore shrimps are likely to be the most important prey of *L. stappersii* in the south of the lake.

Ontogenetic changes in feeding are illustrated in Figures 44 and 45 by frequency of prey occurrence. The data from Kigoma indicated that juveniles fed on copepods, then at c. 100mm on shrimps and *S. tanganicae.* Only large fish were entirely piscivorous. Cannibalism was noted in some months, mainly by adult fish.

*Lates stappersii* from the south of the lake maintained a simple, two prey item diet throughout their life. The zooplanktivorous phase was not found at Mpulungu as young *L. stappersii* (TL **<** 100mm) were not caught. Initially they preyed on shrimps and then gradually the proportion of clupeids increased. Only very large individuals were mainly piscivorous. Thus *L. stappersii* is not entirely a piscivorous predator throughout its life. Fish prey become important in the diet of this predator well over the size of 100mm which was observed earlier (Ellis, 1978; FAO, 1978; Roest, 1992)

It could be argued that commercial catch samples, taken by light attraction methods, are of dubious value, owing to the simultaneous concentration of both predators and prey. Pearce (1991) stated, on the basis of some experimental fishing, that it is unlikely that the occurrence of shrimps in the stomach of *L. stappersii* is an artifact due to light attraction. Stomach samples collected during experimental mid-water trawling in Kigoma and Mpulungu areas in June 1995 were compared with those obtained during the same month from commercial catch samples (Fig. 46) . The diet composition from the commercial and survey samples of the same area were quite similar. Due to better preservation of the stomachs collected during the survey, prey items which are digested quickly such as copepods and shrimps are represented more in survey samples than in commercial catch samples.

## 4. DISCUSSION

### 4.1 Distribution

*Stolothrissa tanganicae* and *L. miodon* have adopted different life strategies. *Stolothrissa tanganicae* spends the larval and juvenile phase in offshore open water where nursery areas are located (Aro *et al.,* in preparation). As the fish grow they move towards the coast and enter into the liftnet fishery area to which they are fully recruited when they reach a length of 56mm, at about 5 months of age.

*Limnothrissa miodon* during the first year of life occurs in inshore, shallow water and moves offshore during its second year. Very large fish are found only in open water where they have a similar feeding behaviour to *L. stappersii,* preying on shrimps and juveniles of *S. tanganicae* (Ndugumbi *et al.* 1976; Poll, 1953; personal observation)

*Stolothrissa tanganicae* is probably a more specialized planktivorous feeder than *Limnothrissa miodon* (Matthes, 1965-66), preying on the offshore zooplankton community. The latter can feed on a wider food spectrum and it preys on the diversified inshore plankton community. When energetic requirements increase, probably related to gonadal development, the fish migrate to offshore waters where they eat fish and shrimps. It still has to be determined whether spawning of *L. miodon* takes place close to the shore or in open water. The high inshore larval abundance reported by Tshibangu and Kinoshita (1995) would indicate that coastal areas are the favourite places for nurseries and perhaps spawning.

*Lates stappersii* **<** 1 yr are caught with *S. tanganicae.* Probably the juveniles of the two species aggregate together and share the same trophic niche. The occurrence of only the 0+ age class in the northern end of the lake does not mean this is a primary nursery area for *L. stappersii.* The young fish can be spawned by adults further south where the lake deepens and expands into the Kigoma sub-basin. Some of the young then spread northwards. A southerly movement occurs from an age of c. 6 months.

Preliminary evidence from pelagic trawl surveys would indicate the existence of nursery areas in the Kigoma basin. The juveniles of the June cohort shown in Figure 32 (in which all samples were pooled) were found entirely in the Kigoma and Rumonge sub-basins. Previously, a nursery area was found by Chapman and van Well (1978b) in the offshore, central part of the lake.

In some areas the catch composition of *L. stappersii* showed clear bimodality (Fig. 31) . It has been proposed, although no evidence has been produced, that the missing length groups (within 130-250mm length range) are not represented in the catch because the fish move inshore out of the usual fishing grounds to prey upon juvenile *S. tanganicae* (Roest, 1988). However both *S. tanganicae* and *L. stappersii* do not spend time inshore in their life cycle. Fishery-independent information (survey data not affected by commercial catch bias) would indicate that *S. tanganicae* juveniles occur mainly in offshore, open water (Aro *et al.,* in preparation) as do the “missing length group” of *L. stappersii.* During the June and November 1995 cruise surveys, length classes within the 130-250mm size interval were well represented and almost all of these were caught in offshore deep water hauls (Fig. 32). In June 1995 the 110-160mm cohort was caught in the East Marungu sub-basin, and in November the 150-200mm cohort was found in pelagic waters in the Rumonge, Kalemie and Moba sub-basins.

*Lates stappersii,* like *S. tanganicae,* spends all its life cycle in the pelagic deep water, and thus preys on this clupeid almost exclusively. The life history of *L. miodon* with the juvenile inshore phase enables the fish to avoid *L. stappersii* and reduce predation pressure on it. Adult *L. miodon* offshore are too large for capture by *L. stappersii.*

### 4.2 Life histories

Growth coefficients of the three species, as estimated from the July 1993-June 1995 data are similar to the most of the previously published estimates (Table 8). As far as the accuracy of length-based methods allow, there is no evidence of different growth pattern within species between parts of the lake.

A more accurate assessment of growth may be achieved from studying otolith daily growth rings. Fish aging by such methods has been unsuccessful for *L. stappersii* (Kimura, 1991a), but may be feasible for the short lived clupeids. Preliminary results of age obtained by Pakkasmaa and Sarvala (1995), for *S. tanganicae* and *L. miodon* otoliths, sampled from the same populations from which length data were obtained, were quite consistent with growth estimates obtained by length based analyses. *Stolothrissa tanganicae* of c. 60mm were aged from otoliths as 150-160 days old and *L. miodon* of 60 and 100mm as 120-160 and 250-350 days old respectively. Converting lengths from the average VBGF, estimated by length frequency distributions to relative age, the above lengths corresponded to 153 days for *S. tanganicae* and 138 and 279 days for *L. miodon.*

The large number of fish, sampled on a regular weekly basis at various sites around the lake, analyzed for the present study to estimate the growth of *S. tanganicae, L. miodon* and *L. stappersii,* and the similarity of the results with earlier studies (Table 8 and Fig. 47) indicate that estimates for each species are reliable. It can be observed (Fig. 47) that the growth of *L. miodon* lies between that of *S. tanganicae* and *L. stappersii.*

The timing of clupeid reproduction as indicated by changes in the monthly GSI does not show any evident seasonality but a highly variable pattern with four apparent peaks during the year in the case of *S. tanganicae* but not clear peaks in the case of *L. miodon.* To evaluate the seasonal allocation of reproductive output of the clupeids, a fecundity index correlated with an index of the spawning population abundance should be used (Craig and Mannini, in preparation) However, seasonal variation of GSI, which shows similar variability throughout the areas studied, would indicate that the reproductive process is continued, although with varying intensity, throughout the year.

As a result of such dynamic reproductive strategies, knowledge on the timing of reproduction of the clupeids is not well defined within and between years (see Coulter, 1991, for a review of results from previous authors). Probably, this is because unlike most temperate clupeids, which have a distinct spawning season and generally live for more than 2 years (Blaxter and Hunter, 1982) , *S. tanganicae* and *L. miodon* spawn almost continuously after becoming sexually mature and are short-lived (longevity of 1.5 and 2.5 yr respectively)

When $L_m$ is reached serial spawning takes place in several clupeid species (Blaxter and Hunter, 1982) and probably Lake Tanganyika clupeids have this reproductive behaviour. Multiple spawning over the whole year could be regarded as an adaptive strategy to increase offspring survival and recruitment in a relatively unstable pelagic environment (Alheit, 1989; Amstrong and Shelton, 1990) . Environmental factors are thought to play a critical role in pelagic environments causing long term fluctuations (LluchBelda, *et al.,* 1989; Shannon *et al.,* 1988). Further, in upwelling systems characterized by pulsed primary production such as Lake Tanganyika (Plisnier *et al,.* 1996) the planktonic larval phase of fish can suffer a high and variable mortality.

At Kigoma although *S. tanganicae* reproduction is continued throughout the year, the reproductive period in May-June gives rise to a cohort which is very successful, having a high survival rate. The abundance of *S. tanganicae* larvae, which is at its highest between May and July, in the stomachs of *L. stappersii* indicates the prey abundance in the environment. The main recruitment pulse to liftnet fishery which takes place from June to October depends on the May-June cohort strength.

It seems that, at least at Kigoma, *S. tanganicae* is very efficient in exploiting a survival window, i.e. a period of high survival hypothesized by Alheit (1989) for small pelagics, which is open during the dry season (from June to September) . This four month long survival window is due to the low local abundance of adult *L. stappersii* (Coenen, 1995; FAO, 1978) and to increased primary and secondary production which in turn is a consequence of the deepening thermocline and the vertical mixing of the water (Plisnier *et al.,* 1996). Production reaches a maximum around November (Hecky, 1991; Kurki, 1996)

*Lates stappersii* reproduction follows a more regular pattern especially in the area of Mpulungu (Fig. 36) which takes place during the wet season. As can be expected by a relatively long-lived species the seasonal reproductive period is fairly constant between years (Chapman and van Well, 1978b; Ellis, 1978)

The size at which 50% of the fish reach sexual maturity and the $L_m/L_\infty$ ratio provide an important insight on the life history of a species. Life history strategies may be linked to the terms of resources allocation to reproduction. Lake Tanganyika clupeids appear to have different strategies. Both *S. tanganicae* and *L. miodon* reach $L_m$ at the same age (8-9 months) but *S. tanganicae* at this age has already completed about 2/3 of its somatic growth while *L. miodon* only half.

The difference can be explained by the life histories of the two species. *Stolothrissa tanganicae* is pelagic throughout its life and is continuously preyed upon mainly by *L. stappersii,* the most important pelagic predator species, and secondarily by *L. miodon.* All available resources are allocated to complete somatic growth so that a body size can be reached which will reduce the risk of predation. The population of *L. stappersii* consists mainly of fish in the length range 200-300mm. Assuming that prey are taken up to 30% of the size of the predator size (Treasurer *et al.,* 1992), *L. stappersii* would capture *S. tanganicae* up to c. 75mm which is very close to the species $L_m$.

Unlike *S. tanganicae, L. miodon* is not a truly pelagic species and most of its first year of life takes place in shallow inshore water to avoid *L. stappersii* predation. Although it can be suggested that this species is exposed to more diversified predation from others *Lates* species and piscivorous cichlids, the inshore environment has a richer source of potential prey than the pelagic. When *L. miodon* migrate offshore as adults they are too large for predation by *L. stappersii*.

Diet composition of *L. stappersii* has not previously been investigated comparatively in different areas. The remarkable differences in the diet composition between the two study areas indicates *L. stappersii* feeding ecology, like that of many fish species, depends on food availability rather than the age of the fish. The southern end of the lake probably has a large shrimp population which may attract and sustain a resident, commercially important, adult stock of *L. stappersii.* Differences in meso and macrozooplankton composition have been reported by Kurki and Vuorinen (1995) and Kurki (1996). How much this explains the present low abundance of *S. tanganicae* in this area is difficult to assess. Certainly a concentration of *L. stappersii* may have a substantial effect on the abundance of the latter. Therefore, the predator-prey relationship between *S. tanganicae* and *L. stappersii* as investigated in the past (Roest, 1988) is now further complicated by the relevance of the shrimp prey.

Large sized *L. miodon* feed on both shrimps and *S. tanganicae* and thus are likely to share the same trophic niche as *L. stappersii.*

It is then likely that the presence of both *L. stappersii* and large *L. miodon* exerts a top-down control, through predation mortality, on *S. tanganicae* effective enough to keep its abundance low at the southern end of the lake. In Kigoma waters shrimp density appears to be lower than in the south (Kurki, 1996) so *L. stappersii* turns to other available prey.

A review of changes which took place from 1960’s within the pelagic fish community in the Mpulungu sub-basin is given by Pearce (1995) . In 1989 a study was carried out by Pearce author on the diet composition of *L. stappersii* in Mpulungu area. At that time *S. tanganicae* was still an important component of the diet comprising, on a monthly basis, from 20% to 70% of the total diet weight (both larvae and adults). The remaining dietary component was mostly shrimp (Pearce, 1995)

It appears that while *S. tanganicae* abundance in the Mpulungu sub-basins has been drastically reduced over the last ten years this has not affected *L. stappersii.*

### 4.3 Fishery exploitation

Lake Tanganyika clupeids are short-lived species with high M and therefore characterized by a quick turn-over. The production/biomass ratio (P/B) is assumed to be equivalent to total mortality (Z) when the growth follows the von Bertalanffy model and mortality is exponential (Allen, 1971). Among *L. stappersii, L. miodon* and *S. tanganicae,* the last, as it can be inferred by its life parameters, has the highest P/B which is expected to be in the order of 4-5.

More uncertain is the P/B estimate for *L. miodon* because of biased Z estimates. The range of Z values available from the present study as well as from previous research (Table 8) would indicate overestimated rates which do not match the expected longevity of 2.5 yr (Lévêque *et al.,* 1977). Mannini (1991) applied length cohort analysis to the *L. miodon* stock of Lake Kivu and obtained Z values not higher than 2 $yr^{-1}$, much lower the value he obtained of 9 $yr^{-1}$ from catch curve analysis applied to the same data (Mannini, 1990). Preliminary Z figure from catch curve analysis applied to June and November 1995 survey data for the whole Lake Tanganyika is of 3 $yr^{-1}$. This estimate is more realistic and less biased than those from commercial catch data. Therefore, P/B of *L. miodon* can be reasonably expected to lie between 2 and 3 $yr^{-1}$.

*Lates stappersii* is the most long lived of the three species and has the lowest natural mortality resulting in the slowest turn-over. A P/B of 1.5 can be regarded as representative for this species.

The population dynamic characteristics such as those of clupeid species of Lake Tanganyika, are thought to make the species quite resilient to fishery exploitation, although many important clupeid fisheries have declined or collapsed (Beverton, 1990). Also, the same biological traits, quick growth and high natural mortality, make them vulnerable to recruitment failure due to environmental changes (Csirke, 1988) which are poorly understood. Sudden and unexpected increase in juvenile mortality can severely reduce recruitment into the adult stock. A relatively longer-lived species such as *L. stappersii* whose (exploited) population is made of several yearly cohorts can withstand these perturbations better.

Simple biomass models illustrated in Figures 48 to 50 outline the dynamics of a typical *S. tanganicae* cohort for the whole lake and of *L. stappersii* cohorts in the Kigoma and Mpulungu areas. The *S. tanganicae* cohort reaches maximum biomass at 5 months when the fish begin to be fully recruited to the fishery. The *L. stappersii* cohort at Kigoma is exploited from 6 months (100mm TL) but fishing mortality is low. The *L. stappersii* stock at Mpulungu enters the exploited phase later at c. 18 months (230mm TL) but fishing effort there is very intense resulting in a sharp biomass decline.

The constants in relative yield per recruit (Y/R)' analysis (Beverton and Holt, 1966; Pauly and Soriano, 1986; Sparre and Venema, 1992) are $L_\infty$, K, M and $L_c$. Normally, when assuming knifeedge recruitment, tropical fish species with high M produce Y'/R curves with a misleading plateau unless, according to Pauly (1994), L/F data are corrected for probability of capture using a selection ogive (i.e. from catch curve analysis)

The aim of $(Y/R)^{-1}$ analysis in the present work was to outline the current status of fishery exploitation of the three species based on knowledge of their dynamics and especially on the selectivity of fishing gears in use and of the consequent $L_c$. Also, a comparison between areas where the same species has different length at entry into the fishery provides information on the appropriateness of current fishing strategies.

Despite $L_c < L_m$ *S. tanganicae* does not appear to be overexploited in the lake (Fig. 51). No assessment can be made for *L. miodon.* The overestimation of Z determines unrealistically high F and, consequently, E rates. Relative (Y/R)' curves in Figure 52 are given only for the sake of comparison between the exploitation patterns in Bujumbura and Mpulungu which are characterized by different length at entry into the respective fisheries. As it can be expected, the very small length at entry into the beach seine fishery in the south has a marked negative impact on both (B/R)' and (Y/R)'.

The shape of the $(Y/R)^{-1}$ curve of *L. stappersii* at Kigoma and Mpulungu (Fig. 53) highlights the effect of the different length at entry of the two fisheries. Currently, *L. stappersii* is lightly exploited in the Kigoma area, although the small $L_c$ would make it easily vulnerable in case of increased fishing mortality. The concentration of industrial fishing effort on adult *L. stappersii* in the south results in intensive exploitation and further increase of fishing effort in the local fishing grounds can lead to critical effects.

## 5. CONCLUSIONS

Life histories of *S. tanganicae, L. miodon* and *L. stappersii* are similar throughout the lake and no substantial evidence has been gathered on possible sub-populations with different life strategies.

The major commercial fish stocks of the lake are those of *S. tanganicae* and *L. stappersii.* The population dynamics of the former makes it a highly productive species which can be quite resilient to exploitation. However it is vulnerable to environmentally induced recruitment failure which can quickly affect the size of the fishable stock. Effective assessment of *S. tanganicae* is therefore difficult. *Lates stappersii* is a relatively long lived, opportunistic predator whose population is made up of several cohorts which makes it less exposed to recruitment failure. The assessment and management of the *L. stappersii* is easier than that for *S. tanganicae.*

The Lake Tanganyika ecosystem is very varied and quite remarkable spatial differences occur. There are for example significant differences between northern and southern areas in fish distribution and feeding ecology. The fishery concentrates on clupeids in the north, on *L. stappersii* in the south and on both clupeids and the centropomid in the Kigoma area. Copepods are the main food of clupeids while shrimps, particularly in the south, are an important food of *L. stappersii.*

Historical ecological changes in the ecosystem have taken place. The disappearance of adult *L. stappersii* from the Bujumbura sub-basin (although the fishery was always small) and the increasing scarcity during the last decade of *S. tanganicae* in the Mpulungu sub-basin cannot be attributed solely to exploitation.

The presence of a “biological gradient” in the pelagic along the longitudinal axis of the lake can only be verified by lakewide surveys. The importance of pelagic shrimps has been highlighted in the present study. The magnitude and dynamics of the shrimp population needs to be assessed by appropriate investigations. In the past, considerable attention has been paid to the *S. tanganicae* and *L. stappersii* predator-prey relationship. Such relationships appear to be more complicated than suggested because of the “shrimp component”.

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## 7. REFERENCES


Algaraja, K., 1984. Simple methods for estimation of parameters for assessing exploited fish stocks. Indian J. Fish., 31: 177-208.

Alheit, J., 1989. Comparative spawning biology of anchovies, sardines and sprats. Rapp. P. -v. Reun. Cons. mt. Explor. Mer, 191: 7-14.

Allen, K.R., 1971. Relation between production and biomass. J. Fish. Res. Bd. Can. 28: 1573-81.

Amstrong, M.J., and P.A. Shelton, 1990. Clupeoid life-history styles in variable environments. Env. Biol. Fish., 28: 77-85.

Aro, E., 1993. Guidelines for sampling pelagic catches on Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-FM/04 (En) 25pp.

Aro, E., 1996. Report of travel of the 5th scientific cruise (16.11-4.12.1995) . In Hanek, G. (ed.), Reports of Travel 61- 75 of project GCP/RAF/271/FIN. FAO-FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/48 (En) : 146-194.

Aro, E., P. Mannini, I.M. Kimosa, E.R. Makere, N.A. Chale, 1995. Report of travel of the 2nd scientific cruise (15-30.06.1995) . In Hanek, G. (ed.), Reports of Travel 61-75 of project GCP/RAF/271/FIN. FAO-FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/48 (En) : 13-74.

Ault, J.S. and N.M. Ehrhardt, 1991. Correction to the Beverton and Holt Z estimator for truncated catch length-frequency distributions. ICLARM Fishbyte, 9(1) : 37-39.

Bertalanffy von, L., 1938. A quantitative theory of organic growth. Human Biol. 10: 181-213.

Beverton, R.J.H., 1990. Small marine pelagic fish and the threat of fishing; are they endangered? J. Fish. Biol., 37 (Supplement A): 5-16.

Beverton, R.J.H. and S.J. Holt, 1956. A review of methods for estimating mortality rates in exploited fish populations, with special references to sources of bias in catch sampling. Rapp. P.-V. Réun. CIEM, 140: 67-83.

Beverton, R.J.H. and S.J. Holt, 1966. Manual of methods for fish stock assessment. Part II. Tables of yield function. FAO Fish. Biol. Tech. Pap., 38: 67 pp.

Blaxter, J.H.S. and J.R. Hunter, 1982. The biology of clupeoid fishes. Adv. Mar. Biol., 20:1-223.

Chapman, D.W. and P. van Well, 1978a. Growth and mortality of *Stolothrissa tanganicae.* Trans. Amer. Fish. Soc. 107: 26-35.

Chapman, D.W. and P. van Well, 1978b. Observations on the biology of *Luciolates stappersii* in Lake Tanganyika (Tanzania). Trans. Am. Fish. Soc., 107(4): 567-573.

Coenen, E.J., 1995. LTR’s fisheries statistics subcomponent: March 1995 update of results for Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/32 (En): 45 pp.

Coulter, G.W., (ed) 1991. Lake Tanganyika and its life. Natural History Museum Publications and Oxford University Press, London, Oxford and New York, 352 Pp.

Csirke, J., 1988. Small shoaling pelagic fish stocks. In Gulland J.A. (ed.) Fish population dynamics: the implications for management, Chichester, John Wiley and Sons Ltd. 271-302.

Ellis, C.M.A., 1971. The size at maturity and breeding seasons of sardines in southern Lake Tanganyika. Afr. J. Trop. Hydrobiol. Fish., 1: 59-66.

Ellis, C.M.A., 1978. Biology of *Luciolates stappersii* in Lake Tanganyika (Burundi). Trans. Amer. Fish. Soc., 107(4): 557-566.

FAO, 1978. Lake Tanganyika Research and Development Project, Tanzania. Fishery biology and stock assessment, based on the work of D.W. Chapman, H. Rufli, P. van Well and F. Roest. FI:DP/URT/71/012, Technical Report 1, 37 pp.

Gunderson, D.R. and P.H. Dygert, 1988. Reproductive effort as a predictor of natural mortality rate. J. Cons. CIEM, 44: 200-9.

Hecky, R.E., 1991. The pelagic ecosystem. In G.W. Coulter (ed.) Lake Tanganyika and its life. Natural History Museum Publications and Oxford University Press, 90-110.

Hyslop, E.J., 1980. Stomach content analysis. A review of methods and their application. J. Fish. Biol. 17: 411-429.

Kihakwi, A.D. and N.A. Chale, 1995. Report of travel to Kipili and Kirando (Tanzania) and Mpulungu and Nsumbu (Zambia), 06- 22.08.1994. In Hanek, G. (ed.), Reports of travel 46-60 of project GCP/RAF/271/FIN. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/30: 63-65.

Kimura, S., 1991a. On the otoliths of *Lates stappersii.* In Kawanabe, H. and M. Nagoshi (eds), Ecological and limnological study on Lake Tanganyika and its adjacent regions, 7: 65.

Kimura, S., 1991b. Growth of *Stolothrissa tanganicae* estimated from daily otolith rings in southern Lake Tanganyika. In Kawanabe, H. and M. Nagoshi (eds), Ecological and limnological study on Lake Tanganyika and its adjacent regions, 7: 60-61.

Kimura, S., 1991c. Growth of *Limnothrissa miodon* estimated from daily otolith rings in southern Lake Tanganyika. In Kawanabe, H. and M. Nagoshi (eds), Ecological and limnological study on Lake Tanganyika and its adjacent regions, 7: 62-64.

Kimura, 5., 1995. Growth of the clupeid fishes, *Stolothrissa tanganicae* and *Limnothrissa miodon,* in the Zambian waters of Lake Tanganyika. J. Fish. Biol., 47: 569-575.

King, M., 1995. Fisheries biology, assessment and management. Fishing News Books, Blackwell Science Ltd, Oxford, 341 pp.

Kurki, H., 1996. The results of zooplankton sampling at three localities in Lake Tanganyika; July 1993 - December 1995. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN, in press.

Kurki, H. and I. Vuorinen, 1995. Zooplankton ecology of Lake Tanganyika. Report on the results of LTR’s scientific sampling programme. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/34 (En, Fr) : 29 pp.

Lévêque, C., J.R. Durand and J.M. Ecoutin, 1977. Relations entre le rapport P/B et la longévité des organisme. Cah. ORSTOM, ser. Hydrobiol., 11: 17-31.

Lluch-Belda, D., R.J.M. Crawford, T. Kawasaki, A.D. MacCall, R.H. Parrish, R.A. Schwartzlose and P.E. Smith, 1989. World-wide fluctuations of sardine and anchovy stocks: the regime problem. S. Afr. J. Mar. Sci., 8: 195-205.

Mannini, P. 1990 - Paramèters de la population de *Limnothrissa miodon* du lac Kivu (1980 - 1989). PNUD/FAO - RWA/87/012/Document de Travail (TR)/32: 41 pp.

Mannini, P. 1991 - Aspects de la dynamique et de l’aménagement du stock de *Limnothrissa miodon* du lac Kivu. PNUD/FAO - RWA/87/012/Document de Travail (TR)/43: 21 pp.

Mannini, P., 1993. Field notes for Fish Biology. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-FM/08 (En): 34pp.

Mannini, P., 1994. Changes in fish data collection work. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN, Office Memorandum dated 7 March 1994: 6pp. plus annex.

Mannini, P. and E. Aro, 1995. Guidelines for catch handling on board *R/V Tanganyika Explorer.* FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-FM/19 (En) : 27pp.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. CIEM, 39(2): 175-92.

Pauly, D., 1983a. Some simple methods for the assessment of tropical fish stocks. FAO Fish. Tech. Pap., (234): 52 p.

Pauly, D., 1983b. Length-converted catch curve. A powerful tool for fisheries research in the tropics. (Part I) . ICLARM Fishbyte, 1(2) : 9-13.

Pauly, D., 1984a. Length-converted catch curve. A powerful tool for fisheries research in the tropics. (Part II) . ICLARM Fishbyte, 2(1): 17-9.

Pauly, D., 1984b. Length-converted catch curve. A powerful tool for fisheries research in the tropics. (Part III: Conclusion). ICLARM Fishbyte, 2(3): 9-10.

Pauly, D., 1987. A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic invertebrates. In Pauly, D and G.R. Morgan (eds), Length-based methods in fisheries research. ICLARM Conference Proceedings 13: 468 pp.

Pauly, D., 1994. Theory and practice of overfishing. In Pauly, D., On the sex of fish and the gender of scientists. Collected essays in fisheries science. Chapman & Hall, 89-103.

Pauly, D. and N. David, 1981. ELEFAN I, a BASIC program for the objective extraction of growth parameters from length-frequency data. Meeresforschung, 28(4): 205-11.

Pauly, D. and J.L. Munro, 1984. Once more on the comparison of growth in fish and invertebrates. ICLARM Fishbyte, 2(2): 21.

Pauly, D. and M.L. Soriano, 1986. Some practical extensions to Beverton and Holt’s relative yield-per-recruit model. In Naclean, J.L., L.B. Dizon and L.V. Hosillo (eds), The First Asian Fisheries Forum. Asian Fisheries Society, Manila, Philippines, 491-496.

Pearce, M.J., 1985. A description and stock assessment of the pelagic fishery in the south-west arm of the Zambian waters of Lake Tanganyika. Report of the Department of Fisheries, Zambia: 1-74.

Pearce, M.J., 1991. The effect of light from commercial fishing boats on the feeding of *Lates stappersii* and on zooplankton abundance and composition. In Kawanabe, H. and M. Nagoshi (eds), Ecological and limnological study on Lake Tanganyika and its adjacent regions, 7: 70-71.

Pearce, M.J., 1995. Effects of exploitation on the pelagic fish community in the south of Lake Tanganyika. In Pitcher, T.J. and P.J.B. Hart (eds), The impact of species changes in African lakes, Chapman & Hall, 425-441.

Peterson, I. and S.J. Wroblewski, 1984. Morality rate of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci., 47: 1117-20.

Plisnier, P.D., 1995. Catch assessment survey in Zambian waters of Lake Tanganyika in 1994. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/41 (En) : 26 pp.

Plisnier, P.D., V. Langenberg, L. Mwape, D. Chitamwebwa, K. Tshibangu and E. Coenen, 1996. Limnological sampling during an annual cycle at three stations on Lake Tanganyika (1993-1994). FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/46 (En): 136 pp.

Poll, M., 1953. Poissons non Cichlidae. Résultats scientifique de exploration hydrobiologique du Lac Tanganyika (1945-47). Vol III, fasc. SA. Institute Royal des Sciences Naturelles de Belgique, Bruxelles, 251 pp.

Rikhter, V.A. and V.N. Efanov, 1976. On one of the approaches to estimation of natural mortality of fish populations. ICNAF Res. Doc., 76/VI/8: 12 pp.

Roest, F., 1978. *Stolothrissa tanganicae:* population dynamics, biomass evolution and life history in the Burundi waters of Lake Tanganyika. CIFA Tech. Pap. 5: 42-62.

Roest, F., 1988. Predator-prey relations in northern Lake Tanganyika and fluctuations in the pelagic fish stocks. In Lewis, D. (ed.), Predator-prey relationships, population dynamics and fisheries productivity’s of large African lakes. CIFA Occas. Pap., 15: 104-129.

Roest, F., 1992. The pelagic fisheries resources of Lake Tanganyika. Mitt. Internat. Verein. Limnol., 23: 11-15.

Roff, D. A., 1986. Predicting body size with life history models. BioScience 36: 316-323.

Roff, D.A., 1992. The evolution of life histories. Theory and Analysis. Chapman & Hall, 535 pp.

Shannon, L.V., R.J.M. Crawford, G.B. Brundrit and L.G. Underhill, 1988. Responses of fish populations in the Benguela ecosystem to environmental change. J. Cons. perm. mt. Explor. Mer, 45(1): 5-12.

Shepherd, J.G., 1987. A weakly parametric method for estimating growth parameters from length composition data. In Pauly, D. and G. R. Morgan (eds.), Length-based methods in fisheries research, ICLARM Conf. Proc., 13: 113-9.

Sparre, P. and S.C. Venema, 1992. Introduction to tropical fish stock assessment. Part I. Manual. FAO Fish. Tech. Pap. 306.1, Rev. 1. FAO, Rome, 376 pp.

Tiercelin, J.J. and A. Mondeguer, 1991. The geology of the Tanganyika Trough. In G.W. Coulter (ed.). Lake Tanganyika and its life. Natural History Museum Publications and Oxford University Press, 7-48.

Treasurer, J.W., R. Owen and E. Bowers, 1992. The population dynamics of pike, *Esox lucius,* and perch, *Percha fluviatilis,* in a simple predator-prey system. Env. Biol. Fishes, 34(1): 65-78.

Tshibangu, K.K. and I. Kinoshita, 1995. Early life histories of two clupeids, *Limnothrissa miodon* and *Stolothrissa tanganicae,* from Lake Tanganyika. Japan. J. Ichthyol., 42(1): 81-87.

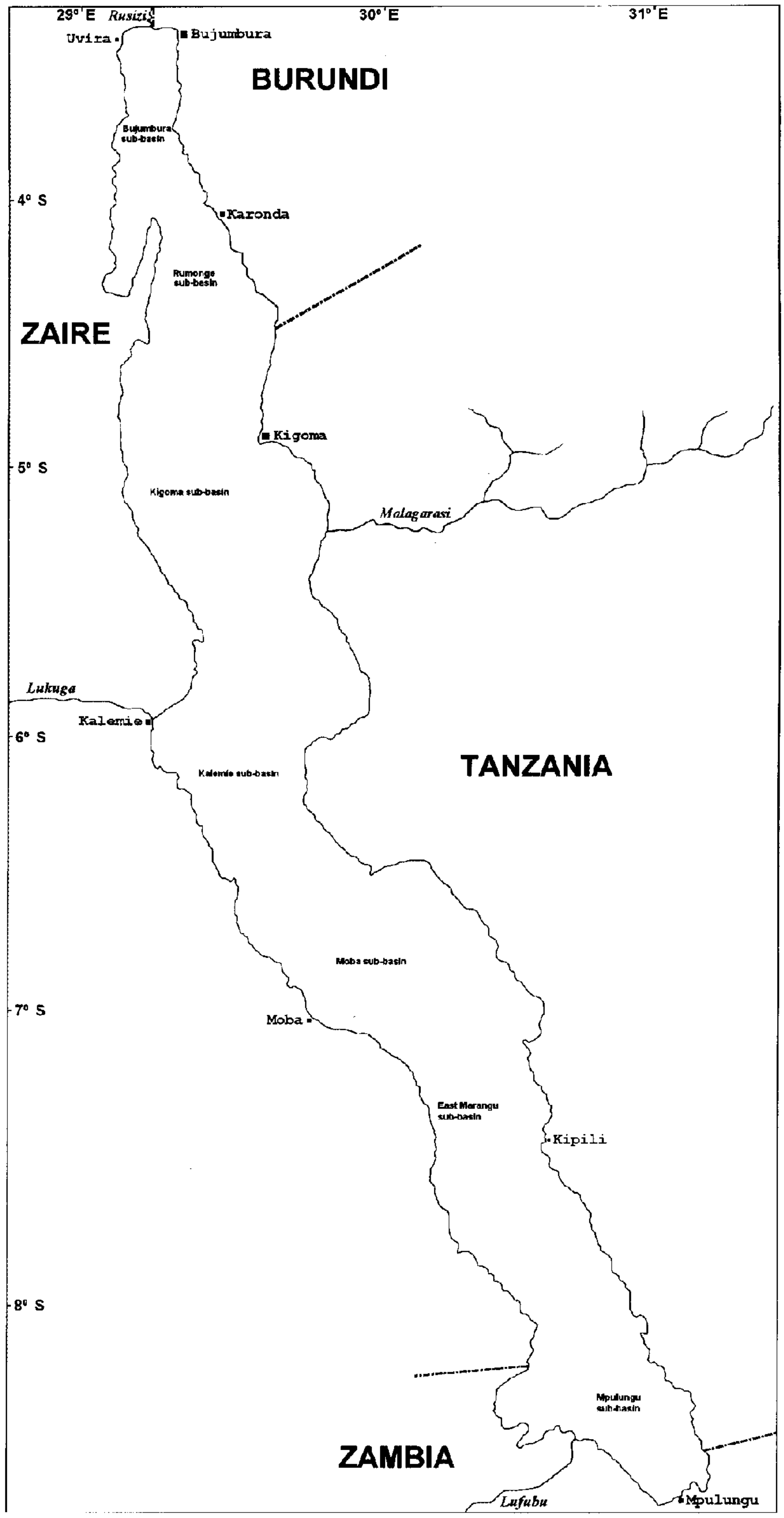



Figure 1. The map shows the sampling sites. Sub-basins are also indicated (for more details see text and Tiercelin and Mondeguer in Coulter, 1991).

| | | | | |
|---|---|---|---|---|
| | | *S. tanganicae* | | |
| Conversion | a | b | r | n |
| $W = a * TL^b$ | $4.0485*10^{-6}$ | 3.11 | 0.97 | 824 |
| TL = a + (b * SL) | 0.8729 | 1.1562 | 0.99 | 211 |
| TL = a + (b * FL) | -1.2572 | 1.0915 | 0.99 | 211 |
| | | *L. miodon* | | |
| Conversion | a | b | r | n |
| $W = a * TL^b$ | $3.9793*10^{-6}$ | 3.13 | 0.99 | 1755 |
| TL = a + (b * SL) | 1.6658 | 1.1873 | 0.99 | 93 |
| TL = a + (b * FL) | -0.6520 | 1.1179 | 0.99 | 93 |
| | | *L. stappersii* | | |
| Conversion | a | b | r | n |
| $W = a * TL^b$ | $6.7978*10^{-6}$ | 2.99 | 0.99 | 452 |
| TL = a + (b * SL) | -0.9087 | 1.2048 | 0.99 | 198 |
| TL = a + (b * FL) | -2.5117 | 1.0845 | 0.99 | 198 |

Table 1. Coefficient values for the interconversion of length and weight statistics for *S. tanganicae*, *L. miodon* and *L stappersii*. The correlation coefficient (r) and the number of fish (n) from which the coefficients were derived are also given.

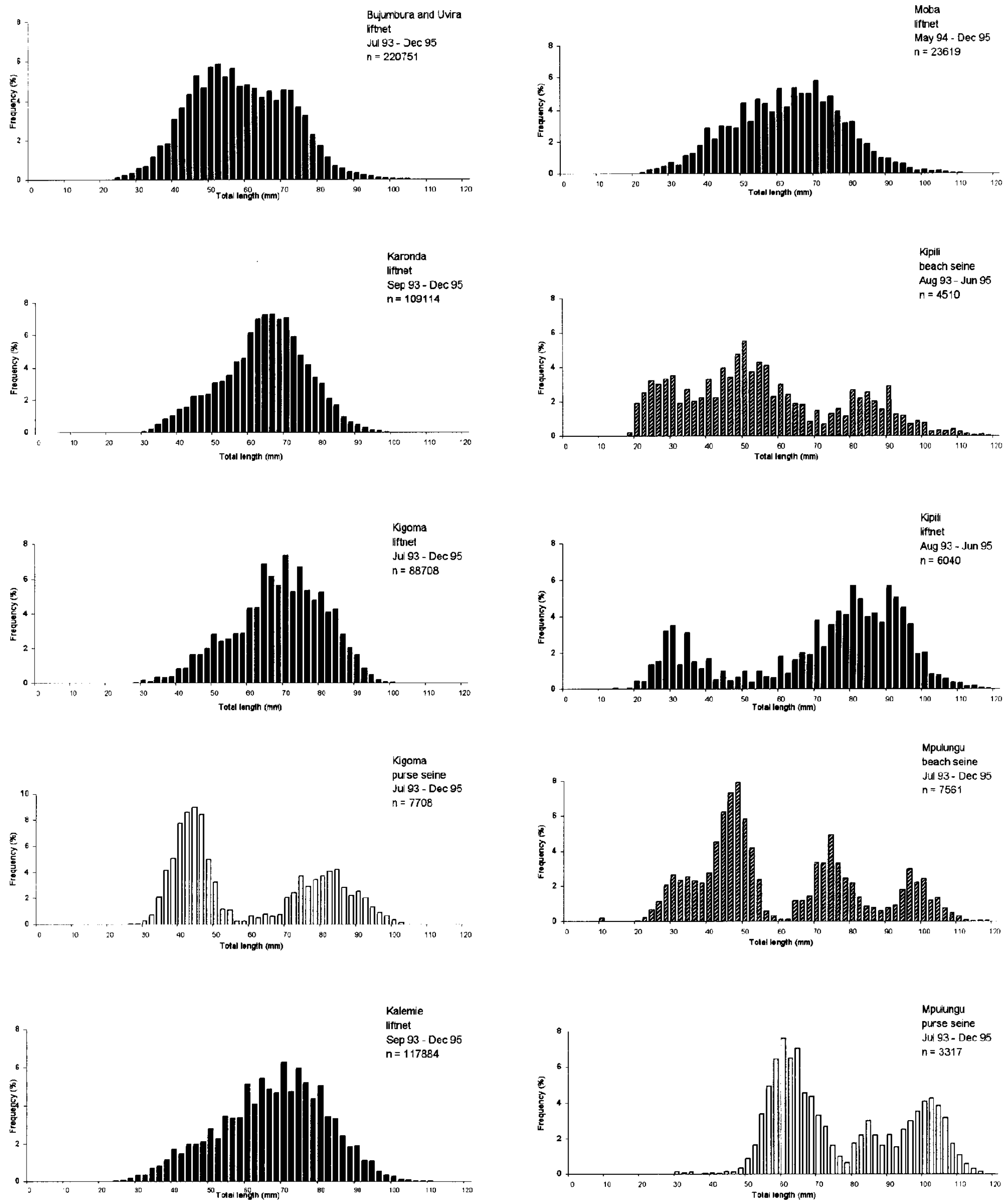



Figure 2. Length composition of the commercial catch of *S. tanganicae* by areas and fishing gears.

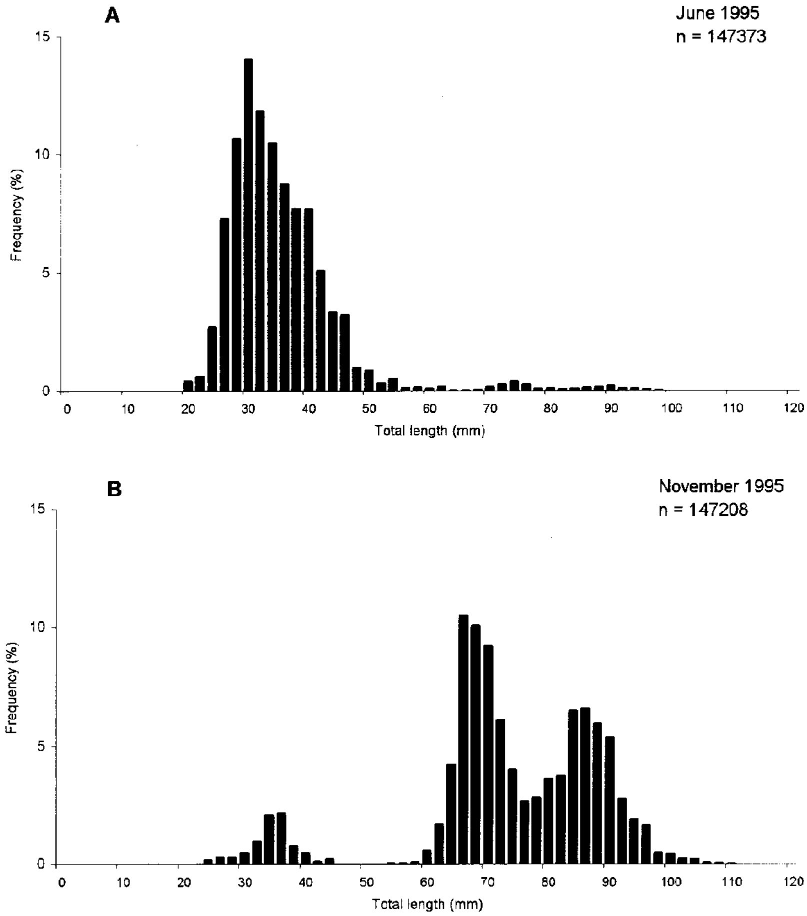



Figure 3. Size distribution of *S. tanganicae* for the whole lake from mid-water trawl surveys. **A**: 16 - 29 June 1995 survey; **B**: 16 November - 4 December 1995 survey.

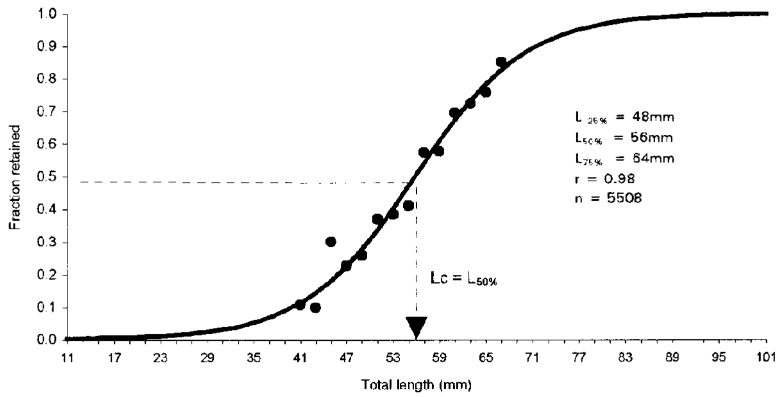



Figure 4. The gear selection ogive for *S. tanganicae* caught in Kigoma waters by a liftnet with a codend mesh size of 10mm. The critical length (Lc) is shown by the dotted line, n is the total sample size. Values for $L_{25\%}$ and $L_{75\%}$ (selection range) were also given.

| Area | Loo TL (mm) | K $yr^{-1}$ | Phi' | Z $yr^{-1}$ I | Z $yr^{-1}$ II | Z $yr^{-1}$ III | M $yr^{-1}$ IV | M $yr^{-1}$ V | M $yr^{-1}$ VI | M $yr^{-1}$ VII | Exploitation rate (E = F/Z) | $L_c$ (TL) mm |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Uvira | 104 | 1.85 | 4.301 | 4.39 (3.54-5.23; 55mm) | 4.50 | 4.49 | 2.7 | 1.5 | 2.0 | 2.8 | 0.37 | 50 |
| Bujumbura | 105 | 1.89 | 4.319 | 6.10 (5.29-6.91; 60mm) | 6.93 | 6.92 | 2.8 | 1.6 | 2.1 | 2.0 | 0.54 | 57 |
| Karonda | 112 | 1.77 | 4.339 | 4.79 (2.46-7.12; 72mm) | 8.68 | 8.67 | 2.6 | 1.9 | 1.9 | 2.9 | 0.45 | 46 |
| Kigoma | 105 | 1.84 | 4.306 | 5.16 (3.32-7.00; 70mm) | 5.25 | 5.24 | 2.7 | 1.7 | 2.0 | 2.7 | 0.47 | 56 |
| Kalemie | 108 | 1.80 | 4.322 | 5.05 (4.57-5.52; 68mm) | 5.60 | 5.59 | 2.7 | 2.0 | 2.0 | 2.8 | 0.47 | 64 |
| Mpulungu | 114 | 2.00 | 4.415 | 4.33 (3.94-4.71; 98mm) | 4.00 | 3.70 | 2.8 | 2.2 | 2.0 | 3.1 | 0.35 | 63 |
| Mean | 108 | 1.86 | 4.334 | 4.97 | 5.83 | 5.77 | 2.7 | 1.8 | 2.0 | 2.7 | 0.44 | 56 |

Table 2. Von Bertalanffy growth model coefficients (Loo and K from the Elefan I method), total (Z) and natural (M) mortality estimates for *S. tanganicae* from various areas. Roman numerals indicate the methods used. **I**: lenght-converted catch curve ( 95% CI and cutoff length, L', in brackets) ; **II**: Beverton and Holt, 1956; **III**:Ault and Ehrhardt, 1991; **IV**: Pauly, 1980; **V**: Rikhter and Efanov, 1976; **VI**: Gunderson and Dygert, 1988; **VII:** Alagaraya, 1984. Exploitation rates are estimated from catch curve's Z and Pauly's M. Mean length at first capture, $L_c$, based on the method of Pauly (1987), except the Kigoma estimate which was obtained from gear selectivity experiments (see text and Figure 4) .

| Sex and areas | a | b | r | $L_m$ (mm) | 95% CI for Lm | n |
|---|---|---|---|---|---|---|
| **Females** | | | | | | |
| Bujumbura & Uvira | 12.291 | -0.144 | 0.997 | 85 | 83-88 | 5524 |
| Kigoma | 18.157 | -0.225 | 0.987 | 81 | 76-86 | 5218 |
| Kalemie | 12.267 | -0.159 | 0.995 | 77 | 74-81 | 4971 |
| Mpulungu | 13.408 | -0.177 | 0.982 | 76 | 69-82 | 559 |
| **Males** | | | | | | |
| Bujumbura & Uvira | 28.221 | -0.350 | 0.996 | 81 | 78-84 | 2942 |
| Kigoma | 19.580 | -0.249 | 0.985 | 79 | 73-85 | 3036 |
| Kalemie | 12.978 | -0.174 | 0.993 | 74 | 70-79 | 4536 |
| Mpulungu | 10.930 | -0.145 | 0.903 | 76 | 55-94 | 354 |

Table 3. Linear regression estimates for the parameters of the logistic equation relating proportion mature to length for *S. tanganicae* (see also text and Figs. 11 to 14). The correlation coefficient (r), predicted length at 50% maturity ($L_m$), 95% confidence interval and sample size (n) are also given.

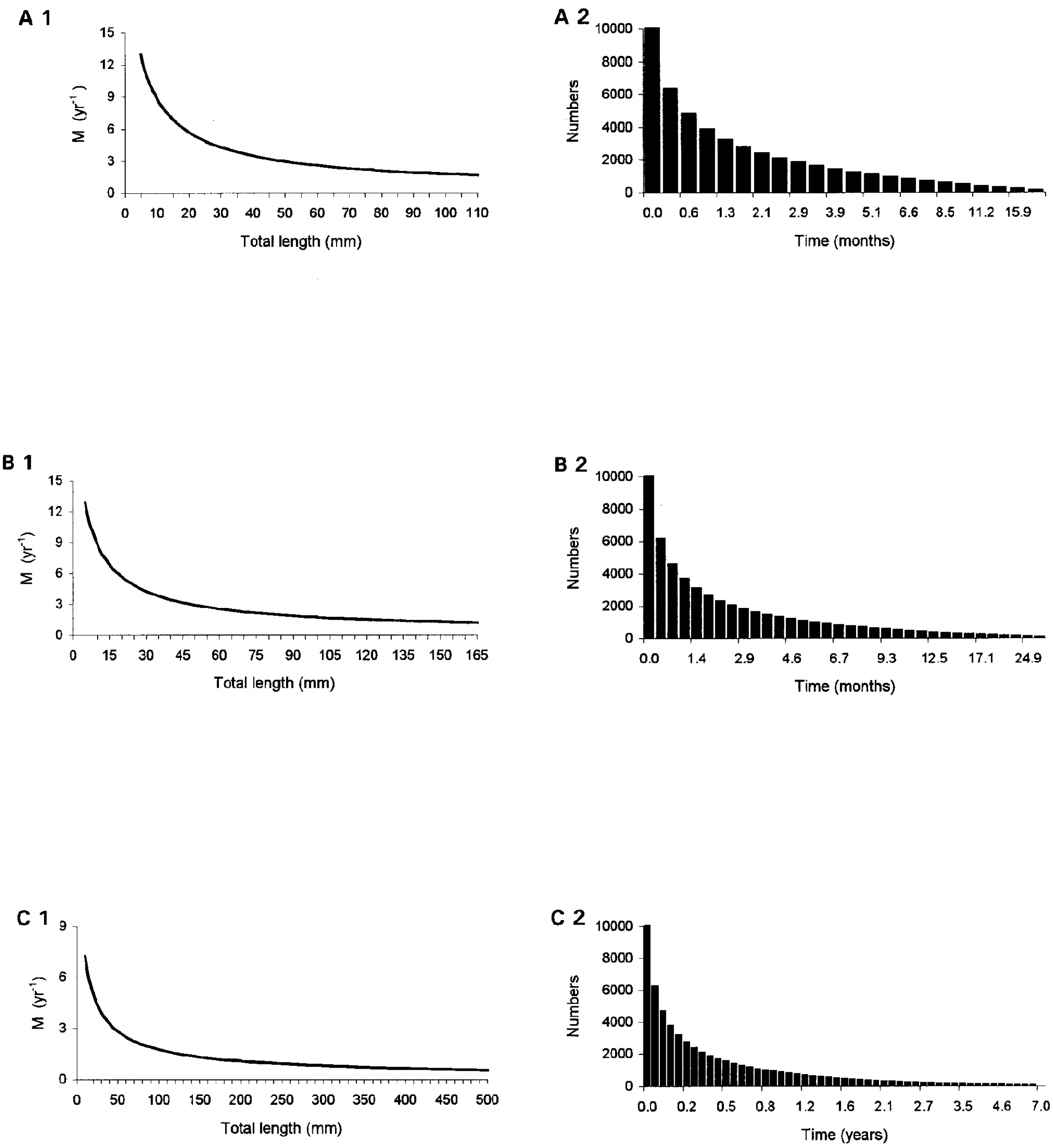



Figure 5. Mortality rate at size (**1**) and development of population numbers (**2**) assuming size-dependent mortality for *S. tanganicae* (**A**), *L. miodon* (**B**) and *L. stappersii* (**C**). Mean VBGF coefficients of each species have been used.

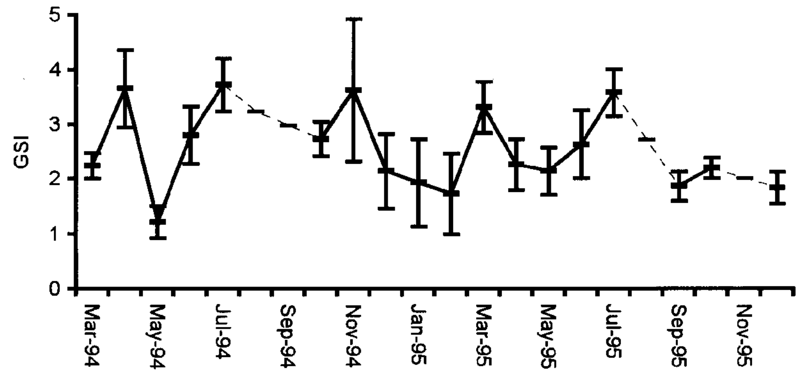



Figure 6. *Stolothrissa tanganicae*, females (Bujumbura samples, n = 786). Monthly mean GSI, error bars indicate 95% confidence interval. Dotted line indicates no data.

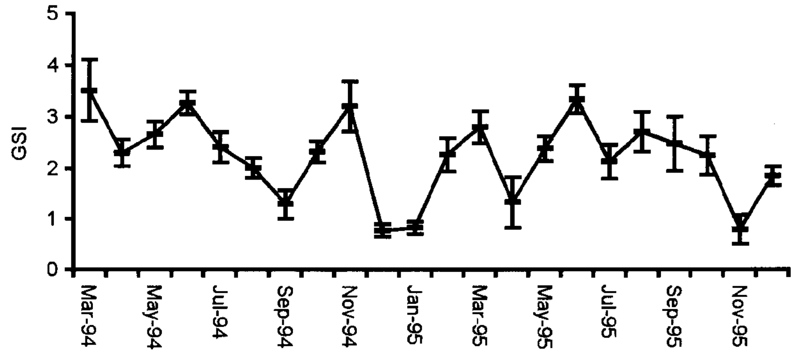



Figure 7. *Stolothrissa tanganicae*, females (Kigoma samples, n = 3019). Monthly mean GSI, error bars indicate 95% confidence interval.

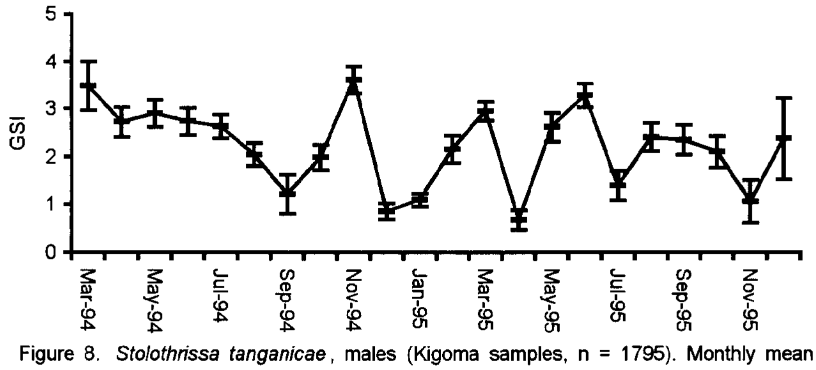
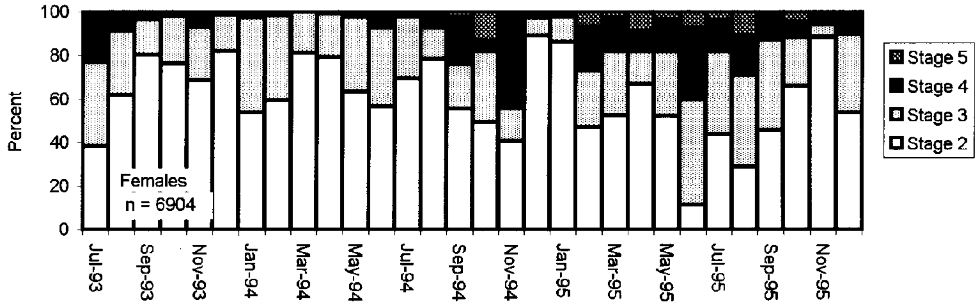



Figure 8. *Stolothrissa tanganicae*, males (Kigoma samples, n = 1795). Monthly mean GSI, error bars indicate 95% confidence interval.



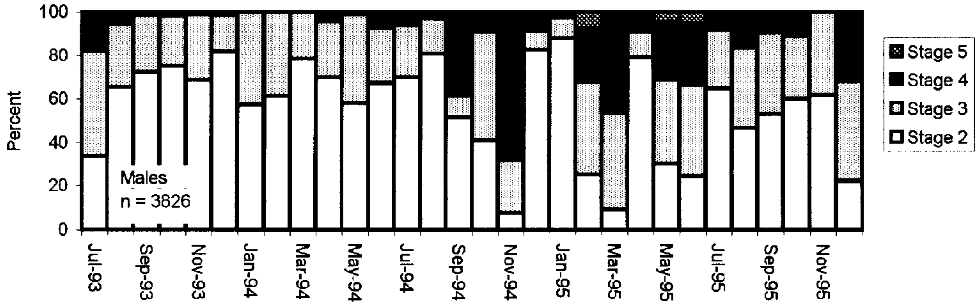
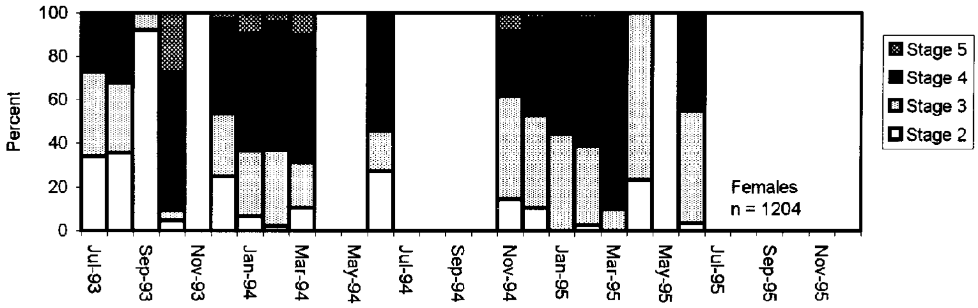




Figure 9. Monthly proportions (percentage) of maturity stages for *S. tanganicae* in Kigoma area, n = sample size.



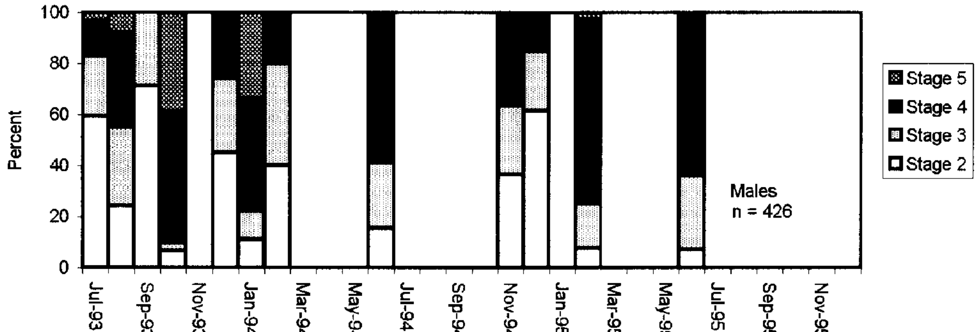




Figure 10. Monthly proportions (percentage) of maturity stages for *S. tanganicae* in Mpulungu area, n = sample size. No fish or only immature fish were caught in the months which are shown blank.

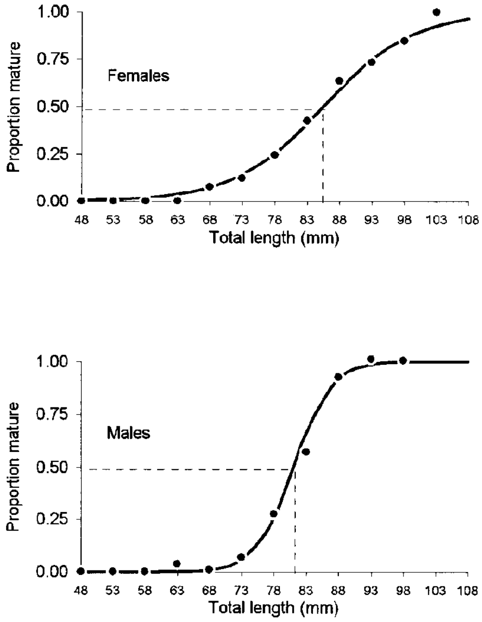



Figure 11. Proportion of mature individuals of *S. tanganicae* from Bujumbura and Uvira pooled samples. Data were fitted to the logistic equation (see Table 3). Dotted line indicates $L_m$.

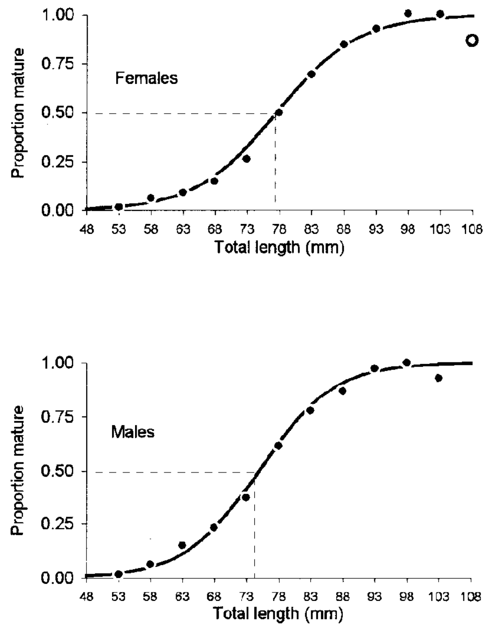



Figure 13. Proportion of mature individuals of *S. tanganicae* from Kalemie samples. Data were fitted to the logistic equation (see Table 3). Open circles have not been included. Dotted line indicates $L_m$.

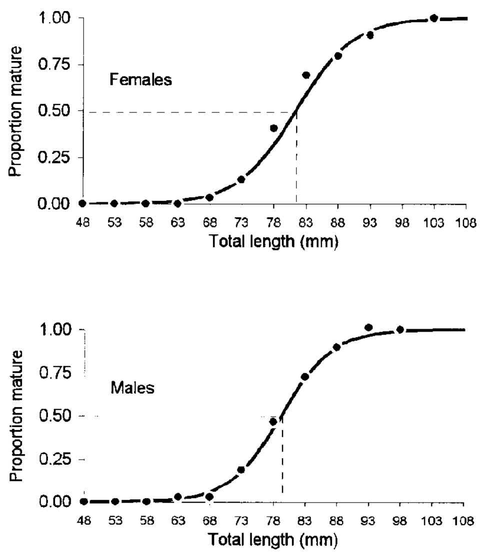



Figure 12. Proportion of mature individuals of *S. tanganicae* from Kigoma samples. Data were fitted to the logistic equation (see Table 3). Dotted line indicates $L_m$.

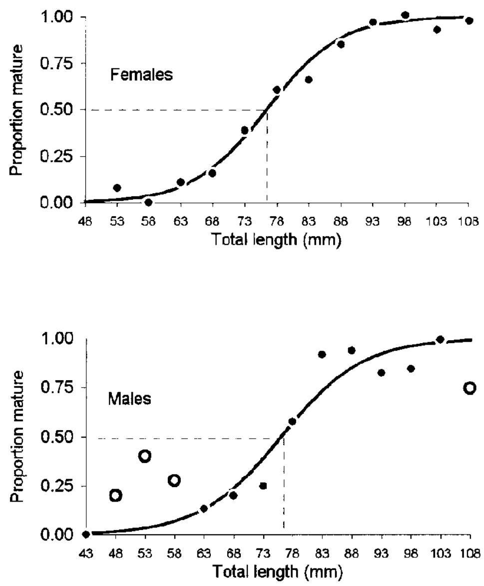
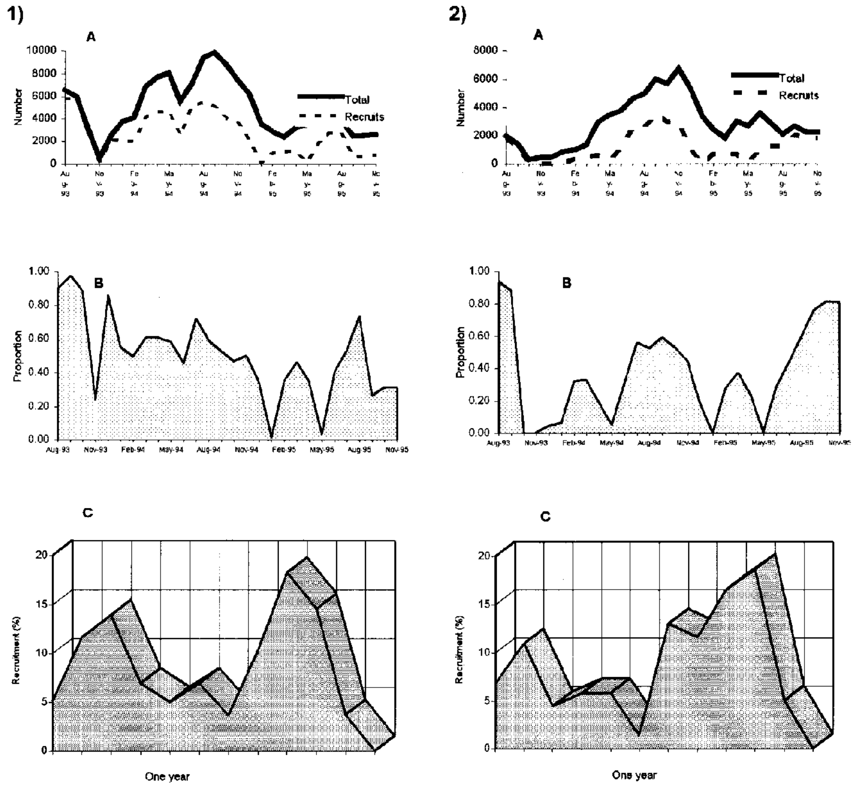



Figure 14. Proportion of mature individuals of *S. tanganicae* from Mpulungu samples. Data were fitted to the logistic equation (see Table 3). Open circles have not been included. Dotted line indicates $L_m$.



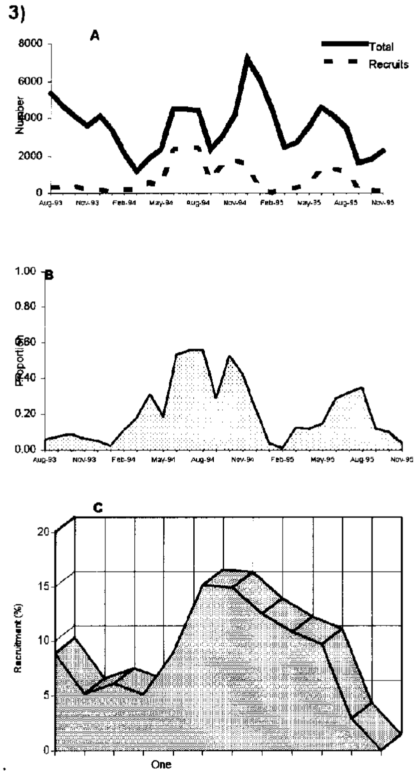
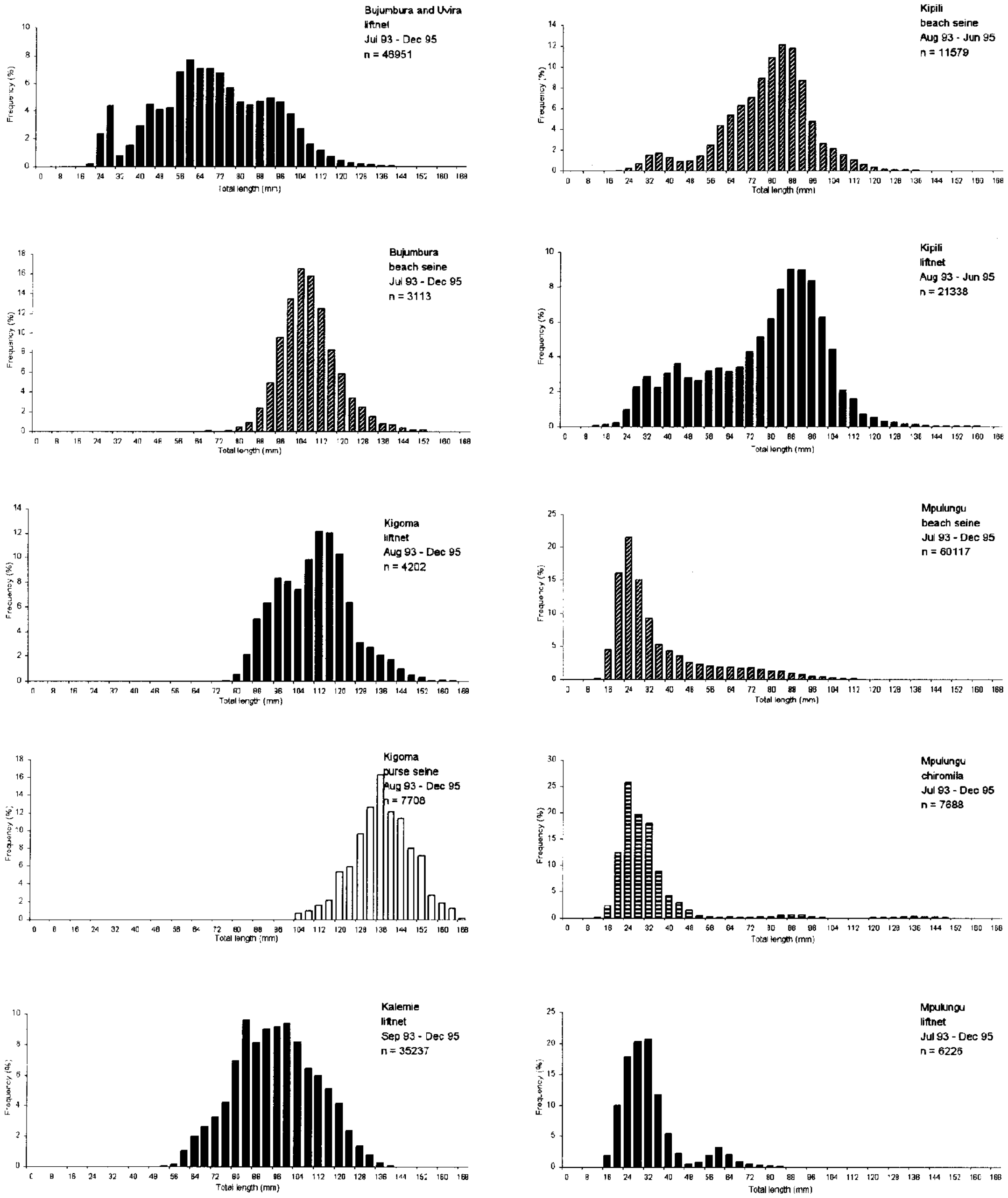




Figure 15. **A**, moving average over three months of *S. tanganicae* total number in samples and number of recruits (TL < 56mm) and, **B**, the proportion of recruits in the samples. **C**, approximation of recruitment pattern as inferred from backward projection onto one year relative time axis of L/F distributions according to VBGF (Pauly, 1983a, 1987). **1)** Bujumbura , **2)** Uvira and **3)** Kigoma.



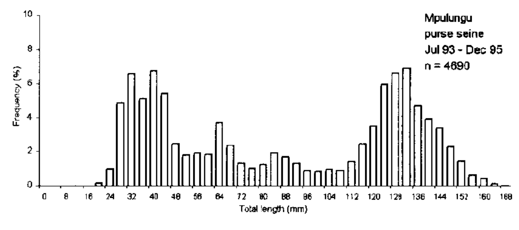
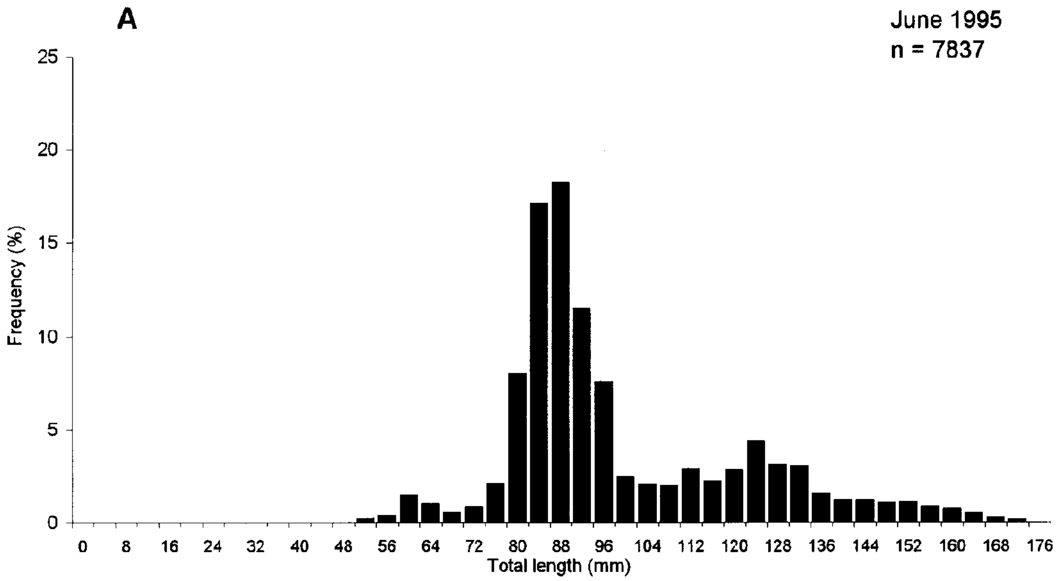




Figure 16. Length composition of the commercial catch of *L miodon* by areas and fishing gears.



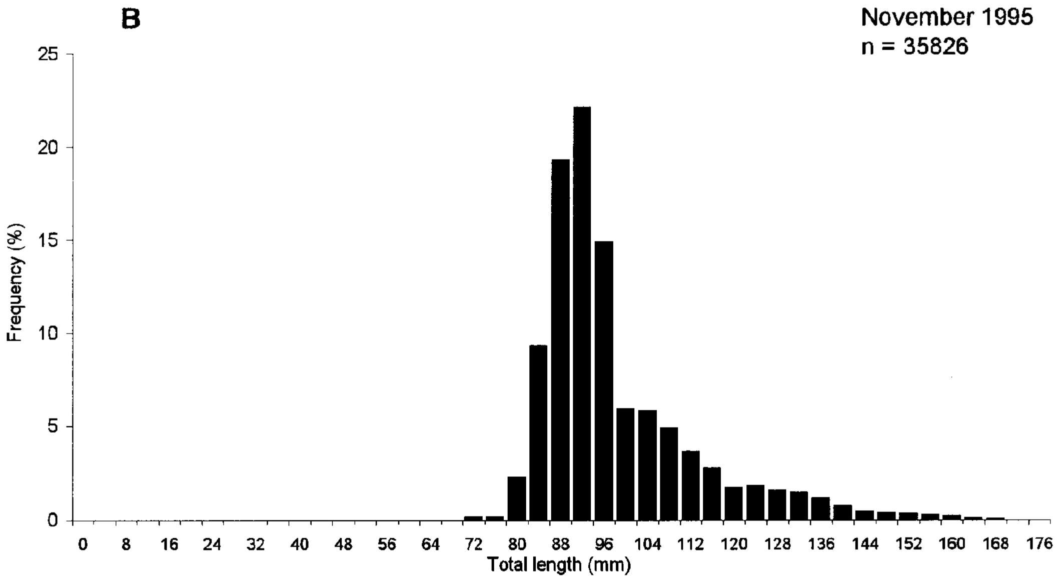




Figure 17. Size distribution of *L. miodon* for the whole lake from mid-water trawl surveys. **A**: 16 - 29 June 1995 survey; **B**: 16 November - 4 December 1995 survey.

| Area | Loo TL (mm) | K $yr^{-1}$ | Phi' | Z $yr^{-1}$ I | Z $yr^{-1}$ II | Z $yr^{-1}$ III | M $yr^{-1}$ IV | M $yr^{-1}$ V | M $yr^{-1}$ VI | M $yr^{-1}$ VII | Exploitation rate (E = F/Z) | $L_c$ (TL) mm |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bujumbura | 180 | 1.04 | 4.528 | 5.08 (4.44-5.72; 58mm) | 5.49 | 5.48 | 1.6 | 1.7 | 1.2 | 1.6 | 0.68 | 55 |
| Kipili | 180 | 1.06 | 4.536 | 6.91 (6.26-7.57; 91mm) | 7.98 | | 1.6 | 1.7 | 1.2 | 1.6 | 0.76 | 76 |
| Mpulungu | 182 | 1.01 | 4.524 | 4.21 (3.92-4.51;126mm) | 6.35 | 6.34 | 1.6 | 2.0 | 1.1 | 1.6 | 0.63 | 15 |
| Mean | 181 | 1.04 | 4.529 | 5.40 | 6.61 | 5.91 | 1.6 | 1.8 | 1.2 | 1.6 | 0.69 | |

Table 4. Von Bertalanffy growth model coefficients (Loo and K from the Elefan I method), total (Z) and natural (M) mortality estimates for *L. miodon* from various areas. Roman numerals indicate the methods used. I: length-converted catch curve (95% CI and cutoff, $L_c$, in brackets); **II**: Beverton and Holt, 1956; **III**:Ault and Ehrhardt, 1991; **IV** Pauly, 1980; **V**: Rikhter and Efanov, 1976; **VI**: Gunderson and Dygert, 1988; **VII**: Alagaraya, 1984. Exploitation rates are estimated from catch curve's Z and Pauly's M (see text). Mean length at first capture, Lc, based on the method of Pauly (1987).

| Sex and areas | a | b | r | $L_m$ (mm) | 95% CI for Lm | n |
|---|---|---|---|---|---|---|
| **Females** | | | | | | |
| Bujumbura & Uvira | 7.852 | -0.076 | 0.941 | 104 | 88-121 | 5116 |
| Kigoma | 6.903 | -0.058 | 0.908 | 119 | 96-142 | 1024 |
| Kalemie | 11.492 | -0.115 | 0.990 | 100 | 94-107 | 2303 |
| Mpulungu | 6.774 | -0.085 | 0.962 | 80 | 68-92 | 1360 |
| **Males** | | | | | | |
| Bujumbura & Uvira | 11.565 | -0.119 | 0.973 | 97 | 87-108 | 2452 |
| Kigoma | 10.776 | -0.124 | 0.915 | 87 | 65-101 | 563 |
| Kalemie | 12.976 | -0.133 | 0.992 | 97 | 92-103 | 2531 |
| Mpulungu | 4.304 | -0.048 | 0.968 | 89 | 76-103 | 950 |

Table 5. Linear regression estimates for parameters of the logistic equation relating proportion mature to length for *L. miodon* (see also text and Figs 27 to 30). The correlation coefficient (r), predicted length at 50% maturity ($L_m$), 95% confidence interval and sample size (n) are also given.

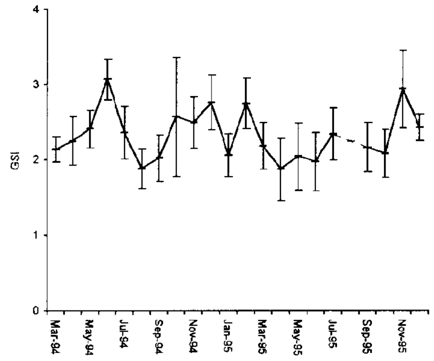



Figure 18. *Limnothrissa miodon*, females (Bujumbura samples, n = 2106). Monthly mean GSI, error bars indicate 95% confidence interval. Dotted line indicates no data.

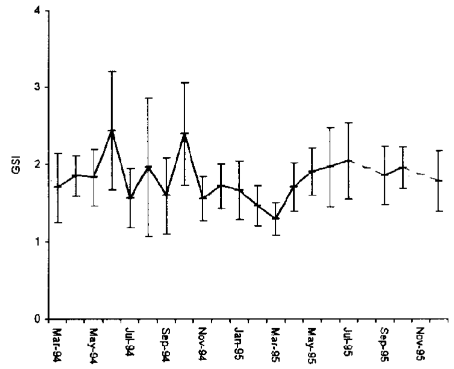



Figure 19. *L. miodon*, males (Bujumbura samples, n = 667). Monthly mean GSI, error bars indicate 95% confidence interval. Dotted line indicates no data.

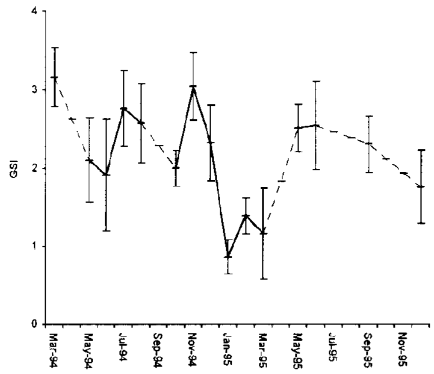



Figure 20. *Limnothrissa miodon*, females (Kigoma samples, n = 864). Monthly mean GSI, error bars indicate 95% confidence interval. Dotted line indicates no data.

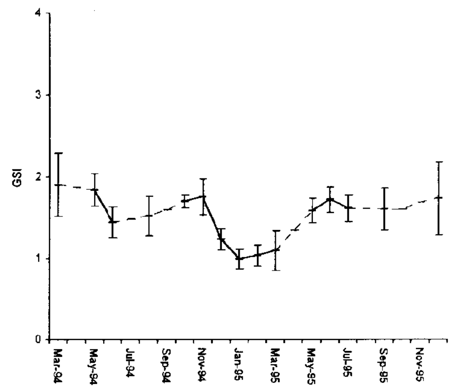



Figure 21. *L. miodon*, males (Kigoma samples, n = 805). Monthly mean GSI, error bars indicate 95% confidence interval. Dotted line indicates no data.

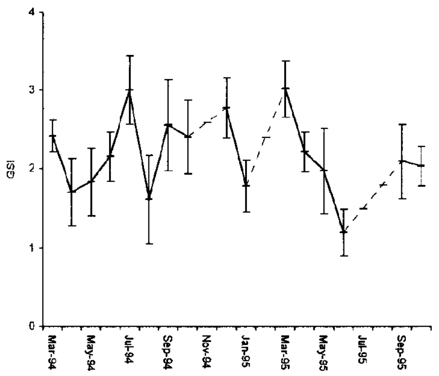



Figure 22. *Limnothrissa miodon*, females (Mpulungu samples, n = 1204). Monthly mean GSI, error bars indicate 95% confidence interval. Dotted line indicates no data.

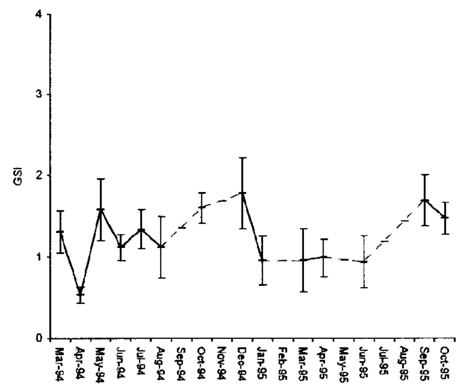



Figure 23. *L. miodon*, males (Mpulungu samples, n = 394). Monthly mean GSI, error bars indicate 95% confidence interval. Dotted line indicates no data.

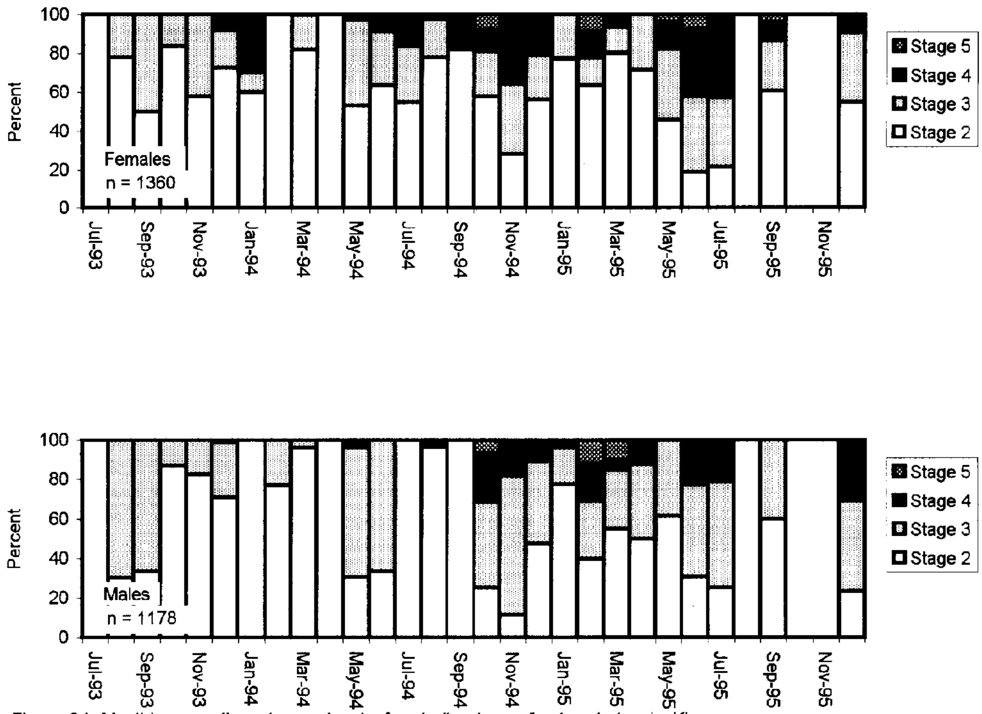



Figure 24. Monthly proportions (percentage) of maturity stages for *L. miodon* in Kigoma area, n = sample size. No fish or only immature fish were caught in the months which are shown blank.

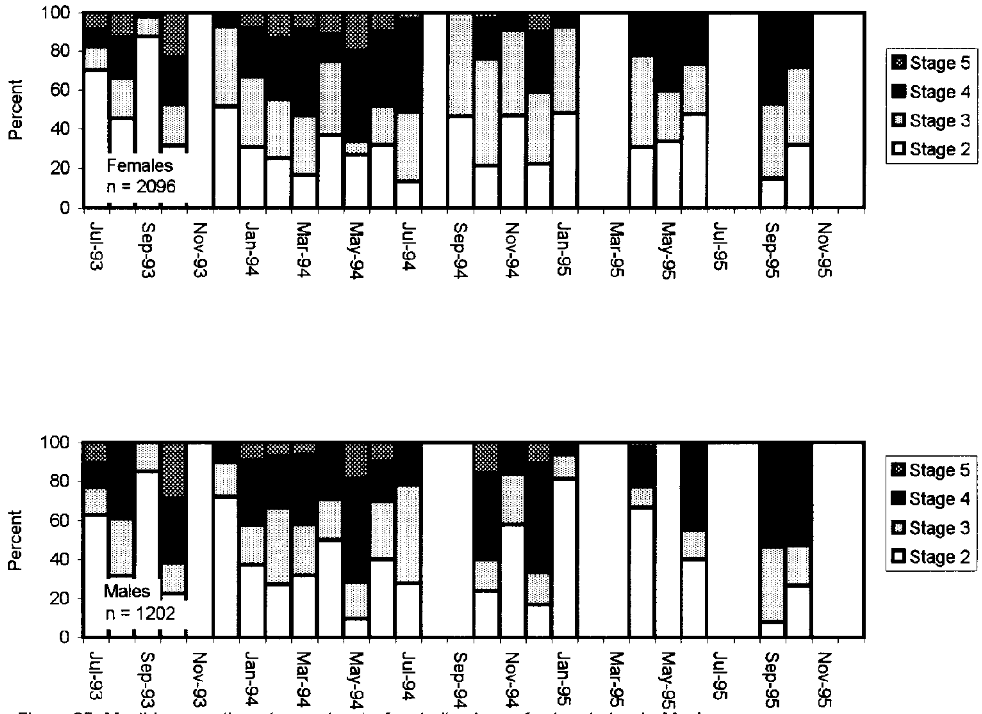



Figure 25. Monthly proportions (percentage) of maturity stages for *L. miodon* in Mpulungu area, n = sample size. No fish or only immature fish were caught in the months which are shown blank

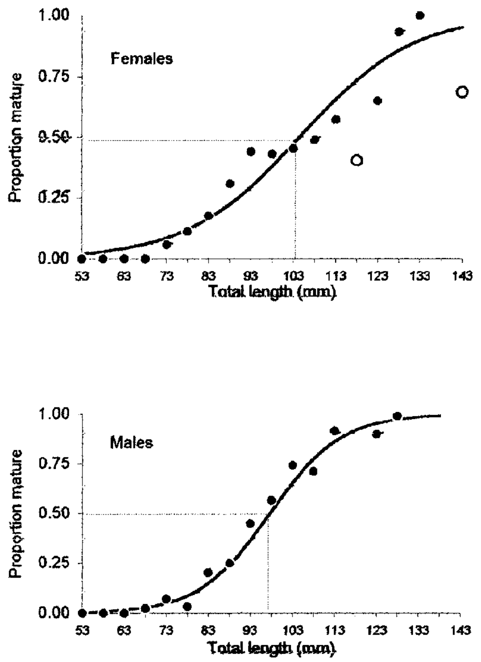



Figure 26. Proportion of mature individuals of *L. miodon* from Bujumbura and Uvira pooled samples. Data were fitted to the logistic equation (see Table 5). Open circles have not been included. Dotted line indicates $L_m$.

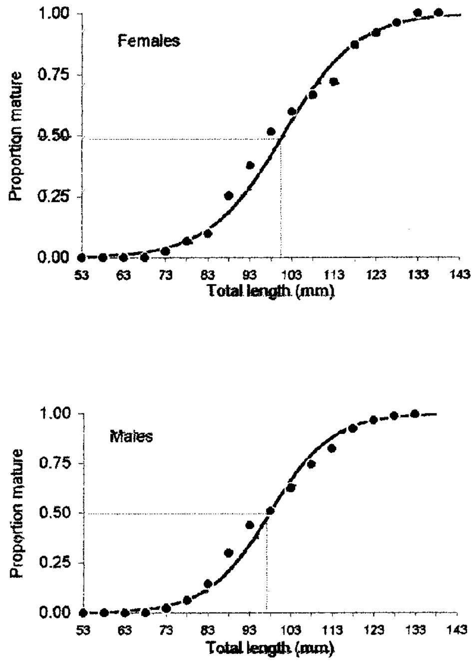



Figure 28. Proportion of mature individuals of *L. miodon* from Kalemie samples. Data were fitted to the logistic equation (see Table 5). Dotted line indicates $L_m$.

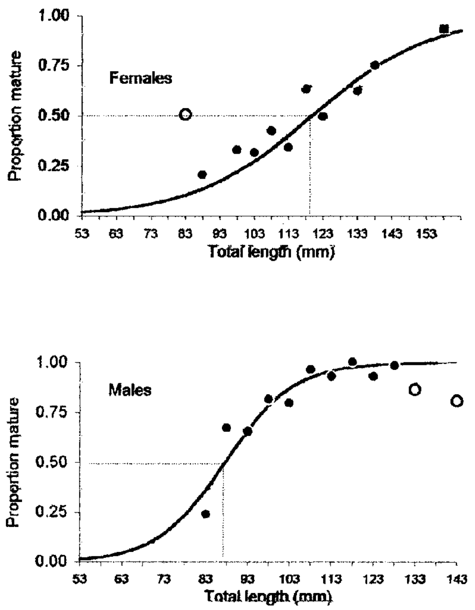



Figure 27. Proportion of mature individuals of *L. miodon* from Kigoma samples. Data were fitted to the logistic equation (see Table 5). Open circles have not been included. Dotted line indicates $L_m$.

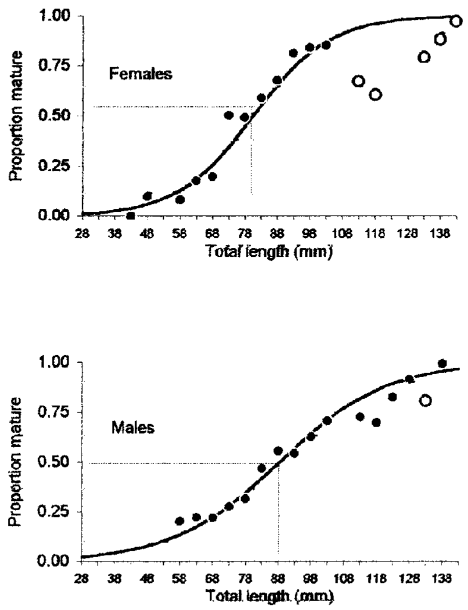



Figure 29. Proportion of mature individuals of *L. miodon* from Mpulungu samples. Data were fitted to the logistic equation (see Table 5). Open circles have not been included. Dotted line indicates $L_m$.

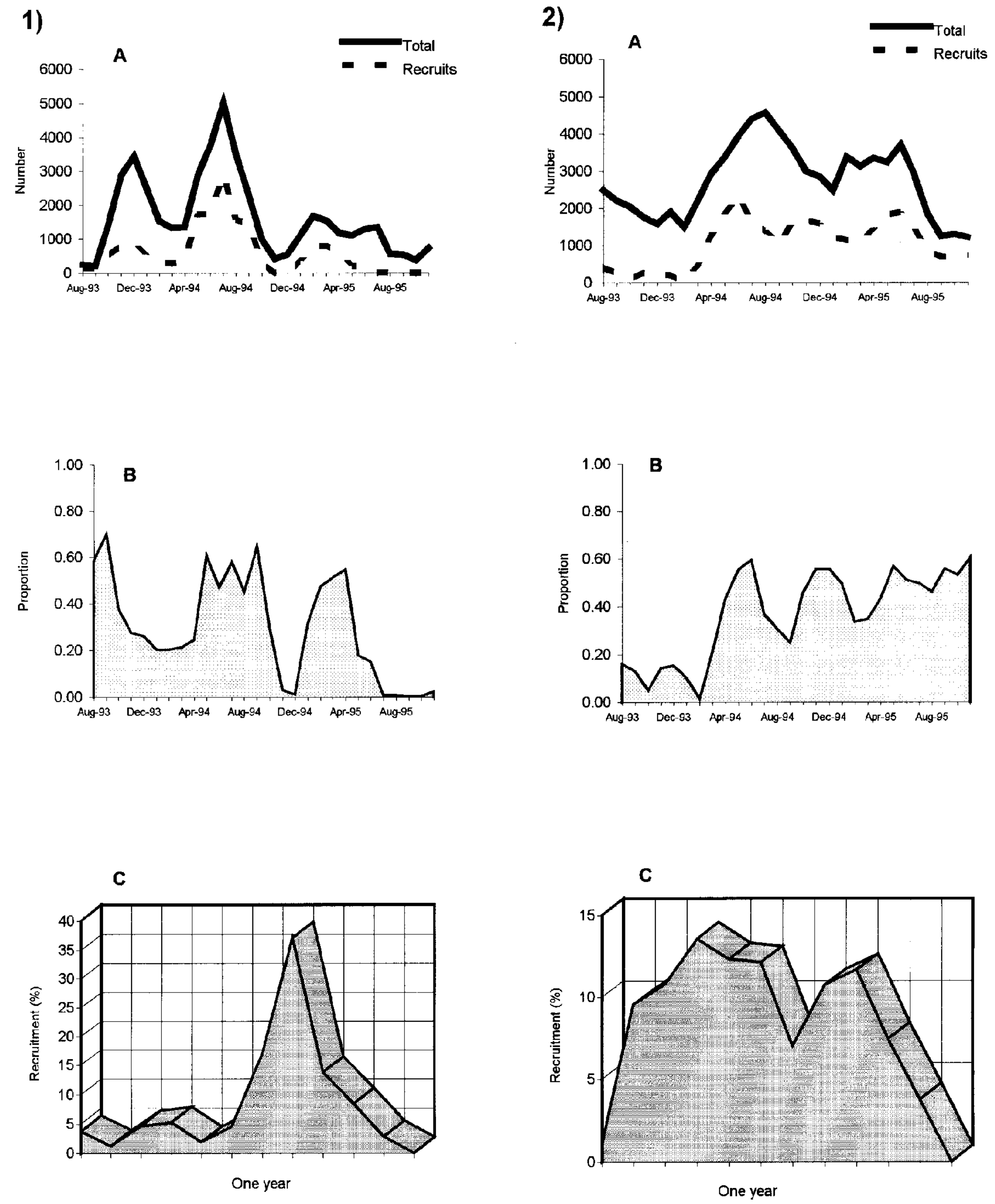
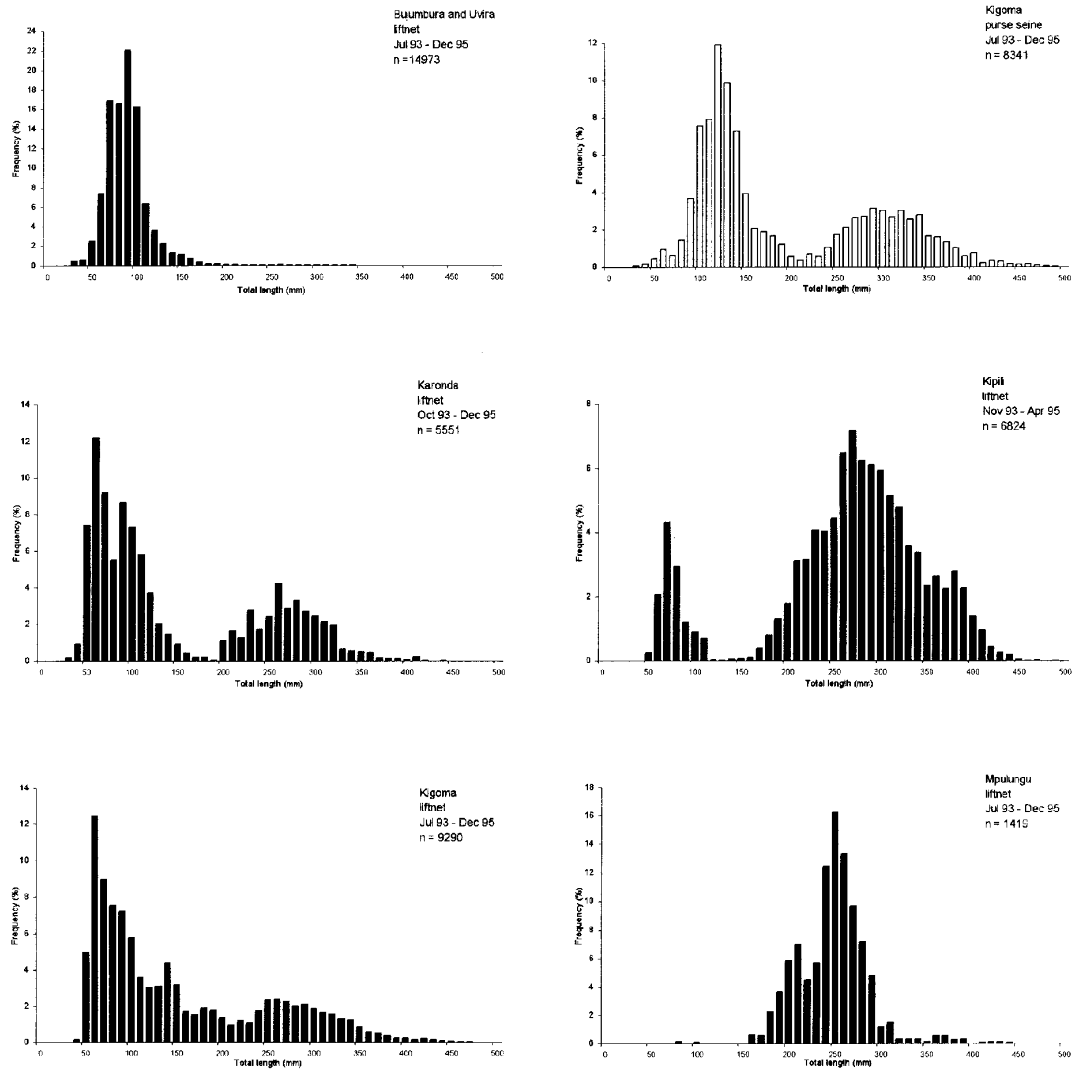



Figure 30. **A**, moving average over three months of *L. miodon* total number in samples and number of recruits and, **B**, the proportion of recruits in the samples. **C**, recruitment pattern as inferred from backward projection onto one year relative time axis of L/F distributions according to VBGF (Pauly, 1983a, 1987). **1)** Bujumbura (recruits: TL < 55mm). **2)** Mpulungu (recruits: TL < 26mm).



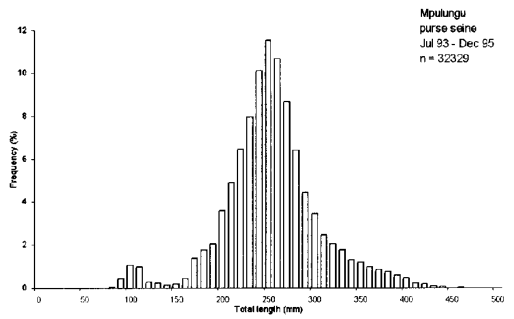
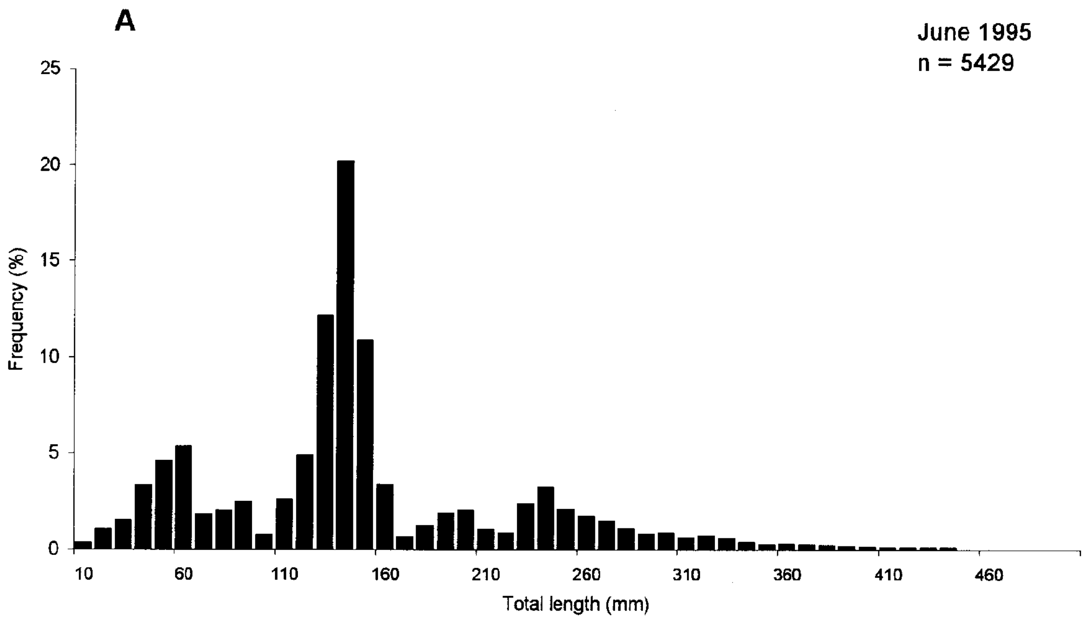




Figure 31. Length composition of the commercial catch of *L. stappersii* by areas and fishing gears.



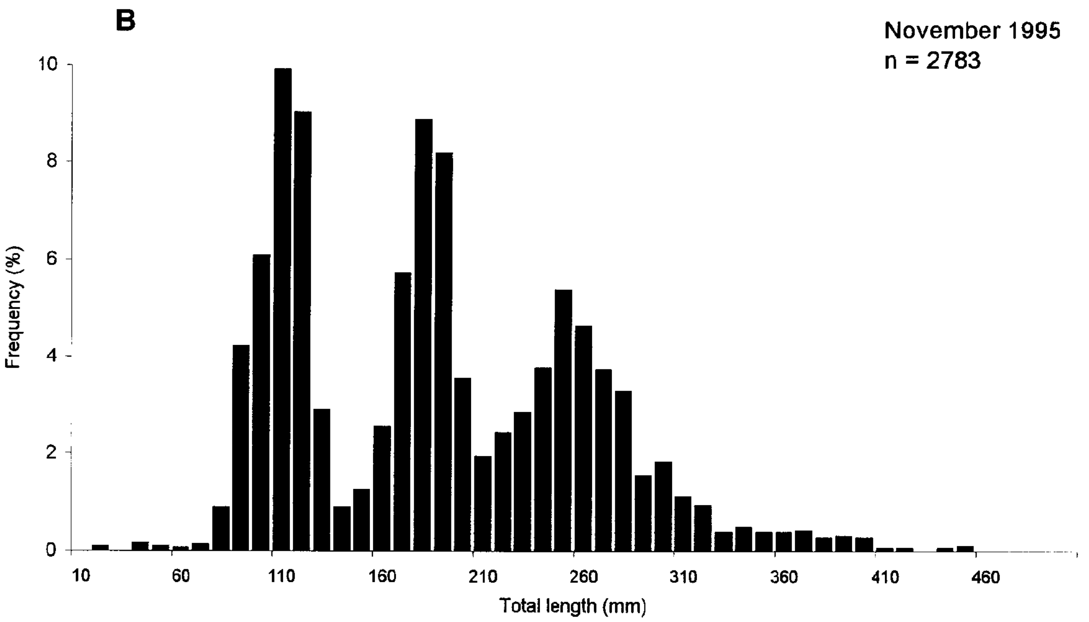




Figure 32. Size distribution of *L. stappersii* for the whole lake from mid-water trawl surveys. **A**: 16 - 29 June 1995 survey; **B**: 16 November - 4 December 1995 survey.

| Area | Loo TL (mm) | K $yr^{-1}$ | Phi' | Z $yr^{-1}$ I | Z $yr^{-1}$ II | Z $yr^{-1}$ III | M $yr^{-1}$ IV | M $yr^{-1}$ V | M $yr^{-1}$ VI | M $yr^{-1}$ VII | Exploitation rate (E = F/Z) | $L_c$ (TL) mm |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Kigoma | 519 | 0.44 | 5.070 | 1.35 (1.25-1.46; 300mm) | 1.16 | 1.15 | 0.9 | 0.9 | 0.5 | 0.7 | 0.37 | 103 |
| | 506 | 0.43 | 5.038 | 1.18 (1.08-1.28; 300mm) | 1.08 | 1.07 | 0.8 | 0.8 | 0.5 | 0.7 | 0.28 | 97 |
| Kipili | 551 | 0.41 | 5.096 | 2.33 (2.07-2.59; 260mm) | 1.82 | 1.80 | 0.8 | 0.9 | 0.5 | 0.6 | 0.65 | 250 |
| | 550 | 0.36 | 5.031 | 2.00 (1.78-2.23; 260mm) | 1.56 | 1.46 | 0.7 | 0.8 | 0.4 | 0.5 | 0.63 | 250 |
| Mpulungu | 510 | 0.42 | 5.036 | 2.11 (1.99-2.22; 250mm) | 2.20 | 2.18 | 0.8 | 0.9 | 0.5 | 0.6 | 0.61 | 234 |
| | 530 | 0.40 | 5.051 | 2.35 (2.20-2.50; 250mm) | 2.30 | 2.29 | 0.8 | 0.9 | 0.5 | 0.6 | 0.66 | 239 |
| Mean | 528 | 0.41 | 5.054 | 1.89 | 1.69 | 1.66 | 0.8 | 0.9 | 0.5 | 0.6 | 0.53 | |

Table 6. Von Bertalanffy growth model coefficients (Loo and K from the Elefan I method), total (Z) and natural (M) mortality estimates for *L. stappersii* from various areas. The second set of growth parameters is from the SLCA method. Roman numerals indicate the methods used. **I**: length-converted catch curve ( 95% CI and cutoff, L', in brackets); **II**: Beverton and Holt, 1956; **III**:Ault and Ehrhardt, 1991; **IV**: Pauly, 1980; **V**: Rikhter and Efanov, 1976; **VI**: Gunderson and Dygert, 1988; **VII**: Alagaraya, 1984. Exploitation rates are estimated from catch curve's Z and Pauly's M. Mean length at first capture, Lc, based on the method of Pauly (1987).

| Sex and areas | a | b | r | Lm (mm) | 95% CI for Lm | n |
|---|---|---|---|---|---|---|
| **Females** | | | | | | |
| Kigoma | 7.189 | -0.026 | 0.912 | 278 | 217-338 | 1687 |
| Mpulungu | 8.130 | -0.034 | 0.96773 | 237 | 214-260 | 4217 |
| **Males** | | | | | | |
| Kigoma | 8.090 | -0.029 | 0.974 | 278 | 253-303 | 1186 |
| Mpulungu | 3.976 | -0.016 | 0.956 | 255 | 213-298 | 5702 |

Table 7. Linear regression estimates for the parameters of the logistic equation relating proportion mature to length for *L. stappersii* (see also text and Figs 39 and 40). The correlation coefficient (r), predicetd length at 50% maturity ($L_m$), 95% confidence intervals and sample size (n) are also given.

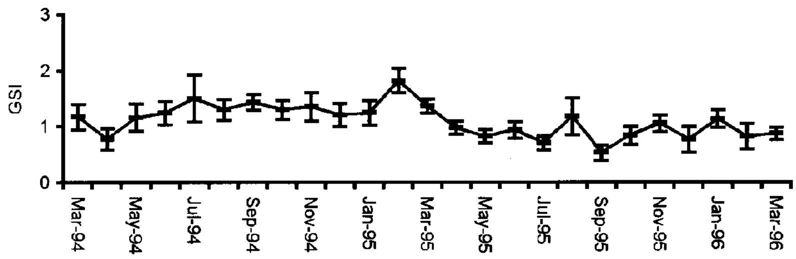



Figure 33. *Lates stappersii*, females (Kigoma samples, n = 2249). Monthly mean GSI, error bars indicate 95% confidence interval.

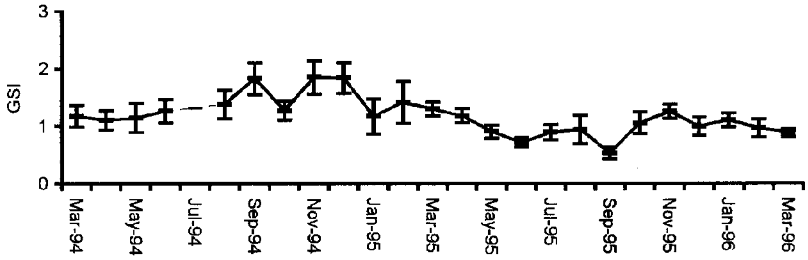



Figure 34. *Lates stappersii*, males (Kigoma samples, n = 1858). Monthly mean GSI, error bars indicate 95% confidence interval. Dotted line is for missing data.

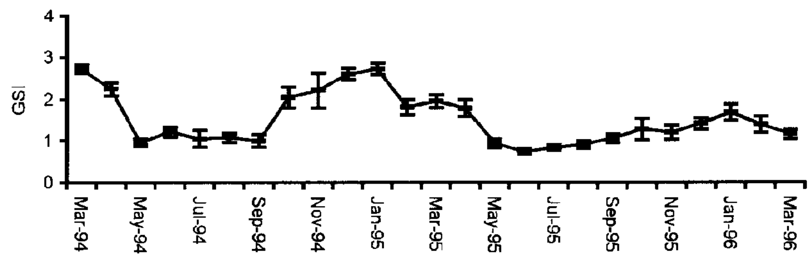



Figure 35. *Lates stappersii*, females (Mpulungu samples, n = 4296). Monthly mean GSI, error bars indicate 95% confidence interval.

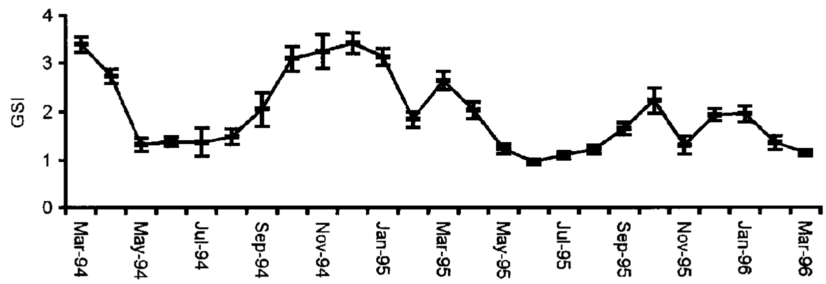



Figure 36. *Lates stappersii*, males (Mpulungu samples, n = 1858). Monthly mean GSI, error bars indicate 95% confidence interval.

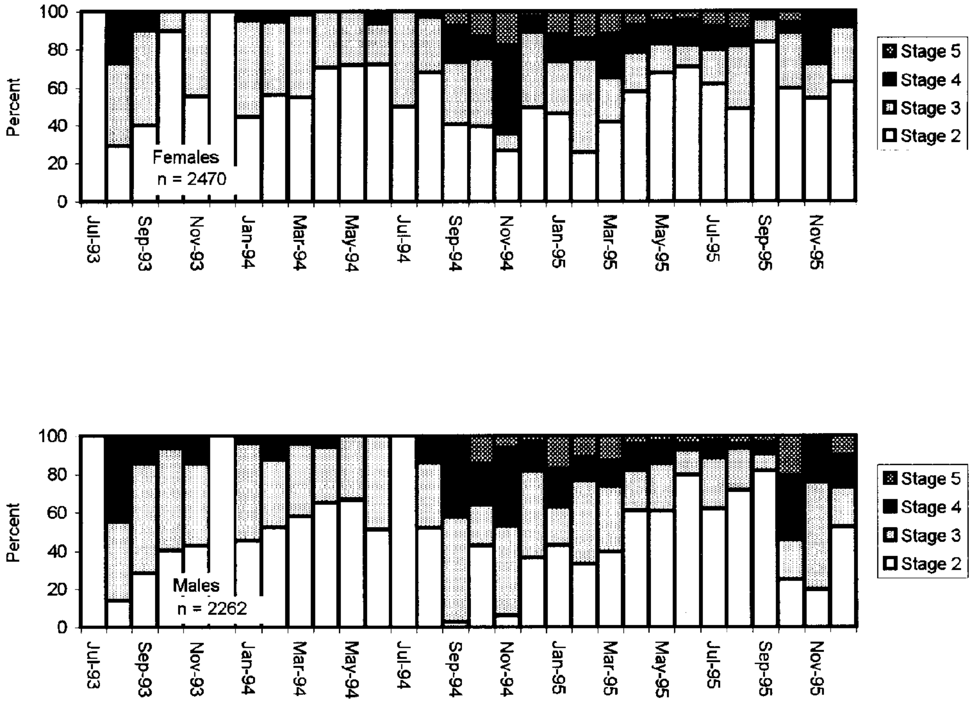



Figure 37. Monthly proportions (percentage) of maturity stages for *L. stappersii* in Kigoma area, n = sample size. No fish or only immature fish were caught in the months which are shown blank.

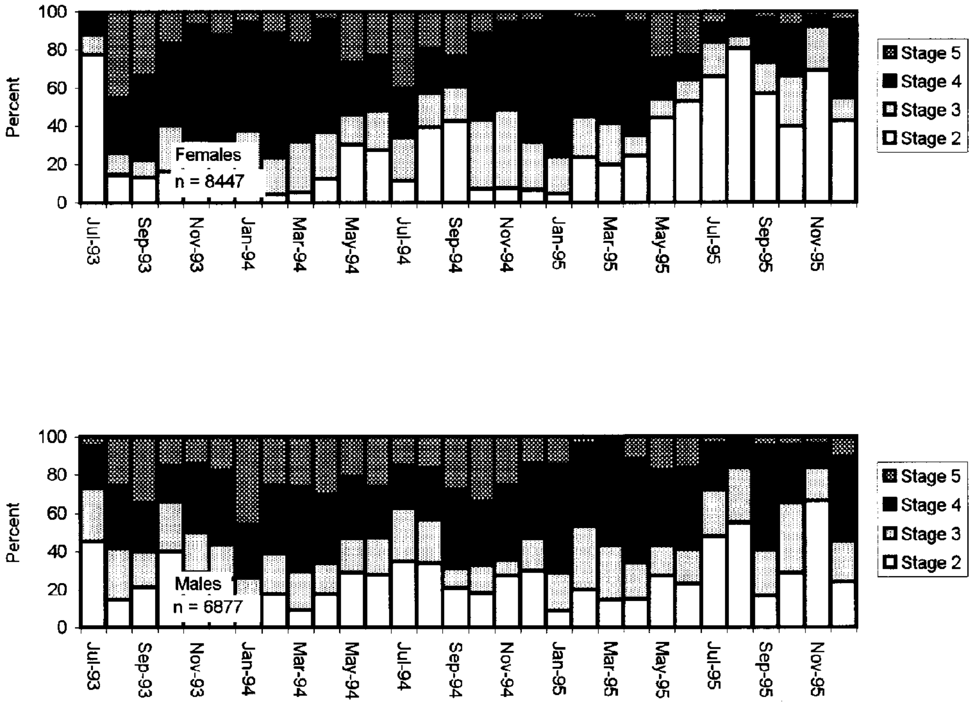



Figure 38. Monthly proportions (percentage) of maturity stages for *L. stappersii* in Mpulungu area, n = sample size.

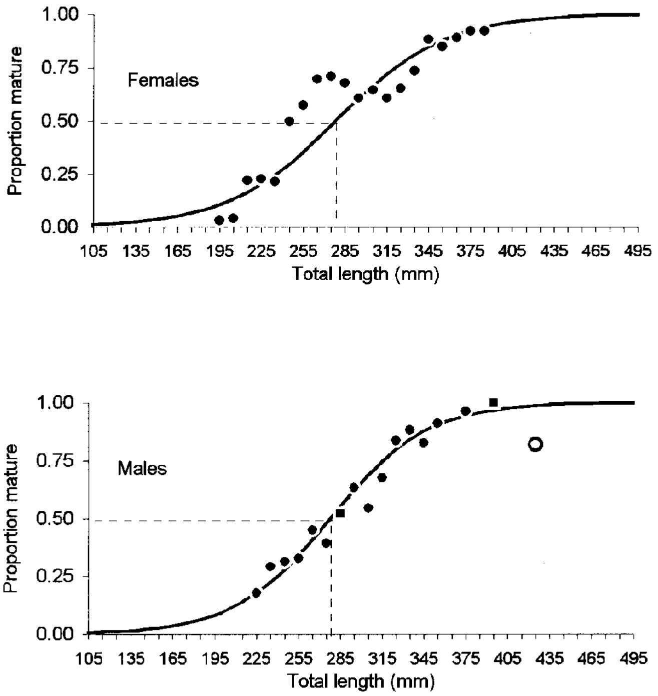



Figure 39. Proportion of mature individuals of *L. stappersii* from Kigoma samples. Data were fitted to the logistic equation (see Table 7). Open circles have not been included.

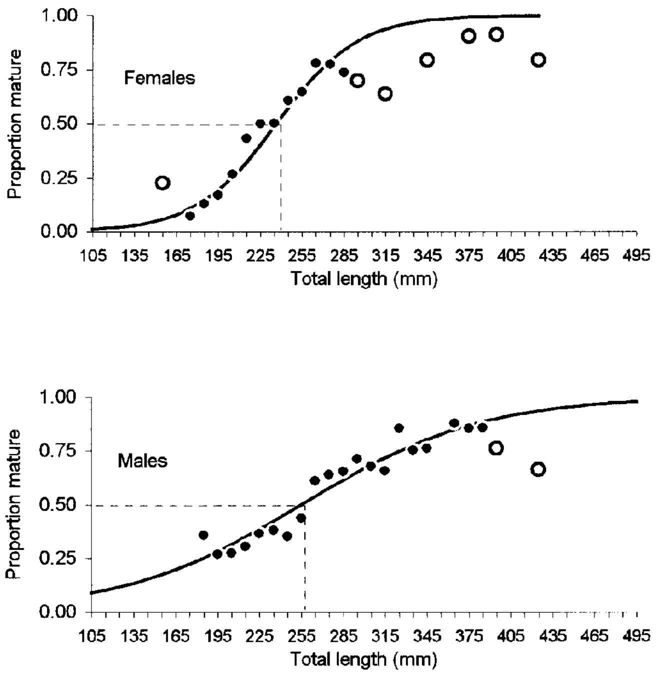



Figure 40. Proportion of mature individuals of *L. stappersii* from Mpulungu samples. Data were fitted to the logistic equation (see Table 7). Open circles have not been included.

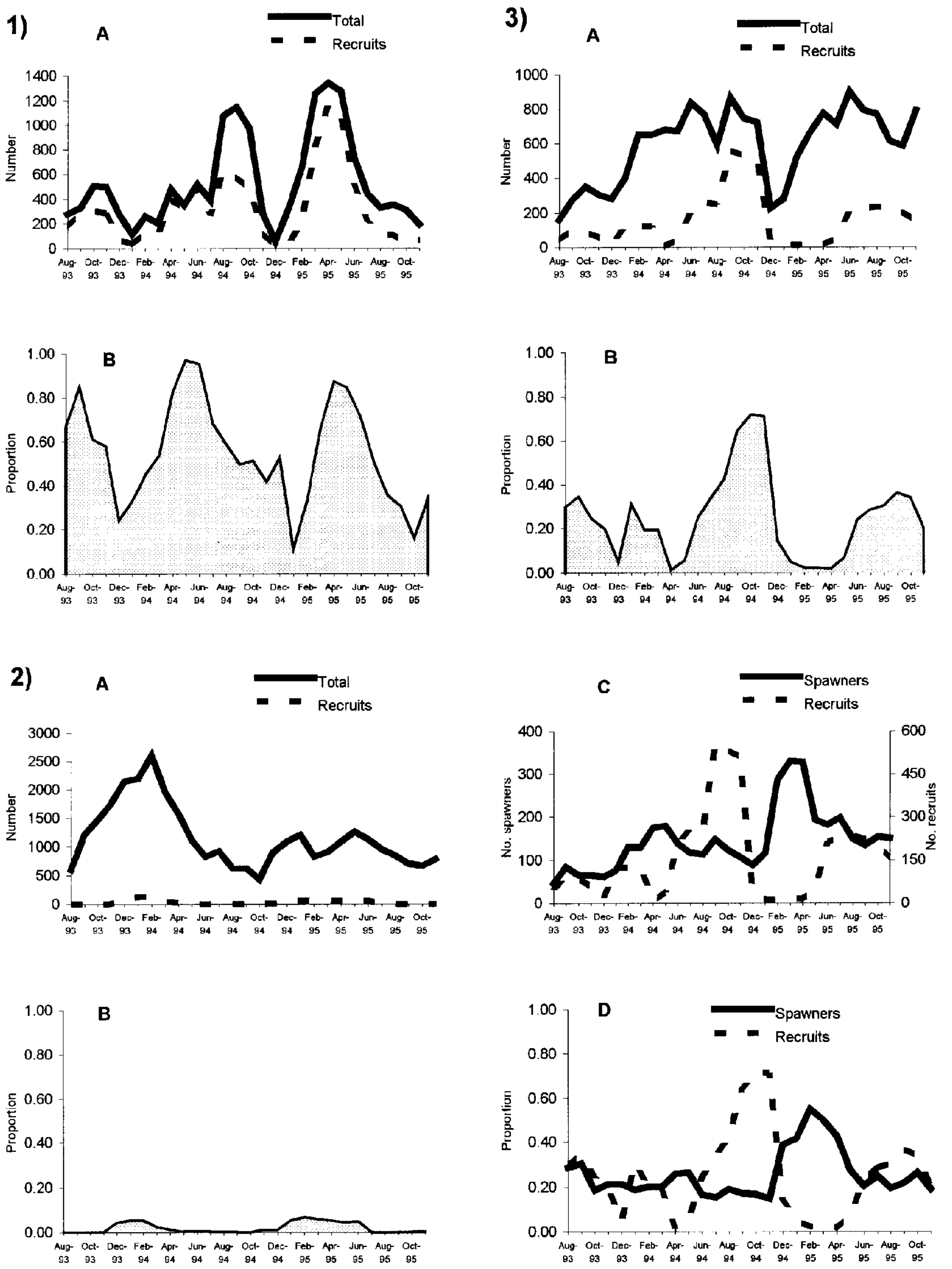



Figure 41. **A**, moving average over three months of *L. stappersii* total number in samples and number of recruits (TL < 90mm) and, **B**, the proportion of recruits in the samples. **1)** Bujumbura and Uvira. **2)** Mpulungu. **3)** Kigoma. **C**, moving average over three months of *L. stappersii* mature individuals (TL > 275mm) and recruits, **D** the proportion of recruits and spawnwers in Kigoma samples.

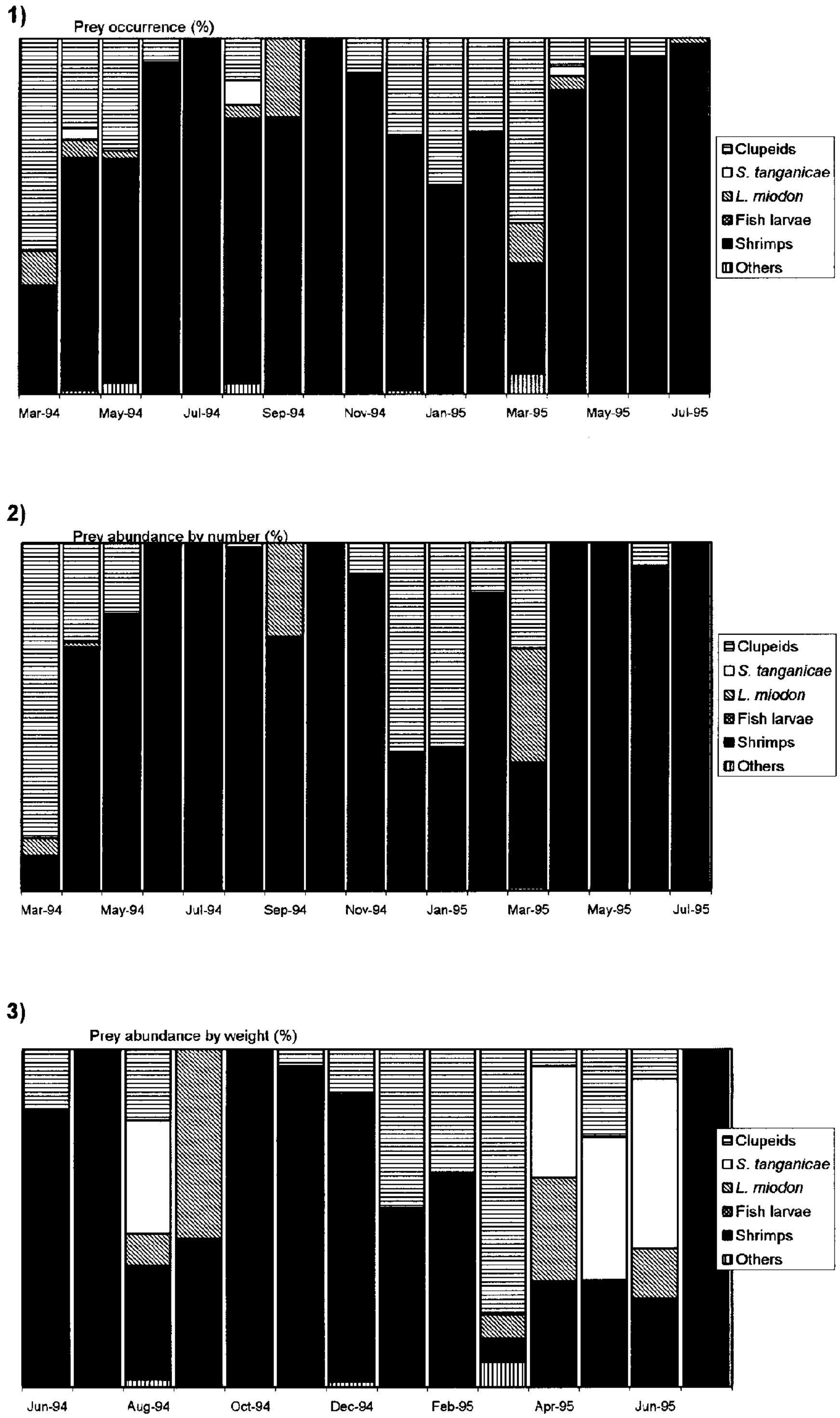



Figure 42. Monthly composition (%) of the diet of *L. stappersii* in the Mpulungu area expressed by **1)** prey occurrence, **2)** prey number and **3)** prey weight. Note time axes are different.

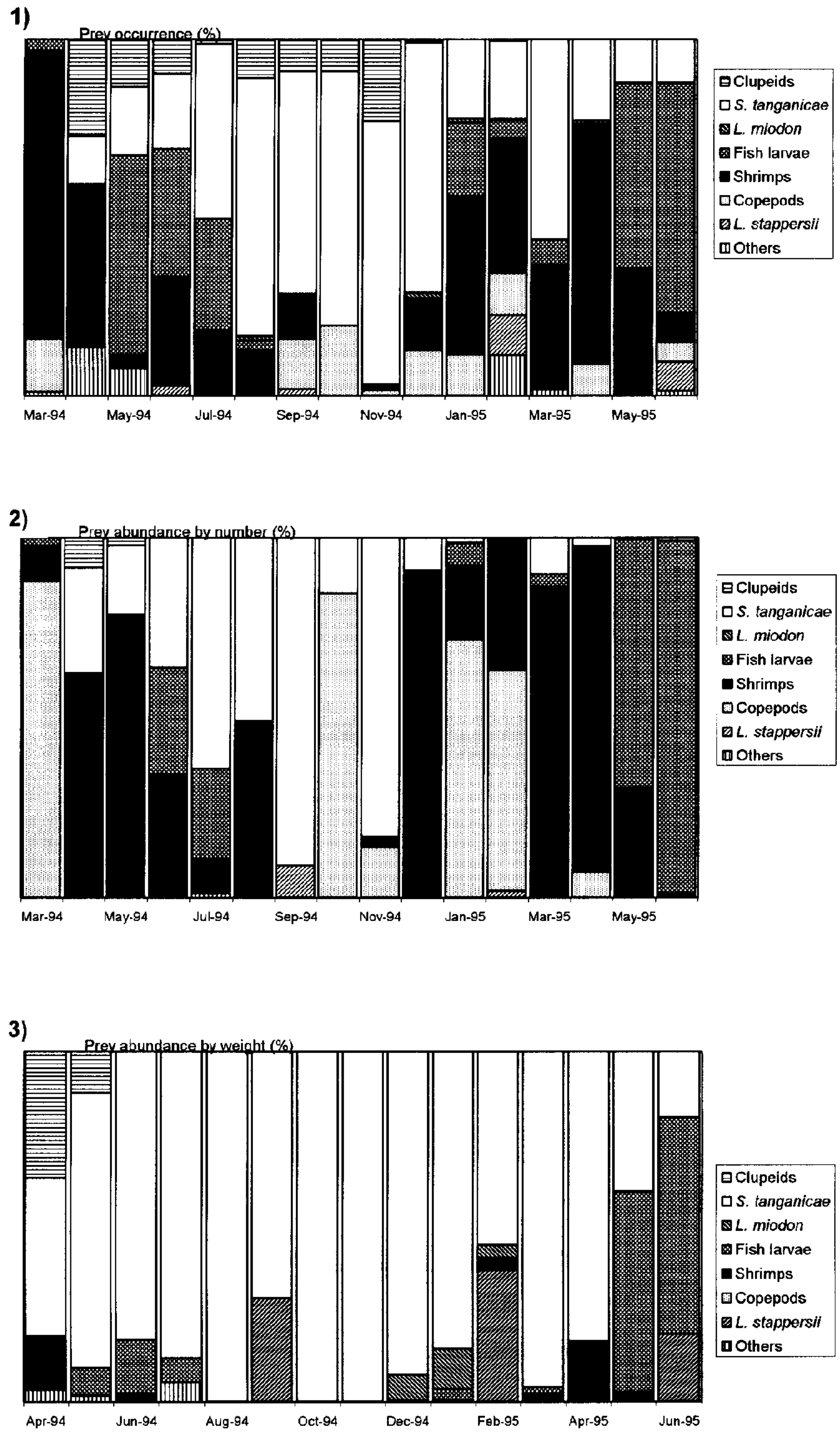



Figure 43. Monthly composition (%) of the diet of *L. stappersii* in Kigoma area expressed by **1)** prey occurrence, **2)** prey number and **3)** prey weight. Note time axes are different.

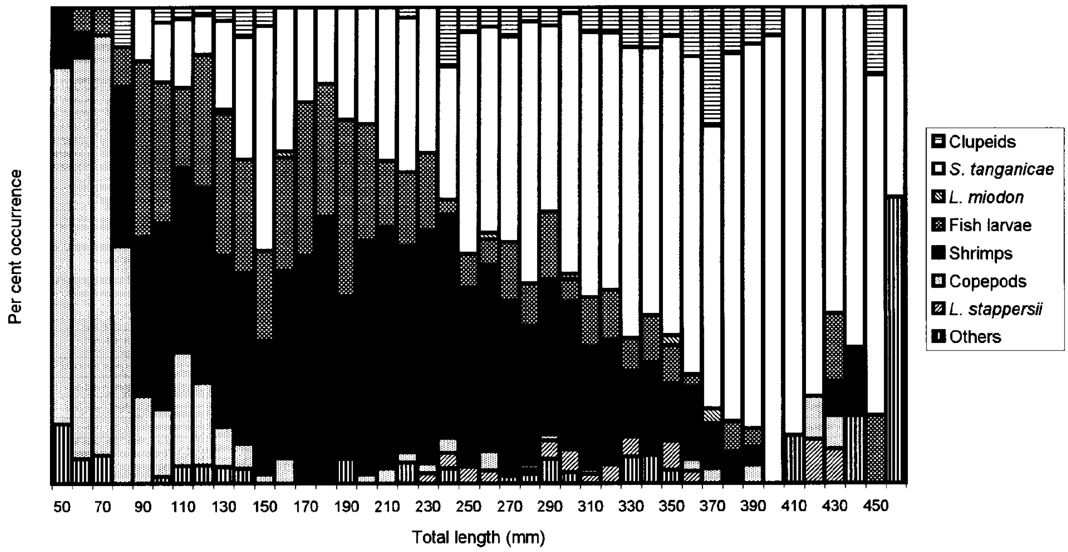



Figure 44. Variation in the diet of *L. stappersii* with size (total length) in the Kigoma area.

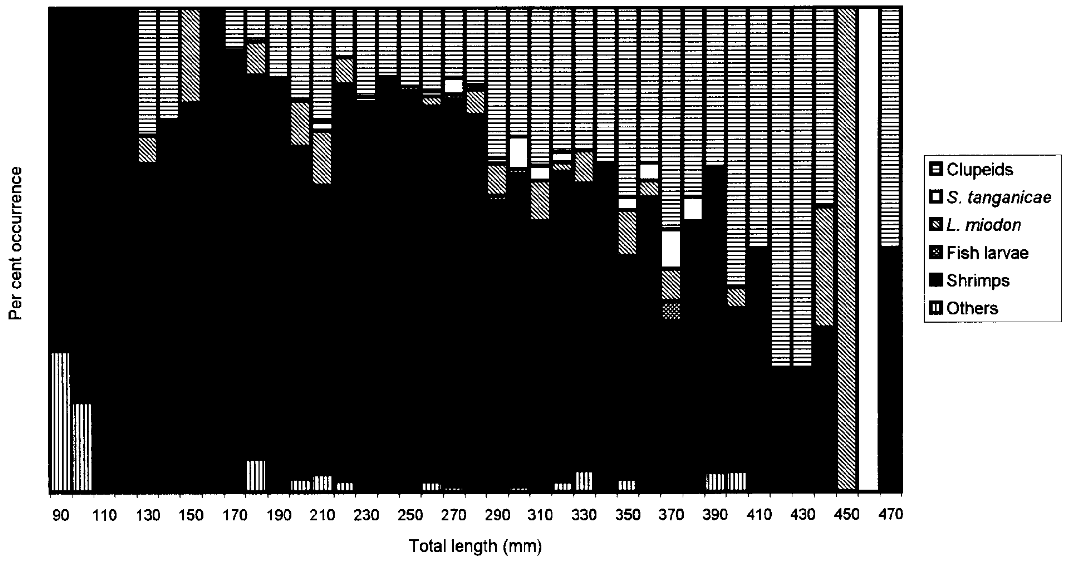



Figure 45. Variation in the diet of *L. stappersii* with size (total length) in the Mpulungu area.

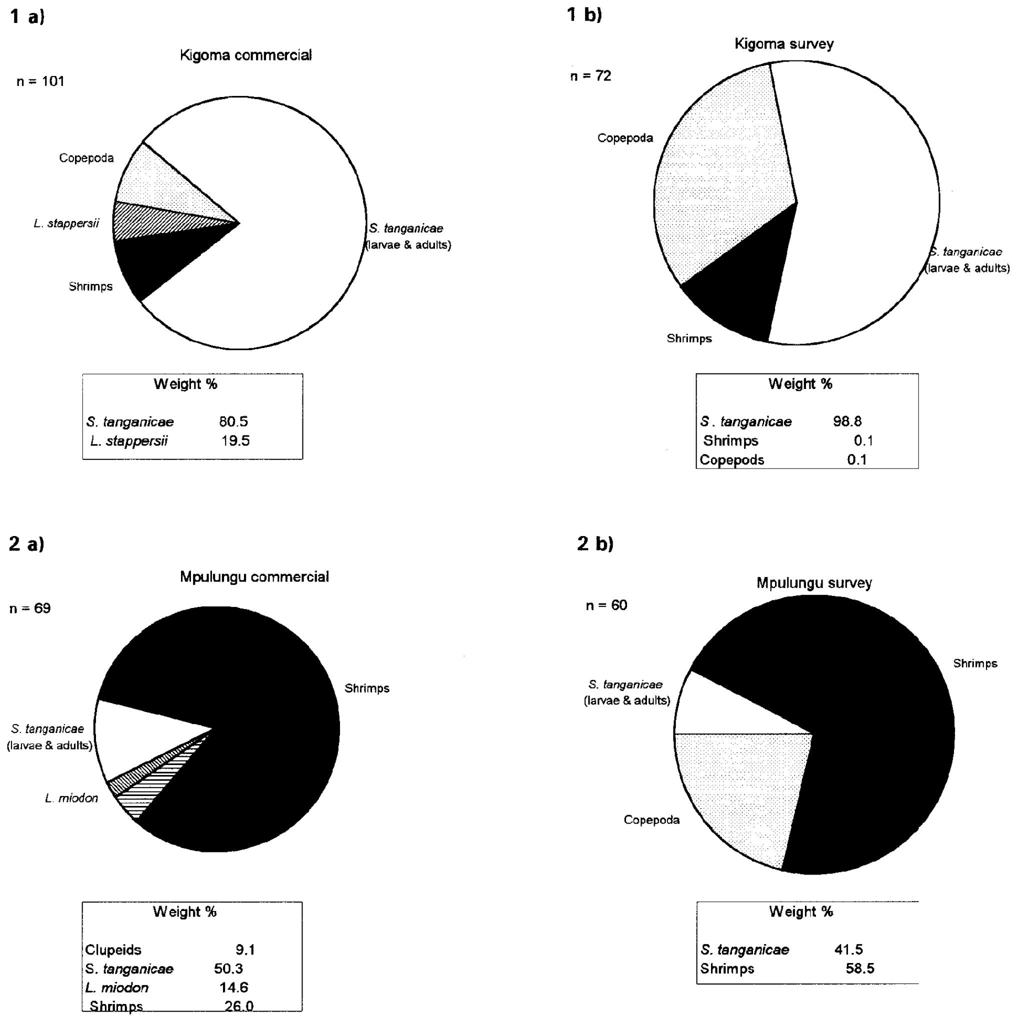



Figure 46. Occurrence (percent frequency) of prey items in *L. stappersii* stomachs in Kigoma (**1**) and Mpulungu (**2**) area from June 1995 commercial catch samples (**a**) and survey samples (**b**), n is the number of non empty stomachs analysed . Weight composition (when available) is shown in text boxes.

| *Stolothrissa tanganicae* | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Area** | **Data** coll. | **Loo** (mm) | **Length** meas. | **K** annual | **Phi'** | **Z** annual | **Source** |
| Bujumbura | 1972-76 | 93.8 | FL | 2.52 | 4.35 | 5.52 | Roest, 1978 |
| " | 1972 | 92 | TL | 3.46 | 4.47 | 5.99 | Moreau et al., 1991 |
| " | 1974 | 100 | TL | 4.00 | 4.60 | 11.43 | " |
| " | 1974 | 90 | TL | 2.00 | 4.21 | | " |
| " | 1980 | 107 | TL | 2.30 | 4.42 | 17.21 | " |
| " | 1981 | 100 | TL | 2.72 | 4.43 | 8.51 | " |
| " | 1982 | 101 | TL | 2.00 | 4.31 | 7.54 | " |
| Uvira | 1988 | 108 | SL | 1.90 | 4.35 | 9.23 | Mulimbwa & Mannini, 1993 |
| " | 1988 | 109 | SL | 2.29 | 4.43 | | " |
| " | 1987-89 | 106 | SL | 2.13 | 4.38 | | Mulimbwa & Shirakara, 1994 |
| " | 1993-95 | 104 | TL | 1.85 | 4.30 | 4.39 | This study |
| Bujumbura | " | 105 | TL | 1.89 | 4.32 | 6.10 | " |
| Karonda | " | 112 | TL | 1.77 | 4.35 | 4.79 | " |
| Kigoma | | 90 | FL | 2.52 | 4.31 | 5.16 | Chapman & van Well, 1978a |
| " | 1993-95 | 105 | TL | 1.84 | 4.31 | 5.16 | This study |
| Kalemie | 1994-95 | 108 | TL | 1.80 | 4.32 | 5.05 | " |
| Mpulungu | 1962 | 91 | TL | 1.62 | 4.13 | 4.62 | Moreau et al., 1991 |
| " | | 110 | | 1.56 | 4.28 | | Pearce, 1985 |
| " | | 112 | | 1.56 | 4.29 | | " |
| " | | 116 | FL | 1.72 | 4.36 | | Kimura, 1991b* |
| " | 1990 | 104 | SL | 1.87 | 4.31 | | Kimura, 1995* |
| " | 1993-95 | 114 | TL | 2.00 | 4.41 | 4.33 | This study |
| *Limnothrissa miodon* | | | | | | | |
| **Area** | **Data** coll. | **Loo** (mm) | **Length** meas. | **K** annual | **Phi'** | **Z** annual | **Source** |
| Bujumbura | 1974 | 165 | TL | 1.15 | 4.50 | 5.76 | Moreau et al., 1991 |
| " | 1980 | 161 | TL | 1.12 | 4.46 | 4.44 | " |
| " | 1981 | 172 | TL | 1.31 | 4.59 | 9.76 | " |
| " | 1982 | 172 | TL | 1.14 | 4.53 | 6.66 | " |
| Uvira | 1988 | 140 | SL | 1.19 | 4.37 | 4.67 | Mulimbwa & Mannini, 1993 |
| " | 1987-1989 | 135 | SL | 1.15 | 4.32 | | Mulimbwa & Shirakara, 1994 |
| Bujumbura | 1993-95 | 180 | TL | 1.04 | 4.53 | 5.08 | This study |
| Kigoma | | 175 | TL | 0.92 | 4.45 | | Ndugumbi et al., 1976 |
| Kipili | 1993-95 | 180 | TL | 1.06 | 4.54 | 6.91 | This study |
| Mpulungu | | 164 | | 0.95 | 4.41 | 5.80 | Pearce, 1985 |
| " | | 178.1 | FL, F | 0.80 | 4.41 | | Kimura, 1991c* |
| " | | 155.6 | FL, M | 0.99 | 4.38 | | " |
| " | 1990 | 155.4 | SL | 0.86 | 4.32 | | Kimura, 1995* |
| " | 1993-95 | 182 | TL | 1.01 | 4.52 | 4.21 | This study |
| *Lates stappersii* | | | | | | | |
| **Area** | **Data** coll. | **Loo** (mm) | **Length** meas. | **K** annual | **Phi'** | **Z** annual | **Source** |
| Bujumbura | 1973-80 | 470 | | 0.40 | 4.95 | 1.78 | Roest, 1988 |
| " | 1982 | 540 | TL | 0.42 | 5.09 | 1.95 | Moreau & Nyakageni, 1992 |
| " | " | 535 | TL, s | 0.36 | 5.01 | | " |
| " | 1983 | 580 | TL | 0.56 | 5.28 | 1.60 | " |
| " | " | 510 | TL, s | 0.35 | 4.96 | | " |
| Uvira | 1988 | 462 | SL (El.) | 0.46 | 4.99 | 2.16 | Mulimbwa & Mannini, 1993 |
| " | " | 480 | SL (SLCA) | 0.38 | 4.94 | 2.02 | " |
| " | " | 456 | SL (Proj.) | 0.45 | 4.97 | 2.16 | " |
| Kigoma | 1971-72 | 455 | FL | 0.25 | 4.71 | | Chapman & van Well, 1978b |
| " | 1974-76 | 450 | FL | 0.40 | 4.91 | | " |
| " | 1993-95 | 519 | TL (El.) | 0.44 | 5.07 | 1.35 | This study |
| " | " | 506 | TL (SLCA) | 0.43 | 5.04 | 1.18 | " |
| Kipili | " | 550 | TL (El.) | 0.41 | 5.09 | 2.33 | " |
| " | " | 550 | TL (SLCA) | 0.36 | 5.04 | 2.00 | " |
| Mpulungu | 1963-83 | 480 | | 0.39 | 4.95 | 2.02 | Pearce, 1985 |
| " | 1993-95 | 510 | TL (El.) | 0.42 | 5.04 | 2.11 | This study |
| " | " | 530 | TL (SLCA) | 0.40 | 5.05 | 2.35 | " |

Table 8. Estimates of growth coefficients (Loo, K) and total mortality rates (Z) from different L/F data sets and authors. El. refers to Elefan 1 method , SLCA to Shepherd length composition analysis. Sources marked with asterisk means growth coefficients were obtained by otolith reading.

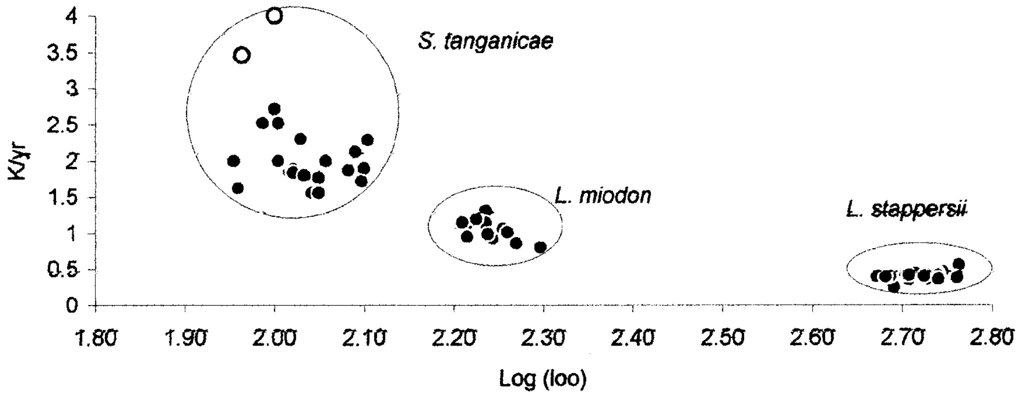



Figure 47. Plots of K against Log (Loo) for *S. tanganicae*, *L. miodon*, *L. stappersii* estimated by various authors. Data are from Table 9, Loo values originally given as standard length or fork length have been converted to total length using conversion parameters from Table 1. Open circles indicate probable overestimates.

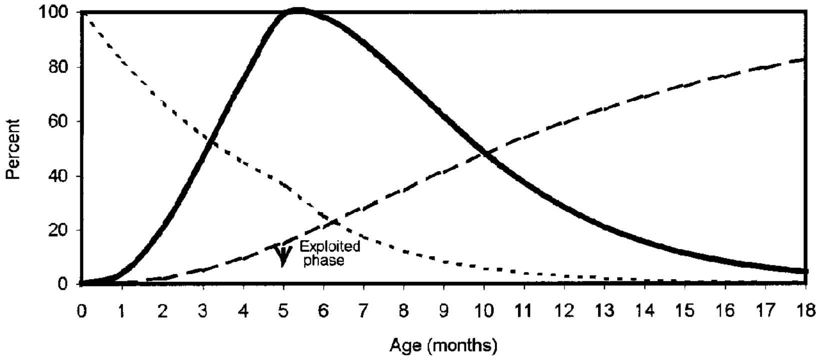



Figure 48. Relative numbers surviving (------) and individual growth in weight (— —), and cohort biomass (——), expressed as percentages of the maximum values against age for *S. tanganicae* (whole lake).

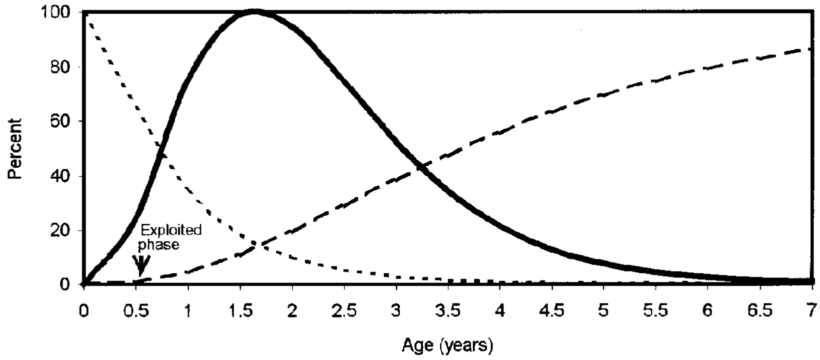



Figure 49. Relative numbers surviving (-------) and individual growth in weight (— —), and cohort biomass (—), expressed as percentages of the maximum values against age for *L. stappersii* (Kigoma).

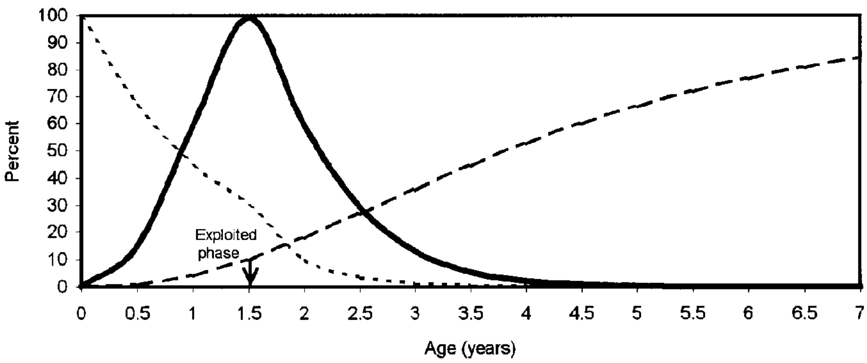



Figure 50. Relative numbers surviving (------) and individual growth in weight (— —), and cohort biomass (——), expressed as percentages of the maximum values against age for *L. stappersii* (Mpulungu).

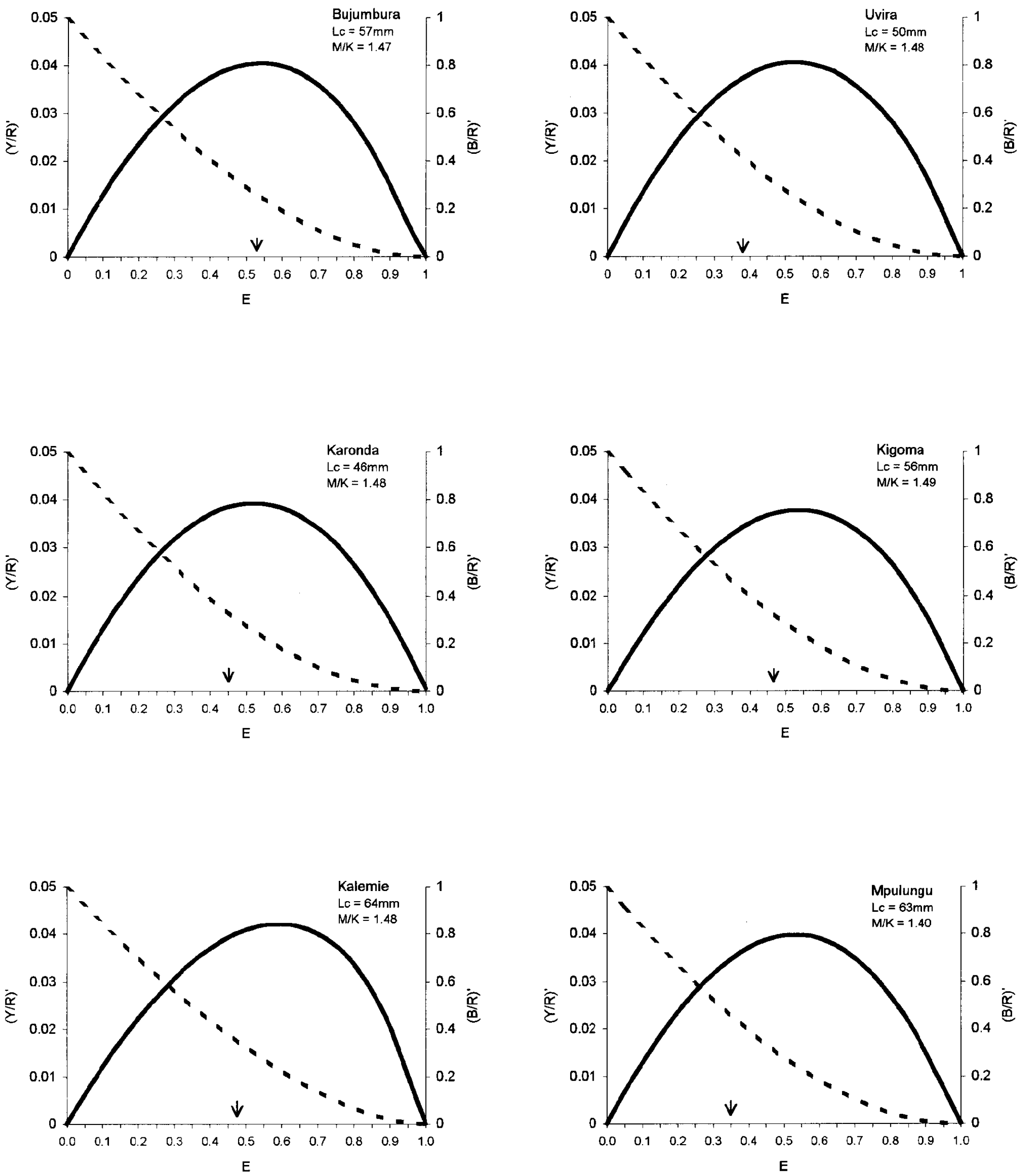



Figure 51. Relative yield per recruit (Y/R)' and biomass per recruit (B/R)', expressed as a function of exploitation rate (E), for *S. tanganicae* for different areas. Arrow indicates estimated current E.

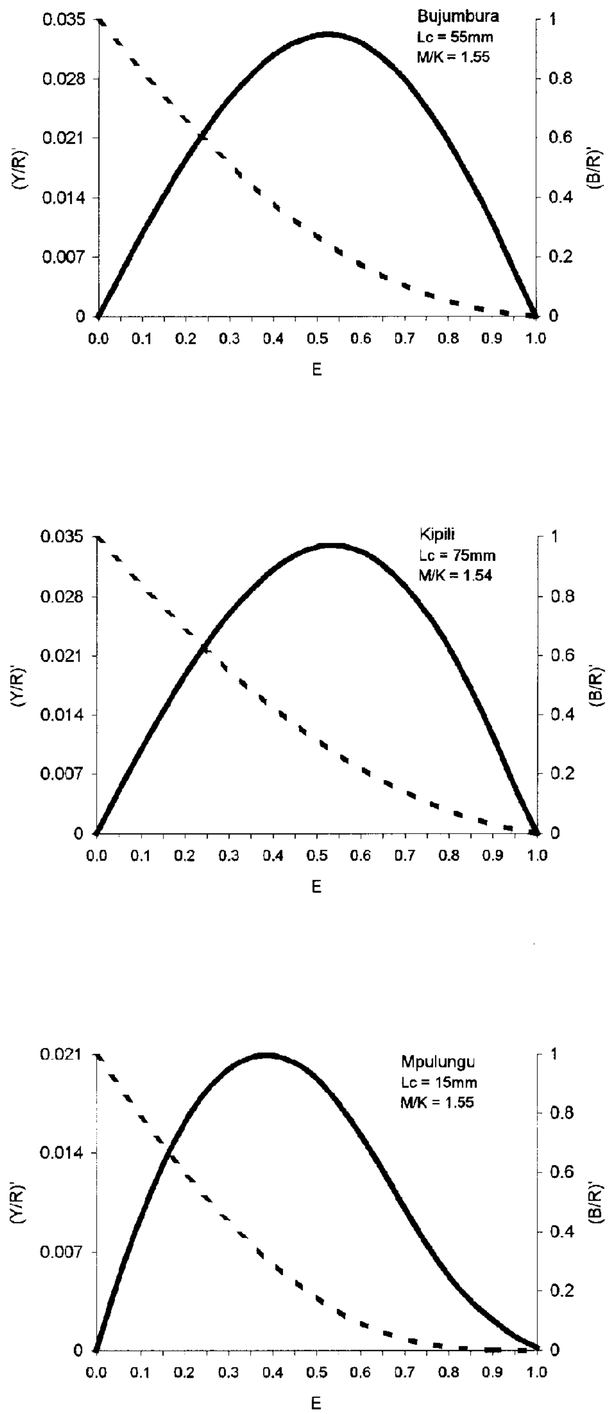
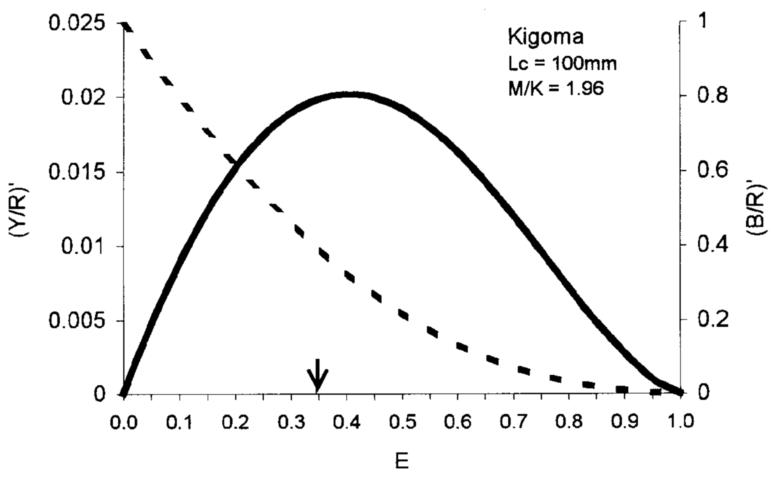



Figure 52. Relative yield per recruit (Y/R)' and biomass per recruit (B/R)', expressed as a function of exploitation rate (E), for *L. miodon* for different areas.



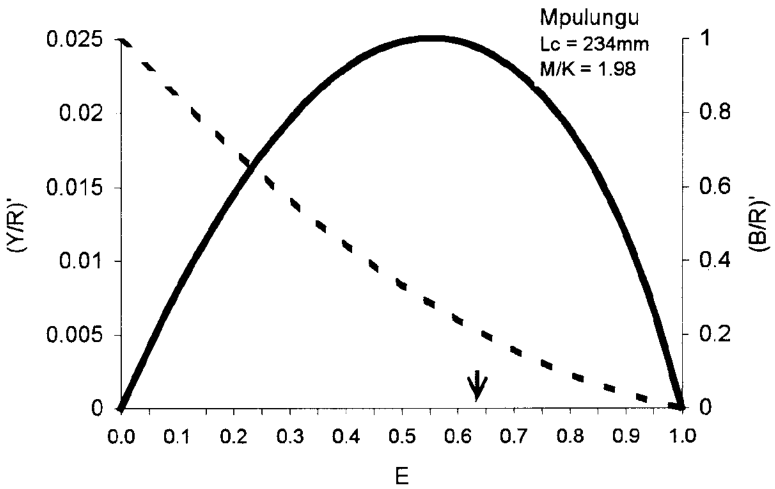




Figure 53. Relative yield per recruit (Y/R)' and biomass per recruit (B/R)', expressed as a function of exploitation rate (E), for *L stappersii* for different areas. Arrow indicates estimated current E.