GCP/RAF/271/FIN-TD/83 (En) August 1998

GEOGRAPHICAL DISTRIBUTION PATTERNS OF PELAGIC FISH AND MACROZOOPLANKTON IN LAKE TANGANYIKA

by
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OF THE UNITED NATIONS

Bujumbura, August 1998

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 Development 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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For bibliographic purposes this document should be cited as follows:

Mannini, P. Geographical distribution patterns of pelagic
1998 fish and macrozooplankton in Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. **GCP/RAF/271/FIN-TD/83 (En): 103 p.**

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TABLE OF CONTENTS

1. Introduction

Scientific knowledge about Lake Tanganyika and its fisheries is often affected by the spatially sparse nature of the available information. The main problem for the understanding of the pelagic ecosystem is that the most of research has been carried out in restricted areas and therefore it has been difficult to obtain results whose validity could extend to the whole lake. Moreover the lake’s remoteness and its huge size create formidable logistical problems to implement lake–wide research.

Coulter (1991a) assembled and discussed all the relevant information on the lake ecosystem from research work done in the last forty years. From Coulter’s work the need to have lake–wide patterns of biotic and abiotic characteristics is evident. The FAO-FINNIDA “Research for the Management of the Fisheries on Lake Tanganyika”, LTR, has attempted to fulfill this need through simultaneous data collection, at fixed localities around the lake, and execution of lake–wide surveys using the R/V Tanganyika Explorer.

Previous lake–wide research comprised three acoustic surveys conducted in 1973, 1975 and 1976 to estimate the pelagic fish biomass (Joahanesson, 1975; Mathisen, 1975; FAO, 1978). Biomass estimates were extremely different between surveys probably due to both fluctuation in fish (particularly clupeids) abundance and different acoustic methodologies used. However, it was apparent that fish biomass was unevenly distributed along the longitudinal axis of the lake. A major limiting factor of these studies in the 1970s was that no integrated fishing could be done and therefore no direct information on fish species and size composition of the acoustic measurements was available.

The present report deals with catch data on the three most important pelagic fish of the lake, and LTR target species, the clupeids *Stolothrissa tanganicae* (Boulenger) and *Limnothrissa miodon* (Regan), and the centropomid *Lates stappersii* (Boulenger). Data were collected during five integrated acoustic and pelagic trawling lake-wide surveys conducted in the 1995-98 period. The principal aim of trawling was for species identification and determination of size composition of the acoustically observed fish. Information on the pelagic shrimps, the atyid *Limnocaridana parvula* (Calman) and the palaemonid *Palaemon moorei* (Calman), and on the fish larvae of the target species was also included.

The purpose of the work is to describe the lake-wide distribution of fish and shrimp distribution and to investigate the relations between species. Also, it integrates the findings of previous work based on commercial fishery–dependent information (Mannini, et *al.,* 1996) to which reference is often made. The results are discussed in the context of the management of the pelagic fish resources.

2. Materials and Methods

2.1 Data collection

Five combined hydroacoustic and pelagic trawling lake–wide surveys were carried out in June (15-29) 1995, November-December (16-3) 1995, April (2–9) 1996, November-December (22–4) 1997 and February (5-19) 1998. The April 1996 surveys covered only the northern half of the lake and had to be prematurely halted due to the breakdown of the hydroacoustic equipment. Due to the unfortunate combination of technical problems, unavailability of scientific staff and especially to the civil unrest in part of the region, survey work could be resumed only in November 1997. The interval of one and half year between the 1995-96 and 1997-98 surveys created severe problems and posed obvious limits to the data comparison and analysis.

The fish and macrozooplankton data collection was carried out as described in Mannini and Aro (1995), and Kurki (1996). The research vessel (*R/V Tanganyika Explorer*) was equipped with a French-type pelagic trawl net and a high speed Gulf-net V sampler. The stretched mesh size of the trawl codend was 8 mm, the vertical and horizontal openings were, depending on the speed, 10-13 m and 25-35 m respectively. The Gulf-net opening diameter was 20 cm and the mesh size was 250 µm. Fish catch were processed on board. Total catch weight, species composition, fish size (total length, TL) distribution and sexual maturity stage were recorded. A five–stage sexual maturity scale was used as described by Aro (1993). Stomach contents of the centropomid predator *L. stappersii* were preserved in 10% formalin for later dietary analysis (Mannini, 1994 based on Hyslop, 1980). Extra sampling work was also carried out for specific research aims (e.g. otolith sampling, clupeid stomach contents, tissue samples for genetic analysis, etc). Gulf–net samples were preserved in 4% formaldehyde for later analysis ashore.

The acoustic survey design consisted of oblique zigzag transects from the East Coast to the West Coast or viceversa. The design changed slightly between surveys (Szczucka, in prep.). Trawl stations were allocated following the acoustic survey design, normally along the acoustic transect across the lake from two to three trawling hauls were carried out. Most of the fishing was done between dusk and dawn; in the present work only night hauls were used unless otherwise indicated. A typical haul lasted one hour at a speed of 3.5 knots (1.8 m^2 s^{-1}). the fishing depth depended on the depth of highest fish density as indicated from the acoustic output. This was generally within the 60-100 m depth range, the minimum and maximum fishing depths were 10 and 130 m respectively. Trawl catches were standardised to numbers and weight caught per 60 mm hauling. The position of the trawl stations used for this work is given in Table 1.

Crustacean zooplankton and fish larvae were sampled by double–oblique tows with a Gulf V high speed plankton net within the 0-100 m depth range at the speed of about 3.3 knots. In June 1995, a Gulf-net tow within the 0-100 m depth range would be carried out first, followed by the trawling station. During the other surveys tows were done in the evening along the acoustic transects but independently from the trawl stations. Gulf–net samples were analysed as described in Bosma *et al.,* (1998).

2.2 Data analysis

The following geomorphological terminology, after Tiercelin and Mondeguer (1991), has been used, unless otherwise indicated, throughout this study. Seven sub-basins were identified by these authors (Figs 1 and 2):

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

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

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

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

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

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

7) Mpulungu sub-basin (100 km long, 25 km wide, 800 m 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 <200 m bottom depth are referred to as inshore areas, while areas >200 m are considered to be offshore, pelagic and open water irrespective of their distance from the coast.

Four bathymetric zones (<200 m, 200-400 m, 400-600 m and >600 m bottom depth) were used as indicative of distance from the coast to configure the inshore–offshore extent.

The Geographical Information System (GIS) EchoBase™ was used to produce thematic maps. The lake surface was divided in 1.5 by 3.6 n mile cells. The inverse distance interpolation method was applied, the interpolated data were calculated according to the formula:

$$D_j = \sum D_i \, w_{ji}$$

where:

D_j is the interpolated value at the node j

D_i is the measured value at the data point i

w_{ji} is the weighting factor, i.e. the inverse distance in square between a data point and the node $w_{ji} = 1/(R_{ji})^2$

The search radius was 20 and 15 n mile for the trawl and Gulf-net respectively.

Estimates of fish population parameters (e.g. growth, mortality, length at sexual maturity, L, length at first capture, L4 were from Mannini *et al.* (1996) unless otherwise indicated. Fish modes from length frequency distributions were identified through the Bhatacharaya's method (1967). The terms "larva", "juvenile"(TL < L) and "adult" (TL ≥ L) used for the fish are according to Blaxter (1988). For *L. stappersii* only "juveniles" was used to indicate fish ≤ 100 mm TL.

The following statistical tests were used and are indicated in the text: One-way ANOVA, Kruskall-Wallis ANOVA, Mann-Whitney U-test, x^2 test and Pearson correlation.

3. Results

3.1 General remarks on the 1995-96 and 1997-98 surveys

The uncorrected (not standardised) total catch composition of each survey, from both night and day hauls, is given in Table 2. The highest total catch was made in February 1998, the lowest was in April 1996. The latter was related to only the northern half of the lake that was surveyed before fishing was stopped for the breakdown of the acoustic equipment.

The three target species contributed from 63% to 89% of the total catch weight. In all but the June 1995 survey, S. *tanganicae* was the main contributor to the catch (up to 85% in November—December 1997), followed in importance by *L. stappersii* and *L. miodon.* The other *Lates* species *(L. mariae, L. angustifrons* and *L. microlepis)* made from 3% to 30% of the catch weight, especially *L. mariae.* Generally, the biomass of these centropomids caught was made by relatively few, large-sized specimens. The by-catch contributed by other species was always < 11% of the total catch and it was mostly composed of the cichlid *Bathybathes* sp. and large specimens of the clarid *Dinopterus cunningtoni.*

The survey data and results were treated as if from two distinct data sets. The first included the three surveys which took place from June 1995 to April 1996, and the second the two surveys carried out in November-December 1997 and in February 1998. The interval of more than one and half years between surveys did not allow for close monitoring of the abundance and distribution dynamics of the target species, especially of the clupeids, due to their short life span and high population turnover rate.

Another factor, which led to some caution in the analysis, was the apparent change in the fishing strategy between the two survey groups. Sampling frequency (i.e. number of hauls) in the last two surveys was reduced by 40% compared to the sampling effort of June and November-December 1995 surveys. Also, the number of daylight fishing hauls increased.

The time of fishing is an important variable when targeting pelagic, schooling fish species. Vertical distributions and diel movements of fish in the pelagic zone are strongly affected by light intensity (Blaxter, 1974). For some pelagic fish it is advisable that light conditions are standardised to ensure consistent and comparable population estimates (Luecke and Wurtsbaugh, 1993). Lake Tanganyika clupeids, especially *S. tanganicae,* school during the day and scatter into layers at night (Chapman, 1976; personal observation). This behaviour is common to several fish species and is believed that daytime aggregation is related to predator avoidance (Johannes, 1992). consequently, fish catchability changed markedly during the diel cycle and this was reflected in the catch rates. In June 1995, November-December 1995 and April 1996, respectively 76%, 86% and 100% of the hauls were carried out nightime. In November-December 1997 and February 1998 the percentage of night hauls decreased from 76% to 52% respectively.

In all surveys the highest catches of clupeids were always made during daylight hours. For example, the highest night catch of *S. tanganicae* amounted to the maximum of 54 kg hr^{-1} in April 1996, while it was possible to achieve a catch rate up to 1181 kg hr^{-1} during the day (February 1998). This was probably related to the fish behaviour changes between day and night. Daylight schooling allowed for the dense, large fish concentrations to be easily targeted and efficiently fished. Throughout the present work, data from night–time trawling were used (unless when otherwise specified). Very high catches made during daylight hours were normally not taken into account except those from the November– December 1997 and February 1998 surveys; the removal of these catches would have had a dramatic effect on the results of these two surveys.

In November-December 1997 one single daylight haul of 533 kg hr^{-1} of *S. tanganicae* contributed 77% of the total catch weight of the entire survey, 88% of the target species weight and 90% of *S. tanganicae* catch. In February 1998 a single one hour daylight trawl daylight caught 1181 kg of *S. tanganicae* equivalent to 66% of that survey total catch, 75% of the target species weight and 93% of the entire *S. tanganicae* catch.

It should be possible to assess from the results of the acoustic biomass estimates whether some of these differences in the two survey groups were due to differences in fishing operations, or to changes in the fish abundance or distribution.

The low number of non–zero catches and the effect of the single hauls with the highest catches in both November-December 1997 and February 1998 surveys made these data unsuitable for some of the analyses performed with data from the other three surveys.

3.2 *Stolothrissa tanganicae*

Stolothrissa tanganicae was caught in 104 of the 131 hauls. Catch rates varied between 0 and 1181 kg hr^{-1} (or 54 kg hr^{-1} considering only night-time catches). The statistical distribution of catch rate in both survey groups was positively skewed indicating a patchy distribution (Fig. 3). The relatively high percentage of zero catches indicated that the species was contiguously distributed and dispersed. The distribution of log-transformed CPUE values was not significantly different between the two survey periods ($X^2_{[10]} = 10.43$, $p > 0.05$).

In all surveys the majority of fish examined for sex maturity were close to maturity or fully mature individuals (Fig. 4). In June and November-December 1995 the majority of both females and males had not yet achieved the full maturity. The proportion of mature, reproducing fishes was highest in April 1996. In November-December 1997 and February 1998 maturing and mature individuals made up the majority of fish sexed. No clear trend was observed for females between the last two periods, while the proportion of reproducing males increased marginally in February.

During the June and November–December 1995 surveys the catches of *S. tanganicae* were higher in the northern half of the lake (Fig. 5). The relative abundance (i.e. relative to the fished layer of water) was always highest in the Kigoma and Karonda sub–basins. However, in November–December *S. tanganicae* showed a less localised distribution, occurring also in the southern basins. The April 1996 survey covered the northern half of the lake only and could not provide a lake-wide pattern of catch rate. In that month CPUE of *S. tanganicae* was higher in the Rumonge and Kigoma sub-basins (Fig. 6a).

Nearly one and half years after the previous survey the distribution of *S. tanganicae* showed a similar pattern to that obtained in 1995 surveys. Although the effect of few outstanding catches was remarkable, the overall picture of CPUE distribution confirmed the highest concentration of *S. tanganicae* in the region defined by the Rumonge, Kigoma and Kalemie sub-basins. The remaining southern areas showed either localised (November–December 1997) or low occurrence (February 1998) of *S. tanganicae* in the catches (Fig. 7).

Mean catch per hour of trawling (CPUE, kg hr^{-1}) was three fold higher (Mann-Whitney test: $P = 0.003$) in November-December (4.401 kg hr^{-1}) than in June 1995 (1.554 kg hr^{-1}). In April, the mean CPUE increased further to 8.120 kg hr^{-1}, significantly higher than in June ($P = 0.014$) but not higher than in November-December 1995 ($P = 0.643$). In November-December 1997 mean CPUE calculated either with and without daylight catches (23.679 and 2.476 kg hr^{-1} respectively) was lower than in February 1998 (66.799 and 4.873 kg hr^{-1} for day and night CPUE respectively). In both cases (with and without day catches) the mean CPUE was not significantly different ($P = 0.543$ and $P = 0.766$).

The June 1995 sampled population was dominated (97% of total number) by juveniles aged between 2 and 3 months while five months later, in November, they had been recruited to the adult stock (Fig. 8). This stock was made up of mainly 7-8 month-old (74% of total number) adult *S. tanganicae,* either close to sexual maturity or mature (TL ≥ L_m,; L_m = 78 mm). This was the spawning stock that originated the juvenile fish of about 3-months old, dominating, in the area sampled, the April stock (Fig. 9).

Sexually maturing fish contributed most (87%) of the sampled stock in November-December 1997. By February 1998 they were being recruited into the adult stock and dominated the size structure of the sample because no juveniles were found (Fig. 10).

During the first two 1995 surveys adult fish were found throughout most of the lake basins. Their relative abundance was unevenly distributed and was generally higher in the northern basins, especially in November and December (Fig. 11), while juvenile fish occurred mainly north of Kalemie (Fig. 12). In April, catches of adults were mainly from the area between Rumonge and Kigoma sub– basins and from the east of Kalemie sub-basin (Fig. 6b). Juveniles were abundant over the most of the region surveyed (Fig. 13a).

Both adult and juvenile *S. tanganicae* in November–December 1997 and February 1998 were mainly found in the northern half of the lake, especially in the area between the south of Rumonge and the north of Kalemie sub–basins (Figs 14 and 15).

Bottom depth was used as an indication of the distance from the coast. *Stolothrissa tanganicae* mean catch rates (in weight) were not different between bottom depth zones either in June and November-December 1995 (Kruskall-Wallis ANOVA: P = 0.206) or in April (P = 0.162). However, the composition of the population at different distances from the coast was not the same. At the time of the June recruitment, the smallest recruits occurred only in offshore waters, while older *S. tanganicae* were found in coastal areas. By November–December the June juveniles were fully recruited to the adult stock and made up the bulk of the population. They were found in all strata and no size–related distribution could be observed. Immature *S. tanganicae,* which at that time made up only a minor part of the population, were found entirely, as in June, in offshore waters (Figs 16 and 19). *Stolothrissa tanganicae* stock in April 1996 was almost entirely made up of juveniles which occurred only in offshore, open waters. The partitioning between offshore juveniles and inshore adults was particularly evident in this month (Figs 17 and 19). Maturing and mature fish in November-December 1997 and February 1998 showed a widespread inshore-offshore distribution, while the small quantity of juveniles present was only in the open areas of the lake (Figs 17, 18 and 19). Generally, *S. tanganicae* tend to move inshore to coastal areas as they grow. The offshore truly pelagic region appears to serve as a nursery during the initial post-larval life stage.

Frequency distribution of log-transformed (Ln(n+1)) samples of *S. tanganicae* larvae (Fig. 20a) indicated that during this life stage they were rather evenly distributed and no evidence of contagious and patchy distribution could be inferred. Larvae were common in 97 (92%) of the 105 Gulf-net tows. No significant difference was found in the mean number of larvae between surveys which ranged from 30 to 43 specimens per 100 m^3 (ANOVA, $F = 0.2955$, $P = 0.88$).

Stolothrissa tanganicae larvae occurred at low densities all over the lake showing increased abundance at the northern end, in the Bujumbura sub–basin, and in the northern part and western arm of the Mpulungu sub–basin. Higher concentrations of larvae were found in November–December 1995 and their presence was confined in the northern basins where the highest density (250 specimens per 100 m^3) was recorded in the Kigoma sub-basin (Fig. 21). Peak larval abundance was recorded in Kigoma and Kalemie areas in April 1996 (Fig. 13b). In November-December 1997 and February 1998 larval numbers were higher in the Kalemie sub-basins (Fig. 22). The available data on the distribution of *S. tanganicae* larvae showed that they were always rare in the southern half of the lake.

Overall, it can be deduced that the northern half of Lake Tanganyika was the area where *S. tanganicae* was prevalent for most of its life cycle.

3.3 *Limnothrissa miodon*

Limnothrissa miodon was caught in 73 of the 131 hauls. Catch rates varied between 0 and 96 kg hr^{-1}. The frequency distribution of catch rate (Fig. 23) between survey groups (June, November–December 1995 and November-December 1997 and February 1998) was very different ($X^2_{[10]} = 26.39$, $P < 0.05$). Between the two survey periods the proportion of zero catches doubled from 23% to 50%, positively skewing the CPUE frequency distribution in November-December 1997 and February 1998.

Sub–samples of fish whose sex and maturity stage could be identified comprised mainly maturing specimens. The highest proportion of mature *L. miodon* was found in April 1996 (Fig. 24).

Catches of *L. miodon* were scattered throughout the lake (Fig. 25) and catch rates were higher (Mann-Whitney test: $P = 0.017$) during the November–December survey than the June 1995 survey (mean CPUE: 3.698 and 1.966 kg hr^{-1} respectively). Catch rate was quite low during April 1996, the highest values were obtained in the Kalemie sub-basin (Fig. 26a). In this month the mean survey CPUE was 2.021 kg hr^{-1}, significantly lower than in the previous survey ($P = 0.003$) but not lower than in June 1995 ($P = 0.469$).

In November-December 1997 and February 1998, *L. miodon* was generally caught in relatively low quantities, and was rather evenly distributed. The higher CPUEs resulted from the northern end of the lake and the eastern area between the Kigoma and

Kalemie sub-basins (Fig. 27). Mean CPUE was 0.231 and 14.683 kg hr^{-1} in 1997 and 1998 respectively. Due to the scanty data, mean values were not tested statistically.

In June 1995, catches of schools of juveniles were made in Bujumbura and Kigoma areas (Fig. 28) and because of their numeric abundance (59% of total *L. miodon* catch number) they had an obvious effect on the size composition of the sampled population (Fig. 29). Only maturing and mature fish were found in NovemberDecember 1995 (Fig. 29). Mature specimens (TL ≥ L_m; L_m = 100 mm) were found to be quite localised in June, while they showed a more dispersed distribution and higher abundance in November–December (Fig. 30).

The size composition of April 1996 catch was mainly composed of sexually mature fish of about one year of age (Fig. 31) sampled in the Rumonge and, mostly, in the (eastern) Kalemie sub-basins (Fig. 26b). Juveniles were rare in the most of the survey area and were almost entirely caught in the Rumonge area (Fig. 32a).

In November-December 1997 the sampled stock comprised mainly fish close to the achievement of sexual maturity, while in February 1998 only young *L. miodon* at an early stage of sexual maturity were found (Fig. 33). Both adults and juveniles were more abundant in hauls made at the northern end of the lake and in the eastern sector of the area between the Kigoma and Kalemie sub–basins (Figs 34 and 35).

There were no differences in mean catch between depth–defined zones (Kruskall-Wallis ANOVA, P = 0.088). Numeric catches of mature *L. miodon* were not different while catches of immature fish were significantly different between inshore-offshore areas (P = 0.01).

Based on evidence from commercial catch data, *L. miodon* is believed to have a size–dependent distribution. Large specimens above the length of 125 mm were rare in the artisanal fishery catch while they were common in the industrial catch taken more offshore (Mannini *et al.,* 1996). *Limnothrissa miodon* >125 mm total length composed 3.5% of the total number sampled from the commercial catch during the July 1993-December 1995 period. Their proportion amounted to 12% of the total number caught in the two 1995 surveys.

Survey data produced further evidence on the inshore–offshore distribution of the species. Large sized *L. miodon* (>125 mm TL) occurred in offshore open water while juveniles were found in more inshore coastal waters (Figs 36, 37, 38 and 39). It appears that the adult stock of *L. miodon* occupy an open water, pelagic habitat.

The frequency distribution of log–transformed numbers of *L. miodon* larvae in the samples indicated that they were rather uniformly distributed within the surveyed areas (Fig. 20b). Larvae were common occurrence in 96 of the 105 Gulf–net tows. The low frequency of zero densities suggested that the larvae did not have a markedly patchy distribution. The mean number of larvae ranged from 18 (April 1996) to 45 (November–December

1997) individuals per 100 m^3 of water, and it was not significantly different between surveys (ANOVA, $F = 2.030$, $P = 0.10$).

Limnothrissa miodon larvae were found, in low concentration, all over the lake, with higher densities being recorded in November-December 1995. In both surveys, *L. miodon* larval concentrations reached a maximum in the Bujumbura and Karonda areas (Fig. 40) . In April 1996 the larval number was even lower and their number reached a maximum in the Kigoma and Kalemie sub-basins (Fig. 32b). Unlike the first two lake-wide surveys in 1995, in November-December 1997 and February 1998 *L. miodon* larvae showed a relatively high density in the southern half of the lake (i.e. Moba, East Marungu and Mpulungu sub–basins). In February no larvae were found north of Kalemie (Fig. 41).

3.4 *Lates stappersii*

Lates stappersii occurred in 86 of the 131 hauls and catch rates varied between 0 and 61 kg hr^1. The distribution of catch rate had few zero catches in the first two surveys carried out in 1995 and the species was caught in the majority (95%) of the hauls. The frequency of zero catches increased drastically in November– December 1997 and February 1998 when it raised from 5% to 47%. The statistical distribution of catch rate became strongly skewed to the right (Fig. 42). The overall CPUE distribution was thus different from that obtained in 1995 ($X^2_{1101} = 38.40$, $P < 0.05$).

The sexual maturity composition of survey samples comprised mainly maturing females (stage II and III), except in April 1996 when the proportion of mature fish was the highest (Fig. 43). Generally males were found in a more advanced maturity stage than females. The proportion of mature individuals appeared to increase from June onwards in 1995–96 and from November–December 1997 to February 1998. In this month the proportion of mature males, as that of females, was the highest (Fig. 43).

Lates stappersii showed, in both 1995 surveys, a wide distribution occurring over the most of the lake (Fig. 44). Higher catch rates were obtained during the June survey in Kalemie, Moba and Mpulungu areas, while in November CPUEs were the highest again in Moba but also in the Kigoma sub–basins. Mean catch rate in the June and November surveys (7.033 and 5.587 kg hr^{-1} respectively) were not significantly different (Mann-whitney test, $P = 0.6$).

In April 1996, *L. stappersii* was caught throughout the survey area (the northern half of the lake) but its relative abundance in the catch was highest in the Kigoma and Kalemie sub-basins (Fig. 45a). Mean CPUE (1.949 kg hr^{-1}) was significantly lower than in June and November-December 1995 surveys ($P = 0.024$ and $P = 0.011$ respectively).

CPUEs of *L. stappersii* in November-December 1997 and February 1998 showed a more localised pattern (Fig. 46) compared to the two 1995 lake-wide surveys, probably due to the high frequency of zero catches together with the lower number of hauls carried out. Catch per hour trawling was low in November-December 1997 and the highest values were obtained in the Kalemie region. Outside this area only very small quantities were caught. The northern half of the lake was still characterised by extremely low catches during the February 1998 survey. In this month *L. stappersii* was found almost entirely in the southern area of the lake from the Kalemie to East Marungu sub-basins. Mean survey CPUE was 0.539 and 3.337 kg hr^{-1} in November-December 1997 and February 1998 respectively. The difference was not statistically tested because of too few data.

In both 1995 surveys the sampled population showed a polymodal distribution (Fig. 47), where 3 to 4 cohorts could be identified. According to the growth pattern from the estimated von Bertalanffy growth function (Mannini *et al.,* 1996), these cohorts comprised the 0+, 1+ and 2+ age groups. The highest frequency of young *L. stappersii* was found in June when the approximately 3 month-old cohort was sampled, and sexually immature fish made up most (87%) of the catch. In November–December, the recruitment into the (exploitable) stock was reduced and the proportion of mature fish increased from 13% to 33%.

The size distribution of the sampled stock in April 1996 (Fig. 48) was characterised by the appearance of a cohort of juveniles of about 3-4 months of age, probably spawned by the adults that occurred at the end of the previous year. This cohort comprised about 70% of the size distribution of the sampled stock while mature fish accounted for less than 10% (it has to be noted, however, that only half of the lake was sampled).

The samples of November–December 1997 consisted of almost entirely juveniles. In February 1998 the size distribution of the catch was more composite with several age groups represented (0+, 1+, 2+ and 4+ could be identified, Fig. 49).

In June 1995 sexually mature *L. stappersii* (TL $\geq L_m$; L_m = 275 mm) were mainly localised in Kalemie, Moba and Mpulungu areas and, in November–December, they appeared to have spread over most of the lake with higher abundance in the Kigoma, Moba and East Marungu sub-basins (Fig. 50). More juveniles were caught in June than in November, however, in both months notable numbers were found only in the northern half of the lake (Fig. 51).

In April 1996 the small proportion of the stock made up of adult fish were found in the south of Kigoma area and, mostly, within the Kalemie sub-basin (Fig. 45b). The juveniles, which at the time dominated the sampled stock, occurred in the northern area of the Kigoma sub-basin (Fig. 52).

Mature *L. stappersii* in the catch were extremely localised in November-December 1997 and February 1998, being present mostly in the Kalemie sub-basins (Fig. 53). Catches of juveniles were scattered in both survey periods but the majority of them was from the Kigoma, and mainly the Kalemie areas. In February 1998 they occurred in the catch from the south of the lake, mostly from the area between Kalemie and Moba (Fig. 54).

Lates stappersii occurred in both the coastal shallow areas and in the open water. The catch rate by weight at different distances from the shore (following the depth profile) was similar (KruskallWallis ANOVA, $P = 0.34$). Mean catches by number for early juveniles (TL **<** 100 mm) were significantly different between depth areas ($P = 0.02$), while catch by number of adult fish (TL **>** 275 mm) was not different ($P = 0.22$).

The youngest fish (approximately smaller than 150 mm TL) showed an ubiquitous occurrence between inshore and offshore waters. However, in the periods where they were more abundant they seemed to occur more along the coastal shelf or relatively close to it than in the deep, open areas. Yet, the simultaneous occurrence in some months (e.g. June 1995, April 1996) of juveniles in both coastal and offshore waters suggested that young *L. stappersii* exhibit of highly mobile behaviour. *Lates stappersii* above the size of 150 mm and sexually mature fish occurred in either coastal or offshore areas. However, offshore their abundance in the catch appeared greater and they dominated the size structure of the stock (Figs. 55, 56, 57 and 58).

Lates stappersii larvae were found in 65 of the 105 Gulf-net tows. The number of specimens per 100 m^3 of water varied from 0 to 96. The frequency distribution of the log–transformed number per sample was positively skewed because of the relative high occurrence of tows with no larvae (Fig. 19c). This suggested that this species, at the larval stage, was randomly dispersed and had a moderately patchy distribution.

In the month of June *L. stappersii* larvae were found in low numbers in the southern half of the lake. Larvae were more abundant and evenly spread in November-December 1995, and the highest density was detected in the Karonda and Kigoma areas (Fig. 59).

In April 1996 no larvae were detected in the samples from the northern half of the lake that was sampled.

In the last two surveys larval distribution appeared to be mainly in the southern areas of the lake (Fig. 60). The highest density, and frequency in samples, of *L. stappersii* larvae resulted in February 1998 in the Moba sub-basin.

The mean number per 100 m^3 ranged from 1 (June 1995) to 30 (February 1998) individuals and there was a significant difference in the mean values between surveys (ANOVA, $F = 20.3356$, $P < 0.001$).

A total of 1040 stomachs, 74% (767) of which contained food remains, were sampled during the June and November 1995 lake–wide surveys. The diet composition was different between the two months ($X^2_{[5]} = 18.64$, $P < 0.05$). In both months *S. tanganicae* and shrimps were the two most important prey items. The occurrence of food items showed that in June shrimps were the commonest prey, followed by *S. tanganicae,* while the opposite was observed in November (Fig. 61). In that month the mean abundance of the main shrimp prey species in the environment was significantly lower than in June while the relative abundance of the fish prey was higher (Mann-Whitney test, $P < 0.05$ and $P < 0.01$ respectively; see also par. 3.5 and 3.2).

Stomach contents were plotted along the longitudinal axis of the lake according to the position of fishing hauls where *L. stappersii* was caught (Fig. 62). The occurrence of prey categories in June showed that the heterogeneous diet composition (mainly made by *S. tanganicae,* clupeid larvae and meso—zooplankton) in the northern half of the lake was replaced by almost exclusively shrimp prey in the southern half. This was in agreement with the geographical pattern resulting from the stomach content analysis of commercial catch samples collected from March 1994 to July 1995 at Kigoma and Mpulungu. In November the diet of *L. stappersii* from the south of the lake changed. Shrimps were much less common and fish prey *(S. tanganicae* larvae and adults, unidentified clupeids) were more frequent. Consequently, in this month in the south of the lake, the diet composition was more heterogeneous than in June, and similar to that which was observed in the northern areas in both June and November—December.

3.5 *Limnocaridina parvula* and *Palaemon moorei*

Preliminary information on the pelagic shrimp populations of Lake Tanganyika was gathered by the use of a Gulf net high speed sampler. The relevance of atyid and palaemonid shrimps within the lake pelagic ecosystem was pointed out by the study on the feeding ecology of *L. stappersii* (Mannini *et al*., in press). The ecological importance of crustacean macrozooplankton appeared to be much higher than had been previously thought and the need to elucidate the relations with other component of the pelagic environment was evident.

The atyid *L. parvula* was caught in 80, and the palaemonid *P. moorei* in 78, of the 105 Gulf-net tows. Their density x 100 m^3 of water varied from 0 to 11212 and 32 individuals for *L. parvula* and *P. moorei* respectively. Both species were not found in about 25% of the samples. The frequency distribution of shrimp catches suggested that both species had a moderately aggregate distribution but the size of *L. parvula* shoals extended over a much wider range than *P. moorei* (Fig. 63). The mean number of *L. parvula* varied from 15 (April 1996) to 1896 x 100 m^3 (November-December 1997) and there was a significant difference between survey means (ANOVA, $F = 7.518$, $P < 0.001$). Mean survey density of *P. moorei* was much lower than that of *L. parvula.* It varied from 3 (April 1996) to 9 (June 1995) shrimps x 100 m^3 and there was no significant difference between survey means ($F = 1.572$, $P = 0.188$).

Of the two pelagic shrimps *L. parvula* was found to be more abundant than *P. moorei.* The density of the first was higher in June than in November—December 1995, and in both months it occurred mainly in the southern basins of the lake, notably Kalemie, Moba and East Marungu (Fig. 64). The distribution of *P. moorei* was throughout the lake, although higher densities were found in the southern half of the lake (Fig. 65). In April 1996

L. parvula was more abundant at the southern edge of the survey area. In the same month *P. moorei* was found scattered at very low abundance (Fig. 66). *Limnocaridina parvula* distribution in November-December 1997 and February 1998 confirmed the observed lake-wide pattern in 1995. In both surveys this shrimp mainly occurred in the southern areas of the lake (Fig. 61). *Palaemon moorei* was found in low numbers, as in the previous surveys, and mainly occurred in the central regions of the lake (Fig. 68).

3.6 Species association and relationships.

Association between species was assessed through the analysis of different data collected during the June 1995 lake-wide survey. Data were gathered by pelagic trawling, Gulf-net sampling and stomach content analysis of *L. stappersii* caught in the trawl net. Also data collected during 1993-95 at fixed stations around the lake were used (see Aro, 1993; Kurki, 1993; Mannini, 1993, for sampling procedures).

Only the results from the June survey were employed because pelagic trawl hauls and Gulf–net tows were carried out within the same areas. Normally, a Gulf–net tow within 0–100 m water column would be carried out first, followed by the trawling station.

Analysis of Gulf-net samples showed that within the 0-100 m water column in pelagic water the occurrence and abundance of larvae of both *S. tanganicae* and *L. miodon* were strongly associated ($P < 0.001$). This could suggest that both species have similar environment requirements and that local factors, which enhance larval survival, are common during their early life stage. The occurrence of *L. parvula* was also correlated with that of *P. moorei* ($P < 0.01$) and with the larvae of *S. tanganicae* ($P < 0.001$) (Tab. 3).

Catch rates (survey CPUE) of *L. stappersii* were positively correlated with *L. parvula* and *P. inoorei* abundance ($P < 0.01$ and $P < 0.05$ respectively), and was probably indicative of the predator-prey relationship. This was confirmed by the significant correlation ($P < 0.01$) between the number of shrimp prey in *L. stappersii* stomach contents and the local abundance of the predator (Tab. 3) : predators gather where prey are abundant.

Abundance of *L. stappersii* was also positively associated with number of *S. tanganicae* prey in their stomachs ($P < 0.05$). Unlike the case between shrimps and *L. stappersii,* the latter and *S. tanganicae* occurrence in the environment was not correlated (Tab. 3) . This could mean a more efficient predator avoidance capability of the clupeid compared to the shrimp.

Juveniles of *L. stappersii* (TL < 100 mm) and *S. tanganicae* are believed, on the basis of commercial catch composition, to form mixed shoals. However, it was unclear whether this behaviour is due to the sharing of the same trophic niche or an artefact due to light attraction during fishing operation. Survey data would confirm this size-related association of *L. stappersii* with *S. tanganicae.* Survey CPUE of young *L. stappersii* and *S. tanganicae,* after logarithmic transformation, showed a high positive correlation ($P < 0.001$; Tab. 3).

The relation between mesozooplankton (copepods) and *S. tanganicae* could not be tested through survey data because copepod data from survey samples were not available. Perhaps indirect evidence of this predator-prey relationship could be inferred from the positive correlation ($r = 0.667$, $P < 0.05$) between local abundance of adult *S. tanganicae* (TL > 78 mm, i.e. fully able to prey on copepods) and number of copepods in *L. stappersii* gastric contents (assuming that copepods had been preyed upon in the same area).

The *S. tanganicae-copepod* relationship could be investigated using the information collected during the sampling work at fixed stations. In all three available data sets a significant positive correlation was found between the index of relative abundance of *S. tanganicae* (CPUE) in the local fishing grounds and the number of copepods (n/m^3). Catch per unit of effort of *S. tanganicae* (mixed clupeid CPUE in Mpulungu data) and copepod production were correlated in the northern end of the lake ($r = 0.585$, $P = 0.001$), in the Kigoma sub-basin ($r = 0.450$, $P = 0.013$) and in the southern end ($r = 0.742$, $P = 0.001$).

Time series of *S. tanganicae* and copepod abundance are given in Figure 69. This showed the similarity in the abundance dynamics of the predator and its prey at Bujumbura and Kigoma, while Mpulungu data were affected by the initial high values and by the shorter time series available. Also, quantities of *S. tanganicae* and *L. miodon* in fisheries statistical records are not reported separately within the clupeids commercial category.

The scatterplots of original data and the distribution of regression predicted values against residuals (Fig. 70) confirmed that while the correlation observed from Bujumbura and Kigoma data may be substantiated, the one from Mpulungu data should be discarded.

4. Discussion

The aim of the lake-wide survey conducted in LT over the period June 1995–February 1998 was to appraise the pelagic fish resources of the lake. The questions to be addressed were:

1) what species of fish are available in the different areas of the lake;

2) what is the spatial and seasonal distribution;

3) what is the size of the stock;

4) what is the annual potential yield;

5) what relations exist between species;

While a complete answer (especially to the third and fourth question) could be possible only when the results of the acoustic survey are available (Szczucka, in prep.), the data analysed for the preparation of the present work outline and highlight relevant traits of the biology of the most important pelagic stocks.

4.1 The *Stolothrissa tanganicae* stock

Stolothrissa tanganicae forms contagious aggregations during the juvenile and adult life. The fish disperse during dark hours and gather in schools during daylight (Chapman, 1976). This species is capable of fast movements that occur mainly during daylight when the schooling behaviour takes place (Chapman *et al.,* 1976).

The pattern observed from the survey catch frequency and CPUE distribution shows that *S. tanganicae* stock is very unevenly distributed in the lake. During most of survey months the stock was found in the northern half of the lake from Kalemie area northwards. The picture obtained from the relative biomass distribution would indicate, once confirmed by the acoustic work findings, that *S. tanganicae* stock is at very low density in the southern half of the lake. Commercial catch composition seems to substantiate this.

Stolothrissa tanganicae contribution to artisanal and industrial catch decreases along the longitudinal axis of the lake becoming negligible at the southern end of the lake (Coenen *et al.,* 1998; Mannini *et al.,* 1996; Plisnier, 1995). The decline of *S. tanganicae* in the south of the lake took place recently. Thirty years ago the species was abundant enough to support (initially together with the large *Lates* spp. and subsequently with *L. stappersii)* the development of the industrial purse seine fishery in Zambia (Coulter, 1970). The reduction of *S. tanganicae* stock in this part of the lake began about ten years ago (Pearce, 1995) and seemingly the species is not yet recovering. It is unlikely that the stock collapsed because of fishery exploitation. In the northern areas, where the fishing effort has been intense since few decades and concentrated in a comparatively small and closed area, *S. tanganicae* has not declined.

Clupeid stocks show considerable fluctuations or collapses principally related to environmental factors which undermine the recruitment process and when several consecutive recruitment periods are very poor the stock size of short–lived species declines quickly.

The adult and juvenile of *S. tanganicae* do not show separate distributions along the longitudinal axis of the lake, both spawners and recruits co–occur within the same areas. On the contrary, the inshore–offshore distribution of juveniles and adults is different and follows a clear pattern.

Stolothrissa tanganicae spawning is believed to take place in coastal areas (Coulter, 1991b, Roest, 1978, 1988) and mature fish have been reported as very rare offshore (Mann *et al.,* 1973). Indeed, mature *S. tanganicae* occur offshore but their occurrence increases from offshore towards the coast, and it could be then possible (but yet to be fully proved) that spawning grounds are along the continental shelf.

Contrary to the earlier statement on the inshore phase of young *S. tanganicae* (Coulter, 1991b; Roest, 1988), which was inferred from fishery–dependent information only, post–larval juveniles concentrate offshore in the open areas of the lake. There is a notable separation between the juveniles and the adult stock and this is also reflected in the fishery exploitation pattern (Mannini *et al.,* 1996). Young *S. tanganicae* move towards shallow water from the length of 30-40 mm (at about the age of 2-3 months) and they are recruited first to the industrial fishery and then to the lift-net fishery. Fishing grounds of the former are normally more distant from the coast than those of the artisanal fishery.

Stolothrissa tanganicae nursery grounds extend over the area of occurrence of the species mainly from the north from Kalemie sub– basin, and across the transversal section of the lake they are delimited by the distance from the coast: in areas shallower than 200 m the presence of juveniles is drastically reduced.

Unlike the post-larval life stage, during the larval stage *S. tanganicae* displays a rather even, homogeneous distribution. The data used for the present work were collected mainly in areas of deep water, however, a previous systematic study in areas at different distances from the coast found that *S. tanganicae* larvae occur mostly offshore (Tshibangu and Kinoshita, 1995). The spatial distribution of *S. tanganicae* larvae reflects that of juveniles and adults, being more abundant in the northern half of the lake than in the southern areas.

On a lake–wide basis the size structure of the *S. tanganicae* stock appears to be typical of that of many tropical short-lived species of fish and invertebrates (e.g. squids and shrimps) characterised by high turnover rates. Depending on the time of the year the stock appears to be composed by no more than two clearly identifiable cohorts whose growth can be easily followed between consecutive periods.

The reproductive process of this species is believed to be continuous throughout the year with peaks that can occur at varying time within the year and around the lake (Chapman and van Well, 1978a; Ellis, 1971; Mannini *et al.,* 1966; Pearce, 1985; Roest, 1977). Survey findings suggest that although mature fish are always present, the spawning stock biomass reach the maximum only in some periods (which probably lasts few months), around the first months of the year, while it is extremely reduced in the following months as consequence of the adult biomass decay. Successful spawning during the wet season months (from November to April–May) could be related with the relatively weaker winds which occur in that period of the year. A significant relationships has been found between larval anchovy *(Engraulis mordax)* mortality rate and frequency of calm periods with low wind speed during the spawning season;

conditions that would favour formation and maintenance of larval feeding microhabitats (Peterman and Bradford, 1987).

The Lake Tanganyika *S. tanganicae* fishery is supported mostly by a single major cohort which is recruited during the dry season and makes the exploitable stock during the successive wet season. The temporal pattern of the principal recruitment pulse to the fishery is similar around the lake (Mannini *et al.*, 1996) and fishery statistics indicate that the bulk of the commercial catch is made from September to December (FAO, 1978; Coulter, 1991b; Coenen *et al.,* 1998). More frequent lake-wide surveys (e.g. bimonthly for a twelve-month cycle) would have allowed better definition of those dynamics.

The striking differences in the catch rate between the first (June, November-December 1995 and April 1996) and the second (NovemberDecember 1997 and February 1998) group of surveys have been introduced and discussed in the initial part of the results section. Also the effects of possible changes in the fishing operations have been discussed. However, it must be noted that, as Dennis and Patil (1988) stated: “Ecological abundance data are intrinsically positive, with a few enormously high data points typically arising in every study”. Such large values, which cause considerably uncertainty for management, can reflect the spatial distribution of the species (McConnaughey and Conquest, 1992). Therefore, if the catch rate pattern observed in 1997—98 surveys (increased frequency of low CPUE values and a single huge catch in each survey) is not an artefact due to the sampling procedure (eventually this will be verified once the acoustic survey results become available) then it could mean that *S. tanganicae* stock, in the period considered, was structured in relatively few (large) schools. Chapman (1975), using acoustic measurements of supposedly clupeid shoals in 1973 (Johannesson, 1975), observed that in one occasion, in the north of the lake, most of the estimated biomass occurred in one large shoal. It is known from technologically developed fisheries that catchability initially increases as stock size decreases, so introducing serious difficulties in the assessment of small pelagic stocks (Beverton, 1990; Garcia and Josse, 1988). Stock expansion and contraction, with large changes in abundance, seems to be typical of clupeids (MacCall, 1990) and such dynamics could apply to *S. tanganicae* as well. Murphy (1977) noted that this population behaviour is characteristic of clupeid fishes, contributing to their susceptibility to overfishing.

It appears then that stock of *S. tanganicae* is not constantly available to the fishery. Apart from the main within-year cycle in abundance reflected in industrial and artisanal catch rates (FAO, 1978; Roest, 1988), the availability of the resource in the local fishing grounds is very irregular due to the high mobility of the schools. In the past drastic changes in biomass have been observed. Two acoustic measurements of fish biomass (probably of *S. tanganicae)* in the northern end of the lake within two weeks in November 1973 yielded estimates of respectively 120000 and 260000 t (Johanessen, 1975). Chapman (1975) found large differences in biomass over 24 hours off Kigoma; Chapman *et* al. (1976) observed that fish schools (assumed to be *S. tanganicae)* move in daytime at rates as high as 68 m min^{-1}. They tracked 68 schools and estimated a median movement rate of 10 m min^{-1}.

The fast movements of *S. tanganicae* schools are primarily determined by two factors: predation avoidance and search for food. Survey results do not show any significant positive association between *S. tanganicae* and *L. stappersii* in the environment. *Stolothrissa tanganicae* is the main fish prey of *L. stappersii* (Mannini *et al.,* in press) and has developed an efficient avoidance mechanism. Indeed, high concentrations of *L. stappersii* preying upon *S. tanganicae* schools were not observed in the present study. There is a known negative relationship between CPUEs of the two species in the same area (Pearce, 1988). At the same time, *S. tanganicae* is very efficient at locating mesozoolankton concentrations as shown by the positive correlation between local abundance of copepods and the commercial fishery CPUE. When the copepod abundance increases in the fishing grounds *S. tanganicae* moves into the area and becomes exposed to exploitation as reflected by the increase of the local catch rates.

4.2 The *Limnothrissa miodon* stock

The *L. miodon* stock is more evenly distributed over the lake than *S. tanganicae* stock which is mostly confined within the northern half of the lake basin. The contribution of *L. miodon* to the lift-net and purse seine pelagic catches is smaller than that of *S. tanganicae* and *L. stappersii,* while it dominates in the catch of the nonselective beach seine fishery operated in shallow, coastal areas over sandy bottoms (Pearce, 1995). This is due to the size— related behaviour of this species. The distribution of *L. miodon* across the lake from the coast to the pelagic area shows that there is separation between immature and mature fish.

The juvenile stock comprising the post larval stage occurs in shallow water where it is exploited by gears in which selectivity is reduced by the use of cloth tissue cover (Kihakwi and Chale, 1974; Mannini et *al.,* 1996). As they grow the young *L. miodon* move offshore and are successively recruited to the lift—net and purse seine fisheries. Large *L. miodon* (> 125 mm) occur almost exclusively offshore, in the central areas of the lake, outside the range of the artisanal fishery. These fish are believed to compete for food with *L. stappersii* preying upon pelagic shrimps and young *S. tanganicae* (Ndugumbi *et al.,* 1976; Poll, 1953; personal observation).

In Lake Kivu, where *L. miodon* has been introduced and is the only pelagic fish, large *L. miodon* display a cannibalistic behaviour preying inshore on juveniles (Reusens, 1987; de Iong *et al.,* 1989). In Lake Tanganyika the natural fish prey of *L. miodon* is young *S. tanganicae,* and cannibalism is probably sporadic. The inshore—offshore separation between the very young and adult fish in Lake Tanganyika has probably evolved to minimise juvenile mortality due to cannibalism and *L. stappersii* predation (the latter is rare inshore).

Fishery–dependent data on *L. miodon* are biased because of the juvenile and adult fish behaviour. The tails of the size composition are normally underrepresented in samples from the exploited population. This causes severe limitations and bias to the study of the population biology and dynamics of this species. For example, total mortality rates estimated through the length converted catch curve method (Pauly, 1983a; 1983b; 1984a; 1984b) will be overestimated. Published total mortality estimates from commercial catch data for *L. miodon* in Lake Tanganyika ranged from 4.2 to 9.8 yr^{-1} averaging 5.9 yr^{-1}, thus leading to overestimated exploitation rates. Using survey data where the adult stock is better represented the total mortality was estimated at 3.1 yr^{-1} (Mannini *et al.,* 1996).

Between the 1995-96 and 1997-98 surveys there was a marked difference in CPUE frequency distribution. *Limnothrissa miodon* catchability changed, as shown by the increased frequency of zero and small catches. The high percentage of zero catches would indicate that the species was much more contiguously distributed in 1997-98 than in 1995-96. The relative frequency of zero CPUEs for schooling species is believed to be a better index of abundance than the mean CPUE (Bannerot and Austin, 1983). This would mean that *L. miodon* abundance is reduced compared to two years earlier. However, it could be that the fishing efficiency was different in the two periods and this was directly reflected in fish catchability. It is possible that the acoustic biomass estimate for *L. miodon* will substantially differ between the two survey periods but it will be difficult to assess whether it is due to a change in the stock size or in fishing efficiency.

4.3 The *Lates stappersii* stock

Lates stappersii is known to be a fast, highly mobile fish capable of movement across the whole lake. However, evidence of massive migration has not yet been proven (Chapman, 1976; Chapman and van Well, 1978b). The species distribution obtained from survey data shows that it can occur in all lake areas. In 1995-96 it was found to be a common species, and the low frequency of zero catches at that time indicates that *L. stappersii* has a homogeneous distribution. However, the relative biomass pattern, outlined by the CPUE distribution, was uneven over the lake basin.

The central body of the lake (from Kigoma to East Marungu) characterised by steep shores, reduced shelf, and where the deepest areas are located (see Fig. 2), appears to be the optimal habitat for the species. In these areas the occurrence of *L. stappersii* reaches the maximum (even though the spatial pattern varies between months).

The difference between the CPUE frequency distribution in 1995 and 1997-98 would indicate that *L. stappersii* was less common and more disperse in the latter period. Also, early young fish dominated the size composition of the 1997 catch. Older cohorts were underrepresented due to the low number of fish caught. *Lates stappersii* is a long–lived species (whose maximum age is estimated from 5 to 7 years) compared to the lake's clupeids, and several annual cohorts contribute to the population structure. It is unlikely that sudden changes in stock size and composition can take place over a short time period. Catchability of *L. stappersii* decreased between the two survey groups, while it may be dubious that this was caused by the fish, it seems possible that the efficiency of the fishing operations changed.

Juvenile and adult *L. stappersii* co-occur within a geographical area but the inshore–offshore distribution is not the same. Juveniles are highly mobile and can occur in either inshore and offshore but apparently they tend to be found more often along the continental shelf and slope, while adults are truly pelagic.

In general *L. stappersii* larvae occur in the same areas where the rest of the stock is found and there is some evidence that the spawning grounds of the species in the south of the lake are in the Moba and East Marungu sub–basins.

The Kigoma sub-basin in the northern half of the lake is the area where the most of the "northern" *L. stappersii* stock is located. This area possibly serves as a spawning ground and nursery for this part of the lake, as shown by the abundance, especially in 1995–96, of both juveniles and sexually mature fish. Adult fish can spread northward but further north of Rumonge they become rare. Only juveniles are found at the northern end of the lake (most probably entering in this area from the south), where they gather, and are exploited by the fishery, with *S. tanganicae* born in the same year. In this area, *L. stappersii* juveniles become rare from about the size of 90-100 mm (c. 6 month-old), when probably a southerly movement occurs (Mannini *et al.,* 1996).

There is no evidence of the existence of *L. stappersii* sub–populations in the lake. Results of population biology work (Mannini *et* al., 1996) do not indicate differences between the lake areas. *Lates stappersii* is a highly mobile species and is capable of moving along the longitudinal axis of the lake (FAO, 1978; Roest, 1992). It may be reasonably assumed that the fish move mainly (and mix) among sub–basins. However, from the perspective of stock management *L. stappersii* can be conceived as being split into a "northern" and "southern" stock. The first is located in the Kigoma and Kalemie sub–basins and is exploited almost exclusively by the artisanal lift-net fishery. The second is located in the Moba and East Marungu sub-basins and it is mostly targeted by the industrial purse seine fishery.

The current exploitation pattern of the northern and southern stock (i.e. the length at entry in the fisheries and the size composition of the commercial catch) is dissimilar. For example, the size composition of the commercial catch and the length at entry in the fishery, L_c, are different. The latter, L_c, although mesh sizes of fishing gears are similar, is estimated at about 100 and 235 mm TL in the Kigoma and Mpulungu areas respectively

(Mannini *et al.,* 1996). In the 1960s adult fish used to occur at the northern end of the lake and were caught by the Burundian industrial fishery (Coulter, 1970; 1976). They became rare and the industrial fishery CPUE has declined steadily since the 1980s (Petit and Kiyuku, 1995; Coenen, 1995). Contemporarily, the artisanal fishery catch of this species has increased. Currently, the contribution of *L. stappersii* to the commercial catch in this part of the lake is about 20 % (Coenen *et al*., 1998) and juveniles make up the bulk of it (Mannini *et al.,* 1996).

It has been suggested that the decline in CPUE at the northern end of the lake may have been caused by climatic changes which reduced water transparency at the northern end, making it unfavourable for visual predation (Plisnier, 1997). Also, it may be that the northern end of the lake is not the prime habitat, compared to other areas, for adult *L. stappersii* whose original relatively low abundance in the area was efficiently and quickly reduced by the combined, heavy industrial and artisanal fishing pressure which developed in succession in that region. By the 1970s the total mortality (Z) was already estimated to be higher at the northern end of the lake than in the Kigoma area (Z = 1.2 yr^{-1} and Z = 0.5 yr^{-1} respectively; Henderson, 1976). It is likely that this was related to the higher fishing pressure (hence fishing mortality) in the north. In the same area the other *Lates* species were quickly reduced by the fishing (Coulter, 1970). Probably *L. stappersii* withstood the local heavy exploitation better than *Lates* spp. due to recruitment from other areas and to the short turnover time.

Lates stappersii has replaced during the 1980s by *S. tanganicae* in the industrial purse seine fishery in the south of the lake (Pearce, 1995), and nowadays *L. stappersii* makes up 95% of the catch (Coenen *et al.,* 1998). The most important, and almost the only industrial fishery of the lake is based in Zambia and exploits the adult stock which originates from the Moba and East Marungu sub–basins. Signs of stock depletion have been observed. Commercial CPUE shows a constant decline since the mid-1980s (Coenen, 1995) and the fishing mortality is higher than in other parts of the lake (Mannini *et al.,* 1996). It is reasonable to believe that the stock targeted by the Zambian industrial fishery is sustained by immigration of fish from the less exploited areas north of the industrial fishing grounds. Should the existing industrial fishery reach these relatively poorly exploited areas (provided that this is practically and economically feasible) and/or a new, well organised industrial fishery develop, uncontrolled, to target *L. stappersii* stock in the areas of its main concentrations, then the stock will probably drastically decline and will not be able to sustain the yields recorded by the Zambian fleet during the last decade.

4.4 Observed relations between species

Early work on the feeding ecology of *L. stappersii* suggested that, although this species preys on fish from the size of about 100 mm, pelagic shrimps can be an important component in the diet, especially in the south of the lake (Pearce, 1985; 1995). However no lake–wide study has been carried out to show whether this is typical in all regions. Recent findings, together with the present results, show that the diet varies between the halves of the lake and that *L. stappersii* is not exclusively a fish predator. A comparative study of *L. stappersii* feeding in the Kigoma and Mpulungu areas showed that the diet composition is more heterogeneous, and *S. tanganicae* prey is a principal component, at Kigoma, while in the south pelagic shrimps are an extremely important food items (Mannini *et al.,* in press).

The study of the diet using samples from commercial catch could be biased by the light attraction used in the fishing by artificially attracting both predator and prey. Comparison of results from samples collected with and without light attraction suggests that this is not the case for Lake Tanganyika species (Pearce, 1991; Mannini *et al.,* in press). However, survey data are free from this potential bias and, indeed, they prove that shrimps play an important role in the feeding regime of *L. stappersii.* There is not only a simple predator-prey relation between *L. stappersii* and *S. tanganicae,* but this also includes the shrimps. Both clupeids and shrimps alternate in the diet composition of the predator depending on the time of the year, area of the lake, and their abundance in the environment. The important southern *L. stappersii* stock seems to be sustained by the shrimps even when *S. tanganicae* abundance is low.

Predator avoidance mechanisms seem to be more efficient for *S. tanganicae* (probably due to the high mobility) than for shrimp prey. It appears that *L. stappersii* efficiently locate shrimp concentrations while there is no significant positive association between abundance of *L. stappersii* and *S. tanganicae* in the environment. Excluding the juveniles, which are planktivorous until they reach the length of about 100 mm, *L. stappersii* stock is sustained by clupeids and shrimps and can opportunistically switch from one to the other depending on their availability in the environment.

The mixed occurrence of juveniles of *L. stappersii* and *S. tanganicae* observed in the commercial catch (Ellis, 1978; Chapman and van Well, 1978b) is not an artefact due to the positive response to light attraction. There is possible competition for food between the young centropomids and the clupeids born in the same year. This competition becomes predation when *L. stappersii* assume a piscivorous behaviour as they grow.

A main factor which explains the rapid changes of *S. tanganicae* abundance observed in local areas and fishing grounds is the abundance of copepod prey. Local concentrations of mesozooplankton are efficiently located and depleted by the clupeids, which then move away seeking new feeding grounds. Therefore, within the yearly abundance cycle, the availability of *S. tanganicae* stock to the fishery is strongly influenced by the timing and distribution, within local areas, of plankton abundance.

4.5 Fishery management considerations

The management of the pelagic fisheries of Lake Tanganyika should necessarily focus on the management of *S. tanganicae* and *L. stappersii* stocks and secondarily on that of *L. miodon.*

The population dynamics of *S. tanganicae* shows the typical characteristics such as short life—span, high mortality rate and turnover rate that make it inherently prone to large fluctuations in the size of the population. Expansion and contraction periods within the environment are characteristic of clupeid species (MacCall, 1990). The reduced occurrence of *S. tanganicae* at the southern end of the lake in the recent past may serve as example.

Natural changes in the size of pelagic fish stock are often caused by environmental factors which affect recruitment success. The commonest effect of climatic factors is to augment or diminish the magnitude of recruitment profoundly over a period of time. For short—lived species like *S. tanganicae,* whose population comprises one or two major cohorts, poor recruitment causes an immediate decline of the catchable stock.

Environmental factors and the dynamics through which they affect exploited fish populations are starting to be elucidated for some of the most important stocks in temperate waters on which large, complex historical (several decades) data sets are available (see Cushing, 1995 for a review). Plisnier (1997) has made a first attempt to identify possible effects of climate on Lake Tanganyika fisheries. However, the negative effects of either environmental variables or fishery overexploitation have the same consequence as recruitment overfishing. The real danger is that when recruitment declines so does the subsequent stock and if the fishing effort remains the same then recruitment overfishing takes place. Collapses due to recruitment overfishing have often been associated with transient environmental changes.

Of the three species which make up the pelagic fishery of the lake *S. tanganicae* has the highest production/biomass ratio (i.e. the highest productivity) and the theoretical annual sustainable catch can be higher than the standing stock biomass. At the same time this species is an ideal candidate for wide stock fluctuations described above. Therefore, it has to be accepted that the *S. tanganicae* fishery is inherently a risky enterprise. This is further complicated by the unpredictable occurrence of the stock in local fishing grounds, which is partly determined by the patchy concentration of copepod plankton.

The exploitation of *S. tanganicae* varies from the moderate level in the central areas of the lake to relatively heavy at the northern end. This reflects the lake-wide distribution of fishing effort targeting *S. tanganicae,* which is highest in the area of Bujumbura and Uvira and decreases further southwards. Consequently, it has been suggested that the overexploitation of the stock is taking place in the north (Coenen *et al.,* 1998).

However, to date there is no evidence of local overfishing in the north of the lake. For example, Shirakihara et *al.* (1992) concluded that the decline in the clupeid catch in the 1980s was caused by natural population decrease and that the stock was not overfished. The most recent fishery statistics show that clupeid yield in 1995 was at the same level as the previous years. Catch rates for lift-net fishery (the most important fishery in the north) show wide variations but not a well defined declining trend.

However, possible indications of local overexploitation exist. It should be noted that commercial catch samples collected from July 1993 to December 1995 in Burundi and Zaire north of Karonda were mostly composed (90% of the total number) by *S. tanganicae* below the length at maturity, which, for this species, is 78 mm (Mannini, *et al.,* 1996). In other lift-net fisheries around the lake (where the same net mesh size of 8–10 mm is used) this proportion ranges from 48% (Kipili) to 72% (Kigoma). It seems unlikely, although it cannot be excluded, that the high proportion of juveniles in the catch at the northern end was due to a series of local good recruitments dominating the size structure of the stock. Also, the mean length in catches is smaller at the north end (59 mm) than in the rest of the lake (from 63 mm at Moba to 72 at Kipili).

All together this may indicate that, at the northern end of the lake, sustainable yield level for *S. tanganicae* has been reached, the spawning stock biomass could be critically low, and no further fishery development is advisable on both the west and east coast north of Karonda. Should it happen, any future, negative *S. tanganicae* stock fluctuation will be further amplified by the removal exerted by the overcapacity of the fishery.

Patterson (1992) proposed a simple general model that relates the response of pelagic stock biomasses to exploitation. The information used was from fisheries for small pelagic fish for which more than five years (generally ten years) of data were available. The model indicates that pelagic stocks (at least those in the model) appear to be in equilibrium for an exploitation rate (**E**) of 0.4. This rate can then be used as a reference for appropriate exploitation strategies.

Tentative estimates of **E** for *S. tanganicae* have been recently obtained (Mannini *et al.,* 1996) and a mean value of 0.4 can be derived for the whole lake. This confirms that currently the *S. tanganicae* stock is, on a lake–wide basis, exploited within safe limits. If acoustic biomass estimates confirm the pattern of *S. tanganicae* abundance distribution observed from the survey catches, in the Kigoma and Kalemie sub-basins further fishing effort development could still take place and should be sustainable. However, it has to be pointed out that in these areas the current **E** is at 0.5 (although such estimates are rather approximate) and a strong increase will further exposed the fishery to the risk of stock collapse should adverse environmental factors induce it.

Nursery areas of *S. tanganicae* and *L. miodon* where juveniles spend the first months of their post-larval life are located in different areas. *Stolothrissa tanganicae* nursery grounds are in the offshore, pelagic waters relatively undisturbed by the fishery. *Limnothrissa miodon* nurseries are in shallow, coastal areas and are exploited (mainly in Zambia) by the highly nonselective beach seine fishery.

There is no evidence that late young and adult *L. miodon* are threatened by excessive fishery pressure. Actually, the exploitation status of the stock is unknown, mainly due to the inshore habitat of the species during the first part of its life cycle. Nursery grounds are in coastal waters, especially in areas with sandy bottoms (Matthes, 1967). Beach seining fishing practices which use nonselective net—cover should not be allowed as there is no rationale for their use. Alternatively, should the complete ban on small mesh—sized beach seines be unfeasible then a system of areas closed to this fishing practice should be established. Moreover, the impact of these nets on the coastal fish community (mainly composed by cichlid species), although not yet fully assessed, makes it preferable to halt their use in favour of the more selective pelagic fishery.

The history of the exploitation of *Lates* spp. shows that when the fishing effort, during the development phase of the lake’s fisheries, reached a relatively high level then the stocks of the most long—lived species with low mortality and slow growth were the first to be fished down (Coulter, 1970). This is a general feature which has been observed in many fisheries of the world (Pauly, 1986; 1998). These species have been replaced in the catch by *L. stappersii* which displays characteristics such as faster growth, shorter longevity and population turnover time that make it able to better withstand increased mortality due to fishery exploitation. This succession in the catch composition of *Lates* spp. has been observed at both the northern and southern end of the lake where the fishery has mostly developed (Coulter, 1991b; Pearce, 1995).

Nowadays at the northern end, which is a closed area with respect to the rest of the lake, where the pelagic fishery started and quickly developed, the catch of *L. stappersii* is mostly made up of juveniles (Mannini *et al.,* 1996). Adults appear in the fishery further south, probably from the Kigoma area. Although environmental factors related to climatic changes (i.e. El Niño— Southern Oscillation) have been suggested to explain the current low occurrence of fish larger than 100 mm TL and adult *L. stappersii* in this area (Plisnier, 1997), excessive fishery exploitation cannot be ruled out. Already in the 1970s the total mortality rate of the species was found higher in the Burundian sector of the lake compared to that in the lightly fished area of Kigoma. This means that the resilience of *L. stappersii* to fishing pressure has, unsurprisingly, a threshold beyond which drastic stock size reduction takes place.

The Zambian industrial fishery, entirely based on *L. stappersii,* is experiencing a decline in catch rates. While the fishing effort has experienced seven—fold growth from 1983 to 1995, increasing from 3 to 23 active purse seiners, CPUE has decreased since the mid–1980s further plummeting by 40% from 1994 to 1996 (Coenen, 1995; Coenen *et al.,* 1998; Paffen et *al.,* 1996). This probably indicates that maximum sustainable yield for the local fishing grounds near Mpulungu have been exceeded. The higher resilience to fishery exploitation shown by *L. stappersii* at the southern end of the lake compared to the north is explained by the high length at entry, L_c = 235 mm TL, in the fishery (mostly adult fish are caught) and by immigration from Moba and East Marungu sub–basins.

The fishing effort targeting *L. stappersii* which is the highest at the southern end, can be translated into higher exploitation rate in the south (E = 0.6) compared to the Kigoma area (E = 0.3) (Mannini *et al.,* 1996). In the long term it can be reasonably expected that fisheries targeting *L. stappersii* will further develop in the area of Moba and East Marungu sub–basins where a significant part, perhaps the most important, of the stock occurs, and is currently exposed to moderate exploitation. Consequently this will further reduce the stock available to the present Zambian-based industrial fishery.

Therefore, in the light of all the above evidence, it is advisable to curtail the increase in the industrial fishing effort (i.e. no more new fishing units should enter into the fishery). If catch rates further decline then consideration must be given to reducing the fishing effort to the level of the 1980s (which could mean as much as 50% reduction of either the fishing fleet size or the number of fishing days). Alternatively, the current industrial fishing effort based in Zambia should be re-distributed in Moba and Kalemie whose industrial units recently moved to Mpulungu because of the economic collapse of the native fishery. Seemingly this was not caused by the fish stock but by excessive taxation and lack of equipment (Mambona, 1996)

In the medium–long term prospective, the management of Lake Tanganyika fisheries will have to face the choice between a management oriented to maximise protein yields or profit. The first is represented by the highly productive, but unstable clupeid fishery, which is accessible and meets the food demand of the growing population. The second is based on the *L. stappersii* fishery which at the industrial level requires fish processing facilities and whose high quality products are suitable for export to rich distant markets (for a discussion on protein or profit oriented management see Turner, 1996).

These two fishery management options are not necessarily in antithesis. Should the present partition pattern of the pelagic stocks persist in the future, then the northern half of the lake could have a management strategy oriented to the clupeid–based fishery and another to the *L. stappersii-based* fishery in the southern areas.

Of general validity for the lake’s fisheries is that open access to commercial fishing should not be continued. License holding must be a legal requirement and, more importantly, must be enforced. Licensing system should not primarily be a taxation mechanism but a way to know, and control, the size of the active fishing community, to communicate with it for fisheries incentives or limitations. It is simply inconceivable, and antithetic to management aims, that exploitation of important fisheries to be *de facto* unmonitored and free. It is a well-known, yet often neglected, truism that fisheries that are unlimited become unprofitable (Graham, 1943).

Finally, the above fishery management considerations will have to be substantiated and verified through the standing stock biomass distribution and figures resulting from the acoustic work (Szczucka, in prep.). It may then be possible to design fishery management scenarios based on the actual size and allocation of the resources.

5. Conclusions

The commercial pelagic fish resources of Lake Tanganyika are composed of three species of which the main two are *S. tanganicae* and *L. stappersii.* The fish pelagic community of the lake is very simple and consequently the offshore fishery by-catch of non-target species is small. The three species are unevenly distributed and differences in their occurrence between areas can be dramatic. The distribution and availability of food resources play an important role to determine the occurrence in the lake of the catchable stocks of *S. tanganicae* and *L. stappersii.* Contagious aggregation and highly patchy distribution characterise both *S. tanganicae* and *L. miodon.*

The distribution of *S. tanganicae,* as observed at the time of the surveys, is not uniform within the lake. It mainly occurs in the northern half of the lake and is much reduced in the remaining southern areas. This appears to be a recent contraction of the distribution range of this species.

Limnothrissa miodon is more evenly distributed than *S. tanganicae.* The two species have a different horizontal age–related distribution across the lake. Nursery grounds of the first are close to the shore while those of *S. tanganicae* are in open, pelagic waters. With growth, *S. tanganicae* tend to move inshore while large *L. miodon* display the opposite movement.

Lates stappersii is common in the most of the lake and the deep, steep basins are areas of higher occurrence. The stock can be considered as divided into northern and southern components exploited by different fisheries at different levels.

Pelagic shrimps are an important prey for *L. stappersii* whose occurrence is positively correlated with their abundance. At low abundance of *S. tanganicae* prey *L. stappersii* can exploit the food resources composed by the shrimps and vice–versa. The occurrence of *S. tanganicae* is linked to that of copepods with whom there is a direct predator–prey relationship determining the local abundance pattern of the clupeid.

It is advisable not to further expand the fishing effort at the northern end of the lake, to ban or strongly limit nonselective beach seining targeting on *L. miodon* juveniles, and to stop or redistribute the industrial fishing growth in the south of the lake.

In view of the future population growth around the lake and of the consequent increase of fishing effort it is necessary that open access to the lake pelagic fisheries must be discontinued and regulated through a licensing system.

6. Acknowledgements

This work would not been possible without the commitment of a number of people of different countries who worked together to conduct the scientific cruises on Lake Tanganyika. It is unfortunately not possible to mention them all. Special acknowledgement is due to LTR Co—ordinator George Hanek who made the project survive through unforeseen and uncontrolled circumstances. Sincere thanks are for the perfect crew of R/V Tanganyika Explorer and for the scientific teams for their commitment to never ending working hours. I wish to thank Eero Aro, Pekka Kotilainen and Petra Paffen with whom I had the good fortune to work on the first surveys. Many thanks are due to Johanna Szczucka who conducted the last cruises. Heini Kurki and Els Bosma are acknowledged to have made available the zooplankton data. I thank Janusz Burczynski who kindly introduced me to the use of the EchoBase software. Finally, I am especially grateful to Ian Cowx for the critical reading of the work.

7. References

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

Bannerot, S.P. and Austin C.B. (1983) Using frequency distributions of catch per unit of effort to measure fish–stock abundance. *Trans. Am. Fish. Soc.* 112, 608–617.

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.

Bhatacharaya, C.G. (1967) A simple method for resolution of distribution in Gaussian components. *Biometrics,* 23, 115-135.

Blaxter, J.H.S. (1974) The role of light in the vertical migration of fish – a review. In: Evans, G.C., R. Bainbridge, and 0. Rackham (Eds) *Light as an ecological factor,* II. Oxford: Blackwell Scientific Publications, pp. 189–210.

Blaxter, J.H.S. (1988). Pattern and variety in development. In: Hoar, W.S. and D. Randall (Eds) *Fish physiology* Xia. Chichester and New York: Academic Press, pp. 1-58.

Bosma, E.M., Muhoza, S. and Zulu, I. (1998) The Gulfnet samples results of five cruises with the R/V Tanganyika Explorer. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. FAO, GCP/RAF/271/FIN-TD/March 1998, 26 pp.

Chapman, D.W. (1975) Characteristics of layers and schools of pelagic fish in Lake Tanganyika. FAO, FI:DP/URT/71/012/16, 10 pp.

Chapman, D.W. (1976) Acoustic estimates of pelagic ichthyomass in Lake Tanganyika with an inexpensive echo sounder. *Trans. Am. Fish. Soc.* 105 (5), 581–587.

Chapman, D.W., Rufli, H., van Well, P. and Ndugumbi, Z. (1976) Movements of pelagic fish in Lake Tanganyika. FAO, FI:DP/URT/71/012/35, 18 pp.

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

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

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

Coenen, E., Paffen, P. and Nikomeze, E (1998) Catch per unit of effort (CPUE) study for different areas and fishing gears of Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. FAO, GCP/RAF/271/FIN-TD/80, 92 pp.

Coulter, G.W. (1970). Populations changes within a group of fish species in Lake Tanganyika following their exploitation. *J. Fish Biol.* 2, 329—353.

Coulter, G.W. (1976) The biology of *Lates* species (Nile perch) in Lake Tanganyika, and the status of the pelagic fishery for *Lates* species and *Luciolates stappersii* (Blgr.). *J. Fish Biol.* 9, 235-259.

Coulter, G.W. (ed.) (1991a) *Lake Tanganyika and its life.* Oxford: British Museum (Natural History) and Oxford University Press. 354 pp.

Coulter, G.W. (1991b) Pelagic fish. In: Coulter, G.W. (Ed.) *Lake Tanganyika and its life.* Oxford: British Museum (Natural History) and Oxford University Press, pp. 111-138.

Cushing, D.H. (1995) *Population production and regulation in the sea: a fisheries perspective.* Cambridge: Cambridge University Press. 354 pp.

Dennis, B. and Patil. G.P. (1988) Applications in ecology. In: Crow, E.L. and K. Shimizu (Eds), *Lognormal distributions: theory and applications.* New York: Marcel Decker, pp. 303—330.

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.

Garcia, S. and Josse, E. (1988) Notes on the assessment of small pelagic species on the basis of length frequency analysis and converted catch curves. *Fishbyte,* 6(1): 16-18.

Graham, M. (1943) The fish gate. London: Faber & Faber.

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

de Iong, H.H., Spliethoff, P.C. and Frank. V.G. (1983) Feeding habits of the clupeid *Limnothrissa miodon* (Boulenger) in Lake Kivu. *Hydrobiologia,* 102, 113–122.

Johannes, M.R.S. (1992) Prey aggregation is correlated with increased predation pressure in lake fish communities. *Can. J. Fish. Aquat. Sci.,* 50:66–73.

Johannesson, K.A. (1975) Preliminary quantitative estimates of pelagic fish stocks in Lake Tanganyika by use of echo integration methods. FAO, EIFAC Tech. Pap. 23, Suppl. 1 (1), 292–306.

Kihakwi, A.D. and Chale, N.A. (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. FAO, GCP/RAF/271/FIN–TD/30, 63–65.

Kurki, H. (1993) Field notes on zooplankton. FAO, GCP/RAF/271/FIN-FM/09, 26 pp.

Kurki, H. (1996) Zooplankton sampling on board R/V Tanganyika Explorer. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. FAO, GCP/RAF/271/FIN-FM/20, 16 pp.

Luecke, C. and Wurtsbaugh, W.A. (1993) Effects of moonlight and daylight on hydroacoustic estimates of pelagic fish abundance. *Trans. Amer. Fish. Soc.* 122, 112-120.

MacCall, A.D. (1990) *Dynamic geography of marine fish populations.* Seattle: University of Washington Press, 153 pp.

Mambona, W.B.C. (1996) Enquête cadre simultanée pour le Lac Tanganyika, Zaïre. FAO/FINNIDA Recherche pour l'aménagement des pêches au lac Tanganyika. FAO, GCP/RAF/271/FIN–TD/47, 100 pp.

Mann, M.J., Bashirwa, F., Ellis, C.M., Nahabakomeye, J.B. and Enderlein, H.O. (1973) A preliminary report on fish biology and stock assessment in Lake Tanganyika (Burundi). FAO, FI:DP/BDI/73/020/5, 1–58.

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

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

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

Mannini, P., Aro, E., Katonda, I., Kissaka, B., Mambona, W.B.C., Milindi, G., Paffen, P. and Verburg, P. (1996) Pelagic fish stocks of Lake Tanganyika: biology and exploitation. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. FAO, GCP/RAF/271/FIN–TD/53, 85 pp.

Mannini, P., Katonda, I., Kissaka, B. and Verburg, P. Feeding ecology of *Lates stappersii* in Lake Tanganyika. *Hydrobiologia* (in press).

Mathisen, O.A. (1975) Preliminary report on a mission (acoustic estimation) for the Lake Tanganyika Fisheries project. FAO, FI:DP/URT/71/012/28, 38 pp.

Matthes, H. (1967) Preliminary investigations into the biology of the Lake Tanganyika Clupeidae. *Fish. Res. Bull. Zambia, 4:* 39-46.

McConnaughey, R.A. and Conquest, L.L. (1992) Trawl survey estimation using a comparative approach based on lognormal theory. *Fish. Bull.* 91, 107-118.

Murphy, G. (1977) Clupeoids. In Gulland, G. (Ed.) *Fish population dynamics.* New York: John Wiley, pp. 283-308.

Ndugumbi, Z., van Well, P. and Chapman, D.W (1976) Biology of *Limnothrissa miodon* in Lake Tanganyika. FAO, FI:DP/URT/71/012/36, 15 pp.

Paffen, P., Lukwesa, P.C. and Mwape, L. (1996) Frame survey results for the Zambian coast of Lake Tanganyika, March 1995, and comparison with past surveys. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. FAO, GCP/RAF/271/FIN–TD/52, 97 pp.

Patterson, K. (1992) Fisheries for small pelagic species: an empirical approach to management targets. *Reviews in Fish Biology and Fisheries,* 2, 321–338.

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

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

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

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

Pauly, D. (1986). Problems of tropical inshore fisheries: fishery research on tropical soft bottom communities and the evolution of its conceptual base. In: Mann–Borgese, E. and Ginsburg, N. (Eds) *Ocean Yearbook* 6, Chicago: University of Chicago Press, pp. 29-37.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. and Torres, F. (1998) Fishing down marine food webs. Science, 279, 860- 863.

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, 60 pp.

Pearce, M.J. (1988). Some effects of *Lates* spp. on pelagic and demersal fish in Zambian waters of Lake Tanganyika. In: Lewis, D. (Ed.) *Predator-prey relationships, population dynamics and fisheries productivities of large african lakes.* FAO, CIFA Occas. Pap. 15, pp. 70-87.

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 Nagoshi, M. (Eds) *Ecological and limnological study on Lake Tanganyika and its adjacent regions, 7,* pp. 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 Hart, P.J.B. (Eds) *The impact of species changes in African lakes.* London: Chapman & Hall, pp. 425-441.

Peterman, R.M. and Bradford. M.J. (1987) Wind speed and mortality rate of a marine fish, the northern anchovy *(Engraulis mordax). Science,* 235: 354-356.

Petit, P. and Kiyuku, A. (1995) Changes in the pelagic fisheries of northern Lake Tanganyika during the 1980s. In Pitcher, T.J. and Hart P.J.B. (Eds) *The impact of species changes in African lakes.* London: Chapman & Hall, pp. 443-453.

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. FAO, GCP/RAF/271/FIN-TD/41, 26 pp.

Plisnier, P.D. (1997) Climate, limnology and fisheries changes of Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. FAO, GCP/RAF/271/FIN-TD/72, 39 pp.

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

Reusens, M. (1987) Programme de recherche halietique au Lac Kivu en particulier sur le *Limnothrissa miodon.* Projet de développement de la pêche au Lac Kivu, UNDP-FAO/RWA/87/012, FAO, Doc. de Travail, 3, 114 pp.

Roest, F. (1977) *Stolothrissa tanganicae:* population dynamics, biomass evolution and life history in the Burundi waters of Lake Tanganyika. FAO, CIFA Occas.Pap. 5, 42—63.

Roest, F. (1978) *Stolothrissa tanganicae:* population dynamics, biomass evolution and life history in the Burundi waters of Lake Tanganyika. FAO, 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 productivities of large african lakes.* FAO, CIFA Occas. Pap. 15, 104—129.

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

Shirakihara, K., Use, K., Kamikawa, S. and Mambona, W.B. (1992) Population changes of sardines in northern Lake Tanganyika. *African Study Monographs,* 13(1), 57-67.

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

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

Turner, G.F. (1994) Maximization of yields from African lakes. In: Cowx, I.G. (Ed.) *Stock Assessment in Inland Fisheries.* Oxford: Blackwell, pp. 465—481.

Table 1. Date and position of fishing hauls carried out in June and November-December 1995, April 1996, November-December 1997 and February 1998 combined hydroacoustic-pelagic trawling surveys. Only the fishing hauls used in the present report are listed.

Date	Start Position		End Position		Date	Start Position		End Position		Date	Start Position		End Position	
	South Lat.	E. Long.	South Lat.	E. Long.		South Lat.	E. Long.	South Lat.	E. Long.		South Lat.	E. Long.	South Lat.	E. Long.
15/6/95	03º28,31	29º16,92	03º31,91	29º17,59	16/11/95	03º26,99	29º09,21	03º26,62	29º12,69	02/04/96	03º25,86	29º14,84	03º29,71	02º91,47
16/6/95	03º43,03	29º13,95	03º46,26	29º15,34	17/11/95	03º28,11	29º15,36	03º02,58	29º18,66	03/04/96	03º32,88	29º15,34	03º37,11	29º15,21
16/6/95	04º14,60	29°25.88'	04º17,22	29º28,37	17/11/95	03º37,30	29º18,78	33º73,90	29º18,22	03/04/96	03º46,05	29º15,12	03º48,72	29º17,98
17/6/95	04º34,05	29º37,50	04º37,79	29º36,45	17/11/95	03º56,51	29º08,39	03º55,53	29º11,91	03/04/96	03º57,67	29º07,62	03º57,40	29º11,61
17/6/95	04º33,91	29º10,02	04º36,27	29º08,64	17/11/95	03º57,69	29º16,11	03º59,65	29º20,34	03/04/96	03º57,39	29º15,46	03º56,48	29º19,40
18/6/95	04º45,62	29º25,81	04º49,29	29º27,07	18/11/95	03º58,09	29º24,05	04º00,92	292º42,27	04/04/96	03º57,09	29º23,91	04º01,30	29º23,07
18/6/95	05º20,47	29º45,63	05º17,38	29º46,63	18/11/95	04º27,87	29º14,21	04º28,66	29º17,58	04/04/96	04º27,56	29º13,44	04º27,68	29º17,35
19/6/95	05º03,95	29º37,91	04º59,32	29º36,95	19/11/95	04º28,42	29º38,59	04º31,13	29º38,49	05/04/96	04º27,36	29º25,72	04º27,60	29º30,04
20/6/95	05º41,49	29º53,15	05º45,14	29º54,25	19/11/95	04º57,37	29º08,06	04º57,06	29º11,42	05/04/96	04º27,65	29º37,38	04º30,37	29º34,64
20/6/95	05º56,60	29º37,30	05º58,24	29º34,56	20/11/95	04º57,29	29º25,72	04º58,05	29º28,90	05/04/96	04º57,39	29º08,70	04º56,90	29º13,05
20/6/95	06º05,51	29º21,16	06º09,24	29º23,19	20/11/95	04º56,39	29º36,47	04º54,70	29º33,53	05/04/96	04º57,30	29º26,00	04º57,49	29º29,86
20/6/95	06º12,26	29º42,03	06º16,58	29º40,22	21/11/95	05º28,03	29º19,47	05º28,64	29º22,70	06/04/96	04º57,40	29º36,23	04º55,48	29º32,40
21/6/95	06º23,72	29º39,55	06º24,86	29º43,40	21/11/95	05º27,39	29º35,59	05º27,31	29º38,70	07/04/96	05º27,08	29º20,03	05º26,80	29º23,84
22/6/95	06º31,79	30º00,16	06º31,15	30º03,91	22/11/95	05º28,05	29º44,50	05º30,75	29º46,66	08/04/96	05º27,46	29º36,33	05º26,94	29º39,76
21/6/95	06º37,22	30º17,06	06º38,03	30º18,46	22/11/95	05º56,90	29º16,27	05º56,50	29º19,69	08/04/96	05º28,94	29º44,54	05º32,19	29º45,59
22/6/95	06º52,58	30º08,68	06º56,15	30º07,23	23/11/95	05º57,09	29º31,24	05º56,80	29º35,16	08/04/96	05º57,46	29º20,52	05º57,77	29º24,10
22/6/95	07º07,04	30º27,57	N/A		23/11/95	05º56,71	29º45,73	05º54,72	29º48,67	08/04/96	05º58,78	29º35,23	05º58,48	29º38,79
22/6/95	07º24,58	30º21,36	07º26,94	30º18,67	24/11/95	06º28,43	29º46,60	06º29,27	29º50,29	09/04/96	05º57,07	29º47,67	05º58,09	29º44,54
23/6/95	07º39,56	30º15,15	07º39,25	30º19,04	24/11/95	06º31,86	29º57,00	06º31,24	30º00,26	09/04/96	06º26,69	29º25,55	06º26,50	29º30,49
23/6/95	07º25,44	30º46,07	07º56,41	30º45,10	24/11/95	06º57,38	29º46,52	06º56,89	29º50,18					
23/6/95	08º04,88	30º51,11	N/A		25/11/95	06º57,68	30º05,61	06º58,44	30º09,45					
24/6/95	08º23,61	30º52,93	08º26,82	30º54,36	25/11/95	06º58,69	30º31,65	07º02,56	30º31,05					
25/6/95	08º32,97	30º50,11	08º30,73	30º47,73	25/11/95	07º27,53	30º40,16	07º27,53	30º17,44					
25/6/95	08º19,60	30º53,35	08º16,07	30º37,15	26/11/95	07º30,82	30º33,49	07º33,25	30º35,78					
26/6/95	07º51,57	30º37,75	07º48,42	30º37,40	26/11/95	07º78,74	30º26,65	08º00,92	30º30,20					
26/6/95	07º32,33	30º34,43	07º29,14	30º32,61	27/11/95	07º58,15	30º40,60	07º59,42	30º04,06					
27/6/95	07º05,18	29º59,50	07º03,36	29º56,65	27/11/95	08º00,75	30º50,87	08º03,89	30º52,07					
27/6/95	06º33,42	29º31,03	06º29,78	29º30,70	27/11/95	08º26,72	30º28,89	08º26,06	30º32,58					
28/6/95	05º51,37	29º21,35	05º48,52	29º23,50	28/11/95	08º27,50	30º51,09	08º27,37	30º54,99					
28/6/95	05º18,16	29º22,90	05º14,66	29º23,53	28/11/95	08º28,47	31º07,03	08º31,80	31º07,27					
29/6/95	05º04,23	29º29,80	50º29,39	29º29,87	29/11/95	07º38,40	30º38,38	07º41,09	30º40,34					
29/6/95	04º18,97	29º22,29	04º14,55	29º21,80	1/12/95	04º56,72	29º36,74	04º56,91	29º32,94					
					3/12/95	04º03,25	29º26,11	03º59,40	29º24,47					

Table 1. Continued.

Date	Start Position		End Position		Date	Start Position		End Position	
	South Lat.	E. Long.	South Lat.	E. Long.		South Lat.	E. Long.	South Lat.	E. Long.
22/11/97	03º27,45	29º15,66	03º30,53	29º15,03	5/2/98	05º27,92	29º26,11	05º30,77	29º23,65
23/11/97	03º40,92	29º14,81	03º44,54	29º14,73	6/2/98	06º01,53	29º34,21	06º02,25	29º30,65
23/11/97	03º50,46	29º15,12	03º53,55	29º13,98	6/2/98	06º11,42	29º36,96	06º12,32	29º40,70
23/11/97	04º01,76	29º11,05	04º00,85	29º14,24	7/2/98	06º58,83	29º48,71	06º59,86	29º52,62
23/11/97	04º03,28	29º17,95	04º06,21	29º21,41	8/2/98	07º13,02	30º24,01	07º14,63	30º22,84
23/11/97	04º20,49	29º24,37	04º23,07	29º21,69	8/2/98	07º43,23	30º37,99	07º44,74	30º41,33
24/11/97	04º40,78	29º09,85	04º44,10	29º09,77	8/2/98	08º03,41	30º42,02	08º04,53	30º45,30
24/11/97	04º43,62	29º35,63	04º47,88	29º35,31	9/2/98	08º19,59	30º40,38	08º22,11	30º37,71
25/11/97	05º04,27	29º39,86	05º00,65	29º37,52	9/2/98	08º28,31	30º29,91	08º27,69	30º31,96
25/11/97	04º58,81	29º12,44	05º02,31	29º13,21	11/2/98	07º51,35	30º30,10	07º50,56	30º26,33
26/11/97	05º12,90	29º42,22	05º15,86	29º43,11	11/1/00	07º37,56	30º26,62	07º35,13	30º28,41
26/11/97	05º14,56	29º20,30	05º14,45	29º15,79	12/2/98	06º49,76	30º05,68	06º49,73	30º02,66
27/11/97	05º32,07	29º44,75	05º35,46	29º46,38	13/2/98	06º34,99	29º36,65	06º33,58	29º40,33
27/11/97	05º52,35	29º28,65	05º52,83	29º32,69	13/2/98	06º04,90	29º40,32	06º03,03	29º42,45
28/11/97	06º06,84	29º38,54	06º10,76	29º39,55	14/2/98	05º35,48	29º37,01	05º33,17	29º39,30
28/11/97	06º17,53	29º23,93	06º21,80	29º25,36	14/2/98	05º24,77	29º43,71	05º22,34	29º44,11
28/11/97	06º31,40	29º53,36	06º32,54	29º57,24	15/2/98	05º13,78	29º43,20	05º11,77	29º42,99
29/11/97	06º39,67	29º34,07	06º38,96	29º37,96	15/2/98	05º08,74	29º41,18	05º05,01	29º39,37
29/11/97	06º37,96	30º13,74	06º40,78	30º16,79	17/2/98	04º46,31	29º15,82	04º45,11	29º18,94
30/11/97	07º38,60	30º19,27	07º40,89	30º16,05	18/2/98	04º35,64	29º22,36	04º34,02	29º17,96
1/12/97	07º56,50	30º43,08	07º59,96	30º44,84	19/2/98	03º24,32	29º19,05	03º28,00	29º17,72
2/12/97	08º07,77	30º49,14	08º08,18	30º53,58	19/2/98	03º28,76	29º18,55	03º25,20	29º19,77
2/12/97	08º30,62	30º55,13	08º31,01	30º59,09					
4/12/97	08º23,50	30º39,37	08º24,82	30º35,00					
4/12/97	08º20,72	30º34,13	08º17,37	30º36,95					

Table 2. Total catch composition of five pelagic trawling surveys carried out in 1995-96 and 1997-98. Values are actual, not standardised, catch from night and daylight hauls.

Survey	Total catch	*S. tanganicae*		*L. miodon*		*L. stappersii*		*Lates* spp.		*Other* spp.	
		kg	%	kg	%	kg	%	kg	%	kg	%
Jun-95	506	48	9.5	65	12.8	224	44.3	145	28.7	24	4.7
Nov-Dec 1995	1408	475	33.7	263	18.7	194	13.8	320	22.7	156	11.1
Apr-96	363	138	38.0	36	9.9	56	15.4	96	26.4	37	10.2
Nov-Dec 1997	771	658	85.3	6	0.8	15	1.9	67	8.7	25	3.2
Feb-98	1544	1097	71.0	215	13.9	63	4.1	39	2.5	130	8.4

Table 3. Correlation coefficients between density (n/100 m^3) of *S. tanganicae* and *L. miodon* larvae, *L. parvula* and *P. moorei* shrimps, survey cpue (kg/hr) of *L. stappersii*, *S. tanganicae* and juvenile *L. stappersii* (TL < 100 mm, n/hr), numeric prey abundance in *L. stappersii* stomach contents of shrimps and *S. tanganicae* prey. Significant correlation are marked: * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

	S. tanganicae larvae	*L. miodon* larvae	*L. parvula*	*P.moorei*	*L. stappersii* cpue	Shrimp prey	*S. tanganicae* prey	*L. stappersii* juveniles	*S. tanganicae* cpue
S. tanganicae larvae		0.746***	0.648***	0.187	0.038	-0.021	-0.187	-0.082	-0.105
L. miodon larvae	0.746***		0.125	0.064	-0.141	-0.136	-0.189	-0.107	-0.151
L. parvula	0.648***	0.125		0.489**	0.534**	0.434	-0.007	-0.024	-0.073
P.moorei	0.187	0.064	0.489**		0.487*	-0.075	0.24	-0.304	-0.192
L. stappersii cpue	0.038	-0.141	0.534**	0.487*		0.674**	0.598*	-0.201	-0.103
Shrimp prey	-0.021	-0.136	0.434	-0.075	0.674**		-0.214	-0.231	-0.293
S. tanganicae prey	-0.187	-0.189	-0.007	0.24	0.598*	-0.214		-0.202	0.319
L. stappersii juveniles	-0.082	-0.107	-0.024	-0.304	-0.201	-0.231	-0.202		0.854***
S. tanganicae cpue	-0.105	-0.151	-0.073	-0.192	-0.103	-0.293	0.319	0.854***	

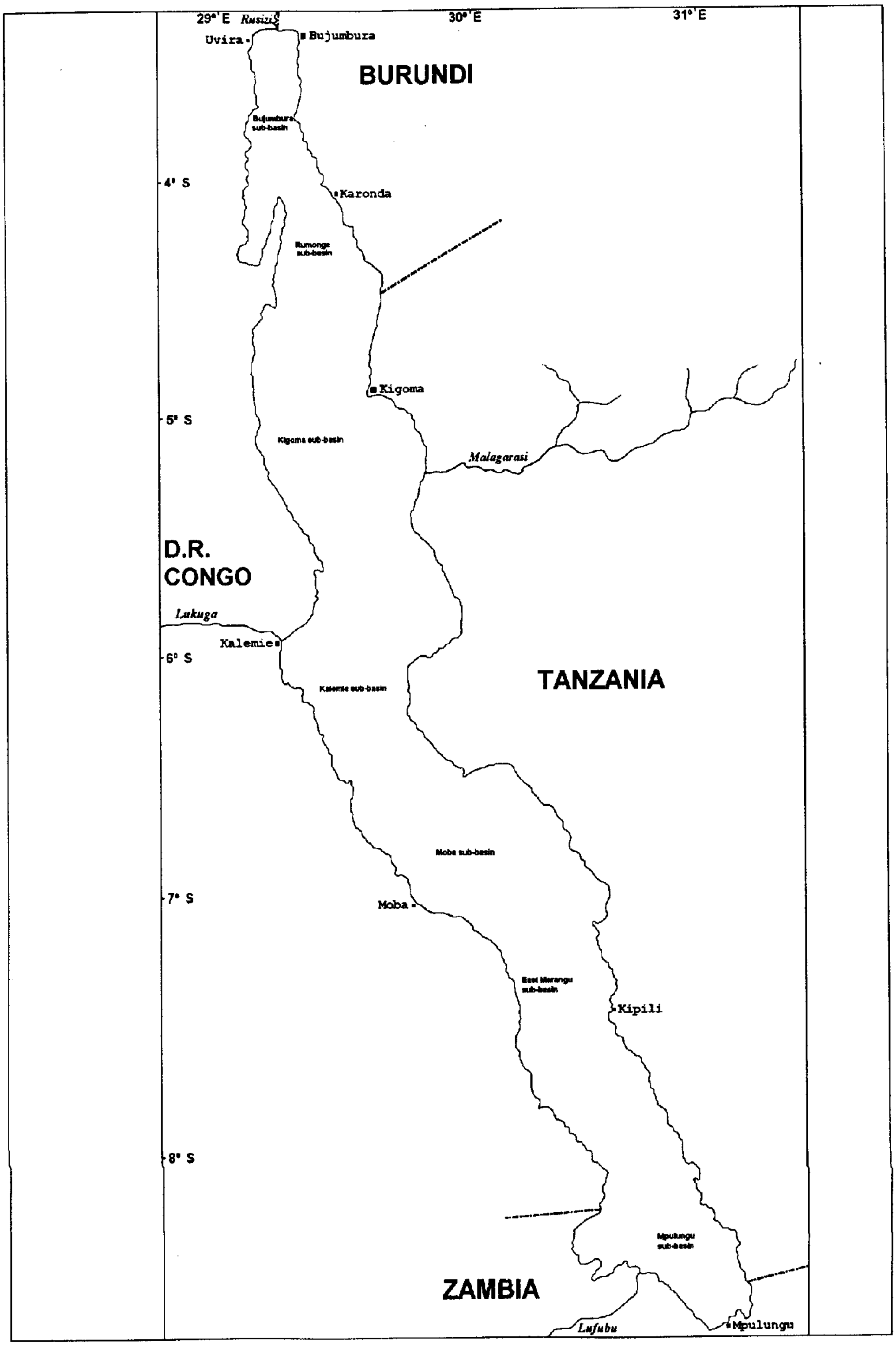


Figure 1. The map shows the major landing sites and villages of the lake. Sub-basins are also indicated (for more details see text and Tiercelin and Mondeguer in Coulter, 1991).

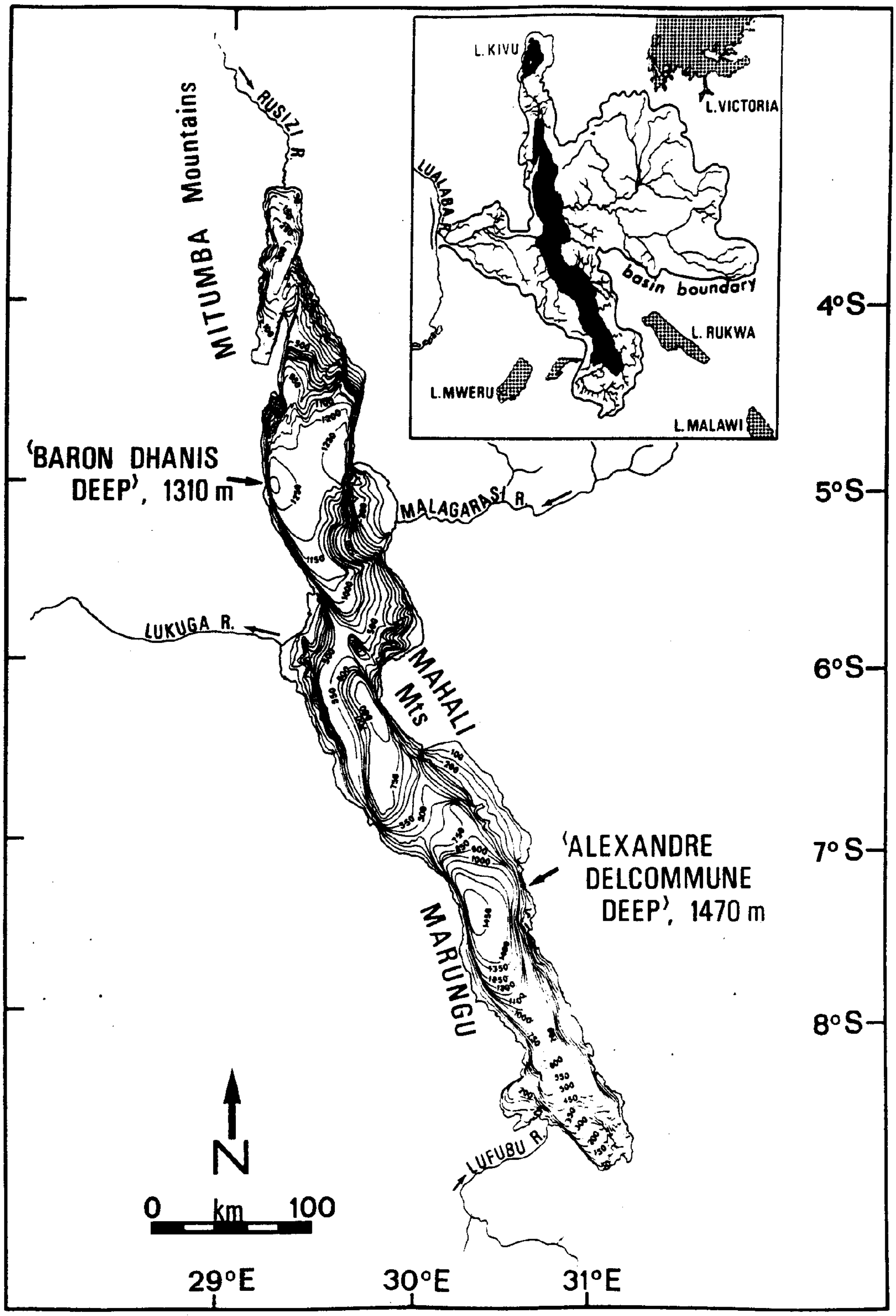


Figure 2. Bathymetry and drainage pattern of Lake Tanganyika (from Coulter, 1991, p. 10),

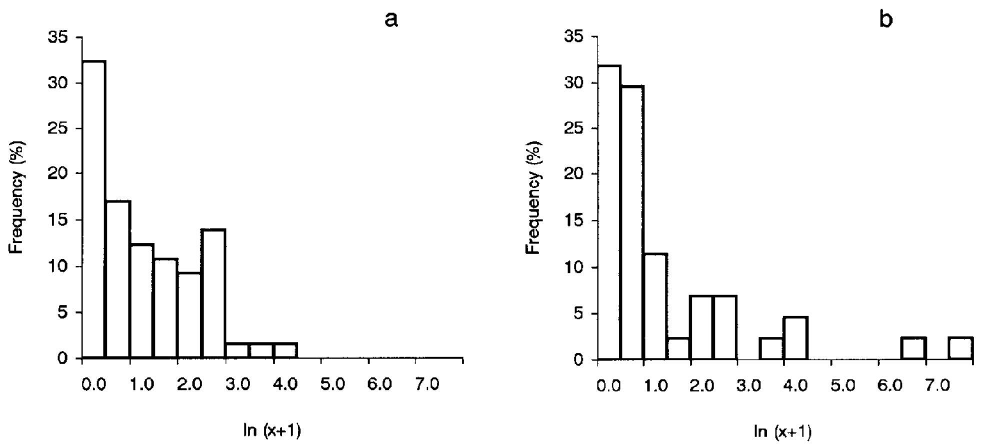


Figure 3. Frequency histograms of ln(x+1) transformed CPUE values derived for *S. tanganicae* from, a, June and November-December 1995 and, b, November-December 1997 and February 1998 pelagic trawl surveys

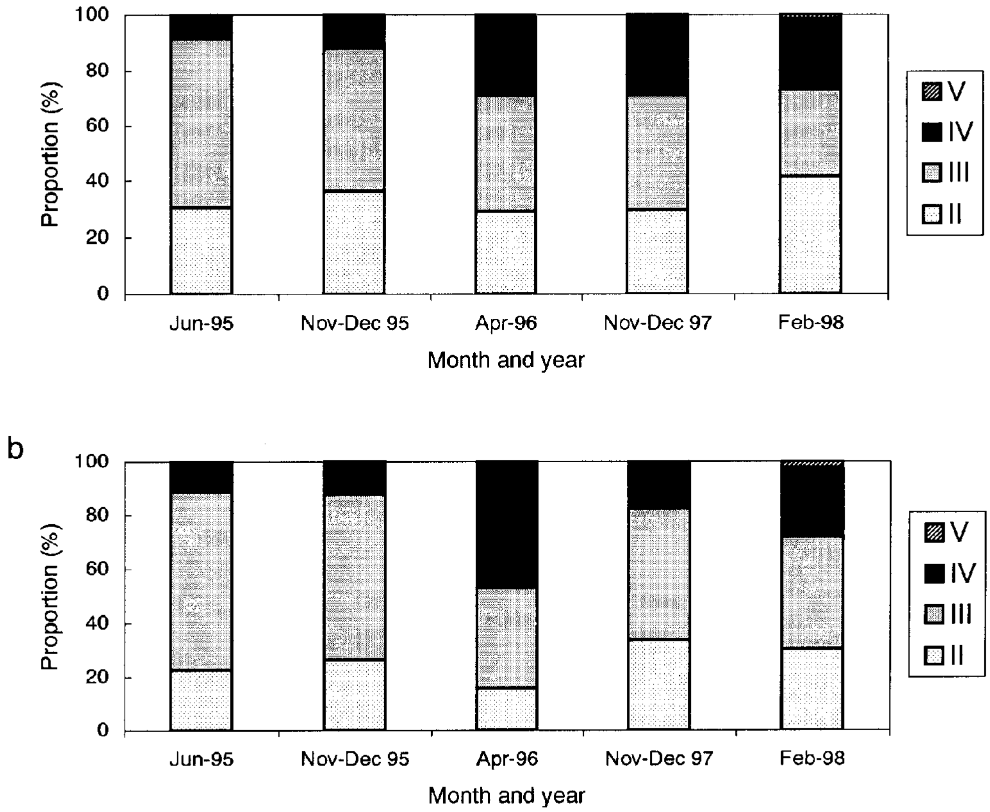


Figure 4. Maturity stages for *S. tanganicae* samples of females (a) and males (b) taken during lake-wide surveys in June (sample size, n=375) and November-December (n=834) 1995, April 1996 (n=507), November-December 1997 (n=673) and February 1998 (n=658).

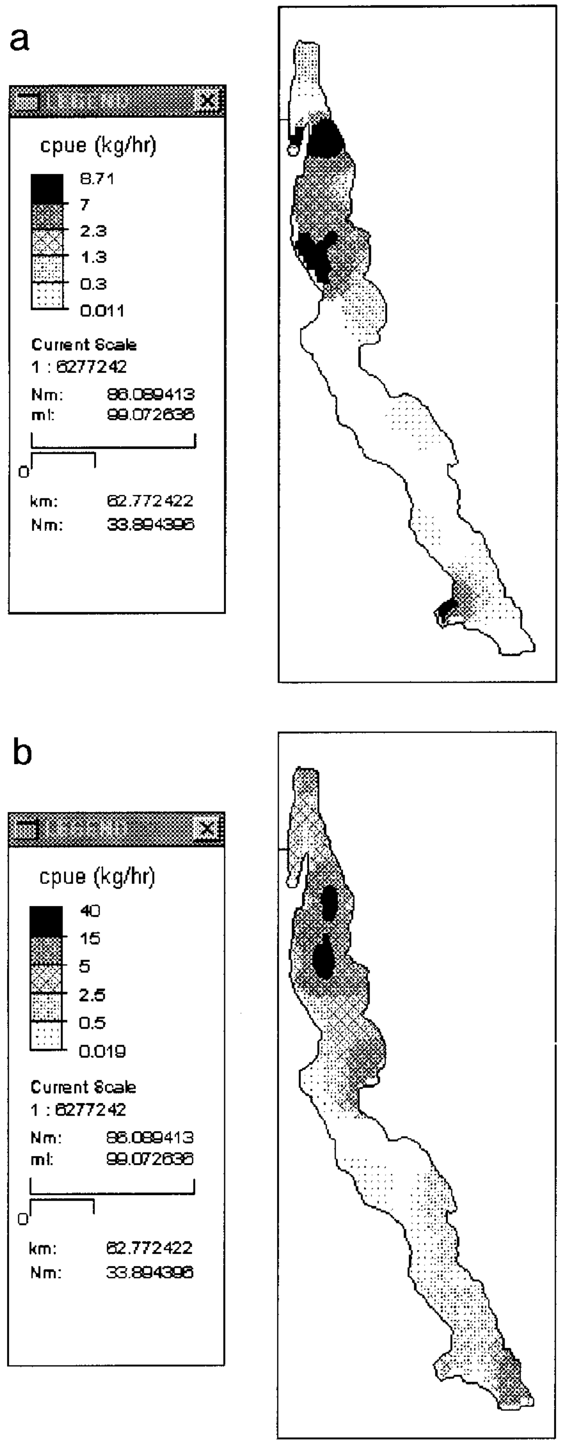


Figure 5. Pelagic trawl catch distribution of *S. tanganicae* in June 1995 (a) and November-December 1995 (b) survey. Catch per unit of effort (kg/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

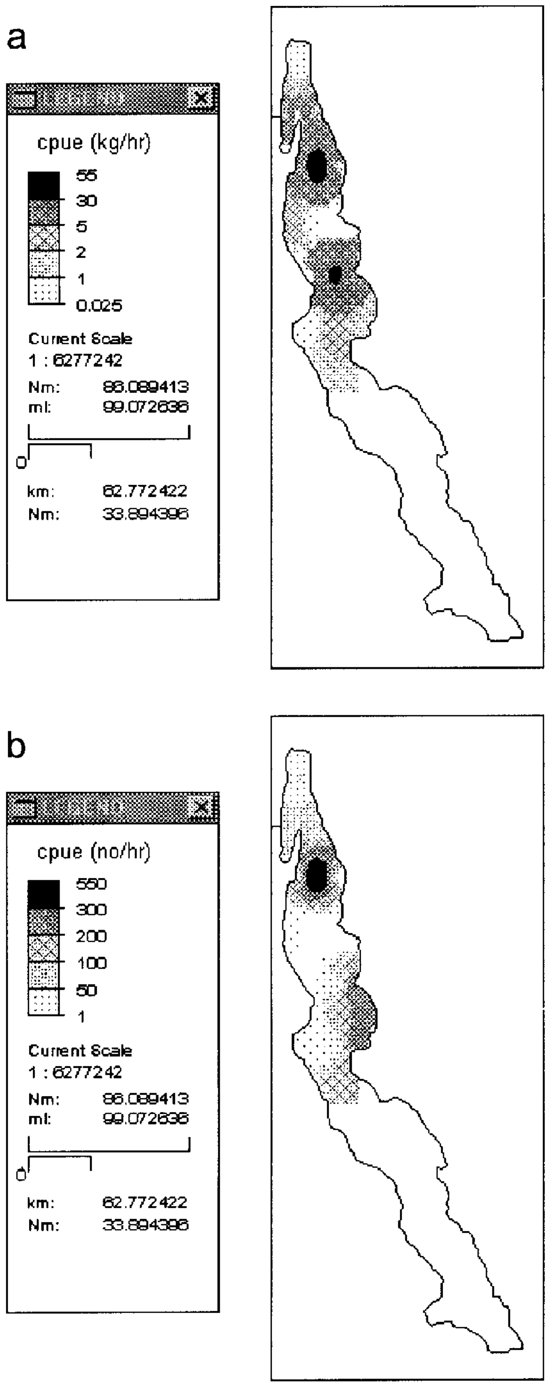


Figure 6. Pelagic trawl catch distribution (a) and number of adults (TL > L_m) caught (b) of *S. tanganicae* in April 1996 survey. Catch per unit of effort (kg/hr) and number of adult fish (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Blank areas mean that interpolation was not possible (no haul made or no zero catch). Note that **pattern scale has unequal intervals**. Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

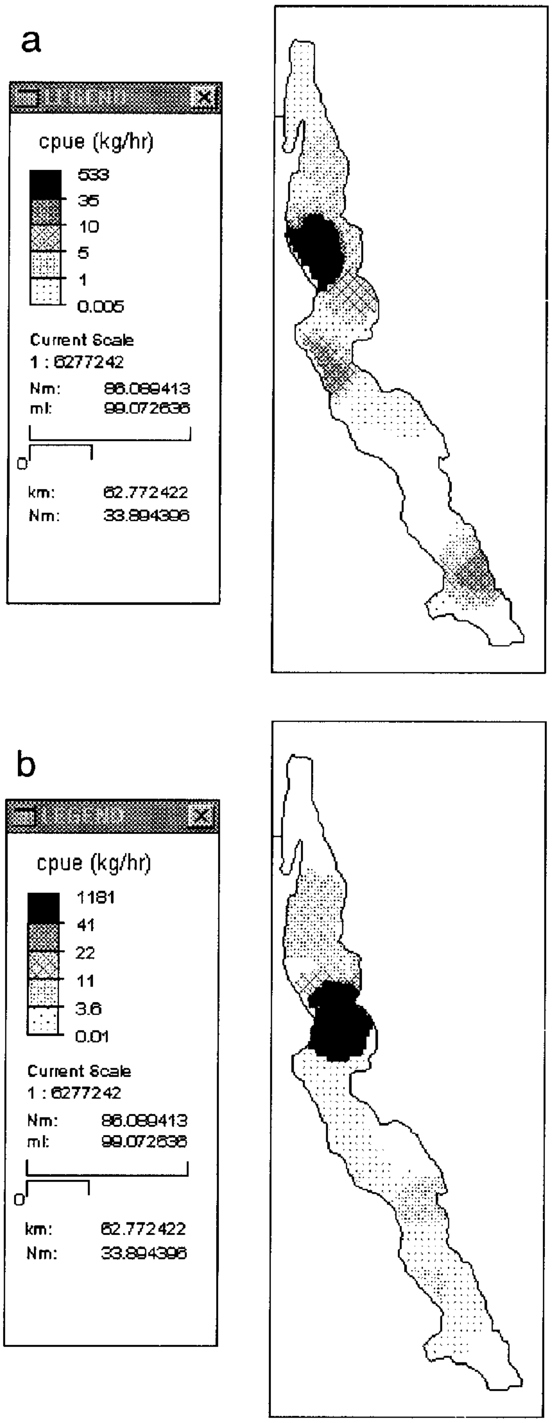
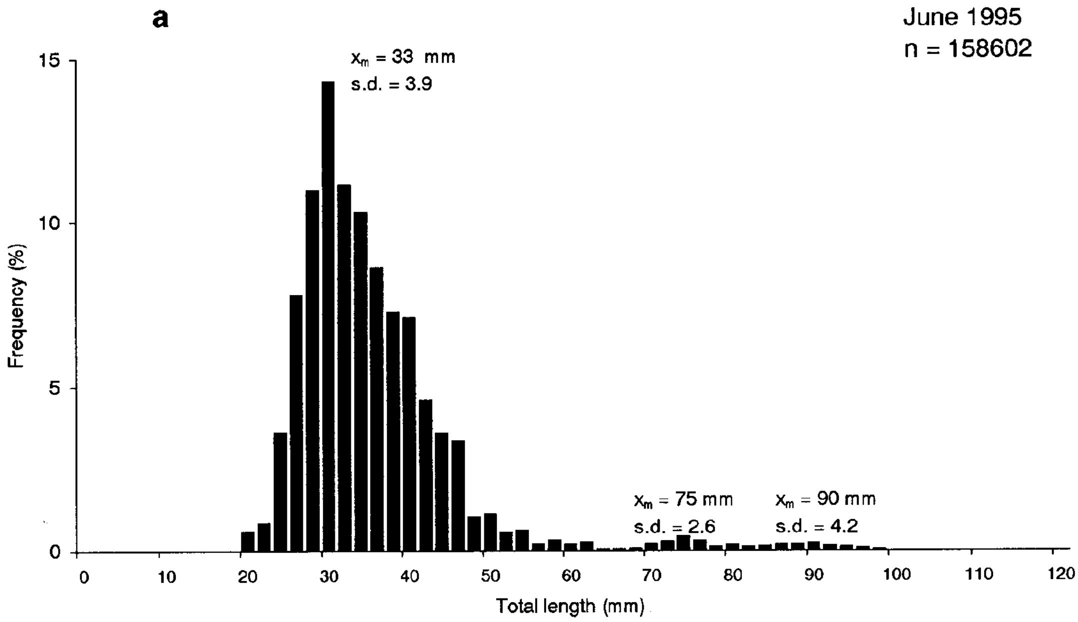


Figure 7. Pelagic trawl catch distribution of *S. tanganicae* in November-December 1997 (a) and February 1998 (b) survey. Catch per unit of effort (kg/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).



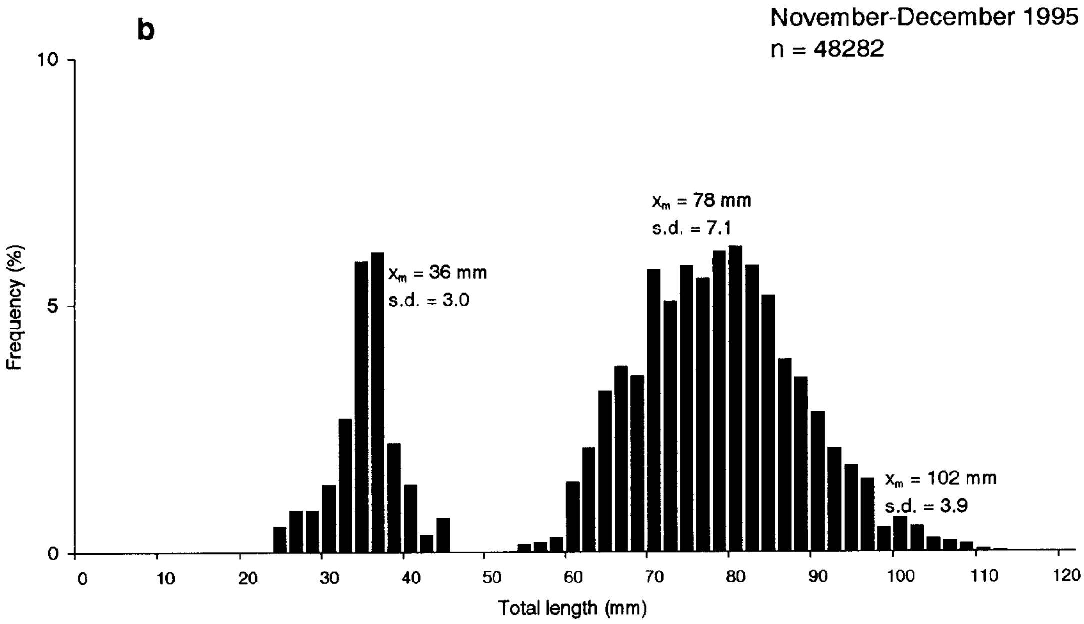


Figure 8. Size distribution of *S. tanganicae* for the whole lake from mid-water trawl surveys. **a**: June 1995 survey; **b**: November-December 1995 survey. N is the sample size, x_m and s.d. are the mean length and standard deviation of identified cohorts after Bhatacharya's decomposition of length distribution.

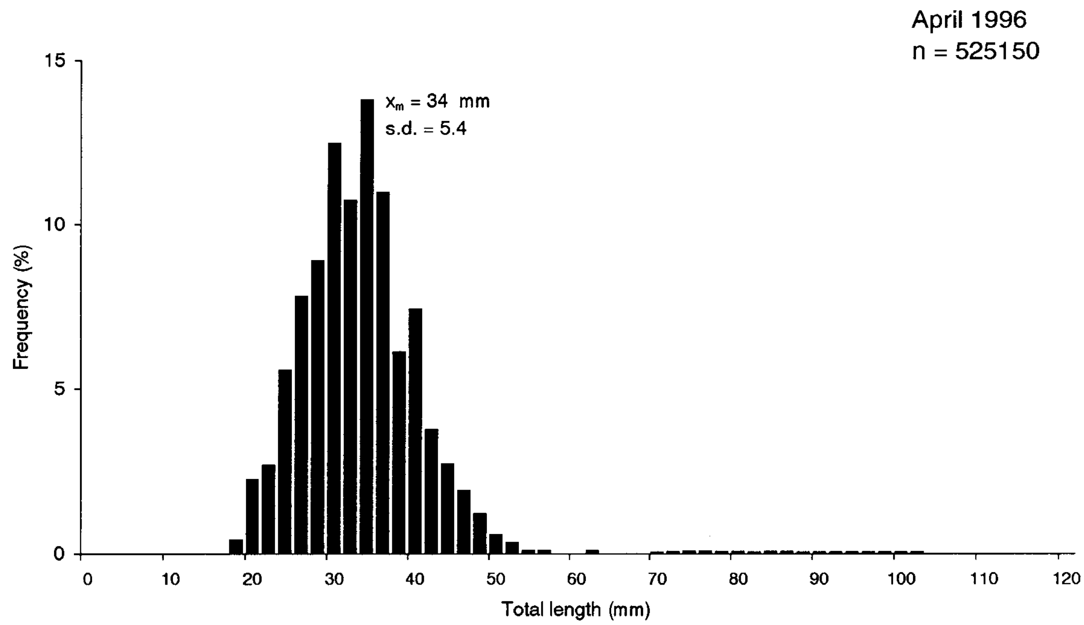


Figure 9. Size distribution of *S. tanganicae* for the whole lake from April 1996 mid-water trawl survey. N is the sample size, x_m and s.d. are the mean length and standard deviation of identified cohort after Bhatacharya's decomposition of length distribution.

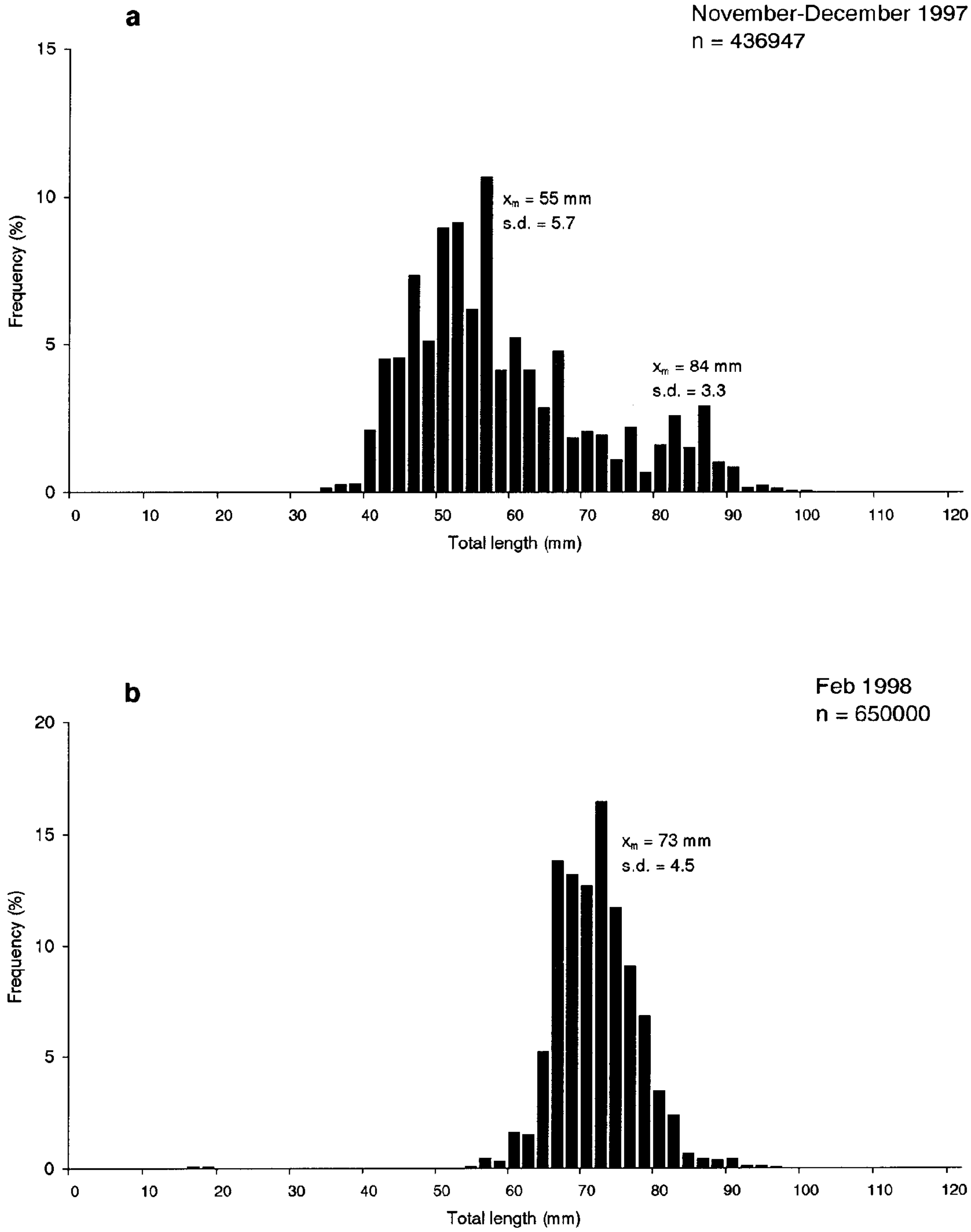


Figure 10. Size distribution of *S. tanganicae* for the whole lake from mid-water trawl surveys. **a**: November-December 1997 survey; **b**: February 1998 survey. N is the sample size, x_m and s.d. are the mean length and standard deviation of identified cohorts after Bhatacharya's decomposition of length distribution.

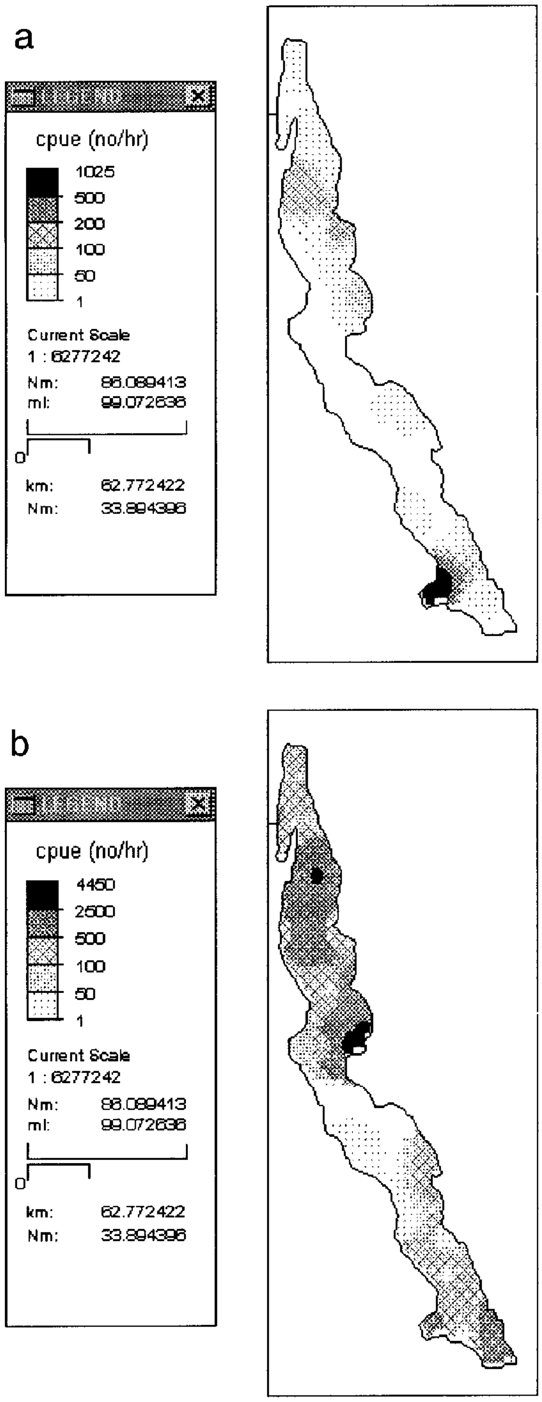


Figure 11. Pelagic trawl catch distribution of adult *S. tanganicae* (TL > L_m) in June 1995 (a) and November December 1995 (b) survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

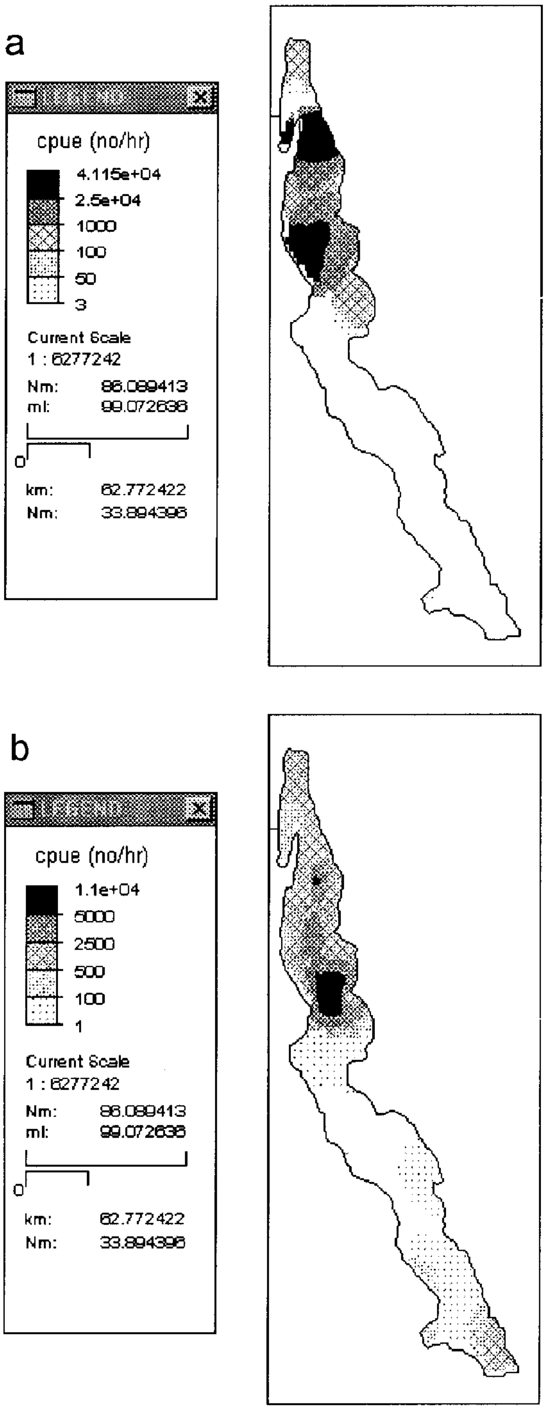


Figure 12. Pelagic trawl catch distribution of young *S. tanganicae* (TL < L_m) in June 1995 (a) and November-December (b) 1995 survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

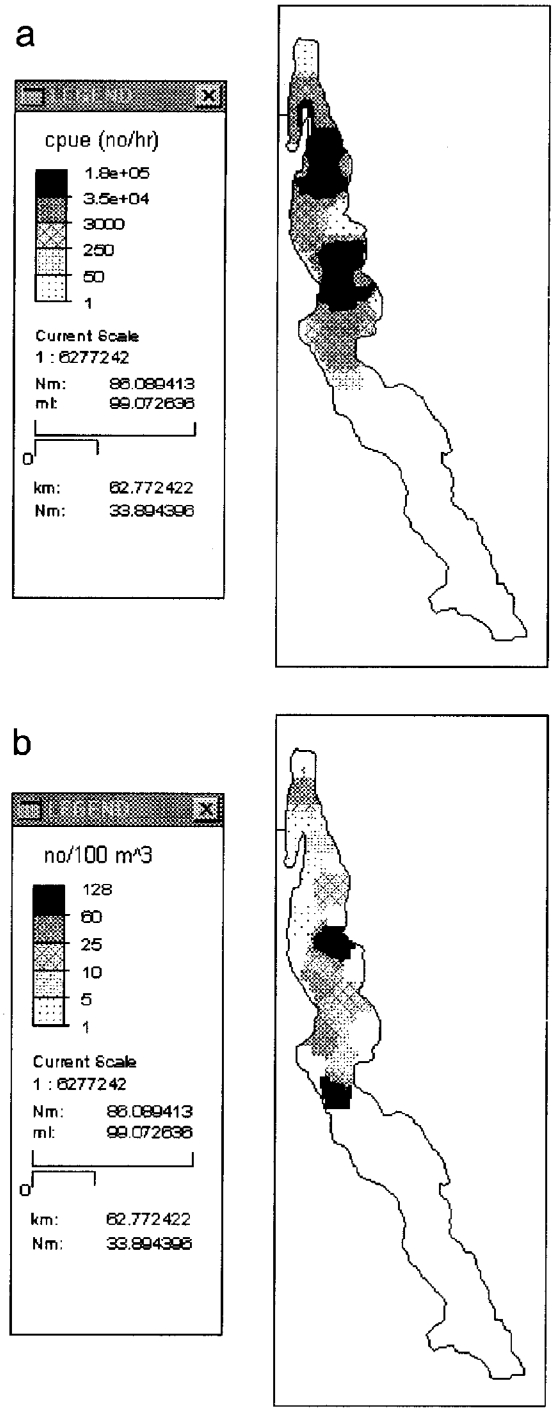


Figure 13. Pelagic trawl catch distribution of (a) young *S. tanganicae* ($TL < L_m$) and distribution of *S. tanganicae* larvae (b) within 0-100 m water column in April 1996 survey. Catch per unit of effort (no/hr) and larval density (no/100 m3) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

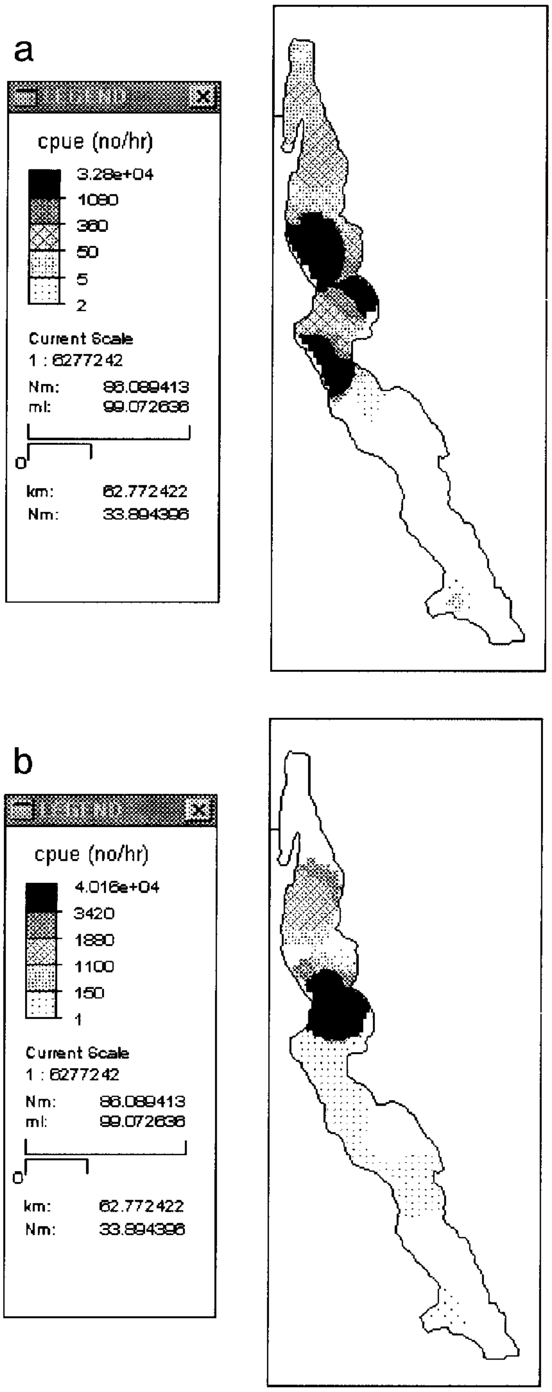


Figure 14. Pelagic trawl catch distribution of adult *S. tanganicae* (TL > L_m) in November-December 1997 (a) and February 1998 (b) survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

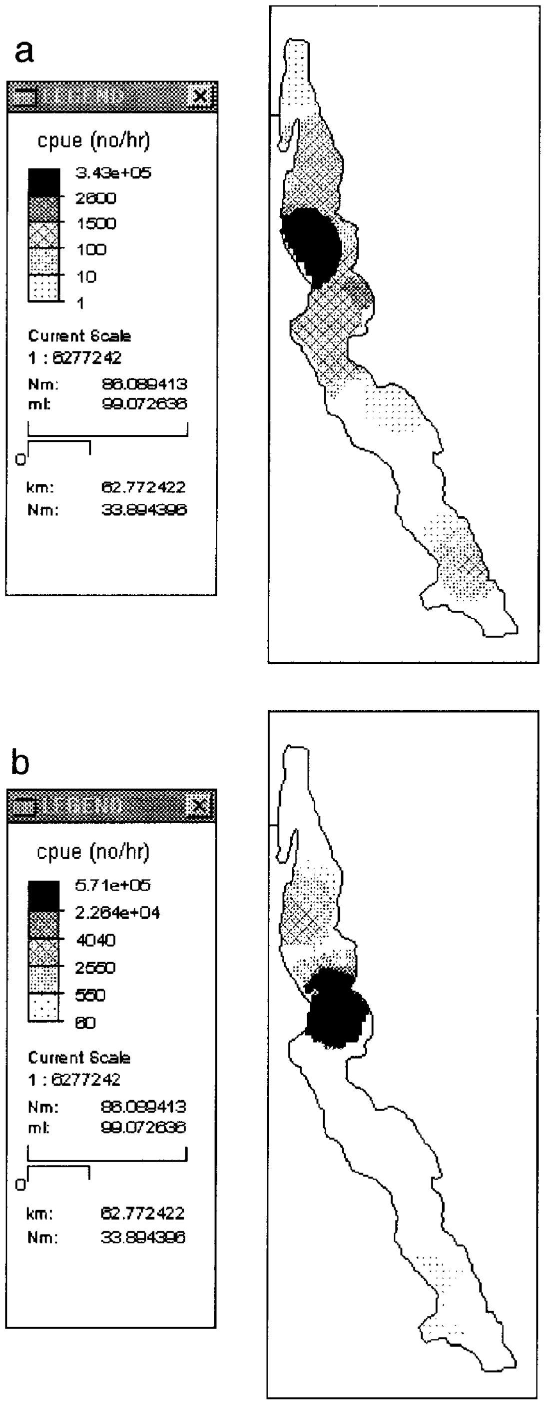


Figure 15. Pelagic trawl catch distribution of young *S. tanganicae* (TL < L_m) in November-December 1997 (a) and February (b) 1998 survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

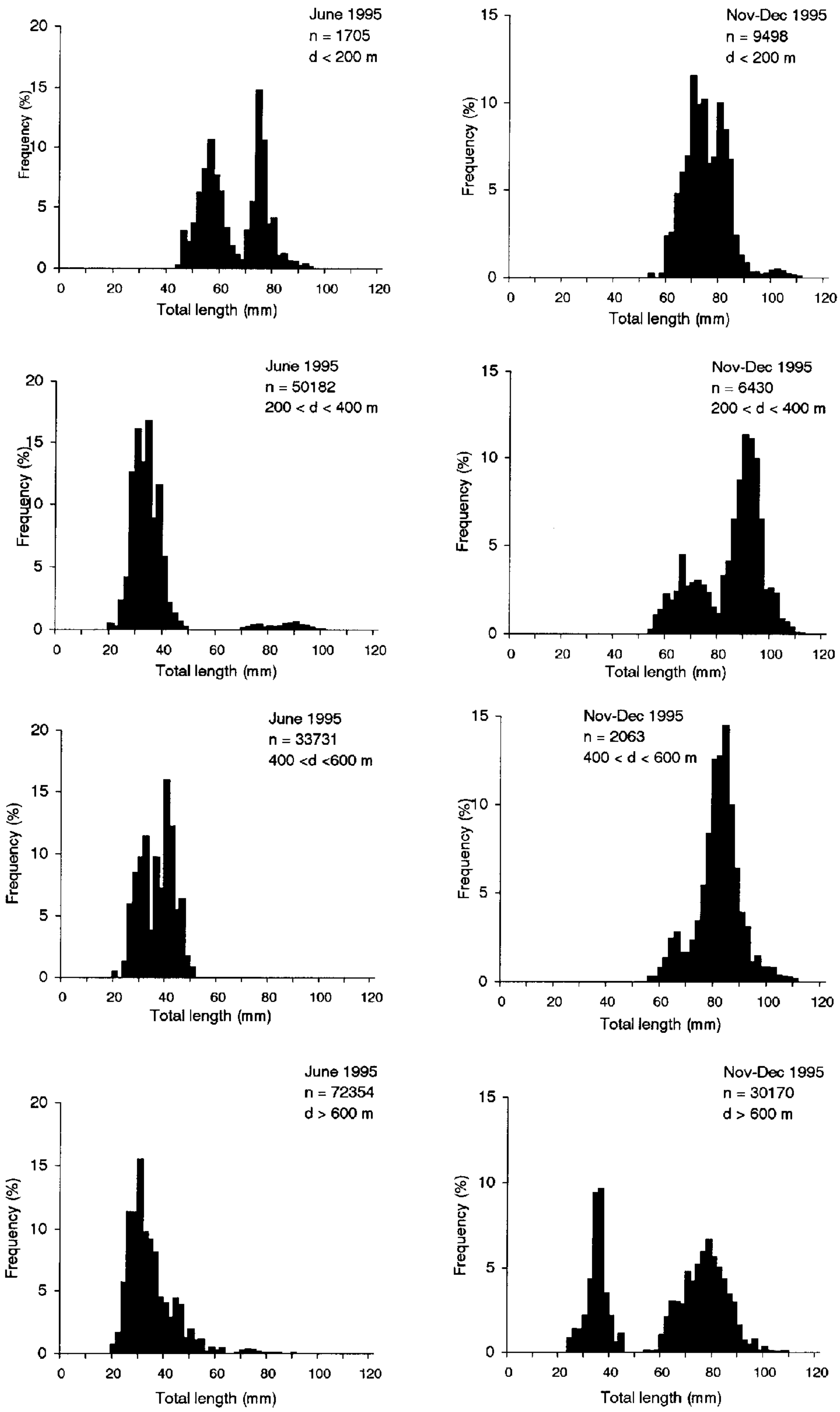


Figure 16. Size distribution of *S. tanganicae* by depth strata in June and November-December 1995. Bottom depth is indicated with d, n is the sample size.

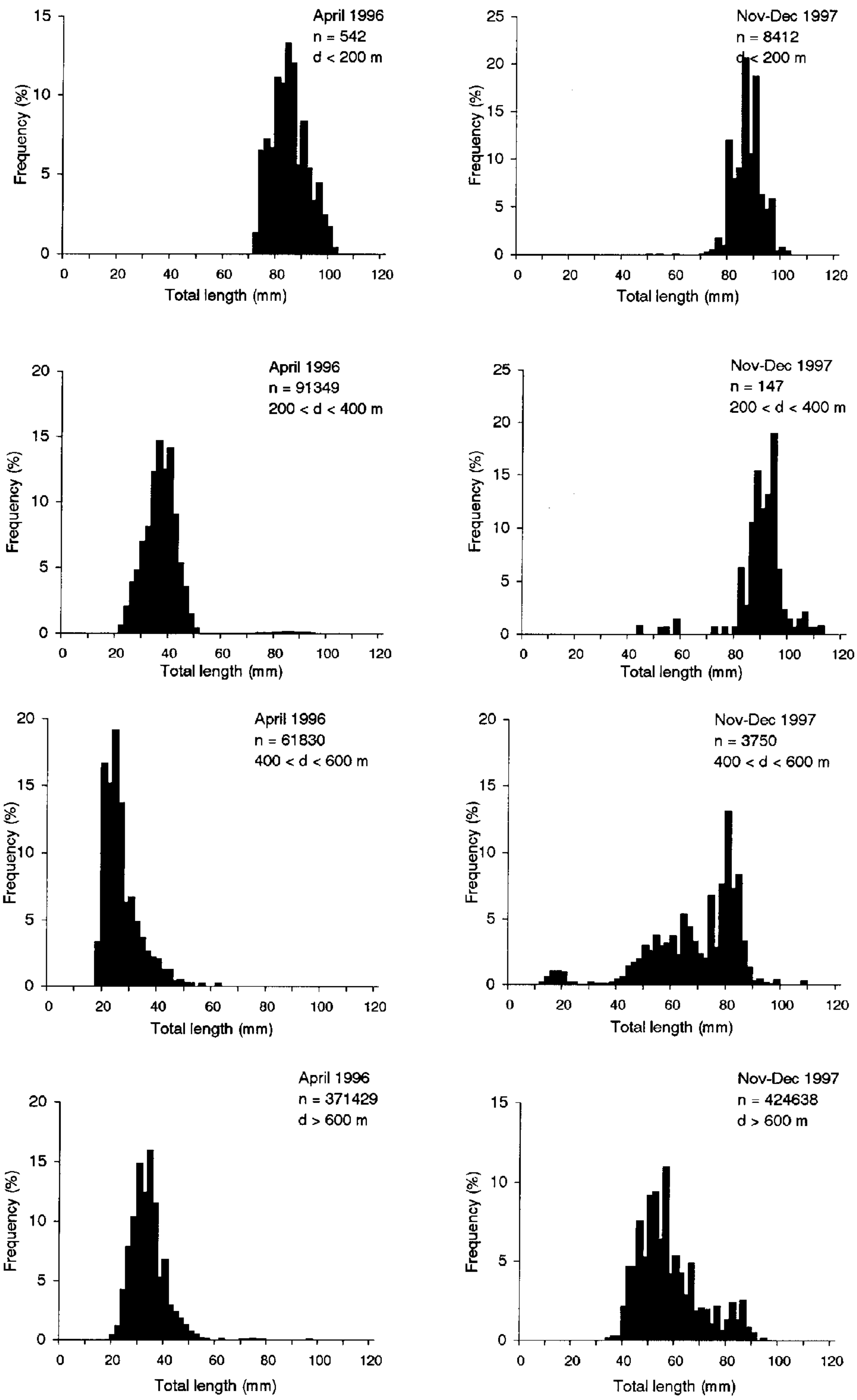


Figure 17. Size distribution of *S. tanganicae* by depth strata in April 1996 and November-December 1997. Bottom depth is indicated with d, n is the sample size.

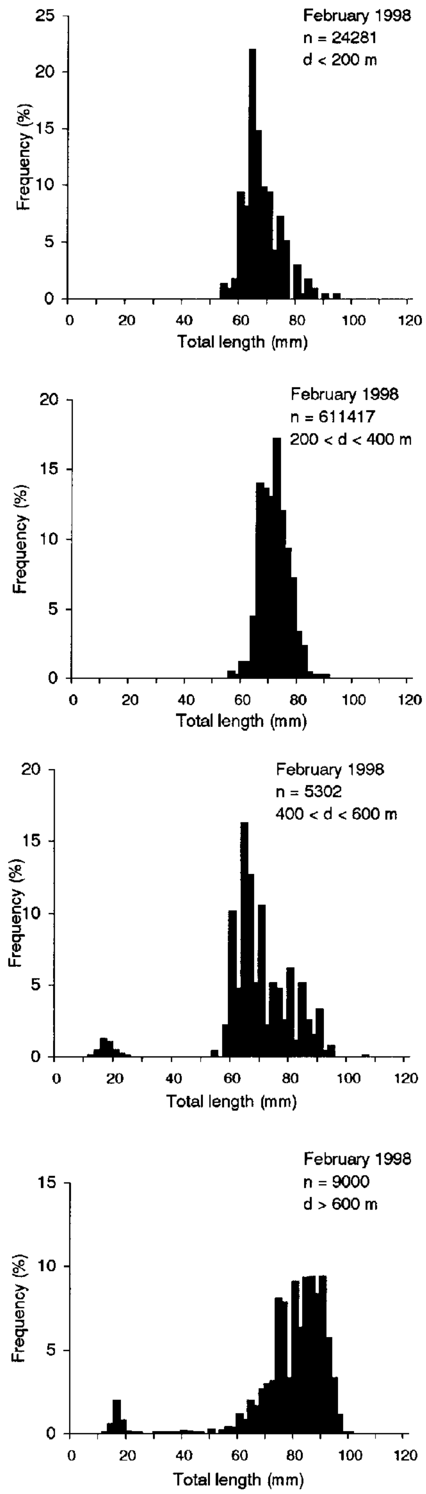


Figure 18. Size distribution of *S. tanganicae* by depth strata in February 1998. Bottom depth is indicated with d, n is the sample size.

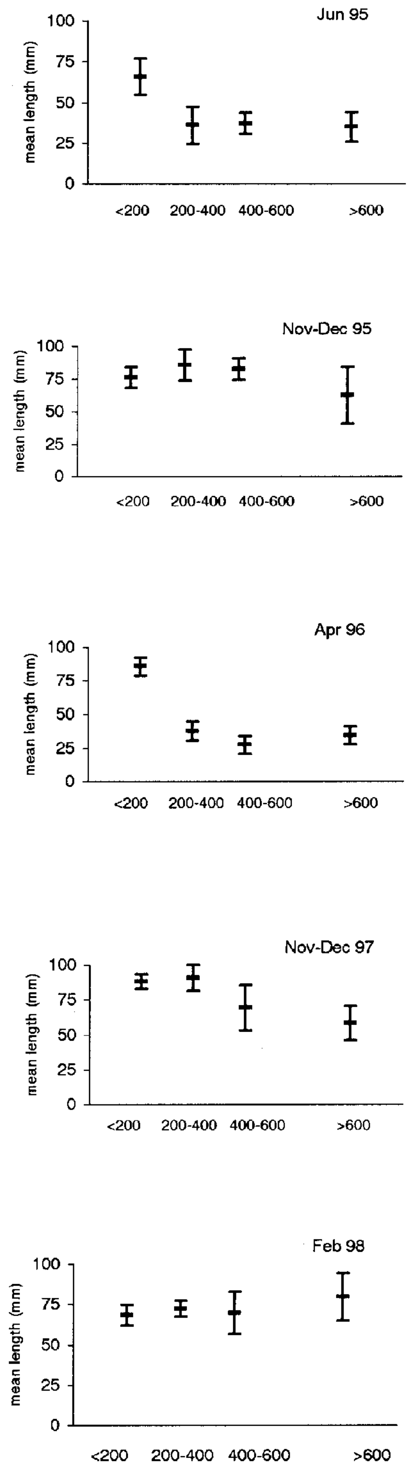


Figure 19. Mean length of *S. tanganicae* in trawl catches from four bottom depth-defined zones (abscissa, m) during five surveys.

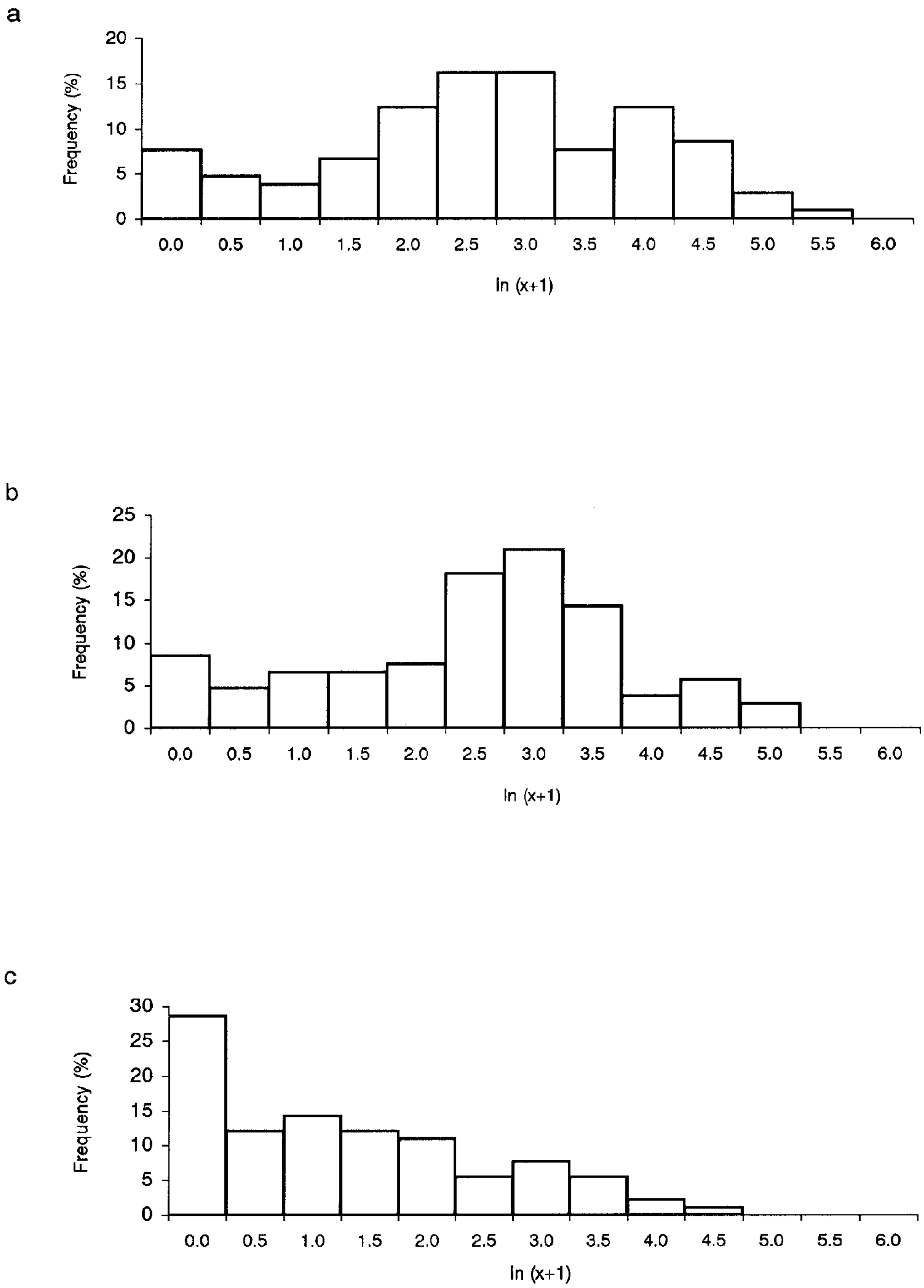


Figure 20. Frequency histograms of ln(x+1) transformed number (n x 100 m^3) of larvae in Gulf-net samples from all surveys. *Stolothrissa tanganicae*, a, *L. miodon*, b, *L. stappersii*, c.

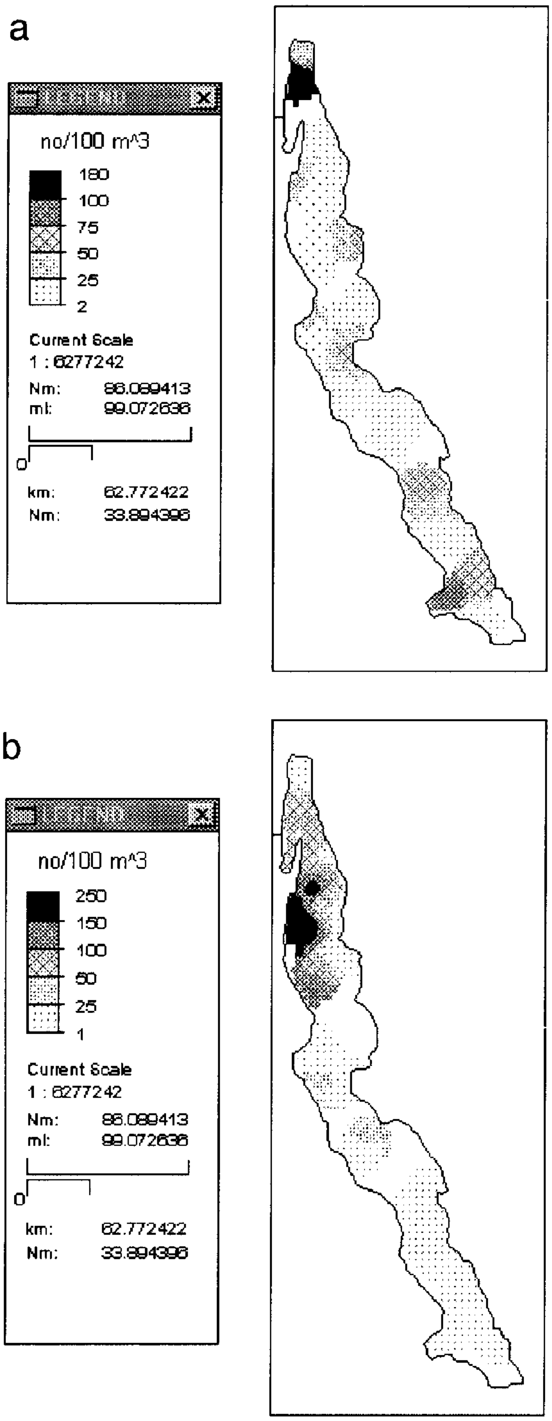


Figure 21. Distribution of *S. tanganicae* larvae within 0-100 m water column in June (a) and November-December (b) 1995. Larval density (no/100 m^3) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no larva recorded or no samples taken). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

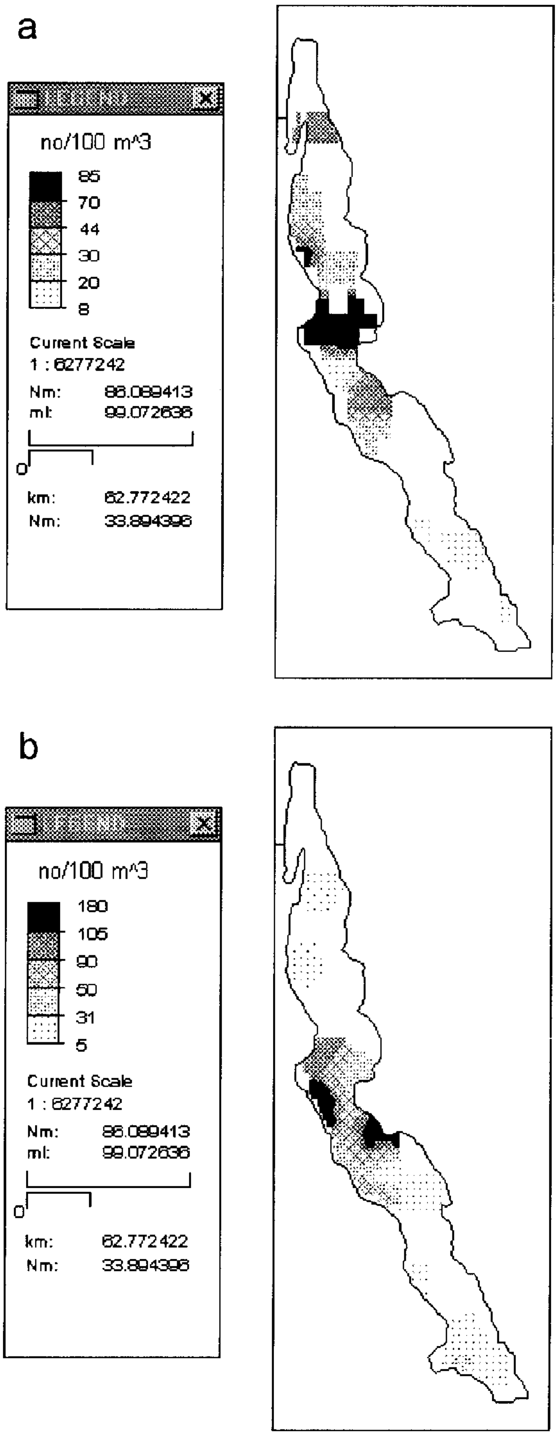


Figure 22. Distribution of *S. tanganicae* larvae within 0-100 m water column in November-December 1997 (a) and February 1998 (b). Larval density (no/100 m^3) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no larva recorded or no samples taken). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles

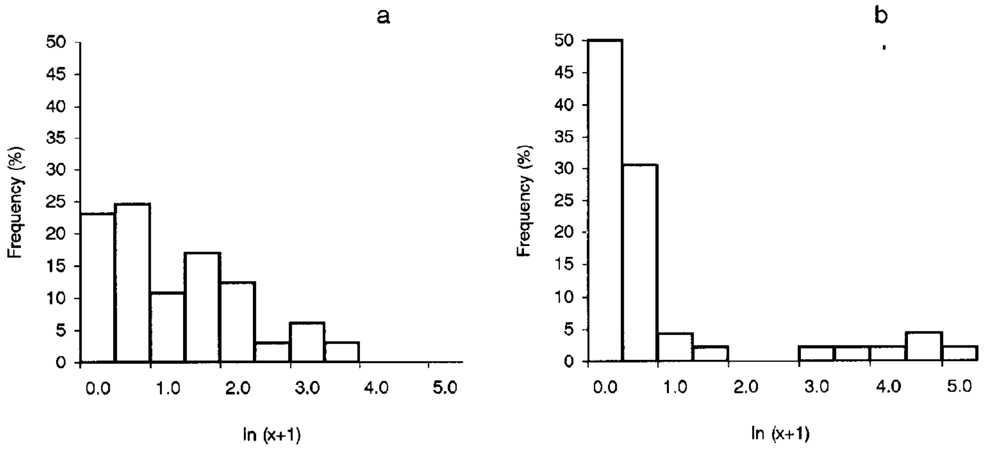
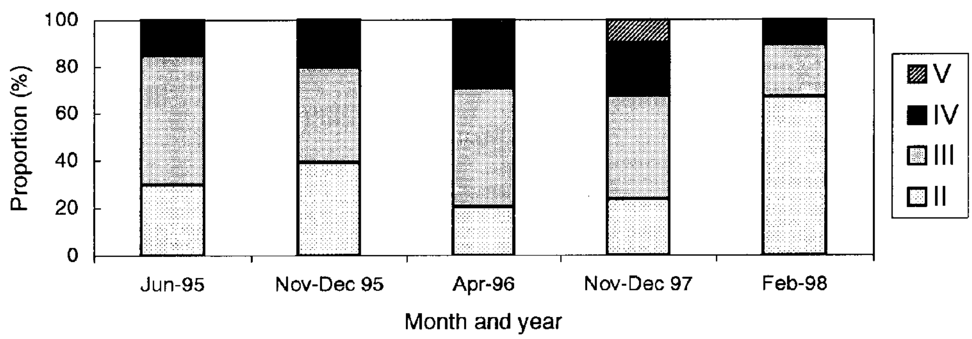


Figure 23. Frequency histograms of ln(x+1) transformed CPUE values derived for *L. miodon* from, a, June and November-December 1995 and, b, November-December 1997 and February 1998 pelagic trawl surveys



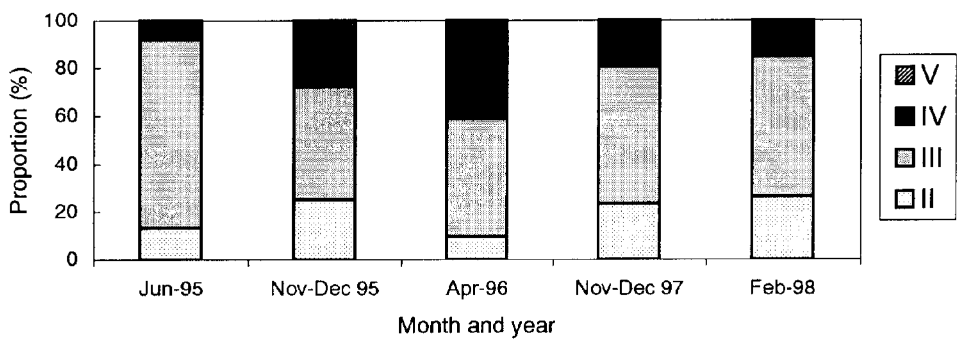


Figure 24. Maturity stages for *L. miodon* samples of females (a) and males (b) taken during lake-wide surveys in June (sample size, n=774) and November-December (n=1080) 1995, April 1996 (n=282), November-December 1997 (n=453) and February 1998 (n=251).

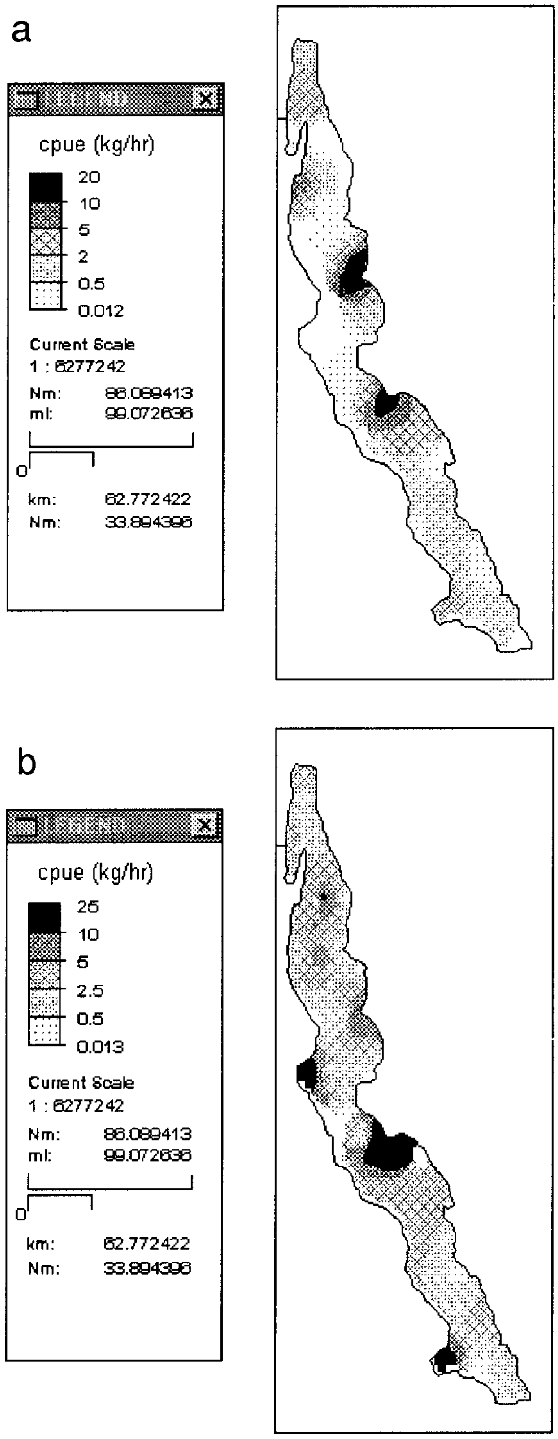


Figure 25. Pelagic trawl catch distribution of *L. miodon* in June 1995 (a) and November-December 1995 (b) survey. Catch per unit of effort (kg/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

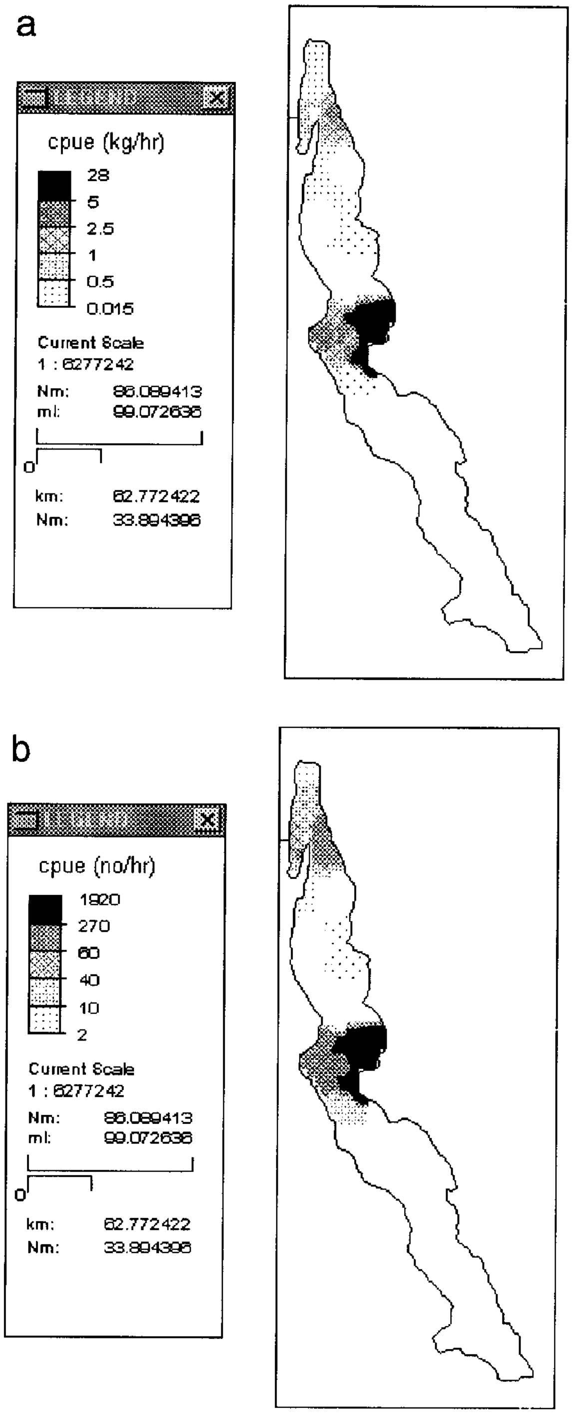
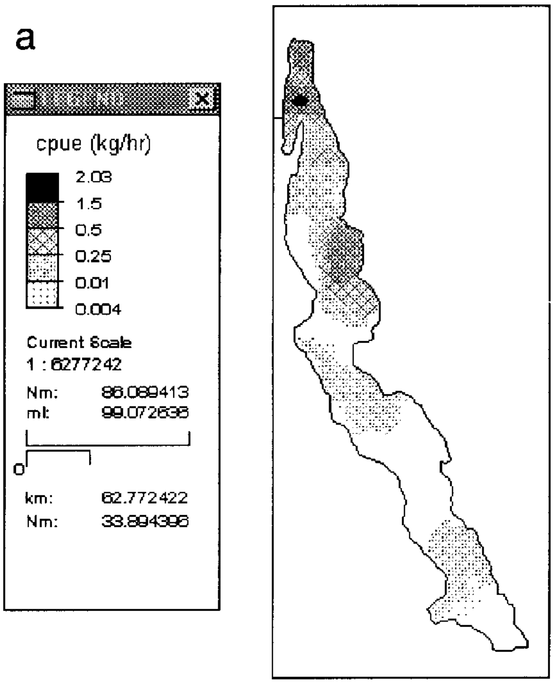


Figure 26. Pelagic trawl catch distribution (a) and number of adults (TL > L_m) caught (b) of *L. miodon* in April 1996 survey. Catch per unit of effort (kg/hr) and number of adult fish (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Blank areas mean that interpolation was not possible (no haul made or no zero catch). Note that **pattern scale has unequal intervals**. Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).



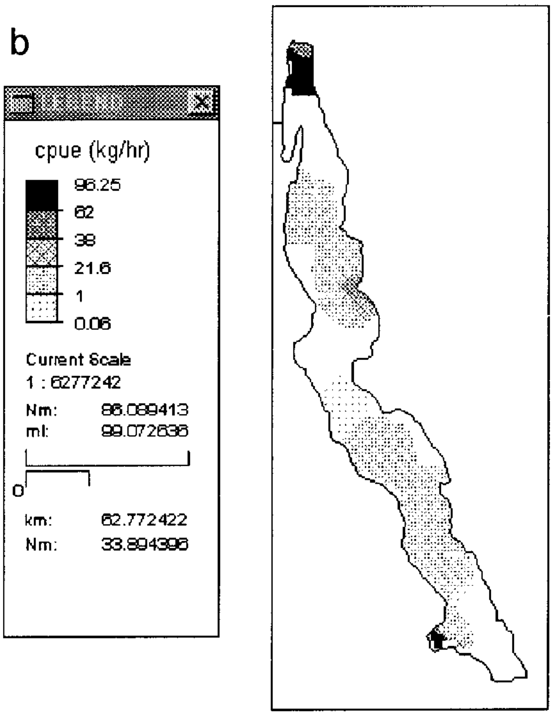


Figure 27. Pelagic trawl catch distribution of *L. miodon* in November-December 1997 (a) and February 1998 (b) survey. Catch per unit of effort (kg/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

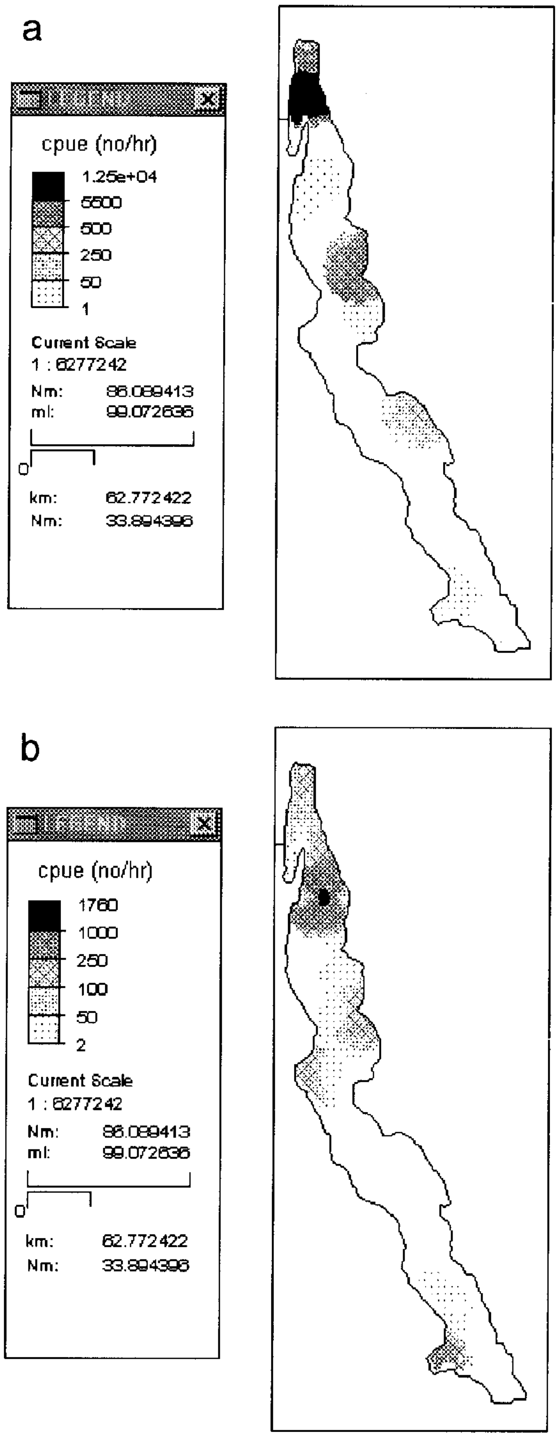


Figure 28. Pelagic trawl catch distribution of young *L. miodon* (TL < L_m) in June 1995 (a) and November-December (b) 1995 survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

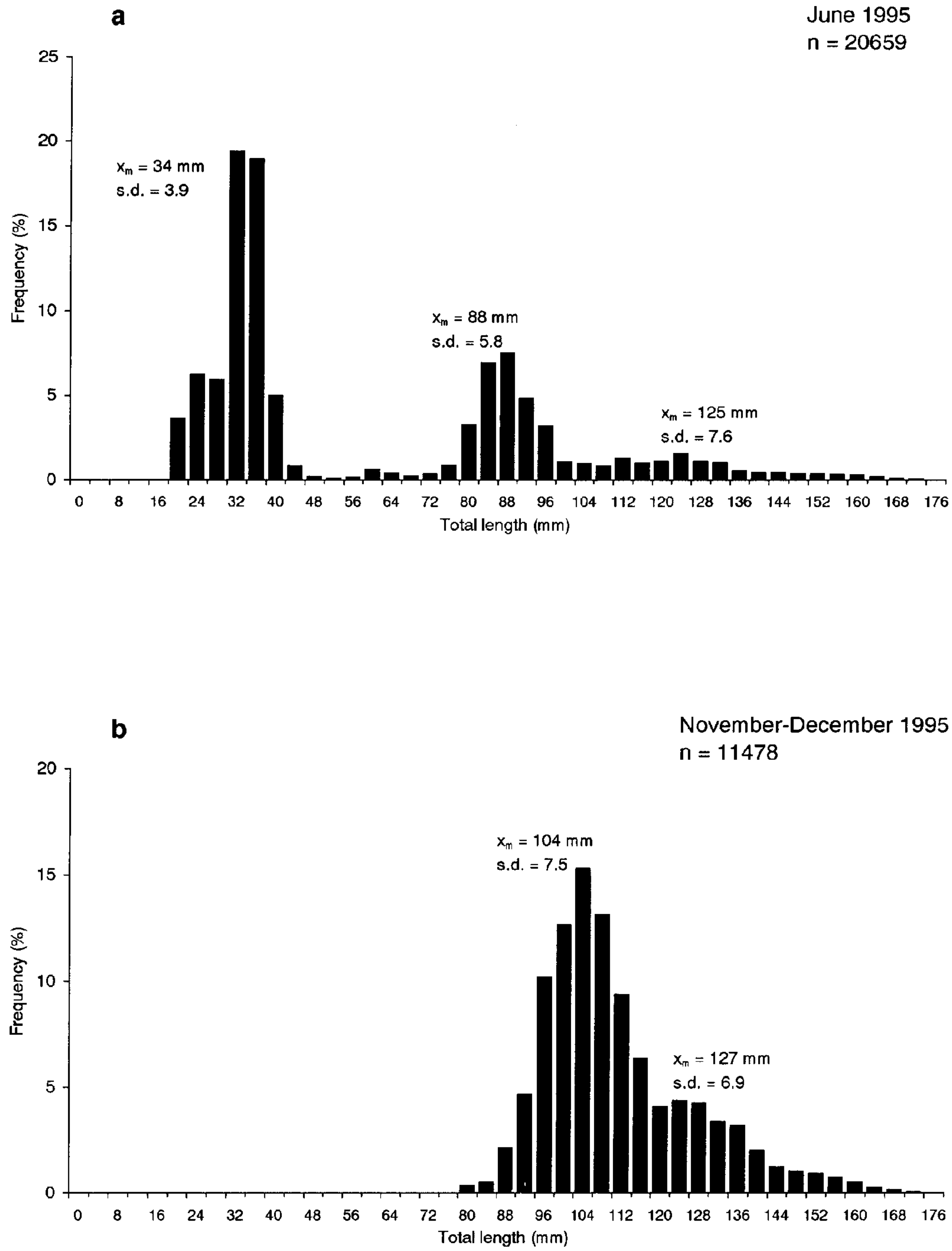


Figure 29. Size distribution of *L. miodon* for the whole lake from mid-water trawl surveys. **a**: June 1995 survey; **b**: November-December 1995 survey. N is the sample size, x_m and s.d. are the mean length and standard deviation of identified cohorts after Bhatacharya's decomposition of length distribution.

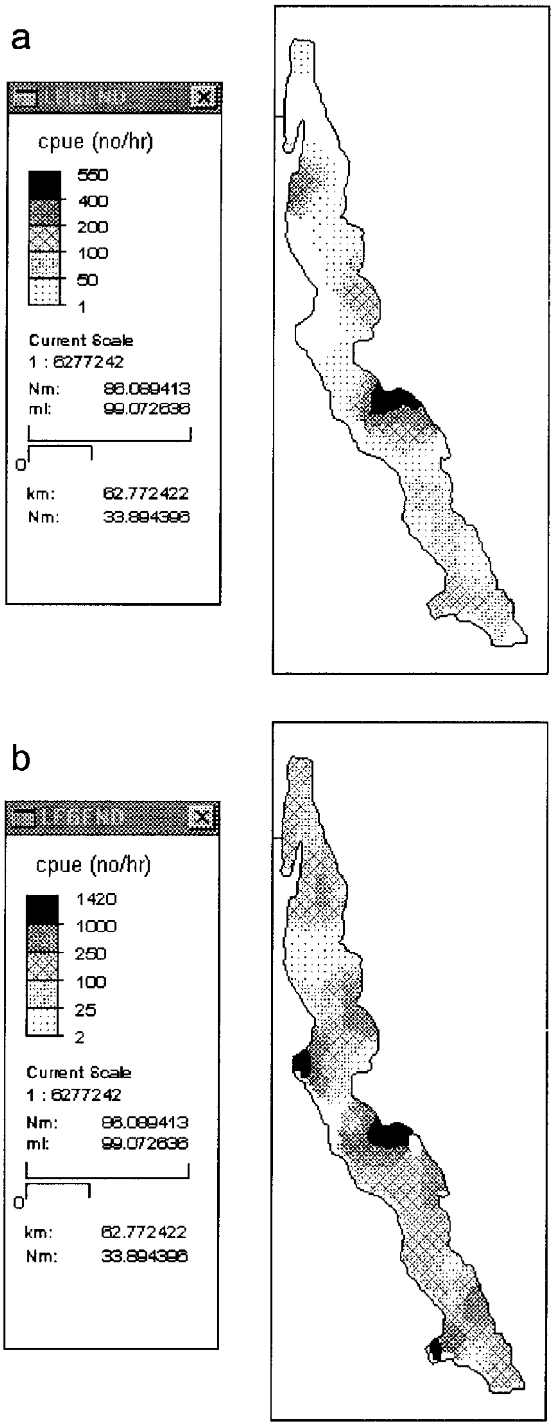


Figure 30. Pelagic trawl catch distribution of adult *L. miodon* (TL > L_m) in June 1995 (a) and November-December 1995 (b) survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals.** Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

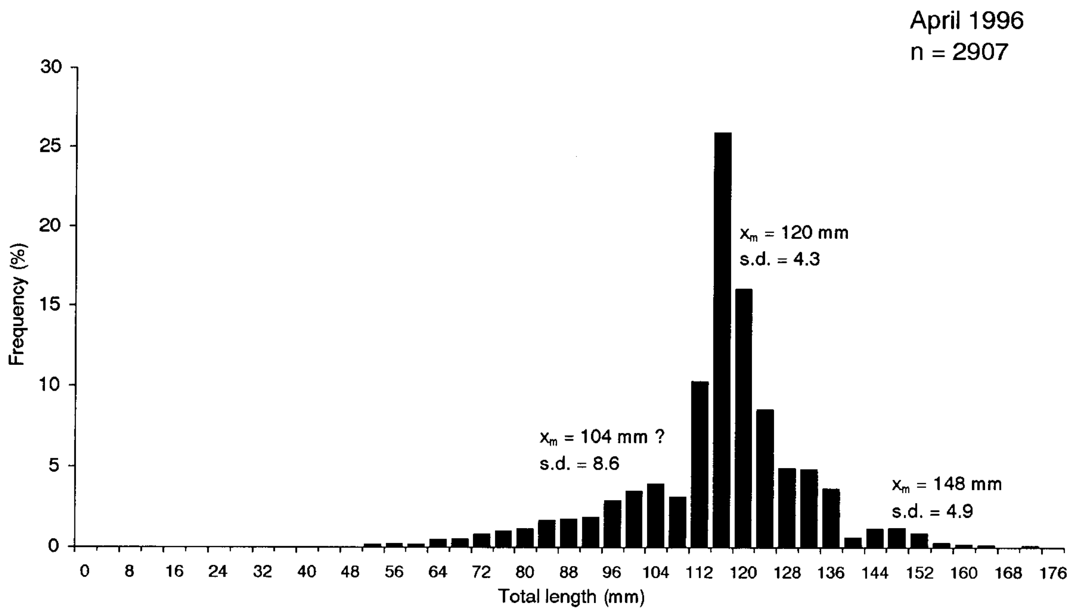


Figure 31. Size distribution of *L. miodon* for the whole lake from April 1996 mid-water trawl survey. N is the sample size, x_m and s.d. are the mean length and standard deviation of identified cohort after Bhatacharya's decomposition of length distribution. Question mark indicates uncertain cohort separation.

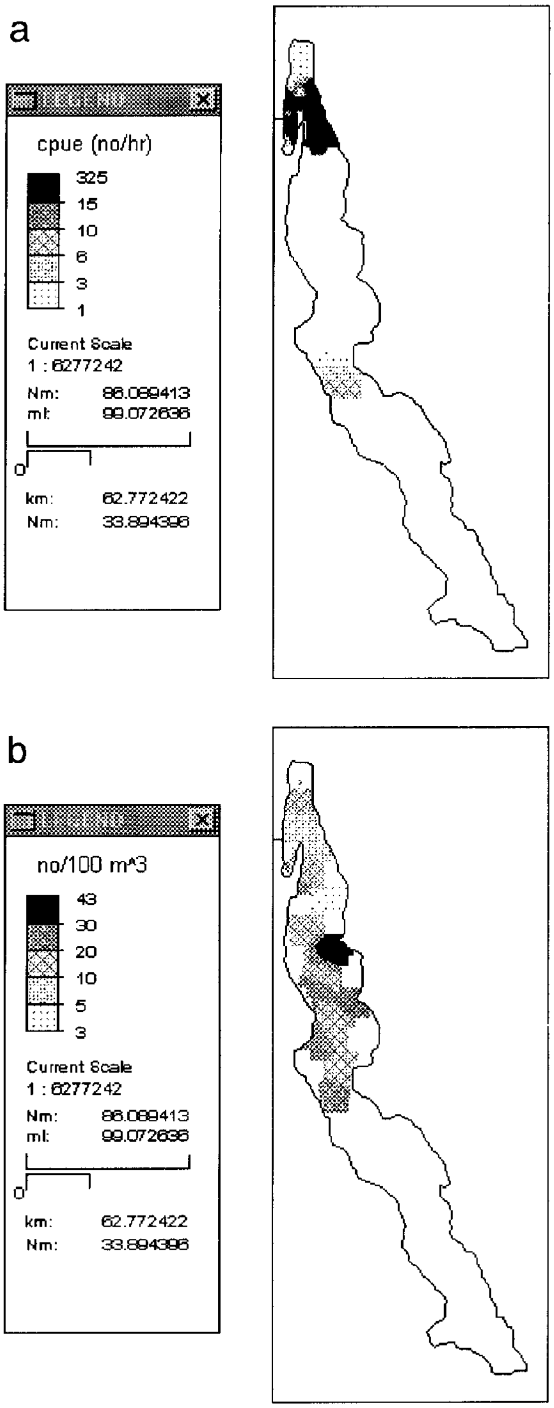


Figure 32. Pelagic trawl catch distribution of (a) young *L miodon* (TL < L_m) and distribution of *L. miodon* larvae (b) within 0-100 m water column in April 1996 survey. Catch per unit of effort (no/hr) and larval density (no/100 m3) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

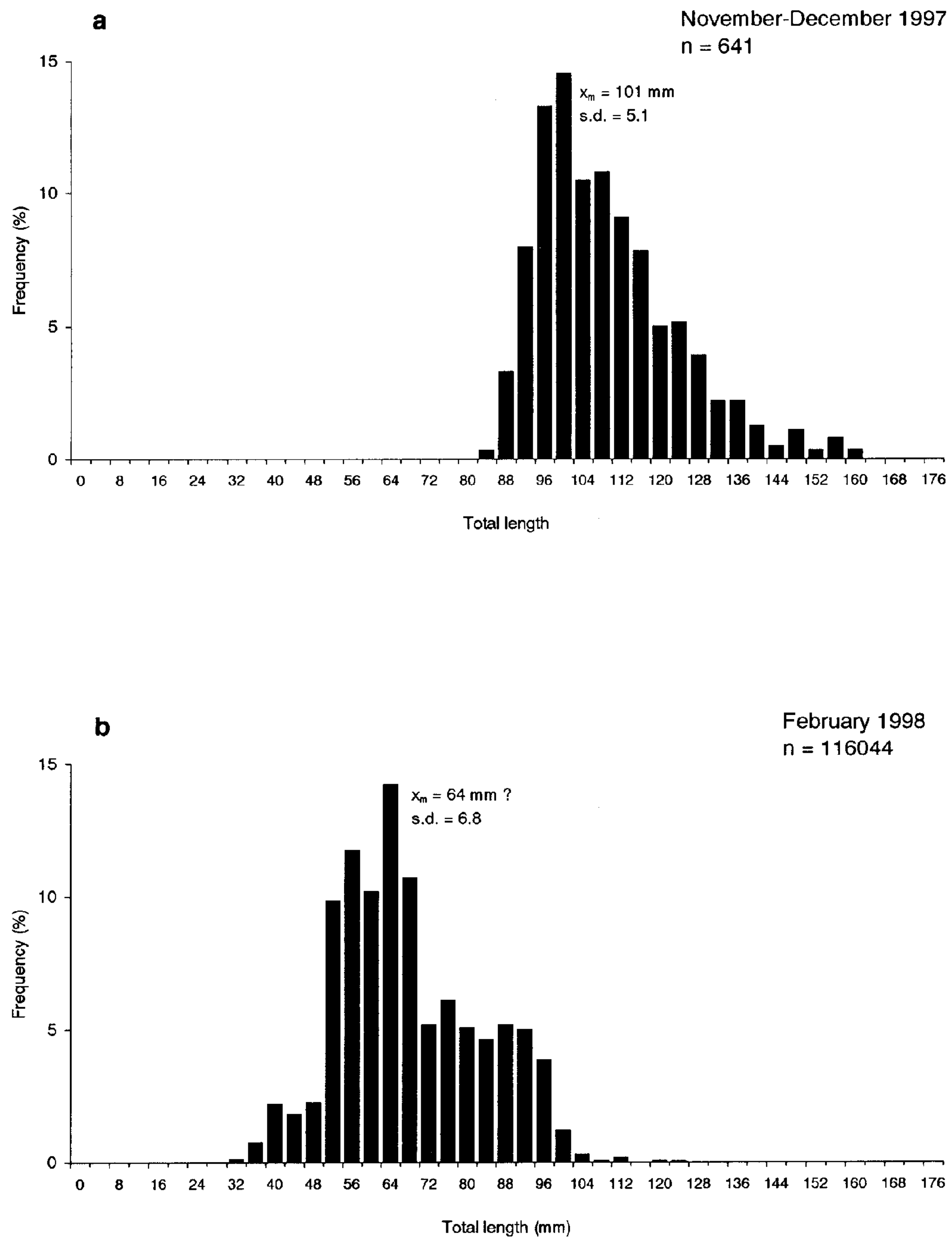


Figure 33. Size distribution of *L. miodon* for the whole lake from mid-water trawl surveys. **a**: November-December 1997 survey; **b**: February 1998 survey. N is the sample size, x_m and s.d. are the mean length and standard deviation of identified cohorts after Bhatacharya's decomposition of length distribution. Question mark indicates uncertain cohort separation.

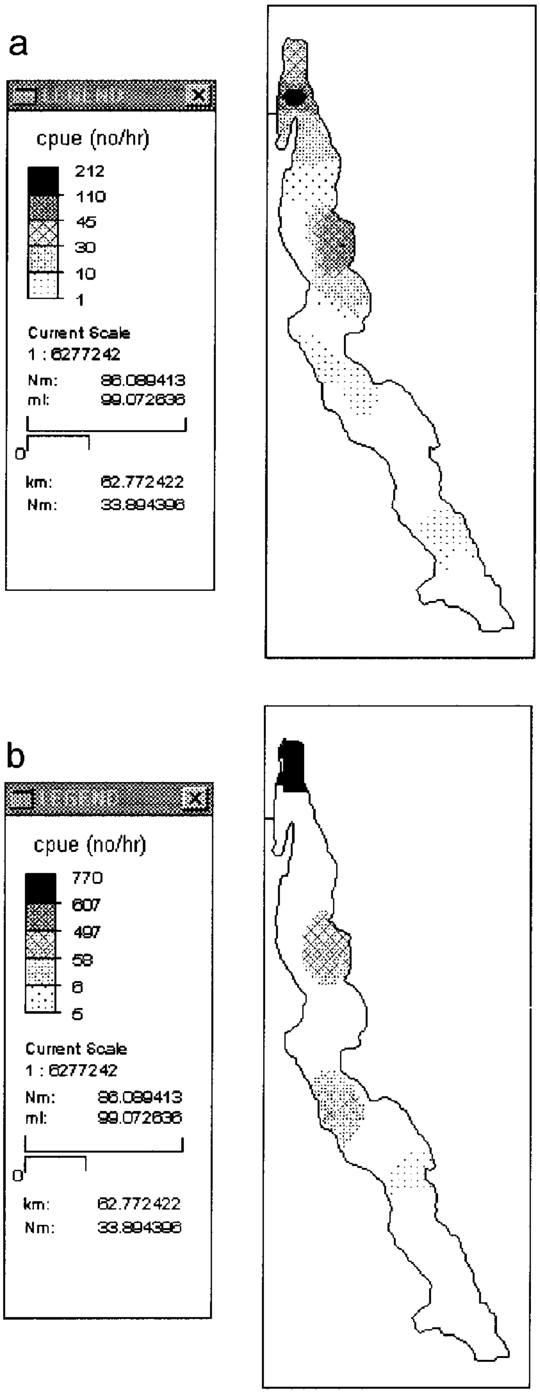


Figure 34. Pelagic trawl catch distribution of adult *L. miodon* (TL > L_m) in November-December 1997 (a) and February 1998 (b) survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

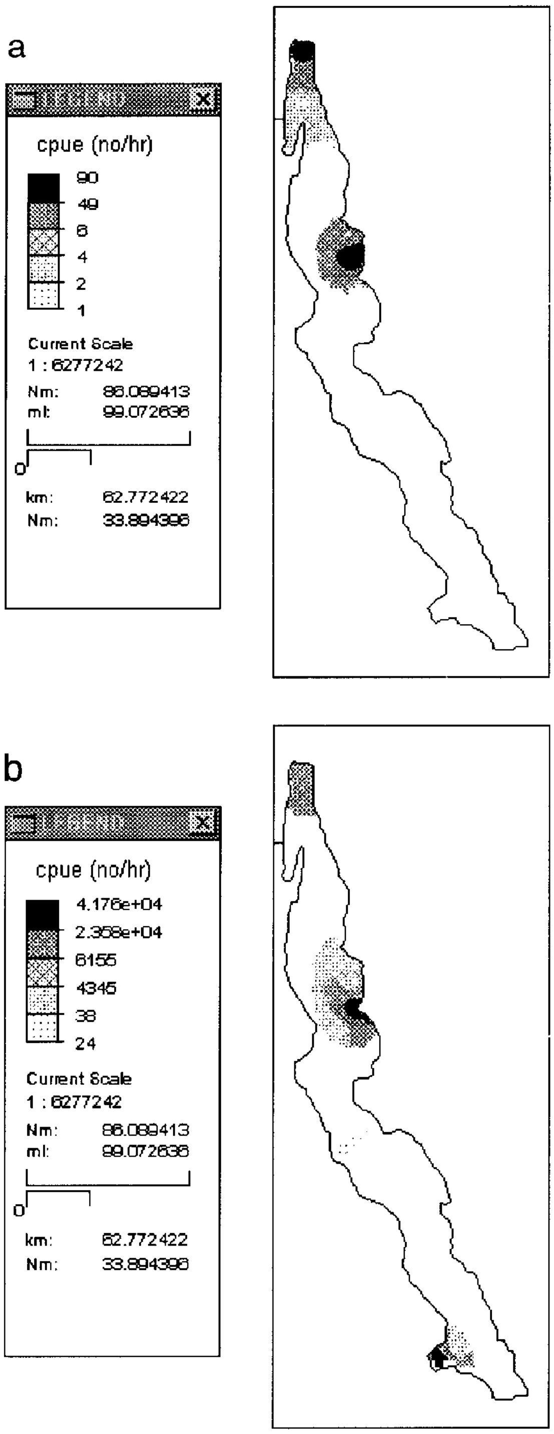


Figure 35. Pelagic trawl catch distribution of young *L. miodon* (TL < L_m) in November-December 1997 (a) and February (b) 1998 survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

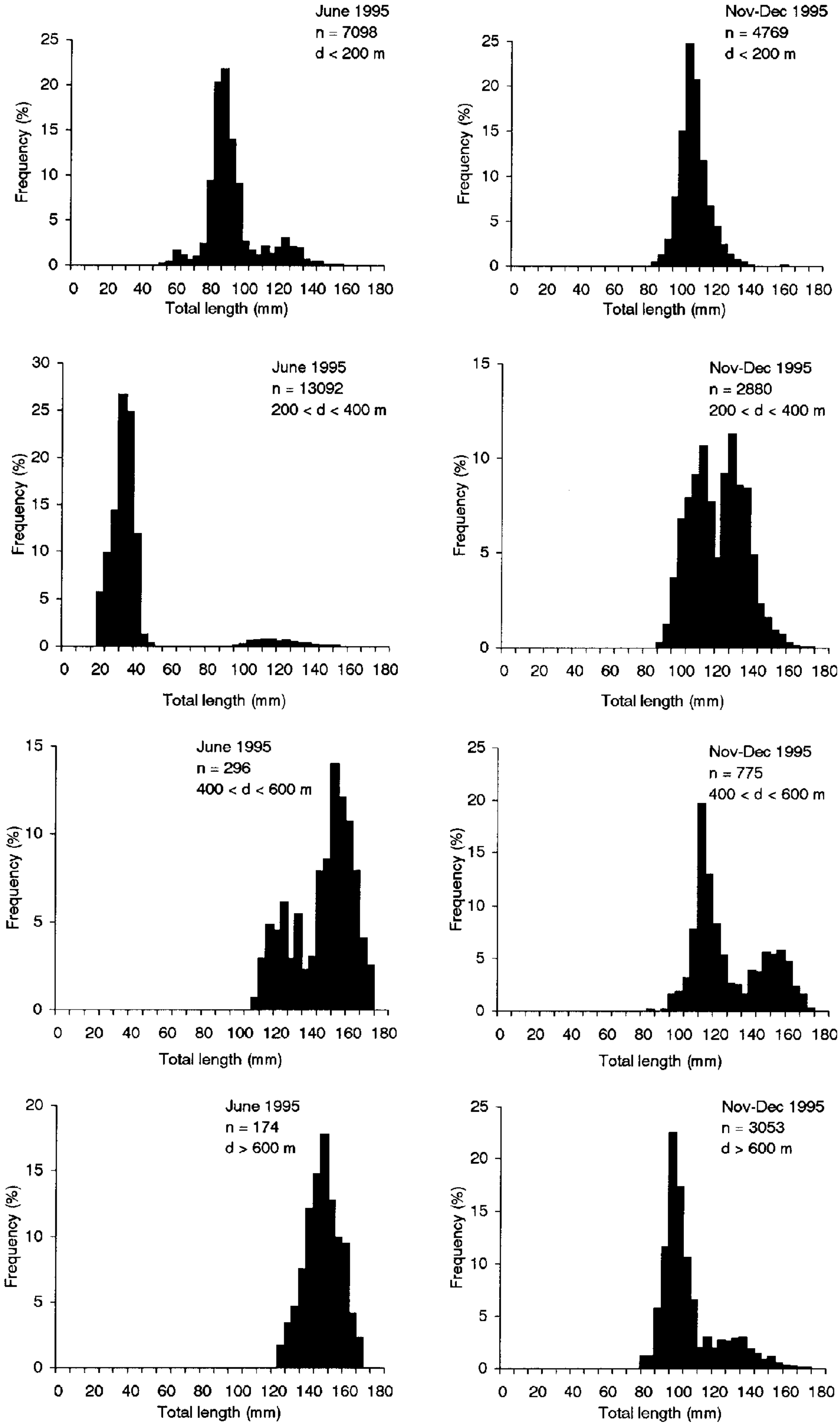


Figure 36. Size distribution of *L. miodon* by depth strata in June and November-December 1995. Bottom depth is indicated with d, n is the sample size.

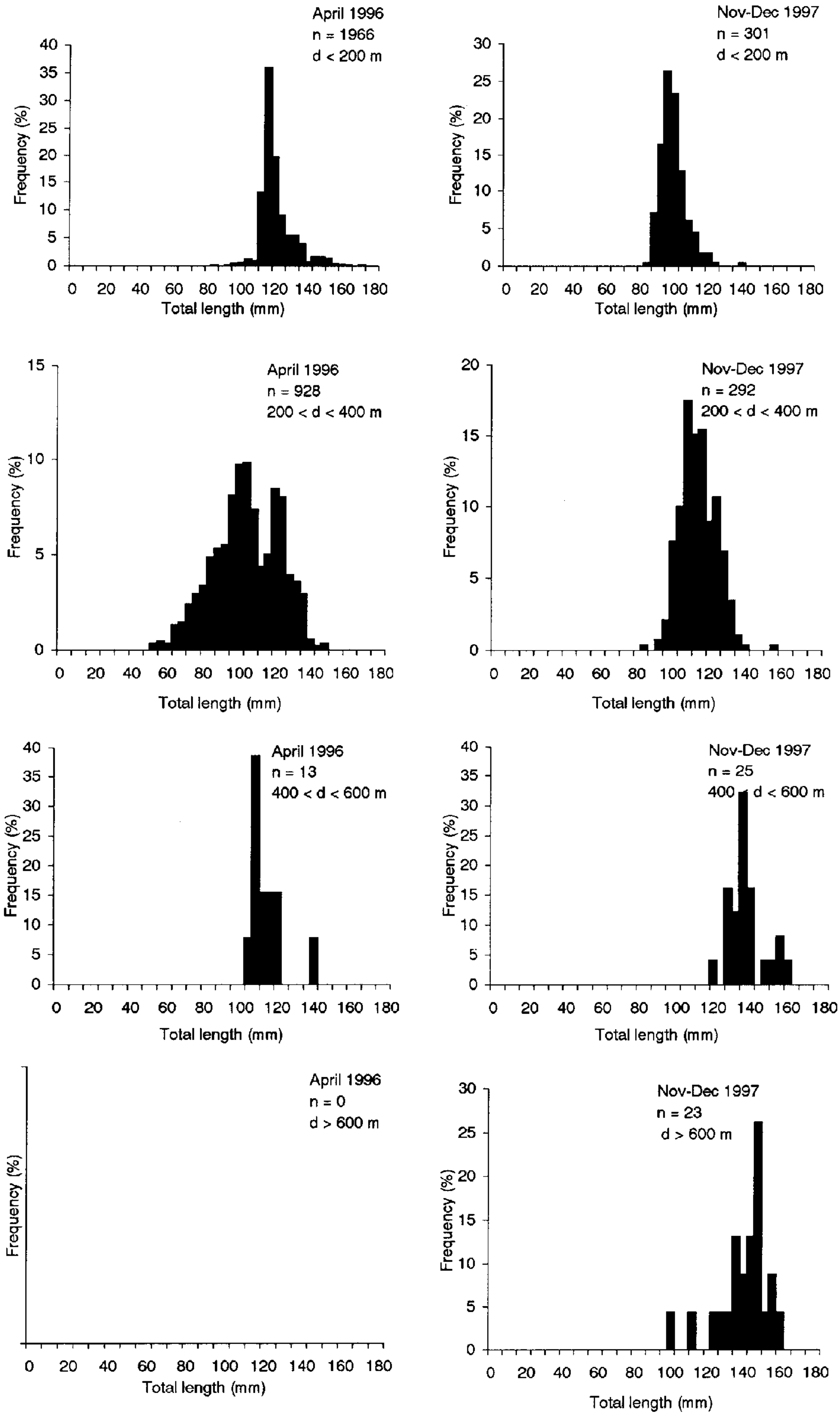


Figure 37. Size distribution of *L.miodon* by depth strata in April 1996 and November-December 1997. Bottom depth is indicated with d, n is the sample size.

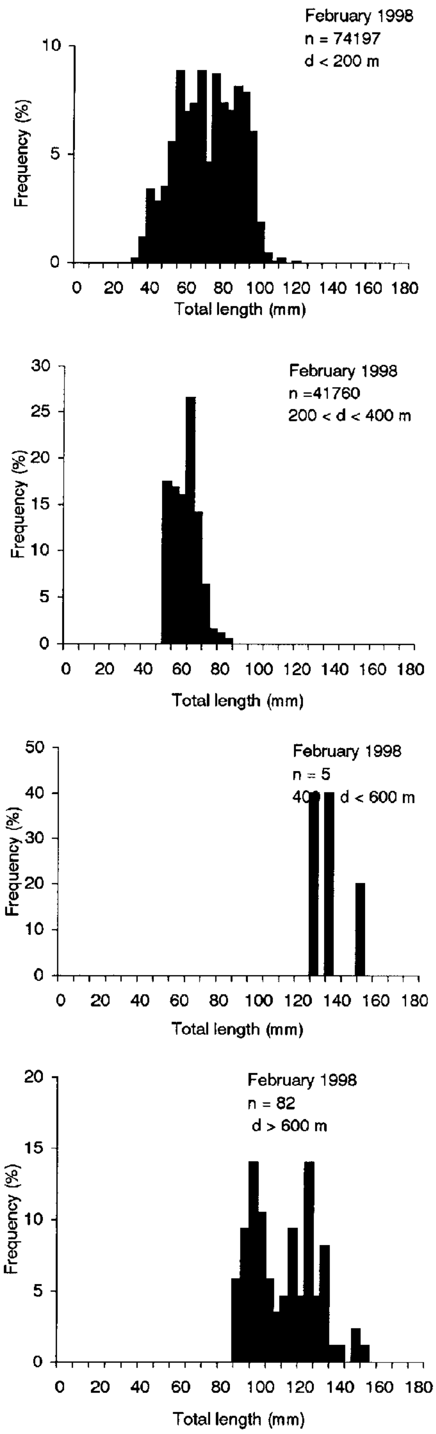


Figure 38. Size distribution of *L. miodon* by depth strata in February 1998. Bottom depth is indicated with d, n is the sample size.

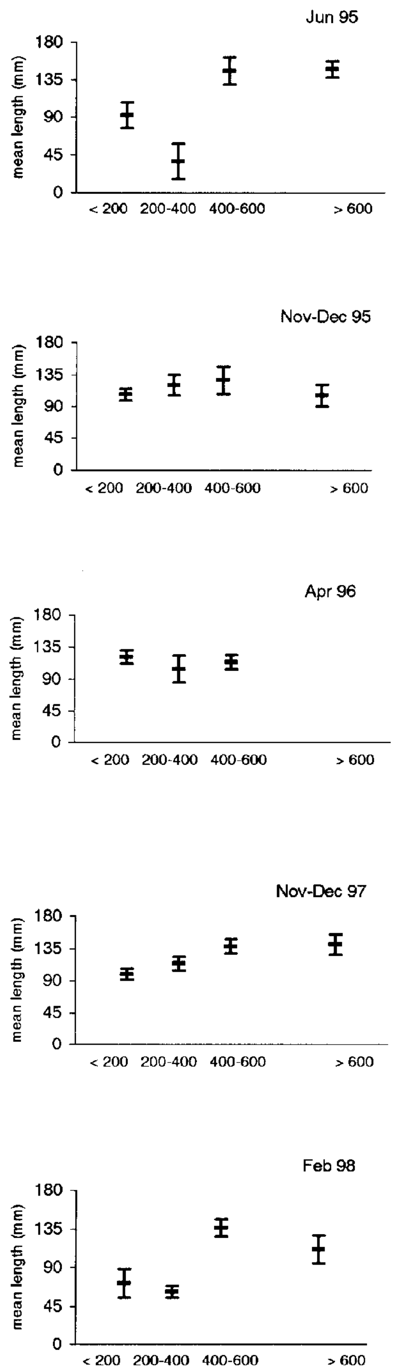


Figure 39. Mean length of *L. miodon* in trawl catches from four bottom depth-defined zones (abscissa, m) during five surveys.

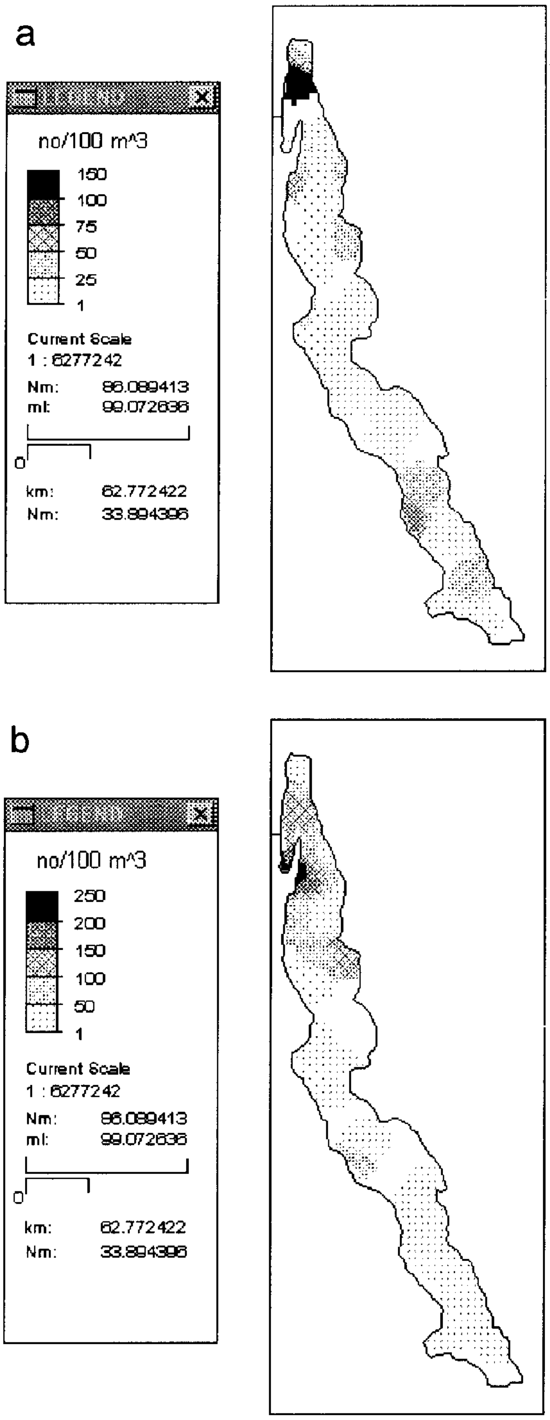


Figure 40. Distribution of *L. miodon* larvae within 0-100 m water column in June (a) and November-December (b) 1995. Larval density (no/100 m^3) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no larva recorded or no samples taken). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

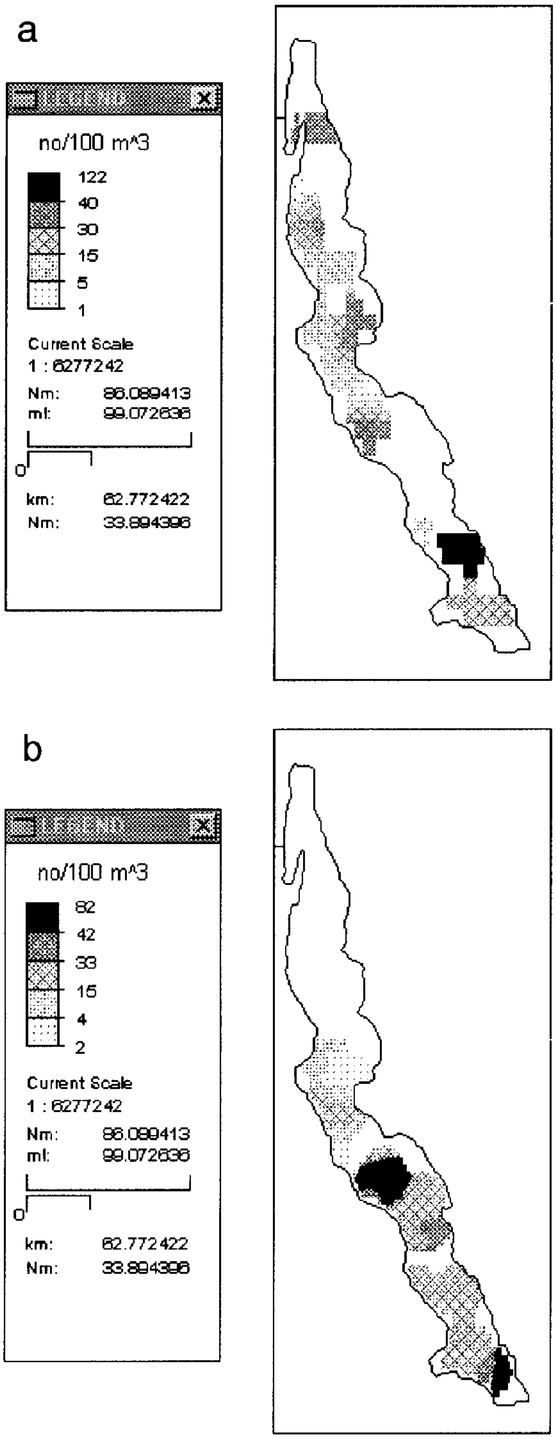


Figure 41. Distribution of *L. miodon* larvae within 0-100 m water column in November-December 1997 (a) and February 1998 (b). Larval density (no/100 m^3) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no larva recorded or no samples taken). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles

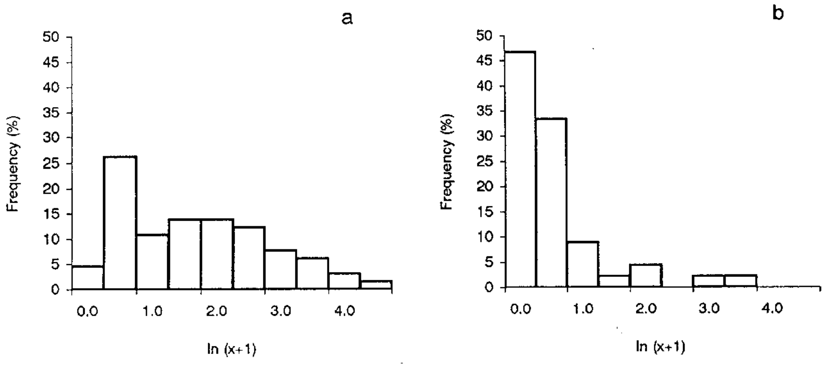


Figure 42. Frequency histograms of ln(x+1) transformed CPUE values derived for *L. stappersii* from, a, June and November-December 1995 and, b, November-December 1997 and February 1998 pelagic trawl surveys

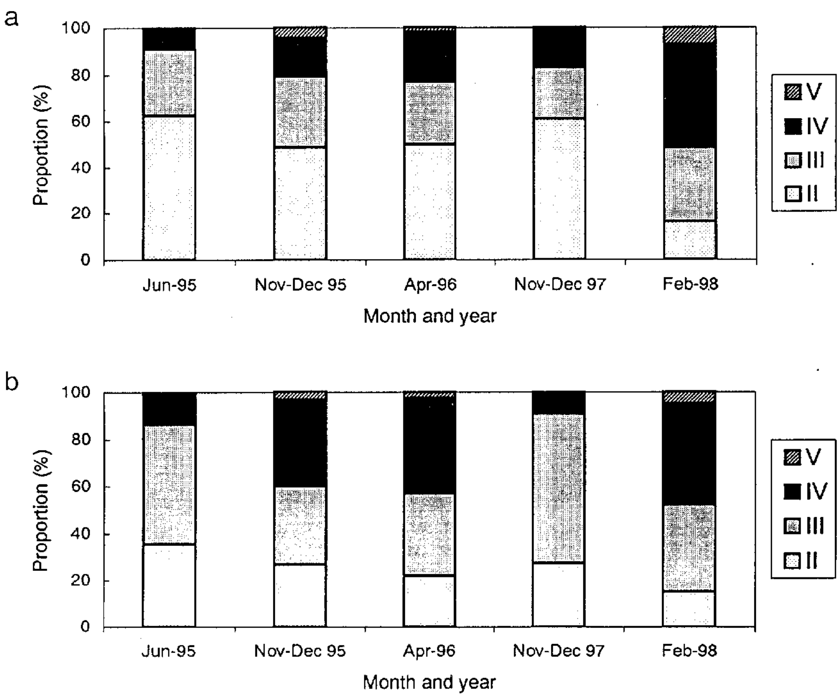


Figure 43. Maturity stages for *L. stappersii* samples of females (a) and males (b) taken during lake-wide surveys in June (sample size, n=671) and November-December (n=861) 1995, April 1996 (n=222), November-December 1997 (n=63) and February 1998 (n=310).

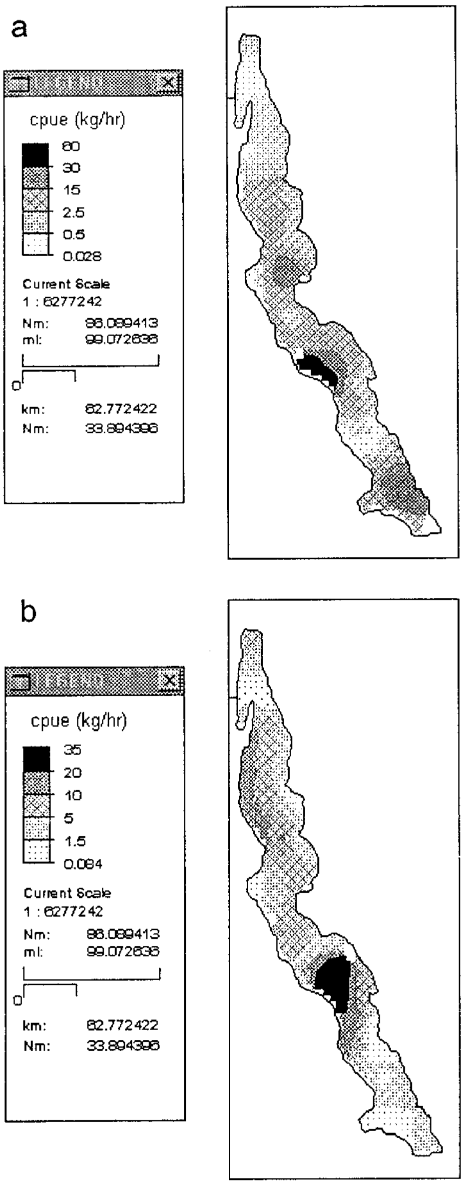


Figure 44. Pelagic trawl catch distribution of *L. stappersii* in June 1995 (a) and November-December 1995 (b) survey. Catch per unit of effort (kg/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

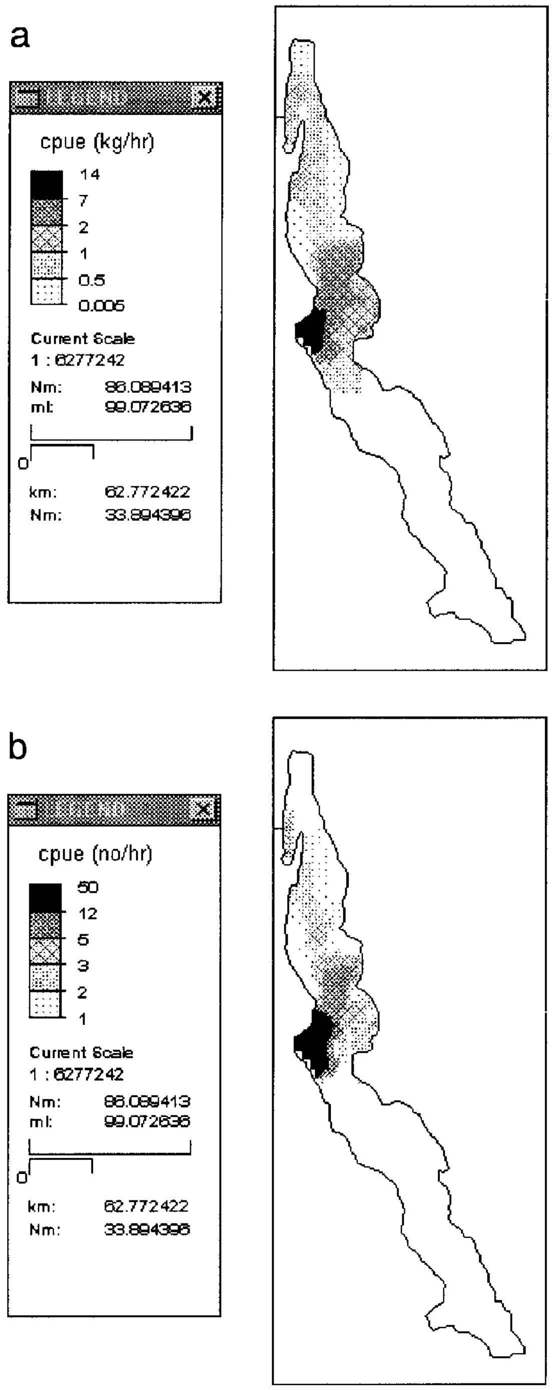


Figure 45. Pelagic trawl catch distribution (a) and number of adults (TL > L_m) caught (b) of *L. stappersii* in April 1996 survey. Catch per unit of effort (kg/hr) and number of adult fish (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Blank areas mean that interpolation was not possible (no haul made or no zero catch). Note that **pattern scale has unequal intervals**. Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

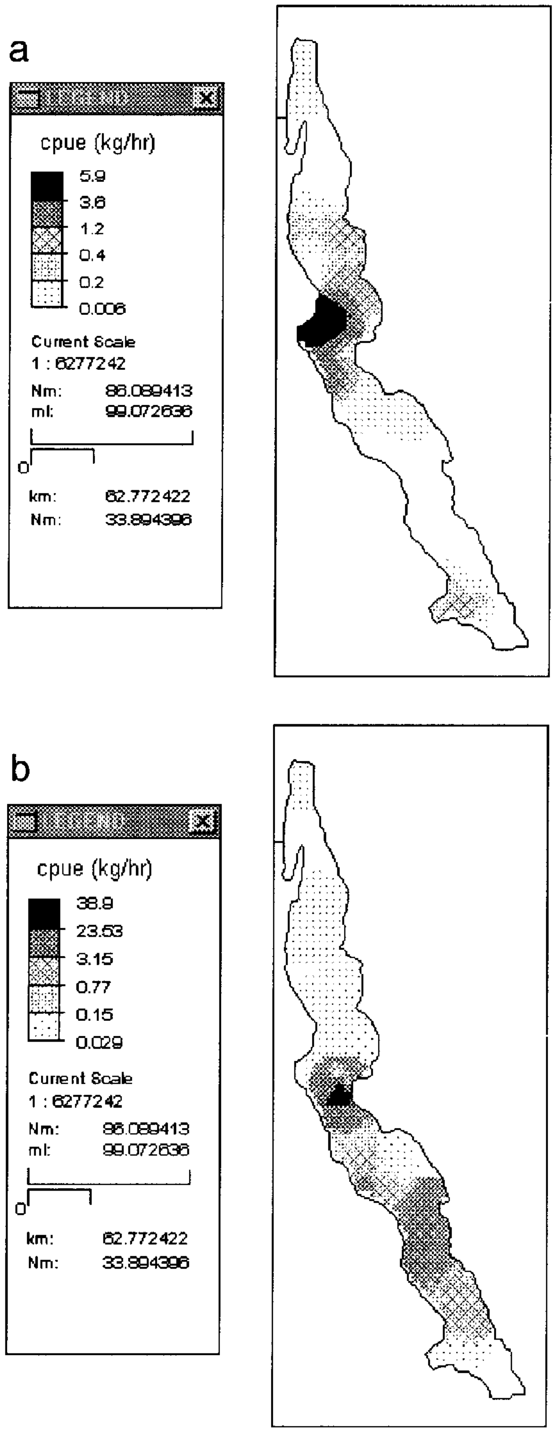


Figure 46. Pelagic trawl catch distribution of *L. stappersii* in November-December 1997 (a) and February 1998 (b) survey. Catch per unit of effort (kg/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

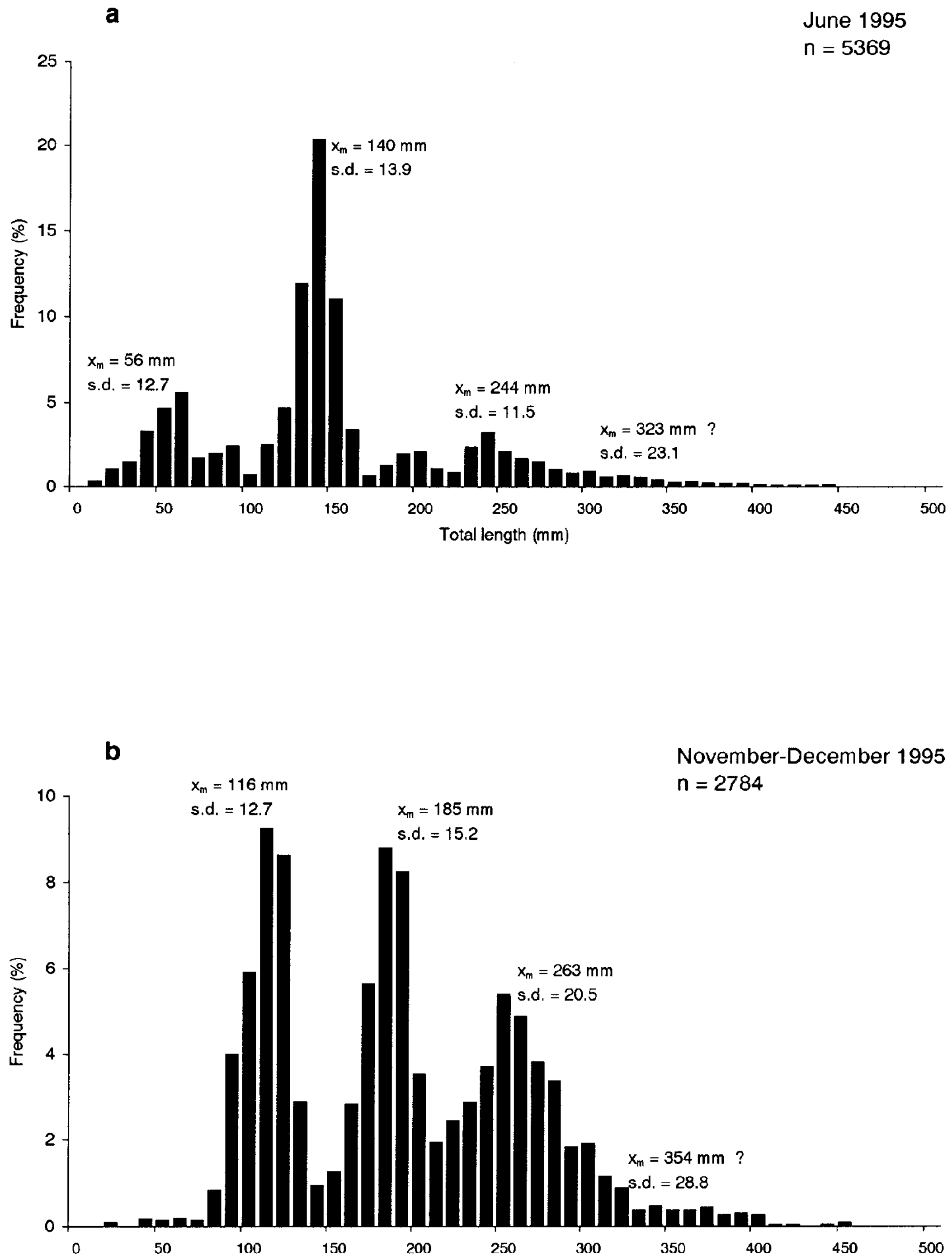


Figure 47. Size distribution of *L. stappersii* for the whole lake from mid-water trawl surveys. **a**: June 1995 survey; **b**: November-December 1995 survey. N is the sample size, x_m and s.d. are the mean length and standard deviation of identified cohorts after Bhatacharya's decomposition of length distribution. Question mark indicates ucertain cohort separation.

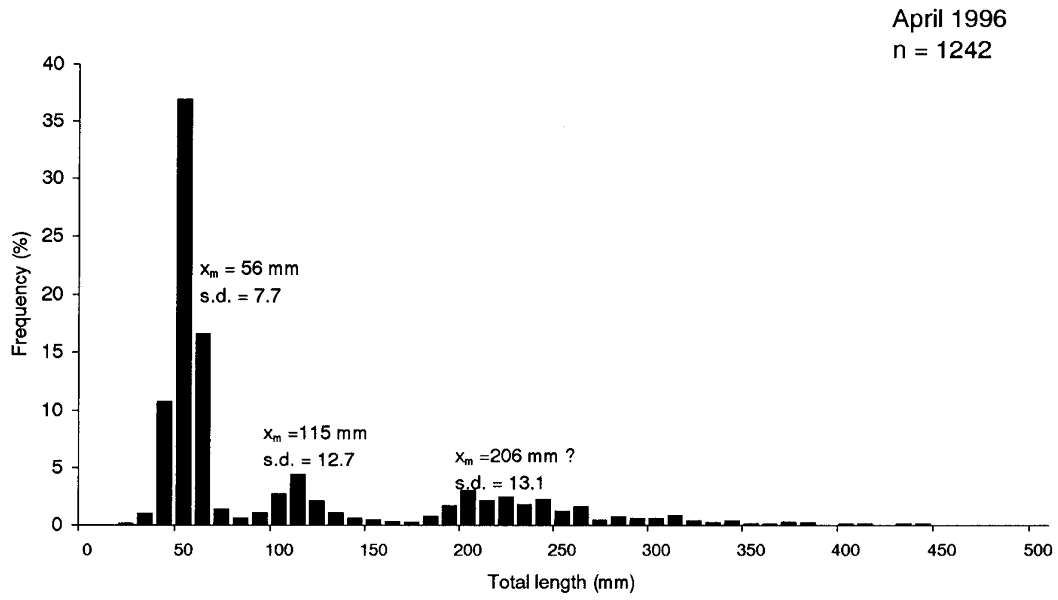


Figure 48. Size distribution of *L. stappersii* for the whole lake from April 1996 mid-water trawl survey. N is the sample size, x_m and s.d. are the mean length and standard deviation of identified cohort after Bhatacharya's decomposition of length distribution. Question mark indicates uncertain cohort separation.

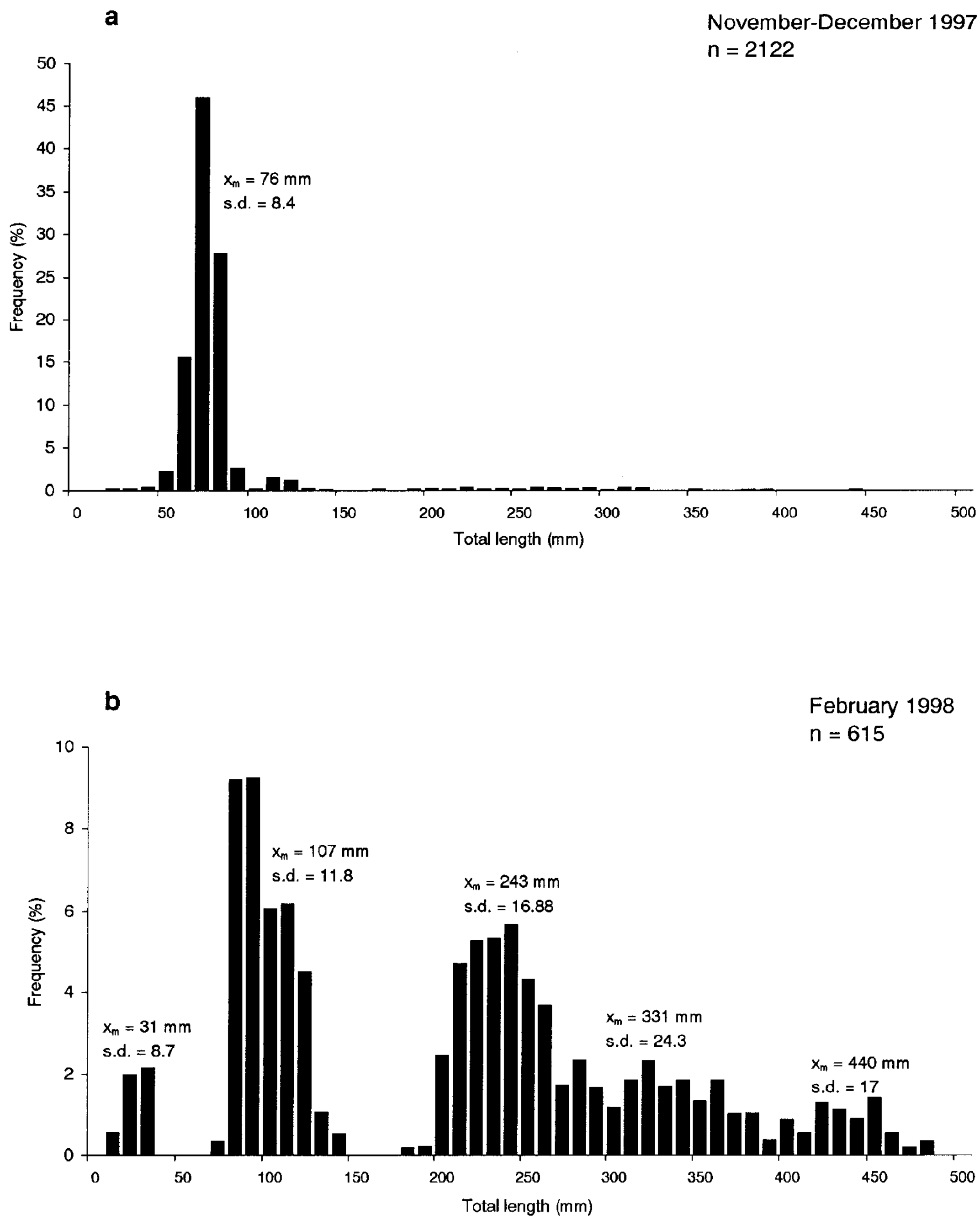
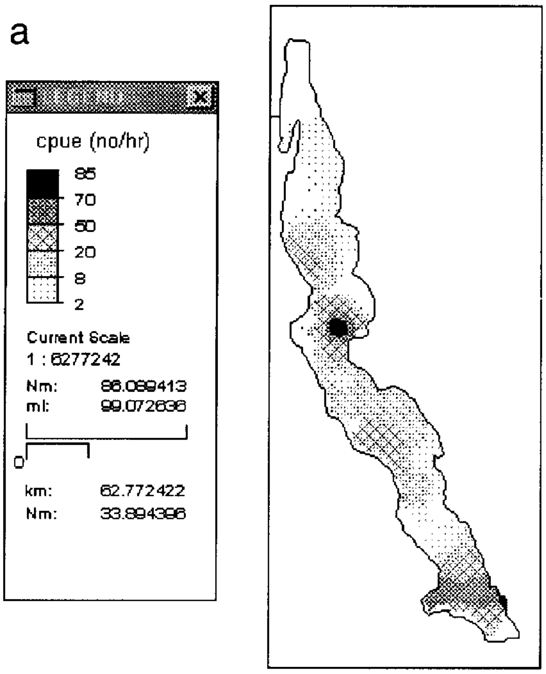


Figure 49. Size distribution of *L. stappersii* for the whole lake from mid-water trawl surveys. **a**: November-December 1997 survey; **b**: February 1998 survey. N is the sample size, x_m and s.d. are the mean length and standard deviation of identified cohorts after Bhatacharya's decomposition of length distribution.

a



b

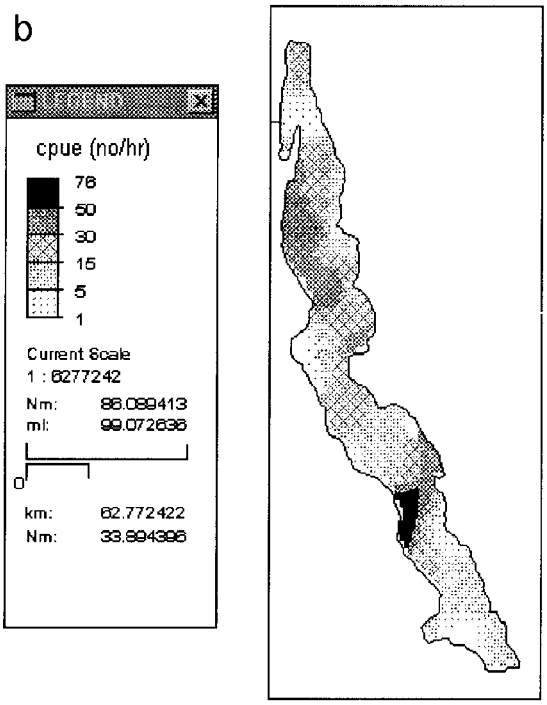


Figure 50. Pelagic trawl catch distribution of adult *L. stappersii* (TL > L_m) in June 1995 (a) and November-December 1995 (b) survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

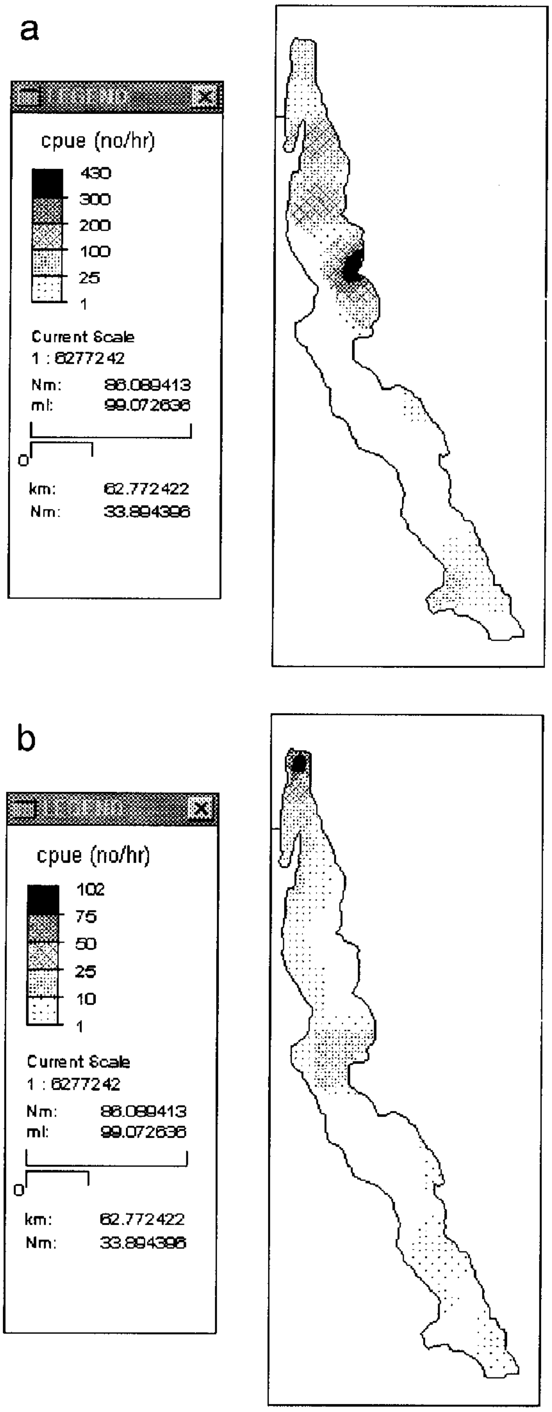


Figure 51. Pelagic trawl catch distribution of young *L. stappersii* (TL < 100 mm) in June 1995 (a) and November-December (b) 1995 survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

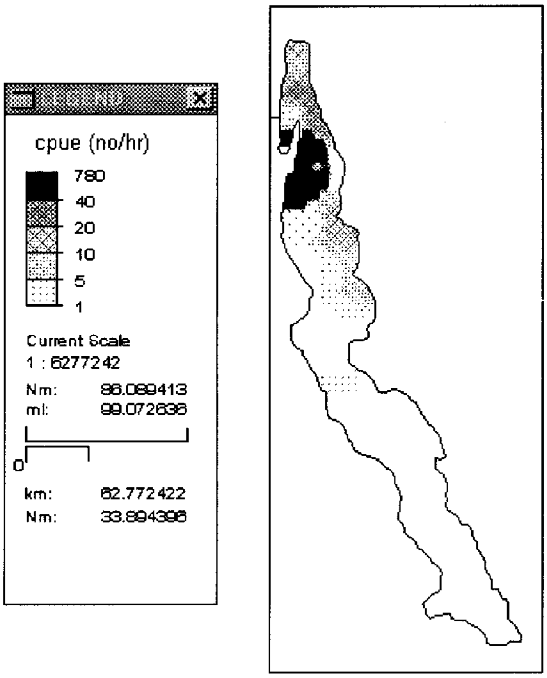


Figure 52. Pelagic trawl catch distribution of young *L. stappersii* (TL < 100 mm) in April 1996 survey. Catch per unit of effort (no/hr) is grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

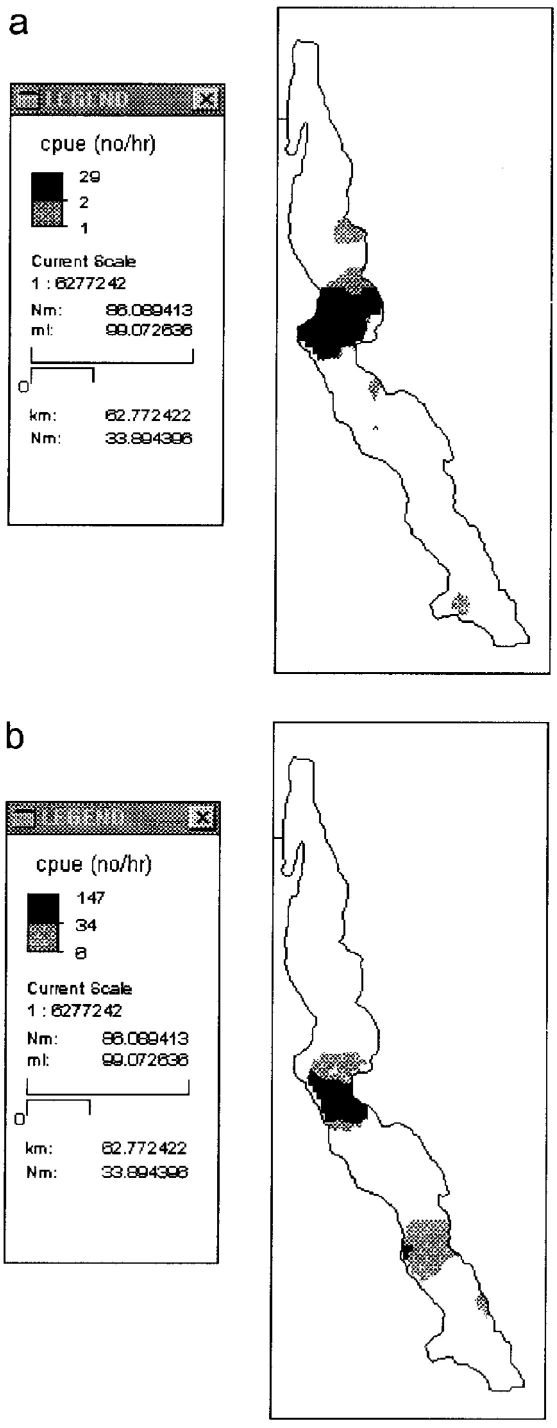


Figure 53. Pelagic trawl catch distribution of adult *L. stappersii* (TL > L_m) in November-December 1997 (a) and February 1998 (b) survey. Catch per unit of effort (no/hr) are grouped in two levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no hauls made or zero catch). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

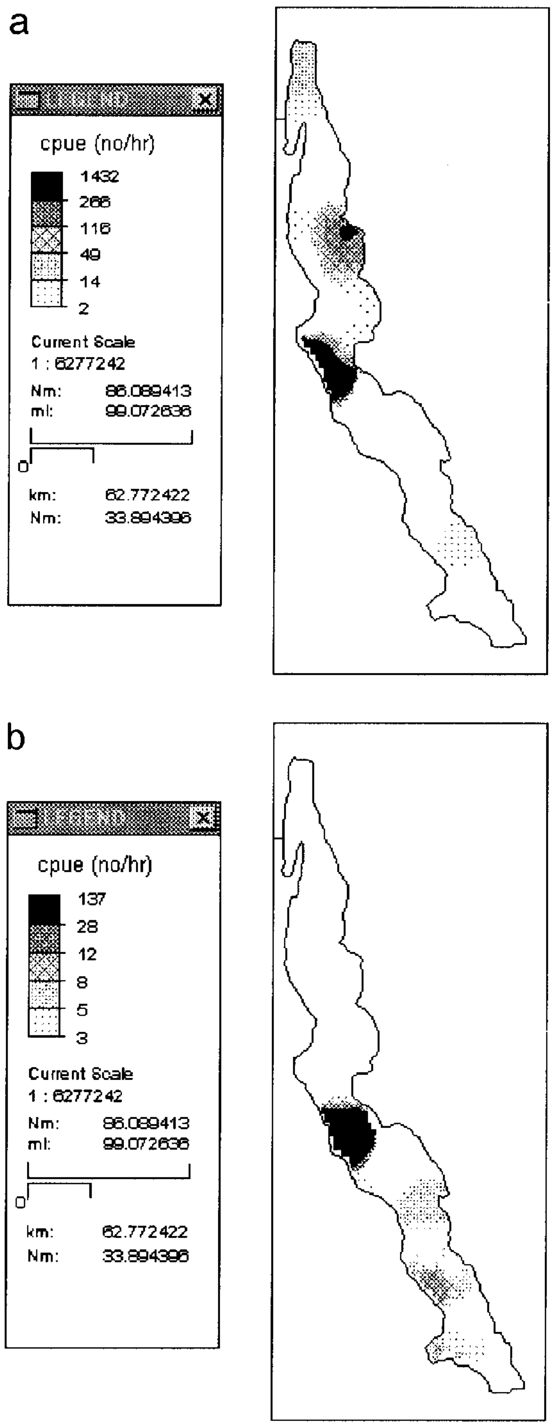


Figure 54. Pelagic trawl catch distribution of young *L. stappersii* (TL < 100 mm) in November-December 1997 (a) and February (b) 1998 survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest catch recorded. Note that **pattern scale has unequal intervals**. Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

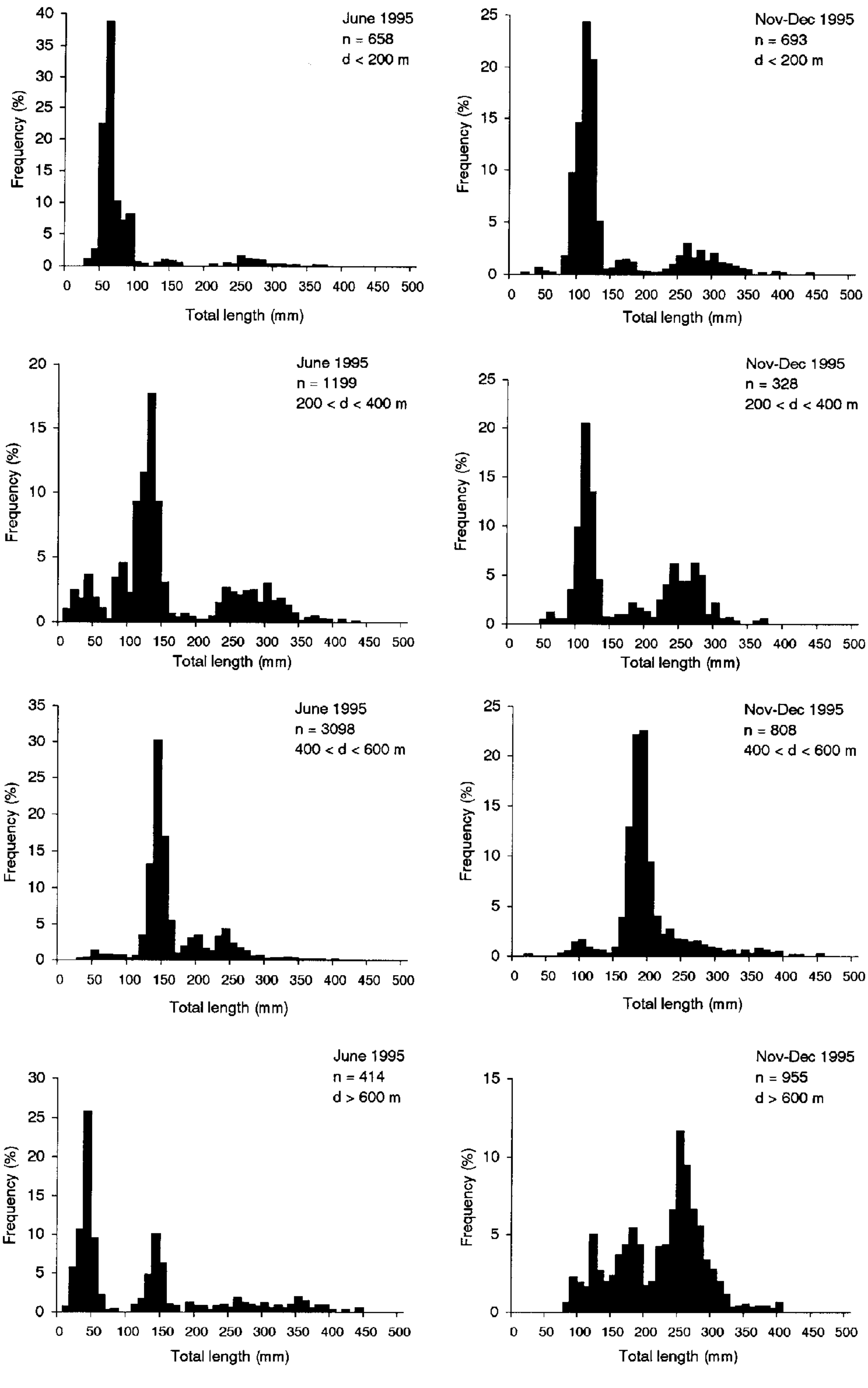


Figure 55. Size distribution of *L. stappersii* by depth strata in June and November-December 1995. Bottom depth is indicated with d, n is the sample size.

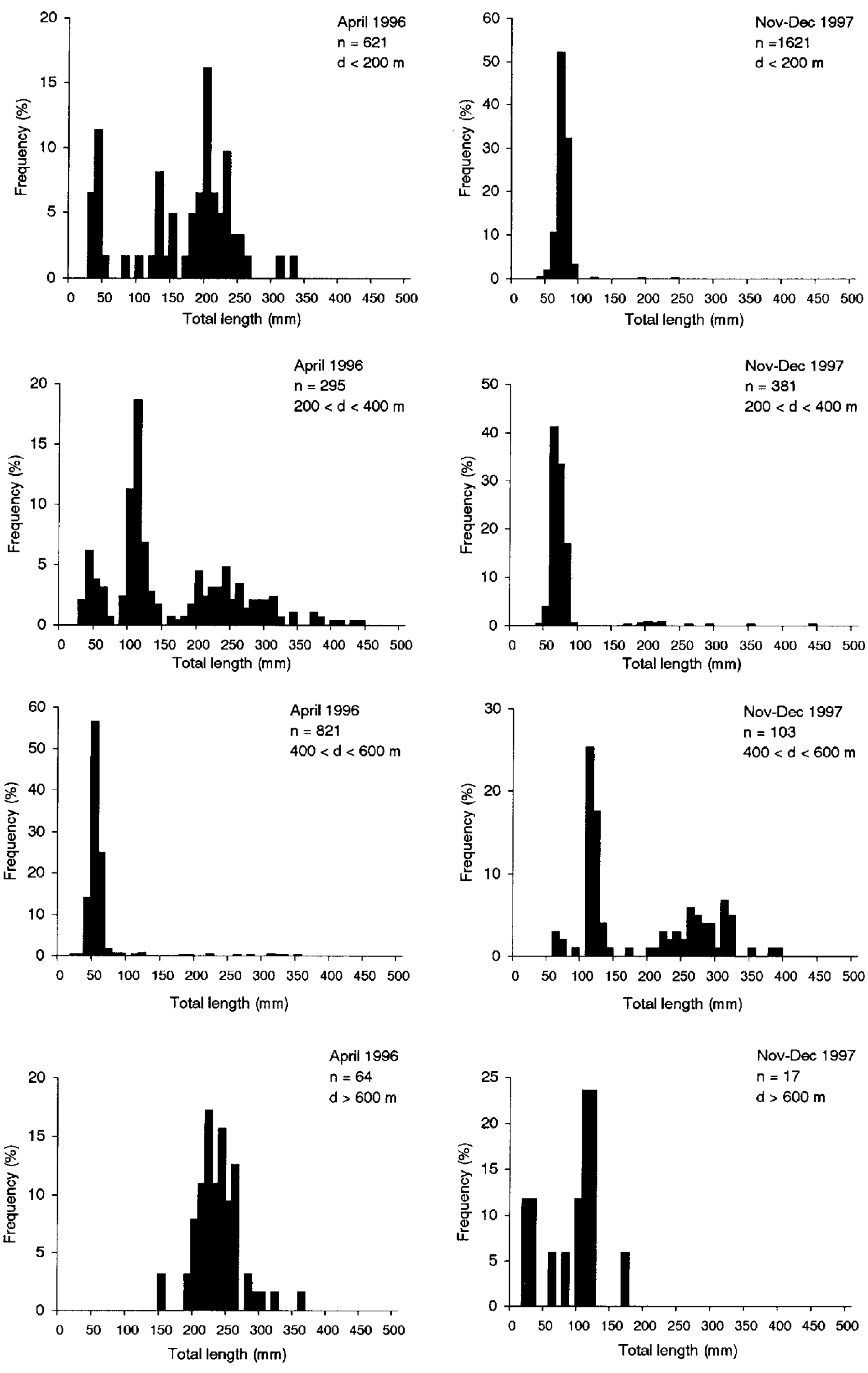


Figure 56. Size distribution of *L. stappersii* by depth strata in April 1996 and November-December 1997. Bottom depth is indicated with d. n is the sample size.

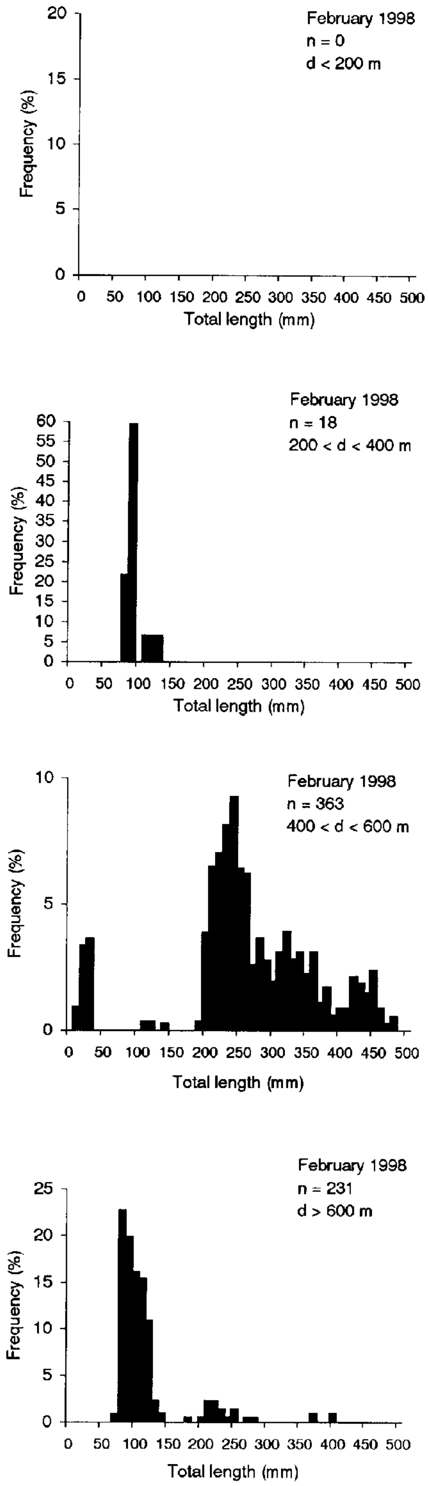


Figure 57. Size distribution of *L. stappersii* by depth strata in February 1998. Bottom depth is indicated with d, n is the sample size.

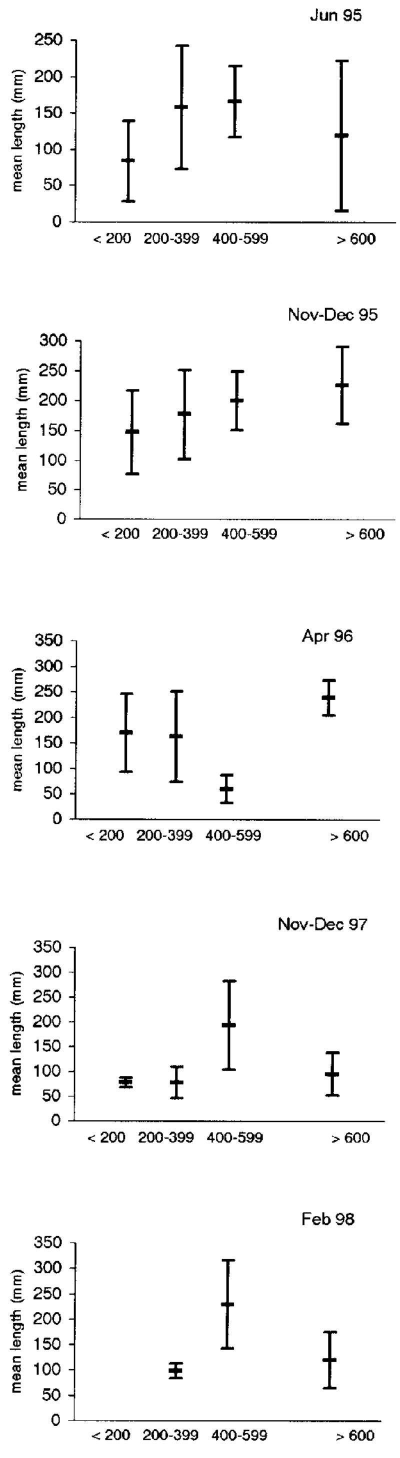


Figure 58. Mean length of *L. stappersii* in trawl catches from four bottom depth-defined zones (abscissa, m) during five surveys.

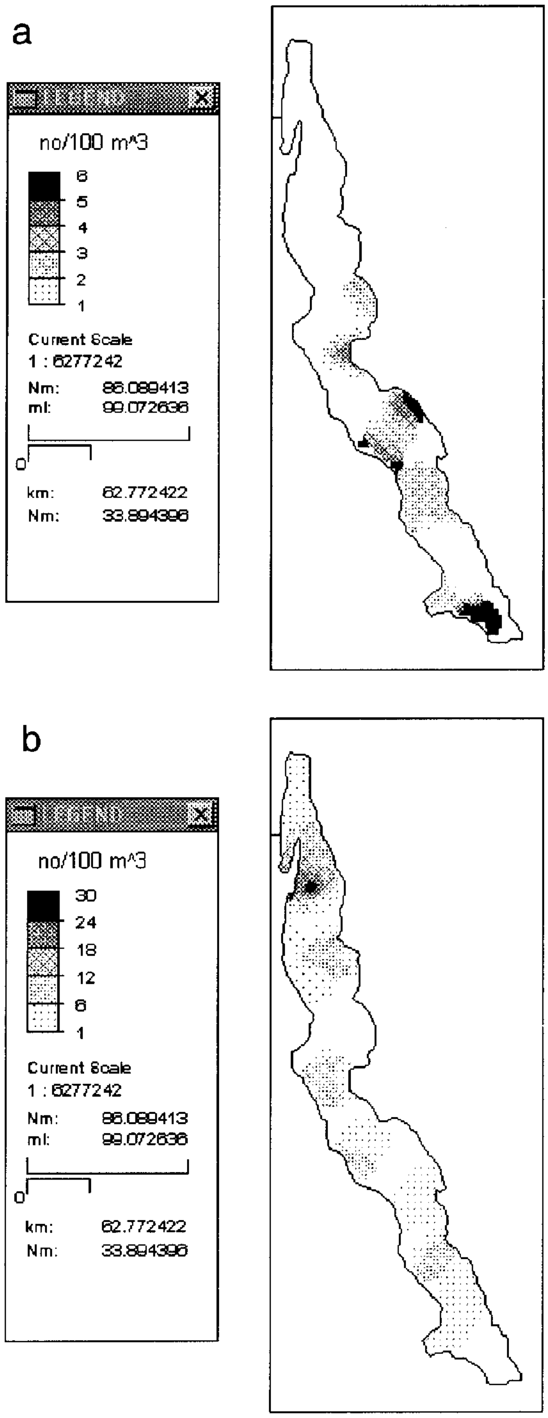
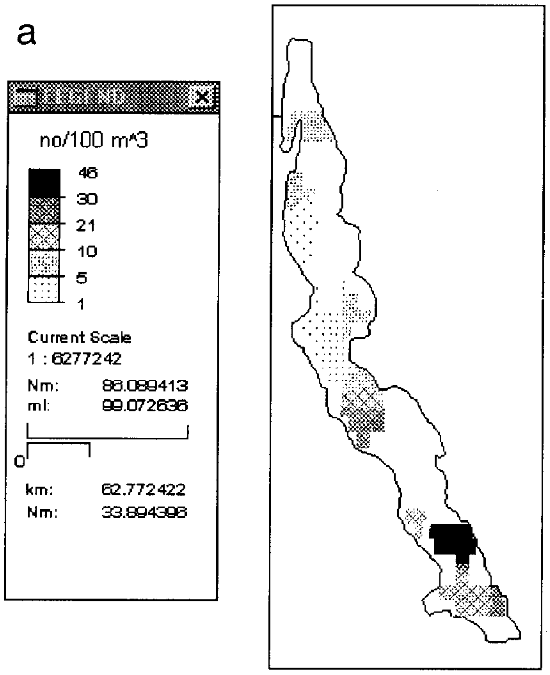


Figure 59. Distribution of *L. stappersii* larvae within 0-100 m water column in June (a) and November-December (b) 1995. Larval density (no/100 m^3) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no larva recorded or no samples taken). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).



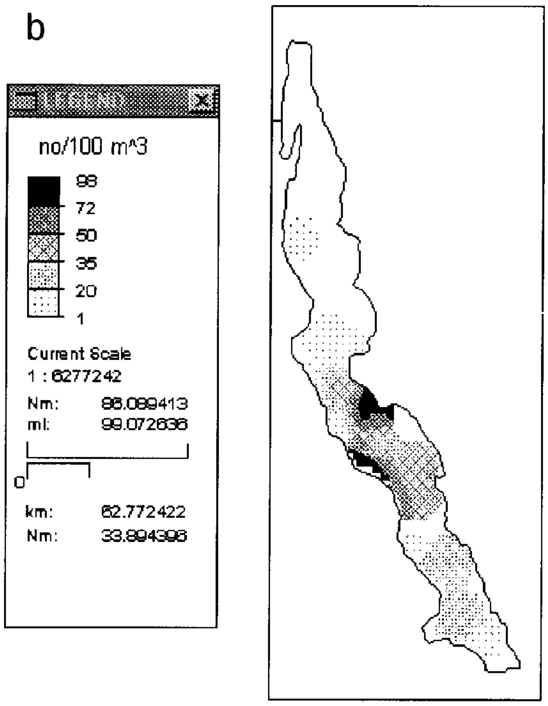


Figure 60. Distribution of *L. stappersii* larvae within 0-100 m water column in November-December 1997 (a) and February 1998 (b). Larval density (no/100 m^3) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no larva recorded or no samples taken). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

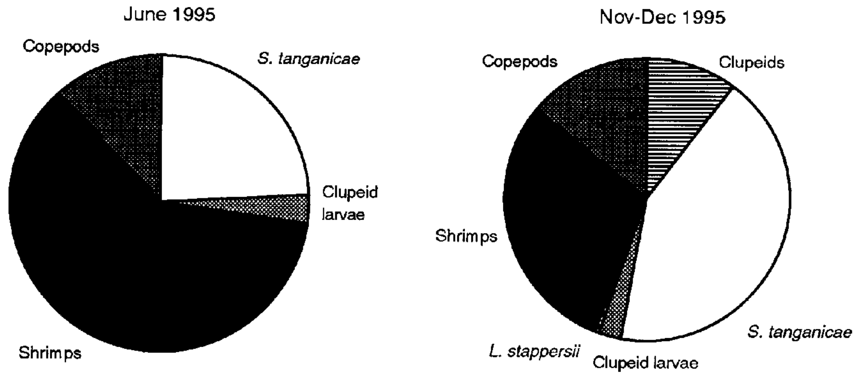


Figure 61. Occurrence of prey items in *L. stappersii* stomach content from June and November-December 1995 survey samples.

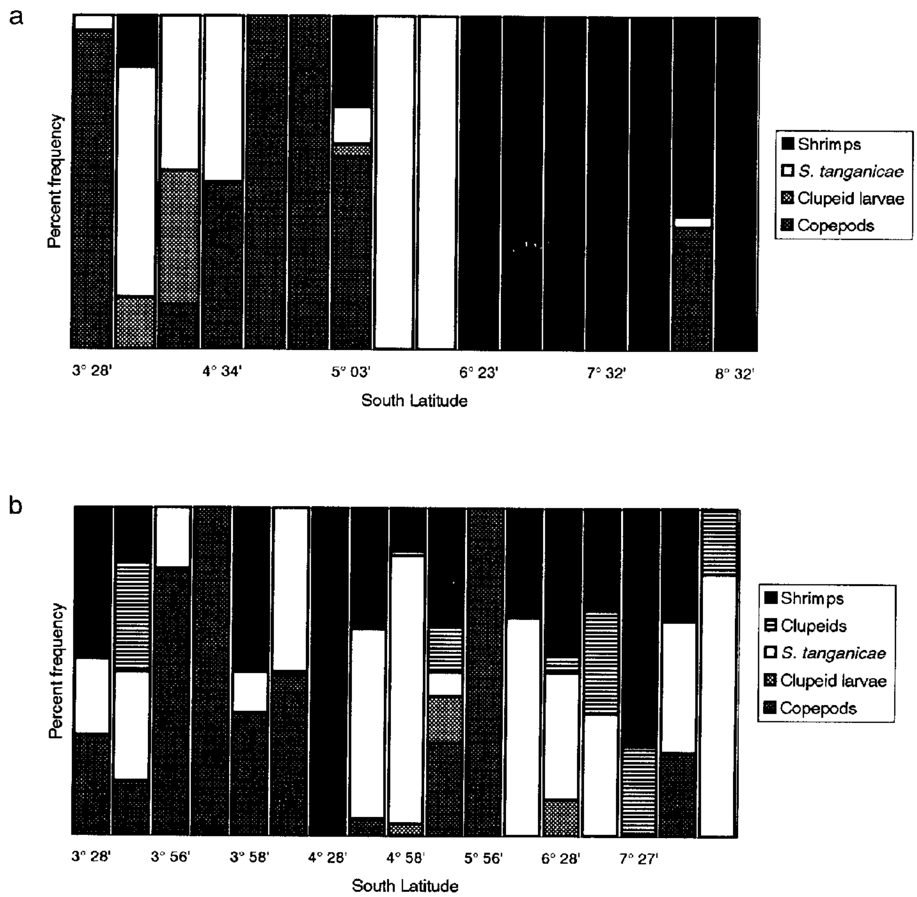
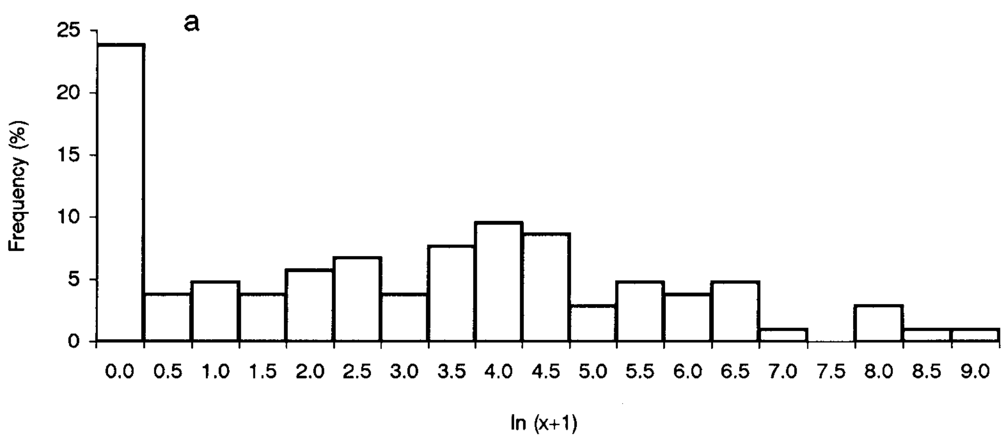


Figure 62. Frequency of prey category in stomach contents of *L. stappersii* caught at different positions along the N-S longitudinal axis of Lake Tanganyika during June 1995 (a) and November 1995 (b) pelagic trawl survey. Note that interval between sampling station positions is not proportional to effective distance.



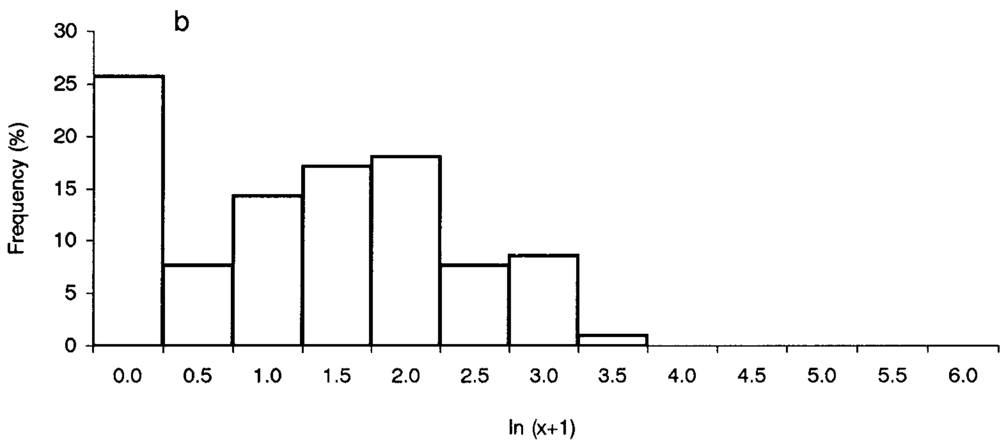
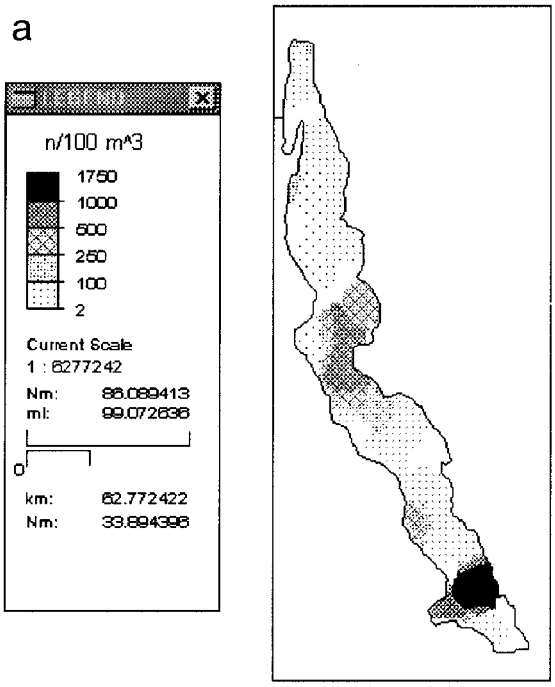


Figure 63. Frequency histograms of ln(x+1) transformed number (n x 100 m^3) of the shrimp *L. parvula*, a, and *P. moorei*, b, in Gulf-net samples from all surveys.

a



b

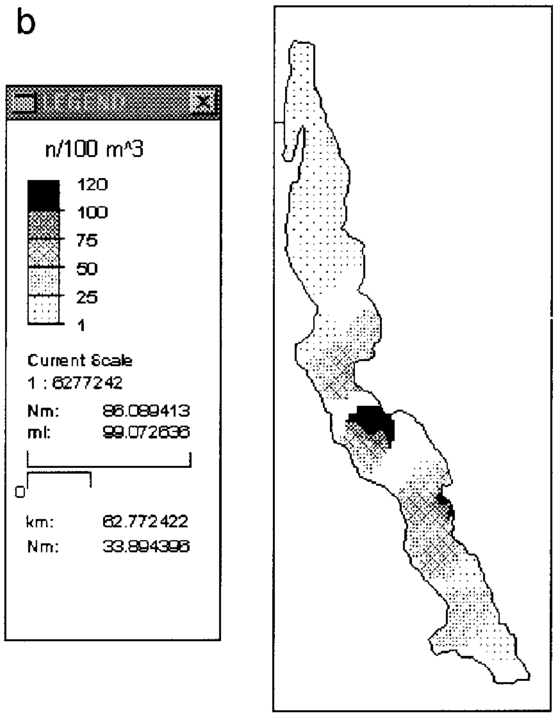


Figure 64. Distribution of *L. parvula* within 0-100 m water column from June (a) and November-December (b) 1995 surveys. Shrimp density (no/100 m^3) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no specimens recorded or no samples taken). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

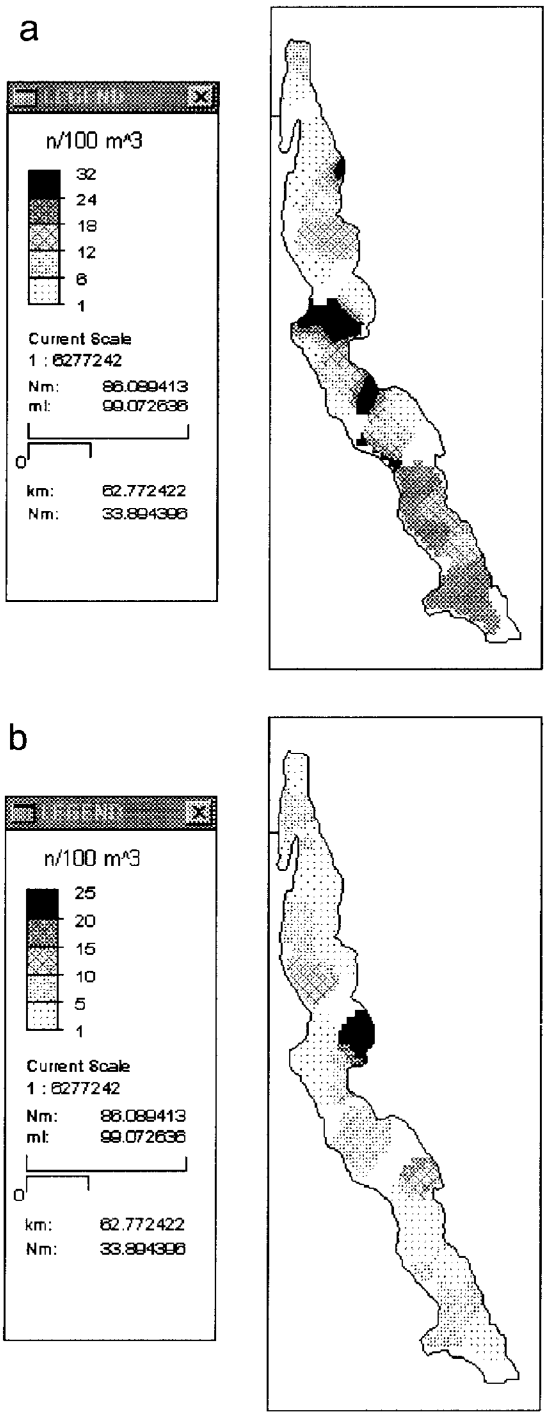


Figure 65. Distribution of *P. moorei* within 0-100 m water column from June (a) and November-December (b) 1995 surveys. Shrimp density (no/100 m^3) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no specimens recorded or no samples taken). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

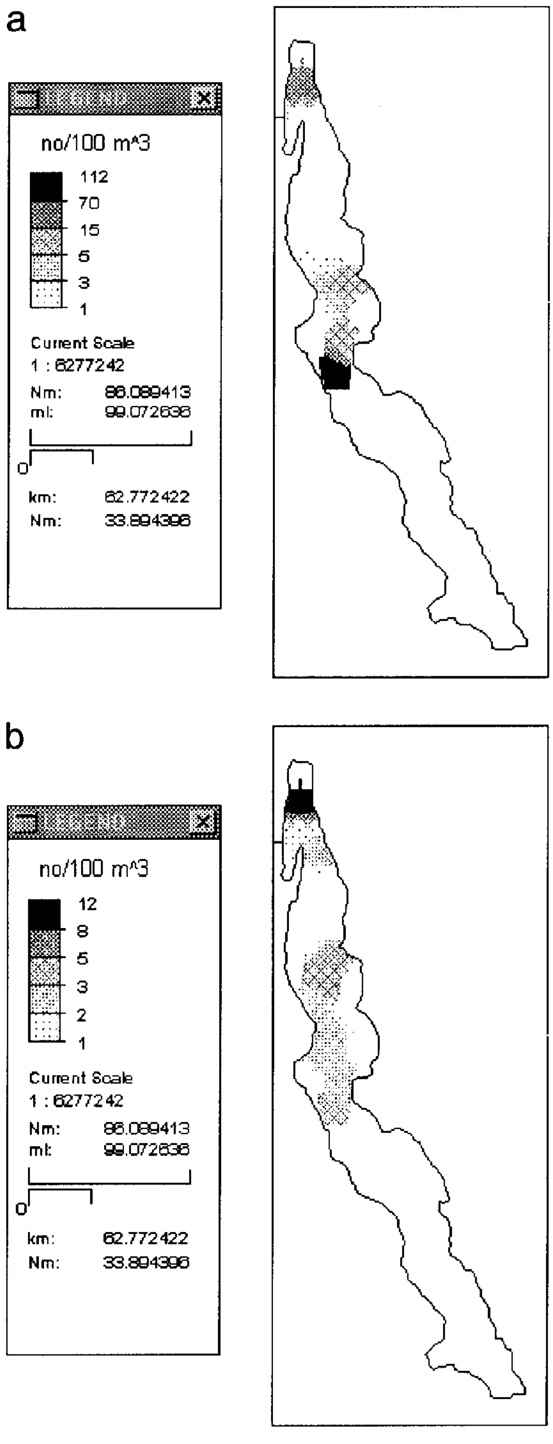


Figure 66. Distribution of *L. parvula* (a) and *P. moorei* (b) within 0-100 m water column from April 1996 survey. Shrimp density (no/100 m^3) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no specimens recorded or no samples taken). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

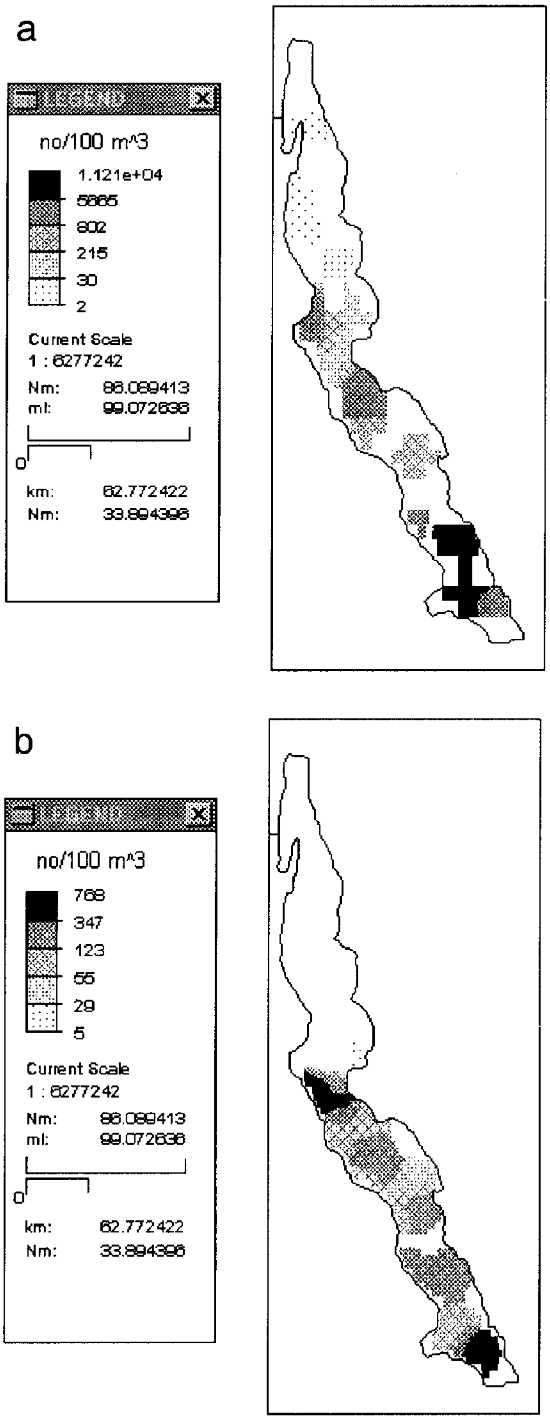


Figure 67. Distribution of *L. parvula* within 0-100 m water column from November-December (a) 1997 and February (b) 1998 surveys. Shrimp density (no/100 m^3) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no specimens recorded or no samples taken). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

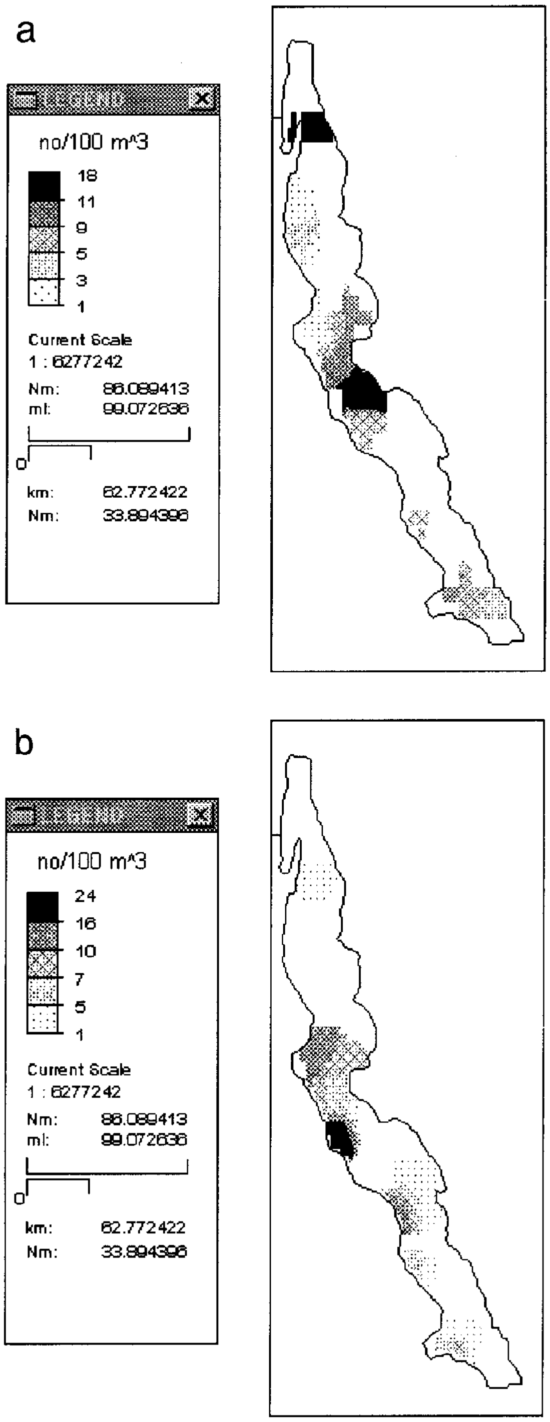


Figure 68. Distribution of *P. moorei* within 0-100 m water column from November-December (a) 1997 and February (b) 1998 surveys. Shrimp density (no/100 m^3) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. Blank areas mean that interpolation was not possible (no specimens recorded or no samples taken). Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statue miles (ml).

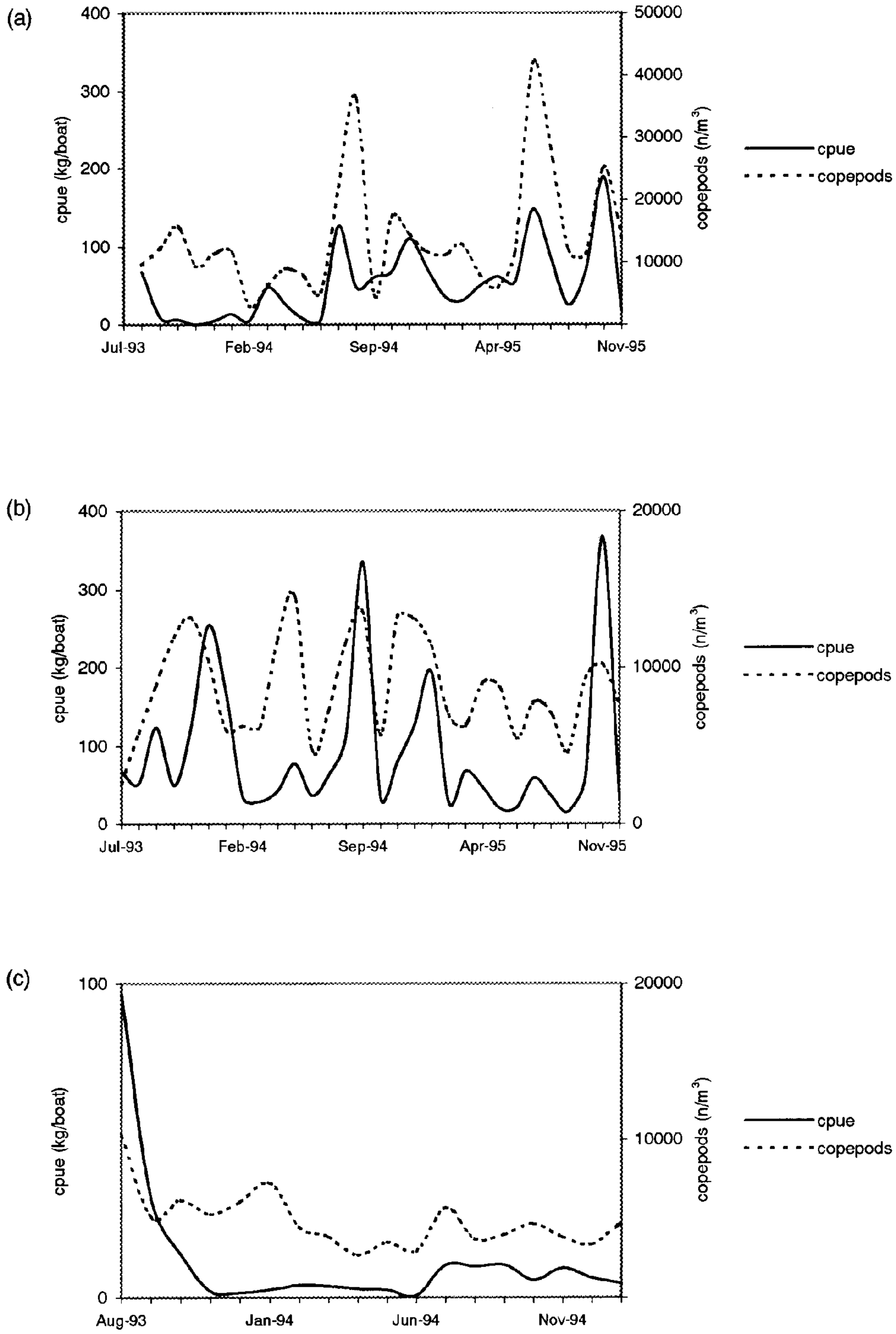


Figure 69. Monthly total number of copepods (n/m^3) and mean cpue (kg/boat) of *S.tanganicae* in Bujumbura (a), Kigoma (b) and mean cpue of clupeids (both *S. tanganicae* and *L. miodon* unsorted) in Mpulungu (c).

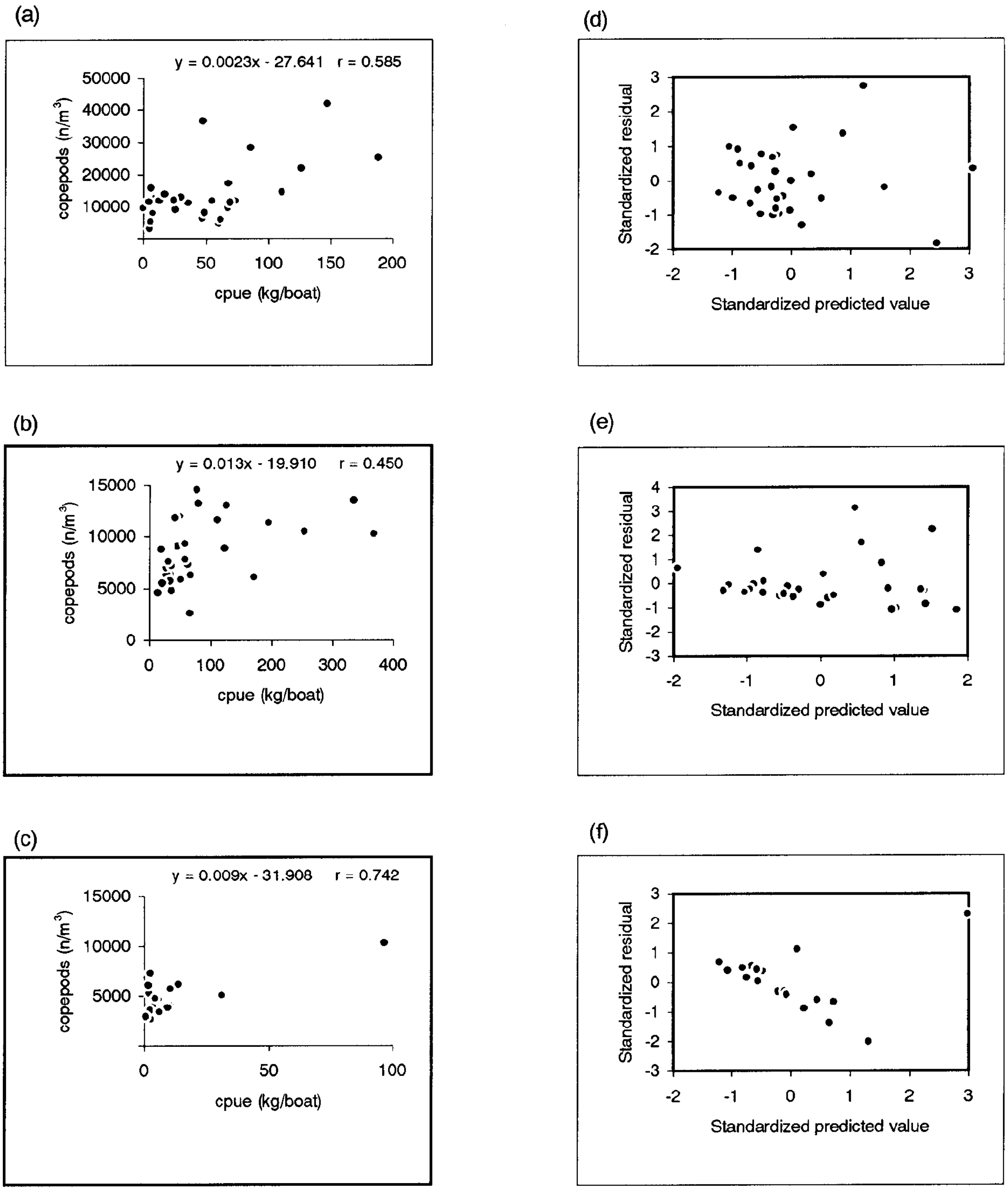


Figure 70. Scatterplot of monthly cpue (kg/boat) and copepods number (n/m^3), and scatterplot of regression predicted values against residuals from Bujumbura (a,d), Kigoma (b, e) and Mpulungu (c,f) data. *Stolothrissa tanganicae* cpue data have been used for Bujumbura and Kigoma. Clupeids cpue (both *S. tanganicae* and *L. miodon* unsorted) was used in Mpulungu.