

**THE UNIVERSITY OF HULL**

**Ecology of the Pelagic Fish Resources of Lake Tanganyika**

being a Thesis submitted for the Degree of  
Doctor of Philosophy  
in the University of Hull

by

Piero Mannini, *Laurea cum laude*

July 1998

## TABLE OF CONTENTS

	page
TITLE PAGE	i
TABLE OF CONTENTS	ii
ABSTRACT	iv
ACKNOWLEDGEMENTS	v
LIST OF SYMBOLS AND ABBREVIATIONS	vi
1. INTRODUCTION	1
2. MATERIAL AND METHODS	15
2.1 Data collection	15
2.1.1 Commercial catch sampling	15
2.1.2 Pelagic trawl surveys	16
2.2 Data analysis	18
3. RESULTS	26
3.1 <i>Stolothrissa tanganyicae</i>	26
3.1.1 Commercial catch composition	26
3.1.2 Gear selectivity	29
3.1.3 Growth and mortality	29
3.1.4 Reproduction	32
3.1.5 Recruitment	35
3.2 <i>Limnothrissa miodon</i>	38
3.2.1 Commercial catch composition	38
3.2.2 Growth and mortality	40
3.2.3 Reproduction	43
3.2.4 Recruitment	44
3.3 <i>Lates stappersii</i>	48
3.3.1 Commercial catch composition	48
3.3.2 Growth and mortality	51
3.3.3 Reproduction	53
3.3.4 Recruitment	57
3.3.5 Feeding ecology	57
3.4 Distribution pattern from survey data	68
3.4.1 General remarks on the 1995-96 and 1997-98 surveys	68
3.4.2 <i>Stolothrissa tanganyicae</i>	71
3.4.3 <i>Limnothrissa miodon</i>	92
3.4.4 <i>Lates stappersii</i>	107
3.4.5 <i>Limnocaridina parvula</i> and <i>Palaemon moorei</i>	131
3.5 Species association and relationships	134
3.6 Fishery exploitation	146

4.	DISCUSSION	154
4.1	Life history traits	154
4.2	Distribution	165
4.2.1	The <i>Stolothrissa tanganyicae</i> stock	165
4.2.2	The <i>Limnothrissa miodon</i> stock	169
4.2.3	The <i>Lates stappersii</i> stock	171
4.3	Observed relations between species	174
4.4	Exploitation status and fishery management implications	175
5.	CONCLUSIONS AND RECOMMENDATIONS	187
5.1	General conclusions	187
5.2	Future research and fishery management	189
	REFERENCES	192
	Appendix 1	209

## ABSTRACT

Most of the scientific knowledge on the pelagic fish (the clupeids *Stolothrissa tanganyicae* and *Limnothrissa miodon* and the centropomid *Lates stappersii*) of Lake Tanganyika is from research carried out in localised areas. This makes it difficult to extend the results to the whole lake. Consequently, there is the need to study the pelagic fish resources on a lake-wide basis using the same data collection procedures.

Within the framework of an international fishery research project, data from the commercial fisheries targeting the pelagic fish stocks were simultaneously collected at various sampling sites in the riparian countries. Fishery-independent data were also obtained from lake-wide research surveys. The life histories of the three fish species appear to be similar throughout the lake. However, fish distribution across the lake is very uneven. The clupeid *S. tanganyicae* mostly occur in the northern half of the lake and is much reduced in southern areas. This appears to be a recent contraction of the distribution range of this species. *Limnothrissa miodon* is more evenly distributed than *S. tanganyicae*. The two species have a different inshore-offshore, size-related distribution across the lake. Nursery grounds of the first are close to the shore while those of *S. tanganyicae* are in open, pelagic waters. With increase in size, *S. tanganyicae* tend to move inshore while large *L. miodon* display the opposite movement. *Lates stappersii* stock, although relatively common, tends to be at higher concentration in the deep, steep central and southern basins. The feeding ecology of *L. stappersii* varies depending on the area and prey availability, but is mainly based on *S. tanganyicae* and pelagic shrimps. Local occurrence of *S. tanganyicae* is associated with that of copepod prey.

The fish stocks experience different exploitation rates across the lake. While the fishing pressure is not excessive in the most of the lake areas, in others local overfishing is taking place. The biological characteristics of the pelagic fish species are discussed for the management of the lake fisheries. Fisheries management options are formulated on the basis of the assessment of the current exploitation levels.

## ACKNOWLEDGEMENTS

I wish to thank the Food and Agriculture Organization (FAO) of the United Nations and the Finnish International Development Agency (FINNIDA) for the use of data from the regional project on “Research for the Management of the Fisheries on Lake Tanganyika”. Special acknowledgements are for the project co-ordinator George Hanek, first of all for his friendship, and for his continuing effort to make the project survive through unforeseen and uncontrolled circumstances.

This work would not have been possible without the commitment of a number of people from different countries who worked together on Lake Tanganyika. It is unfortunately not feasible to mention them all but at a minimum I must thank: Deodatus Chitamwebwa, Eric Coenen, Ibrahim Katonda, Balthazar Kissaka, Victor Langenberg, Charlie Mambona, George Milindi, Lawrence Mwape, Pier Denis Plisnier, and Piet Verburg. Sincere thanks also go to the 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 for making available the zooplankton data. I am also grateful to Heini and Eero Seppälä for their friendship when we worked together in Tanzania. I thank Janusz Burczynski who kindly introduced me to the use of the EchoBase GIS software. I would like to express my gratitude to John Craig for his advice and criticism at the early stages of this work.

I am indebted to Julia Cowx for her support and friendship during my stay in Hull. I am infinitely grateful to my family for their continuous help of all kind during the years I have spent abroad, and also to have taken care of my dogs while I was in the UK, thus overturning their (of my parents!) life routine. Without the encouragement, supervision and criticism of Ian Cowx this work would have been just an idea. Finally, I thank Daniela for being my wife.

## LIST OF SYMBOLS AND ABBREVIATIONS

- $\phi'$  phi prime, i.e. a length based index of growth performance equal to  $\log_{10}K + 2\log_{10}L_{\infty}$ , where  $K$  and  $L_{\infty}$  are parameters of the von Bertalanffy Growth Function.
- C.V. coefficient of variation; the standard deviation expressed as a percentage of the mean.
- $B'/R$  relative biomass per recruit
- CPUE catch per unit of effort
- $E$  exploitation rate;  $E = F/Z$ .
- $E_{max}$  value of  $E$  associated with the highest  $Y'/R$  value for a given value of  $L_c$ .
- $F$  instantaneous rate of fishing mortality ( $\text{time}^{-1}$ );  $F = Z - M$ .
- FL fork length; the length of a fish measured from the tip of the snout to the tip of the shortest central rays of the caudal fin.
- $K$  parameter of the von Bertalanffy Growth Function, of dimension  $\text{time}^{-1}$ , expressing the rate at which asymptotic length is approached.
- $L'$  a length not smaller than the smallest length of fish fully represented in catch samples (e.g. cut-off length in length-converted catch curve analysis)
- L/F length-frequencies.
- $L_{25}$  length at which 25% of the fish will be vulnerable to the gear.
- $L_{50}$  length at which 50% of the fish will be vulnerable to the gear.
- $L_{75}$  length at which 75% of the fish will be vulnerable to the gear.
- $L_c$  mean length of fish at first capture; equivalent to  $L_{50}$ .
- $L_{\infty}$  asymptotic length, a parameter of the von Bertalanffy Growth Function expressing the mean length the fish of a given stock would reach if they were to grow for an infinitely long period.
- $L_m$  mean length at first maturity of the fish of a given population.
- $L_{max}$  maximum length by the fish of a given stock.
- $M$  instantaneous rate of natural mortality ( $\text{time}^{-1}$ );  $M = Z - F$ .

- P/B* production/biomass ratio, or turnover rate.
- SL* standard length, the length of a fish measured from the tip of the snout to the tip of the fleshy part of the caudal peduncle excluding the caudal fin.
- TL* total length, the length of a fish measured from the tip of the snout to the tip of the longest rays of the caudal fin, when the caudal fin lobes are aligned with the main body axis.
- VBGF* von Bertalanffy Growth Function, used to describe the growth in length and weight of fish.
- W* symbol for the individual body weight of a fish.
- Y'/R* relative yield per recruit.
- Z* instantaneous rate of total mortality ( $\text{time}^{-1}$ );  $Z = M + F$ .

## 1. INTRODUCTION

Major lakes and reservoirs in central, eastern and southern Africa, although very different, all have a thriving pelagic community which supports highly productive, important commercial fisheries (Marshall, 1984; Pitcher, 1995).

Much interest has focused on the pelagic fish communities of African inland waters because they are easily exploitable fish resources. This has arisen for two main reasons. First, increase in the human population linked to a higher market demand for fishery products has led to excessive exploitation and the subsequent decline of many inshore stocks, mainly cichlids, traditionally targeted by commercial fisheries. Secondly, some small pelagic species introduced in new environments (e.g. large reservoirs) have been able to sustain the rapid development of profitable fisheries. Overviews of the taxonomy and geographical distribution of small African freshwater pelagic fish are provided in Marshall (1984) and Wandera (1990).

Productivity of the pelagic ecosystem is due to high ecotrophic efficiency and the relative simplicity of the open water ecosystem. Usually, the fish assemblage in the pelagic zone can be characterised as clupeid dominated (*Stolothrissa tanganyicae* Boulenger, *Limnothrissa miodon* Regan) (lakes Tanganyika, Kivu, Kariba, Cahora Bassa) or cyprinid dominated (*Rastrineobola argentea* Pellegrin, *Engraulicypris sardella* Günther) (lakes Victoria, Malawi). Lake Tanganyika was originally characterised by autochthonous clupeid fish but *L. miodon* was deliberately and successfully introduced into Lake Kivu (Collart, 1960) and Kariba (Bell-Cross and Bell-Cross, 1971; Junor and Begg, 1971), and from the latter it spread to Cahora Bassa (Bernacsek and Lopes, 1984).

The three largest African lakes, Victoria (0°50' S, 32°50' E), Tanganyika (3°23' S, 29°40' E) and Malawi (10°45' S, 34°30' E) all have unique pelagic fish communities which support important fisheries. However, the pelagic ecosystem of the three lakes differs markedly.



Lake Victoria is the largest African lake (68000 km<sup>2</sup>), the third largest in the world. It is much shallower (mean depth: 20 m; max. depth: 70 m) than Lake Tanganyika (mean depth: 570 m; max. depth: 1470 m) and Lake Malawi (mean depth: 426 m; max. depth: 756 m), and used to have a unique haplochromine cichlid fish fauna which has been much reduced in the past three decades. The sharp decline of the haplochromine populations caused much concern amongst scientists around the world (e.g. Barel, *et al.*, 1985), and can be attributed mainly to three factors: fishery exploitation, Nile perch (*Lates niloticus* L.) predation and eutrophication.

Introductions of non indigenous tilapiines began in 1953 (Welcomme, 1966; 1967), and *L. niloticus* was first introduced into Lake Victoria in 1954 (EAFPRO, 1960; Fryer, 1960; Hamblyn, 1960; Anderson, 1961; Beadle, 1981). Evidence of reduced abundance in the catch of haplochromines and *Oreochromis esculentus* Graham dates back to at least the late 1970s (Benda, 1979, 1981; Marten, 1979; Okemwa, 1984) and concern about localised overfishing was even being expressed much earlier (Graham, 1929; Beauchamp, 1955; Garrod, 1960; Mann, 1970; Jackson, 1971), long before Nile perch appeared in the lake.

Cichlid populations, displaying life history characteristics such as relative slow growth, low fecundity, and highly developed and complex parental care (Witte and Goudswaard, 1985; Ribbink, 1987), have poor resilience to intensive exploitation. Predation pressure, coupled with the already high fishing mortality in certain areas, quickly led to the reduction of *Haplochromis* stocks to exceedingly low levels.

For twenty years, while traditional catches continued to decline, catches of *L. niloticus* were minimal. Then in the early 1980s the Nile perch population boomed and by 1990 the total annual catch from Lake Victoria increased to over 500 000 t (Gréboval and Mannini, 1992; Reynolds *et al.*, 1995). The lake now supports a thriving fishery and ancillary industries (Reynolds and Gréboval, 1988). The fishery now largely comprises three species: the exotics *L. niloticus* and *Oreochromis niloticus* L., and a native zooplanktivorous, pelagic cyprinid *R. argentea* (Kudhongonia and Chitamwebwa, 1995).

The rapid depletion of the main prey did not induce a corresponding decrease in the predator population because *L. niloticus* opportunistically switched to other available food resources, namely *R. argentea* and the atyid shrimp *Caridina nilotica* Roux. Stocks of these two species, the importance of which within the lake's ecosystem has been given relatively scant attention in the past, have greatly contributed to the maintenance of the predator population and its high catch rates.

Information on the population of the formerly rare *C. nilotica* is very limited, the few quantitative data available indicate a strong increase in the Mwanza Gulf (Witte *et al.*, 1992; Goldschmidt *et al.*, 1993). The cause of the increase of prawns is not yet understood. Hecky (1993) hypothesised that the expansion of *C. nilotica* was favoured by the eutrophication resulting from human riparian activities such as clearing and burning of forest and savannah, and agriculture in the watershed.

The small pelagic *R. argentea* is nowadays the second most important commercial species of Lake Victoria and probably the only native fish that has not been negatively affected by the presence of *L. niloticus*. It is difficult to establish whether the *R. argentea* population has actually expanded during the last decade or so. Certainly the catch rates of this cyprinid increased strongly during the 1980s (Wanink, 1991; Witte *et al.*, 1992). It is possible that *R. argentea* has benefited to some extent from the decline of planktivorous haplochromines due to the predation by *L. niloticus* (Wanink, 1989). The difference between zooplanktivorous haplochromines and *R. argentea* in ability to coexist with *L. niloticus* may be due to their difference in reproductive strategies. *Rastrineobola argentea* has a mean fecundity which is higher than that of haplochromines (Bruton, 1990; Wanink, 1991).

Lake Malawi has not undergone such human-induced, drastic changes as Lake Victoria. Lake Malawi is a West Rift lake and its physical characteristics are more like that of Lake Tanganyika than of Lake Victoria. Lake Malawi has the same general form and appearance as Lake Tanganyika, and, especially in the northern half, the escarpment is steep and great depths are found relatively close to the shore. Moreover, the climatic regime and the wind-induced circulation of water masses are

similar in both lakes (Beadle, 1981). Also common is the high number of fish species and the remarkably high level of endemism amounting to, at least, 93% (Lake Malawi) and 80% (Lake Tanganyika) of the total number of known species. Endemism rate is even higher when only the cichlid fish are considered reaching 97 and 98% in Lake Malawi and Lake Tanganyika respectively (Beadle, 1981; Table 8.2, p. 144).

However, the fish fauna of Lake Malawi is very different from that of Lake Tanganyika. For instance, the pelagic waters of Lake Tanganyika are occupied by centropomid *Lates* spp. of soudanian origin, and by clupeid species which probably originated from the Congo basin, while none of Lake Malawi fish species are believed to have a similar origin (Beadle, 1981).

Historically much of research had been confined to inshore regions with the exception of the FAO Fishery Expansion Project (FAO, 1982) which extended its investigations offshore. Recently, the UK/SADC Pelagic Fish Resource Assessment Project (Menz, 1995) carried out the most detailed studies on the pelagic ecosystem of the lake.

The Lake Malawi fishery takes place predominantly in coastal waters, mainly in the south where it has been estimated that 80% of the lake's total catch is made (Turner, 1995). About two hundred fish species are exploited in the south-east arm of the lake. The bulk of the catch is made up of haplochromine and tilapiine species. A moderate fishery exploitation occurs offshore mainly targeting on the cyprinid *E. sardella*.

*Engraulicypris sardella* was believed to be the most important pelagic species of the lake until the UK/SADC project proved that the true nature of the offshore fish community was much more complex. It showed that at least eight cichlid fish species are quantitatively important in the pelagic ecosystem (Allison, *et al.*, 1995a). The lakefly *Chaoborus edulis* Edwards at the larval stage is an important component of the diet of many fish species (Allison, *et al.*, 1995b) and, consequently, supports fish production. It may be hypothesised that larval *C. edulis* being placed in the food web

between mesozooplankton and fish has an ecological role and importance similar to that of the shrimps *Limnocaridina parvula* (Calman) and *Palaemon moorei* (Calman) in Lake Tanganyika and of *C. nilotica* in Lake Victoria.

The pelagic fishery is expected to further expand. The UK/SADC project indicated a potential offshore yield of 33300 t yr<sup>-1</sup> that would double the lake's total catch (Thompson, 1995), although there are still many uncertainties about the level of sustainable yield (A. Menz, pers. comm.).

Lake Tanganyika is situated in the western branch of the Rift Valley system between 3°23' and 8°50' S at an altitude of 773 m above sea level. The lake is an international water body shared by four states: Tanzania in the east, Zambia in the south, Democratic Republic of Congo (ex-Zaire) in the West and Burundi in the north-east (Figs 1 and 2). The length of the shoreline is 1825 km (Coenen, *et al.*, 1993), the maximum length of the lake is 673 km and the maximum width 50 km. The surface area is 32900 km<sup>2</sup>; thus it is the second largest African lake after Victoria. The maximum depth is 1470 m, the mean depth 570 m, and the total water volume is 18900 km<sup>3</sup> (Beadle, 1981; Coulter, 1991a). Lake Tanganyika is the second deepest lake in the world after Lake Baikal in Siberia, whose maximum depth is 1741 m. Only the surface water to a depth of c. 80-100 m at the northern end, and c. 200 m in the south is oxygenated, below that level there is a large volume of anoxic water (Plisnier *et al.*, 1996). The surface temperature varies between 23 and 27°C throughout the year.

There are two main seasons within a year in the Lake Tanganyika region. The wet season extends from October/November to May, and is characterised by weak winds, high humidity, considerable precipitation and frequent thunderstorms. The dry season from June to September/October has moderate precipitation and strong, regular southerly winds. The seasonal changes of weather and winds results from austral and boreal trade winds, which determine the dynamics of the Inter-Tropical Convergence Zone (ITCZ) and its active wet zone movement (Huttula *et al.*, 1994). These major climatic patterns, and particularly the winds, regulate the seasonal thermal regime of the lake (Coulter, 1963; Coulter and Spiegel, 1991), evaporation

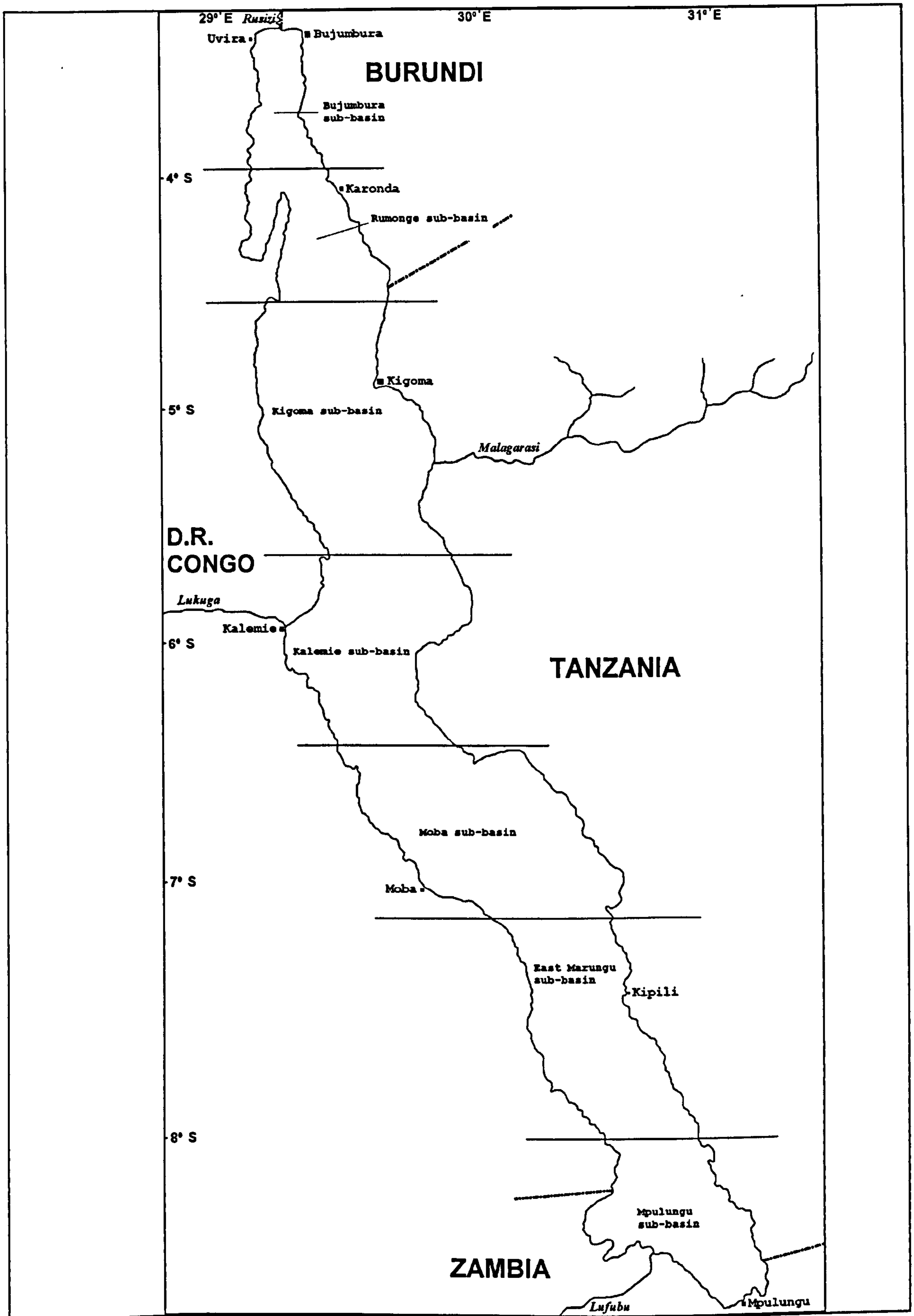


Figure 1. The map shows the major landing sites and villages of the lake. Sub-basins are also indicated and approximately defined by horizontal lines (for more details see text and Tiercelin and Mondeguer in Coulter, 1991).

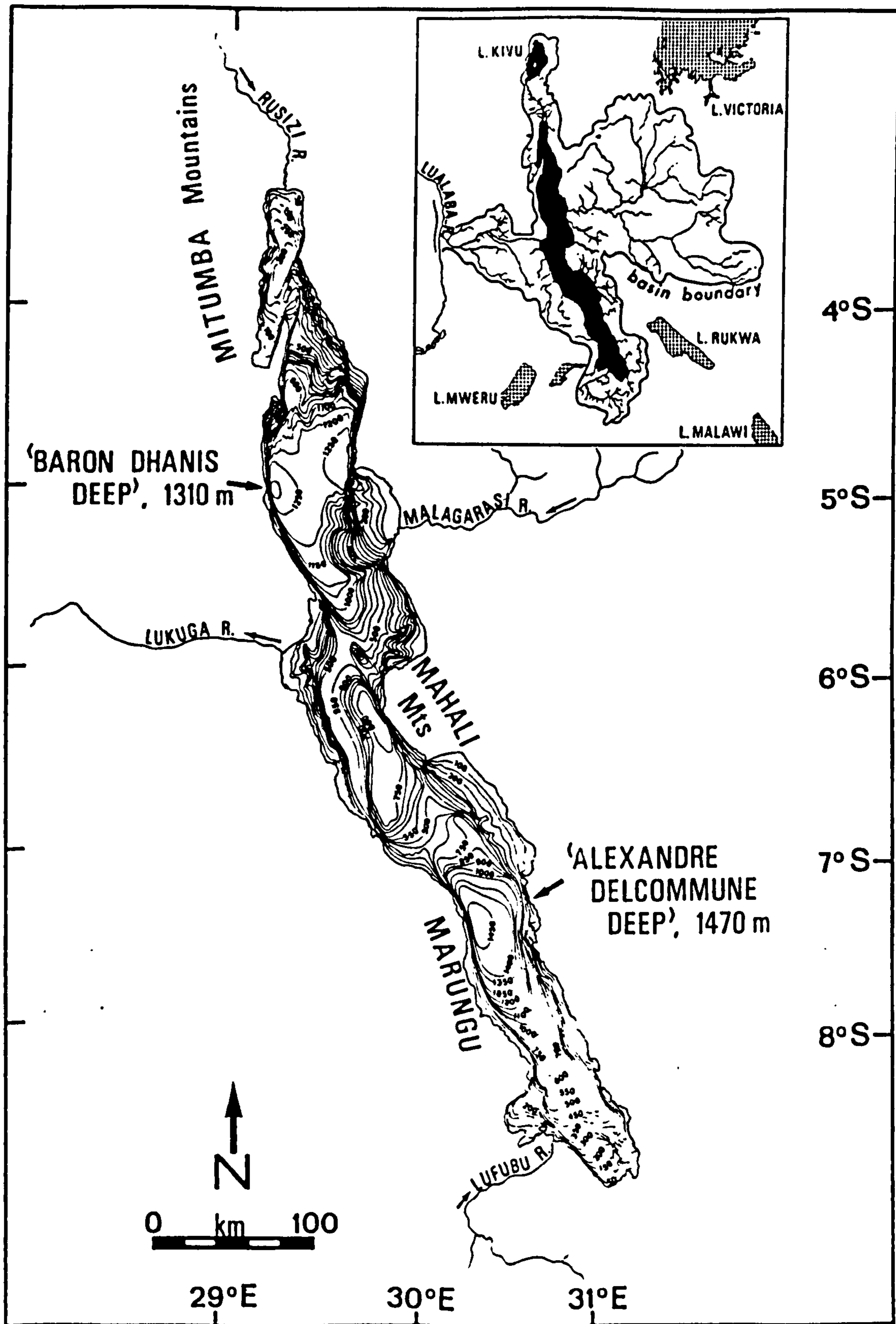


Figure 2. Bathymetry and drainage pattern of Lake Tanganyika (from Coulter, 1991, p. 10).

(Coulter and Spiegel, 1991), water flows and the vertical mixing and transport of water masses (Degens *et al.*, 1971).

The lake is characterised by seasonal upwelling events and the knowledge of their temporal and spatial dynamics has been recently increased by the work of Plisnier *et al.* (1996) and Tuomainen *et al.* (1997).

The main upwelling takes place at the end of the dry season late in the south part of the lake along the steep slopes of the basin. In the south, during the dry season starting in May-June, south-east winds drive surface water northwards causing the deepening of the thermocline in the north. The volume of warm water accumulated in the north depends on the strength of the wind. At the south end of the lake the winds cool the epilimnion by convection and wind mixing, and the thermocline rises in the water column. Deep currents of cold water return to the south and cause upwelling and further cooling. At the onset of the wet season, around October, the south east winds cease, surface temperature starts to increase and vertical stratification begins to be re-established. A secondary upwelling (weaker when compared to the southern upwelling) takes place at the north of the lake in October-November.

The fauna of Lake Tanganyika is richer, either in terms of number of species and endemism, than in any other African lake (Beadle, 1981). The antiquity of the lake has provided the time necessary for speciation processes to develop. Lake Tanganyika has more fish families than any other lake in the world (Coulter, 1991a). All species of the families Clupeidae (*S. tanganyicae* and *L. miodon*) and Centropomidae (*Lates stappersii* Boulenger, *L. mariae* Steindachner, *L. microlepis* Boulenger and *L. angustifrons* Boulenger) to which the most important pelagic fish stocks belong, are endemic.

Lake Tanganyika is known for its productive pelagic fisheries, which is reported to yield higher catches per unit area than in most great lakes of the world (Coulter, 1981, 1991a; Hecky *et al.*, 1981; Lindqvist and Mikkola, 1989; Hecky *et al.*, 1981; Roest, 1992).

Lift nets and purse seines are the main pelagic fisheries of Lake Tanganyika. The first can be classified as an artisanal fishery while the second is considered as industrial. Both these fishing methods use lamps to attract the fish.

Lift nets were first introduced in the north of the lake and are currently the commonest fishing practice. However, they are rare in the south, probably because they are less effective in wind-exposed areas which are common in that part of the lake (Ngomirakiza and Haling, 1972). Purse seine fishing began in Burundi in the early 1950s by Greek fishermen (Collart, 1958) who introduced the traditional "lampara" fishing method common in the Eastern Mediterranean. The method was adopted by the purse seine fleets based at Kalemie, Moba, Kigoma and Mpulungu, all ports with easy access to markets. At the present the most important purse seine fishery is based in Zambia at Mpulungu while it has almost completely disappeared from the rest of the lake due to a combination of socio-economic factors discussed later.

Historical fishery statistics are affected by difficulty in collecting the information from the huge coastline (1828 km) which has an extremely poor communications network. Fishery data on catch and effort are fragmentary for most of the lake with the exception of Burundi (artisanal and industrial fisheries) and Zambia (industrial fishery).

The development and decline of the industrial fishery in Burundi is represented in Figure 3a. It is believed that the collapse was due to the development of the artisanal fishery (Fig. 3b) with improved technology during the 1980s (Roest, 1992; Petit and Kiyuku, 1995). This would have led to competition between the industrial and artisanal fisheries both operating in a relatively small portion of the lake. Also, it has been suggested that fishery exploitation is not the main cause of the decreased industrial catch, and climatic factors could have been the determining factor (Plisnier, 1997). However, artisanal catch rates from the same area do not appear to have gone through a similar decline (Fig. 3); it seems unlikely that environmental changes have had negative effects only on the stock exploited by the industrial



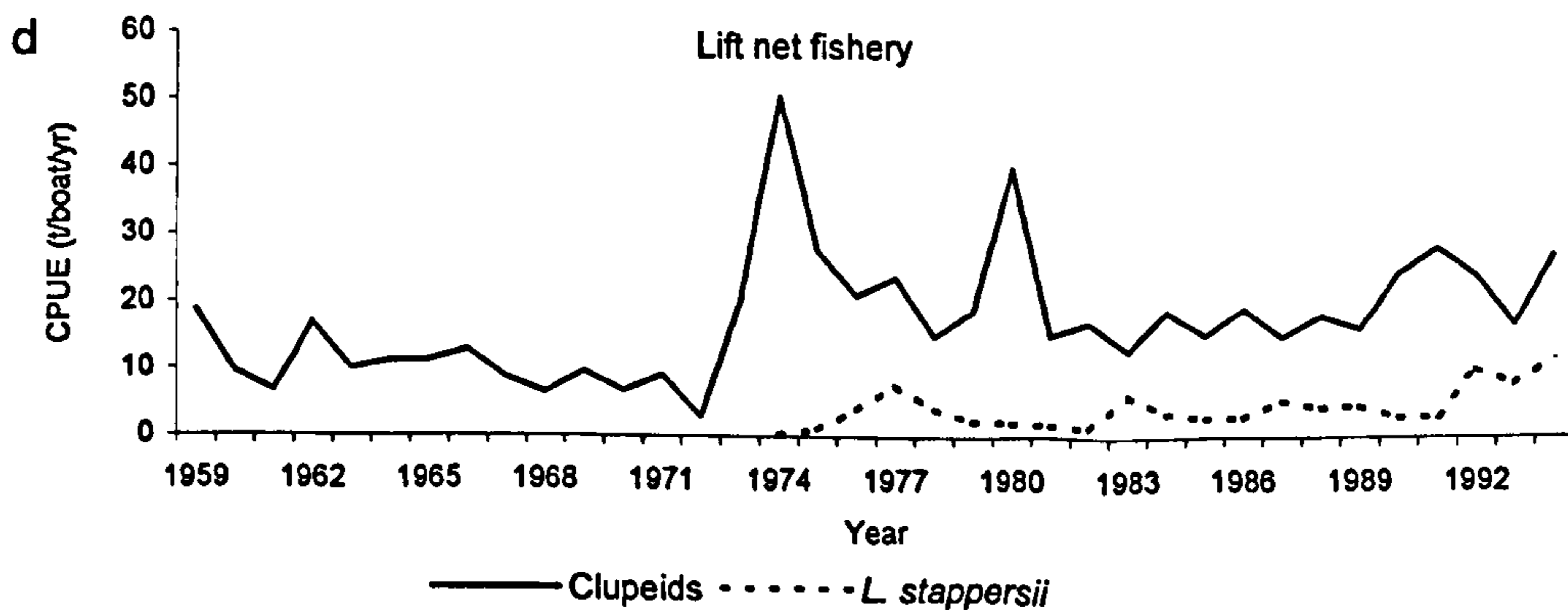
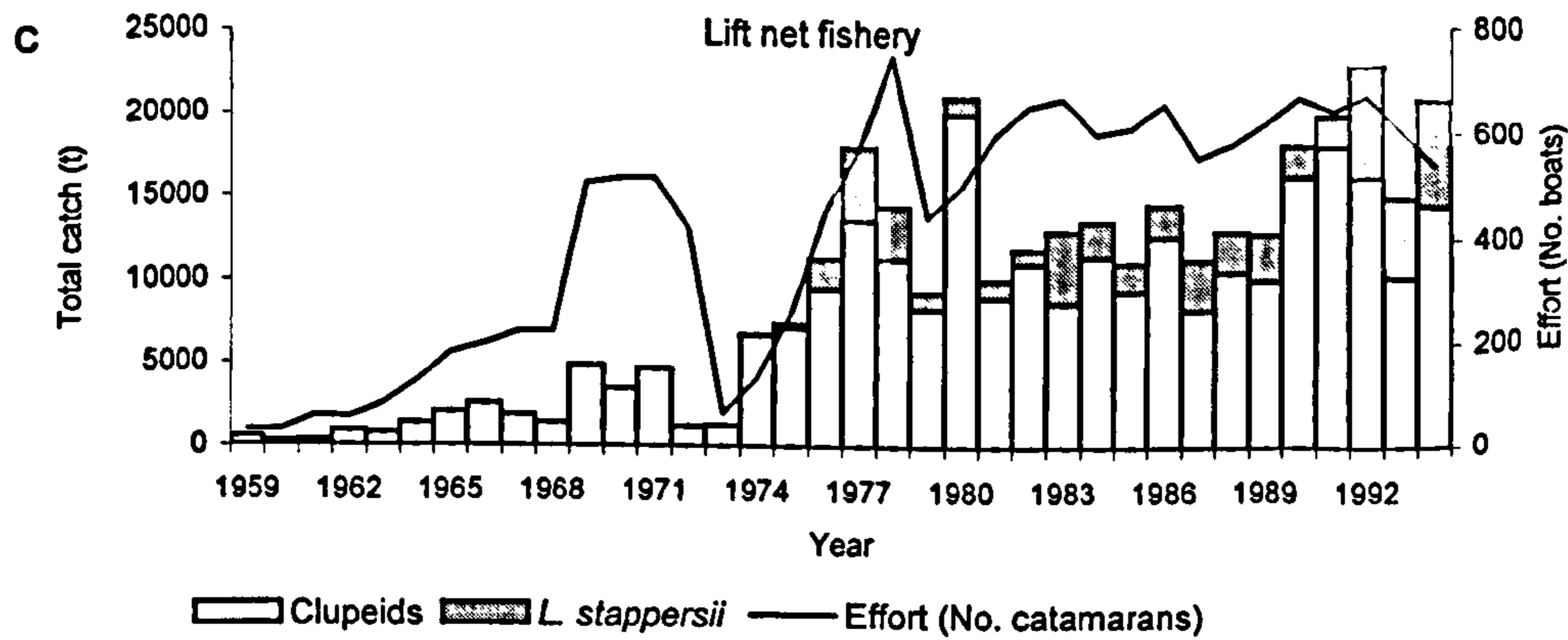
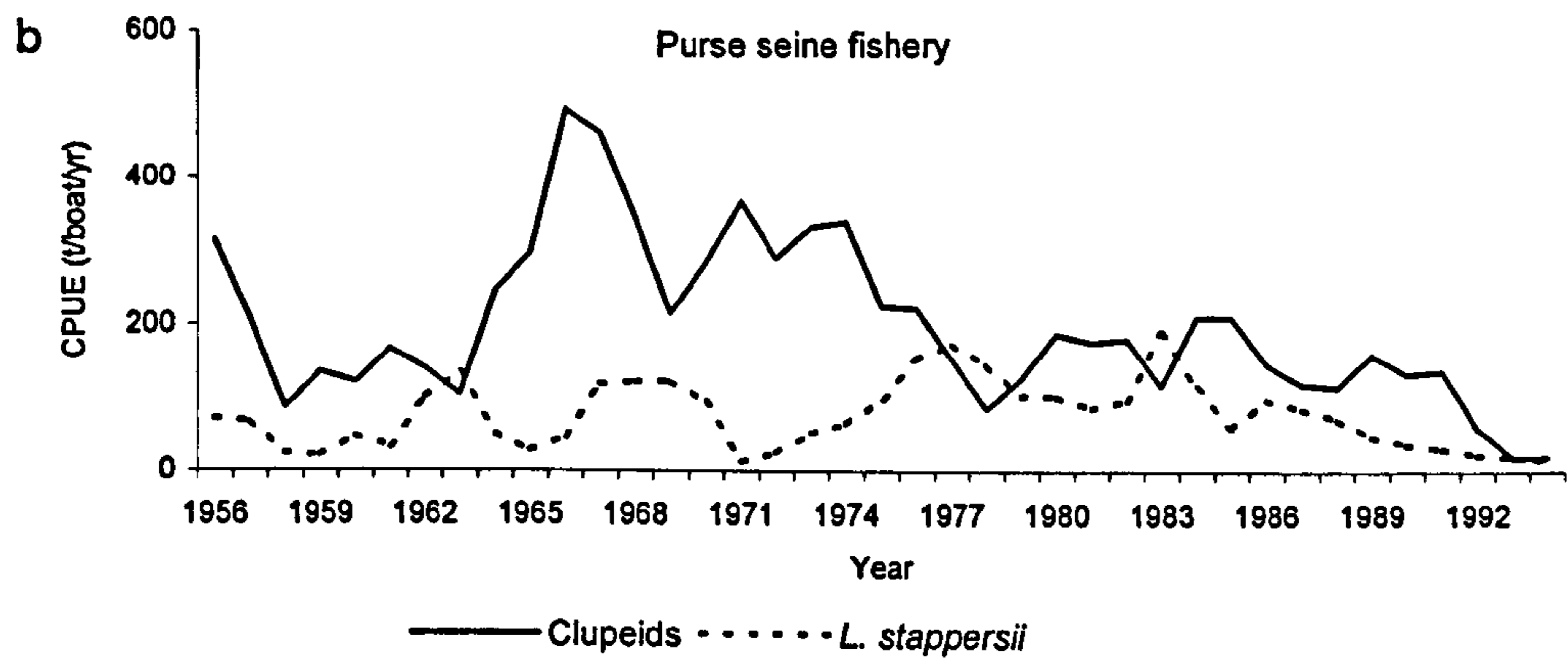
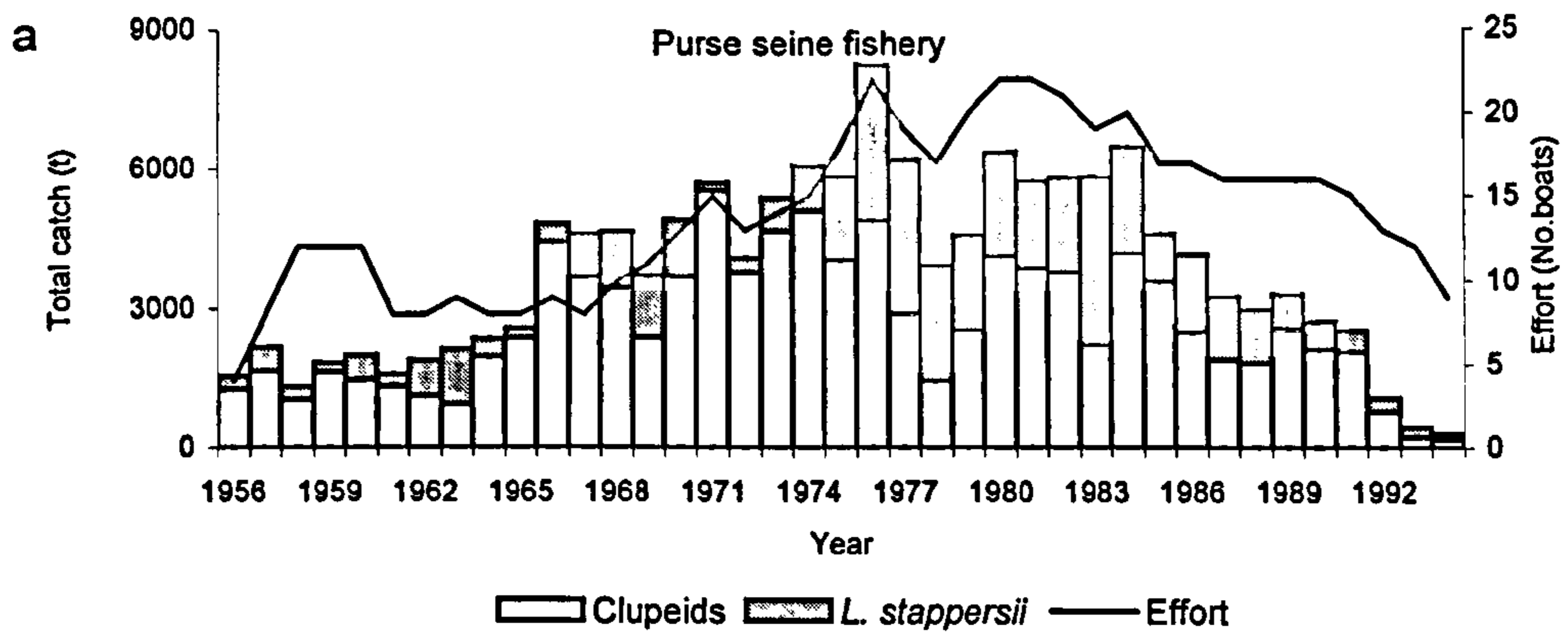


Figure 3. Annual total catch and effort of the Burundian purse seine (a, b) and liftnet (c, d) fisheries. Source: Coenen, 1995; Coenen *et al.*, 1998.

fishery. The most recent fishery statistics from Burundi indicate that while the artisanal fishery during the last few years has maintained a constant level of production, estimated at about 20000 t yr<sup>-1</sup>, the industrial fishery catch dropped in 1994 to a historical minimum of 326 t (Coenen *et al.*, 1998). The economic unprofitability of the fishery, coupled with the civil war affecting the region, forced most of the purse seiners to stop fishing or to move further south, mainly to Zambia. Only two industrial fishing units, from the twenty-two active at the beginning of the 1980s, were still in Burundi in 1995.

The trend in total catch, mostly of the lift net fishery, from Tanzania indicates that since the late 1980s the fish yield fluctuated around 60-50000 t yr<sup>-1</sup> (Fig. 4). However, the reliability of fishery statistics from this sector of the lake is dubious (Coenen *et al.*, 1998; E. Lymo, Fish. Dept., Dar es Salaam, pers. comm.; pers. obs.).

When the purse seine fishery commenced in Zambia the main target was the large top predator *Lates* spp. which was soon overfished (Coulter, 1970) forcing the fishery to switch to the clupeid stock. *Lates stappersii* replaced almost entirely the clupeids in the catch from the mid 1980s. The effort has strongly increased during the last twenty years and sustainable yields from the local fishing grounds appear to have been exceeded as shown by the decline of both catch and CPUE (Fig. 5).

The most recent lake-wide frame survey carried out in 1995 (Paffen *et al.*, 1997), assessed the artisanal lift net fishery as 3104 units, and the industrial fishery as 52 units, of which only 28 were active. The large majority are based at the southern end of the lake. Coenen *et al.* (1998) estimated the 1995 total catch from all lake fisheries (traditional, artisanal and industrial) at 196 570 t. The catch from only those fisheries targeting the pelagic stocks was estimated at 169 280 t, which highlights the importance, either as source of income or food, of the pelagic fish resources.

Scientific knowledge about Lake Tanganyika and its fisheries is often affected by the spatially fragmentary nature of the available information. The main problem for the understanding of the pelagic ecosystem is that most research has been carried out in restricted areas and therefore it has been difficult to obtain results, the validity of

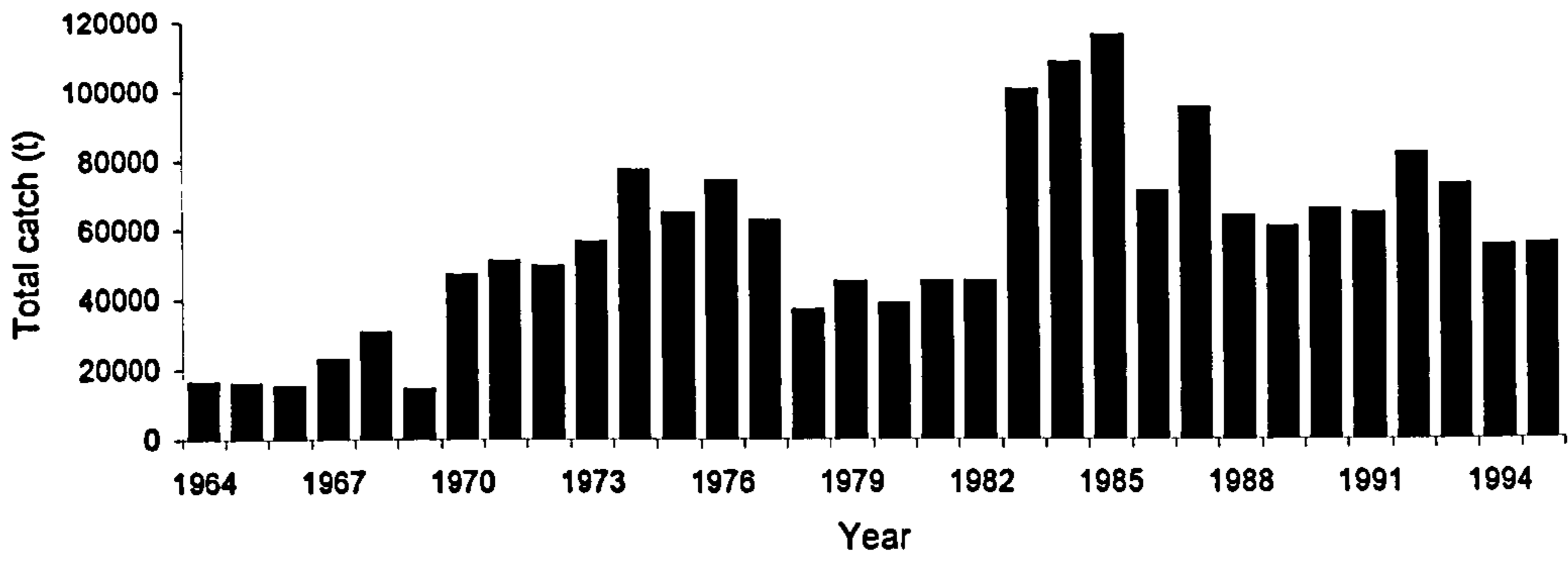


Figure 4. Annual total catch in Tanzanian sector of Lake Tanganyika. Source: Coenen, 1995; Coenen *et al.*, 1998.

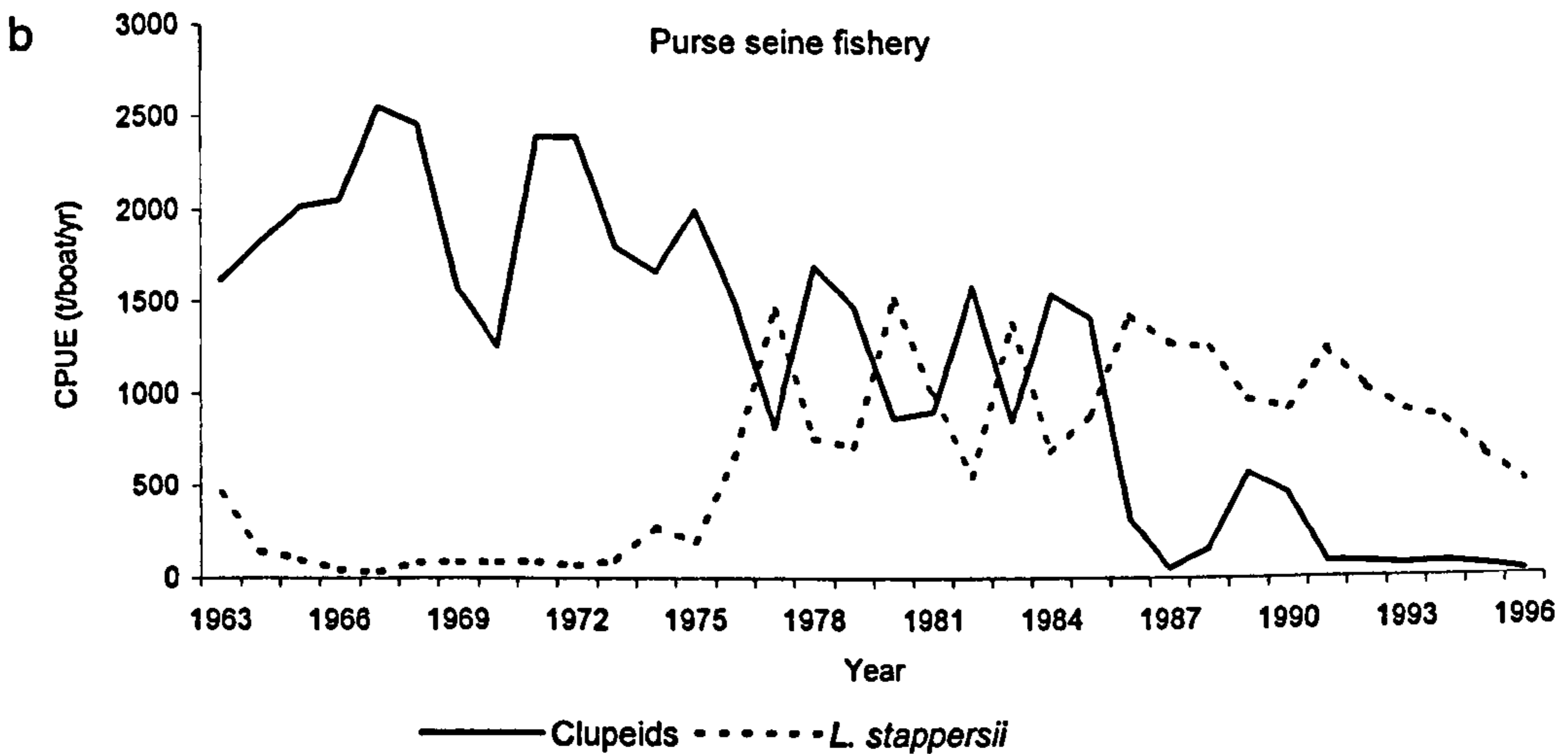
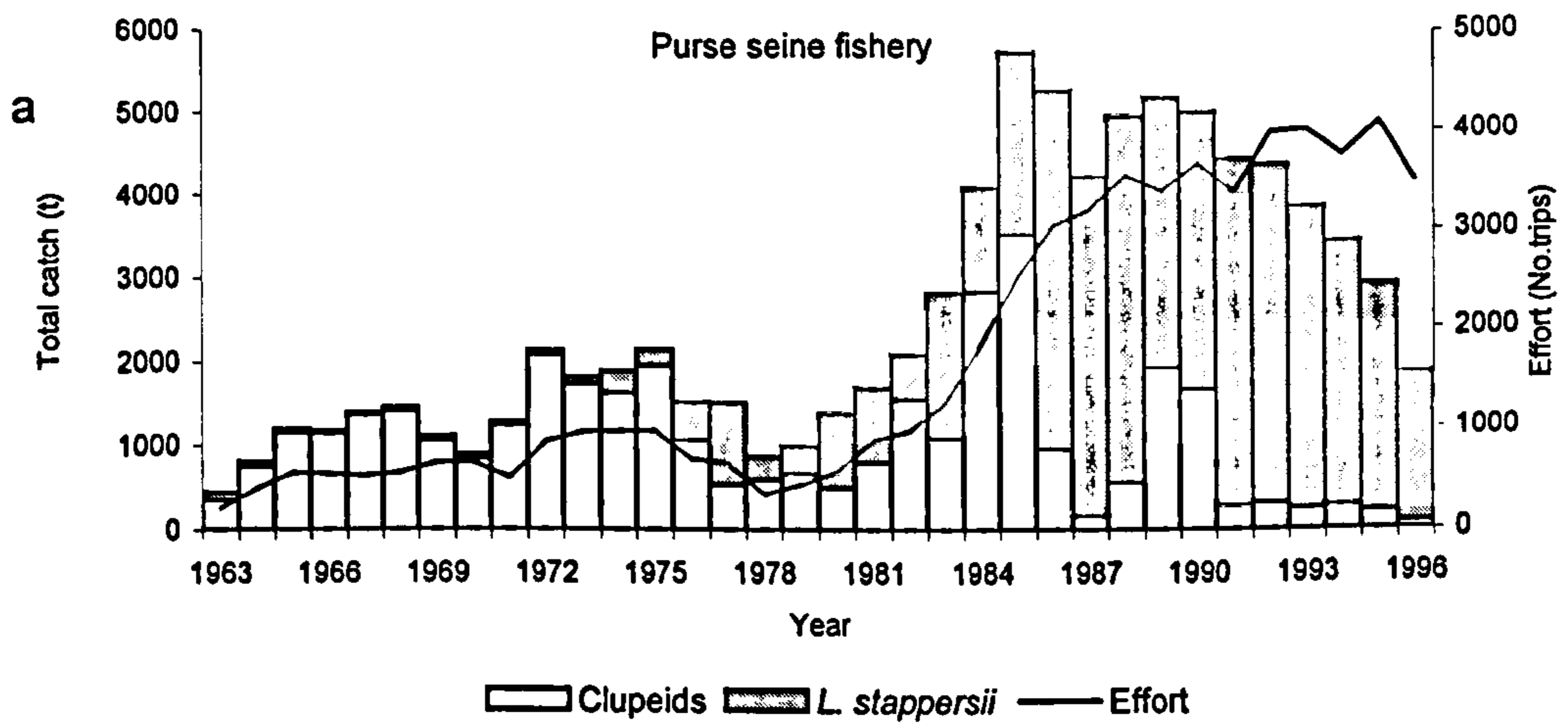


Figure 5. Annual total catch, a, and effort, b, of the Zambian purse seine fishery. Source: Coenen, 1995; Coenen *et al.*, 1998.

which extends 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 over in the last forty years. In the past, research on the main commercial pelagic fish was carried out over different time periods and with varied sampling methods. The results are difficult to compare and there is a lack of data about the biology and exploitation of the major stocks in different areas of the lake.

Previous lake-wide research comprised three acoustic surveys conducted in 1973, 1975 and 1976 to estimate the pelagic fish biomass (Johanesson, 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 combined acoustic and pelagic trawl surveys could not be done and therefore no direct information on fish species and size composition of the acoustic measurements was available.

From the review of previous work the need for a lake-wide understanding of the biotic and abiotic characteristics is evident. The FAO-FINNIDA "Research for the Management of the Fisheries on Lake Tanganyika", henceforth LTR, attempted to fulfil this need through simultaneous data collection, at fixed localities around the lake, and the execution of lake-wide pelagic trawl surveys using the R/V *Tanganyika Explorer*.

This work describes the lake-wide distribution of pelagic fish and shrimp and investigates the relations between species. The main aims are:

- to outline the main characteristics of the population ecology of the main pelagic fish stocks of the lake (*S. tanganyicae*, *L. stappersii* and *L. miodon*);

- to identify possible differences in the life cycle of the commercial fish species in different areas of the lake;
- to identify the spatial distribution patterns of the pelagic fish and shrimp, and to discuss the factors responsible for the observed patterns;
- to investigate the feeding ecology of the centropomid predator *L. stappersii* between different areas of the lake in relation to the distribution of this species;
- to assess the current fishery exploitation status of the resources, and to evaluate fisheries management implications and options on the basis of the biological characteristics of the species and of the assessment of the exploitation levels.

## 2. MATERIALS AND METHODS

### 2.1 Data collection

In fisheries research two main sources of data may be used: those available from sampling the commercial fishery (fishery-dependent data) and those which can be collected from research vessels (fishery-independent data). Commercial catch sampling is necessary since the effects that fishing has on fish stocks must be evaluated. Also, this is a valuable data source for fishery research because the data are relatively inexpensive and easy to obtain. However, the main disadvantages are that commercial catches at best form a haphazard and typically biased sample of the fish population, particularly when the fishery is based on artificial aggregation (e.g. light attraction) of the fish. Research surveys are free by the biases due to the fishing fleet behaviour. The sampling strategy can be better adapted to the fish behaviour and the sampling conditions are under control. The main limitation is that research surveys are generally very expensive. Both data sources were used for the present work.

#### 2.1.1 Commercial catch sampling

The collection of fisheries data from various areas around the lake (Fig. 1) was carried out following standardised procedures (Aro, 1993; Mannini, 1993). Fish were sampled weekly from commercial fish catches from July 1993 to December 1995, but at some sampling sites data collection was continued until July 1996. The commercial gears used targeted the pelagic fish stocks. Thus in the northern sector of the lake (Bujumbura, Uvira and Karonda) samples came from the artisanal liftnet fishery, and in the Kigoma area from both the industrial (purse seine) and artisanal lift net fishery. In the western sector (Kalemie and Moba), catches from the liftnet fishery were sampled. In the south (Kipili and Mpulungu) the beach seine fishery was included for fish collection as this gear efficiently catches small pelagics during some phases of their life cycle. Fish were also sampled from the industrial purse seine fishery and from the minor liftnet and chiromila fisheries. The latter is a fishing method where the net is set in open water and forms approximately a quarter sphere. A lamp boat attracts the fish which are manoeuvred in the encircling net and the footrope is hauled up.

Overall, a total of 3602 fish samples were collected from the commercial catch in the four riparian countries. Total number of samples by species was 1467 for *S. tanganyicae* (589 212 specimens), 1168 for *L. miodon* (208 849 specimens) and 967 for *L. stappersii* (78 727 specimens).

Fish total length (TL, mm) was measured for the purpose of length-frequency (L/F) analysis, and stage of sexual maturity (Aro, 1993) were recorded from length-stratified subsamples throughout the study. From March 1994 to December 1995 individual body weight (W, g), gonad weight (g) and, in case of *L. stappersii*, stomach contents (from March 1994 to June and July 1995 at Kigoma and Mpulungu respectively) were collected from length-stratified subsamples. The stomachs were preserved in 10% formalin and later prey were identified as precisely as possible (Mannini, 1994).

### 2.1.2 Pelagic trawl surveys

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 an unfortunate combination of technical problems, unavailability of scientific staff and especially to the civil unrest in part of the region, survey work was not resumed until November 1997. The interval of one and half years between the 1995-96 and 1997-98 surveys created severe problems and posed obvious limitations on the data comparison and analysis.

The fish and macrozooplankton data collection was carried out as described by Mannini and Aro (1995), and Kurki (1996a). The research vessel (R/V *Tanganyika Explorer*; 26 m, 160 t) 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  $\mu$ m. Fish catch was processed on board. Total catch weight, species composition, fish size (total length,

TL mm) distribution and sexual maturity stage were measured. A five-stage sexual maturity scale, as described by Aro (1993), was used. Stomach contents of the centropomid predator *L. stappersii* were preserved in 10% formalin for later dietary analysis. Extra sampling work was also carried out for specific research aims (e.g. otolith sampling, clupeid stomach contents, tissue samples for genetic analysis). Gulf-net samples were preserved in 4% formaldehyde for later analysis ashore.

Trawl stations were allocated following the acoustic survey design. Normally two to three trawl hauls were carried out along the acoustic transect across the lake. The survey design consisted of zig-zag tracks from the East Coast to the West Coast or vice-versa. The transects were generally confined to water depths exceeding 100 m, for safety reasons, particularly because of the uncertainty on bottom depth profile from the available bathymetric chart. 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 ( $1.8 \text{ m s}^{-1}$ ). 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. Therefore, fish abundance results are relative to the fished layer of water. Trawl catches were standardised to numbers and weight caught per 60 min hauling. Position of trawl and Gulf-net sampling stations was taken from a Global Positioning System (GPS) navigational unit. The position of the trawl stations used for this work is given in Appendix 1. The results of the acoustic surveys (i.e. fish biomass estimates) were not available at the time of the preparation of this work.

Crustacean zooplankton and fish larvae were sampled by towing a Gulf V high speed plankton net within the 0-100 m depth range at a speed of about 3.3 knots for 33 min. In June 1995, a Gulf-net tow within the 0-100 m depth range was carried out first, followed by the trawling. During the other surveys, Gulf-net tows were done in the evening along the acoustic transects but independently from the trawl. Gulf-net samples were analysed as described in Bosma *et al.*, (1998). Samples were preserved in 4% formaldehyde. Subsampling of macrozooplankton was done by using a Folsom splitter. Each sample was split until a subsample of approximately 300 specimens was obtained. All specimens of a subsample were identified and counted.



## 2.2 Data analysis

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

- 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.

For the analysis of survey data, 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. Bottom depth was detected by echosounder readings.

Fish growth can typically be described by the von Bertalanffy function. Von Bertalanffy Growth Function (VBGF) coefficients (von Bertalanffy, 1938) were estimated for *S. tanganyicae*, *L. miodon* and *L. stappersii* from the main study areas. For growth in length the function takes the form

$$L_t = L_\infty (1 - e^{-K(t-t_0)})$$

where  $L_t$  is the predicted mean length of the fish of a given population (or stock) at age  $t$ ,  $L_\infty$  is the mean asymptotic length, i.e. the length the fish would reach at an infinitely high age,  $K$  is a parameter of dimension  $\text{time}^{-1}$  expressing the rate at which asymptotic length is approached,  $t_0$  is the theoretical age the fish would have at length zero had they always grown as described by the VBGF. In the present work  $t_0 = 0$  was used.

The Electronic Length Frequency Analysis, ELEFAN I, (Pauly and David, 1981; Pauly, 1987) and Shepherd Length Composition Analysis, SLCA, (Shepherd, 1987) were used to estimate the coefficients. To verify the gross accuracy of growth parameters, the growth performance index,  $\phi'$ ,  $\phi'$ , (Pauly and Munro, 1984) was calculated.

$$\phi' = \log_{10} K + 2 \log_{10} L_\infty$$

Not all data sets were used to estimate VBGF coefficients. Some were discarded because they were unsuitable for length-based analysis (i.e. lack of evidence of modal class progression). Modes from survey length frequency distributions were identified through the Bhattacharaya's method (1967). When necessary length was converted to relative age using the inverse von Bertalanffy growth equation (Sparre and Venema, 1992).

$$t(L) = t_0 - 1/K \cdot \ln(1 - L/L_\infty)$$

In fisheries science, mortality is usually expressed as instantaneous rate:

$$N_0 = N_t \cdot e^{(-Z \cdot \Delta t)}$$

where  $N_0$  and  $N_t$  are successive numbers present in a population, affected by a total mortality rate  $Z$  during a time interval  $\Delta t$ . Total mortality,  $Z$ , is the coefficient of proportionality accounting for the total number of deaths. The coefficients of proportionality for deaths due to fishing mortality,  $F$ , and due to natural mortality,  $M$ , can be added so that:

$$Z = F + M$$

The fraction of deaths caused by fishing,  $F/Z$ , is called the exploitation rate,  $E$ .

Annual total mortality rates ( $Z \text{ yr}^{-1}$ ) and natural mortality ( $M \text{ yr}^{-1}$ ) rates were estimated using different methods. Although modelling natural mortality for the whole lifespan with a single function is an oversimplification of the true situation, there is not yet valid alternative to empirical modelling (Caddy, 1991). The following models were used

Pauly's equation (Pauly, 1980)

$$\ln M = -0.0152 - 0.279 \cdot \ln L_{\infty} + 0.6543 \cdot \ln K + 0.463 \cdot \ln T$$

where  $L_{\infty}$  and  $K$  are VBGF parameters and  $T$  is the average annual water temperature at the surface in degrees centigrade. Temperature ( $T = 25.5^{\circ}$ ) was obtained from weekly measurements made between July 1993 and July 1995 at Bujumbura, Kigoma and Mpulungu (Craig, 1997). The  $M$  values from this equation were reduced by 20% for both clupeid species following the suggestion of Pauly in the case of small schooling pelagics (Pauly, 1983a).

Rikhter and Efanov's method (Rikhter and Efanov, 1976)

$$M = 1.521 / (T_m^{0.720}) - 0.155$$

where  $T_m$  is the mean age at first maturity.

Gunderson and Dygert method (Gunderson and Dygert, 1988)

$$M = 0.07 + (1.06 \cdot K^{-yr}).$$

Alagaraja method for M corresponding to a 1% survival (Alagaraja, 1984)

$$M = -\ln(0.01) / T_m.$$

In addition to the estimation of a constant natural mortality,  $M$  values for different life stages were calculated using the size-dependent equation for  $M$  developed by Peterson and Wroblewski (1984). The model is based on the information from size spectra of suspended particles in the sea where  $M$  for a given size is predicted to be a power function of the mean weight. Peterson and Wroblewski derived the relationship:

$$M_w \propto W^{-c}$$

where  $M_w$  is the instantaneous rate of natural mortality and  $W$  is the weight. The constant of proportionality depends upon a number of metabolic parameters, and the exponent  $c$  is equal to the exponent in the allometric relationship between growth and metabolic rate. Estimates of these parameters for pelagic fish lead to the equation:

$$M_w = 192 \cdot W^{-0.25}$$

where the time scale is per year and weight is measured in grams.

Annual total mortality rates were estimated using three methods. The length converted catch curve (LCCC) analysis (Pauly, 1983a, 1983b, 1984a and 1984b) was considered as the reference having become one of the standard methods of estimating mortality (Gulland and Rosemberg, 1992). The function takes the form:

$$\ln(N_i / \Delta t_i) = a + b \cdot t_i$$

where  $N$  is the number of fish in length class  $i$ ,  $\Delta t$  is the time needed for the fish to grow

through length class  $i$ ,  $t$  is the relative age (when  $t_0 = 0$ ) corresponding to the mid-length of class  $i$ ,  $a$  and  $b$  are the regression intercept and slope respectively, and  $-b$  is an estimate of  $Z$ .

One of the most important assumptions to estimate  $Z$  is that the sample should, as far as possible, be representative of the stock. Therefore, for each species LCCC was carried out from fish collected during the lake-wide combined hydroacoustic and mid-water trawling surveys of June and November-December 1995.

Beverton and Holt model (Beverton and Holt, 1956)

$$Z = K \cdot \frac{L_{\infty} - \bar{L}_c}{L_c - L_c}$$

where  $L_c$  is the mean length of fish at first capture (i.e. length at which 50% of the fish will be vulnerable to the gear) and  $\bar{L}_c$  is the mean length computed from  $L_c$  upward.

Ault and Ehrhardt method (Ault and Ehrhardt, 1991; Ehrhardt and Ault, 1992).

$$\left( \frac{L_{\infty} - L_{\max}}{L - L'} \right)^{Z/K} = \left( \frac{A(L')}{A(L_{\max})} \right)$$

where

$$A(L') = Z(L' + \bar{L}) + K(L_{\infty} - \bar{L})$$

and

$$A(L_{\max}) = Z(L_{\max} - \bar{L}) + K(L_{\infty} - \bar{L})$$

where  $\bar{L}$  is the mean length of fish,  $L_{\max}$  is the maximum length reached by the fish of a given stock, and  $L'$  is the length for which all fish of that length and longer are under full exploitation.

The gonado-somatic index (GSI = gonad weight/total body weight x 100) was calculated to determine the seasonal pattern of gonad development. Mean length at sexual maturity

was estimated by fitting a logistic curve to the adjusted proportion ( $P$ ) of sexually mature individuals by linear regression (King, 1995). The logistic curve took the form:

$$P = \frac{1}{(1 + \exp(b(L - L_m))}$$

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

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

$$L_m = L_\infty \left( \frac{1}{1 + \frac{M}{3K}} \right)$$

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

Only the feeding of *L. stappersii* was investigated while information on the diet of both clupeid species was obtained from the available literature cited in the text. Prey composition of the diet of *L. stappersii* was determined from stomach contents. Prey taxa were identified as precisely as their condition would allow and their importance expressed in terms of their % frequency occurrence (F) and % diet by number ( $C_n$ ) and weight ( $D_n$ ) (Hylsop, 1980):

$$F = 100N_i N_s^{-1}$$

where  $N_i$  is the number of stomachs containing prey type  $i$  and  $N_s$  is the number of stomachs examined which contained food.

$$C_n = 100 \sum N_{ni} \left( \sum N_p \right)^{-1}$$

where  $\sum N_{ni}$  is the total number of individuals of prey  $i$  and  $\sum N_p$  is the total number of prey items in all stomachs.

$$D_n = 100 \sum W_{ni} \left( \sum W_p \right)^{-1}$$

where  $\sum W_{ni}$  is the total weight of prey  $i$  and  $\sum W_p$  is the total weight of prey items in all stomachs.

When prey identification at species level was not possible the following categories were used: "Clupeids" for unidentified clupeid fish, "Shrimps" for both *L. parvula* and *P. moorei*, "Others" for other fish species than clupeids.

Changes in fish yield for different values of  $F$  (or exploitation rate,  $E = F/Z$ ) were modelled using the relative yield per recruit ( $Y/R$ ) model of Beverton and Holt (1964, 1966; Sparre and Venema, 1992) defined by:

$$Y/R = E(1-c)^{M/K} \left\{ 1 - \frac{3(1-c)}{1 + \frac{(1-E)}{(M/K)}} + \frac{3(1-c)^2}{1 + \frac{2(1-E)}{(M/K)}} - \frac{(1-c)^3}{1 + \frac{3(1-E)}{(M/K)}} \right\}$$

where  $c = L_c/L_\infty$ , and  $E = F/Z$

Relative biomass per recruit ( $B'/R$ ) is computed from the relationship:

$$B'/R = (Y'/R) / F.$$

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:

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

where:

$D_j$  is the interpolated value at the point  $j$ ;

$D_i$  is the measured value at the data point  $i$ ;

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

The search radii were 20 and 15 n mile for the trawl and Gulf-net respectively.

The terms “larva”, “juvenile” ( $TL < L_m$ ) and “adult” ( $TL \geq L_m$ ) used for the fish are according to Blaxter (1988). For *L. stappersii* only “juveniles” was used to indicate fish  $\leq 100$  mm TL.

The following statistical tests were used and are indicated in the text: One-way ANOVA, Kruskal-Wallis ANOVA, Mann-Whitney U-test, Chi-square ( $\chi^2$ ) test, Kolmogorov-Smirnov two-sample test, Cross-correlation and Pearson correlation (Sokal and Rohlf, 1981; Box and Jenkins, 1976; Kinnear and Gray, 1997).





### 3. RESULTS

Results from commercial catch sampling (fishery dependent data) are given by species and by sampled areas, and are followed by results on fish distribution from survey sampling. Functional relationships between total length (TL), standard length (SL), fork length (FL) and weight (W), needed for the study, are given in Table 1.

#### 3.1 *Stolothrissa tanganicae*

##### 3.1.1 Commercial catch composition

Only the liftnet fishery exploited the *S. tanganicae* stock in northern areas of the lake, but the catch composition differed between the northern end (Bujumbura and Uvira) and Karonda. In the former area immature fish made a greater contribution to the catch. Further south, in the Kigoma sub-basin, *S. tanganicae* was the main target of liftnets, but the juveniles were better represented in the purse seine catches (Fig. 6). As the mesh size of liftnets and purse seines was similar (stretched mesh of 8-10mm and 10mm respectively), the appearance of juveniles in the purse seine fishery was probably due to the operation of the purse seiners in offshore nursery areas, outside the usual range of the liftnet fishery which was within 5 km of Kigoma port.

In the south of the lake, the youngest *S. tanganicae* were caught by beach seines but not by purse seines (Fig. 6). However, comparison with the catch composition of other areas is difficult because of the use of unselective beach seine nets (mosquito netting is used to cover the codend) in the Mpulungu area. Currently *S. tanganicae* is not the main exploited species in the south but a supplementary species since its presence in the catches was scarce and sporadic (Pearce, 1995; Plisnier, 1995).

The proportion of *S. tanganicae* in the liftnet sampled catch from Kipili waters was lower than that of *L. miodon* (22% of the total number for both species), and it was negligible (0.9%) in the Mpulungu liftnet catch. The numeric abundance of

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

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

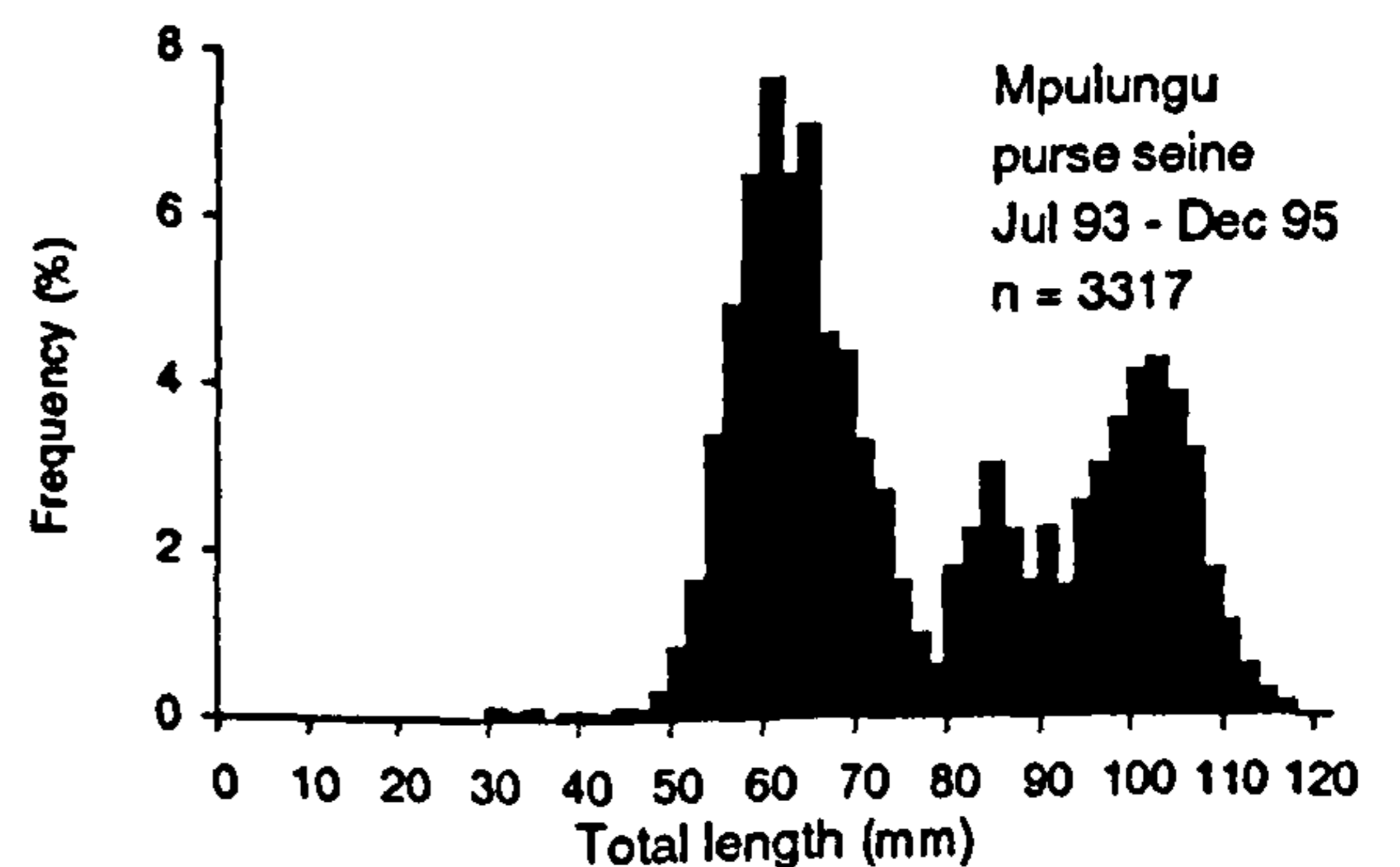
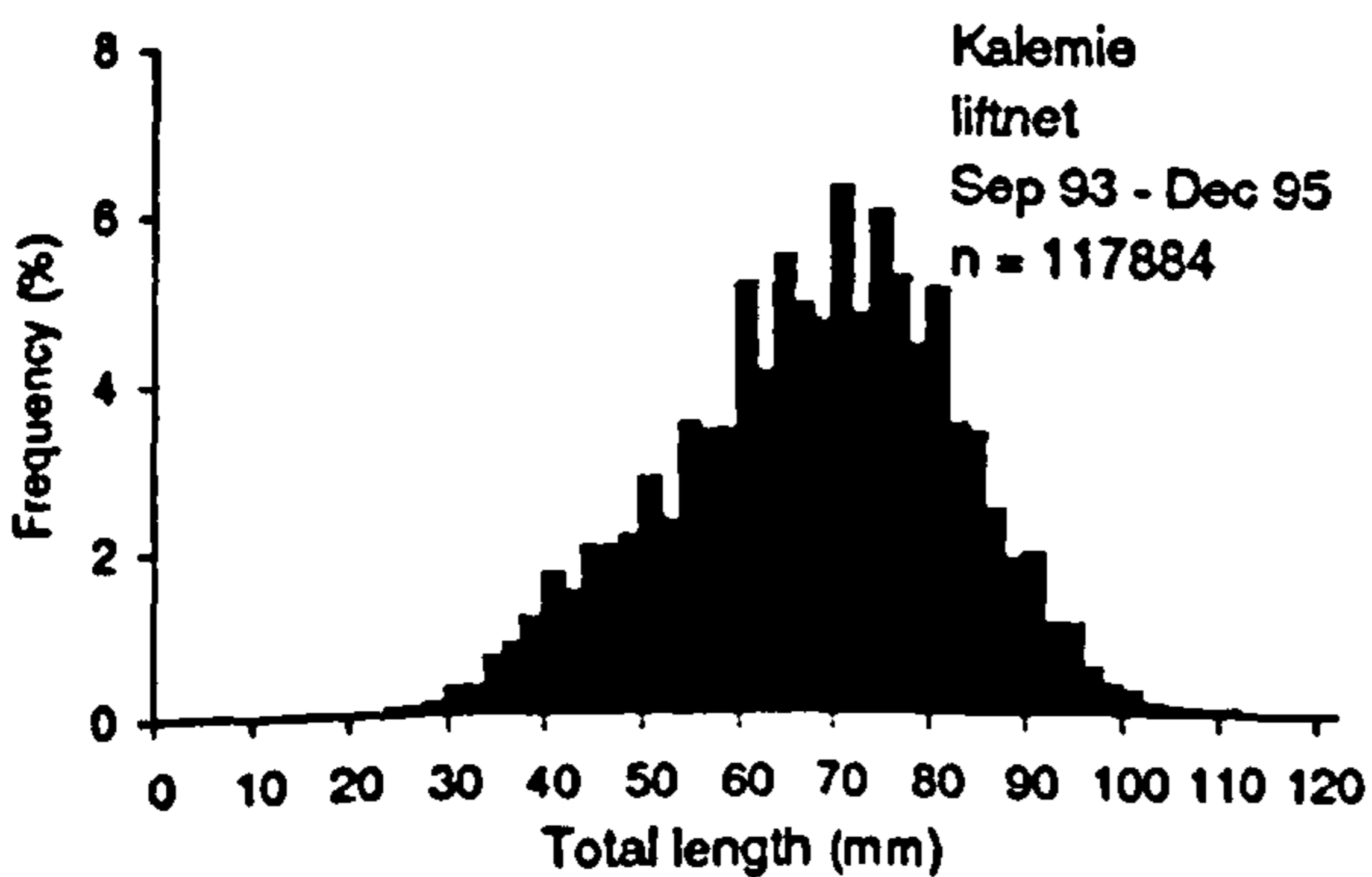
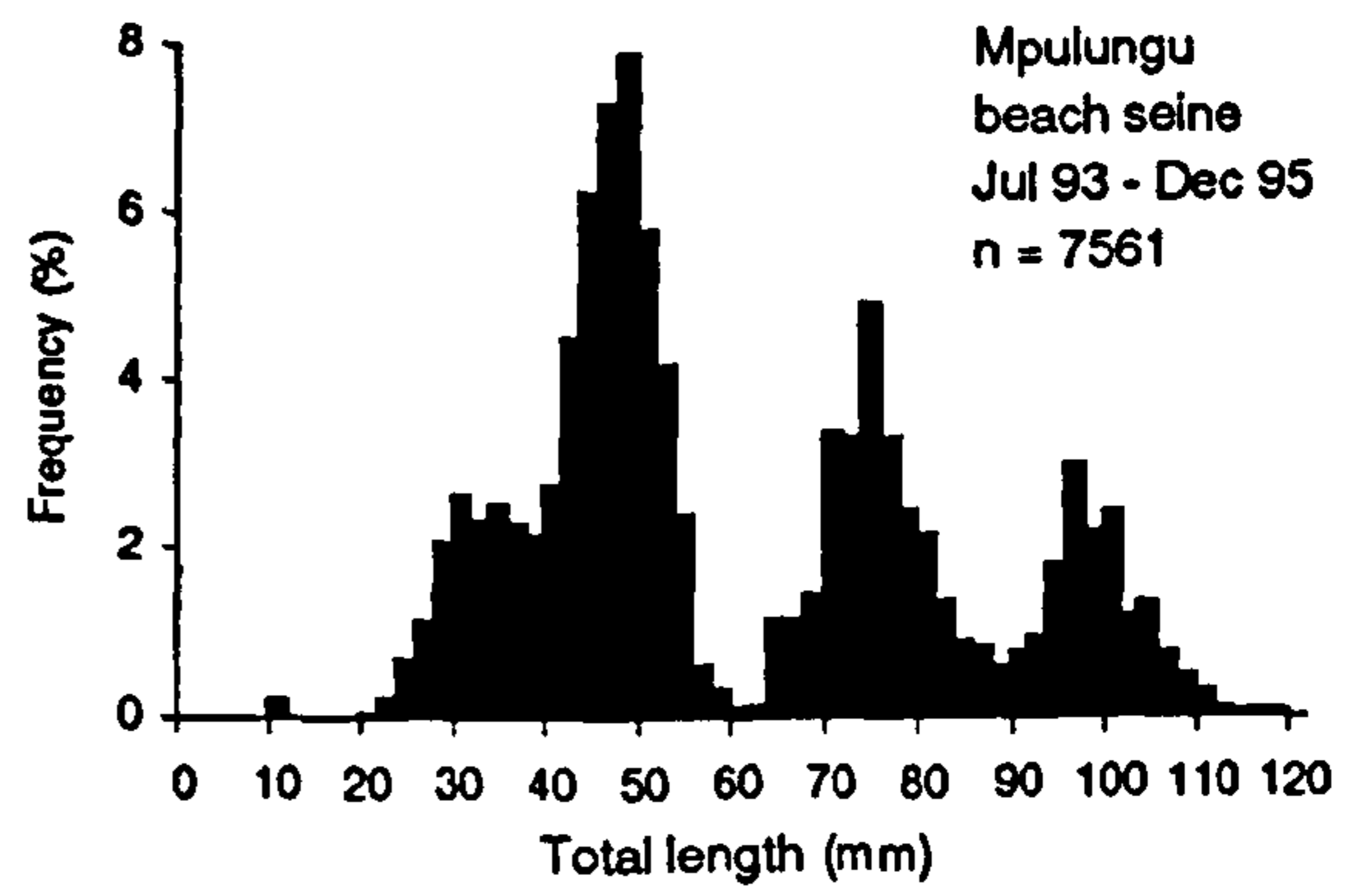
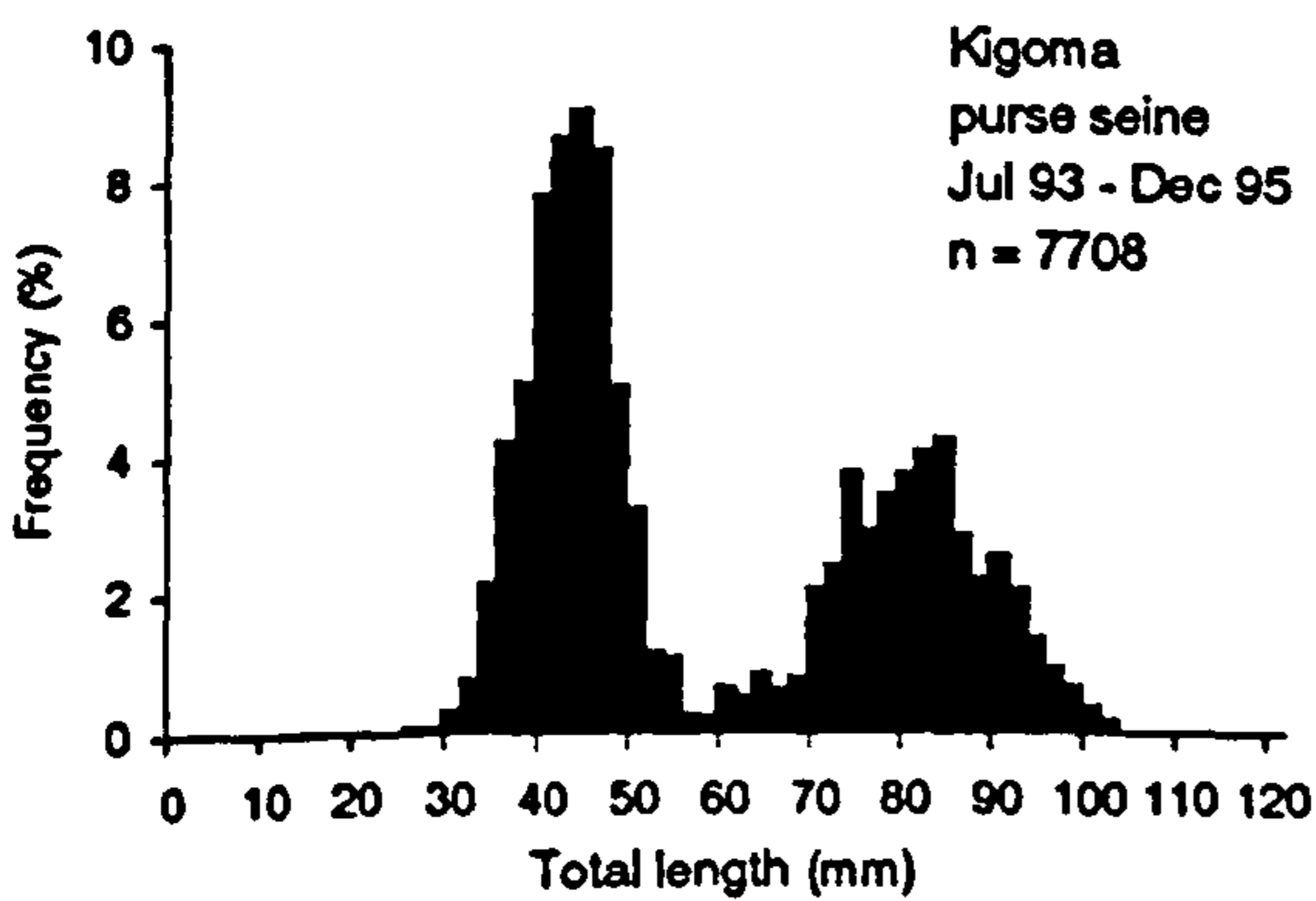
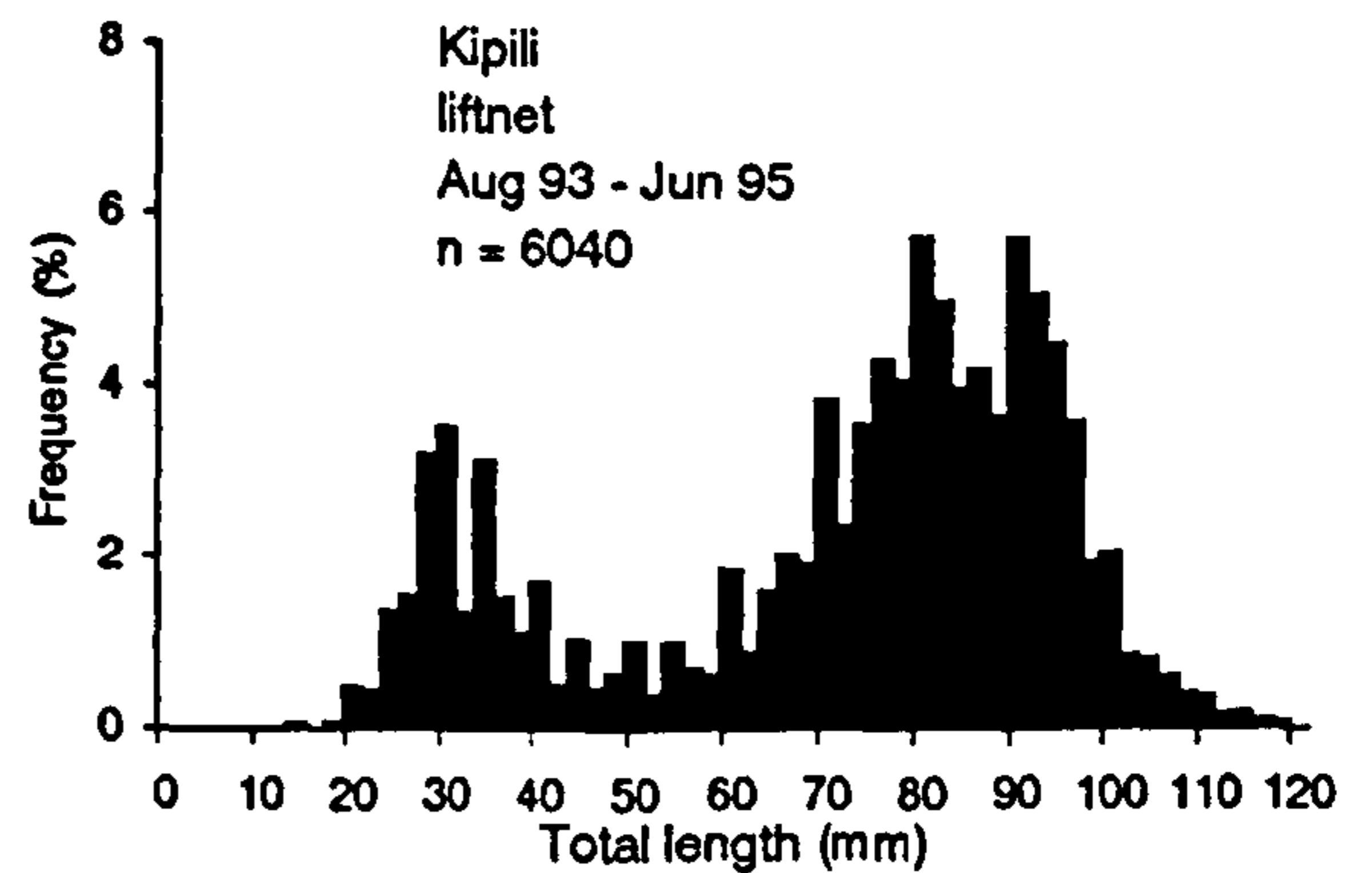
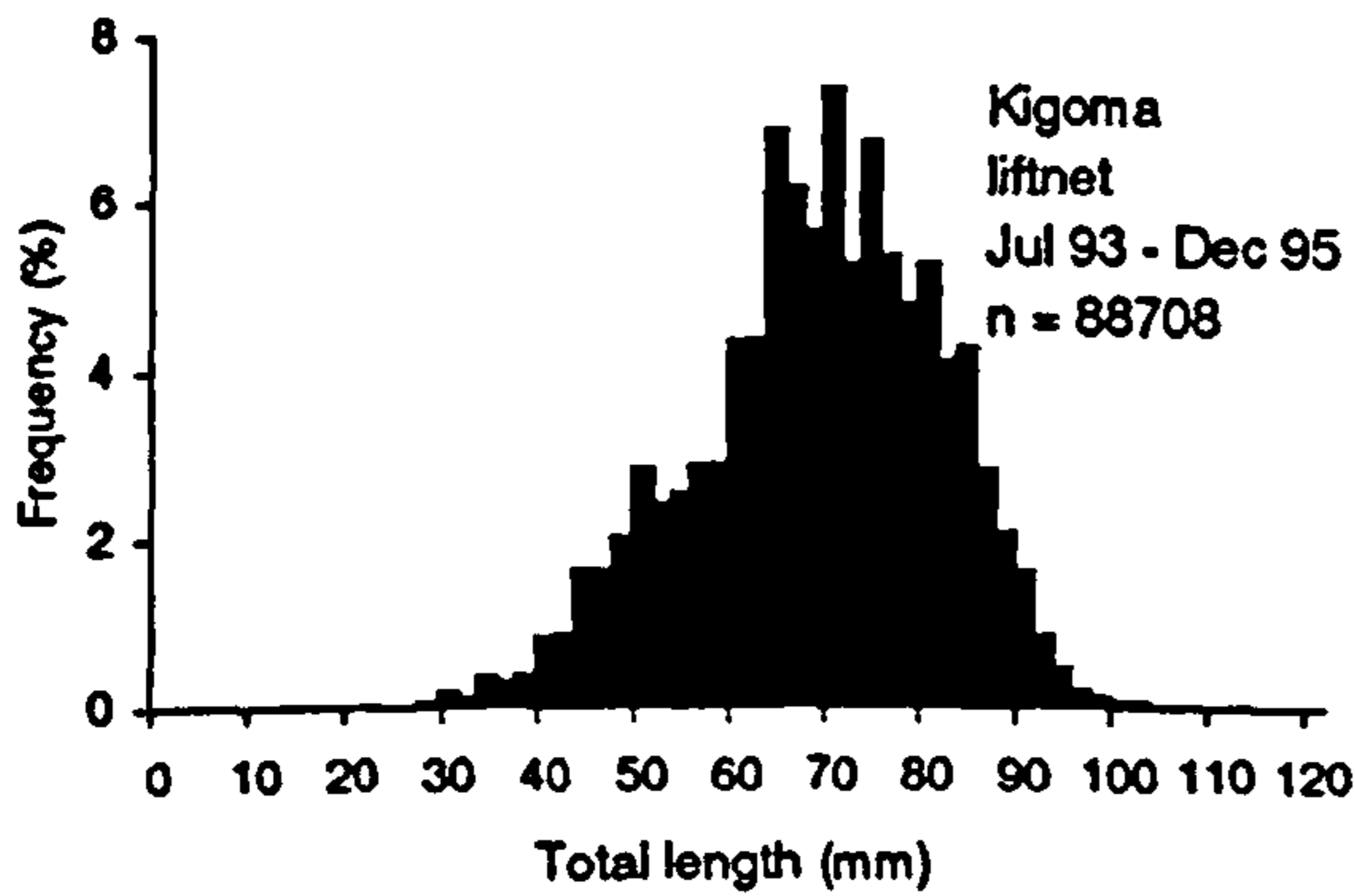
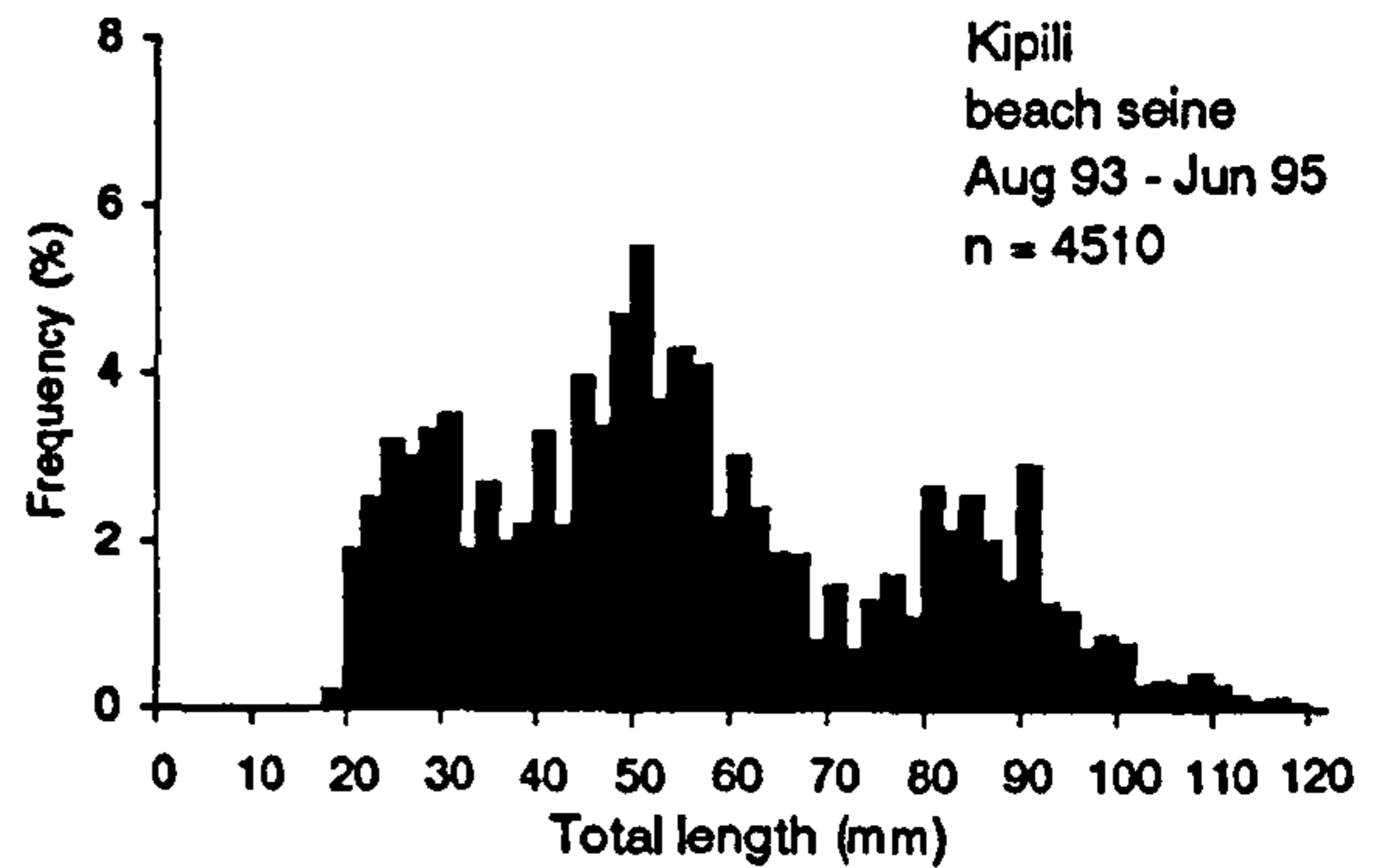
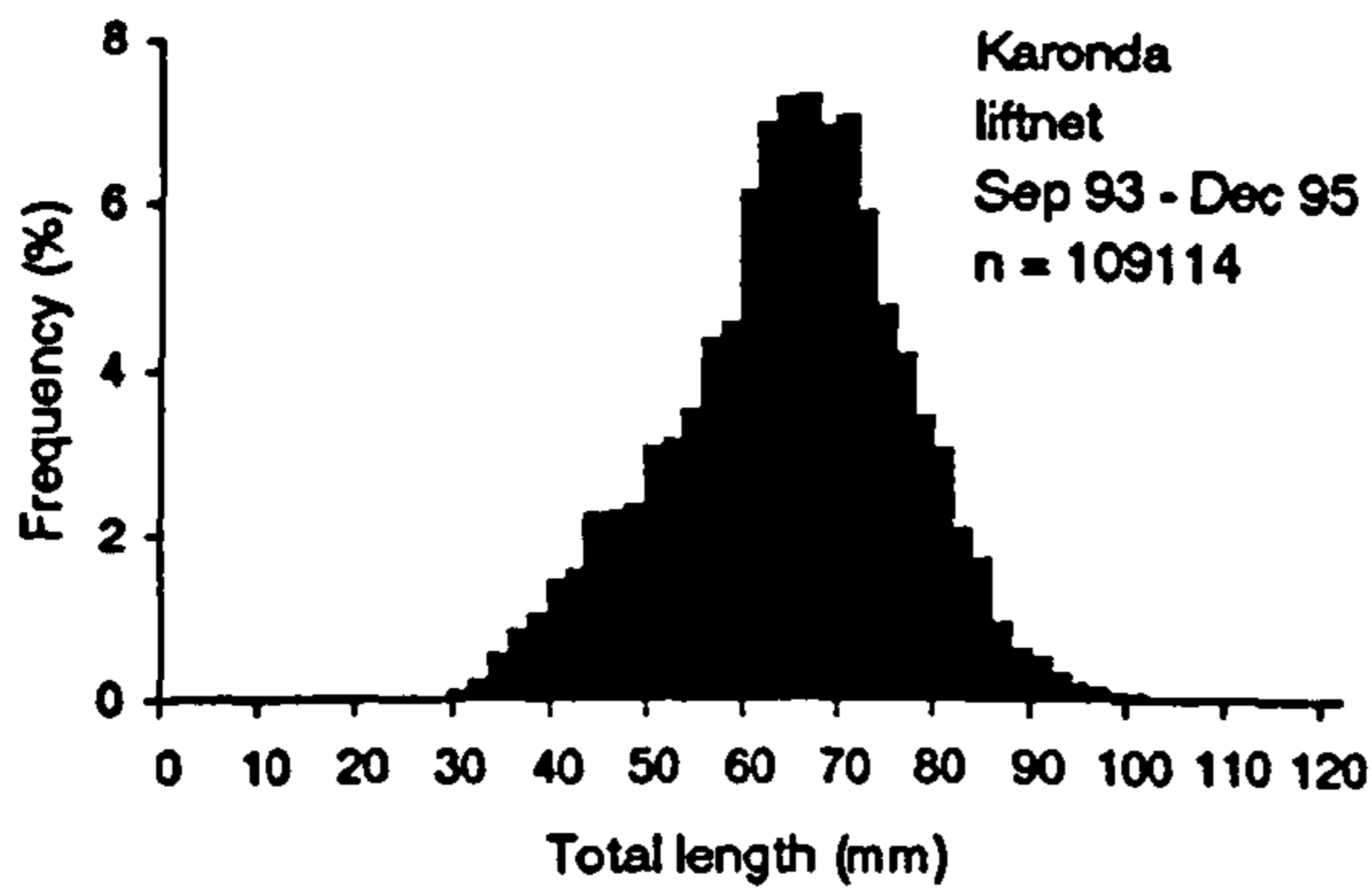
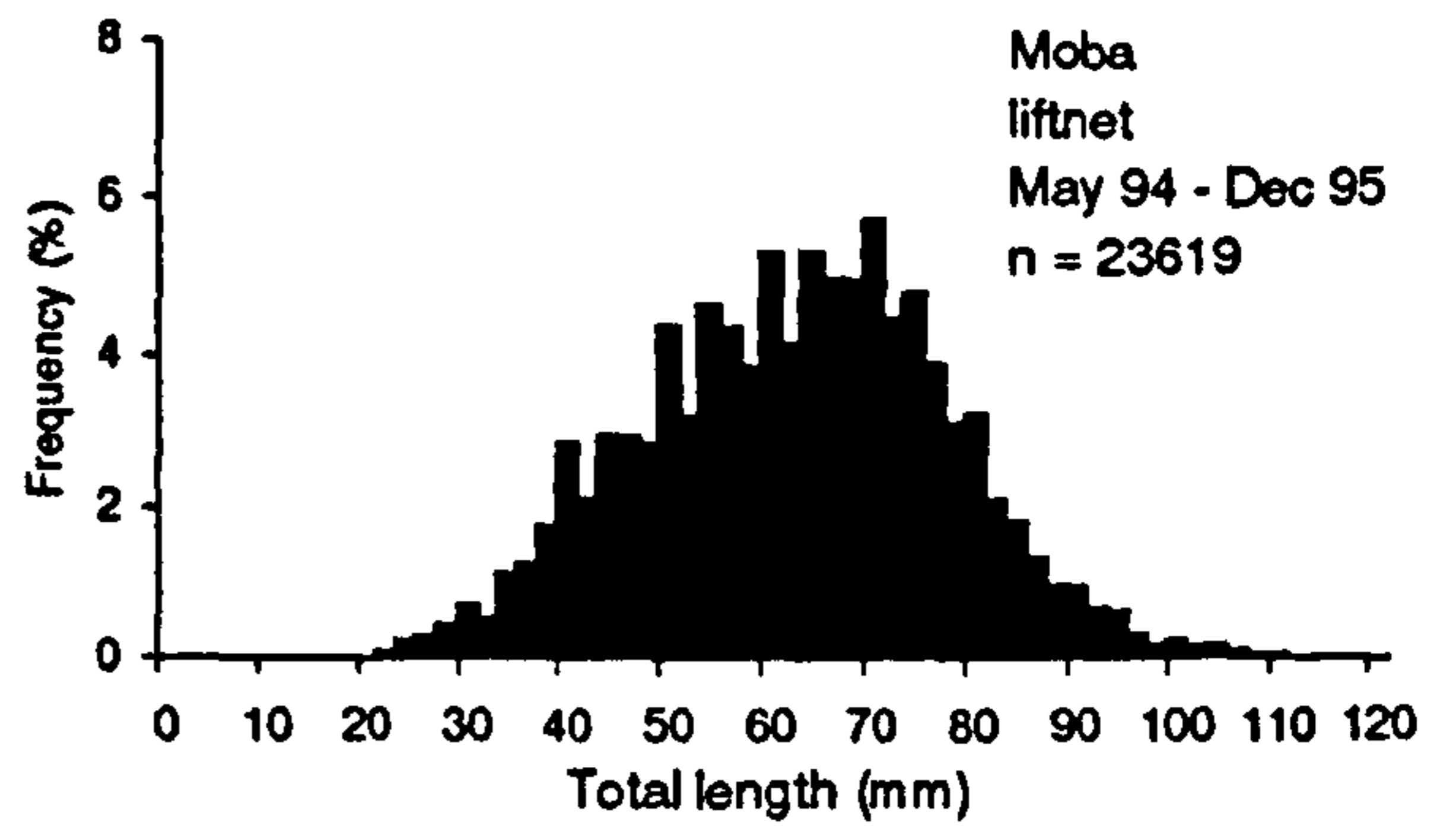
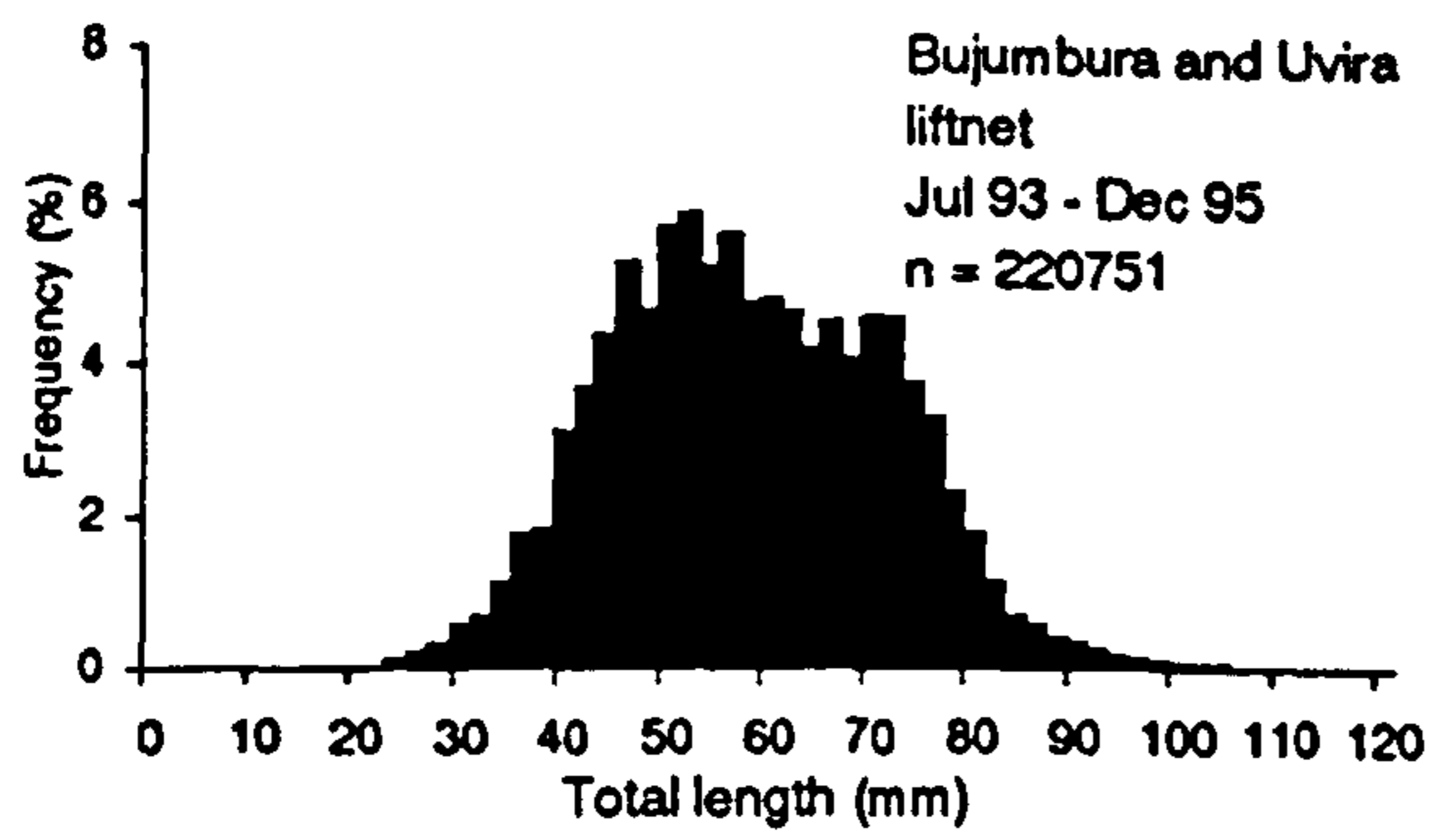


Figure 6. Length composition of the commercial catch of *S. tanganyicae* by area and fishing gear.

*S. tanganyicae* in the beach seine catch was 28% of the total for both clupeid species at Kipili and only 11% at Mpulungu.

### 3.1.2 Gear selectivity

A critical length,  $L_c$ , of 56 mm was estimated for liftnets from covered codend experiments in Kigoma waters, (Fig. 7). The liftnet gear used on Lake Tanganyika is similar (construction scheme, net mesh size and fishing operation) throughout the lake and therefore the selection ogive can reasonably be regarded as typical for *S. tanganyicae* (it might be smaller at the northern end where the size composition of the catch was skewed toward small length classes, see Bujumbura and Uvira L/F distribution in Fig. 6).

Critical length,  $L_c$ , estimates made from the catch curve of the various L/F distributions are given in Table 2. The resulting mean length at first capture for all areas was the same as that obtained from the selectivity experiments.

### 3.1.3 Growth and mortality

Growth coefficients of *S. tanganyicae* estimated from data sets from all around the lake were similar (coefficient of variation, CV, of mean phi' was 0.97) except for those from Mpulungu data (Table 2). The asymptotic length and the rate of growth to this length ( $L_\infty$  and  $K$  coefficients of the VBGF) ranged between 104 and 114 mm and 1.80 and 2.00 yr<sup>-1</sup> respectively. Overall, the growth of *S. tanganyicae*, during the study period, was the same throughout the lake. Longevity was estimated at 1.5 yr.

Total and natural mortality rates derived by different methods are given in Table 2. Mean estimates of  $Z$  ranged from 4.97 to 5.83 yr<sup>-1</sup> depending on the method used. Total mortality was also estimated by catch curve analysis of cruise survey data and a  $Z$  value of 4.56 yr<sup>-1</sup> was obtained ( $r = 0.99$ ; 95% CI = 4.22-4.90; first length included

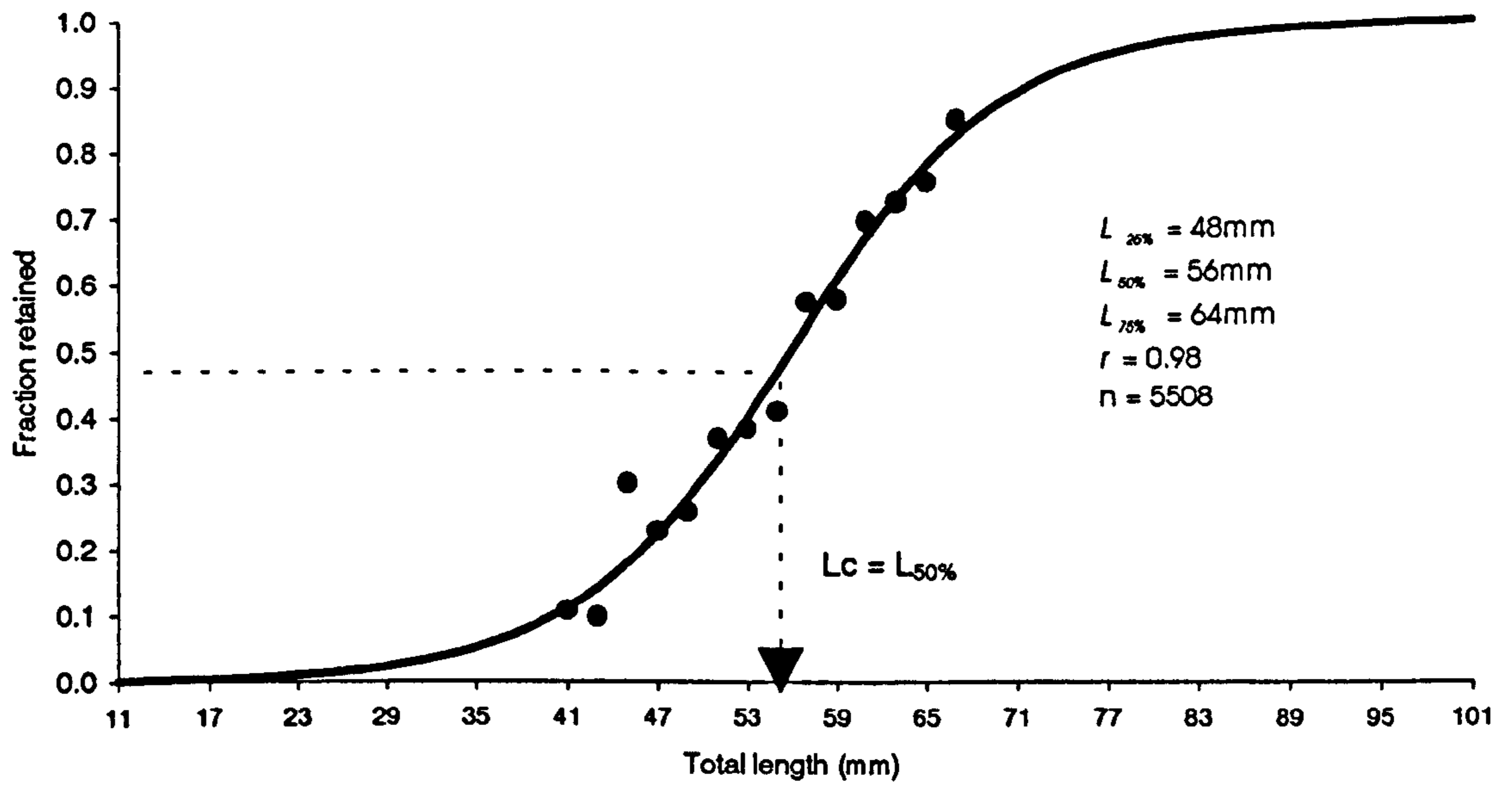


Figure 7. The gear selection ogive for *S. tanganyicae* caught in Kigoma waters by a liftnet with a codend mesh size of 10 mm. The critical length ( $L_c$ ) is shown by the dotted line,  $n$  is the total sample size. Values for  $L_{25\%}$  and  $L_{75\%}$  (selection range) were also given.

Table 2. Von Bertalanffy growth model coefficients ( $L_{\infty}$  and  $K$  from the Elefan I method), total ( $Z$ ) and natural ( $M$ ) mortality estimates for *S. tanganyicae* from various areas. Roman numerals indicate the methods used. I: length-converted catch curve (95% CI and cutoff length,  $L'$ , in brackets); II: Beverton and Holt, 1956; III: Ault and Ehrhardt, 1991; IV: Pauly, 1980; V: Rikhter and Efanov, 1976; VI: Gunderson and Dygert, 1988; VII: Alagaraya, 1984. Exploitation rates ( $E$ ) are estimated from catch curve's  $Z$  and Pauly's  $M$ . Mean length at first capture,  $L_c$ , based on the method of Pauly (1987), except the Kigoma estimate which was obtained from gear selectivity experiments (see text and Figure 7). Whole lake area refers to  $Z$  estimate obtained from survey data and using the mean  $L_{\infty}$  and  $K$  estimated from commercial catch data as input parameters.

Area	$L_{\infty}$ TL (mm)	$K$ yr <sup>-1</sup>	$\Phi$	$Z$ yr <sup>-1</sup> I	$Z$ yr <sup>-1</sup> II	$Z$ yr <sup>-1</sup> III	$M$ yr <sup>-1</sup> IV	$M$ yr <sup>-1</sup> V	$M$ yr <sup>-1</sup> VI	$M$ yr <sup>-1</sup> VII	$E$ ( $E = F/Z$ )	$L_c$ (TL) mm
Uvira	104	1.85	4.301	4.39 (3.54-5.23; 55mm)	4.50	4.49	2.7	1.5	2.0	2.8	0.37	50
Bujumbura	105	1.89	4.319	6.10 (5.29-6.91; 60mm)	6.93	6.92	2.8	1.6	2.1	2.0	0.54	57
Karonda	112	1.77	4.339	4.79 (2.46-7.12; 72mm)	8.68	8.67	2.6	1.9	1.9	2.9	0.45	46
Kigoma	105	1.84	4.306	5.16 (3.32-7.00; 70mm)	5.25	5.24	2.7	1.7	2.0	2.7	0.47	56
Kalemie	108	1.80	4.322	5.05 (4.57-5.52; 68mm)	5.60	5.59	2.7	2.0	2.0	2.8	0.47	64
Mpulungu	114	2.00	4.415	4.33 (3.94-4.71; 98mm)	4.00	3.70	2.8	2.2	2.0	3.1	0.35	63
Mean	108	1.86	4.334	4.97	5.83	5.77	2.7	1.8	2.0	2.7	0.44	56
Whole lake				4.56 (4.22-4.90; 70mm)								

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

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

in the regression,  $L'$ , i.e. size at which fish are fully vulnerable to the fishing gear, = 70 mm). The values derived give a broad range for the estimate of  $Z$  (Table 2). However, a  $Z$  value for *S. tanganyicae* between 4 to 5 yr<sup>-1</sup> is probably appropriate for fish fully recruited to the fishery. This would also be substantiated by the fishery-independent  $Z$  estimate of 4.56 obtained through survey data. A total mortality rate of this order would imply that 99% of a cohort will die within one year.

As with  $Z$  rates,  $M$  rates were estimated by different methods (Table 2). Mean values for the whole lake ranged from 1.8 to 2.7 yr<sup>-1</sup>. The overall mean of 2.3 yr<sup>-1</sup> was probably representative of natural mortality for *S. tanganyicae* throughout the lake.

Size dependent natural mortality rate estimates (Peterson and Wroblewski, 1984) and relative population number at age are given in Figure 8a and 8b. The overall mean  $M$  value from all sizes was 3.7 yr<sup>-1</sup> and that of adults was 1.9 yr<sup>-1</sup>.

Due to the uncertainty in mortality estimates of both  $Z$  and  $M$  and of the consequent fishing mortality,  $F$  (where  $F = Z - M$ ), the exploitation rates,  $E$ , were considered tentative. They ranged from 0.35 to 0.47 resulting in a mean rate of 0.44 and did not indicate any apparent overexploitation of the stocks.

#### 3.1.4 Reproduction

During the year, the gonado-somatic index, GSI, of *S. tanganyicae* increased at intervals of 3-4 months (Fig. 9) for females from Bujumbura and Kigoma and males from Kigoma. There were insufficient numbers of males from Bujumbura and of either sex from Mpulungu for analysis.

During the 21-month period of the study (March 1994 - December 1995), no major differences were found in the *S. tanganyicae* GSI pattern between the northern and Kigoma areas. At Bujumbura GSI of females increased in April, July and November. At Kigoma both sexes showed increased values at about March, May-June and

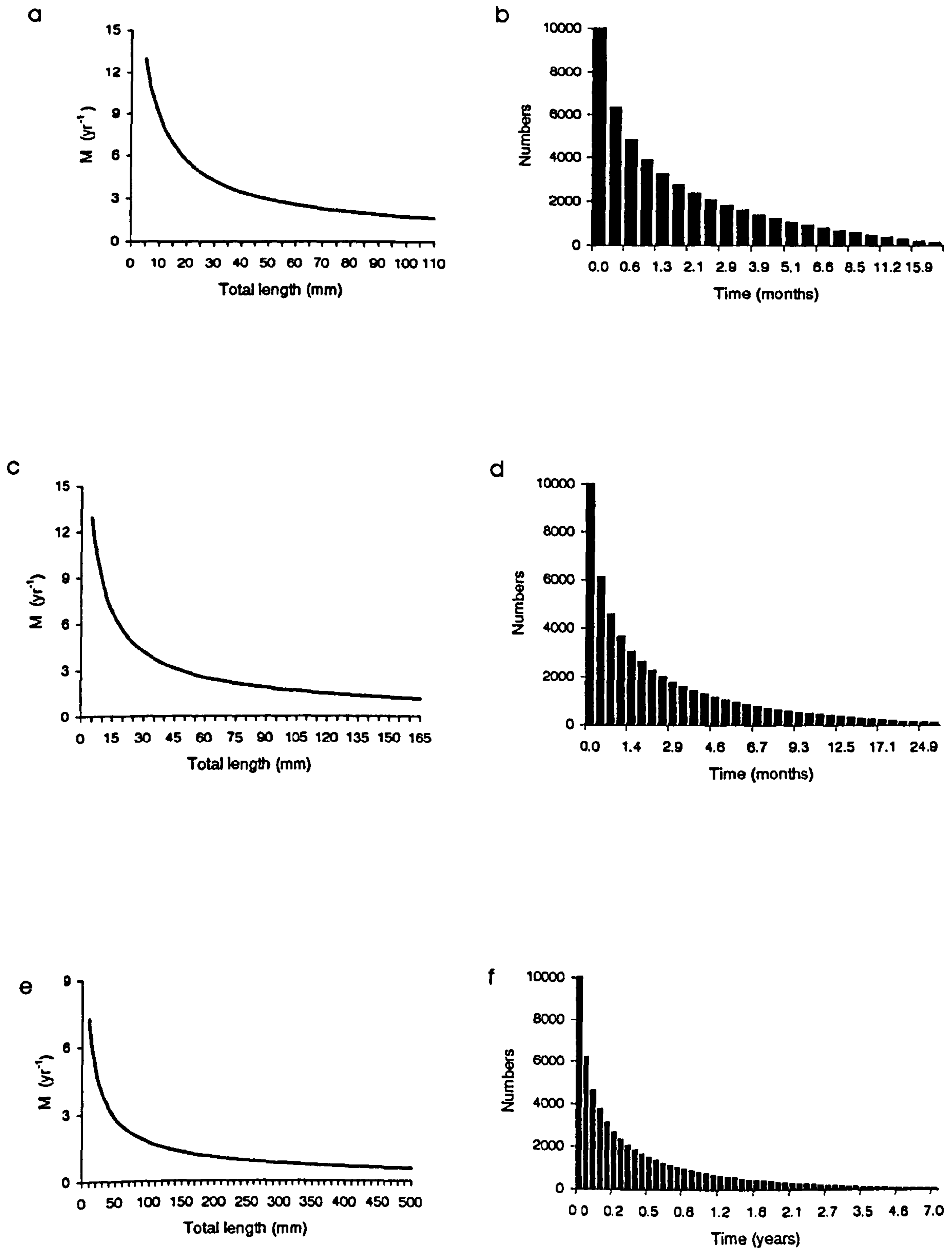


Figure 8. Mortality rate at size (a, c, e) and relative population numbers at age (b, d, f) assuming size-dependent mortality for *S. tanganycae* (a, b), *L. miodon* (c, d) and *L. stappersii* (e, f). Mean VBGF coefficients of each species have been used.



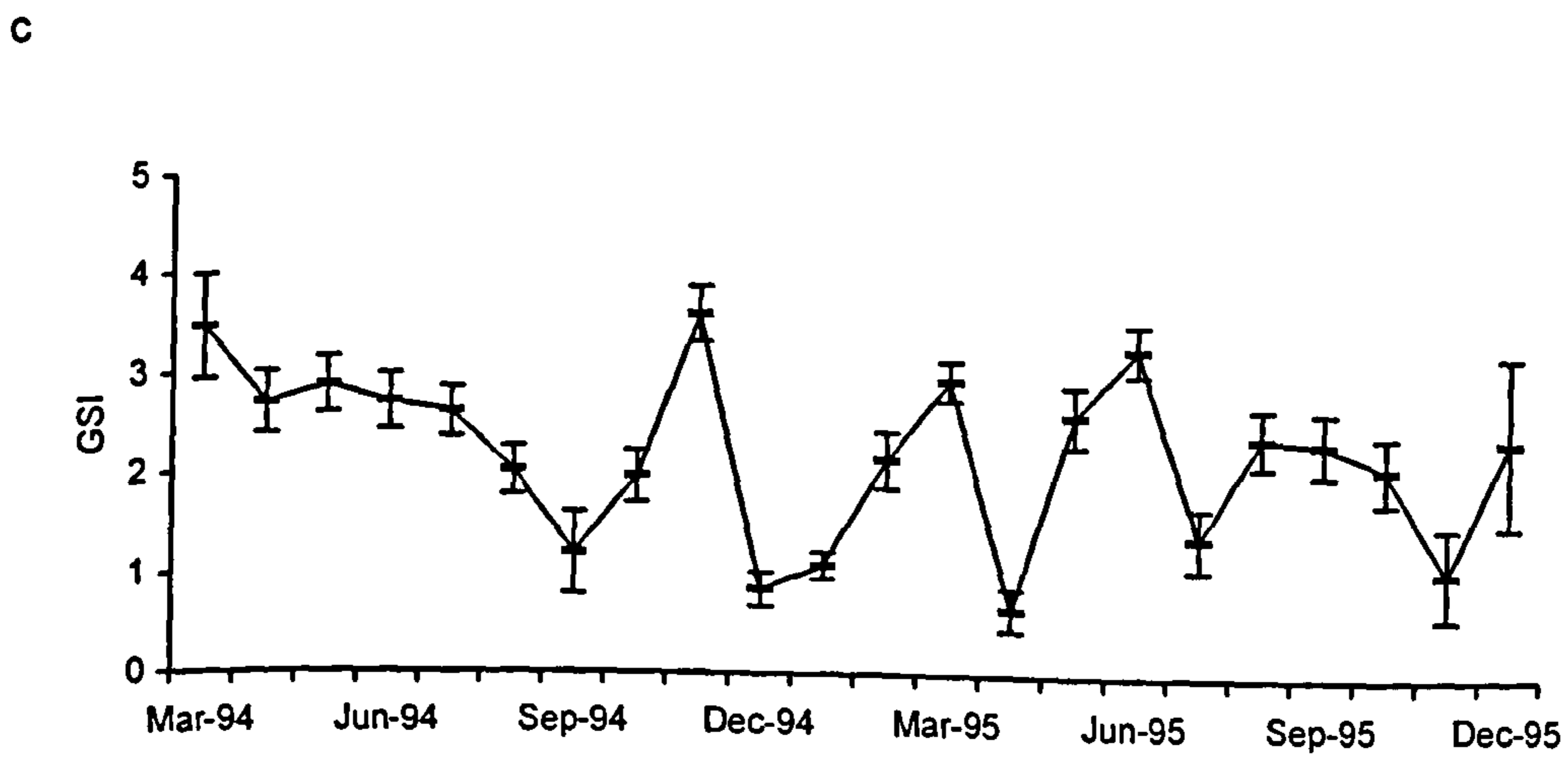
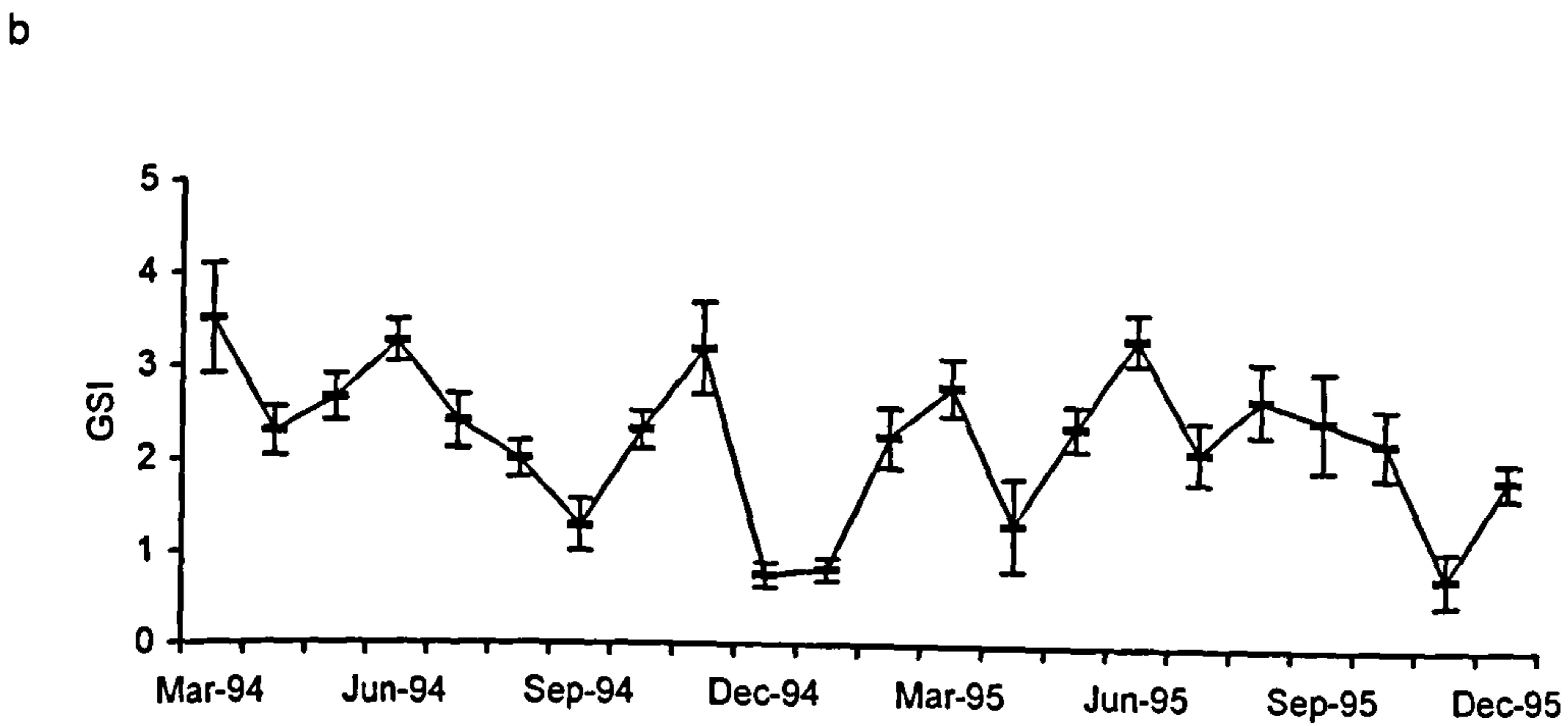
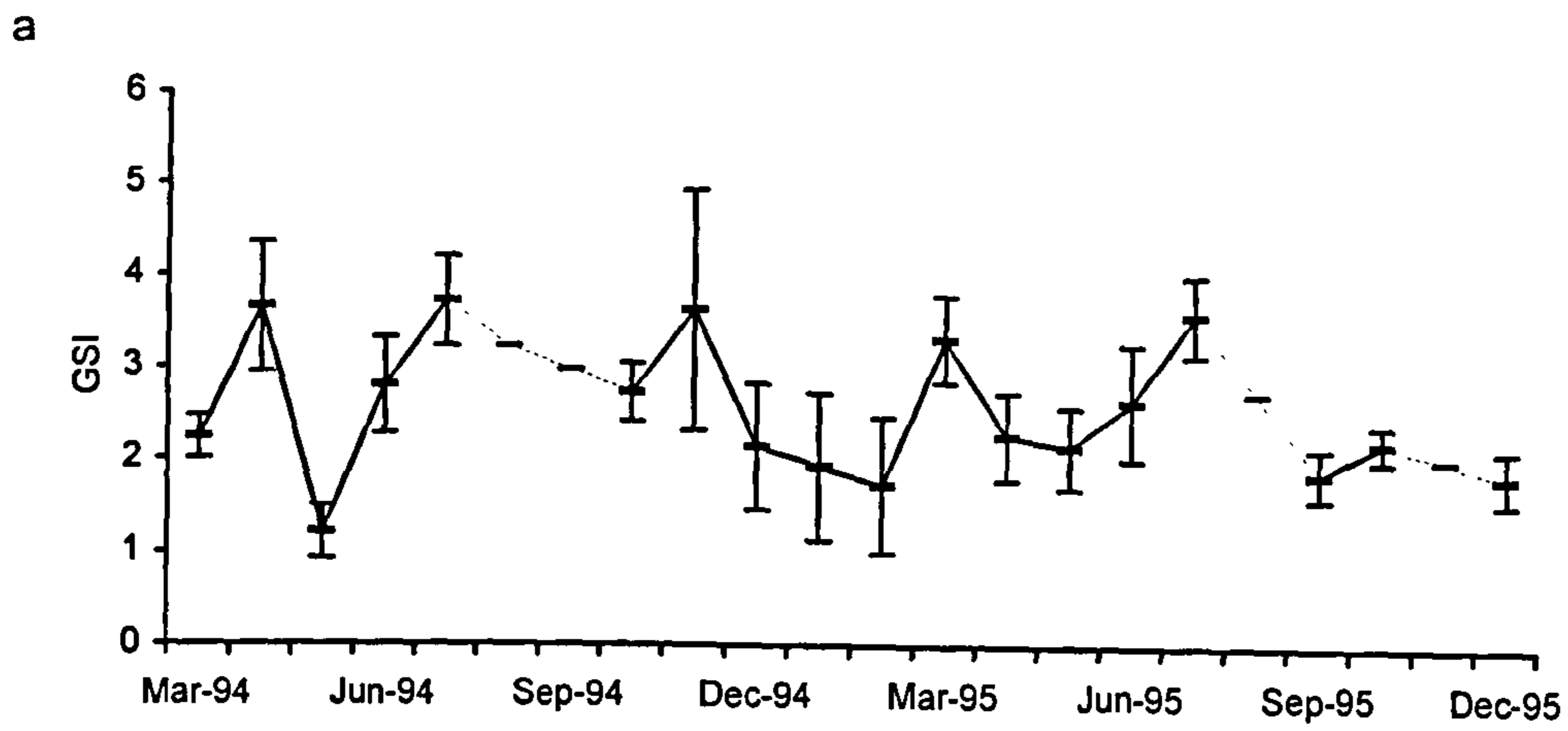


Figure 9. Monthly mean GSI for *S. tanganyicae* from a, Bujumbura samples of females (n = 786) and, Kigoma samples of, b, females (n = 3019) and, c, males (n = 1795). Error bars indicate 95% confidence interval. Dotted line indicates no data.

November.

The percentage frequency of maturity stages (Fig. 10) showed that at Kigoma the catch consisted mainly of fish at the early stages of sexual maturity. The sexual maturity pattern was unclear. It seemed that the frequency of mature individuals increased every 4 months with a temporal pattern close to that of the GSI: i.e. at around May, June and July, September, October and November (in 1994 but not in 1993), and February and March. The correspondence between the occurrence of mature fish and the higher GSI values suggested that reproductive pulses occur around March, May-June and November.

Unfortunately, data from the north of the lake were rejected because they were biased by overestimation of maturity stage II, which was due to the misinterpretation of maturity stage keys by laboratory staff.

There were insufficient fish captured to confirm the reproductive cycles for Mpulungu. Data were scarce and when caught *S. tanganyicae* individuals were either entirely juveniles or sexually mature adults and the simultaneous occurrence of both was rare.

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

### 3.1.5 Recruitment

Recruitment of juveniles (i.e. individuals at or below  $L_c$ ) to the liftnet fishery in the

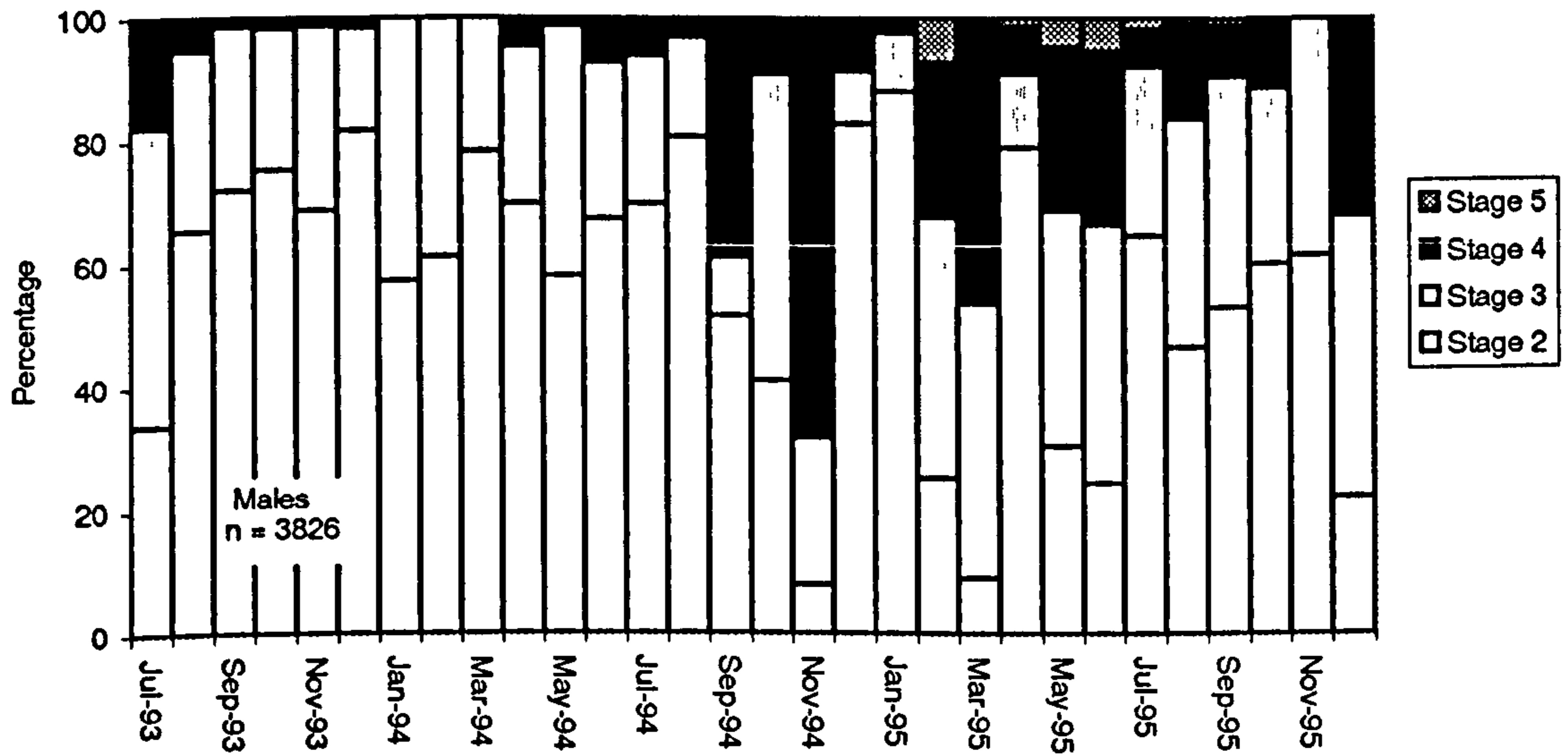
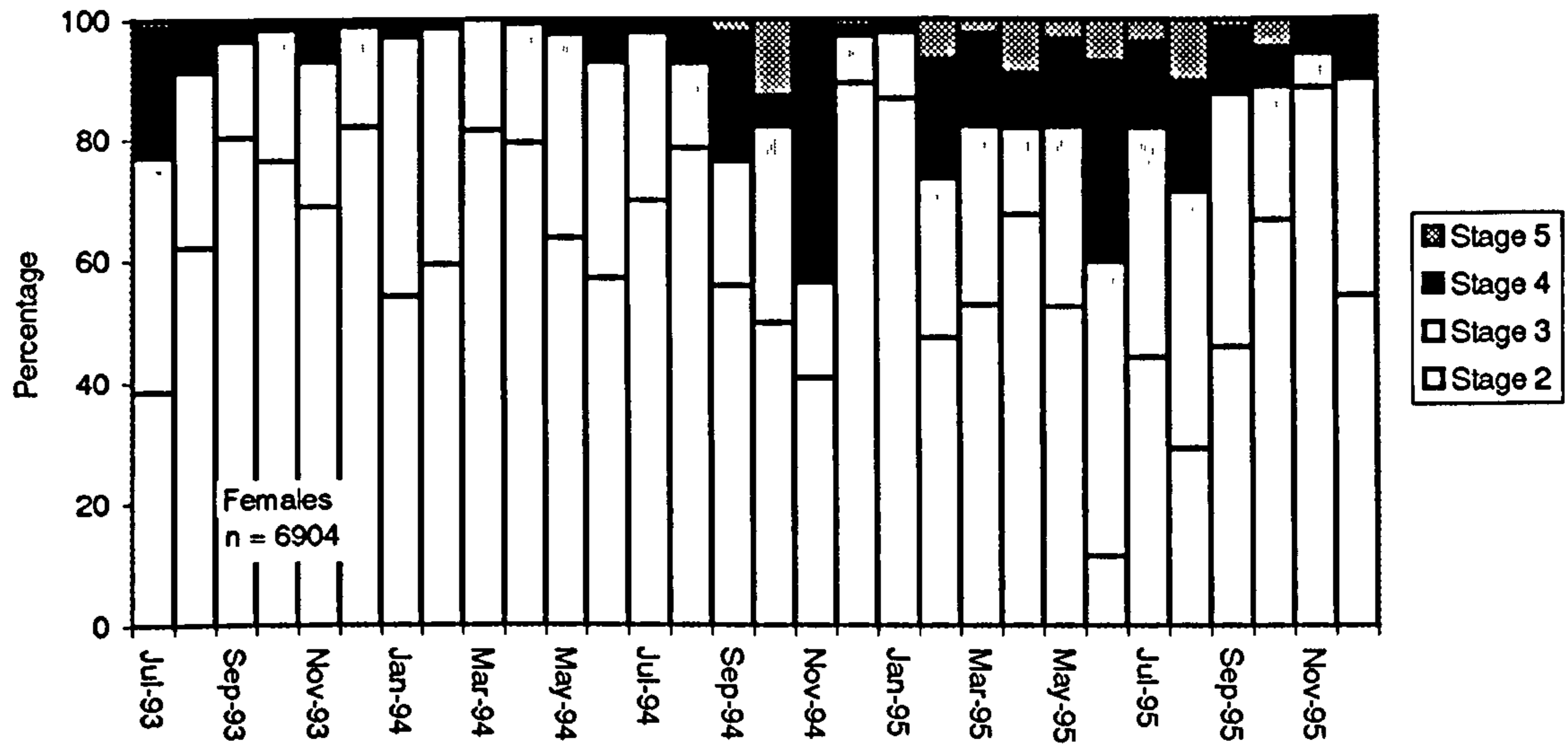


Figure 10. Monthly proportions (percentage) of maturity stages for *S. tanganycae* in Kigoma area, n = sample size.

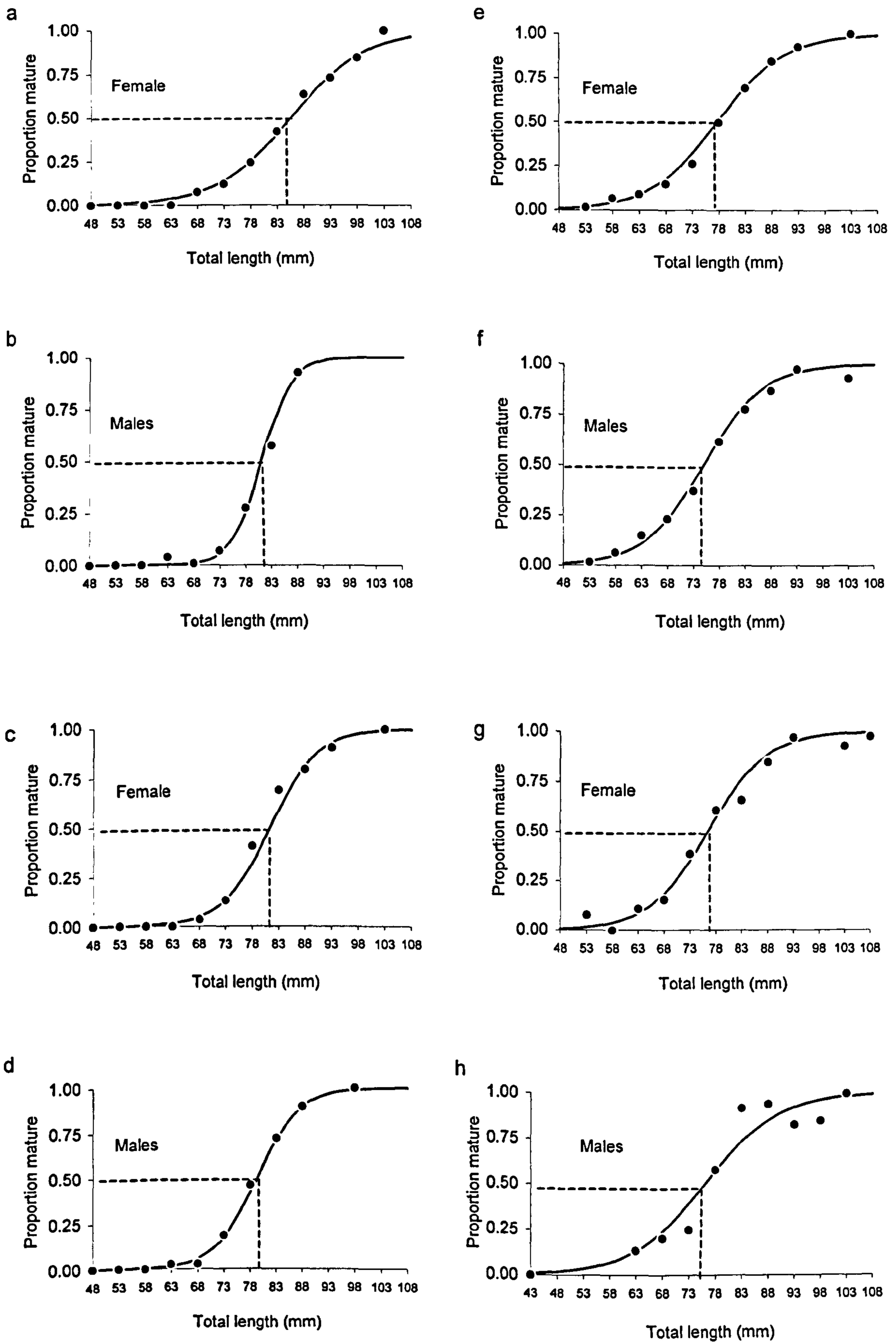


Figure 11. Proportion of mature individuals of *S. tanganicae* from (a, b) Bujumbura and Uvira pooled samples, (c, d) Kigoma, (e, f) Kalemie and (g, h) Mpulungu samples. Data were fitted to the logistic equation (see Table 3, p. 31). Dotted line indicates  $L_m$ .

Bujumbura area appeared to occur throughout the year. The proportion of recruits within the sampled population was often > 50% (Fig. 12a). However, within the thirty-month period, increased abundance of recruits was always observed during the dry season (Fig. 12b), from July to August-September, (lasting longer in 1993 but not in subsequent years). In 1994 the recruitment started during the wet season (March) and continued into the dry season.

The recruitment pattern to the Uvira liftnet fishery was more regular and seasonal (Fig. 12c). In a twelve-month cycle there were two recruitment periods. Early in the year a first, minor, pulse extended over three months (from February to April) and the main recruitment period lasted from June/July to October/November. The appearance of higher proportions of recruits (Fig. 12d) indicated that the main recruitment pulse always took place during the dry season starting in July and ending by October (in 1993) or December (1994 and 1995).

The recruitment of *S. tanganyicae* to the Kigoma fishing grounds (Fig. 12e) was similar to that of Uvira with respect to the major recruitment period from June to December 1994, but in 1995 it ended in August. The proportion of recruits above the mean regularly occurred each year starting from May (1996), June (1995) or July (1996) lasting for two to five months (Fig. 12f). In 1996 a three-month recruitment pulse was also observed around February.

Overall, the principal recruitment season of *S. tanganyicae* in the Kigoma area and in the north of the lake took place from June to November, i.e. during the dry season and the beginning of the wet season.

## 3.2 *Limnothrissa miodon*

### 3.2.1 Commercial catch composition

Liftnets and beach seines exploited different parts of the *L. miodon* stock in the north.

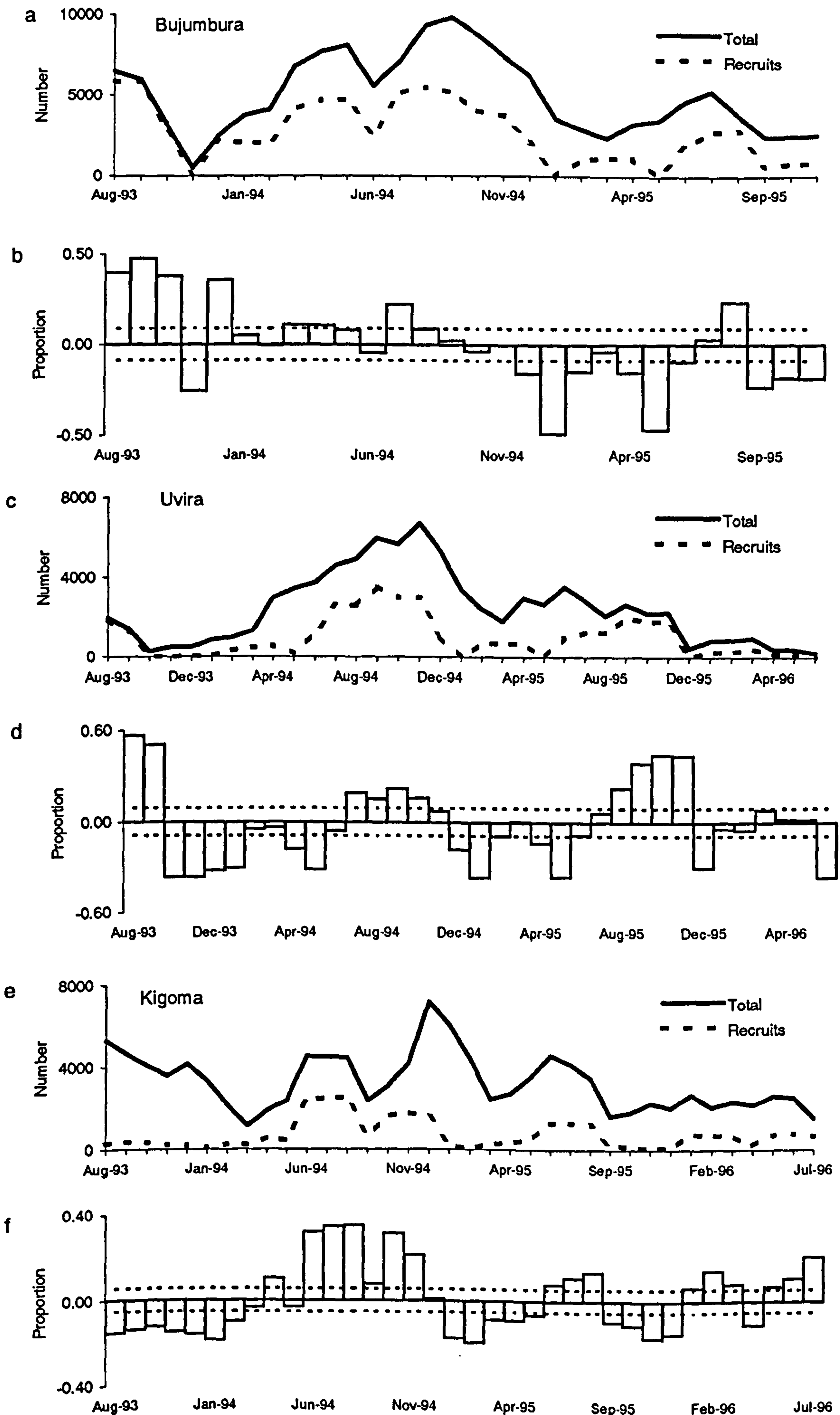


Figure 12. Moving average (a, c, e) over three months of *S. tanganycae* total number in samples and number of recruits (TL < 55 mm) and deviation from mean recruit proportion (b, d, f) in Bujumbura, Uvira and Kigoma samples. Dashed lines in b, d and f, are the upper and lower 95% confidence limits of the mean.

The liftnet catch consisted mainly of immature fish whereas mostly adults were caught by the modest beach seine operation (Fig. 13) because of the highly selective 20 mm mesh size of the net used in that area.

Only the adult *L. miodon* stock was exploited in Kigoma waters and the largest individuals were caught only in the purse seine fishery operating in more open water. The *L. miodon* size distributions at Kigoma and at the southern end of the lake were different (Fig. 13). At Mpulungu beach seines and liftnets used mosquito netting as codend covers and these gears harvested the inshore stock of young *L. miodon*. Consequently  $L_c$  resulted of 15 mm. Thus, *L. miodon* in that area is exposed to fishing mortality from the age of about one month. As in Kigoma waters, the very large fish occurred almost exclusively offshore and were caught by the purse seines.

The length distribution of liftnets and beach seine catches in the Kipili area was similar because both these gears, when targeting clupeids, operated along the coastal zone (Kihakwi and Challe, 1995; pers. obs.). They were often equipped with small mesh codend covers. Length composition from both gears was characterised by a sharp decline to the right. This was not due to mortality but to emigration of large *L. miodon* (TL > 125 mm) from the fishing grounds to more open waters.

### 3.2.2 Growth and mortality

Only the L/F distributions from Bujumbura, Kipili and Mpulungu were suitable for VBGF coefficient estimation (Table 4). The other available data sets did not show any evidence of modal class progression with time, therefore they could not be used with length-based methods. The resulting growth patterns were the same for the three areas (CV of mean  $\phi'$  was 0.13). The values of  $L_\infty$  and  $K$  ranged from 180 to 182 mm and 1.01 and 1.06 yr<sup>-1</sup> respectively. Longevity of *L. miodon* was estimated at 2.5 yr.

All  $Z$  estimates of *L. miodon* are high considering the longevity of the species (Table 4). Total mortality rates obtained from catch curve analysis ranged from 5.40 to 6.61

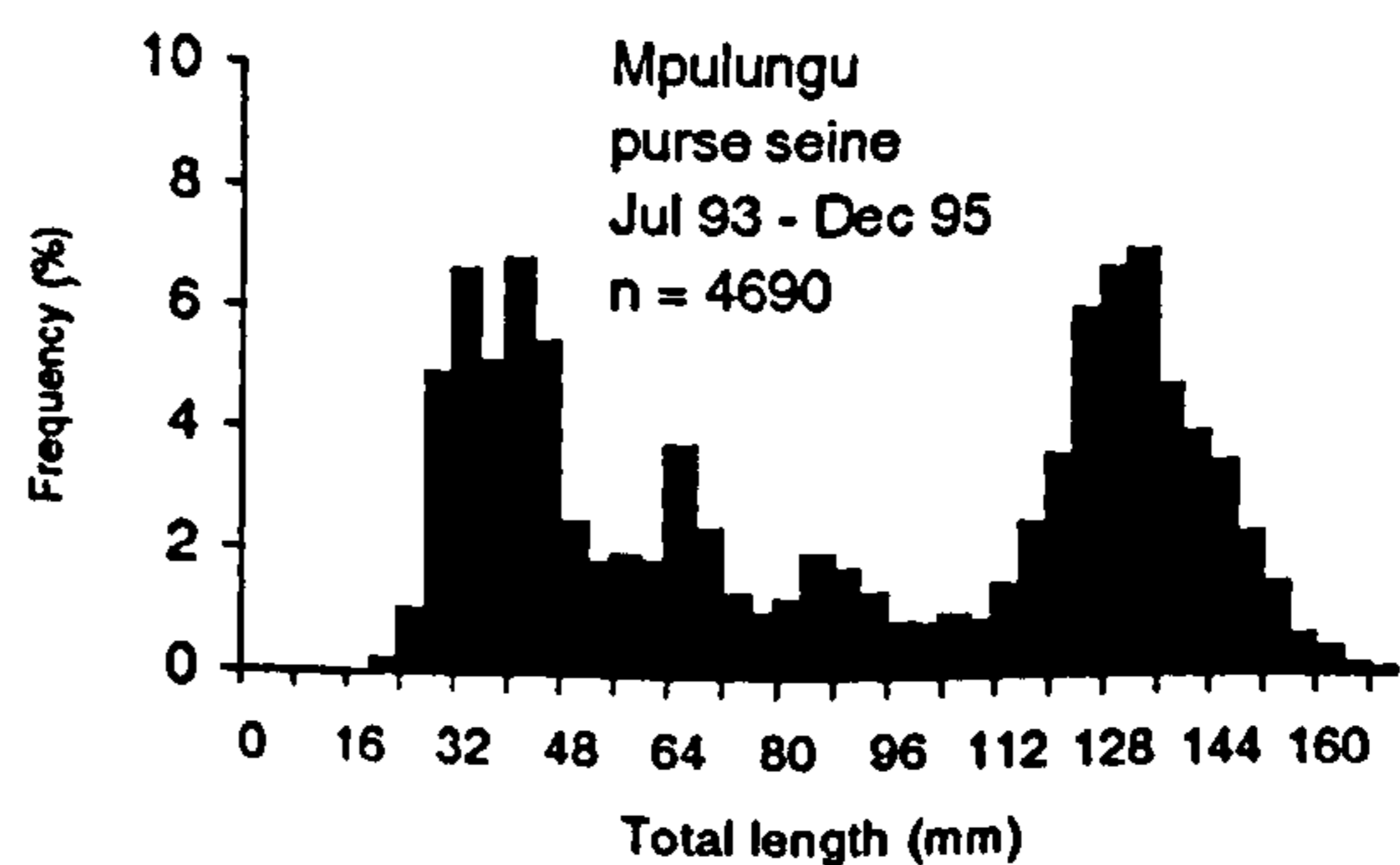
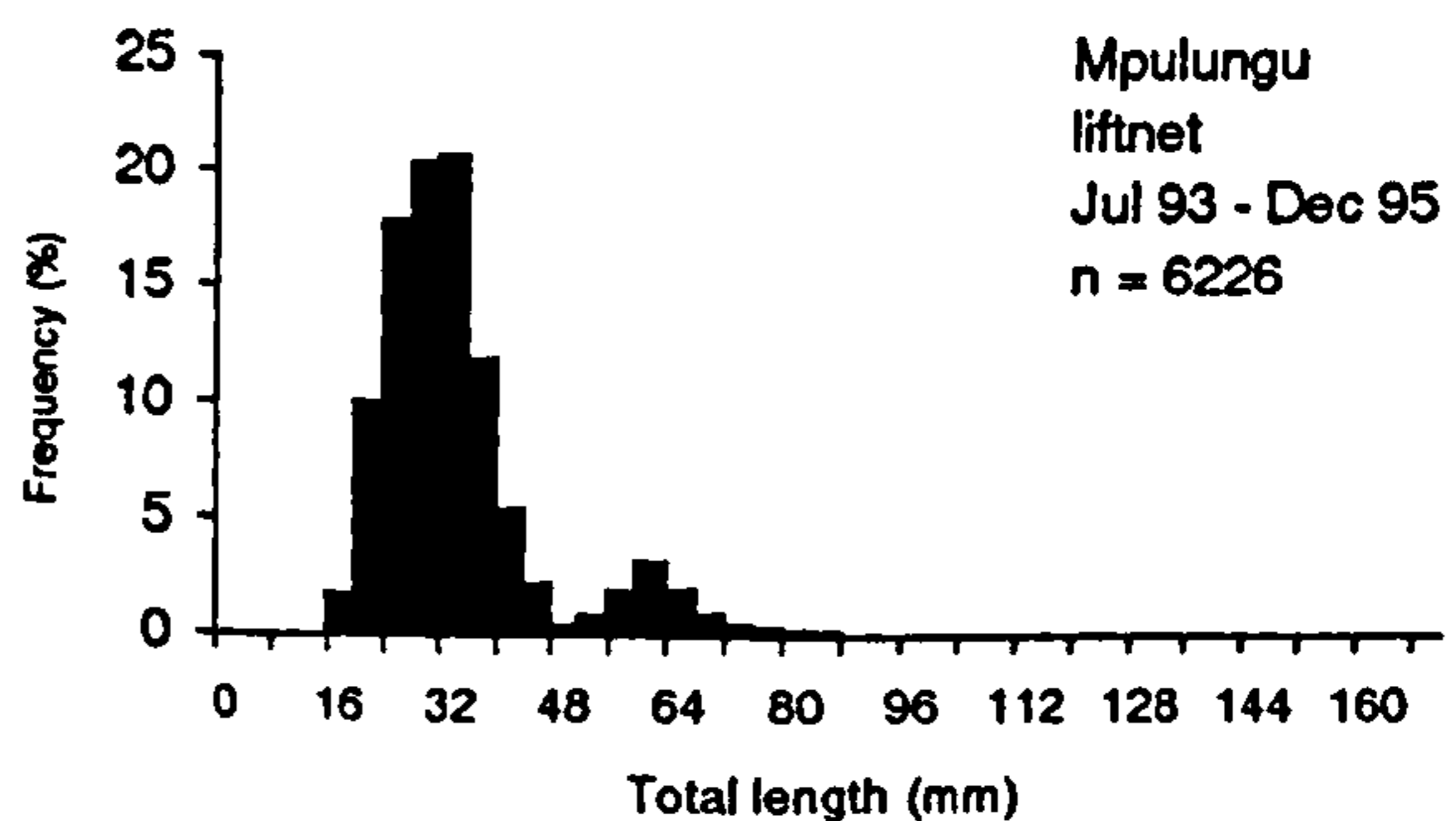
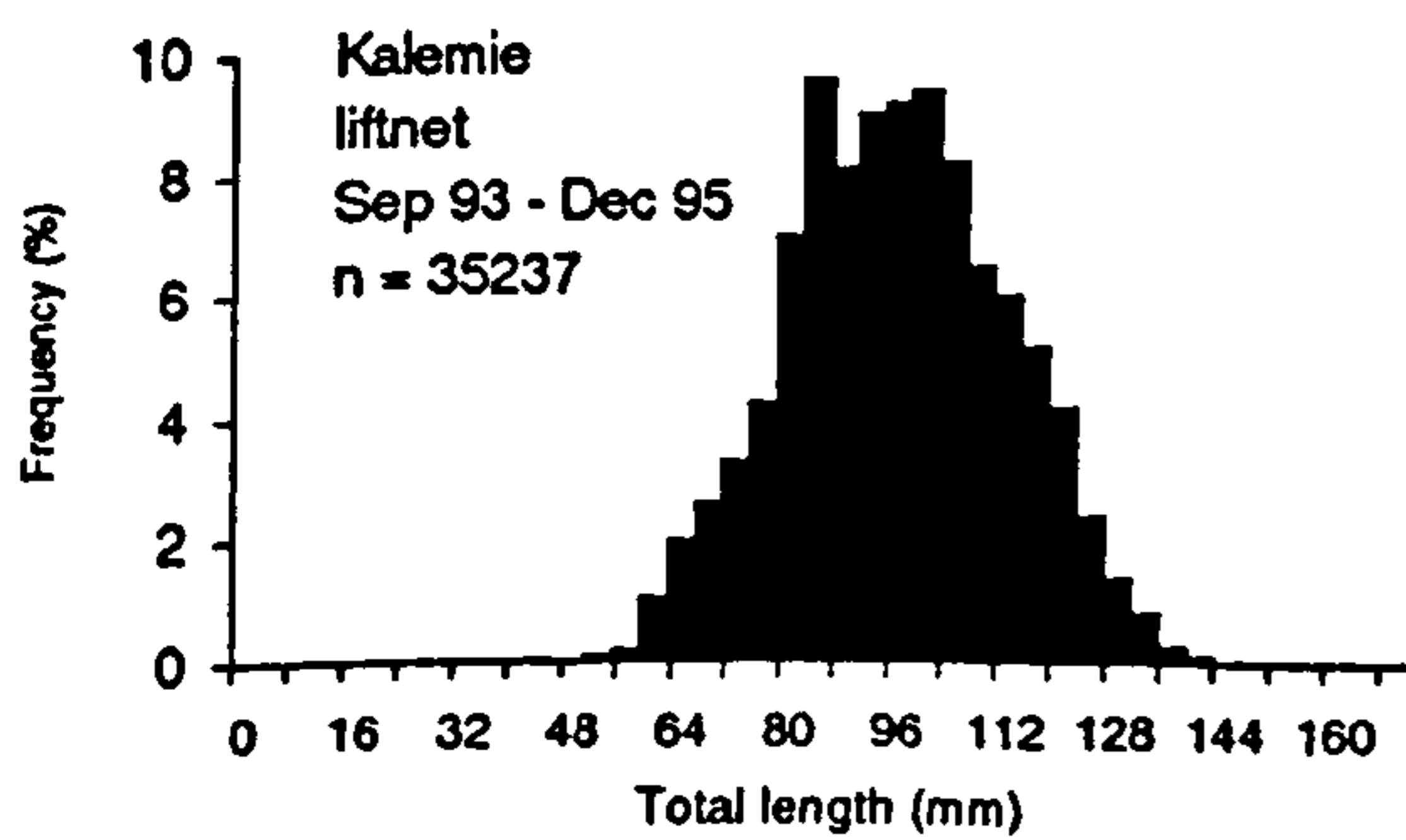
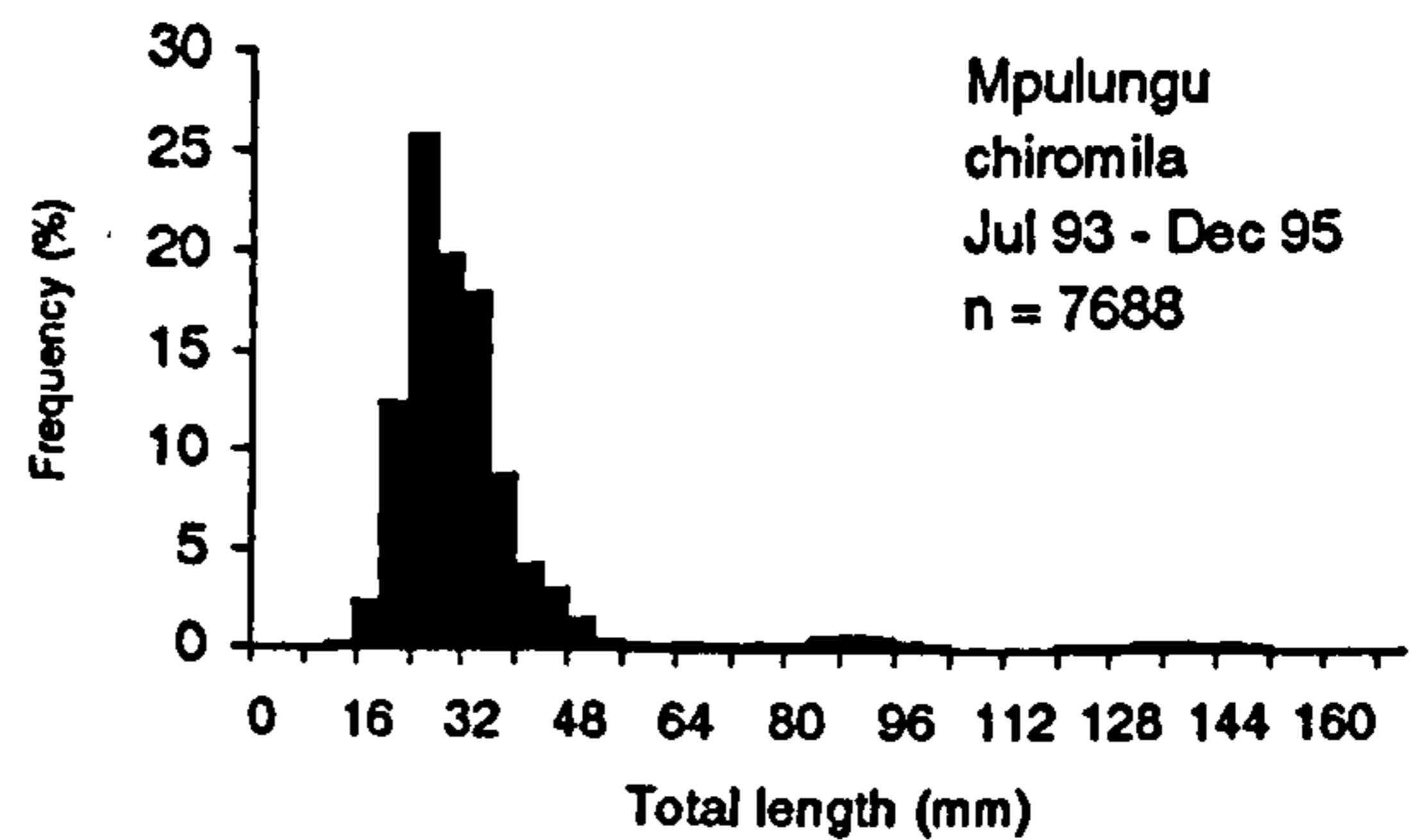
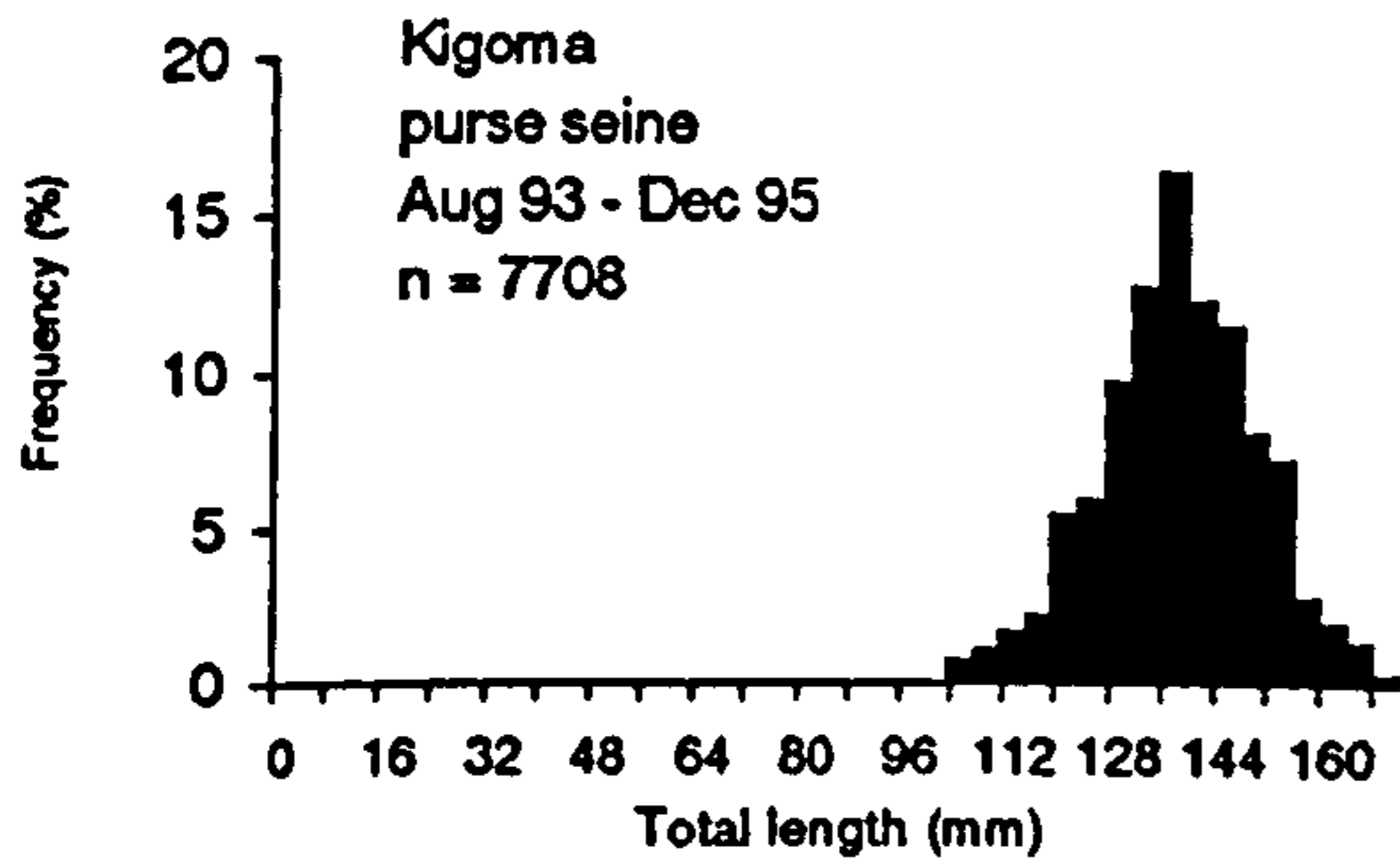
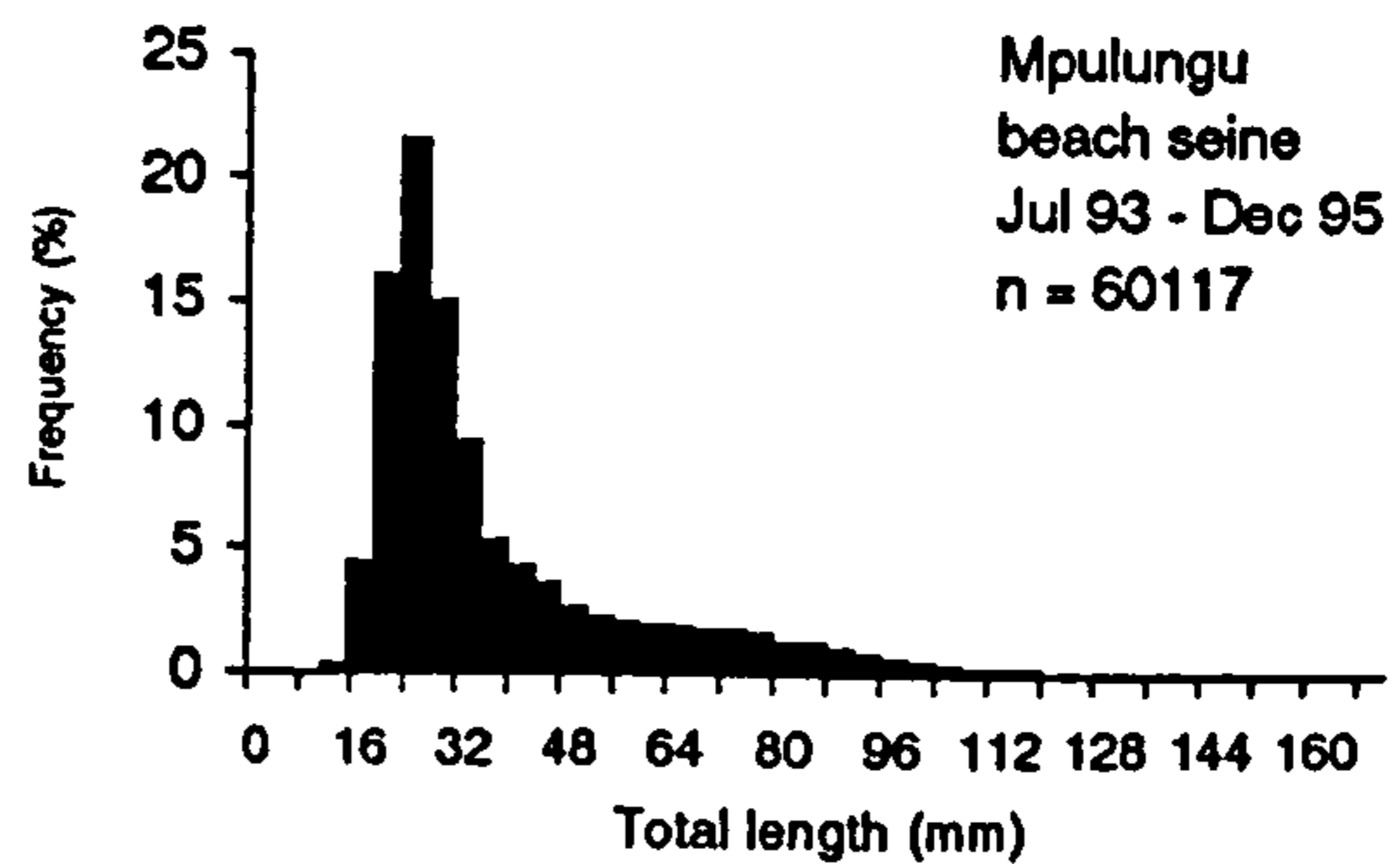
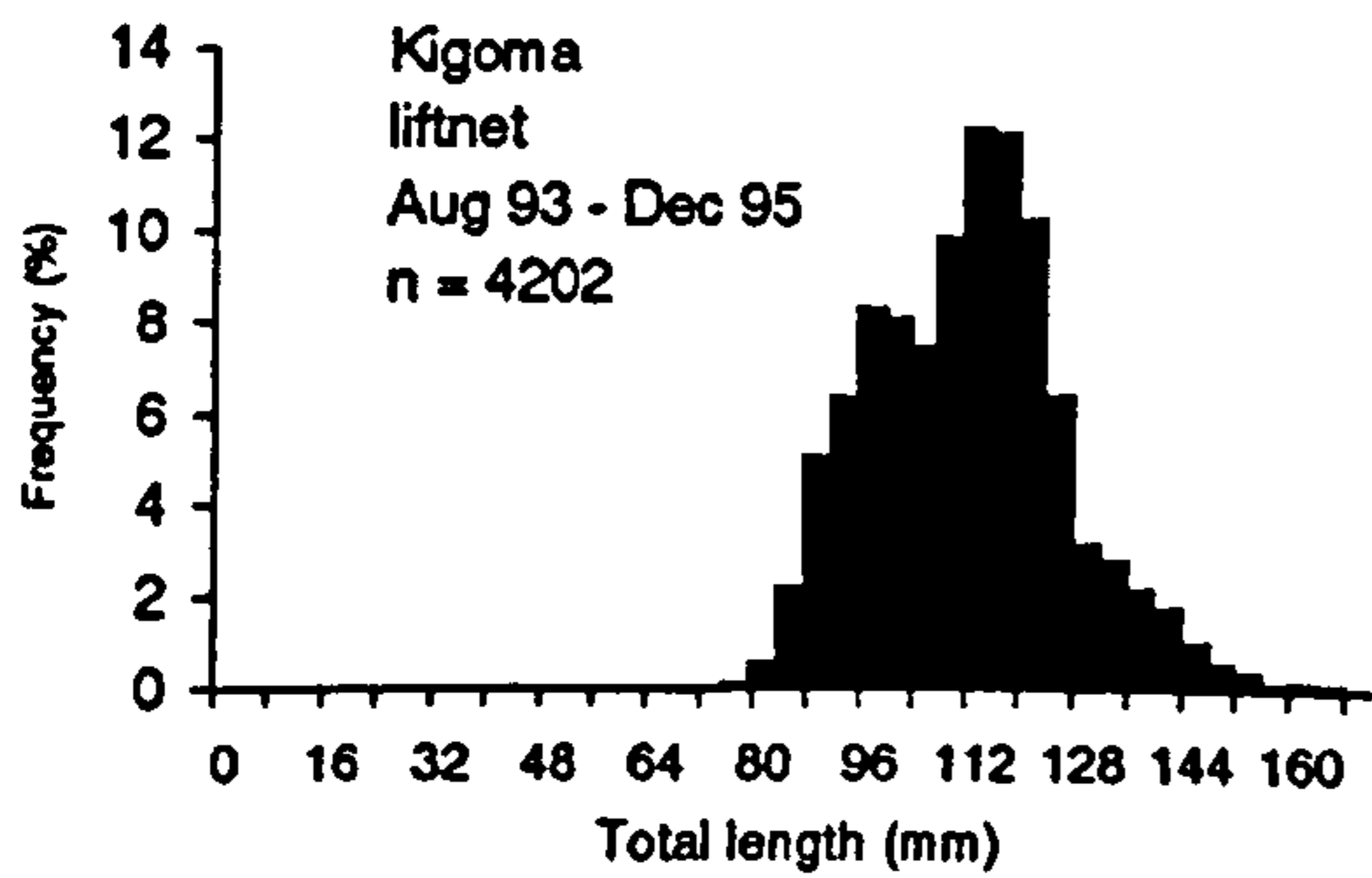
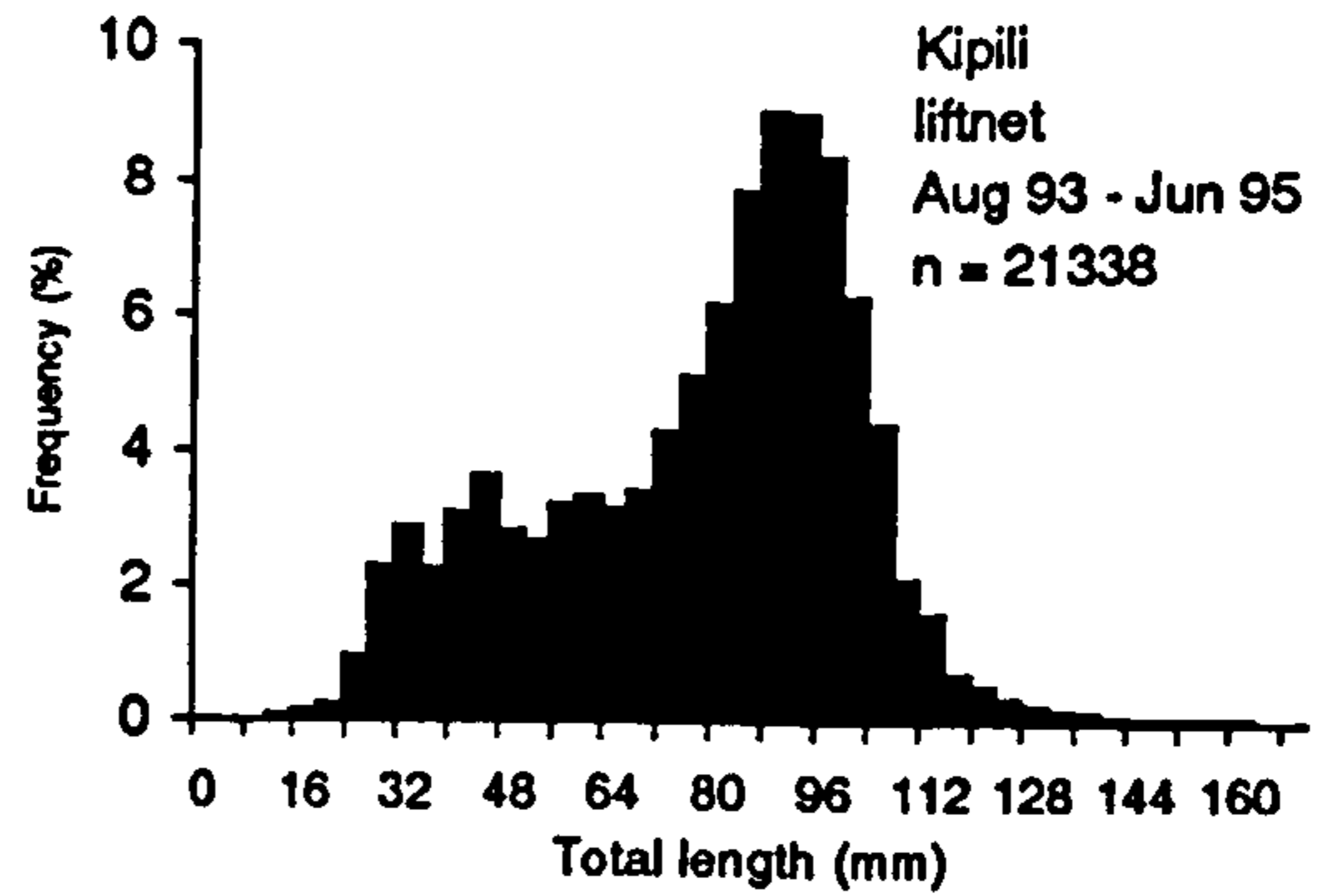
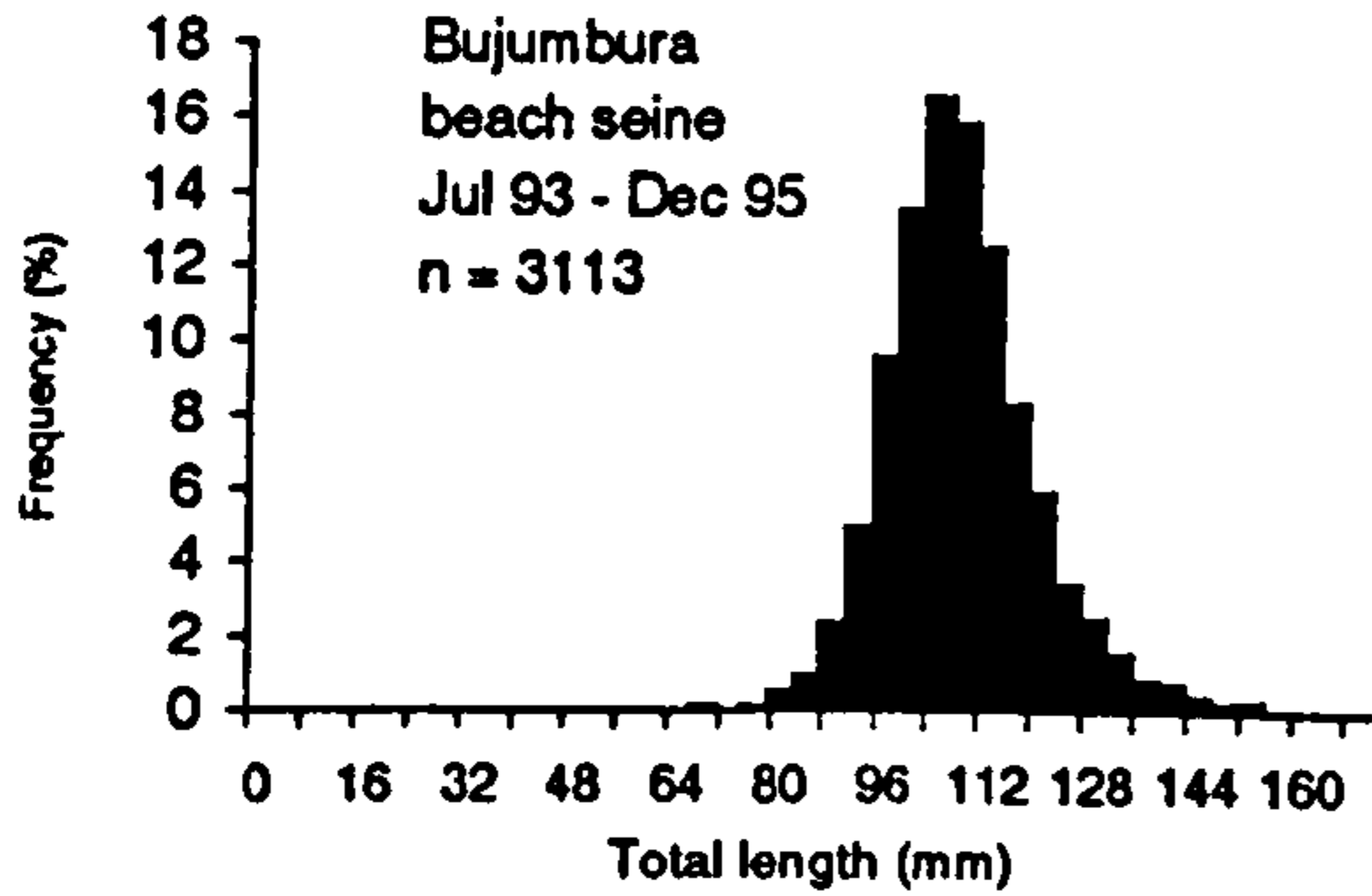
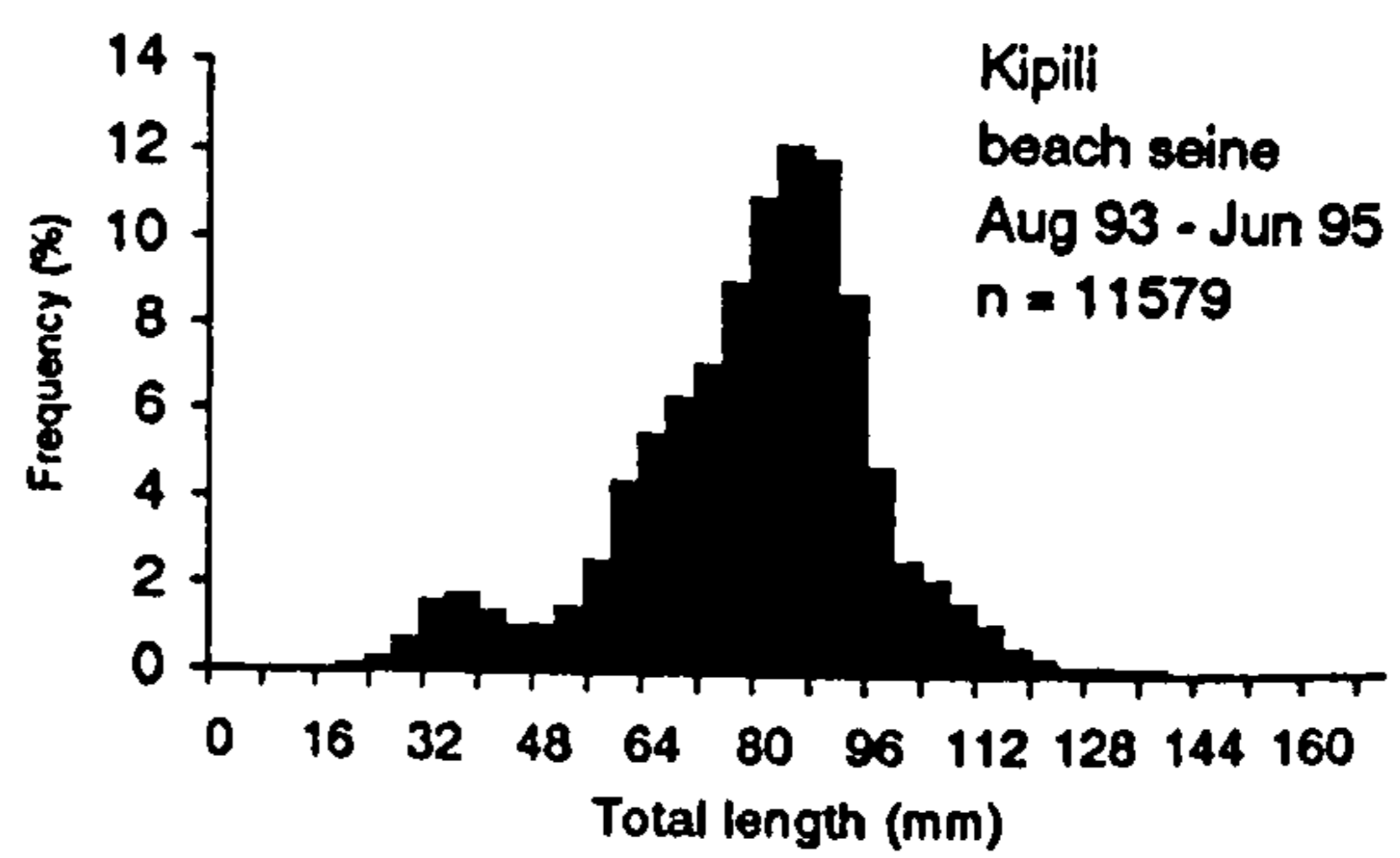
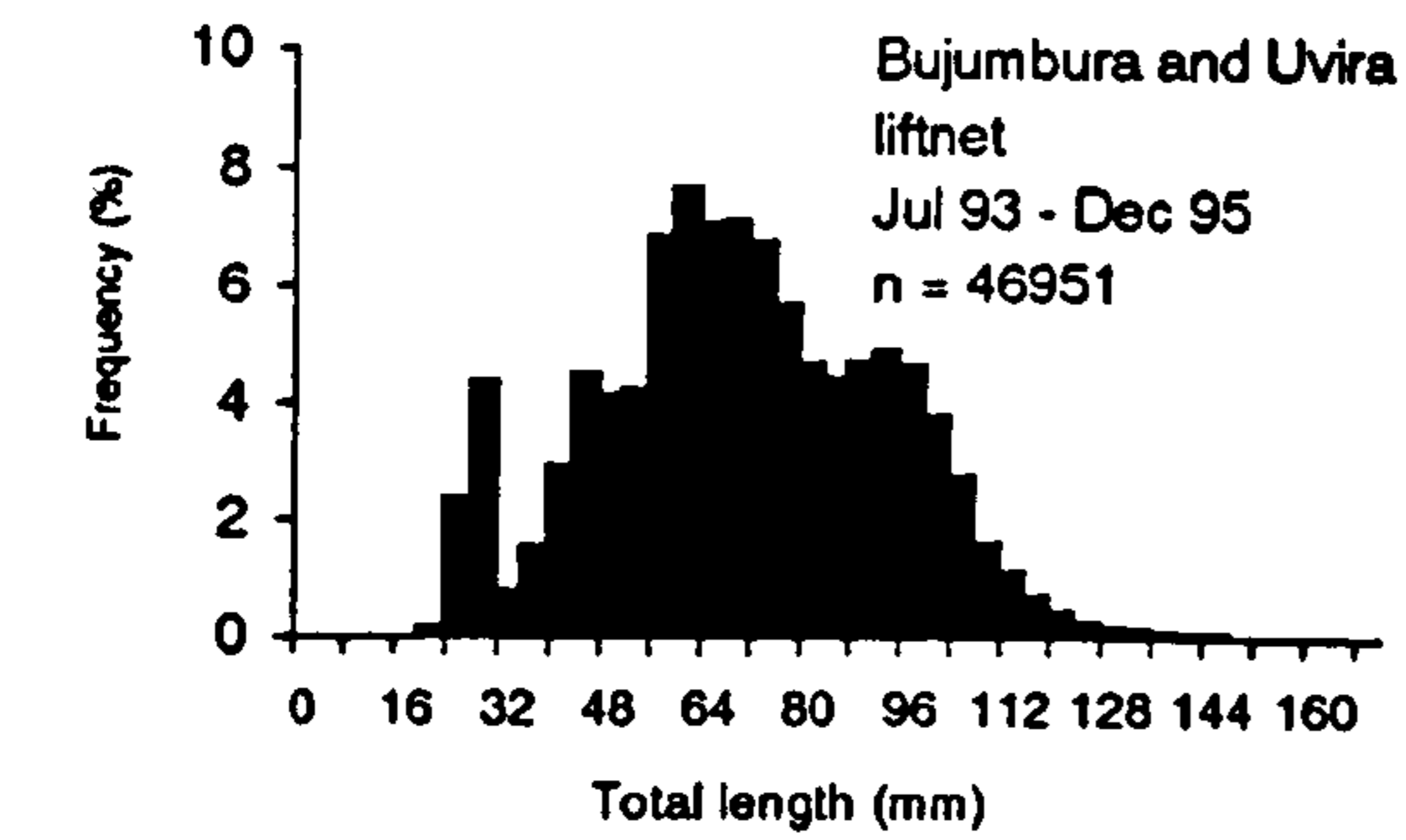


Figure 13. Length composition of the commercial catch of *L. miodon* by area and fishing gear.



Table 4. Von Bertalanffy growth model coefficients ( $L_{\infty}$  and  $K$  from the Elefan I method), total ( $Z$ ) and natural ( $M$ ) mortality estimates for *L. miodon* from various areas. Roman numerals indicate the methods used. I: length-converted catch curve (95% CI and cutoff length,  $L'$ , in brackets); II: Beverton and Holt, 1956; III: Ault and Ehrhardt, 1991; IV: Pauly, 1980; V: Rikhter and Efanov, 1976; VI: Gunderson and Dygert, 1988; VII: Alagaraya, 1984. Exploitation rates ( $E$ ) are estimated from catch curve's  $Z$  and Pauly's  $M$  (see text). Mean length at first capture,  $L_c$ , based on the method of Pauly (1987). Whole lake area refers to  $Z$  estimate obtained from survey data and using the mean  $L_{\infty}$  and  $K$  estimated from commercial catch data as input parameters.

Area	$L_{\infty}$ TL (mm)	$K$ yr <sup>-1</sup>	$\Phi_i$	$Z$ yr <sup>-1</sup> I	$Z$ yr <sup>-1</sup> II	$Z$ yr <sup>-1</sup> III	$M$ yr <sup>-1</sup> IV	$M$ yr <sup>-1</sup> V	$M$ yr <sup>-1</sup> VI	$M$ yr <sup>-1</sup> VII	$E$ ( $E = F/Z$ )	$L_c$ (TL) mm
Bujumbura	180	1.04	4.528	5.08 (4.44-5.72; 58mm)	5.49	5.48	1.6	1.7	1.2	1.6	0.68	55
Kipili	180	1.06	4.536	6.91 (6.26-7.57; 91mm)	7.98		1.6	1.7	1.2	1.6	0.76	76
Mpulungu	182	1.01	4.524	4.21 (3.92-4.51; 126mm)	6.35	6.34	1.6	2.0	1.1	1.6	0.63	15
Mean	181	1.04	4.529	5.40	6.61	5.91	1.6	1.8	1.2	1.6	0.69	
Whole lake				3.13 (3.00-3.26; 84mm)								

Table 5. Linear regression estimates for parameters of the logistic equation relating proportion mature to length for *L. miodon* (see also text and Fig 17). The correlation coefficient ( $r$ ), predicted length at 50% maturity ( $L_m$ ), 95% confidence interval and sample size ( $n$ ) are also given.

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

$\text{yr}^{-1}$  (mean values from various methods given in Table 4). Total mortality of *L. miodon* should not be expected to be higher than *S. tanganycae* mortality rate (compare longevity), otherwise the fish would die well before the achievement of the full growth. This probable overestimation, mainly evident from Kipili and Bujumbura  $Z$  values, could have been due to offshore emigration of fully grown individuals from the fishing grounds. Where fishing gears were not operated offshore, the right side of the *L. miodon* catch curve shows a sharp decline. This would lead to higher values of the regression slope and thus of  $Z$ . Truncated distributions were not encountered from samples collected by offshore nets such as purse seines (see Fig. 13).

Survey data appeared to be more representative of the *L. miodon* population (see also section 3.4.3). From catch curve analysis, applied to the pooled L/F distributions from both surveys,  $Z$  was estimated as  $3.13 \text{ yr}^{-1}$  ( $r = 0.99$ ; 95% CI = 3.00-3.26;  $L' = 84$  mm) which appears more realistic than the  $Z$  estimates obtained from the fishery data.

Natural mortality rates calculated as constant values throughout the life (means from each method) ranged from 1.2 to  $1.8 \text{ yr}^{-1}$ . From the Peterson and Wroblewski model (1984) the overall mean  $M$  value for all sizes was  $2.8 \text{ yr}^{-1}$  and that of adults only was  $1.4 \text{ yr}^{-1}$  were calculated (Figs 8c and 8d).

As  $Z$  from the commercial fishery data was considered overestimated, the fishery mortality ( $F = Z - M$ ) was also overestimated and the resulting  $E$  meaningless. To obtain a more reliable indication of  $E$ ,  $Z$  from survey data was used together with  $M = 1.6 \text{ yr}^{-1}$  obtained from Pauly's method. Then  $F$  was estimated at  $1.1 \text{ yr}^{-1}$  thus leading to  $E = 0.4$ , which would mean that, on lakewide basis, *L. miodon* is not too heavily exploited by the fishery.

### 3.2.3 Reproduction

From all the study areas the reproductive pattern, as indicated by GSI, of *L. miodon*

showed less marked periodicity than *S. tanganyicae*. The reproductive effort of *L. miodon* reflected in gonadal development appeared to be almost constant in the north of the lake while monthly variations, of dubious meaning, were noted in the Kigoma and Mpulungu data (Fig. 14). As there were high variability and lack of data for some months no pattern could be identified. It might seem that female GSI from the three data sets increased around June-July and November but this observation must be treated with caution. The male GSI pattern was even more unclear due to missing data or wide confidence intervals of monthly means. As stated earlier, data on *L. miodon* from commercial catches were thought to be poorly representative of the population, and this has possibly affected the reproductive analysis.

The percentage distribution of maturity stages from the Kigoma samples (Fig. 15) indicated that the greatest number of mature fish were found twice a year (May-July and September-November). In the south only the period July 1993 to July 1994 could be considered due to the scarcity of adult fish during the rest of the sampling programme (Fig. 16). During this period mature *L. miodon* occurred for the most of the year with the highest frequency from January to July. Data from the north of the lake are not presented as maturity stage II was overestimated.

The mean value of  $L_m$  for *L. miodon* was 101 mm (CV 13.8) for females and 95 mm (CV 7.6) for males (Fig. 17; Table 5). The optimal  $L_m$  theory (Roff, 1986, 1992) predicted  $L_m = 130$  mm which is much higher than the lengths obtained from the logistic model. This value is probably unrealistic as only a very small fraction of the population would attain it.

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

#### 3.2.4 Recruitment

In the north, *L. miodon* had a main recruitment period during the 1994 dry season

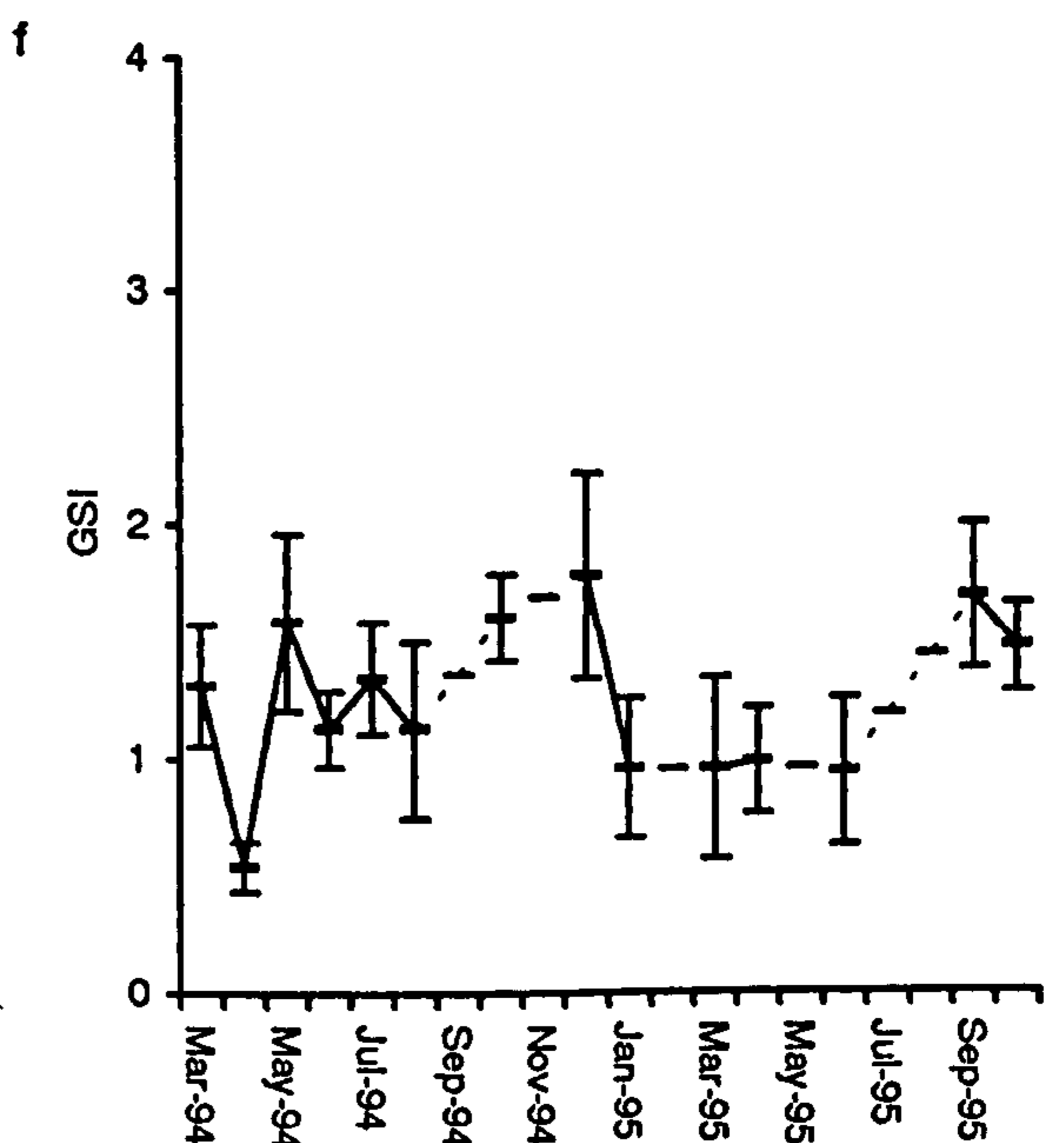
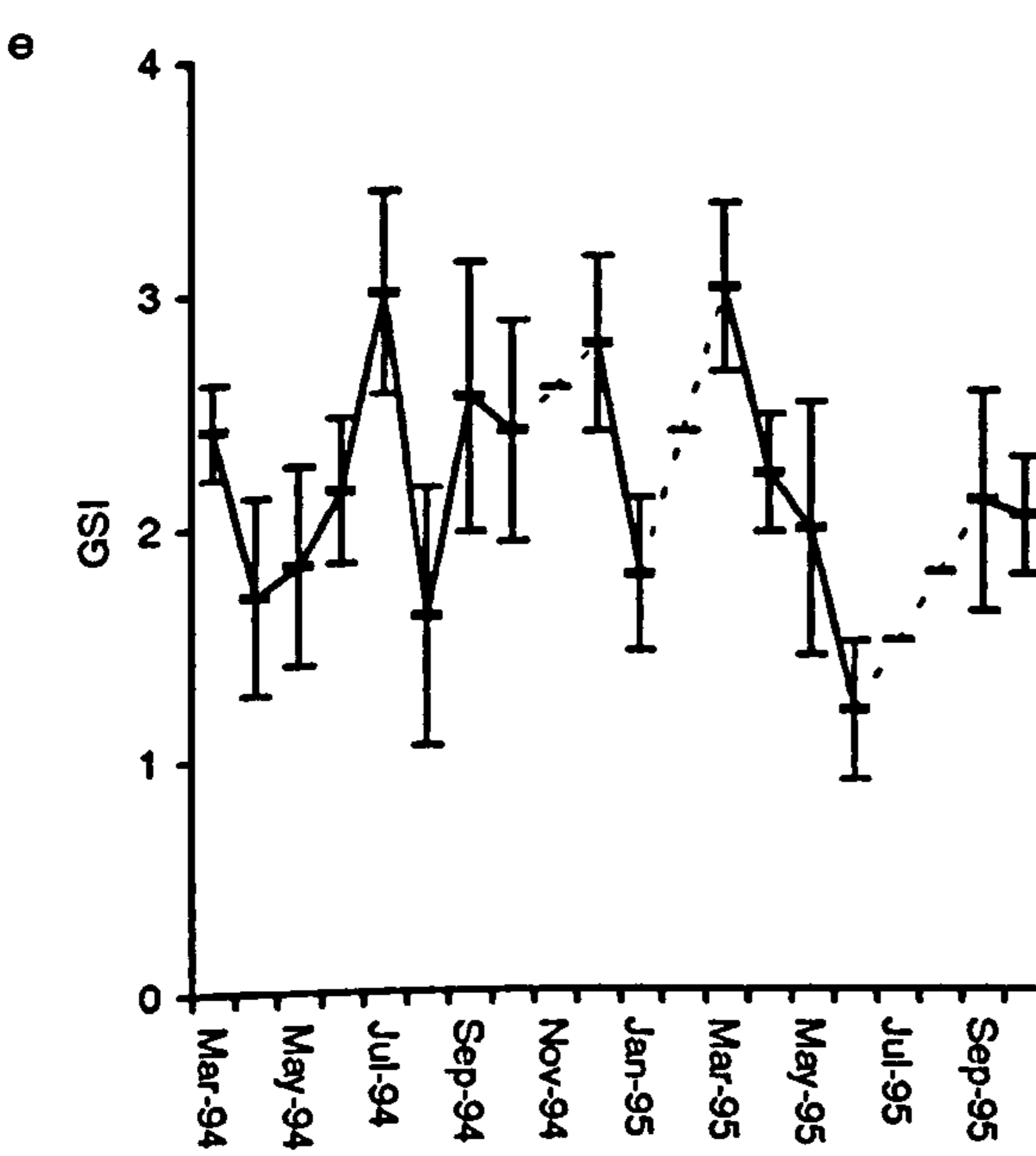
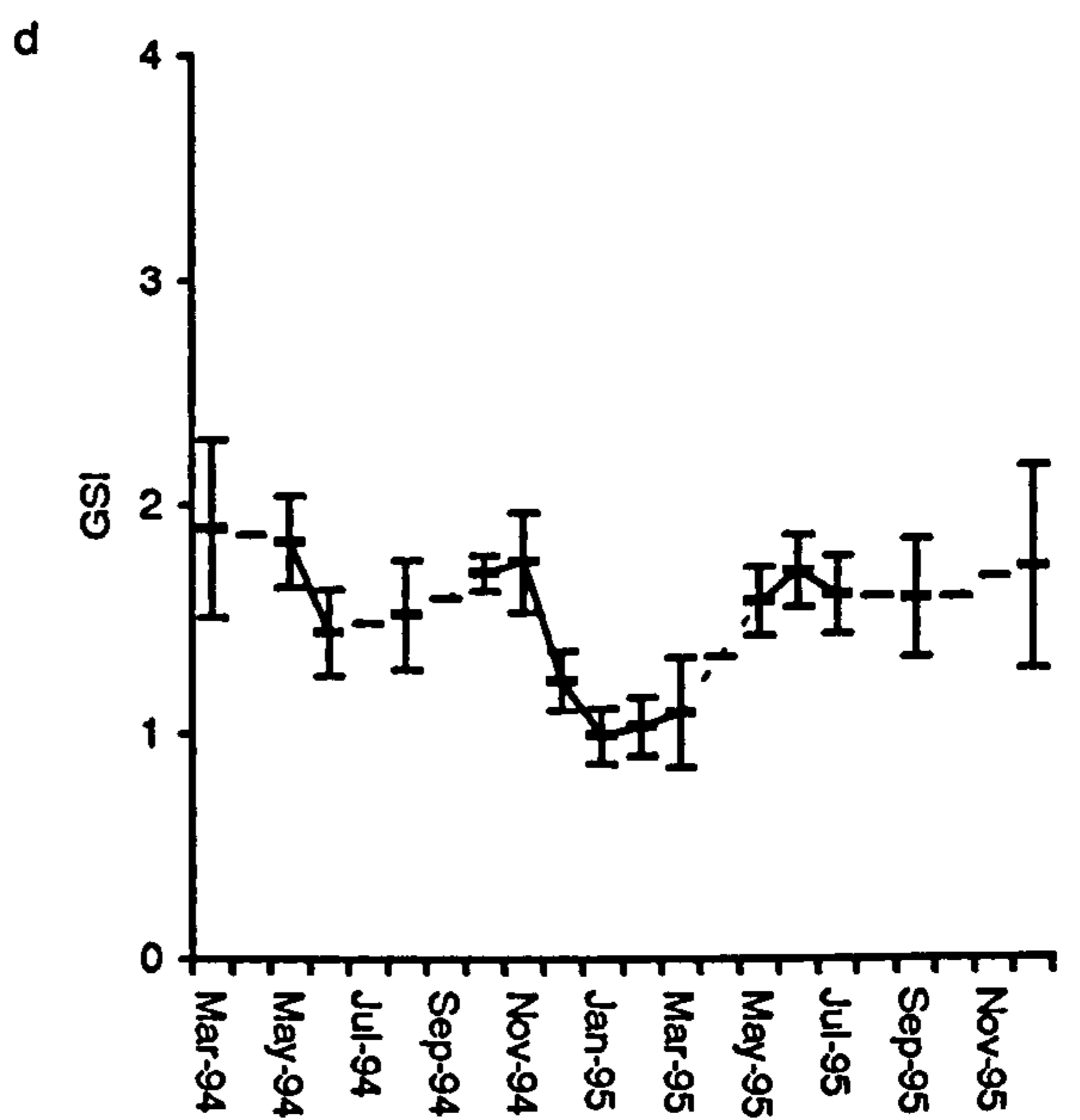
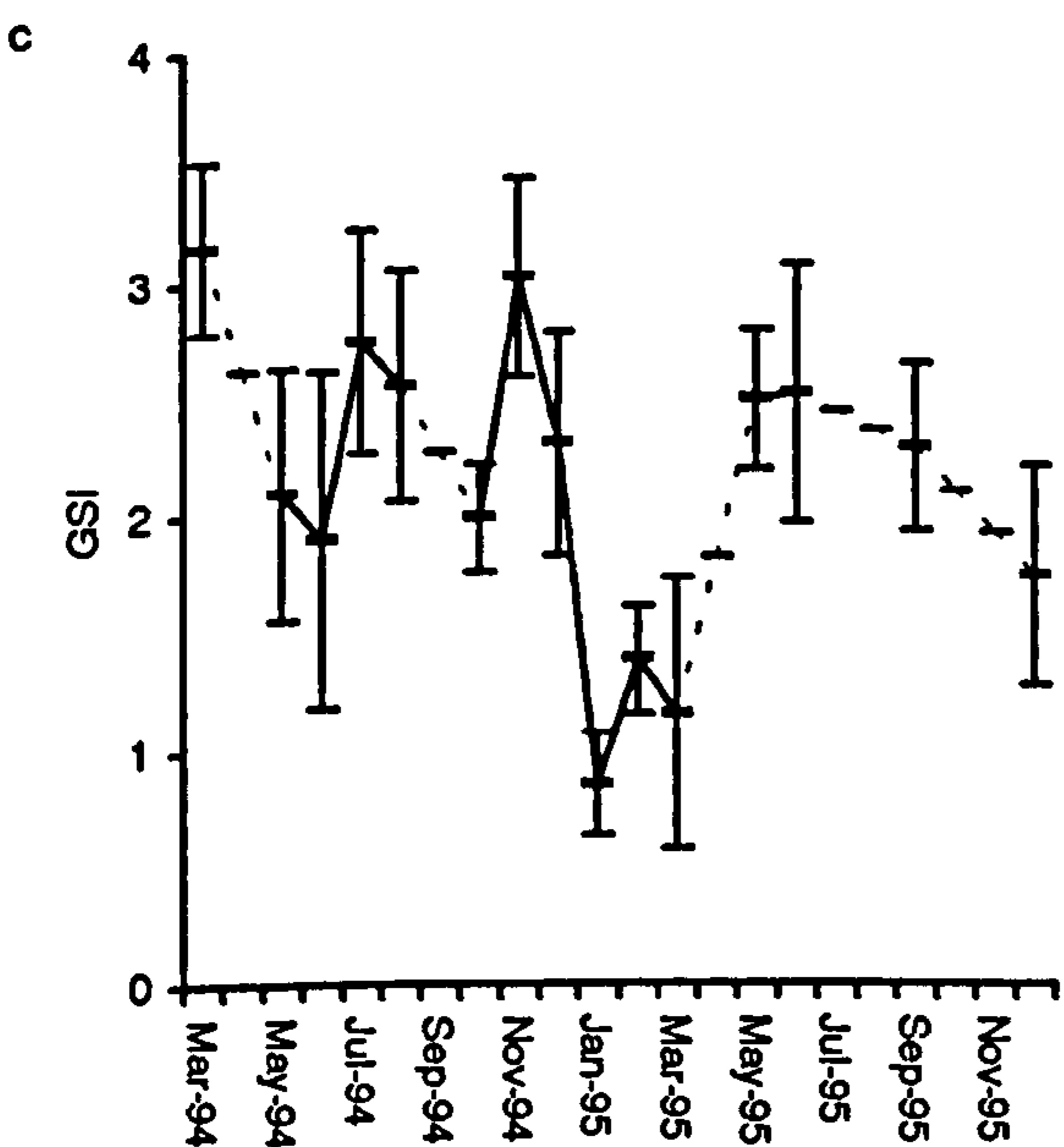
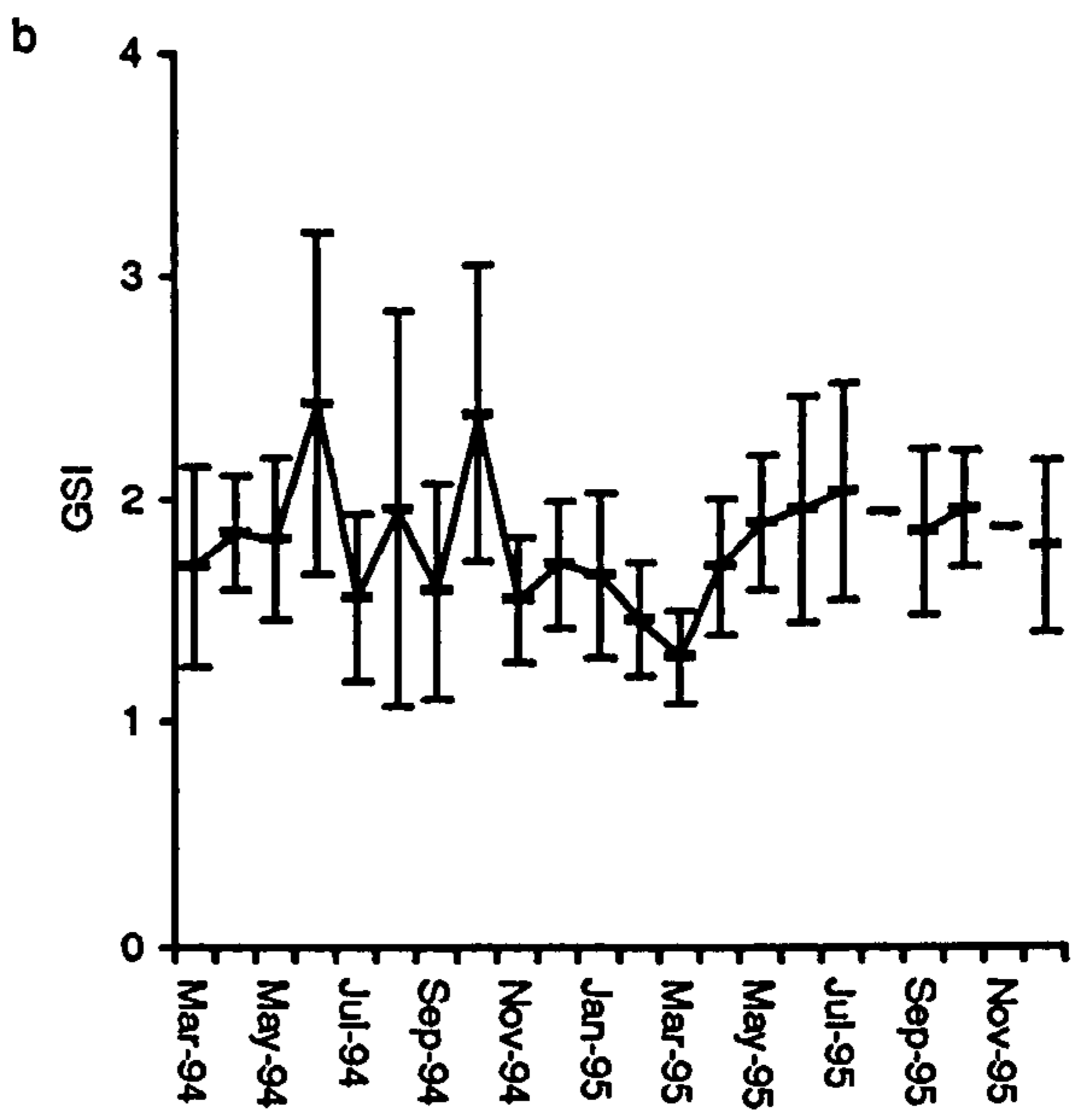
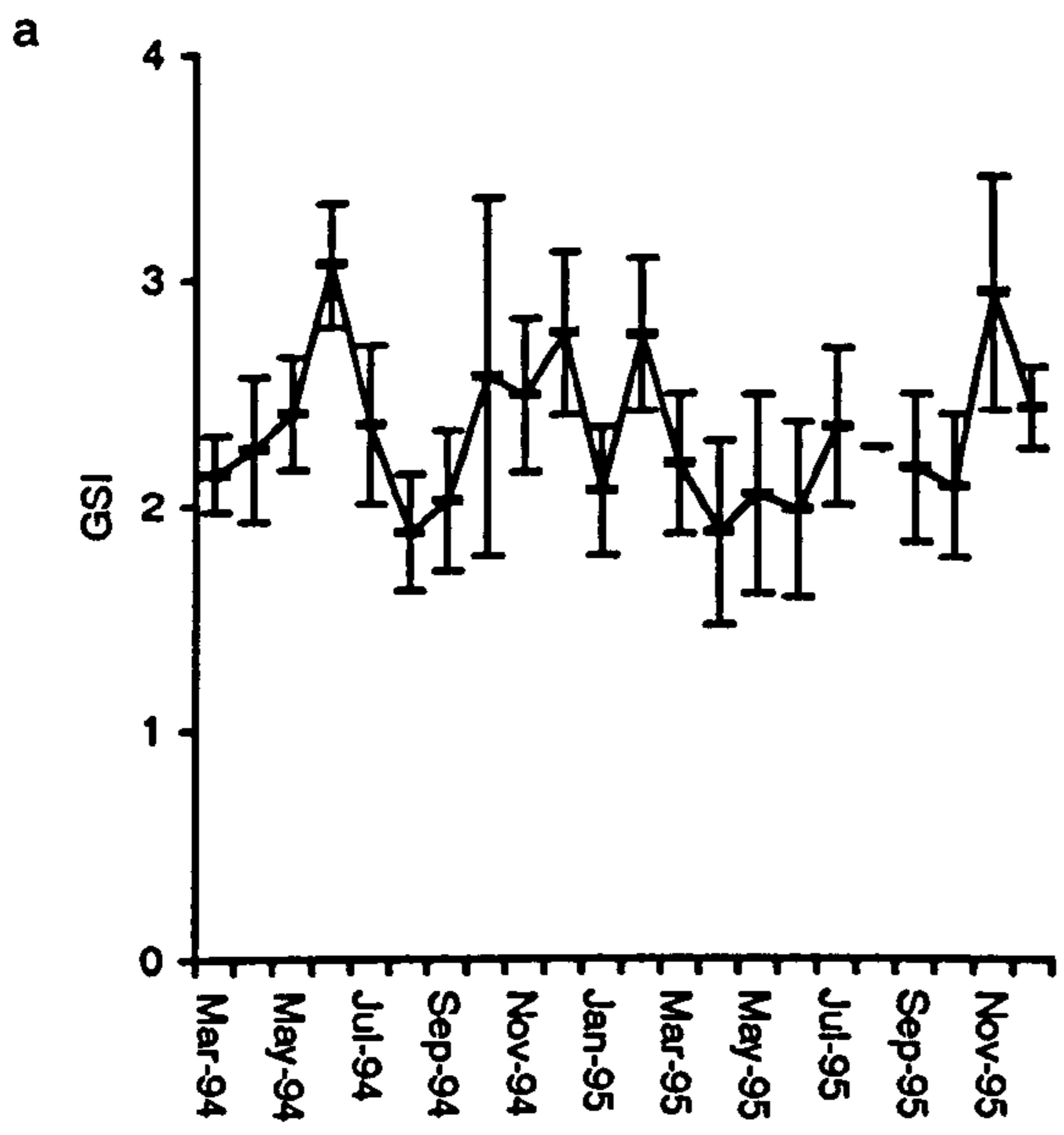


Figure 14. Monthly mean GSI of: a, *L. miodon* females (n = 2106), b, males (n = 667) from Bujumbura samples; c, females (n = 864), d, males (n = 805) from Kigoma samples; e, females (n = 1204), f, males (n = 394) from Mpulungu samples. Error bars indicate 95% confidence interval. Dotted line indicates no data.

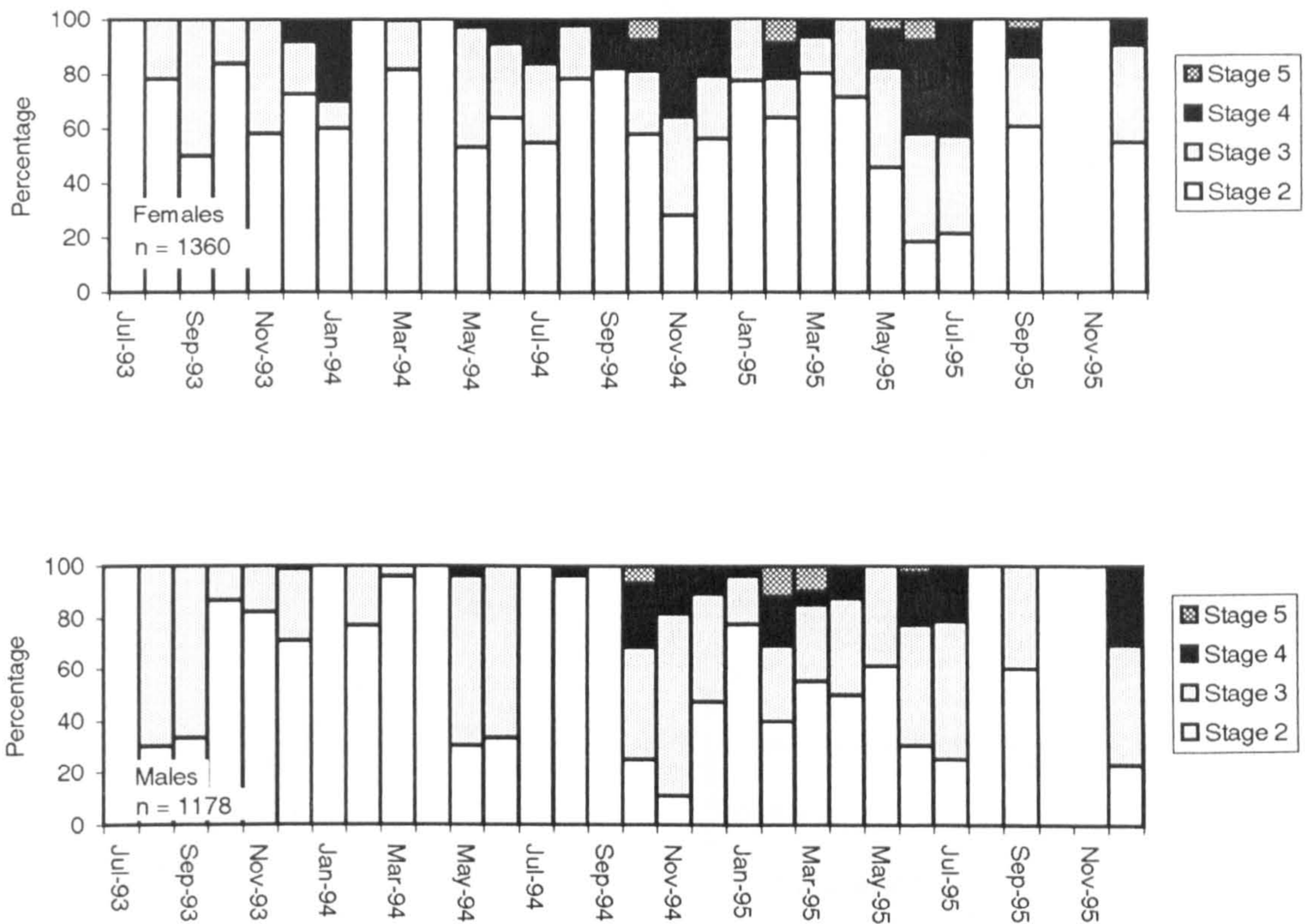


Figure 15. Monthly proportions (percentage) of maturity stages for *L. miodon* in Kigoma area, n = sample size. No fish or only immature fish were caught in the months which are shown 100% blank.

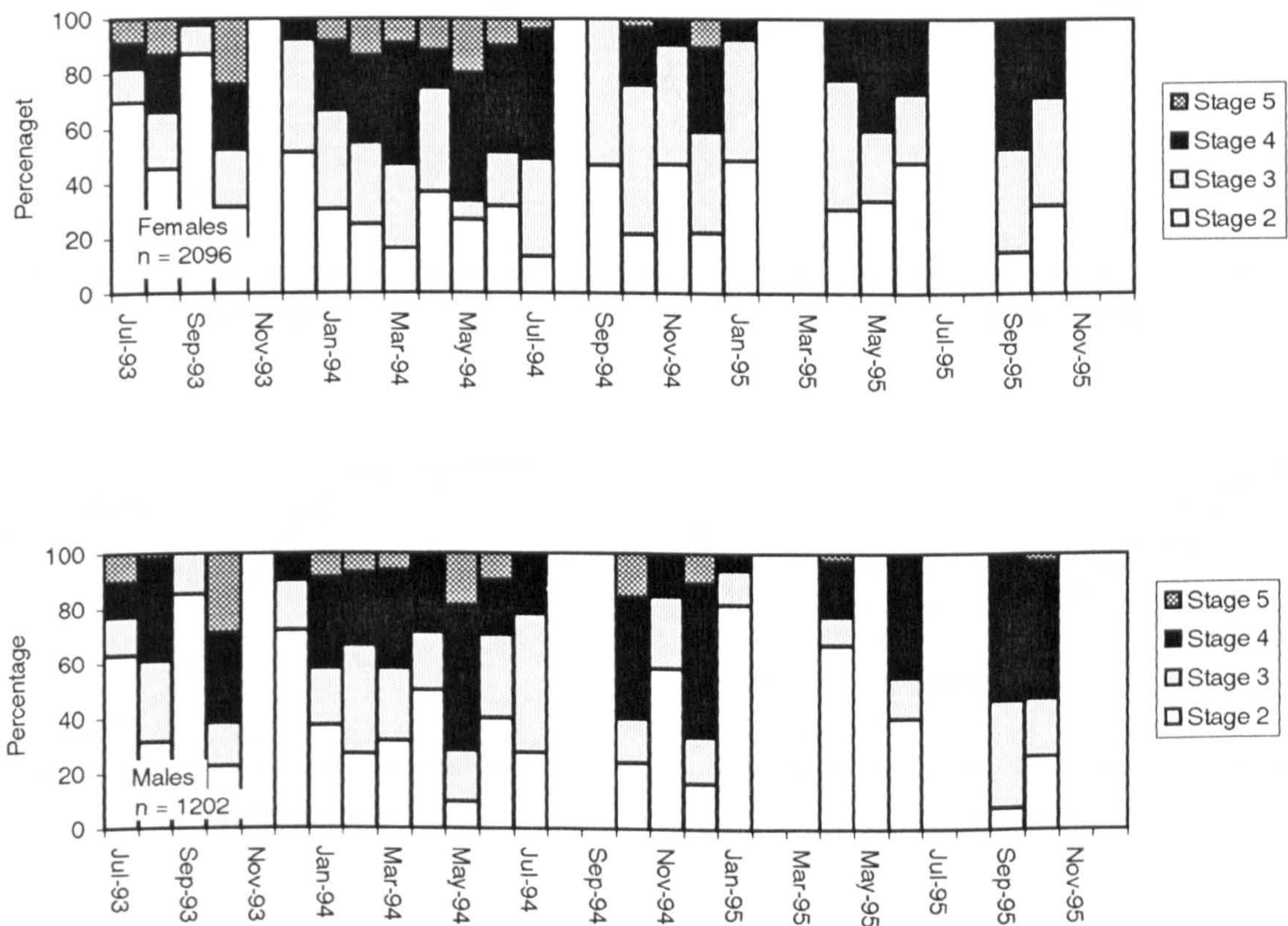


Figure 16. Monthly proportions (percentage) of maturity stages for *L. miodon* in Mpulungu area, n = sample size. No fish or only immature fish were caught in the months which are shown 100% blank.

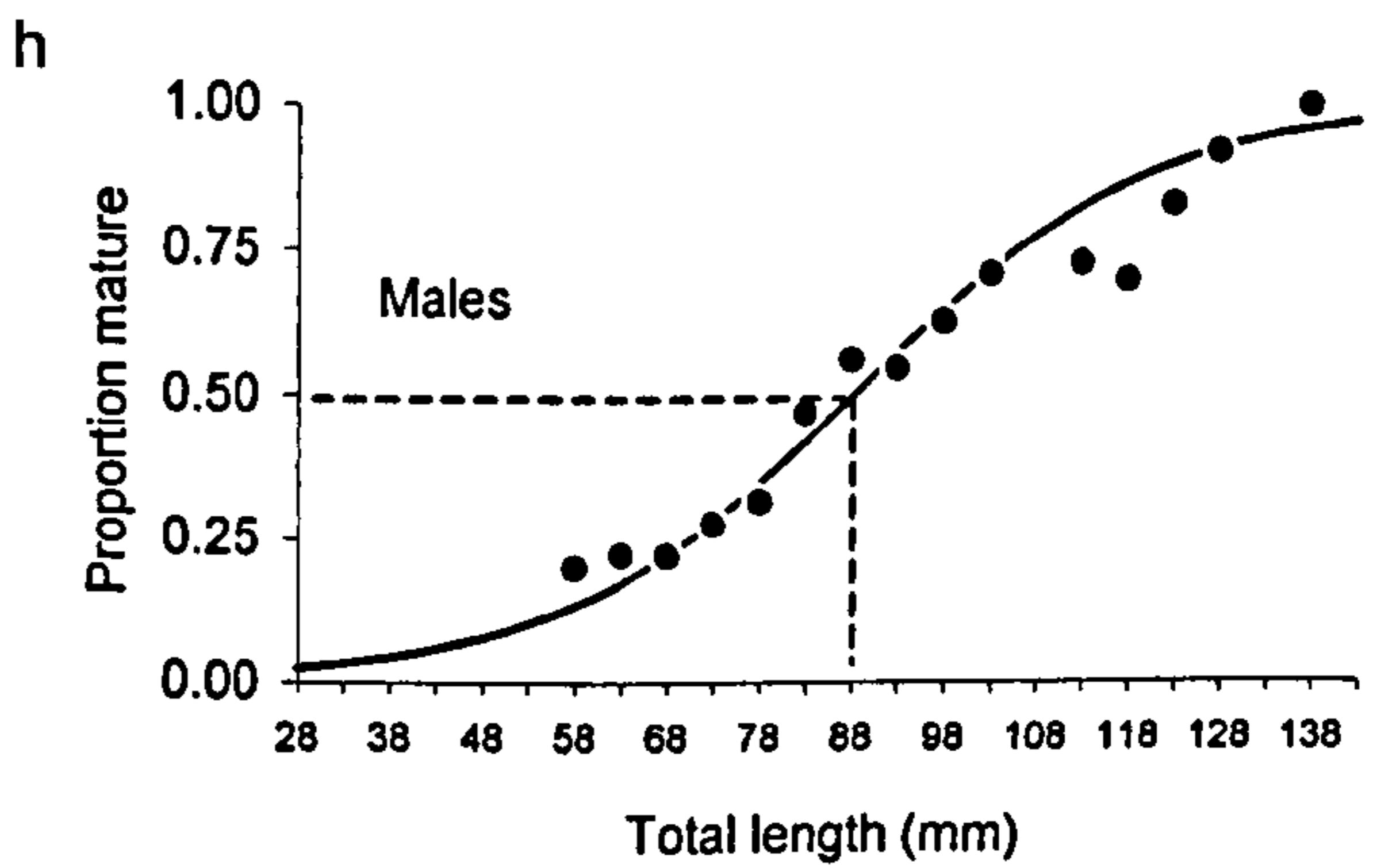
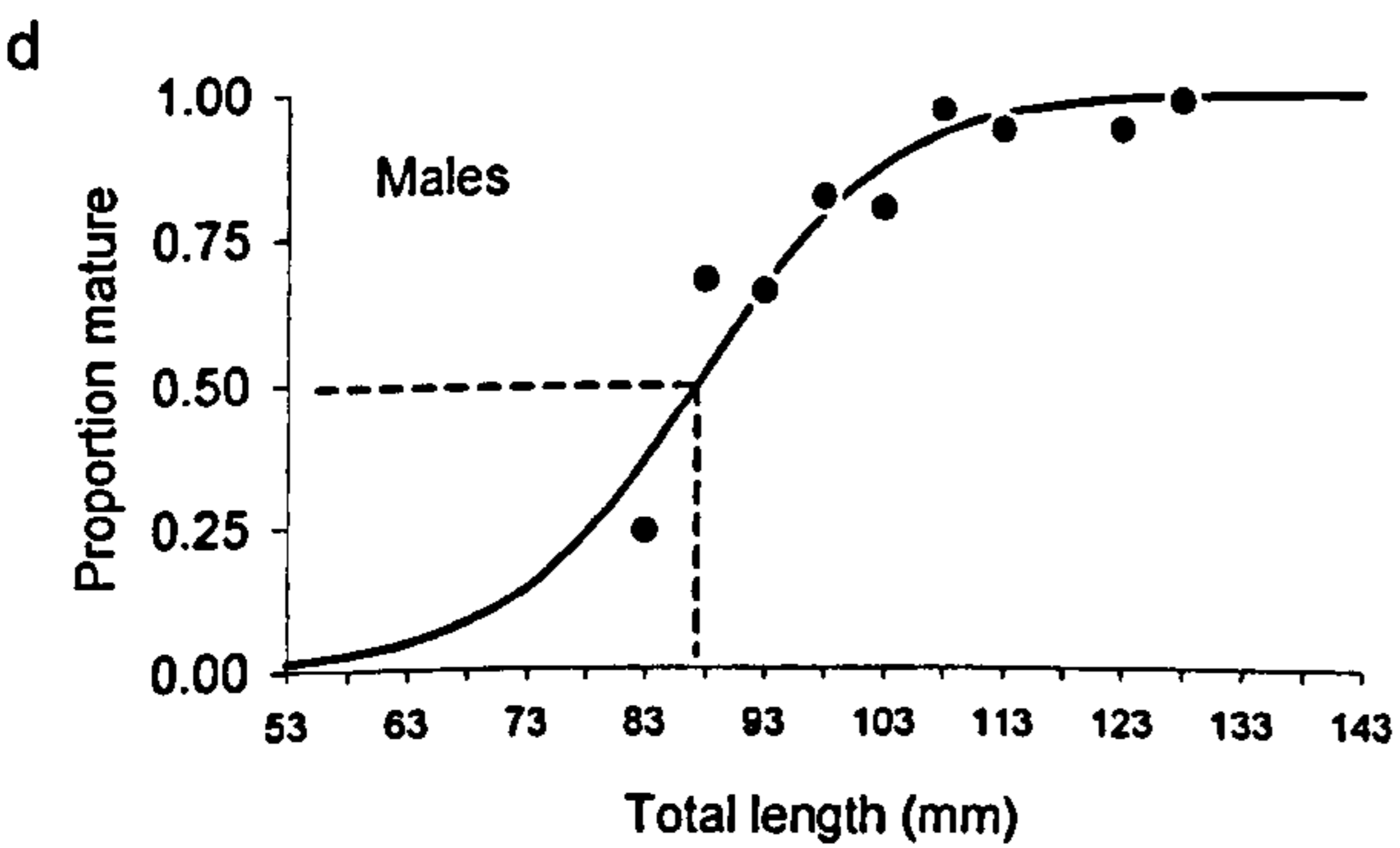
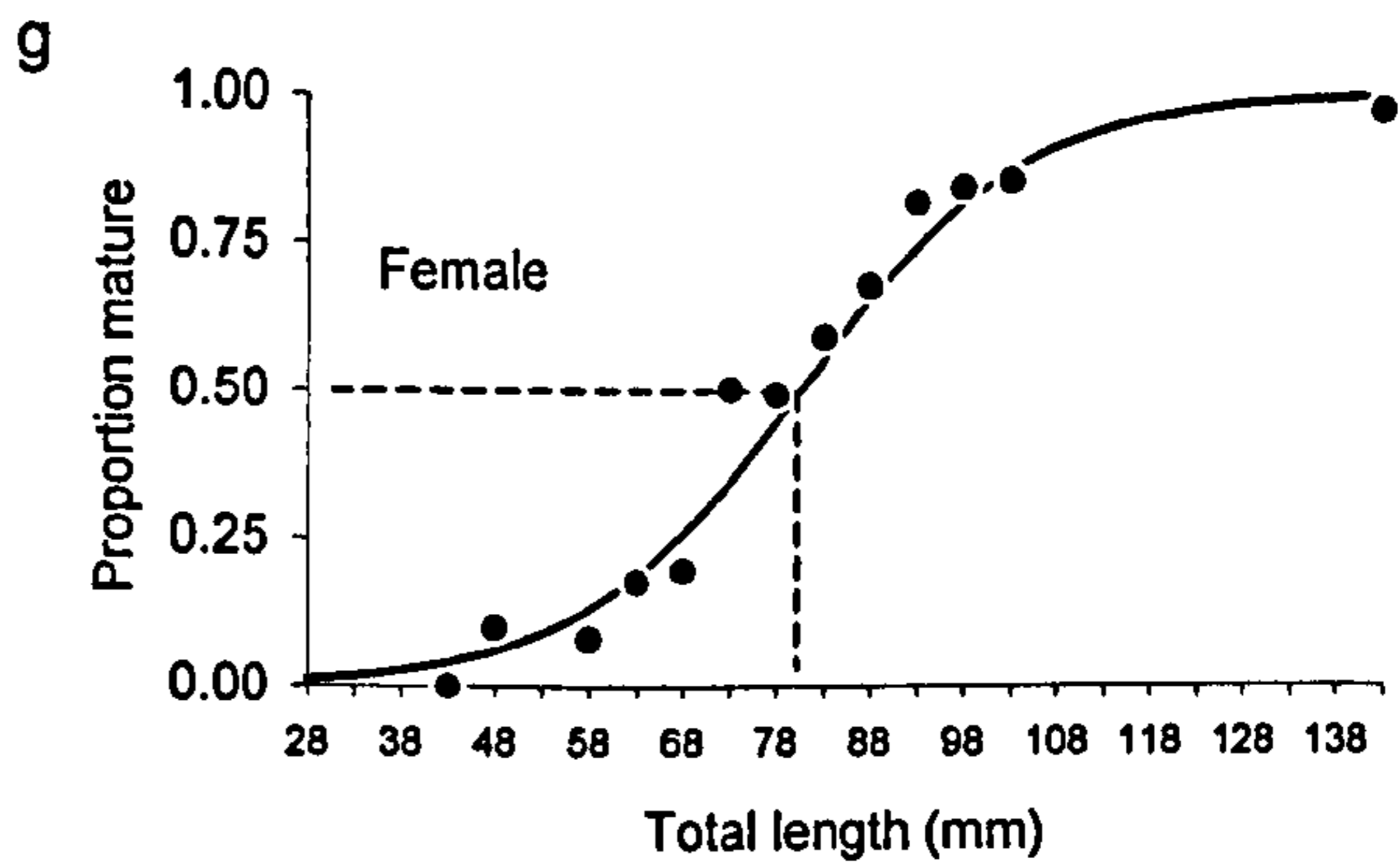
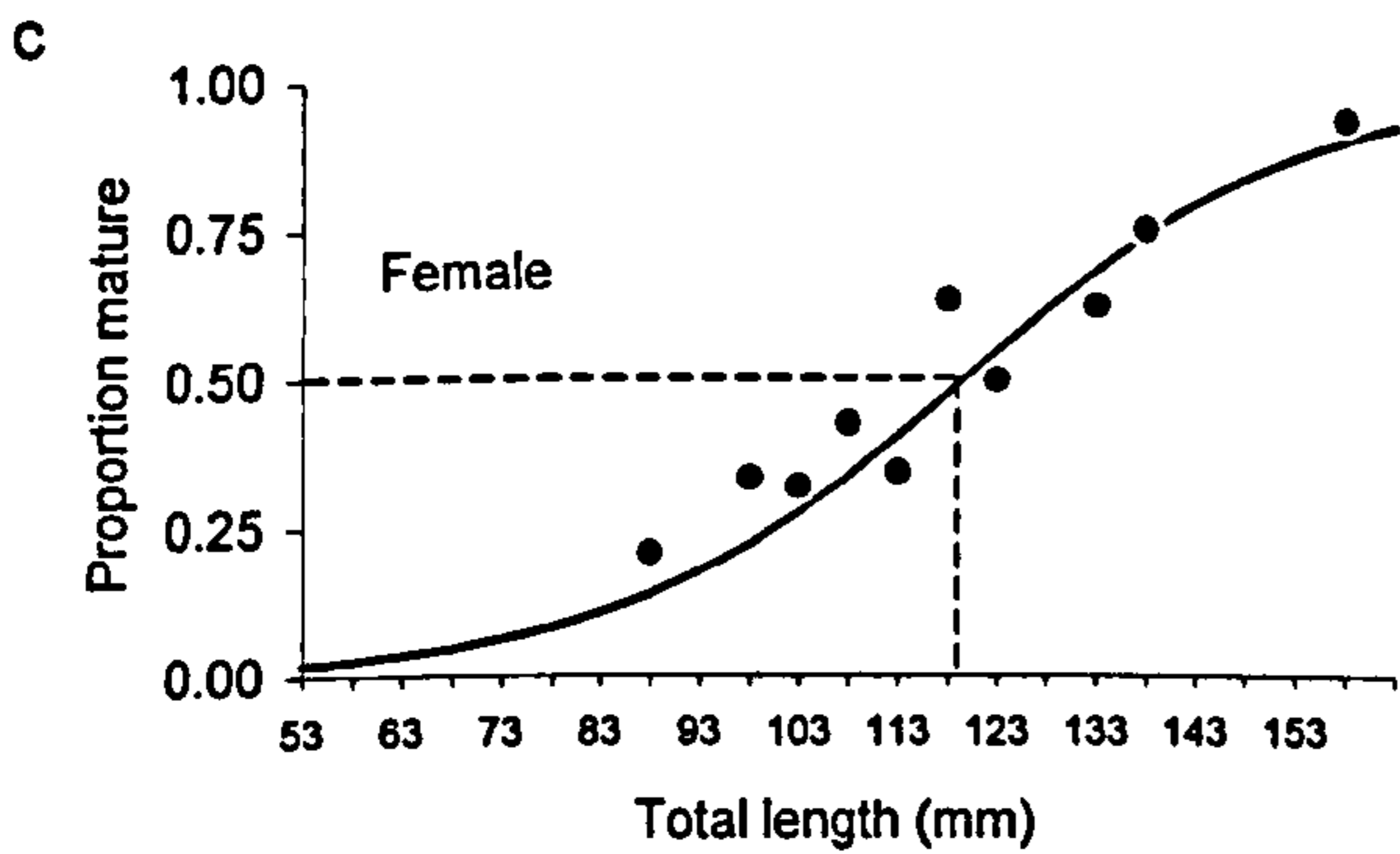
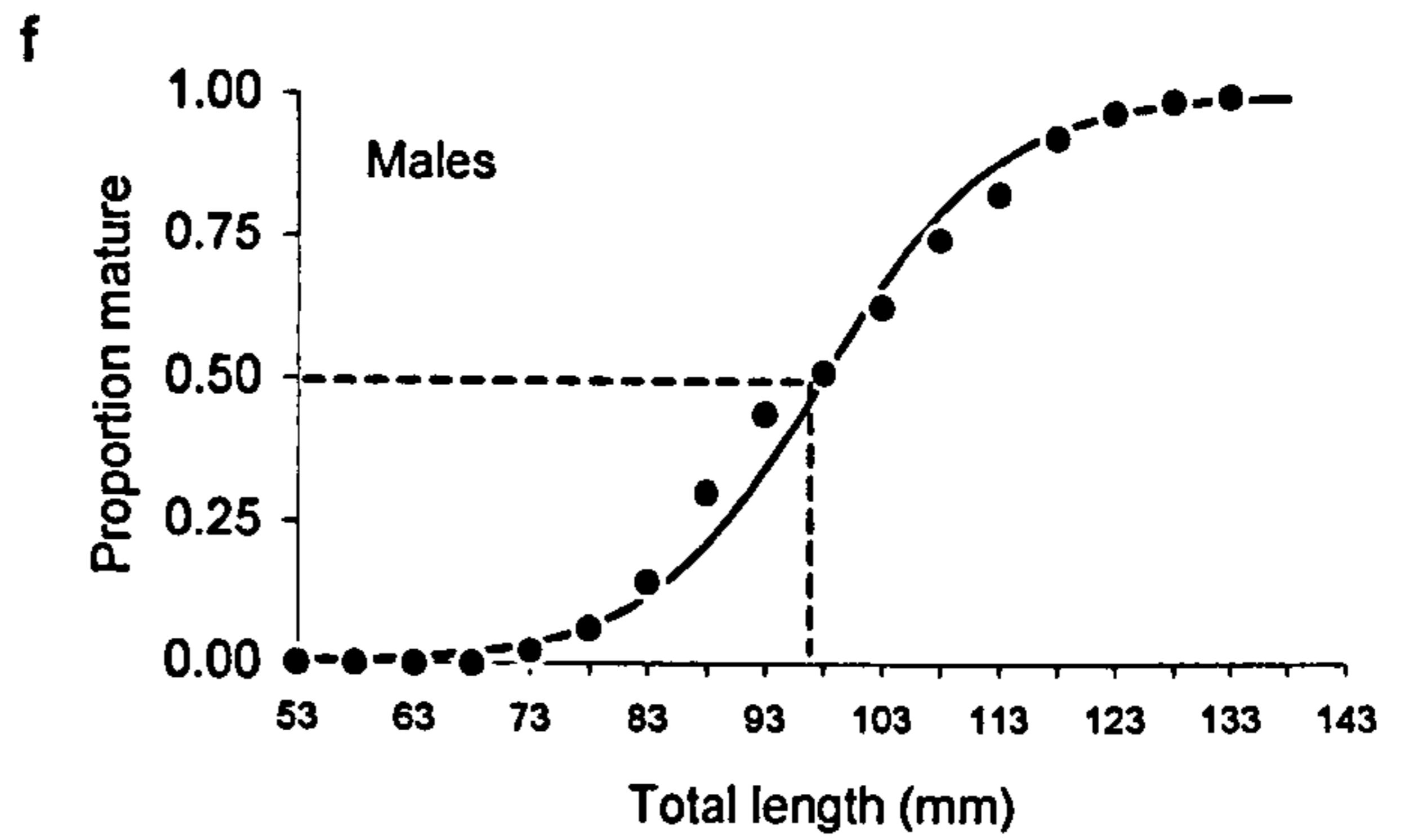
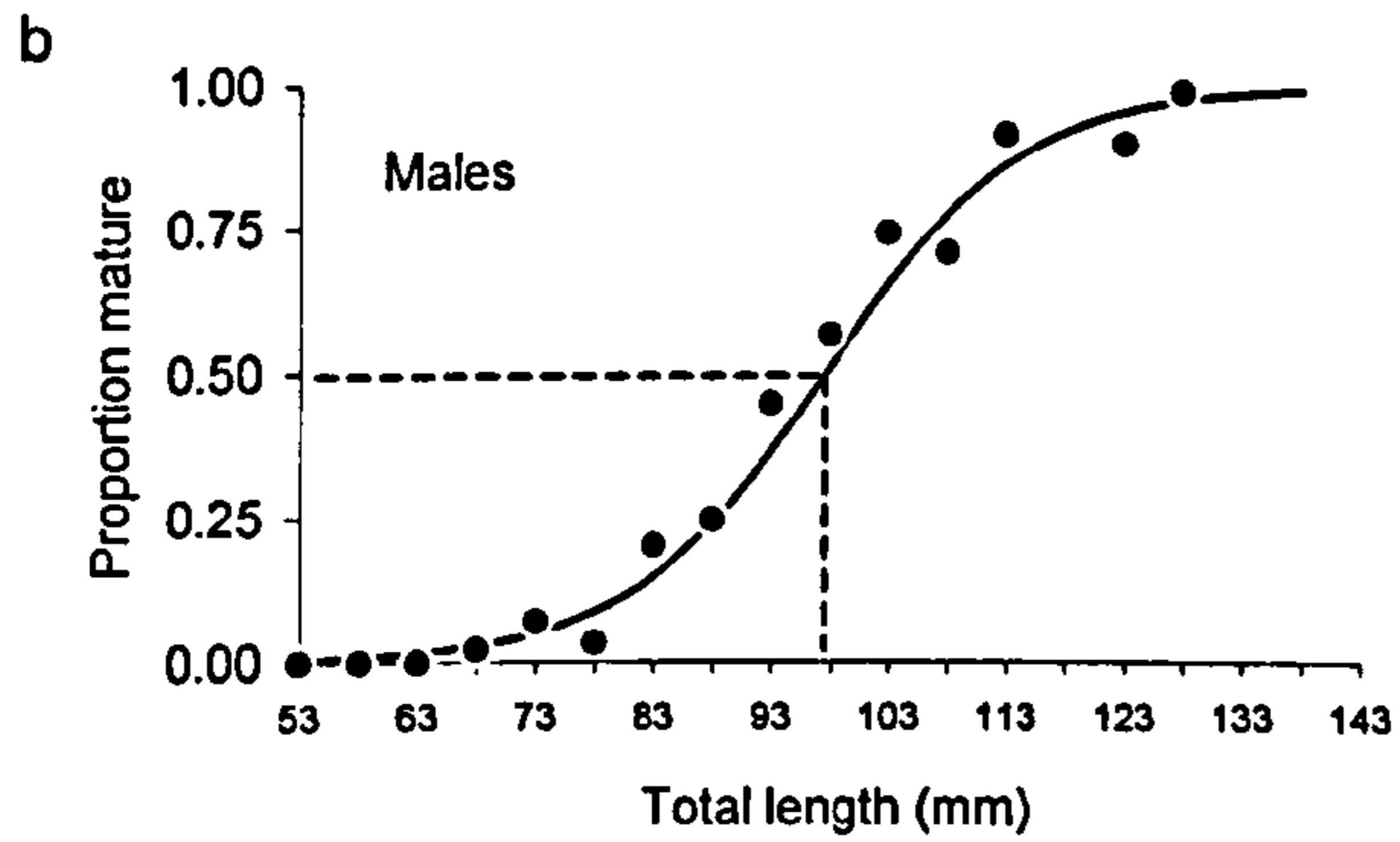
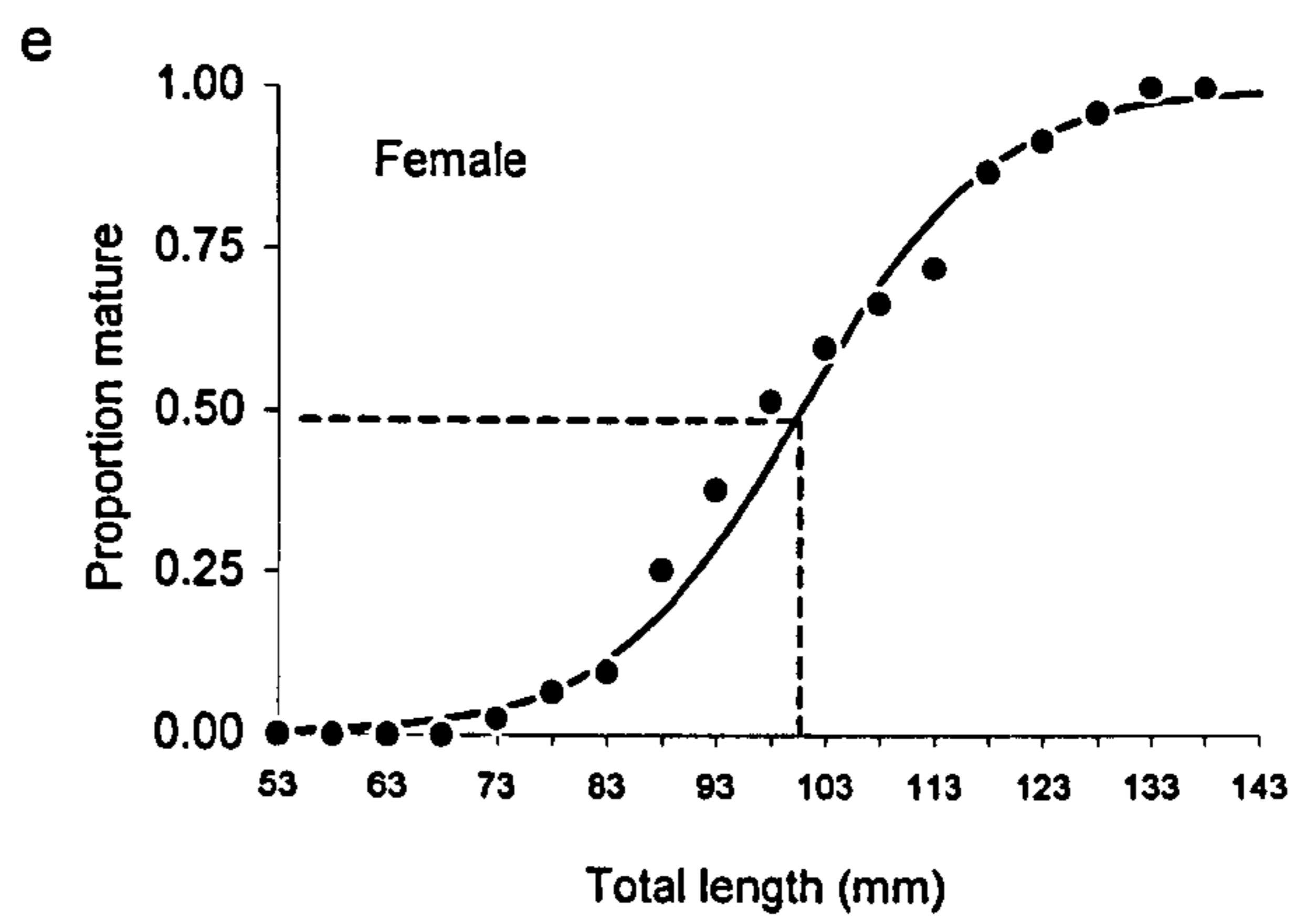
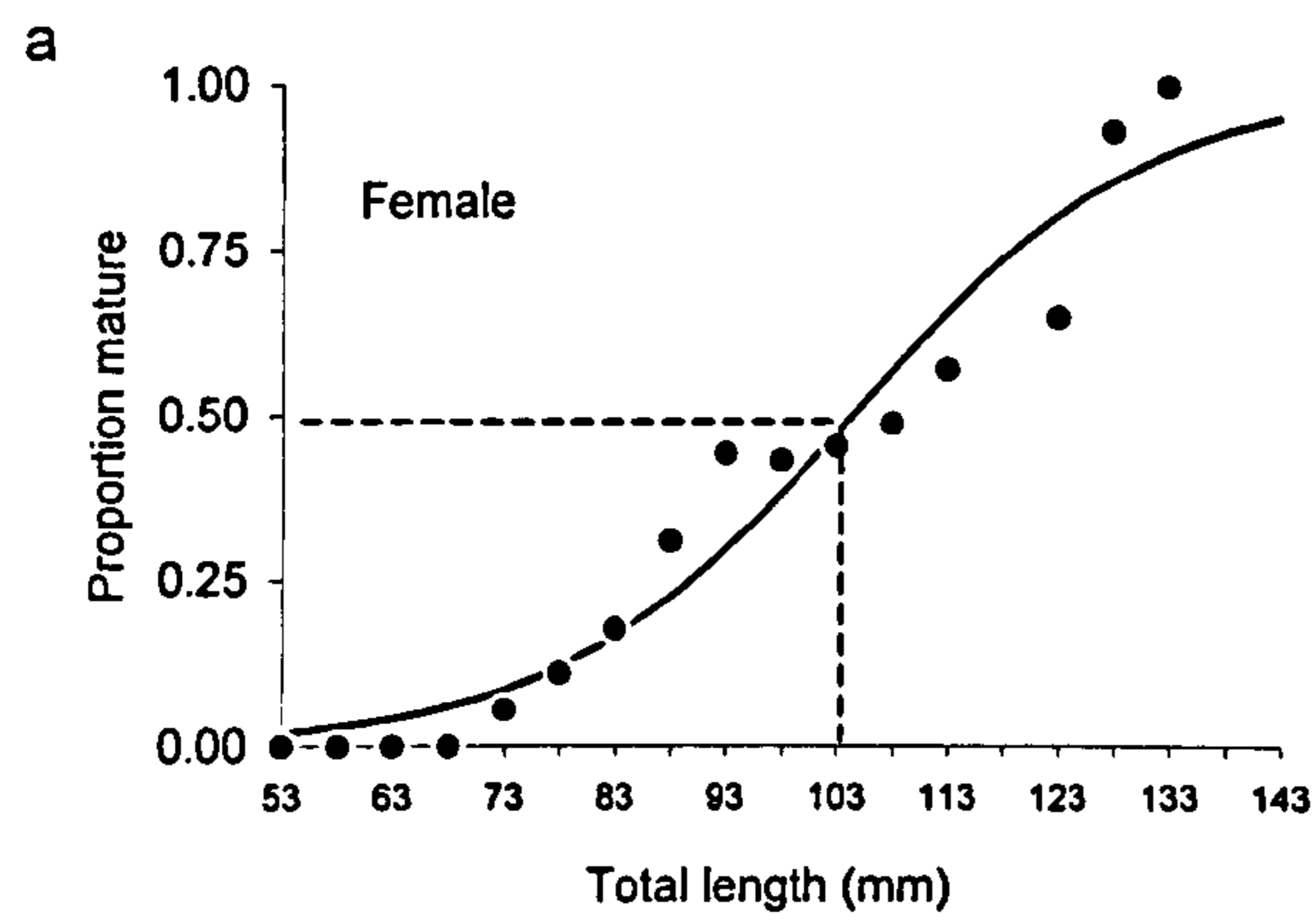


Figure 17. Proportion of mature individuals of *L. miodon* from (a, b) Bujumbura and Uvira pooled samples, (c, d) Kigoma, (e, f) Kalemie, and (g, h) Mpulungu samples. Data were fitted to the logistic equation (see Table 5, p. 42). Dotted line indicates  $L_m$ .

which was not repeated in 1995 (Fig. 18a). Other pulses occurred in November-December 1993 but this did not occur in 1994 and seems to have been delayed until February-March 1995.

Monthly deviations from mean proportion of recruits in the samples (Fig. 18b) highlighted that in two years (1993-94) out of three *L. miodon* recruitment lasted from two to five months during the dry season. In 1993 it started in August and in 1994 in May, in both years it ended by October. In 1995, unlike the preceding two, the main recruitment phase started in January and was over by May.

Recruitment to the beach seine fishery at the southern end of the lake was sustained throughout the year with increased intensity at the onset of the dry season (April/June) (Fig. 18c). The apparent lack of recruits during the second half of 1993 was probably due to the overlooking of unselective fishing gears (such as beach seines with mosquito netting as codend covers) at the initial stage of the sampling programme. However, over the two-year period (1994-96) the proportion of recruits was higher from April-May to June-July and from September and November until December and January (Fig. 18d).

### 3.3 *Lates stappersii*

#### 3.3.1 Commercial catch composition.

Only open water gears exploited *L. stappersii* and virtually no adult fish occurred in catches north of the Rumonge sub-basin. Young individuals were caught in the northern area until they reached a length of 100 mm. Although Kigoma and Mpulungu purse seine fishing units are identical the composition of the catch was very different. Kigoma catch data showed a bimodal length frequency distribution composed of juveniles and adults while the Mpulungu catch consisted mainly of adult fish (Fig. 19). The values of  $L_c$  were very different in the two areas being 103 mm for Kigoma and 234 mm for Mpulungu. The Mpulungu industrial fishery is now entirely based on this

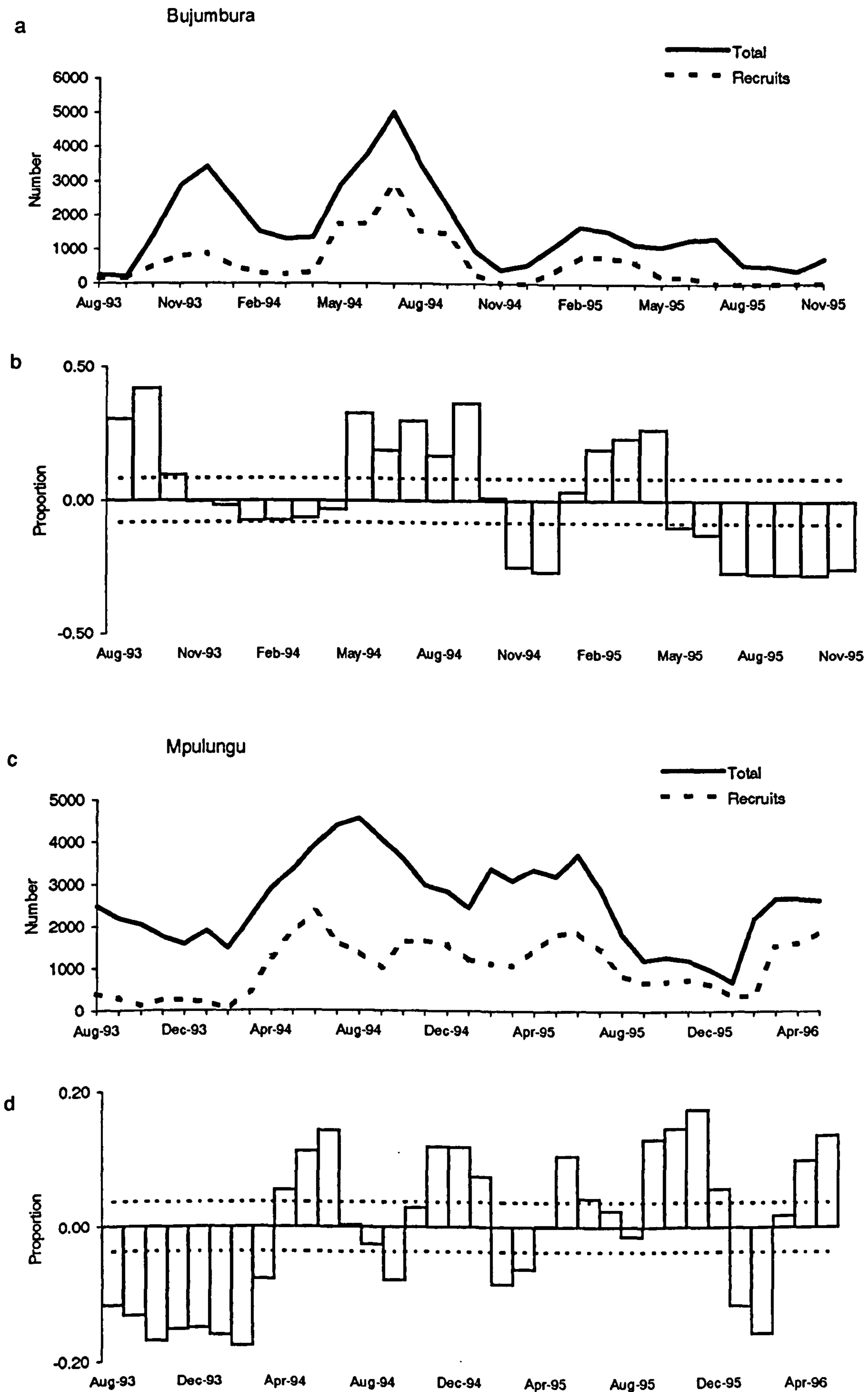


Figure 18. Moving average (a, c) over three months of *L. miodon* total number in samples and number of recruits and deviation from mean recruit proportion (b, d) in Bujumbura and Mpulungu samples. Body length of recruits was TL < 55 mm for Bujumbura and TL < 20 mm for Mpulungu data. Dashed lines in b and d are the upper and lower 95% confidence limits of the mean.



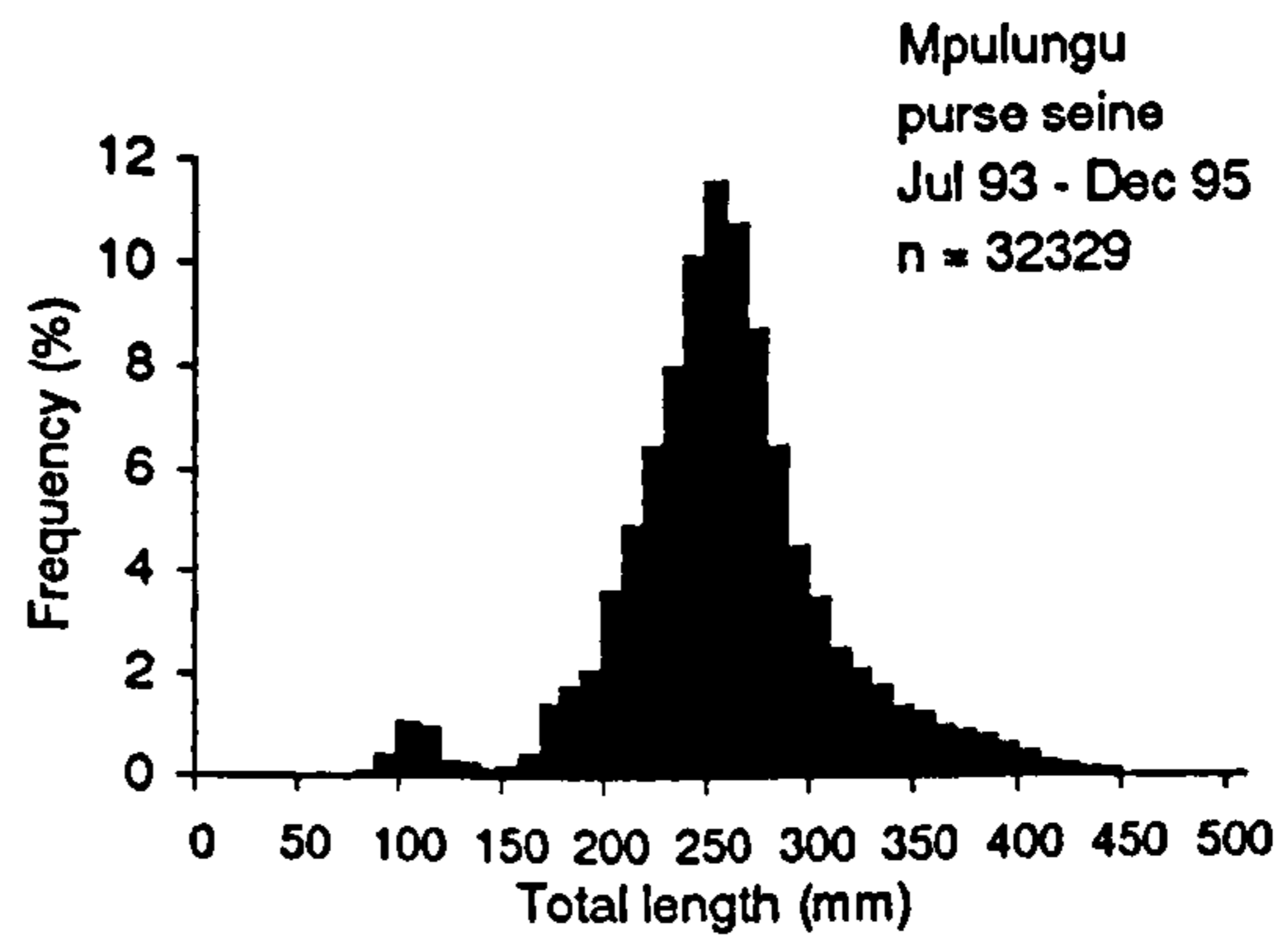
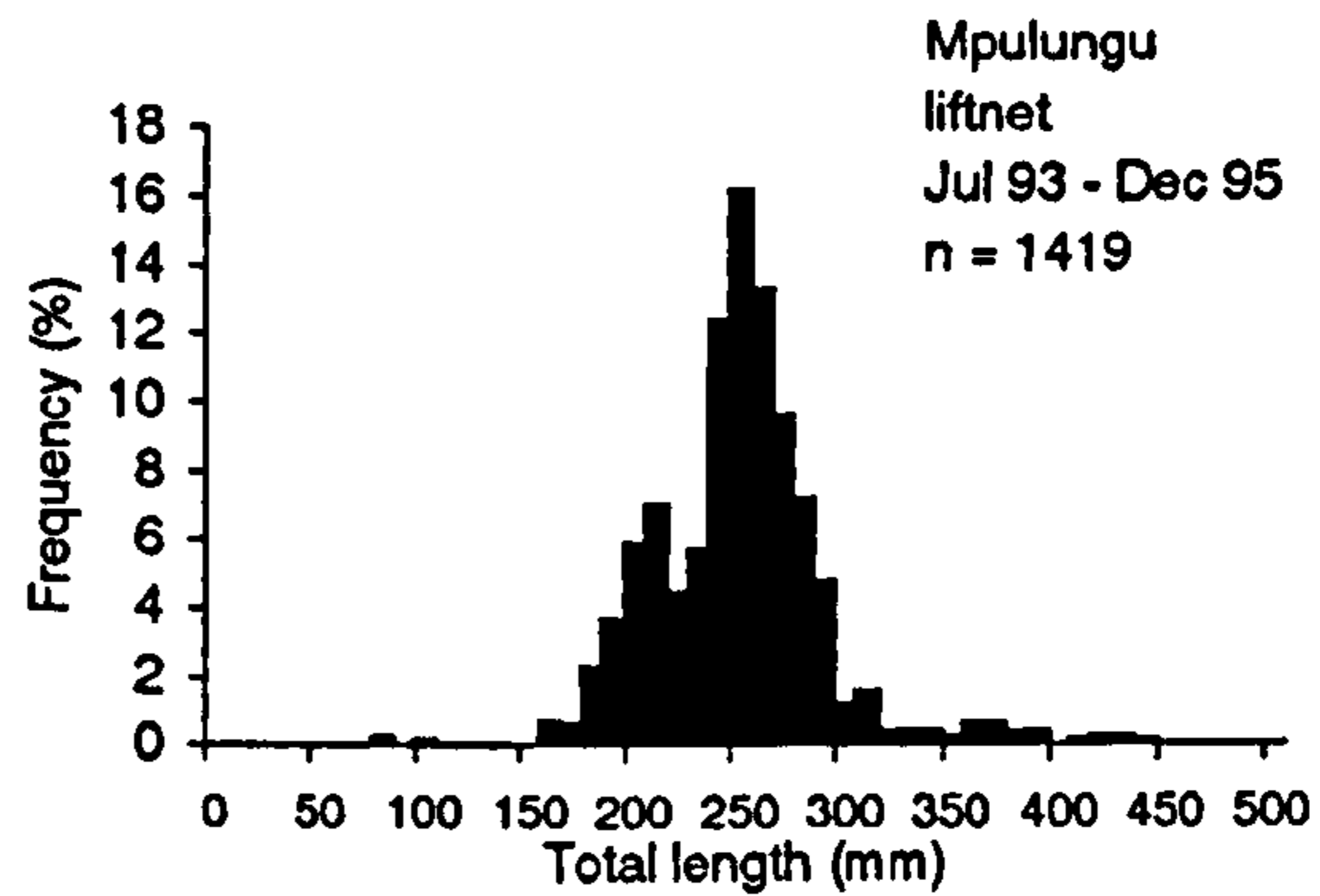
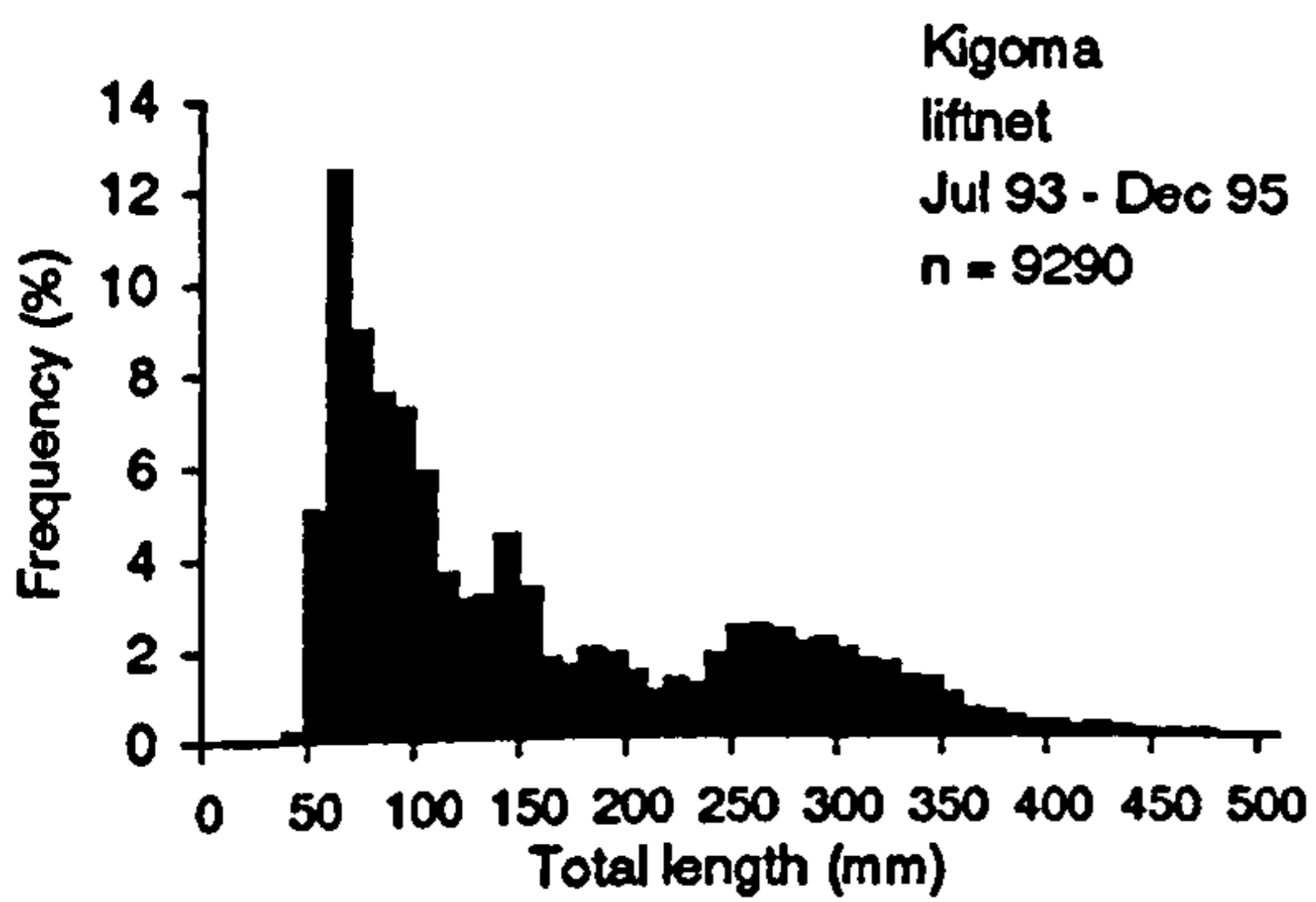
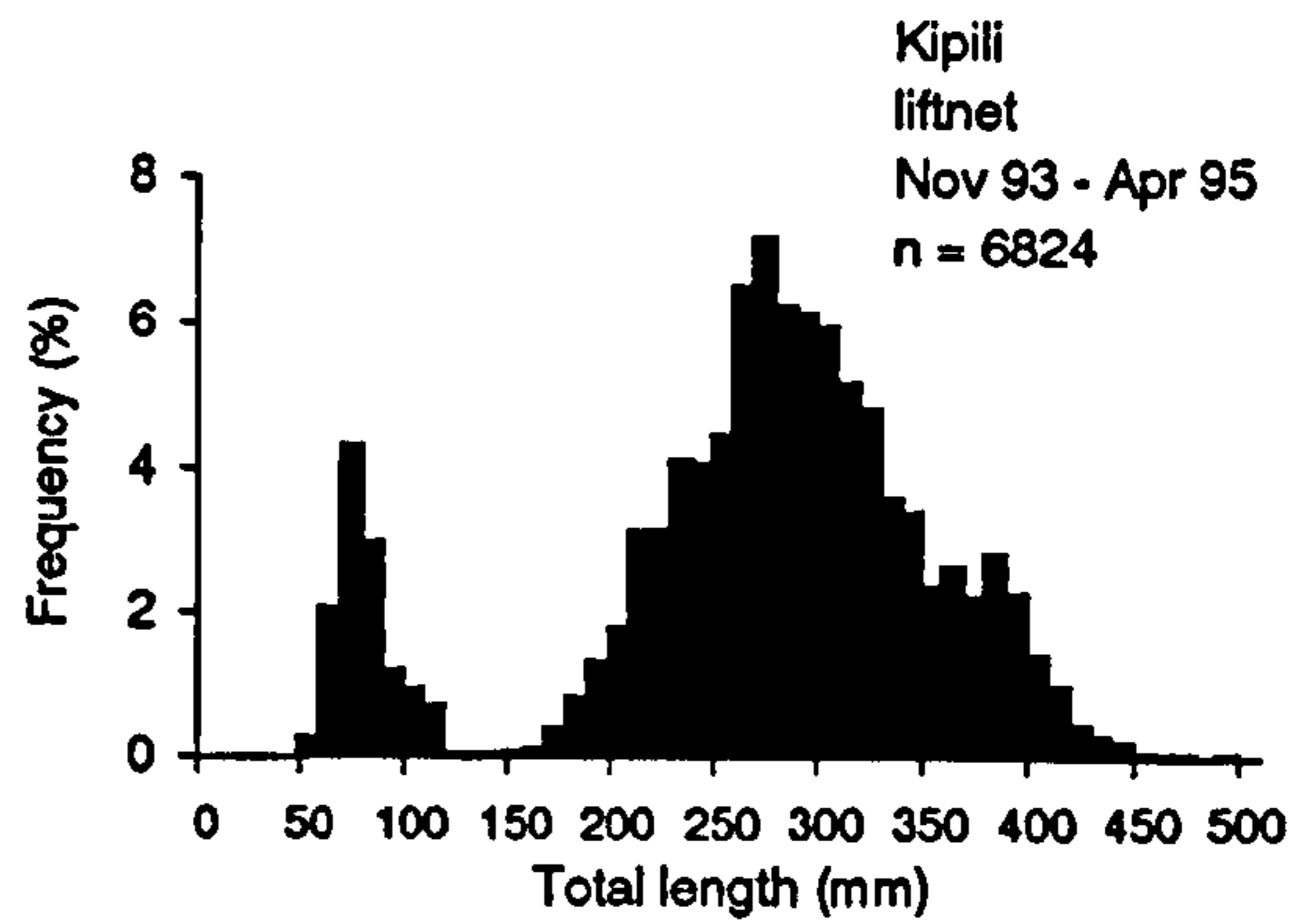
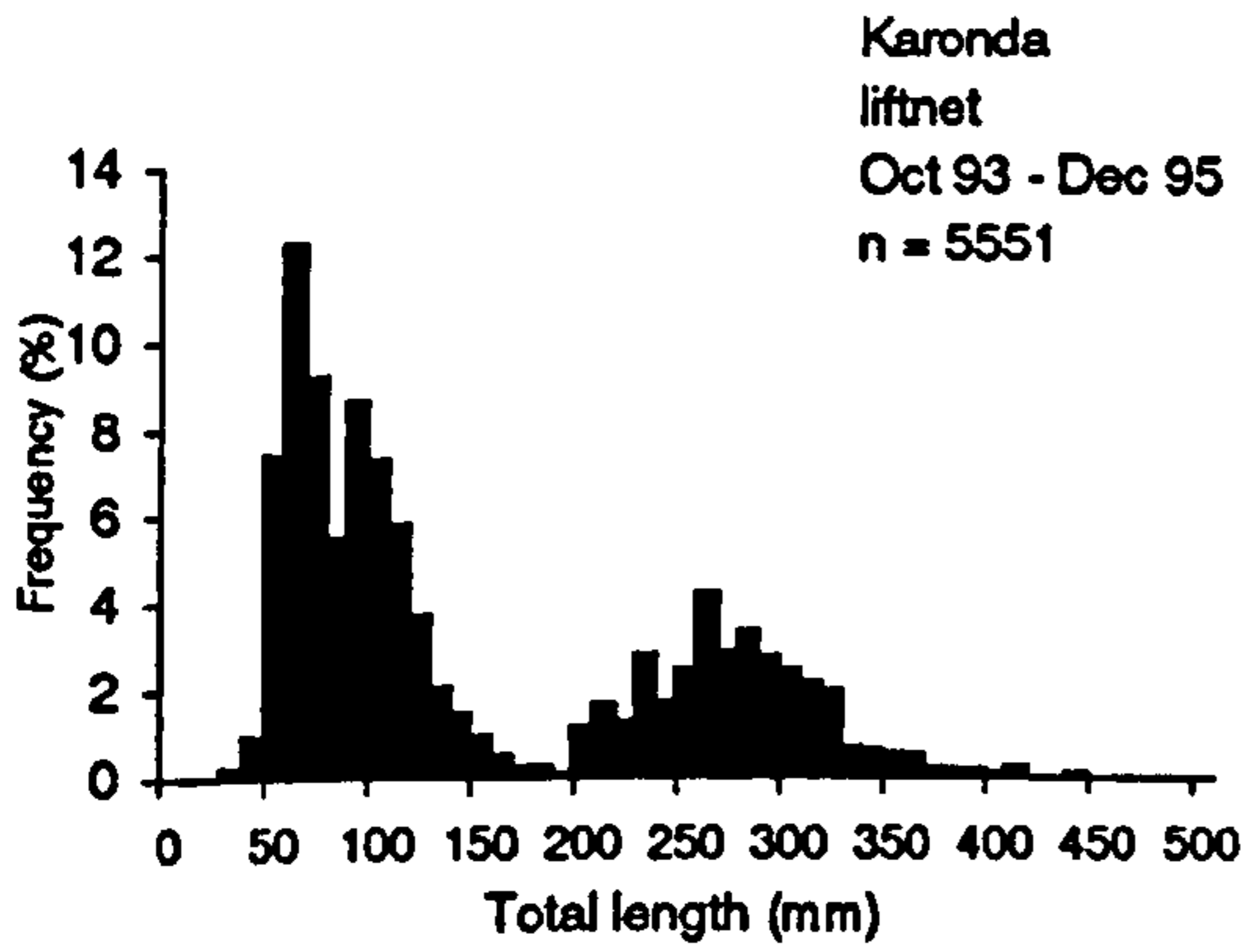
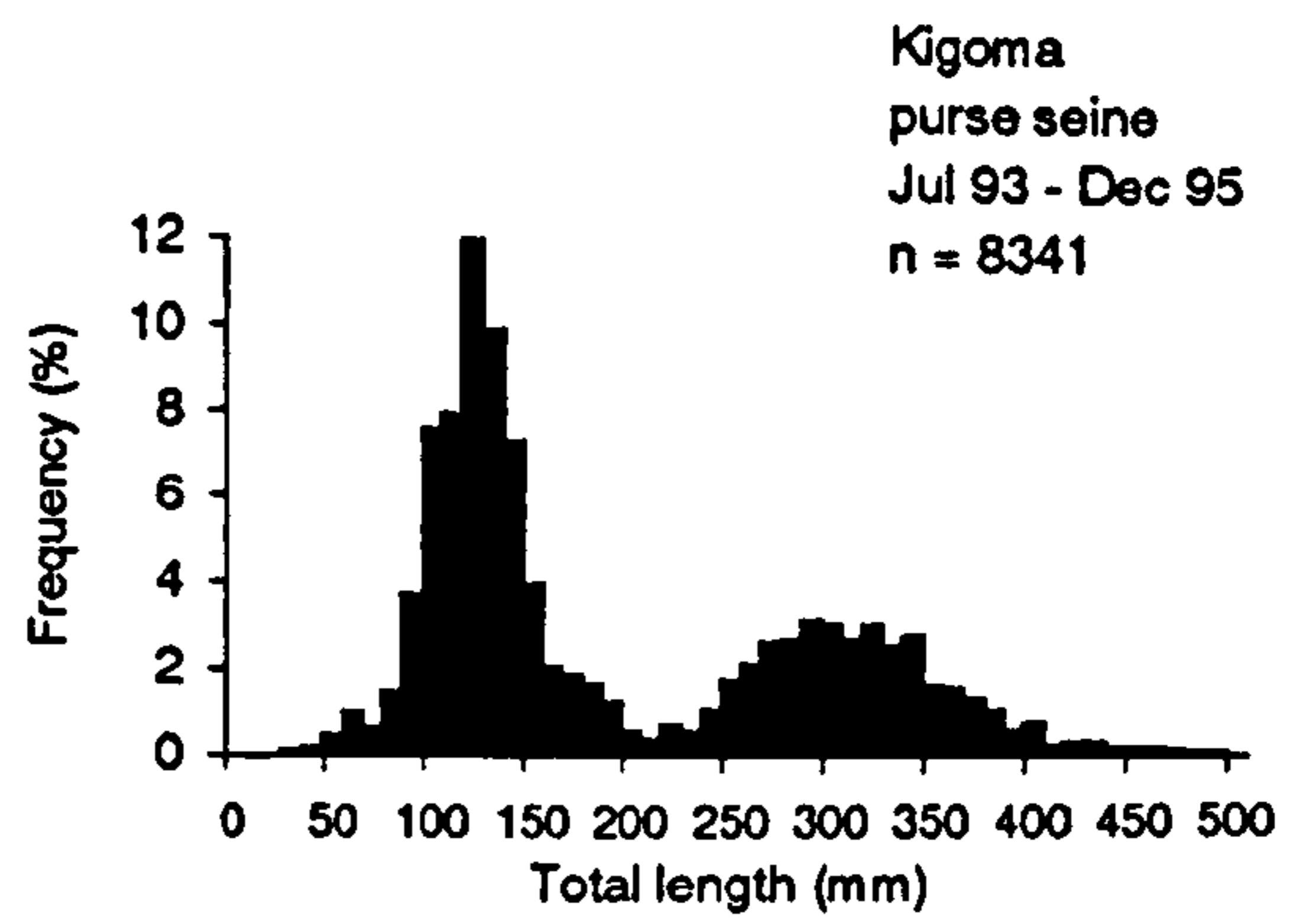
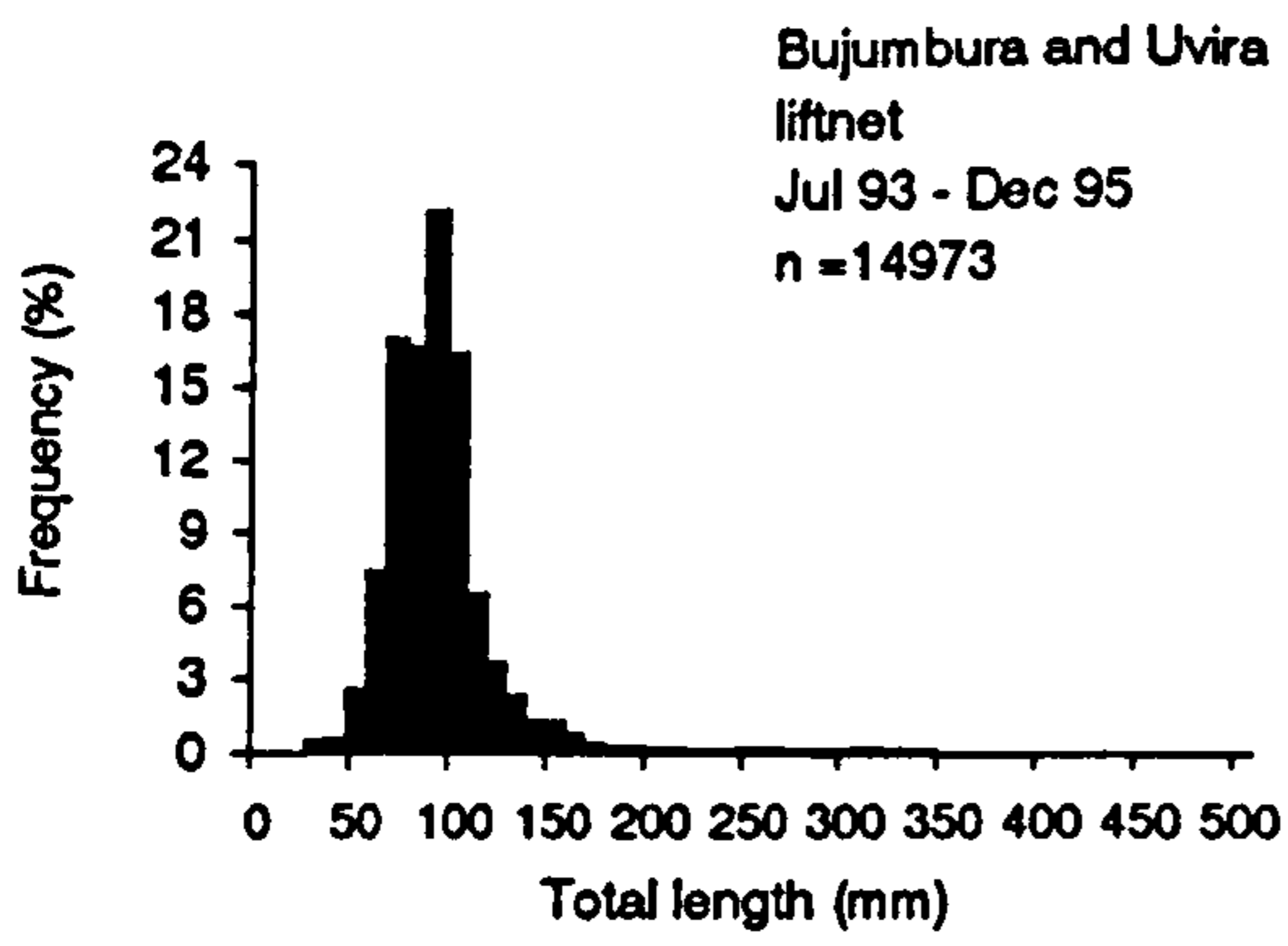


Figure 19. Length composition of the commercial catch of *L. stappersii* by area and fishing gear.

adult fish concentration in the south. However, juveniles were very rare in the commercial catch. The fact that an abundant adult stock exists in the south of the lake for the most of the year, including the reproductive period (see 3.3.3), suggested that one or several important nursery areas should occur, further north, outside the fishing grounds of the purse seine fishery.

### 3.3.2 Growth and mortality

Growth model coefficients for *L. stappersii* estimated by ELEFAN I and SLCA methods (Table 6) were close ( $CV$  of mean  $\Phi'$  was 0.50) ranging from 510 and 551 mm and 0.36 and 0.44  $\text{yr}^{-1}$  for  $L_{\infty}$  and  $K$  respectively. The major differences were from the Kipili data and these were probably due to the small number of available L/F distributions. The maximum lifespan of *L. stappersii* is about 7 yr with the majority of fish dying between the 5<sup>th</sup> and 6<sup>th</sup> year of life.

Mean values of mortality rates derived from the different methods ranged from 1.66 to 1.89  $\text{yr}^{-1}$  and 0.6 to 0.9  $\text{yr}^{-1}$  for  $Z$  and  $M$  respectively (Table 6). Total mortality was considerably higher in the south of the lake (mean  $Z$  from all methods was 2.24) than in the Kigoma area (mean  $Z = 1.17$ ). Catch curve analysis of survey data estimated  $Z = 1.90 \text{ yr}^{-1}$  ( $r = 0.98$ ; 95% CI = 1.75-2.06;  $L' = 140$  mm) which lies between the Kigoma and Mpulungu estimates. The estimates of  $M$  from the Peterson and Wroblewski model (1984) gave mean  $M = 1.4 \text{ yr}^{-1}$  and an adult mean  $M = 0.7 \text{ yr}^{-1}$  (Figs 8e and 8f).

Despite the inaccuracy in extrapolating  $F$  from  $Z$ - $M$  and thus the exploitation rate ( $E = F/Z$ ) it seems evident that the heaviest exploitation is experienced by *L. stappersii* in the southern area. The exploitation rate was below 0.4 at Kigoma and 0.6 at Mpulungu. This is a consequence related to the allocation of the fishing effort, and thus fishing mortality, for this species which is the highest in this area of the lake.

Table 6. Von Bertalanffy growth model coefficients ( $L_{\infty}$  and  $K$  from the Elefan I method), total ( $Z$ ) and natural ( $M$ ) mortality estimates for *L. stappersii* from various areas. The second set of growth parameters is from the SLCA method. Roman numerals indicate the methods used. I: length-converted catch curve (95% CI and cutoff length,  $L'$ , in brackets); II: Beverton and Holt, 1956; III: Ault and Ehrhardt, 1991; IV: Pauly, 1980; V: Rikhter and Efanov, 1976; VI: Gunderson and Dygert, 1988; VII: Alagaraya, 1984. Exploitation rates ( $E$ ) are estimated from catch curve's  $Z$  and Pauly's  $M$ . Mean length at first capture,  $L_c$ , based on the method of Pauly (1987). Whole lake area refers to  $Z$  estimate obtained from survey data and using the mean  $L_{\infty}$  and  $K$  estimated from commercial catch data as input parameters.

Area	$L_{\infty}$ TL (mm)	$K$ yr <sup>-1</sup>	$\Phi'$	$Z$ yr <sup>-1</sup> I	$Z$ yr <sup>-1</sup> II	$Z$ yr <sup>-1</sup> III	$M$ yr <sup>-1</sup> IV	$M$ yr <sup>-1</sup> V	$M$ yr <sup>-1</sup> VI	$M$ yr <sup>-1</sup> VII	$E$ ( $E = F/Z$ )	$L_c$ (TL) mm
Kigoma	519	0.44	5.070	1.35 (1.25-1.46; 300mm)	1.16	1.15	0.9	0.9	0.5	0.7	0.37	103
	506	0.43	5.038	1.18 (1.08-1.28; 300mm)	1.08	1.07	0.8	0.8	0.5	0.7	0.28	97
Kipili	551	0.41	5.096	2.33 (2.07-2.59; 260mm)	1.82	1.80	0.8	0.9	0.5	0.6	0.65	250
	550	0.36	5.031	2.00 (1.78-2.23; 260mm)	1.56	1.46	0.7	0.8	0.4	0.5	0.63	250
Mpulungu	510	0.42	5.036	2.11 (1.99-2.22; 250mm)	2.20	2.18	0.8	0.9	0.5	0.6	0.61	234
	530	0.40	5.051	2.35 (2.20-2.50; 250mm)	2.30	2.29	0.8	0.9	0.5	0.6	0.66	239
Mean	528	0.41	5.054	1.89	1.69	1.66	0.8	0.9	0.5	0.6	0.53	
Whole lake				1.90 (1.75-2.06; 140mm)								

Table 7. Linear regression estimates for the parameters of the logistic equation relating proportion mature to length for *L. stappersii* (see also text and Figs 23 and 24). The correlation coefficient ( $r$ ), predicted length at 50% maturity ( $L_m$ ), 95% confidence intervals and sample size ( $n$ ) are also given.

Sex and areas	a	b	r	$L_m$ (mm)	95% CI for $L_m$	n
<b>Females</b>						
Kigoma	7.189	-0.026	0.912	278	217-338	1687
Mpulungu	8.130	-0.034	0.9677	237	214-260	4217
<b>Males</b>						
Kigoma	8.090	-0.029	0.974	278	253-303	1186
Mpulungu	3.976	-0.016	0.956	255	213-298	5702

### 3.3.3 Reproduction

The changes in the monthly mean values of the GSI of *L. stappersii* differ between Kigoma and Mpulungu (Fig. 20). Kigoma data did not show a clear seasonal pattern, while at Mpulungu the reproductive effort, as shown by the GSI, clearly increased from October to March. Common to both the Kigoma and Mpulungu data was the apparent decrease in GSI mean values during the second sampling year (March 1995 - March 1996).

The composition by sexual maturity stage of the catch showed that while in the Kigoma area both immature and adult *L. stappersii* were equally exploited (Fig. 21), in the south the catch consisted mainly of mature fish (Fig. 22). In the Kigoma area the proportion (%) of mature fish increased mainly between September and March. The occurrence pattern of mature *L. stappersii* was very clear at Mpulungu where within a one-year cycle the maturation started during the transition from the dry to wet season (September-October) to end around April, probably reflecting the time of spawning.

Mean length at maturity ( $L_m$ ) could be estimated only from the Kigoma and Mpulungu samples due to the absence of adult fish in the samples from the north of the lake (Figs 23 and 24).  $L_m$  was 278 mm for both sexes at Kigoma and  $L_m = 237$  mm and  $L_m = 255$  mm for females and males respectively at Mpulungu (Table 7). At Mpulungu the  $L_m$  estimate for females was affected by the occurrence of large-sized individuals which were not fully mature. The mean  $L_m$  for both sexes was 16% smaller than  $L_m = 311$  mm predicted by the optimal  $L_m$  theory (Roff, 1986, 1992).

*Lates stappersii* becomes sexually mature during the second year of life at an age of about 1.7 yr. It reached this maturity relatively early during the growth process:  $L_m/L_8$  ratio is 0.51.

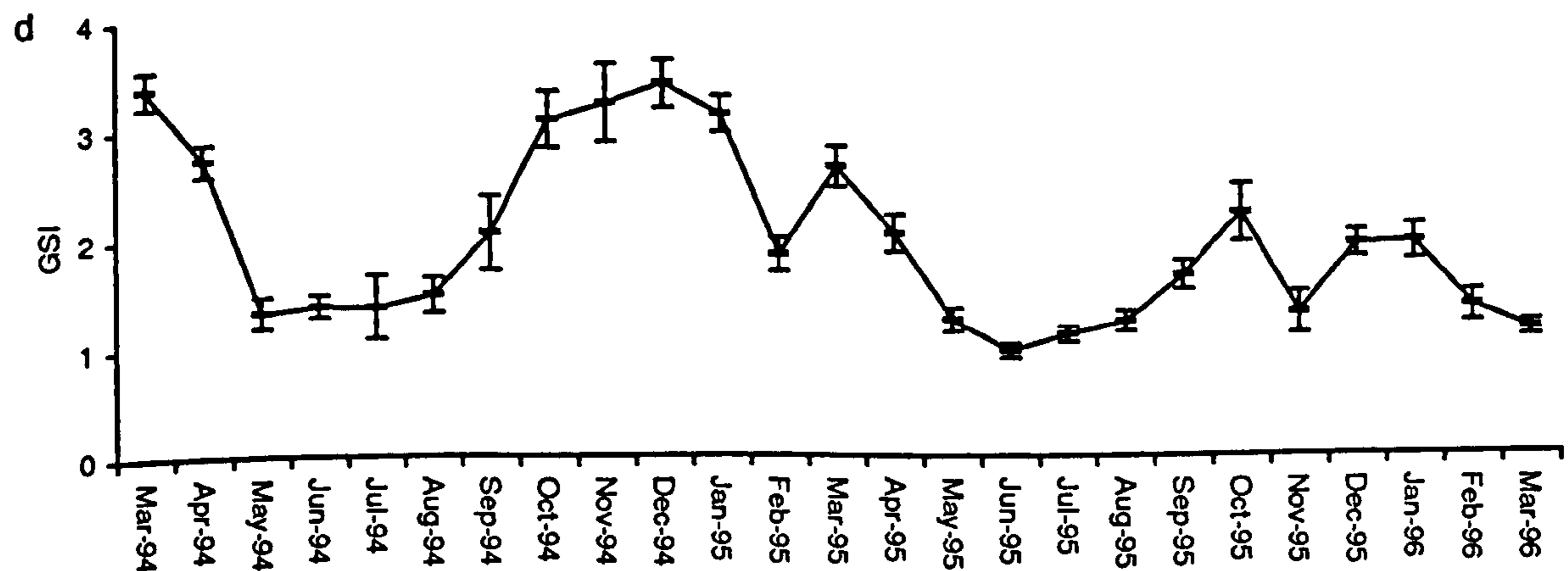
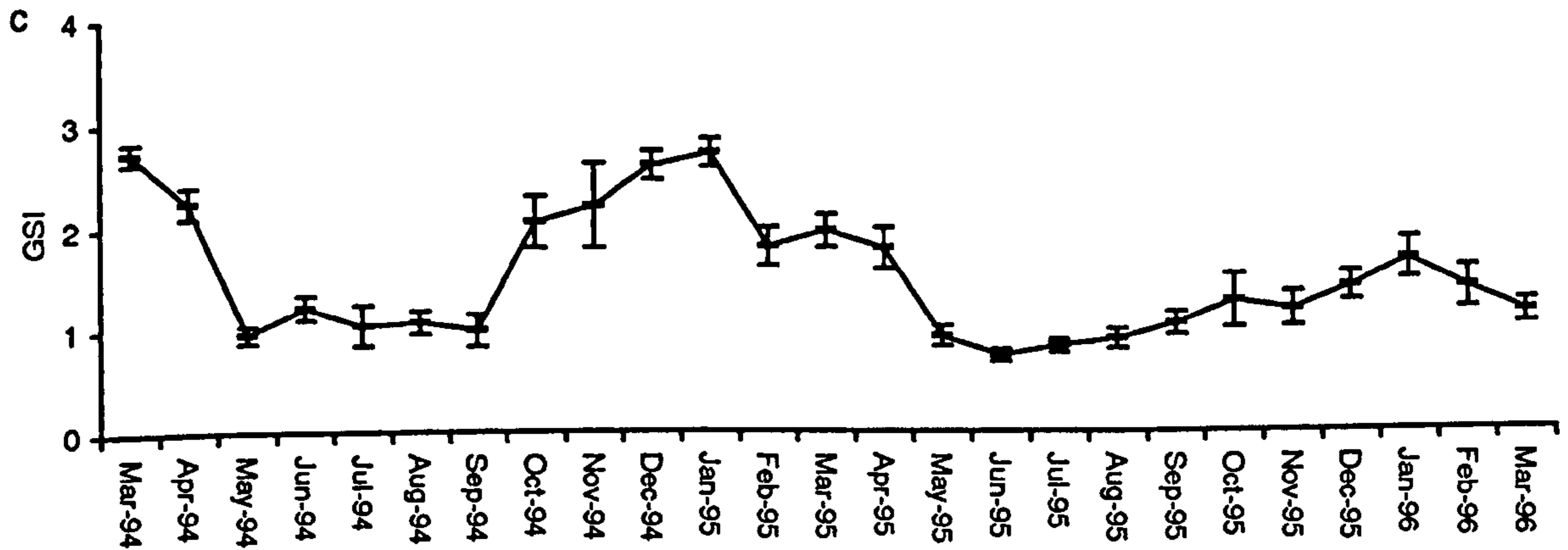
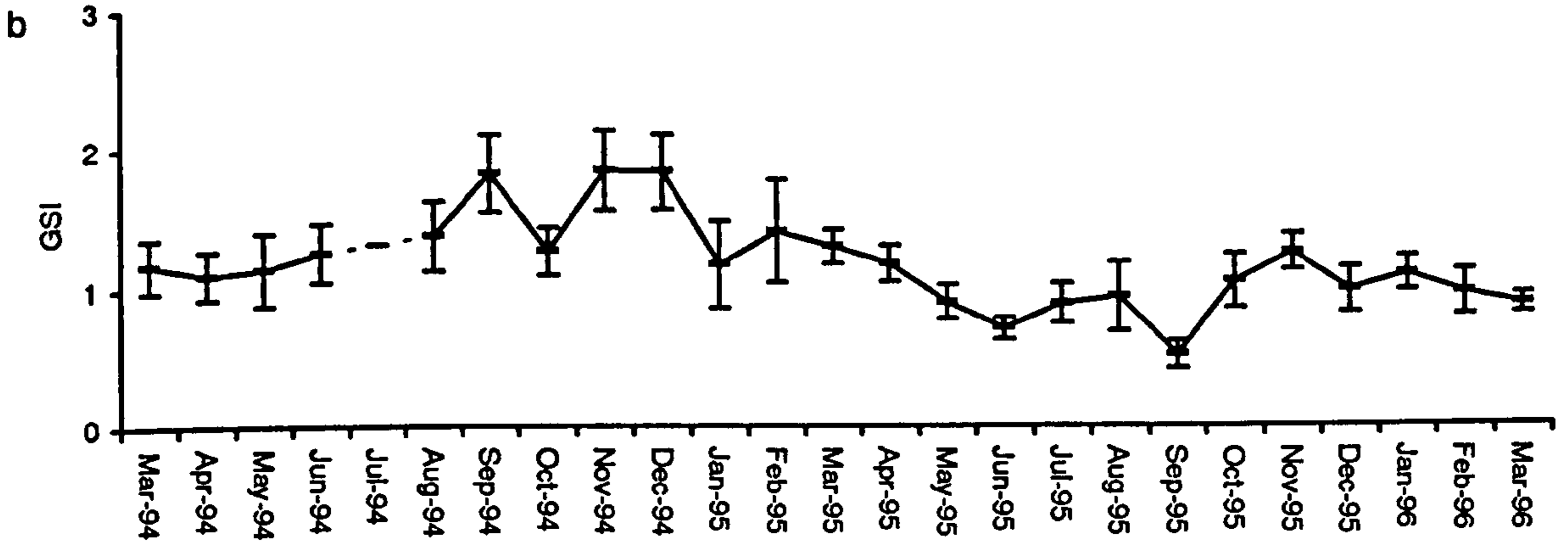
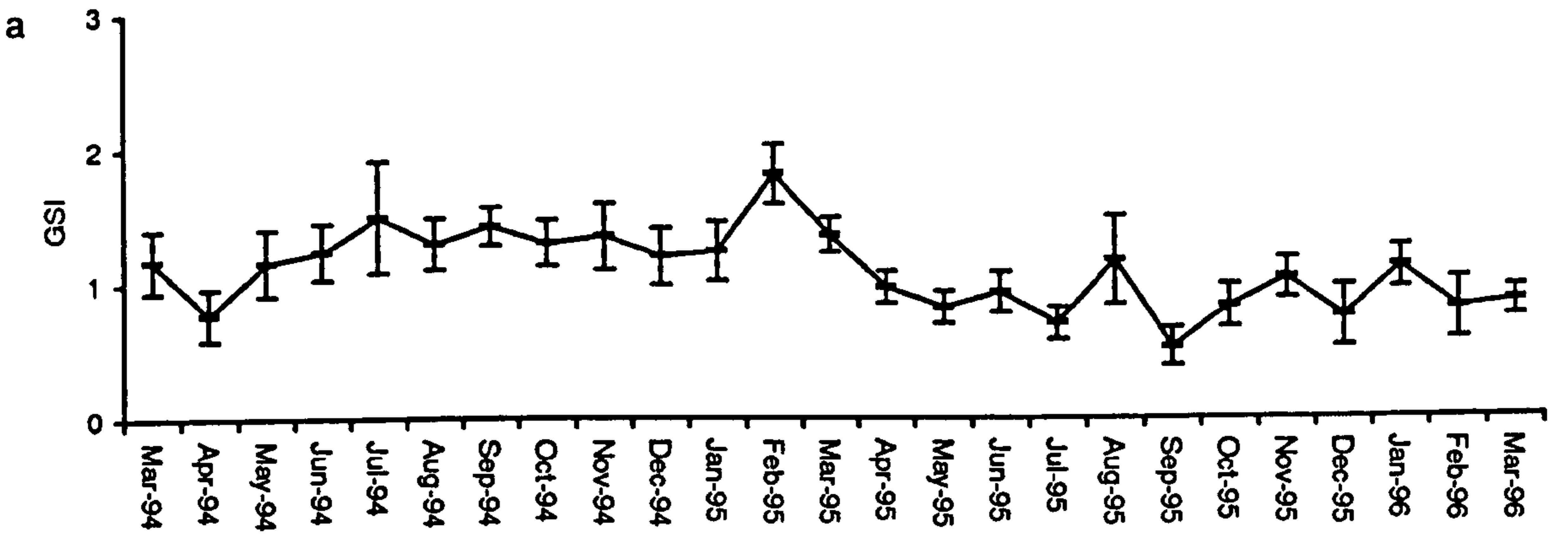


Figure 20. Monthly mean GSI of : a, *L. stappersii* females (n = 2828) and, b, males (n = 2506) from Kigoma samples; c, females (n = 4960) and, d, males (n = 4422) from Mpulungu samples. Error bars indicate 95% confidence interval of the mean.

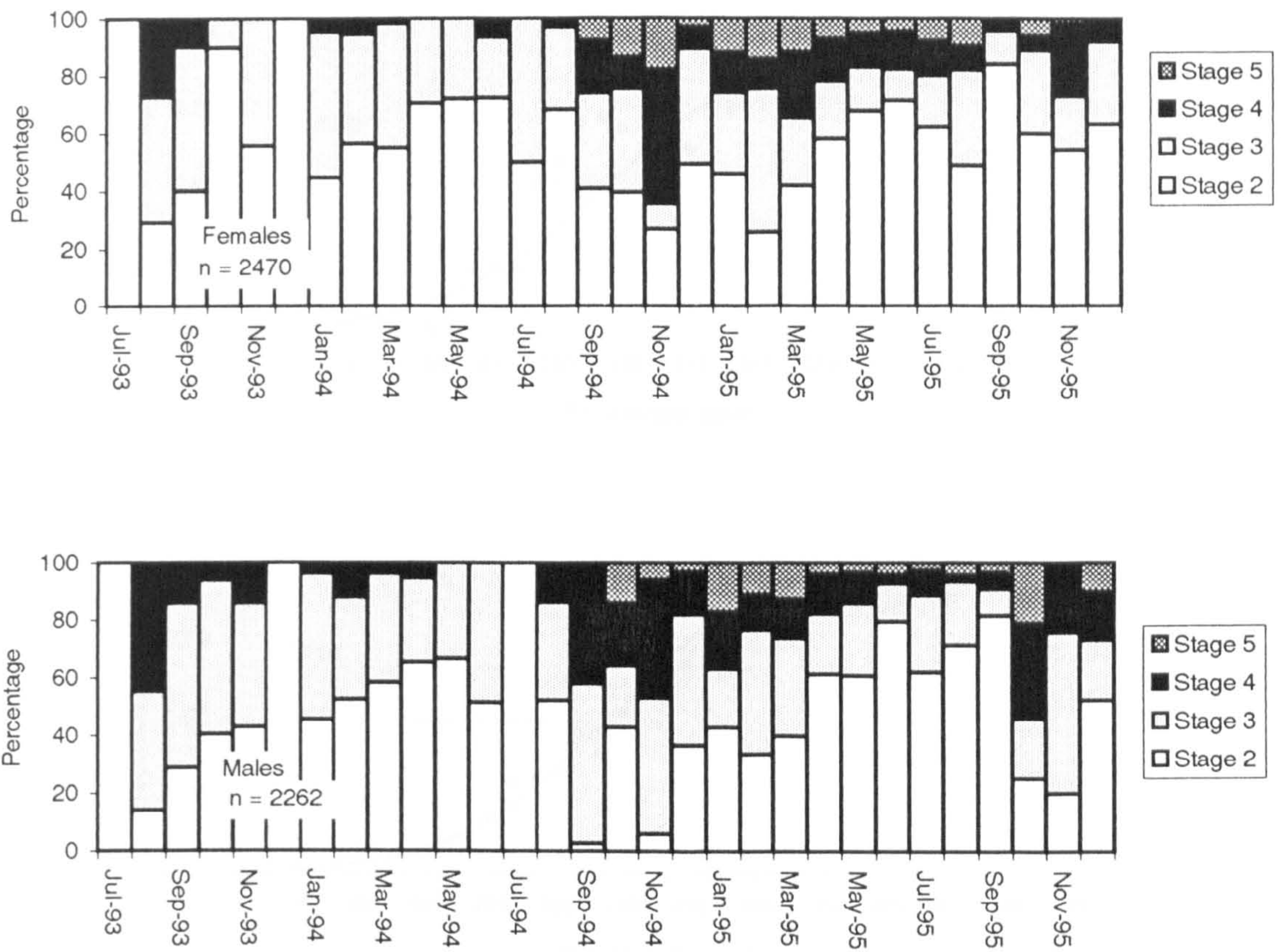


Figure 21. Monthly proportion (percentage) of maturity stages for *L. stappersii* in Kigoma area, n = sample size. No fish or only immature fish were caught in July and December 1993 (females), and in July, December 1993 1993 and July 1994 (males).

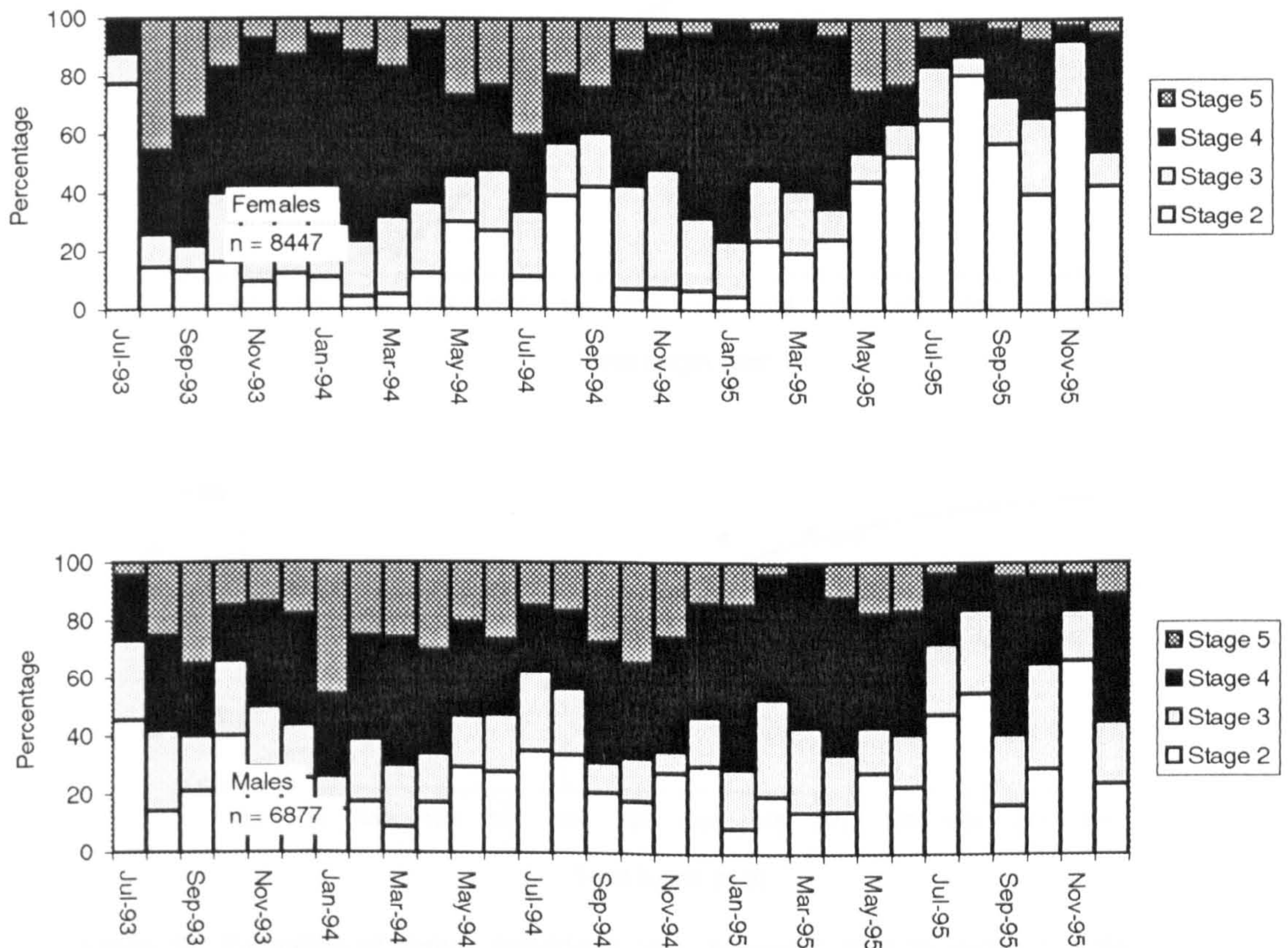


Figure 22. Monthly proportion (percentage) of maturity stages for *L. stappersii* in Mpulungu area, n = sample size.

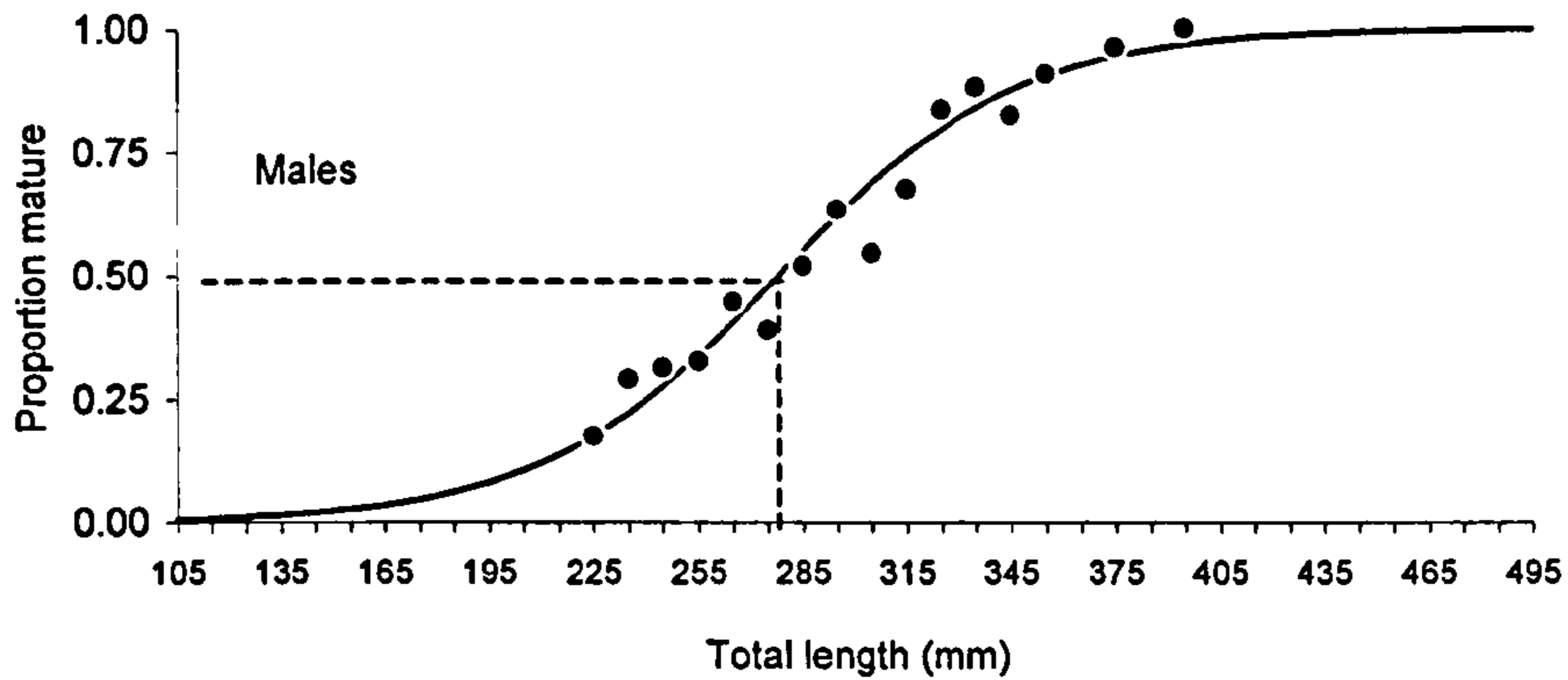
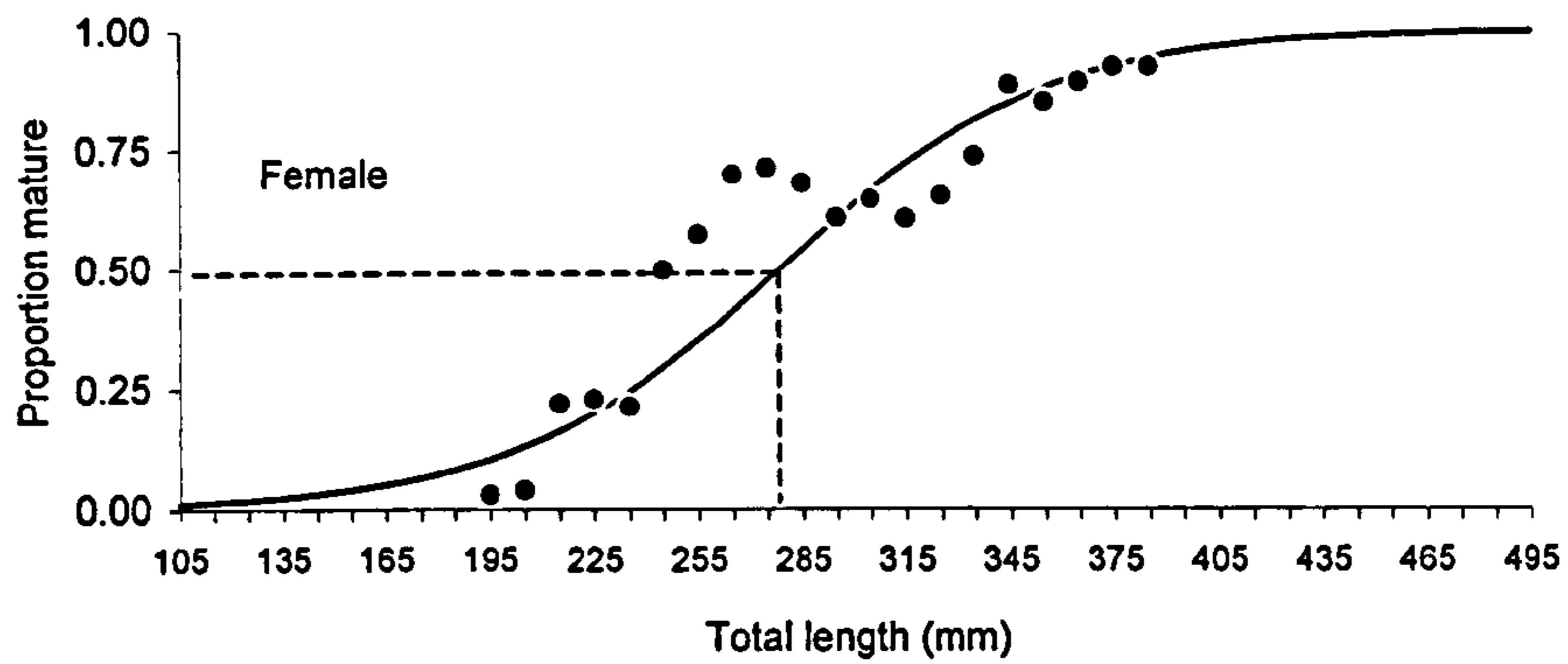


Figure 23. Proportion of mature individuals of *L. stappersii* from Kigoma samples. Data were fitted to the logistic equation (see Table 7, p. 52). Dotted line indicates  $L_m$ .

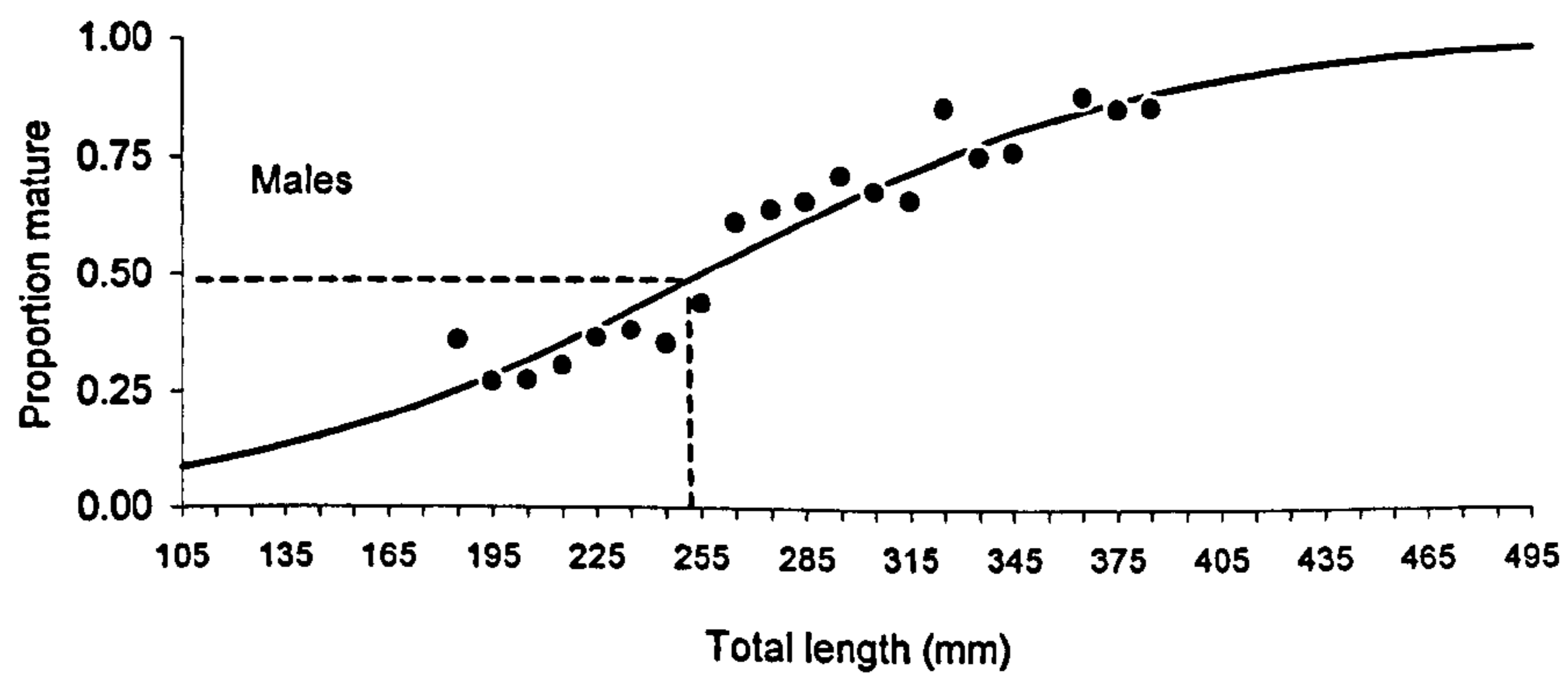
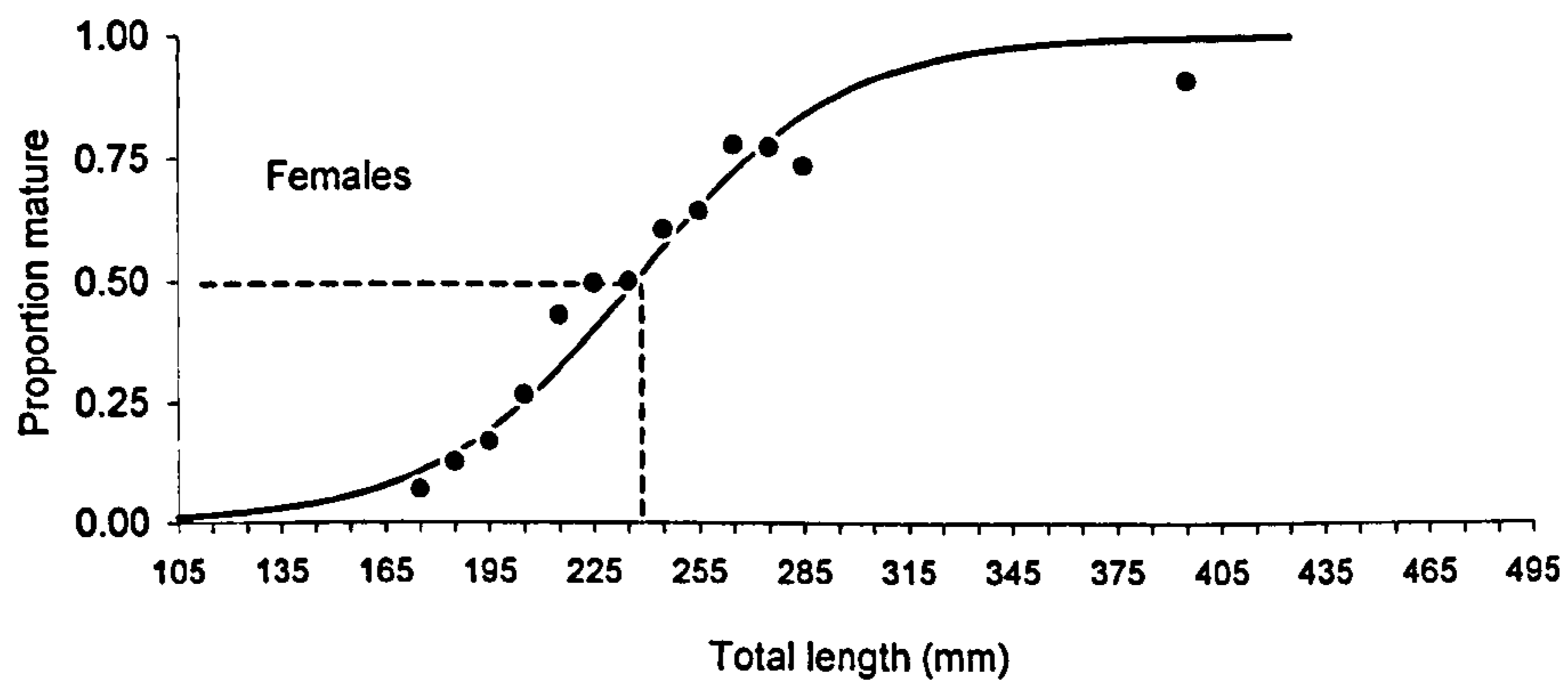


Figure 24. Proportion of mature individuals of *L. stappersii* from Mpulungu samples. Data were fitted to the logistic equation (see Table 7, p. 52). Dotted line indicates  $L_m$ .

### 3.3.4 Recruitment

No adult *L. stappersii* were caught by liftnets in the north of the lake. Within an annual cycle only one major recruitment pulse took place lasting four to five months from the end of the wet season (April-May) throughout the dry season with a possible extension to the onset of the next wet season (Figs 25a and 25b).

The recruitment to the Kigoma fishing grounds was similar to that of the north but, the single annual recruitment period started later around July extending through the dry season and ending in October-November (Figs 25c and 25d).

Both time series from northern and Kigoma areas indicated that *L. stappersii* has a single recruitment phase within the year and this was centred during the months of the dry season. As stated earlier, in the south of the lake, *L. stappersii* juveniles are never recruited to the purse seine fishery and only the adult stock is exploited.

Only in Kigoma were juveniles and adults found together in both liftnet and purse seine catches. The higher occurrences of sexually mature individuals (fish of TL >  $L_m$ ) were followed about 4 months later by the appearance of juvenile recruits in the catch (Figs 26a and 26b). This time lag between spawning and recruitment to the Kigoma fishery was also evident from the cross-correlation function (Fig. 27) which showed a strong positive association between mature fish and recruits on a time lag of four months.

### 3.3.5 Feeding ecology

A total of 4195 *L. stappersii* stomachs (1596 from Mpulungu and 2599 from Kigoma) were examined. No significant difference ( $\chi^2_{[8]} = 14.42, P > 0.05$ ) was found between the diet of males and females. In each month of the study no more than 11% of the stomachs examined were empty. Stomach fullness was mainly "nearly empty" or "half



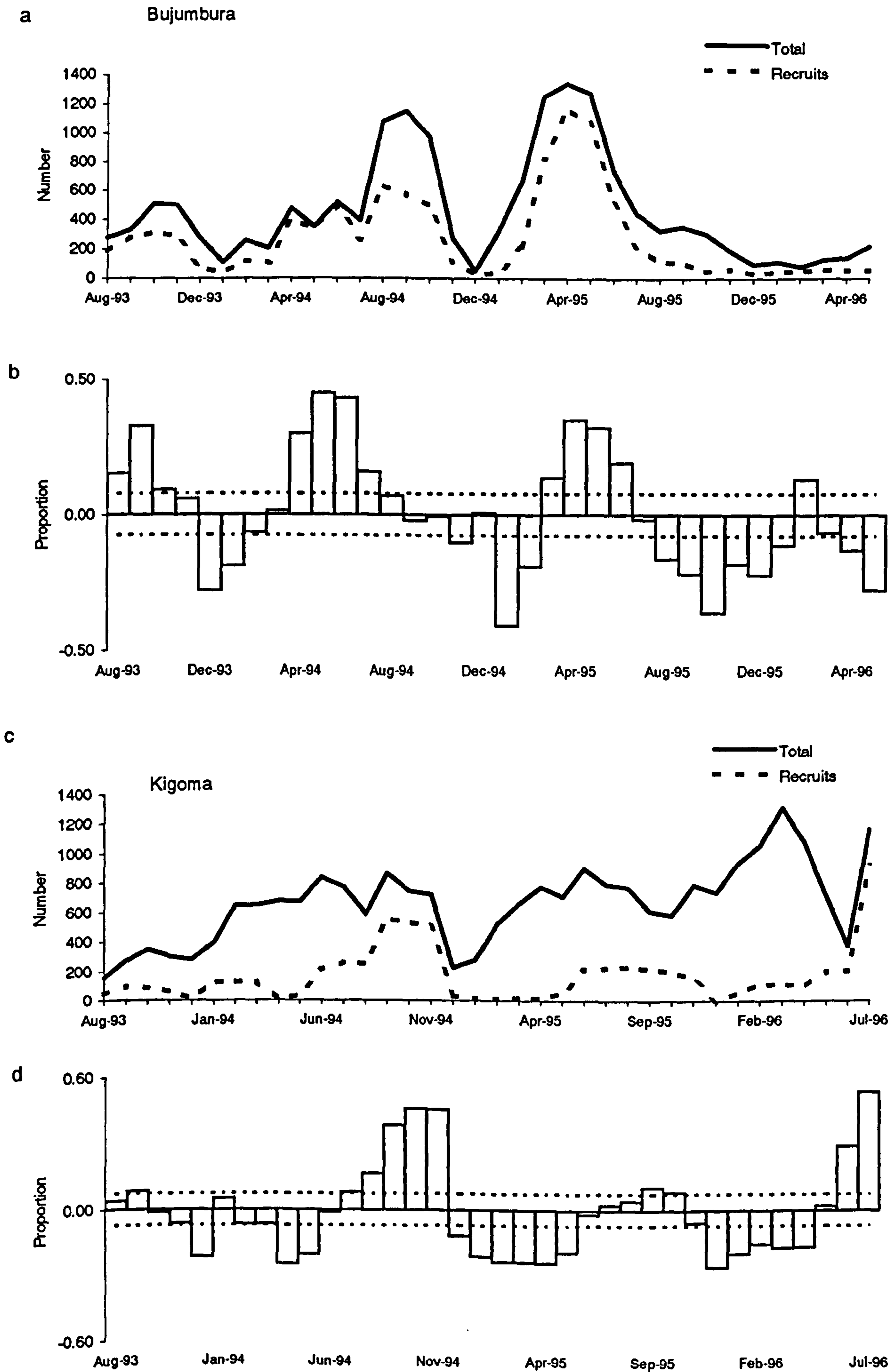


Figure 25. Moving average (a, c) over three months of *L. stappersii* total number in samples and number of recruits (TL < 90 mm) and deviation from mean recruit proportion (b, d) in Bujumbura and Kigoma samples. Dashed lines in b and d are the upper and lower 95% confidence limits of the mean.

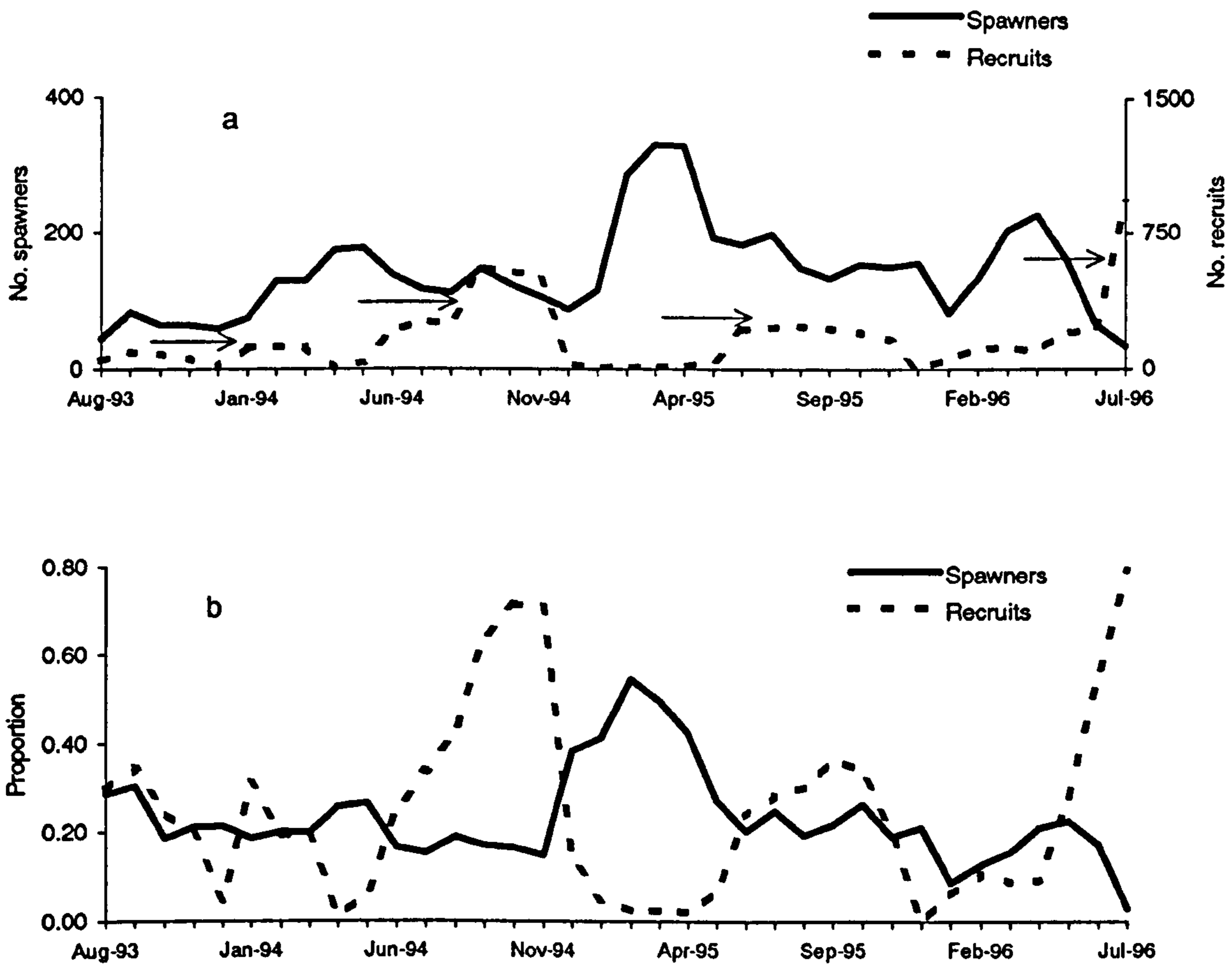


Figure 26. a, moving average over three months of *L. stappersii* mature individuals (TL > 275 mm) and recruits (TL < 90 mm), arrows indicate possible links between occurrence of spawners and recruits and, b, their proportion in Kigoma samples.

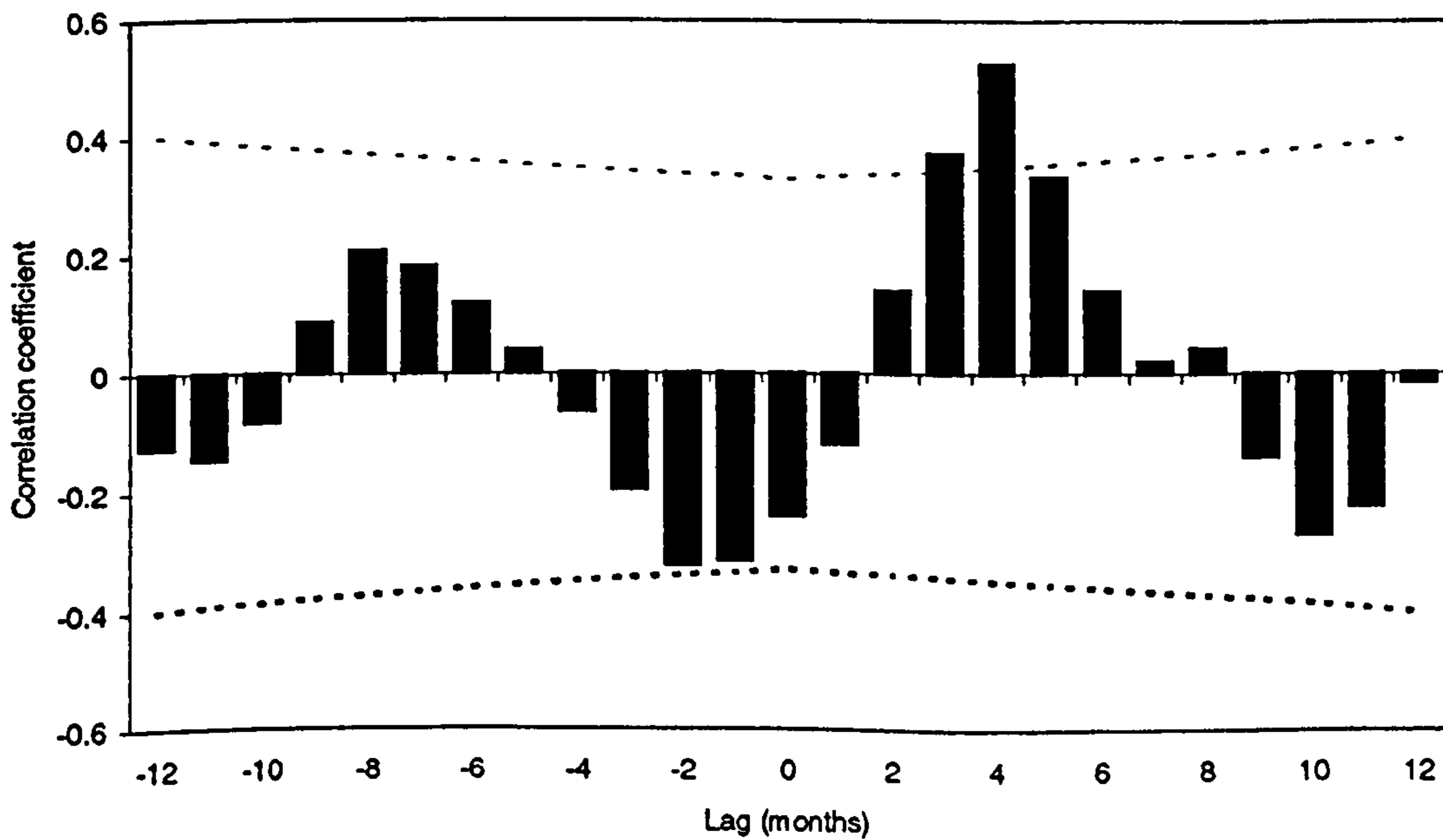


Figure. 27 Cross-correlation function of  $\ln(\text{no})$  spawners with  $\ln(\text{no})$  recruits of *L. stappersii* in Kigoma samples. Dashed lines indicate 95% confidence levels.

full" (45% and 25% at Mpulungu and 41% and 32% of total stomachs at Kigoma, respectively). The diet composition was found to be significantly different between Kigoma and Mpulungu ( $\chi^2_{[6]} = 84.7, P < 0.05$ ).

The diet of *L. stappersii* in the south was based almost entirely upon clupeids and shrimps (Fig. 28). The atyid shrimps *L. parvula*, followed by the palaemonid *P. moorei*, were the main prey for the most of the year. *Limnothrissa miodon* was the commonest fish prey at Mpulungu among the identified clupeids. Clupeid larvae were rare in the stomach contents of fish from this part of the lake.

Around Kigoma, *L. stappersii* displayed a more heterogeneous food spectrum, including mesozooplankton (copepods) and *S. tanganyicae* larvae (Fig. 29). *Stolothrissa tanganyicae* was the most common fish prey, its frequency in the stomachs was greatest between July and January when the catch of this species in the fisheries was also highest. *S. tanganyicae* larvae were important in the diet, especially from May to July, when, in this part of the lake, the main reproductive phase of *S. tanganyicae* takes place. From July, larvae abundance decreased and *L. stappersii* fed on juveniles and adults. The appearance of copepods in the diet of *L. stappersii* from September to January was due to large numbers of young *L. stappersii* in the sample. These fish are planktivorous feeders. Shrimps were common prey throughout the year although their relative contribution varied.

Ontogenetic changes in feeding are illustrated in Figures 30 and 31. *Lates stappersii* caught from the south of the lake maintained a simple, two prey item diet throughout their life. The zooplanktivorous phase was not found at Mpulungu as young *L. stappersii* (TL <100 mm) were not caught. Initially at the size of approximately 90 mm they preyed on shrimps and then gradually the proportion of clupeids increased with size. Only very large individuals were mainly piscivorous. The data from Kigoma indicated that juveniles fed on copepods, and then at a size of approximately 100 mm on shrimps and *S. tanganyicae*. Only large fish were entirely piscivorous. Food availability was more important than size of the predator in prey selection. Cannibalism was noted in some months, mainly by adult fish.

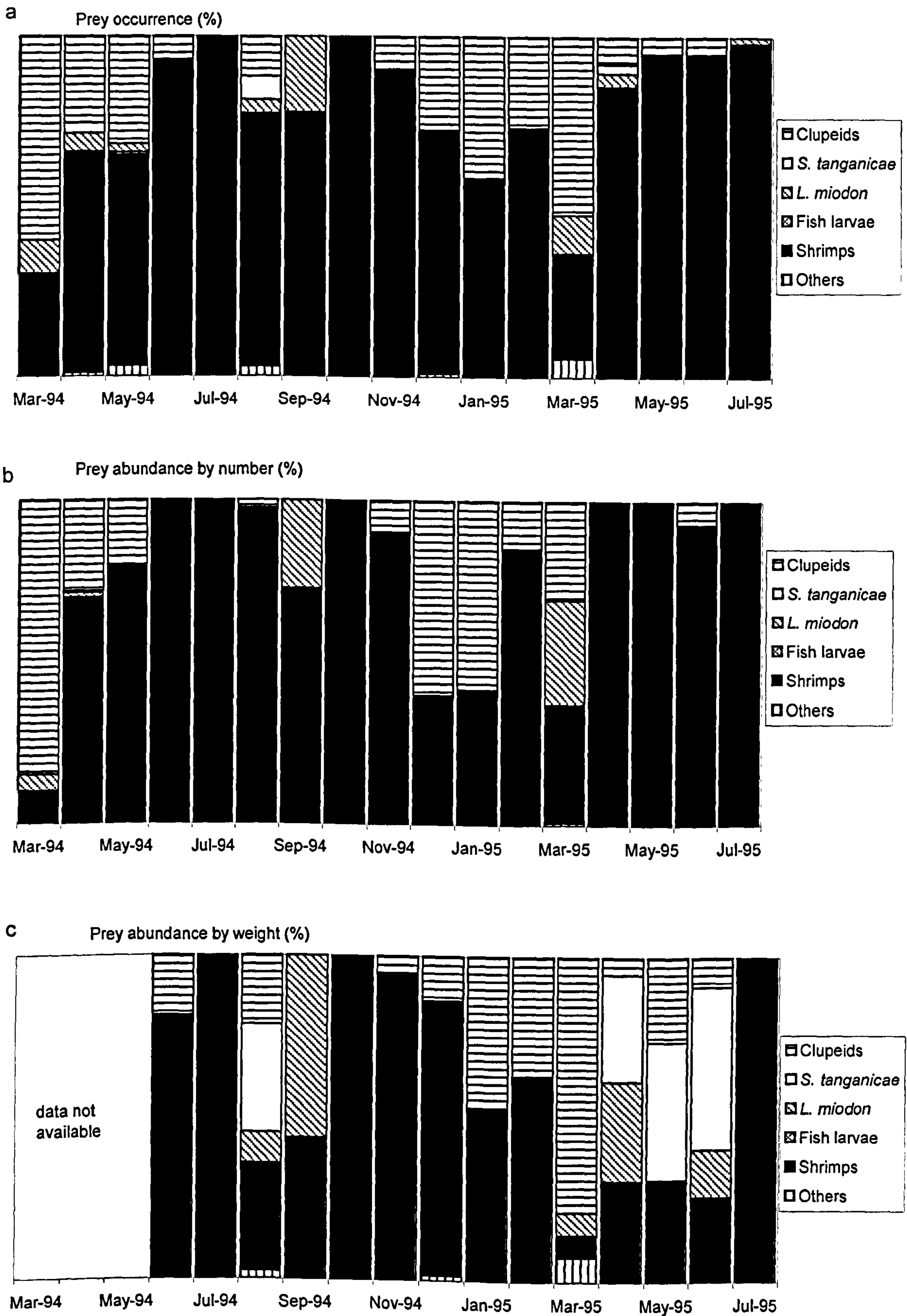


Figure 28. Monthly composition (%) of the diet of *L. stappersii* in the Mpulungu area expressed by, a, prey occurrence, b, prey number and, c, prey weight.

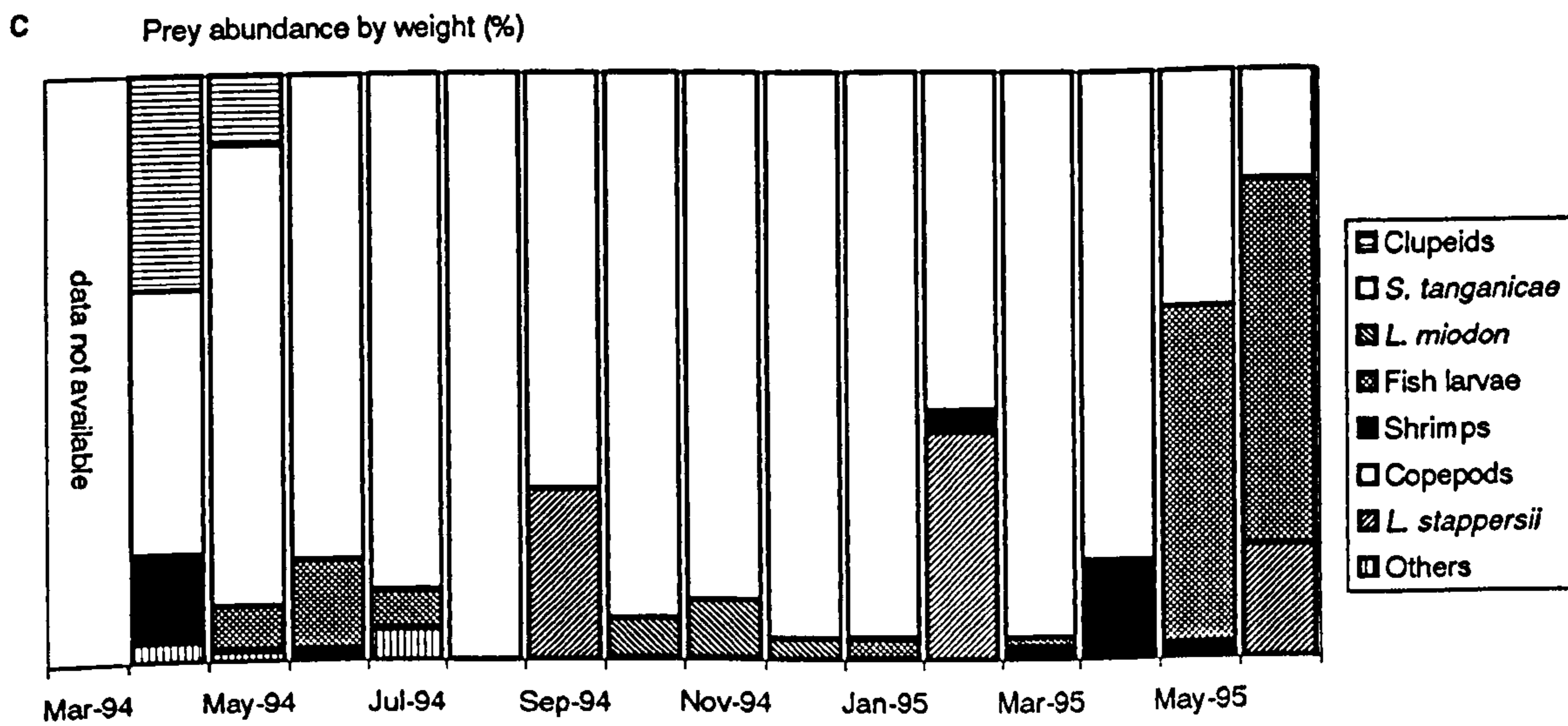
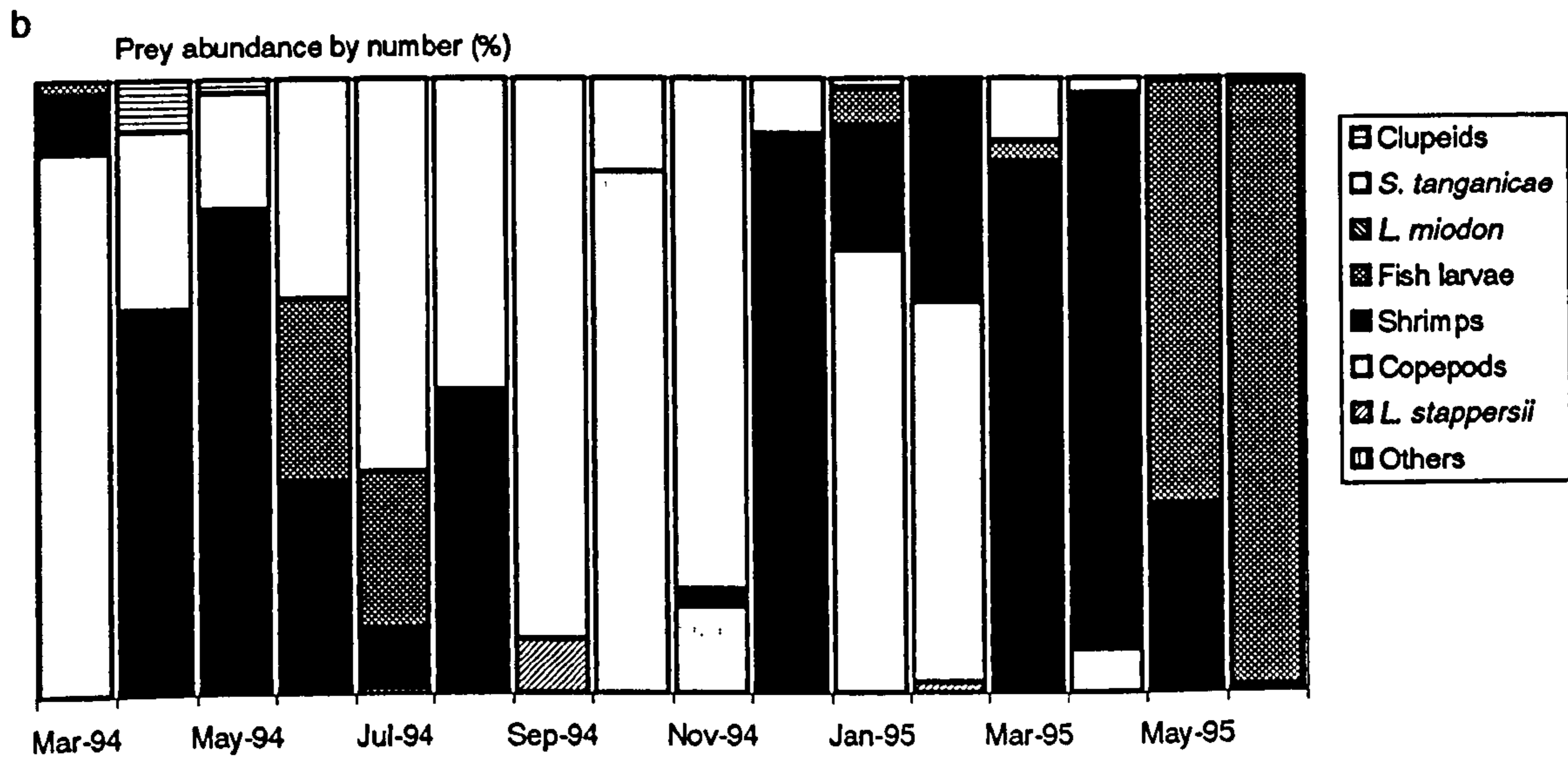
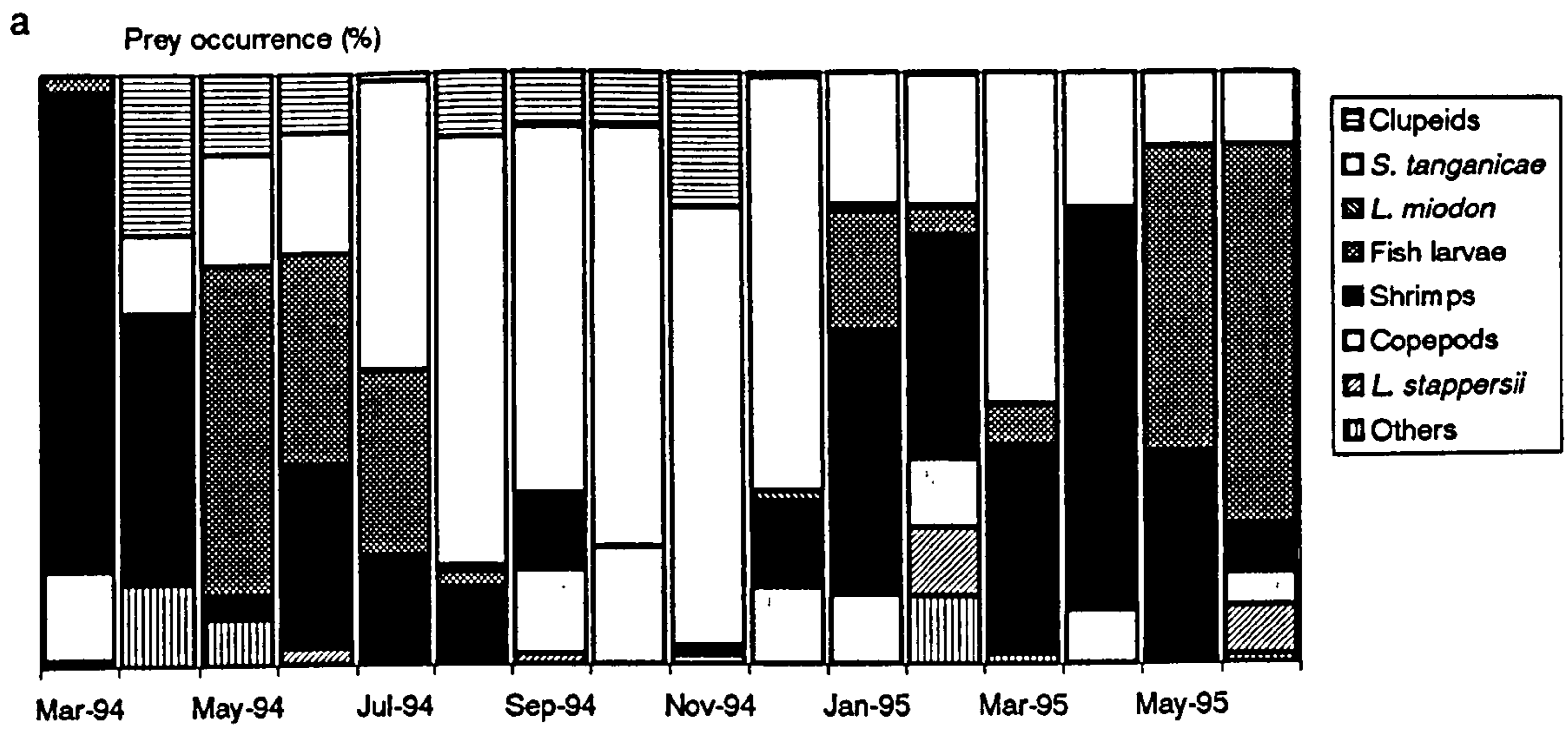


Figure 29. Monthly composition (%) of the diet of *L. stappersii* in Kigoma area expressed by, a, prey occurrence, b, prey number and, c, prey weight.

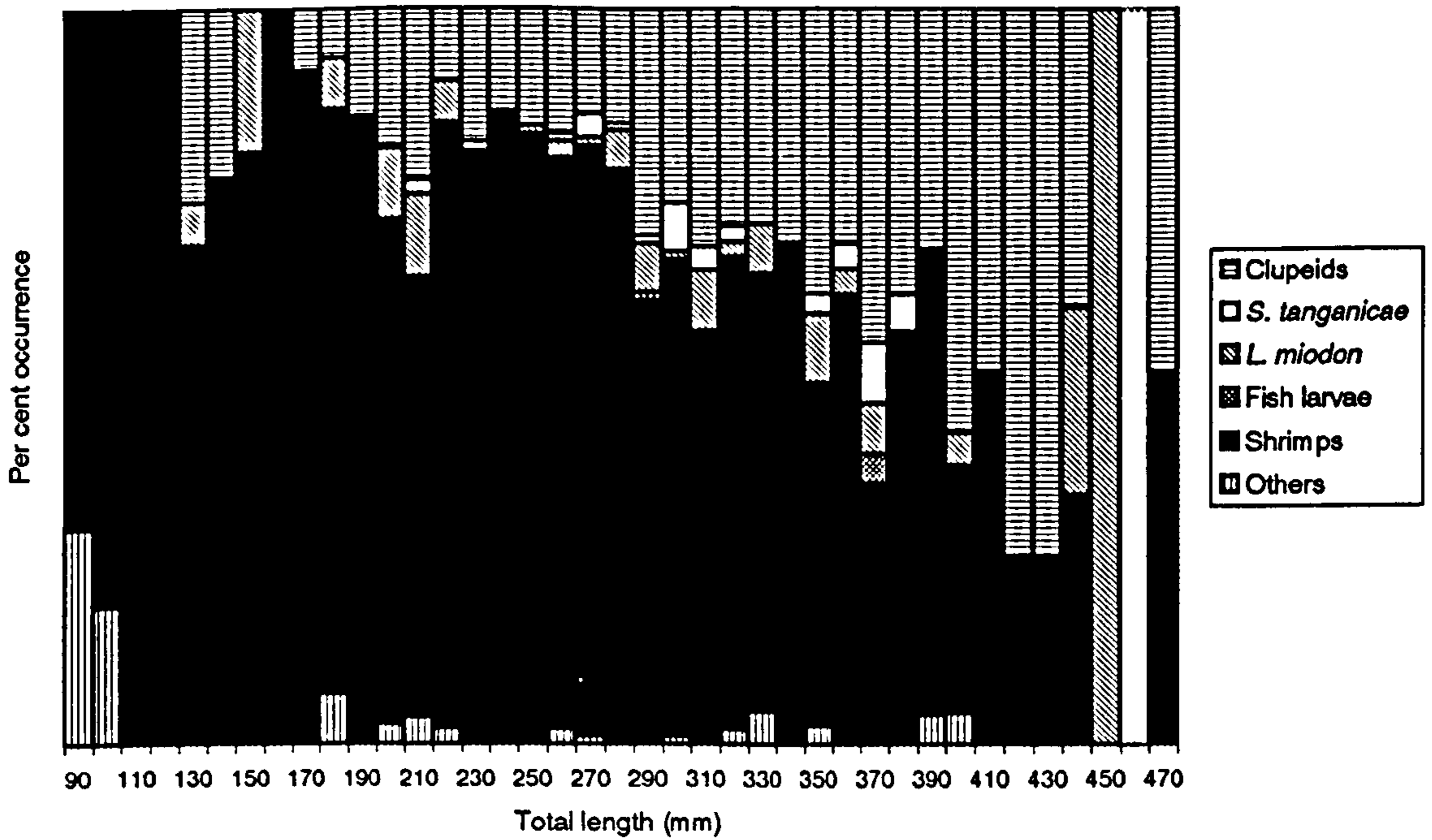


Figure 30. Variation in the diet of *L. stappersii* with size (total length) in the Mpulungu area. Note that there are no data for the 460 mm length class.

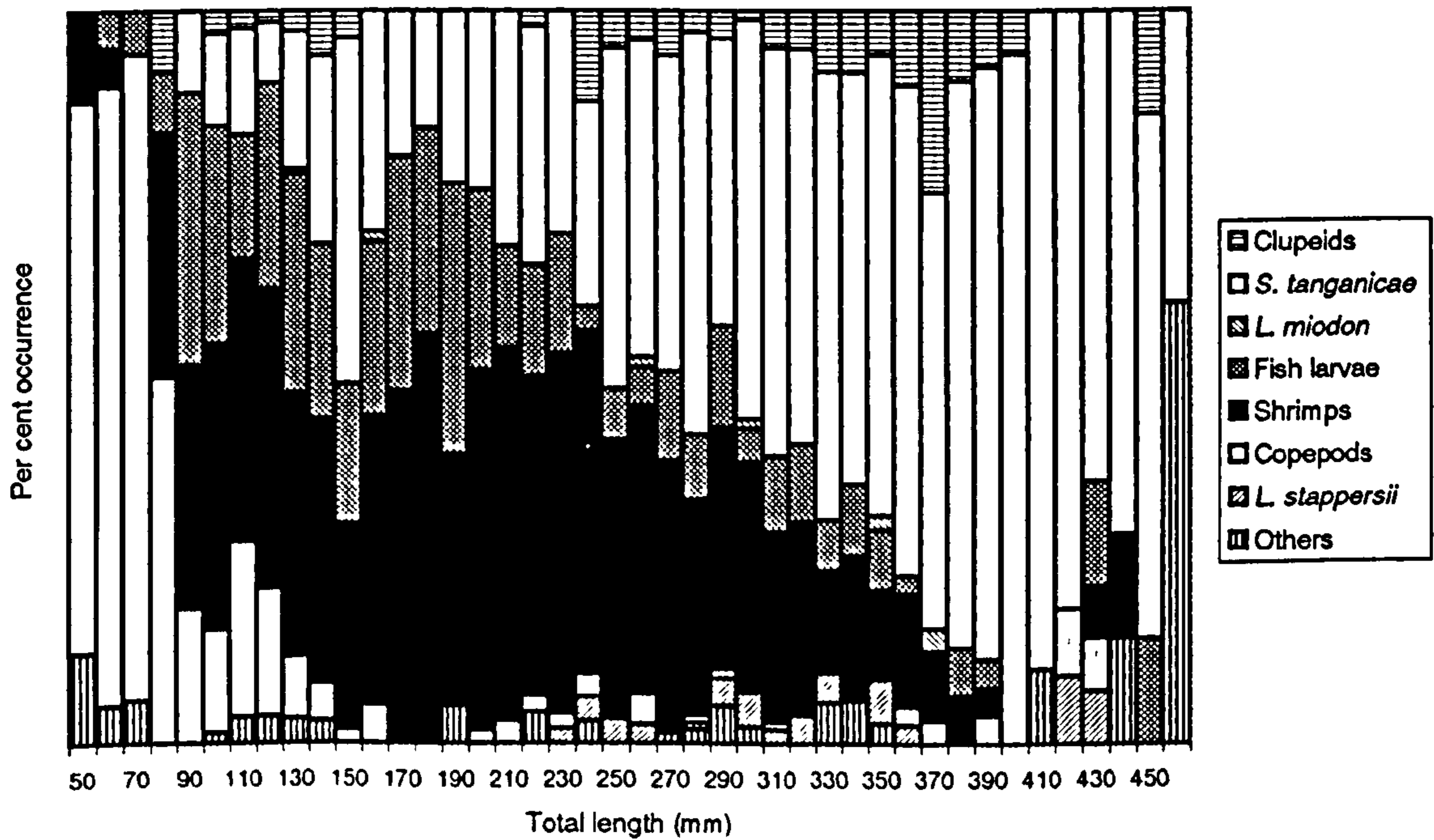


Figure 31. Variation in the diet of *L. stappersii* with size (total length) in the Kigoma area. Note that there are no data for the 400 mm length class.

It could be argued that commercial catch samples, taken by light attraction methods, are of dubious value, owing to the simultaneous concentration of both predators and prey. However, Pearce (1991) stated, on the basis of some experimental fishing, that it is unlikely that the occurrence of shrimps in the stomach of *L. stappersii* is an artefact due to light attraction. Stomach samples collected during experimental mid-water trawling in Kigoma and Mpulungu areas in June 1995 were compared with those obtained during the same month from commercial catch samples (Fig. 32). The diet composition from the commercial and survey samples of the same area appeared similar. However, no statistically significant difference was found between commercial and survey data ( $\chi^2_{[3]} = 2.84, P > 0.05$ ) only in the Mpulungu area. The difference between the two data sets are partly explained by the better preservation of the stomachs collected during the survey, prey items which are digested quickly such as copepods and shrimps are represented more in survey samples than in commercial catch samples. Also, young planktivorous *L. stappersii* were better represented in the size distributions obtained from the survey than from the commercial catch samples (Fig. 33).

A total of 1040 stomachs, 74% (767) of which contained food remains, were sampled during the June and November-December 1995 lake-wide surveys. The diet composition was different between the two months ( $\chi^2_{[5]} = 18.64, P < 0.05$ ). In both months *S. tanganyicae* 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. tanganyicae*, while the opposite was observed in November (Fig. 34). 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 section 3.4.2 and 3.5).

Stomach contents were plotted along the longitudinal axis of the lake according to the position of fishing hauls where *L. stappersii* were caught (Fig. 35). The occurrence of prey categories in June showed that the heterogeneous diet composition (mainly made

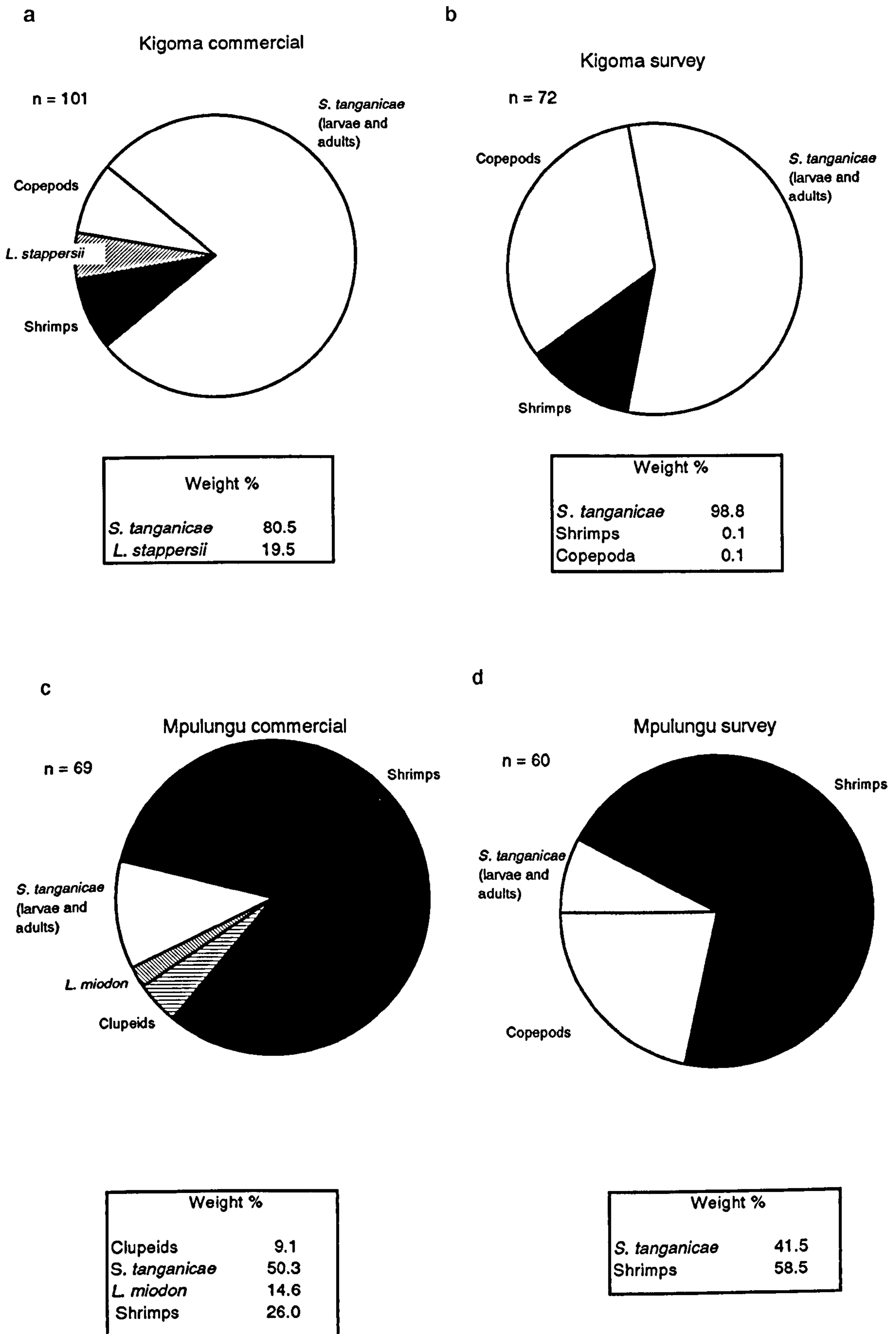


Figure 32. Occurrence (%) of prey items in *L. stappersii* stomachs in the Kigoma (a, b) and Mpulungu (c, d) area from June 1995 commercial catch samples (a, c) and survey samples (b, d), n is the number of non empty stomachs analysed. Weight composition (when available) is shown in text boxes.



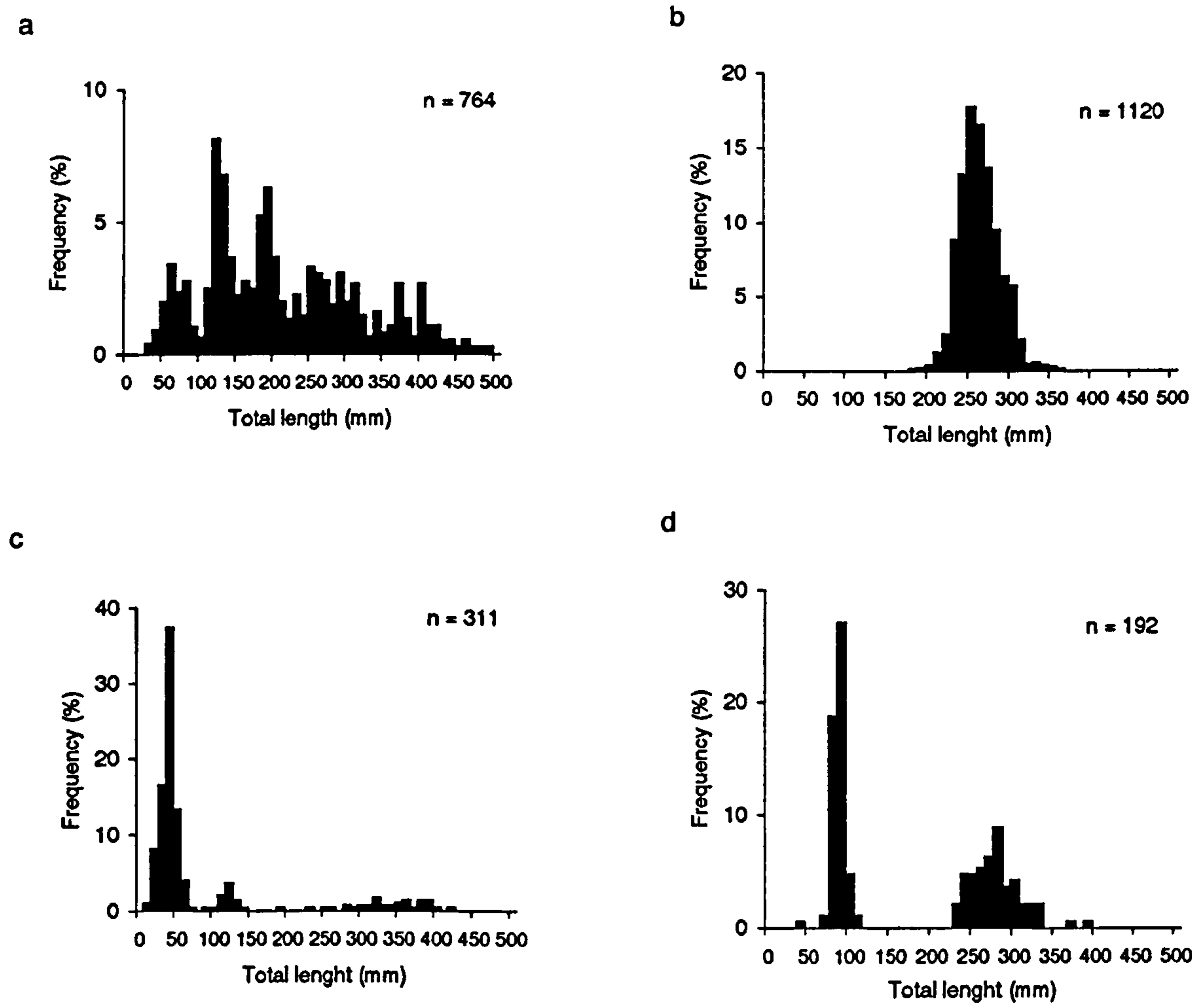


Figure 33. Length composition of the commercial catch samples (a, b) and survey samples (c, d) of *L. stappersii* collected in the Kigoma (a, c) and Mpulungu area (b, d) area, n is the sample size.

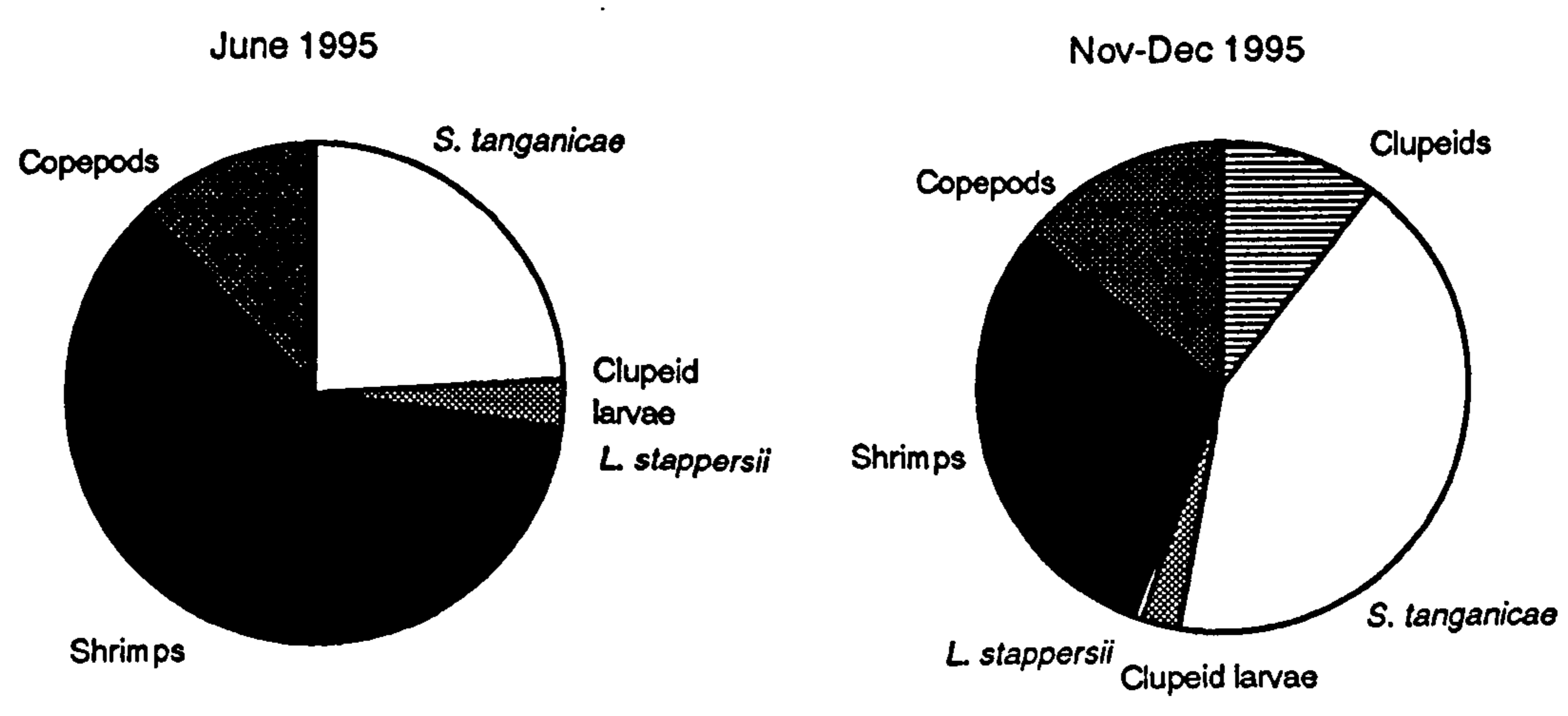


Figure 34. Occurrence of prey items in *L. stappersii* stomach content from June and November-December 1995 survey samples.

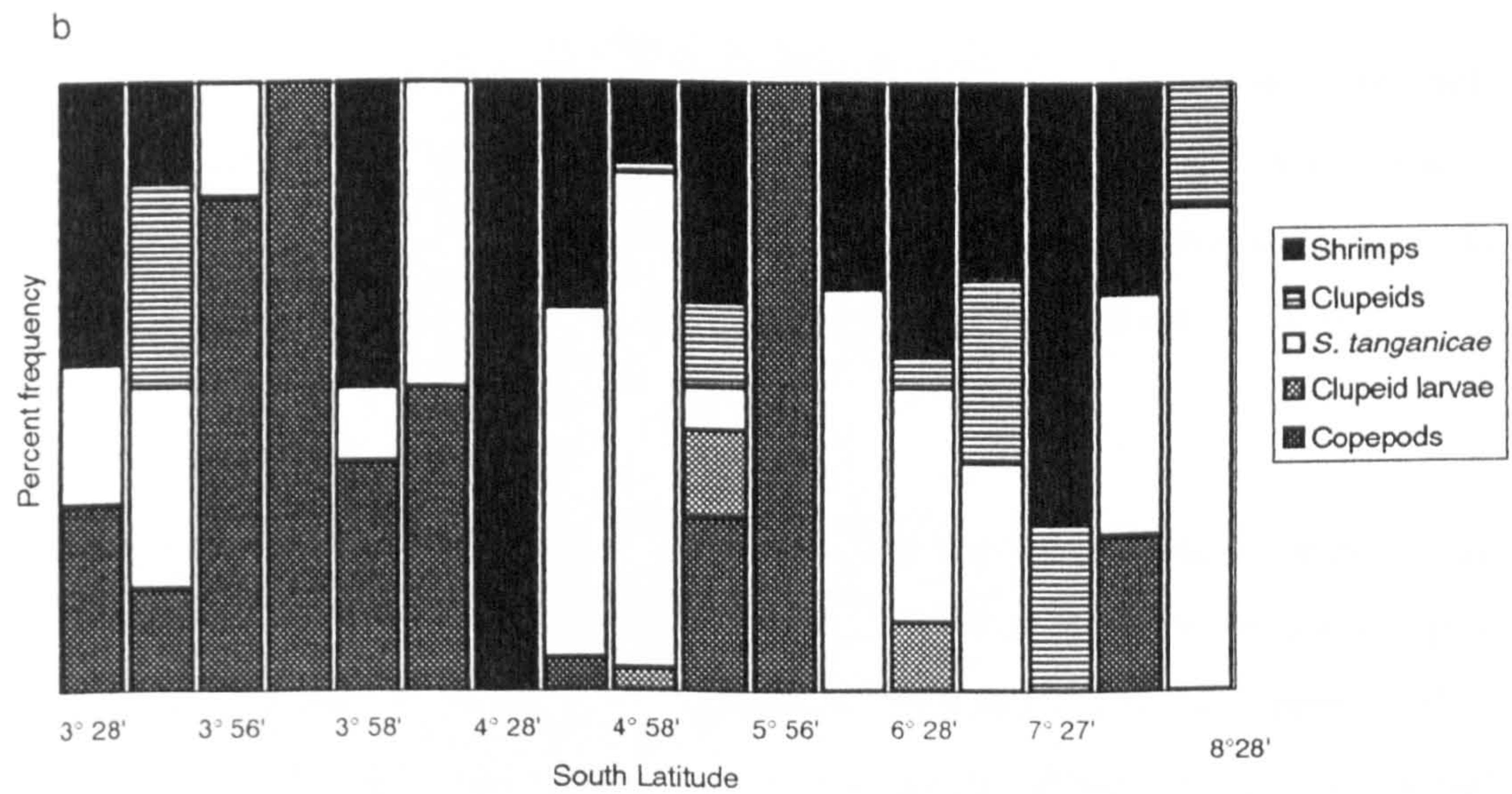
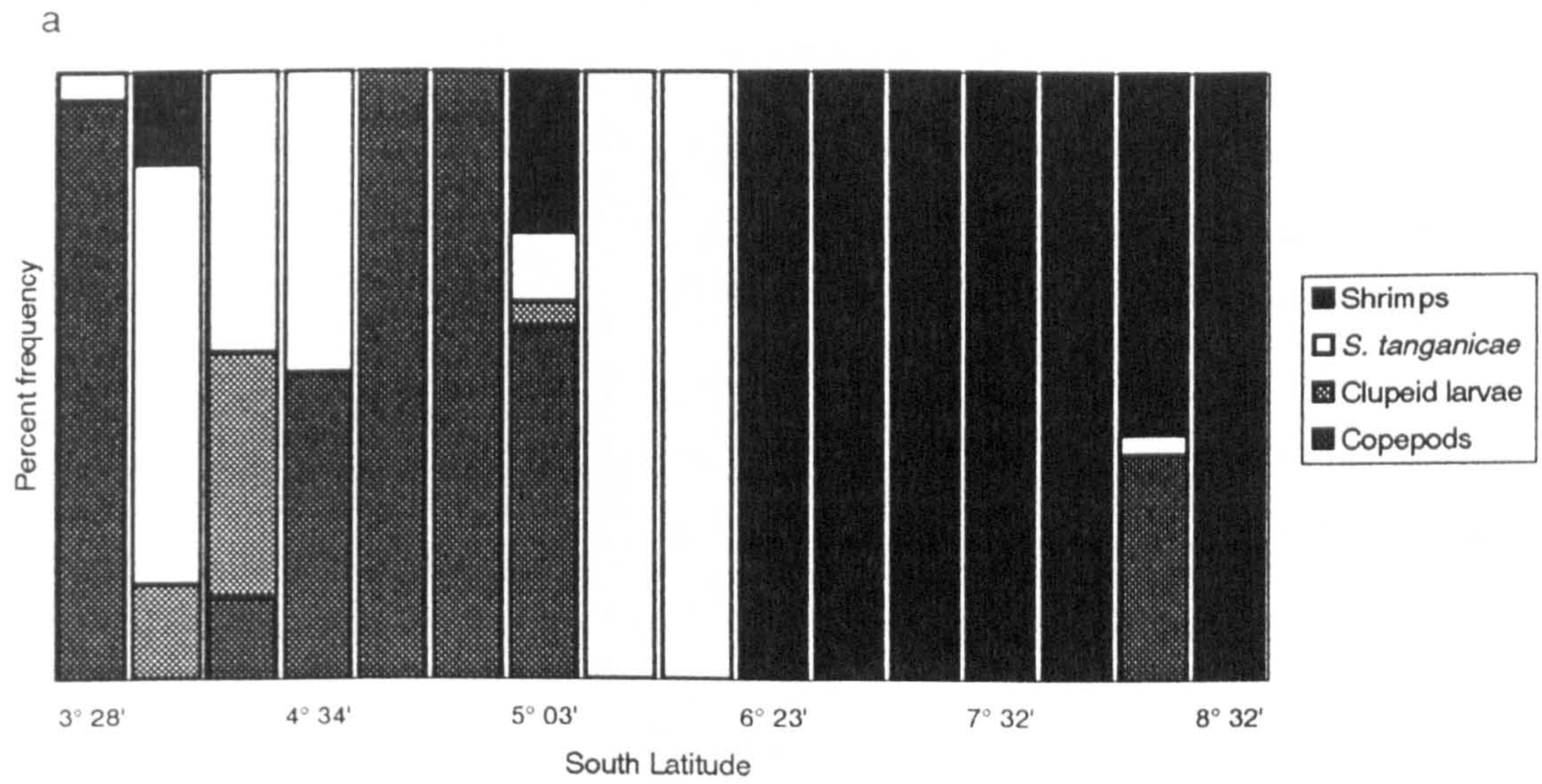


Figure 35. Frequency of prey category in stomach contents of *L. stappersii* caught at different positions along the N-S longitudinal axis of Lake Tanganyika during June 1995 (a) and November 1995 (b) pelagic trawl survey. Note that interval between sampling station positions is not proportional to effective distance.

by *S. tanganyicae*, 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. tanganyicae* 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.

### 3.4 Distribution patterns from survey data

#### 3.4.1 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 8. 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 being surveyed before fishing was stopped as a result of 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. tanganyicae* 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* Boulenger.

The survey data and results were treated as if from two distinct data sets. The first

Table 8. 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 kg	<i>S. tanganicae</i>		<i>L. miodon</i>		<i>L. stappersii</i>		<i>Lates</i> spp.		<i>Other</i> 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

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 the 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. tanganyicae*, school during the day and scatter into layers at night (Chapman, 1976; pers. obs.). This behaviour is common to several fish species and it 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 nighttime. 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. tanganyicae* amounted to the maximum of 54 kg hr<sup>-1</sup> in April 1996, while it was possible to achieve a catch rate up to 1181 kg hr<sup>-1</sup> 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 analysis, 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<sup>-1</sup> of *S. tanganyicae* contributed 77% of the total catch weight of the entire survey, 88% of the target species weight and 90% of *S. tanganyicae* catch. In February 1998 a single one hour daylight trawl caught 1181 kg of *S. tanganyicae* equivalent to 66% of that survey total catch, 75% of the target species weight and 93% of the entire *S. tanganyicae* 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.

#### 3.4.2 *Stolothrissa tanganyicae*

*Stolothrissa tanganyicae* was caught in 104 of the 131 hauls. Catch rates varied between 0 and 1181 kg hr<sup>-1</sup> (or 54 kg hr<sup>-1</sup> considering only night-time catches). The statistical distribution of catch rate in both survey groups was positively skewed indicating a patchy distribution (Fig. 36). The relatively high percentage of zero catches indicated that the species was contagiously distributed and dispersed. The

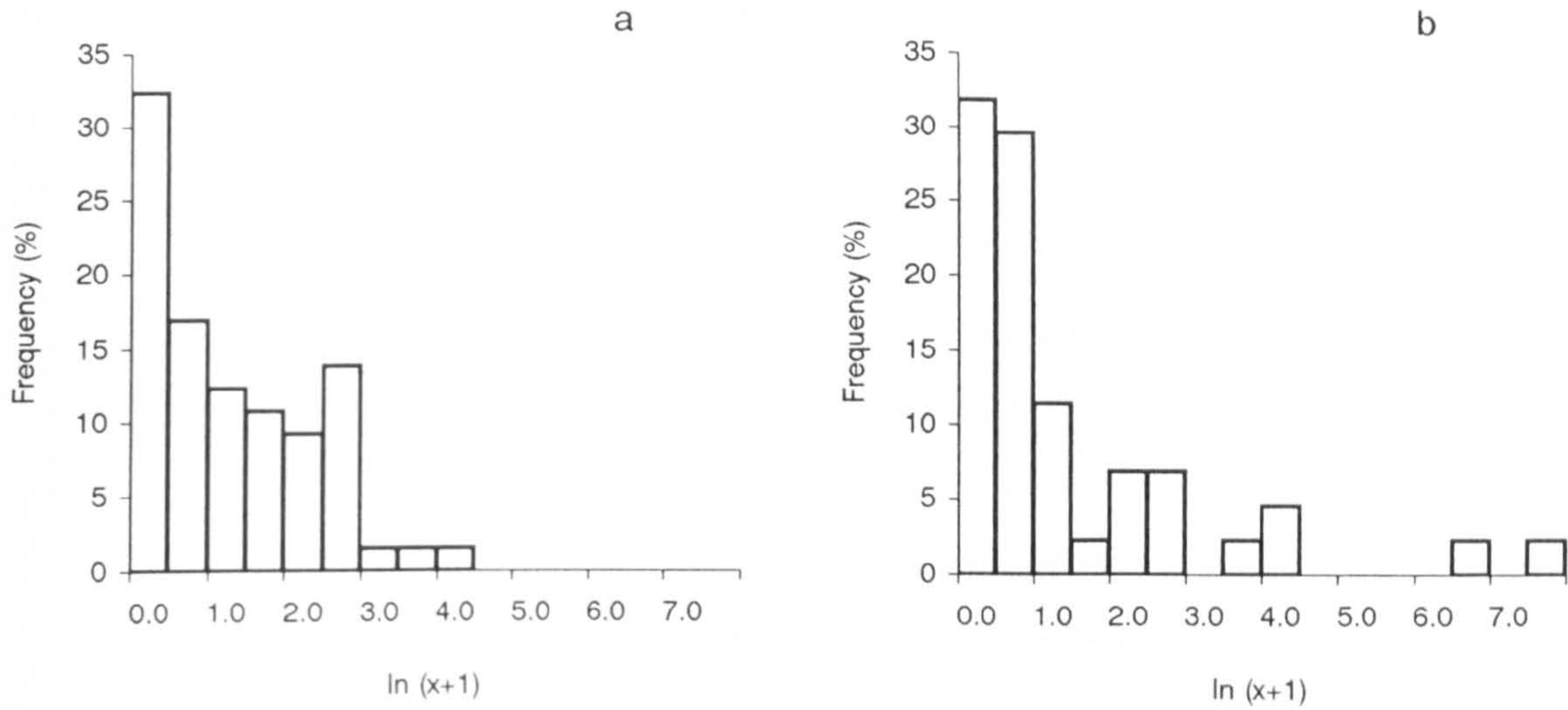


Figure 36. Frequency histograms of  $\ln(x+1)$  transformed CPUE values derived for *S. tanganyicae* from, a, June and November-December 1995 and, b, November-December 1997 and February 1998 pelagic trawl surveys

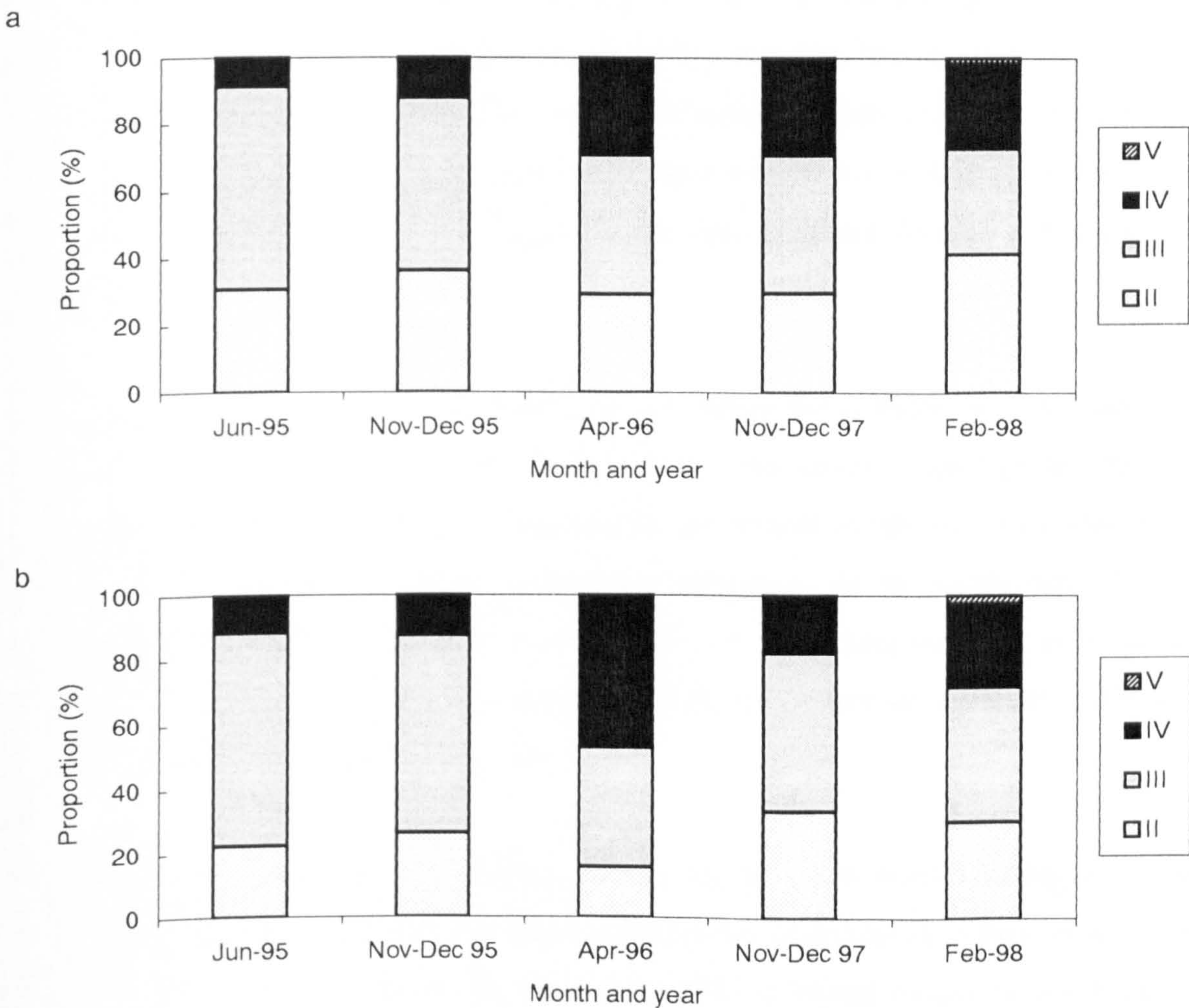


Figure 37. Maturity stages for *S. tanganyicae* samples of females (a) and males (b) taken during lake-wide surveys in June (sample size,  $n=375$ ) and November-December ( $n=834$ ) 1995, April 1996 ( $n=507$ ), November-December 1997 ( $n=673$ ) and February 1998 ( $n=658$ ).

distribution of log-transformed CPUE values was not significantly different between the two survey periods ( $\chi^2_{[10]} = 10.43, P > 0.05$ ).

In all surveys the majority of fish examined for sex maturity were close to maturity or fully mature individuals (Fig. 37). 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.

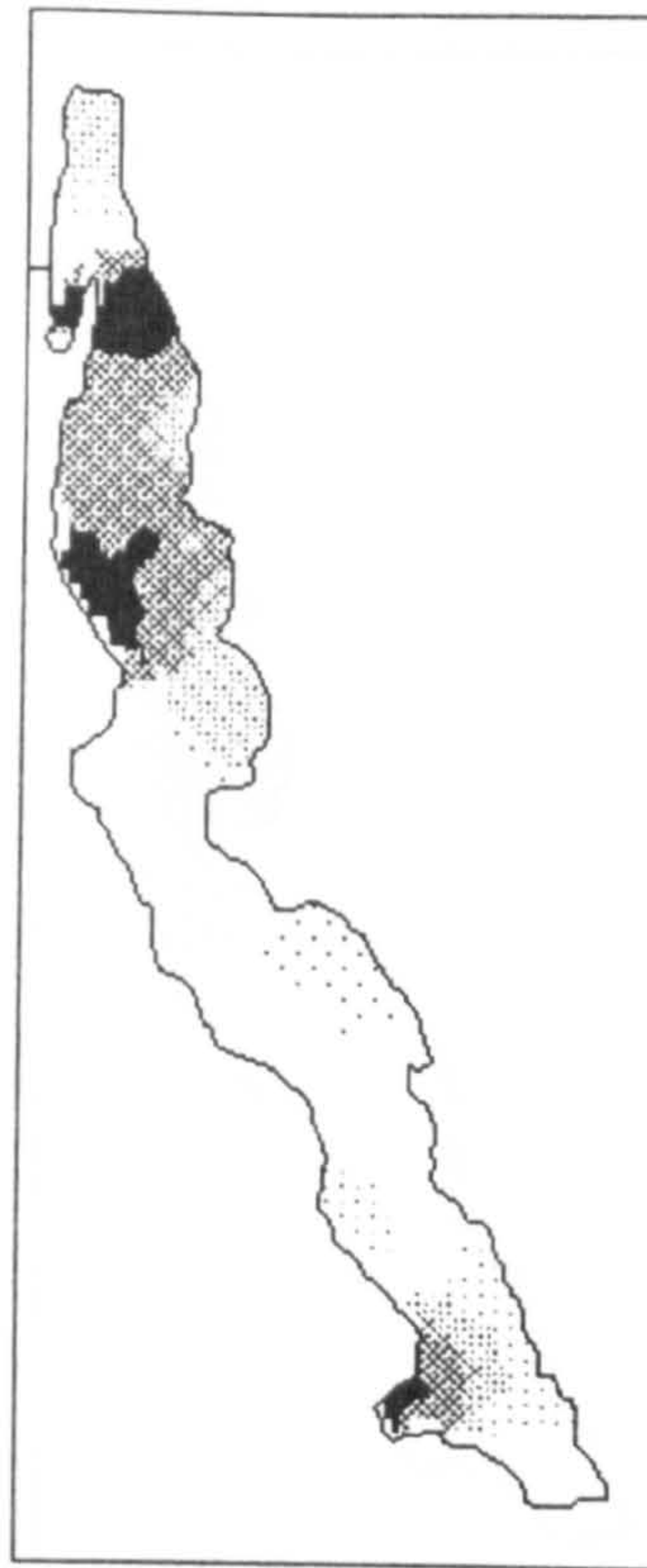
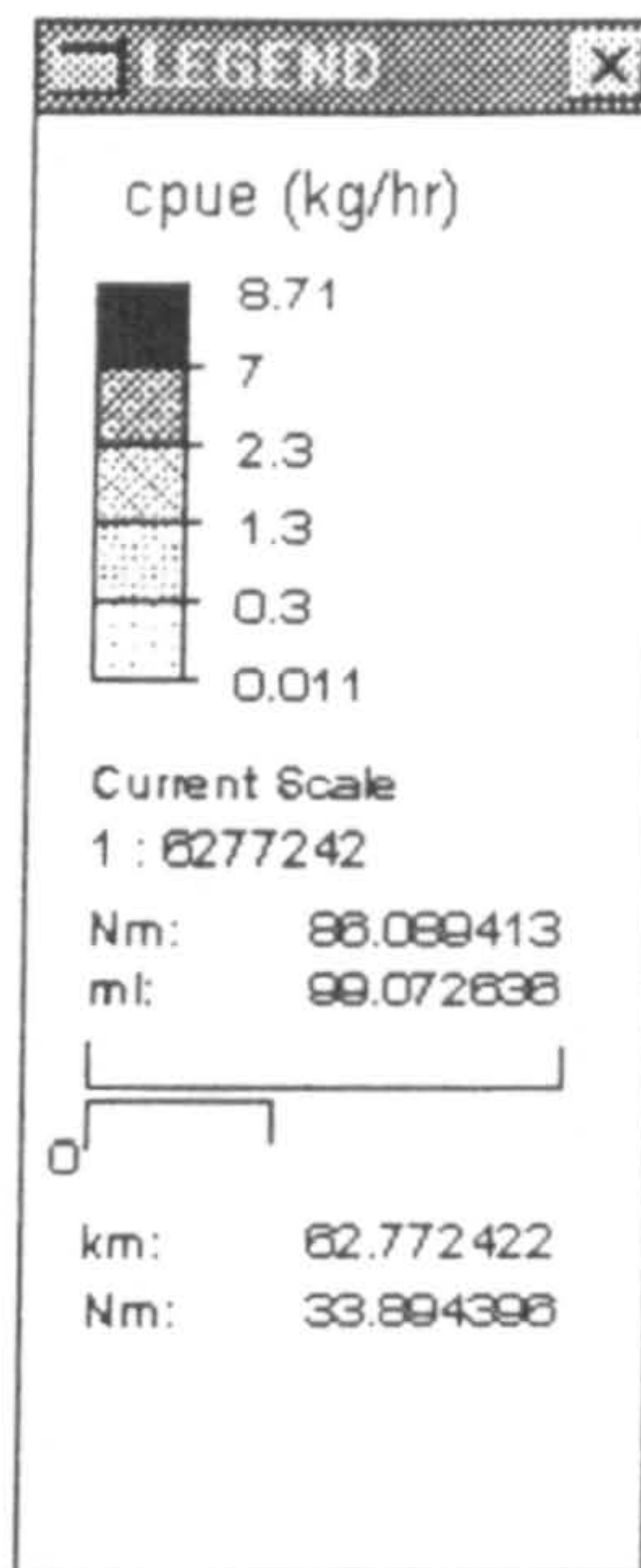
During the June and November-December 1995 surveys the catches of *S. tanganyicae* were higher in the northern half of the lake (Fig. 38). The relative abundance in both periods was always highest in the Kigoma and Karonda sub-basins. However, in November-December *S. tanganyicae* showed a less localised 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. tanganyicae* was higher in the Rumonge and Kigoma sub-basins (Fig. 39a).

Nearly one and half years after the previous survey the distribution of *S. tanganyicae* showed a similar pattern to that obtained in the 1995 surveys. Although the effect of a few outstanding catches was considerable, the overall picture of CPUE distribution confirmed the highest concentration of *S. tanganyicae* 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. tanganyicae* in the catches (Fig. 40).

Mean catch per hour of trawling (CPUE, kg hr<sup>-1</sup>) was three fold higher (Mann-Whitney test:  $P = 0.003$ ) in November-December (4.401 kg hr<sup>-1</sup>) than in June 1995 (1.554 kg hr<sup>-1</sup>). In April 1996, the mean CPUE increased further to 8.120 kg hr<sup>-1</sup>, significantly higher than in June ( $P = 0.014$ ) but not higher than in November-



a



b

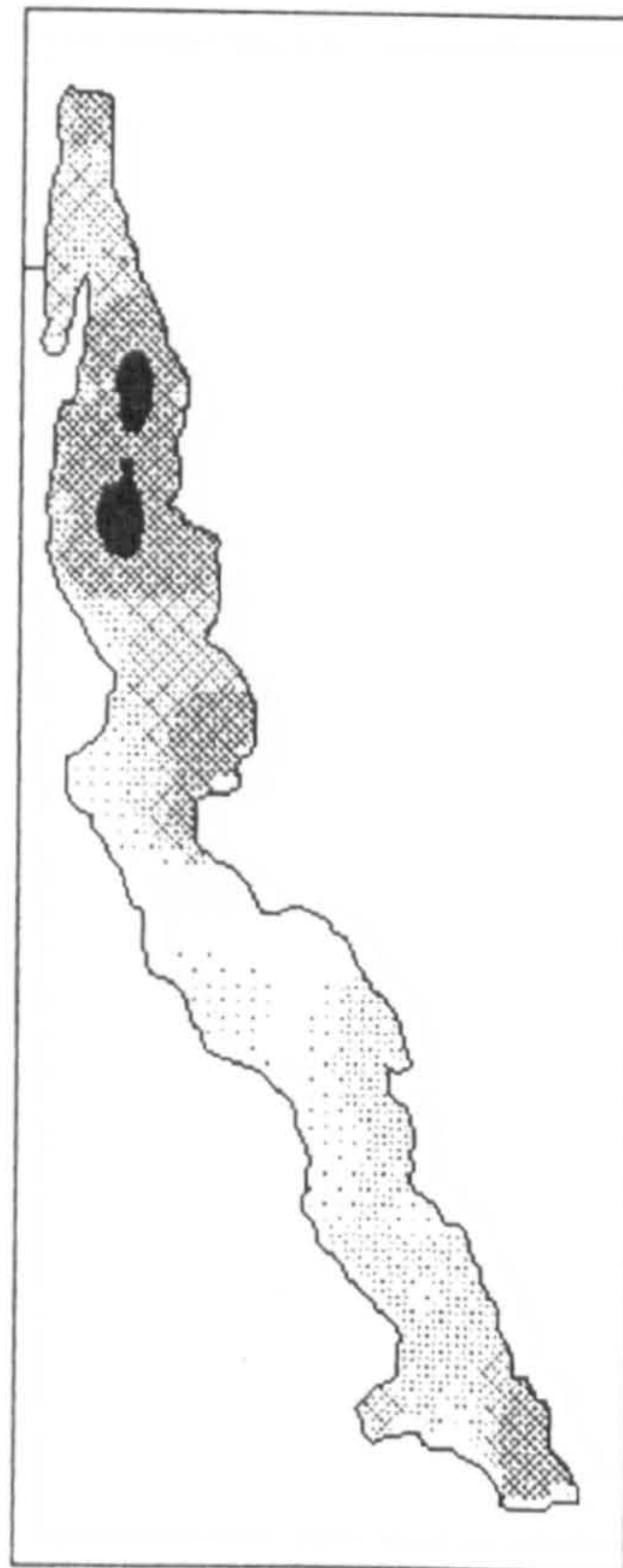
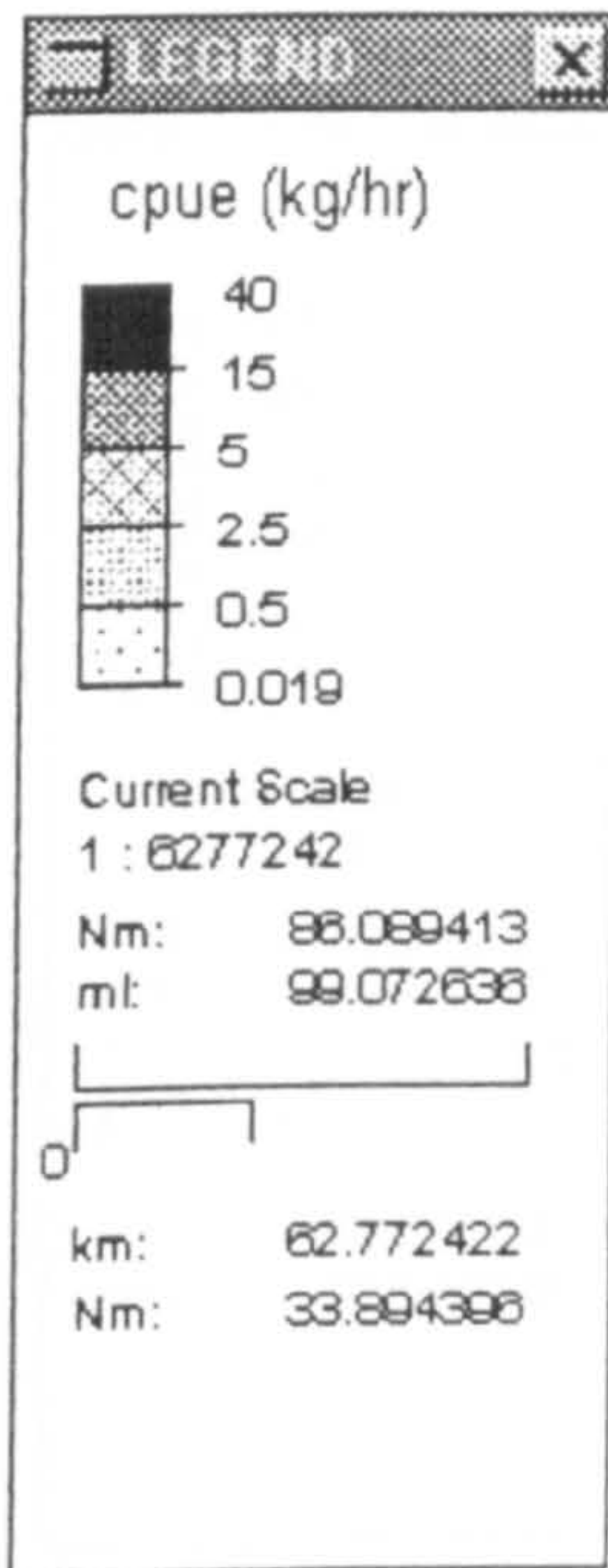
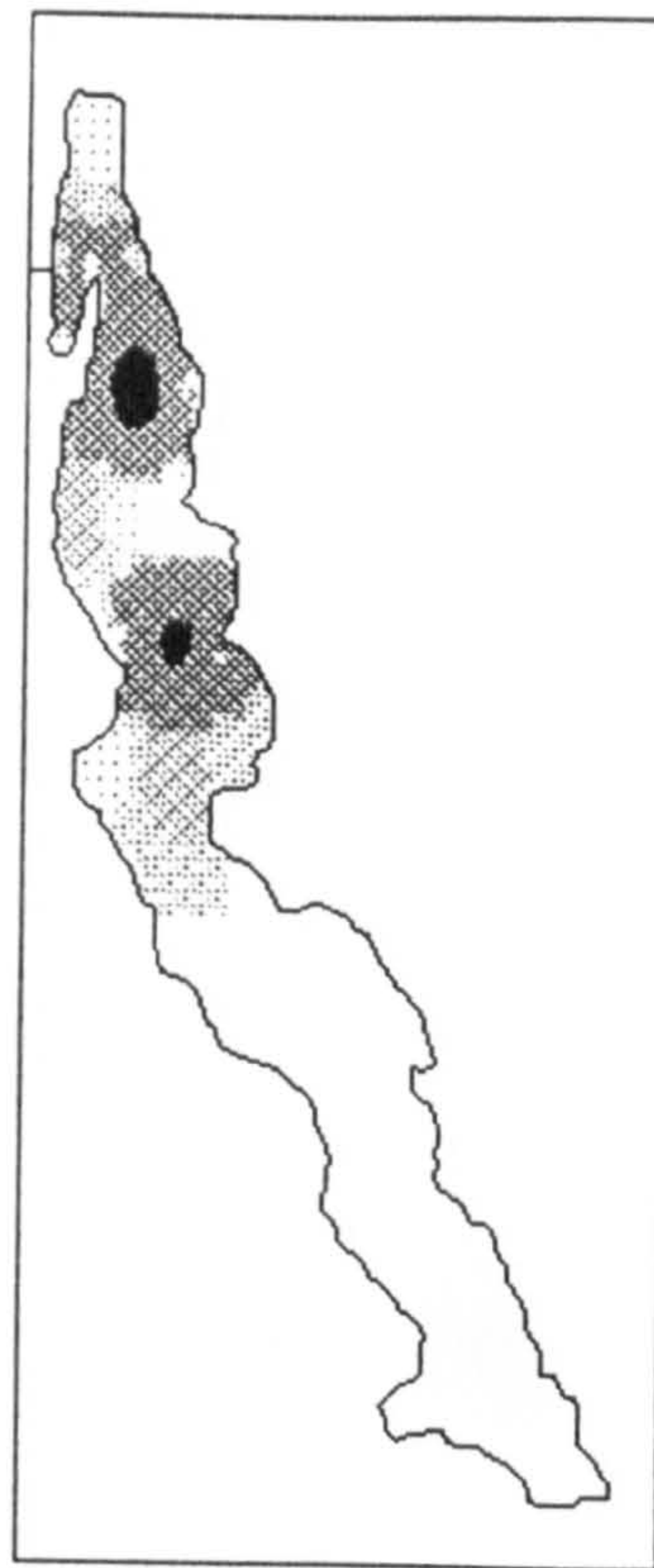
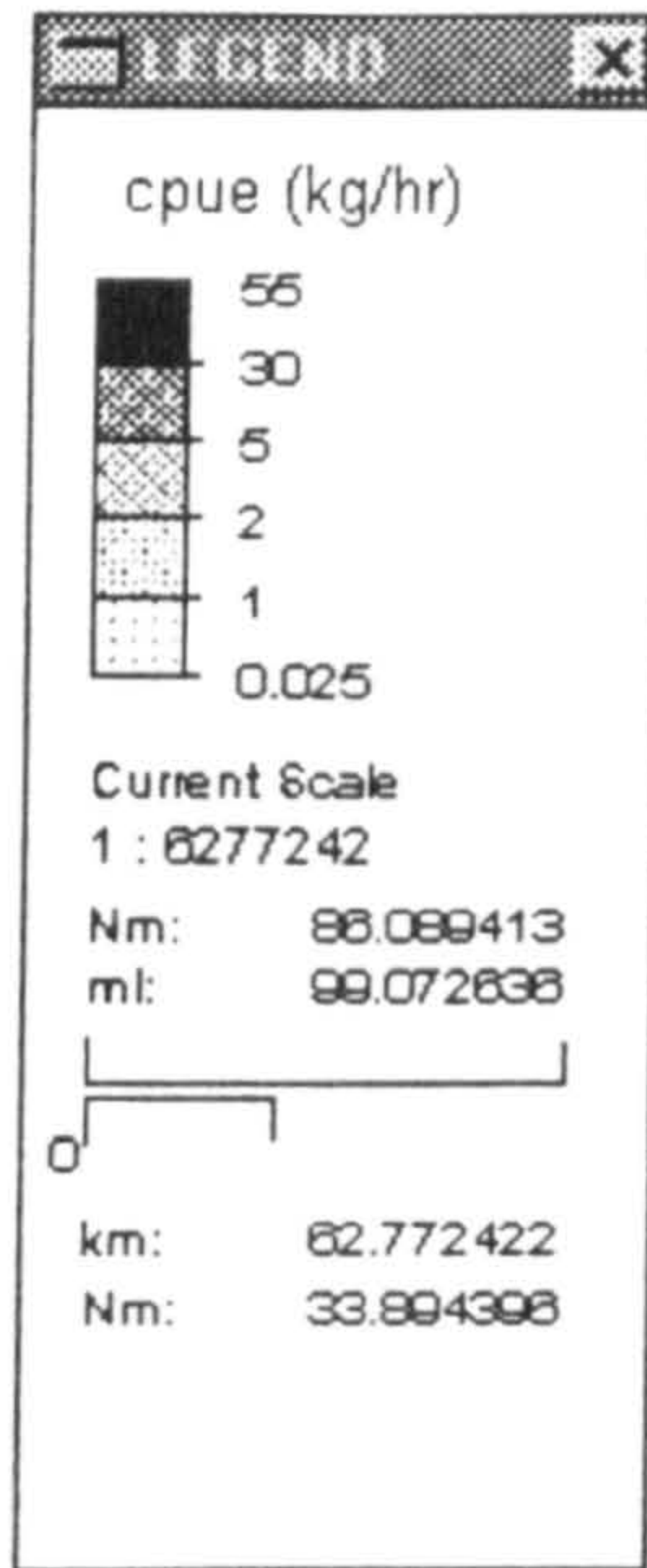


Figure 38. Pelagic trawl catch distribution of *S. tanganyicae* in June 1995 (a) and November-December 1995 (b) survey. Catch per unit of effort (kg/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. 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 statute miles (mi).

a



b

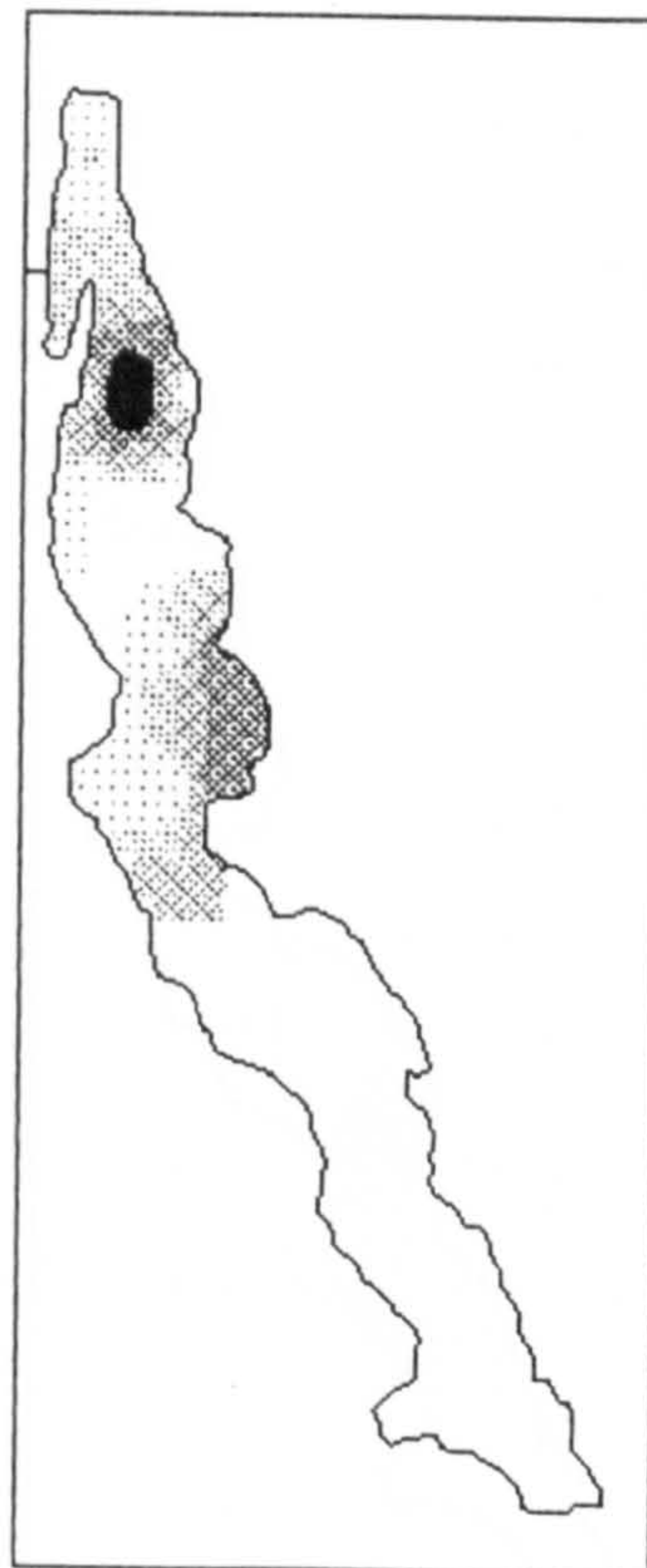
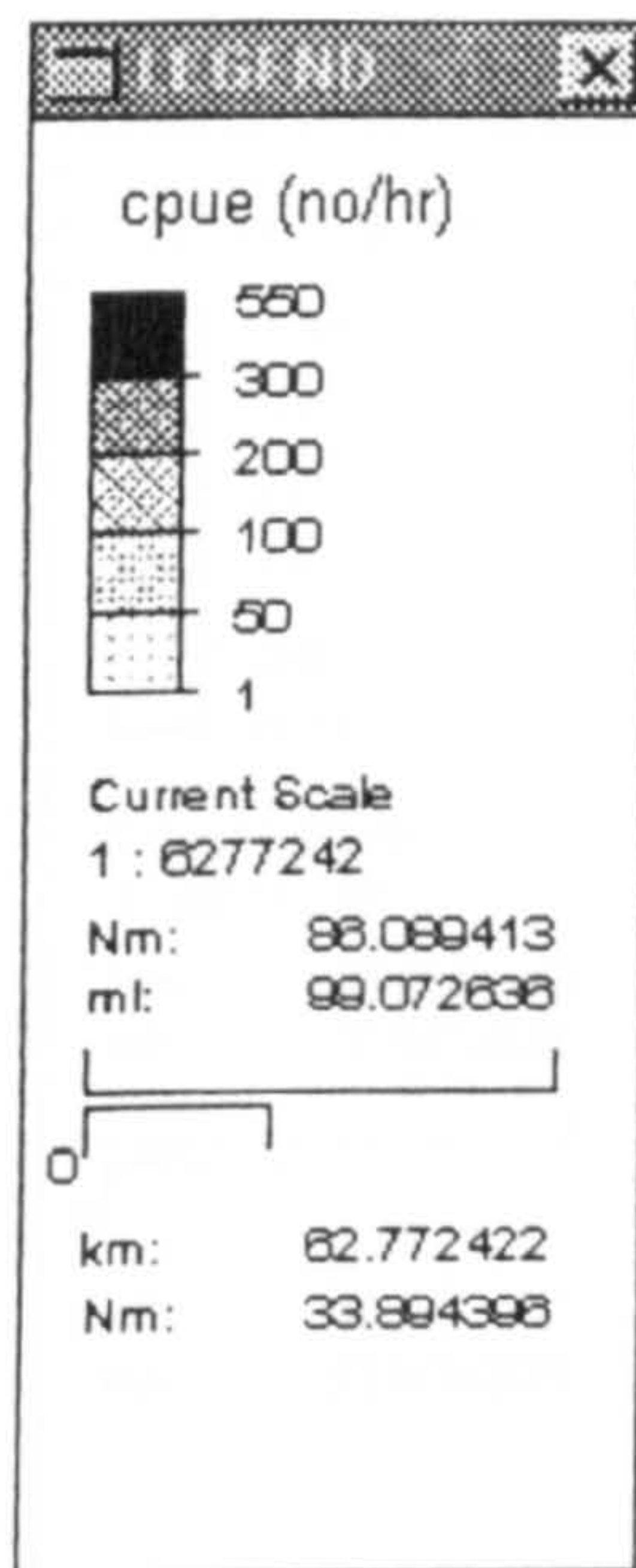


Figure 39. Pelagic trawl catch distribution (a) and number of adults ( $TL > L_m$ ) caught (b) of *S. tanganyicae* in April 1996 survey. Catch per unit of effort (kg/hr) and number of adult fish (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. 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 statute miles (ml).

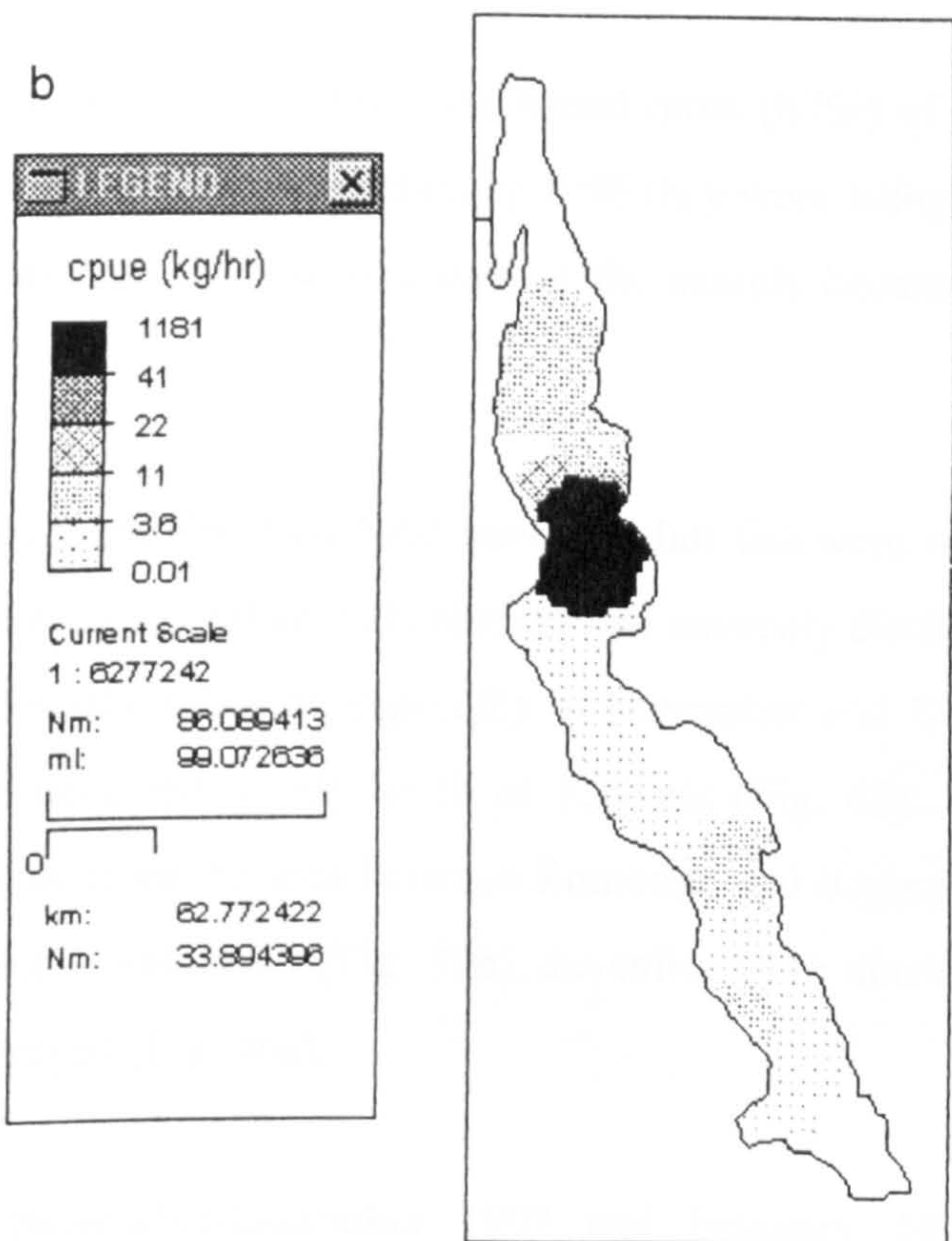
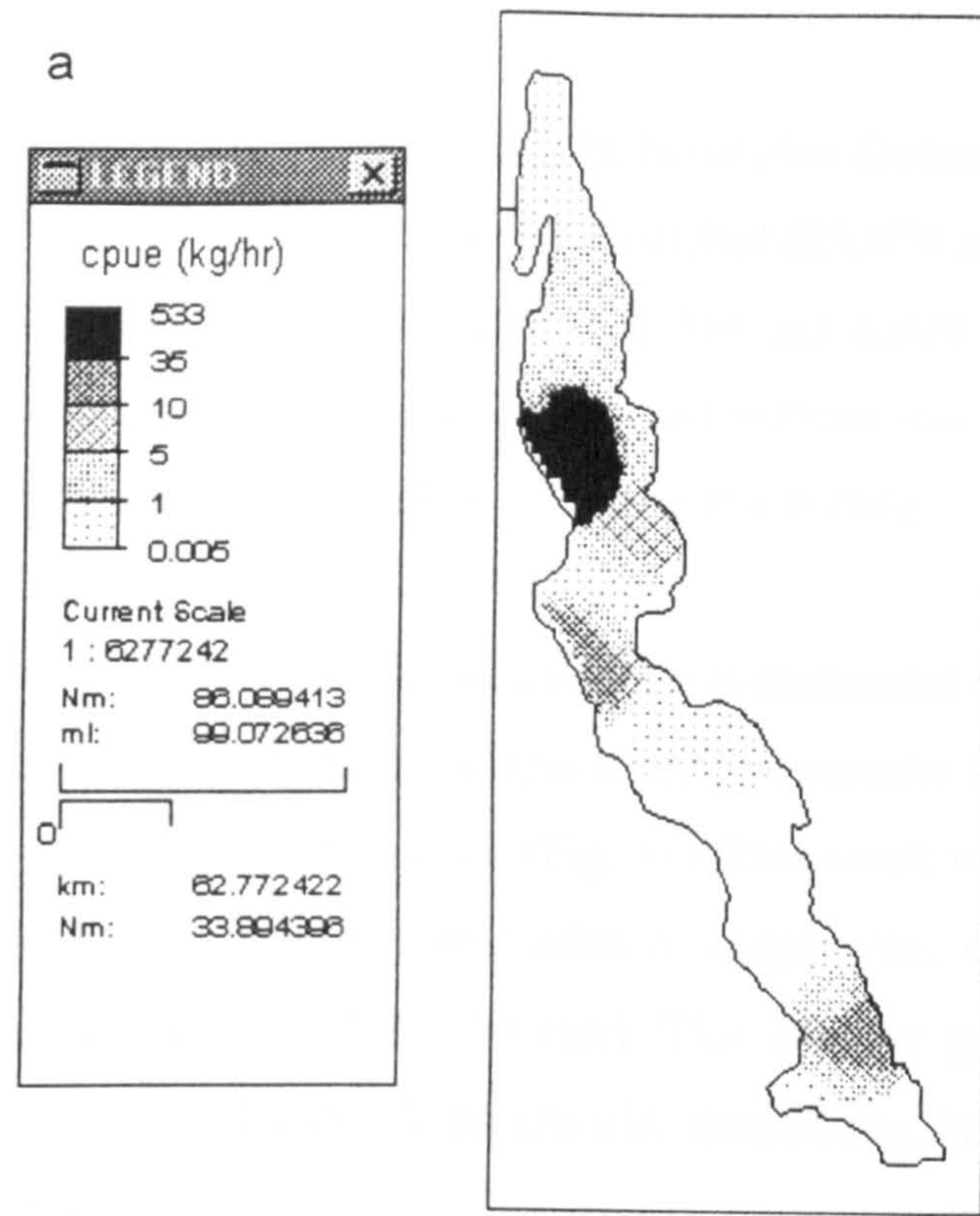


Figure 40. Pelagic trawl catch distribution of *S. tanganyicae* in November-December 1997 (a) and February 1998 (b) survey. Catch per unit of effort (kg/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. 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 statute miles (ml).

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<sup>-1</sup> respectively) was lower than in February 1998 (66.799 and 4.873 kg hr<sup>-1</sup> 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. 41). This stock was made up of mainly 7-8 month-old (74% of total number) adult *S. tanganyicae*, either close to sexual maturity or mature ( $TL \geq L_m$ ;  $L_m = 78$  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. 42).

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 caught (Fig. 43).

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. 44), while juvenile fish occurred mainly north of Kalemie (Fig. 45). 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. 39b). Juveniles were abundant over the most of the region surveyed (Fig. 46a).

In November-December 1997 and February 1998 both adult and juvenile *S. tanganyicae* 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 47 and 48).

Bottom depth was used as an indication of the distance from the coast. *Stolothrissa*

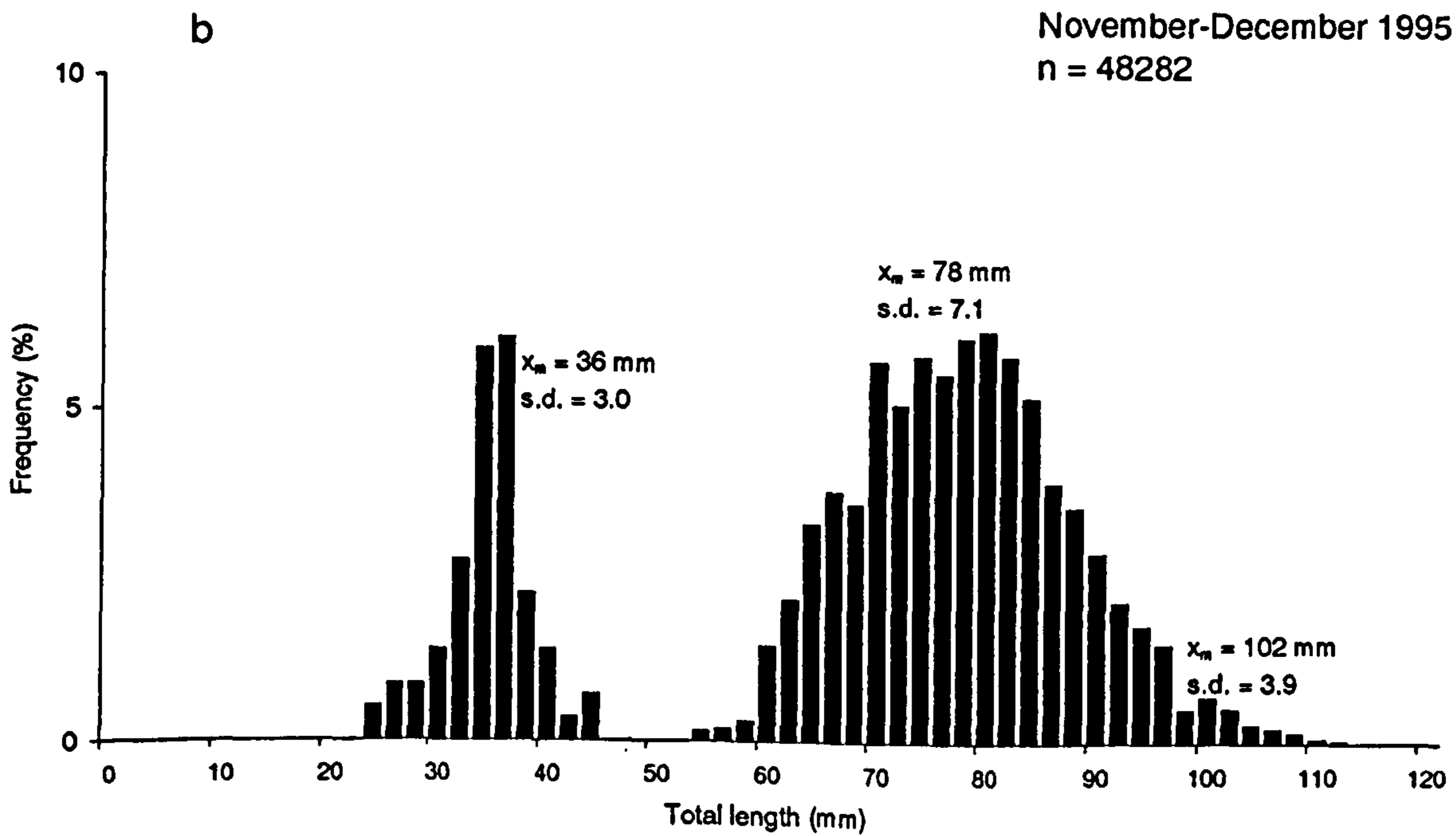
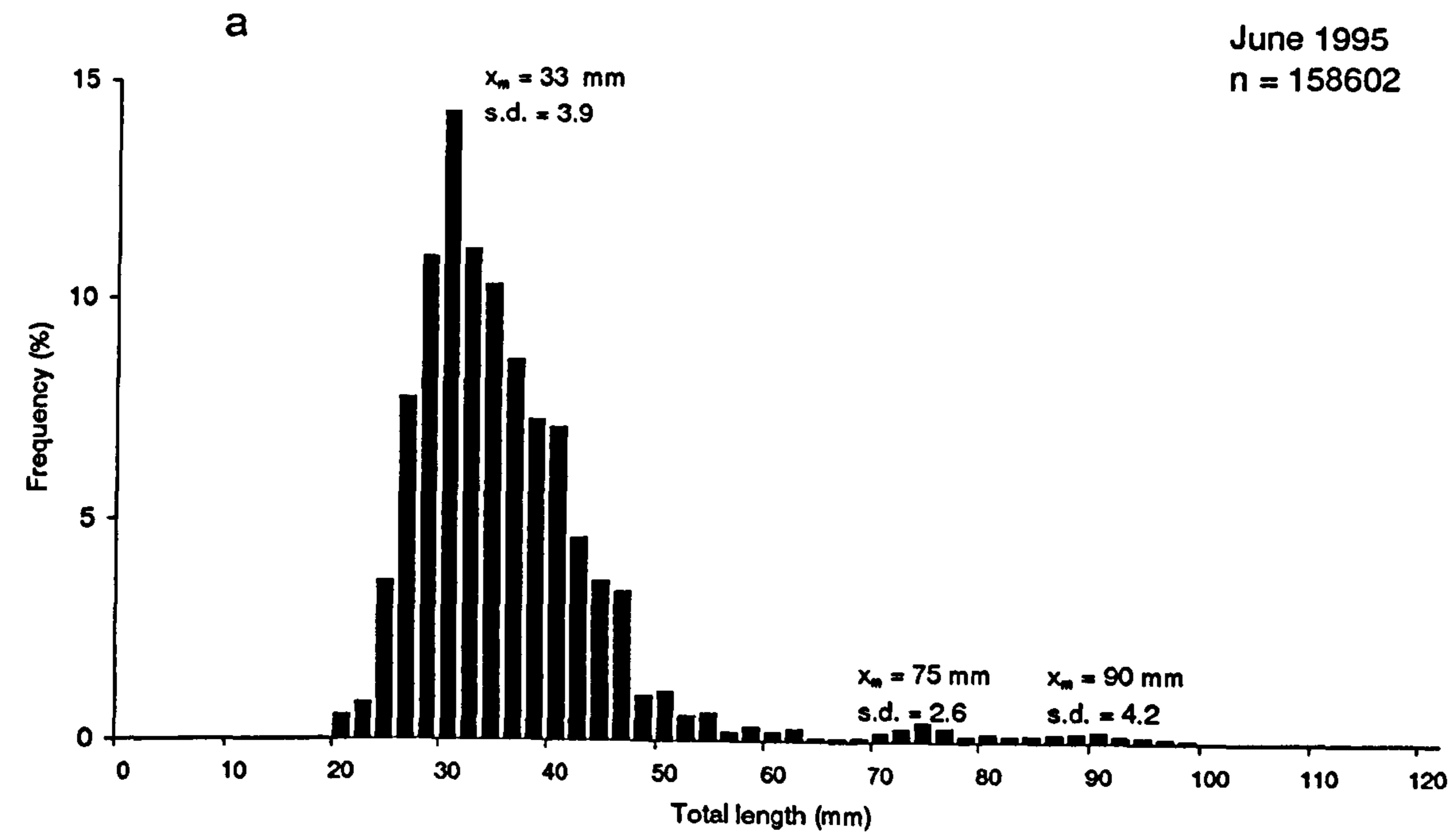


Figure 41. Size distribution of *S. tanganycae* for the whole lake from mid-water trawl surveys. a: June 1995 survey; b: November-December 1995 survey. N is the sample size,  $x_m$  and s.d. are the mean length and standard deviation of identified cohorts after Bhattacharya's decomposition of length distribution.

April 1996  
n = 525150

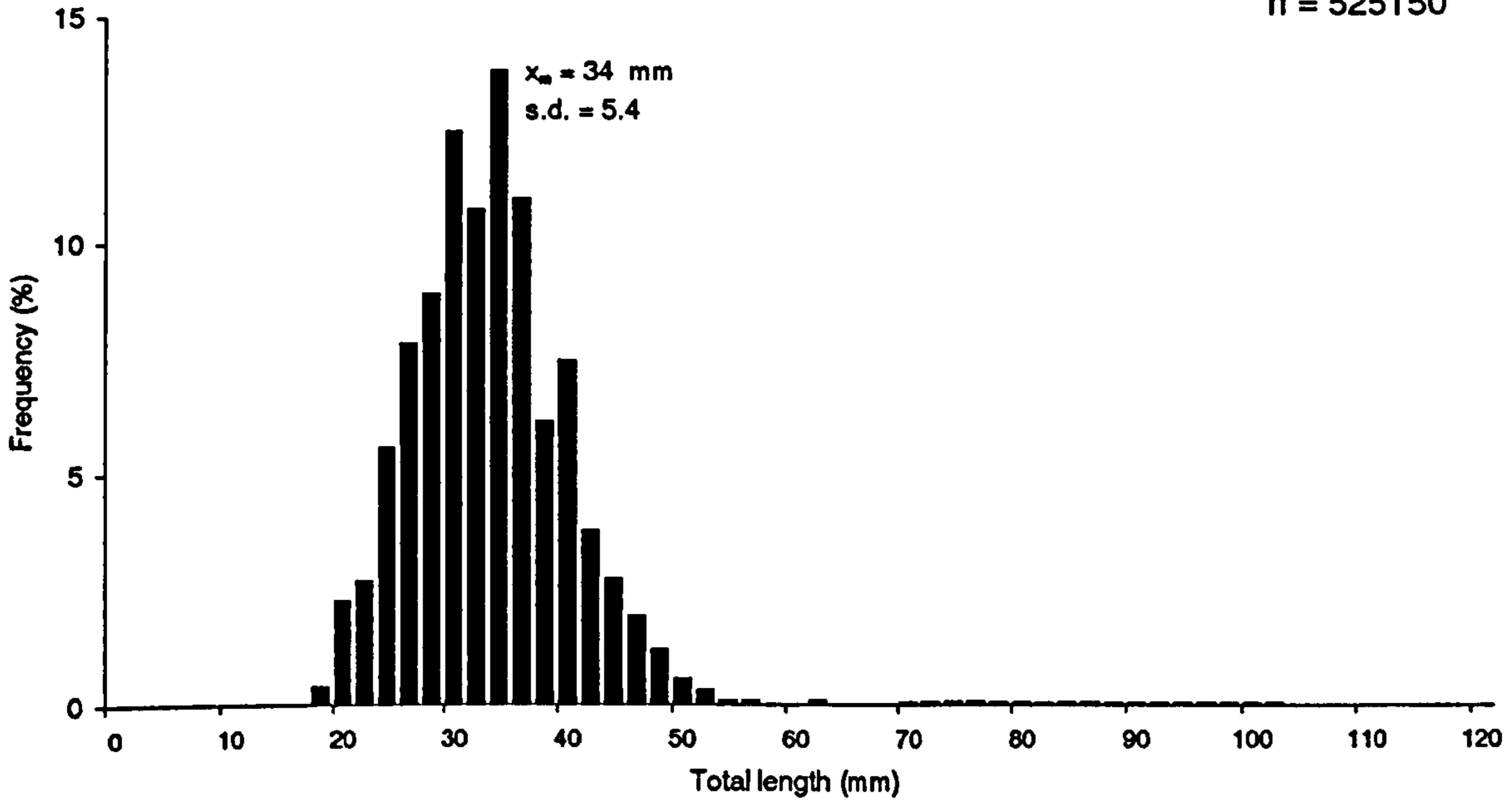


Figure 42. Size distribution of *S. tanganycae* for the whole lake from April 1996 mid-water trawl survey. N is the sample size,  $x_m$  and s.d. are the mean length and standard deviation of identified cohort after Bhattacharya's decomposition of length distribution.

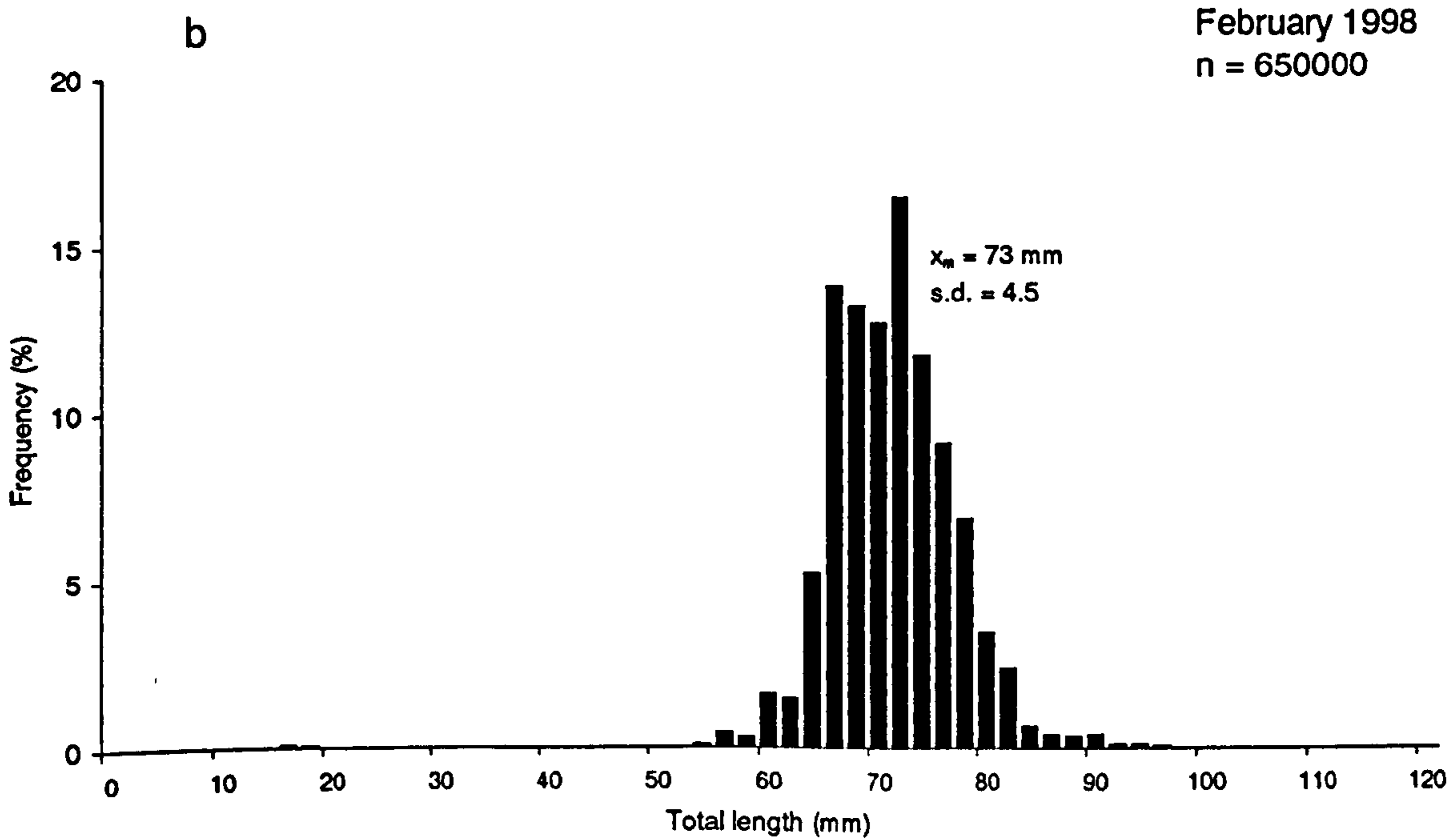
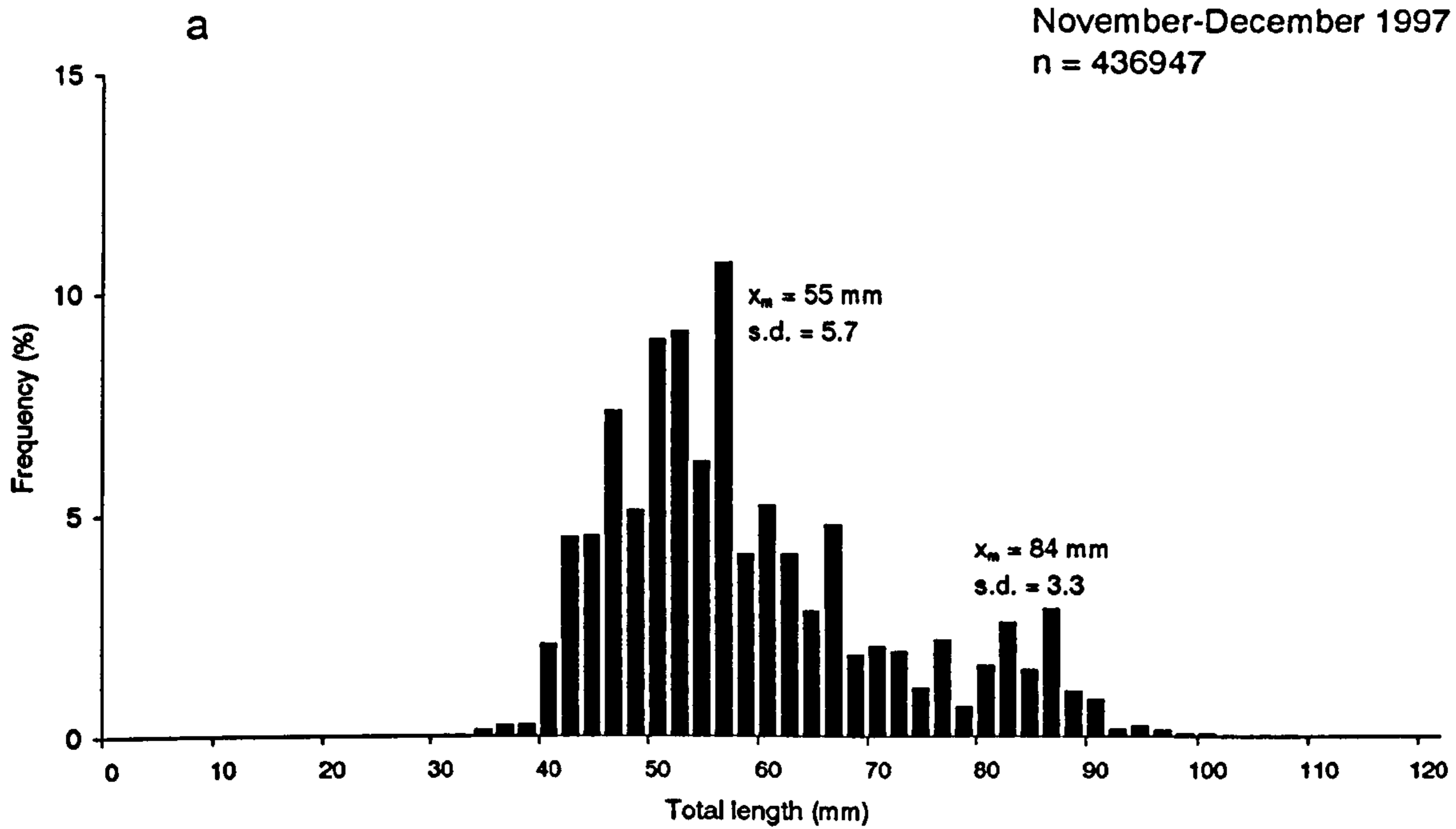


Figure 43. Size distribution of *S. tanganyicae* for the whole lake from mid-water trawl surveys. a: November-December 1997 survey; b: February 1998 survey. N is the sample size,  $x_m$  and s.d. are the mean length and standard deviation of identified cohorts after Bhattacharya's decomposition of length distribution.

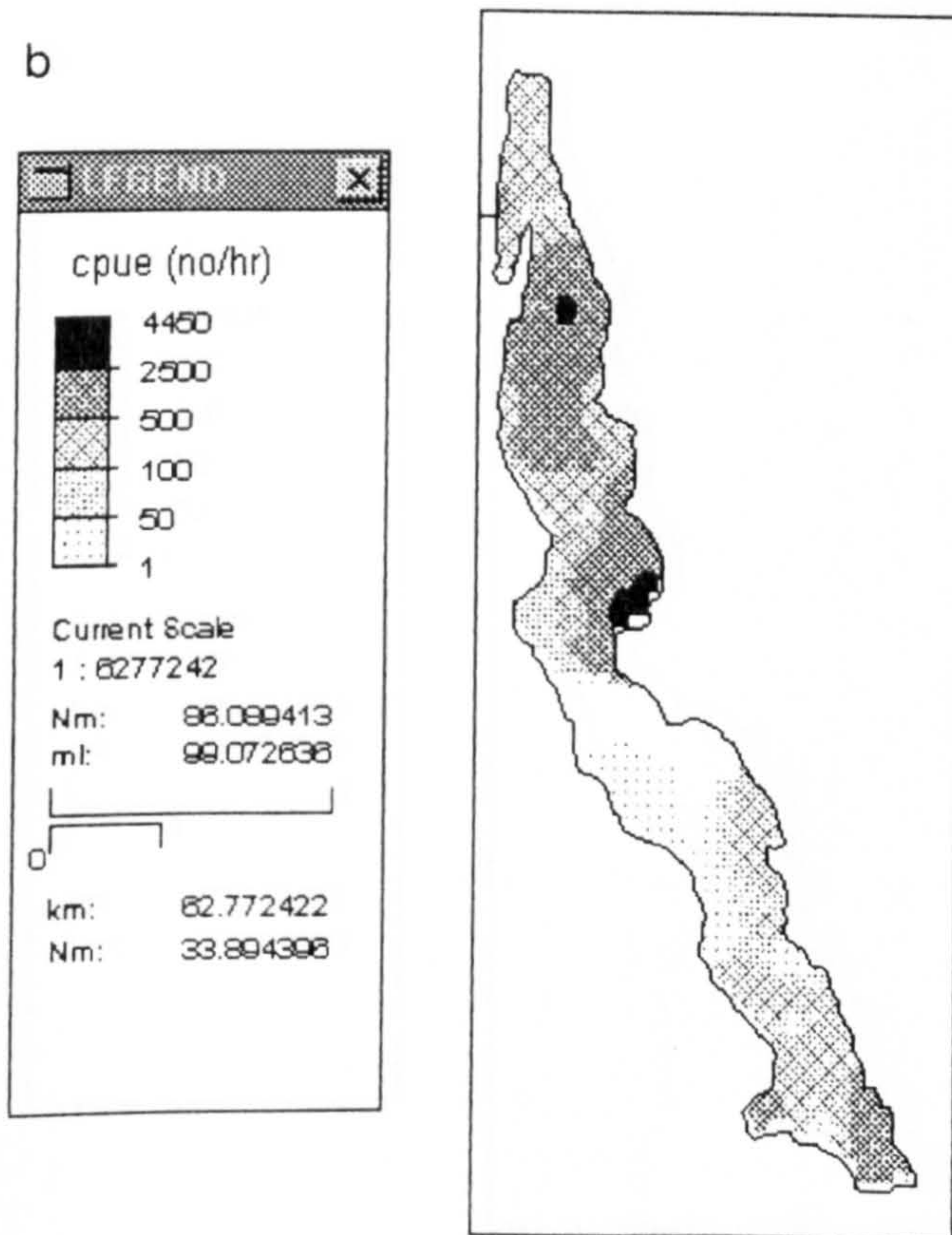
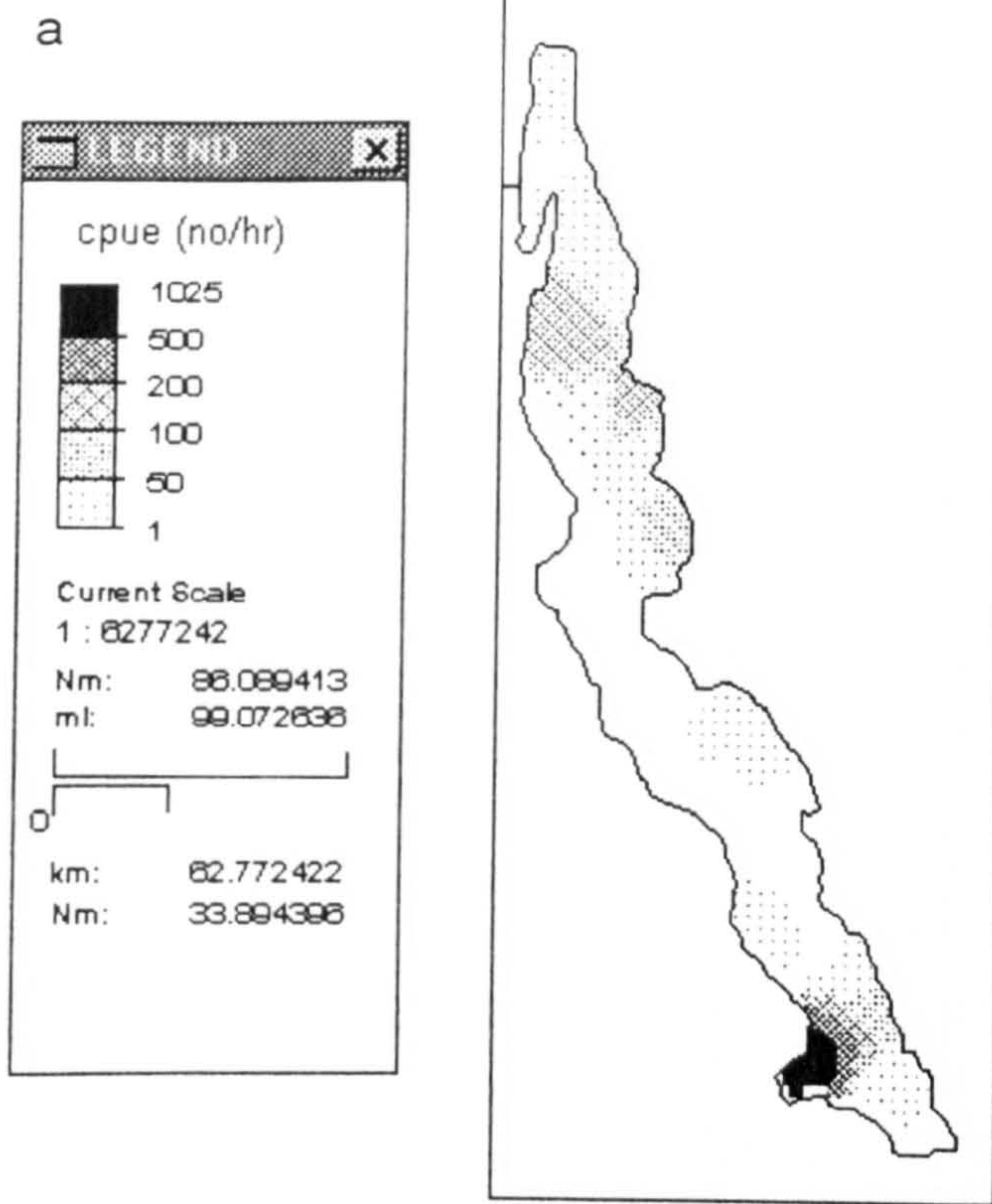
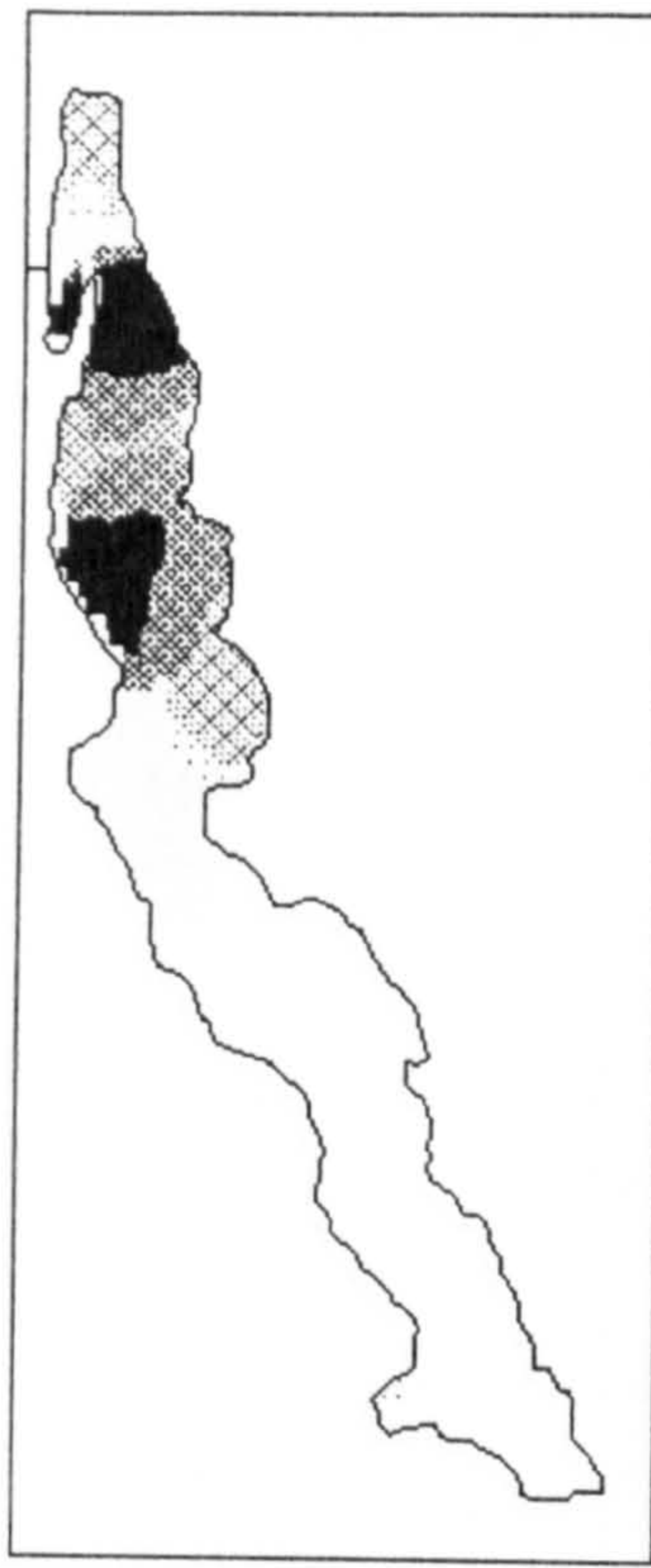
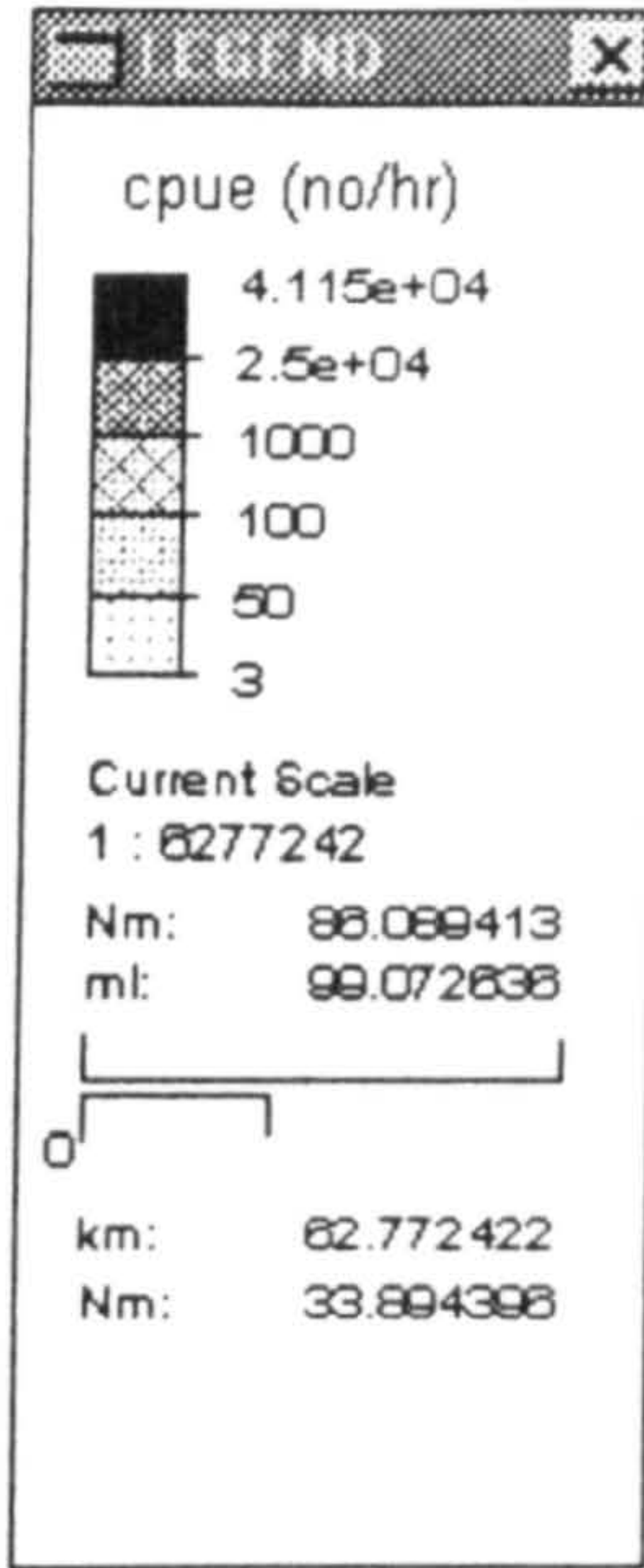


Figure 44. Pelagic trawl catch distribution of adult *S. tanganyicae* ( $TL > L_m$ ) in June 1995 (a) and November-December 1995 (b) survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale 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 statute miles (mi).



a



b

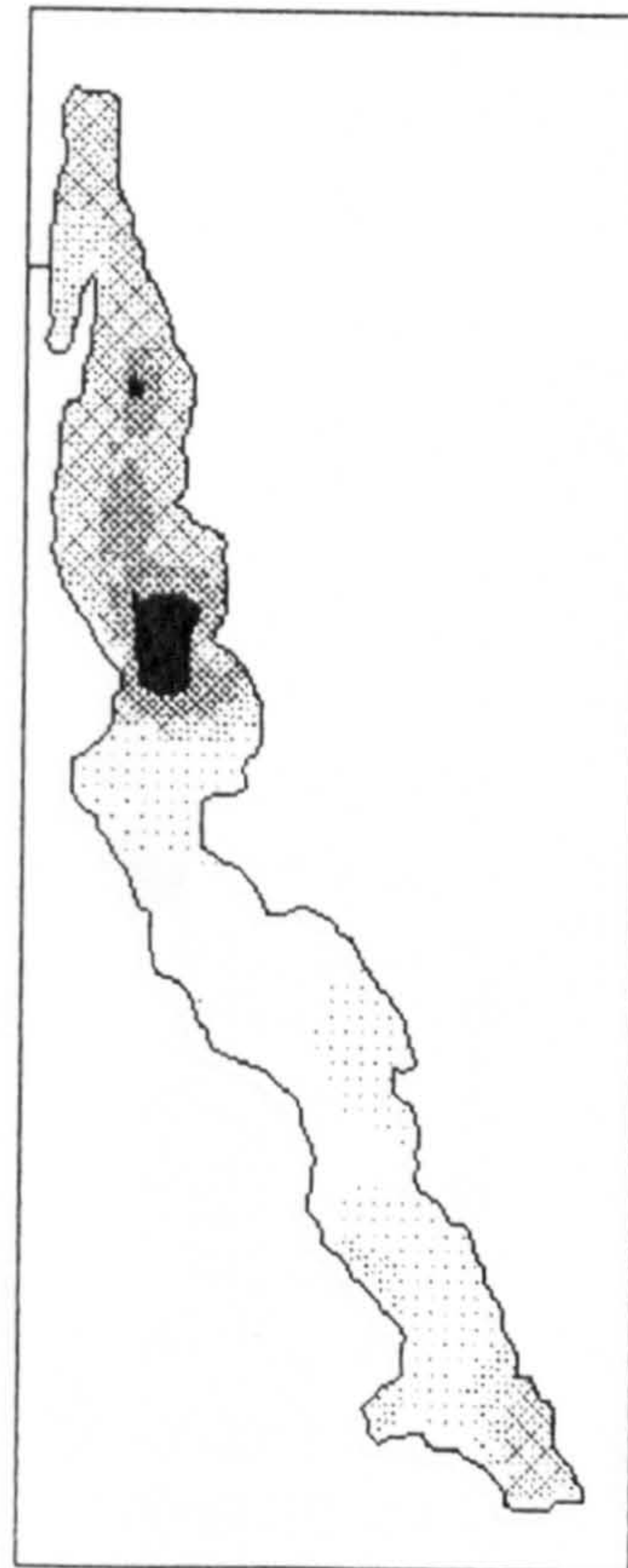
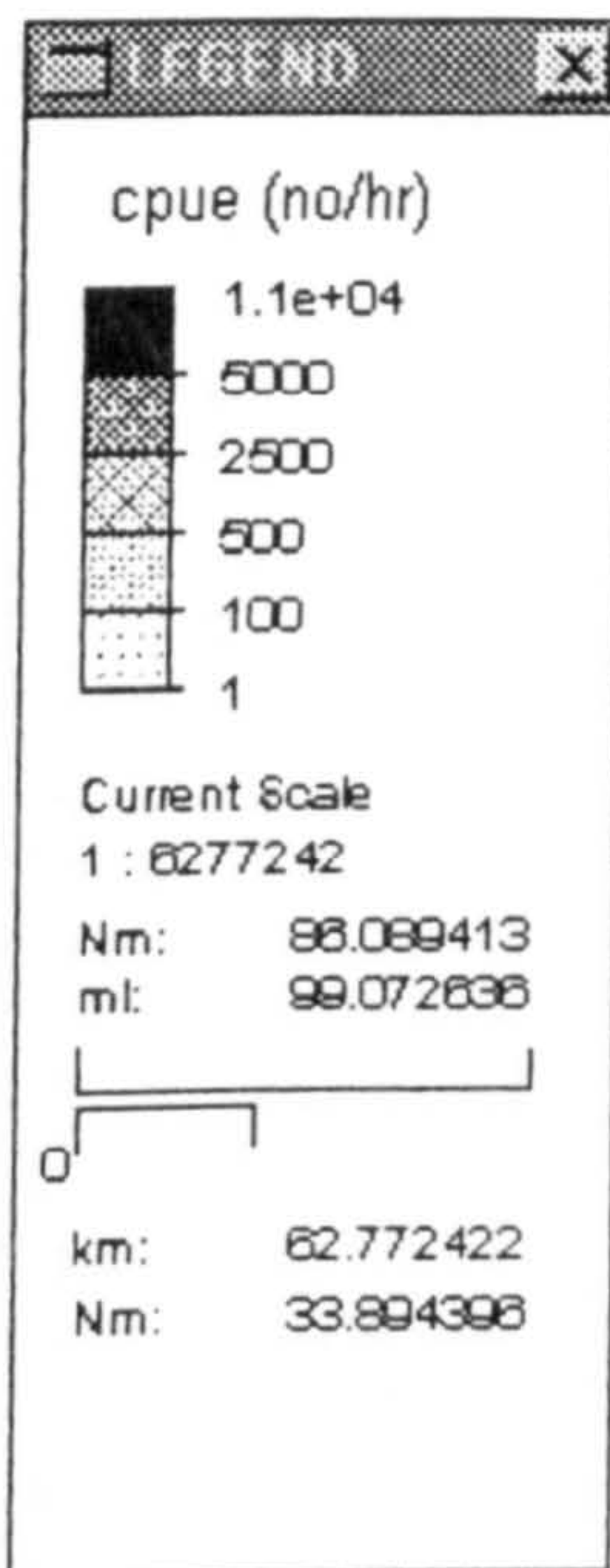


Figure 45. Pelagic trawl catch distribution of young *S. tanganyicae* ( $TL < L_m$ ) in June 1995 (a) and November-December (b) 1995 survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale 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 statute miles (ml).

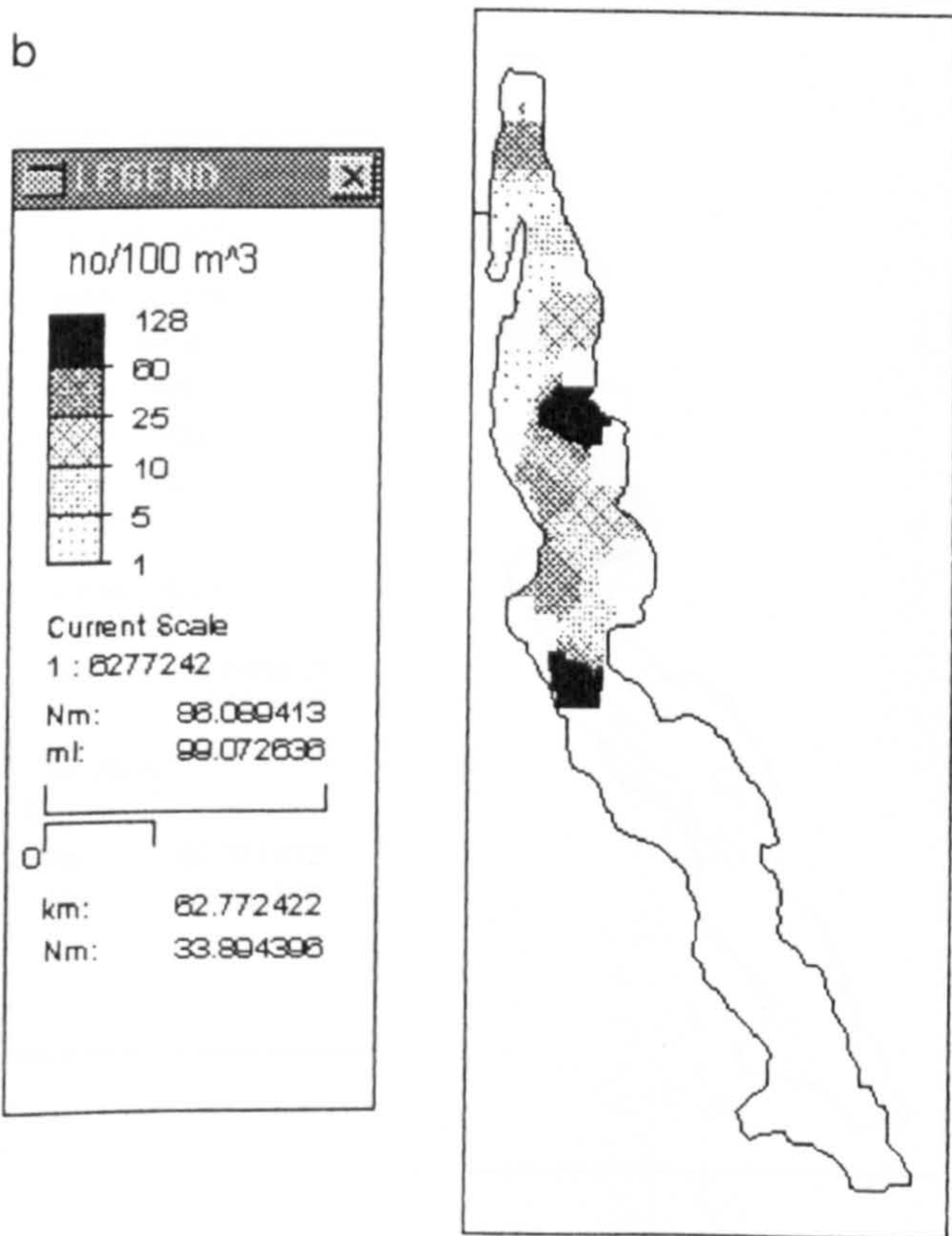
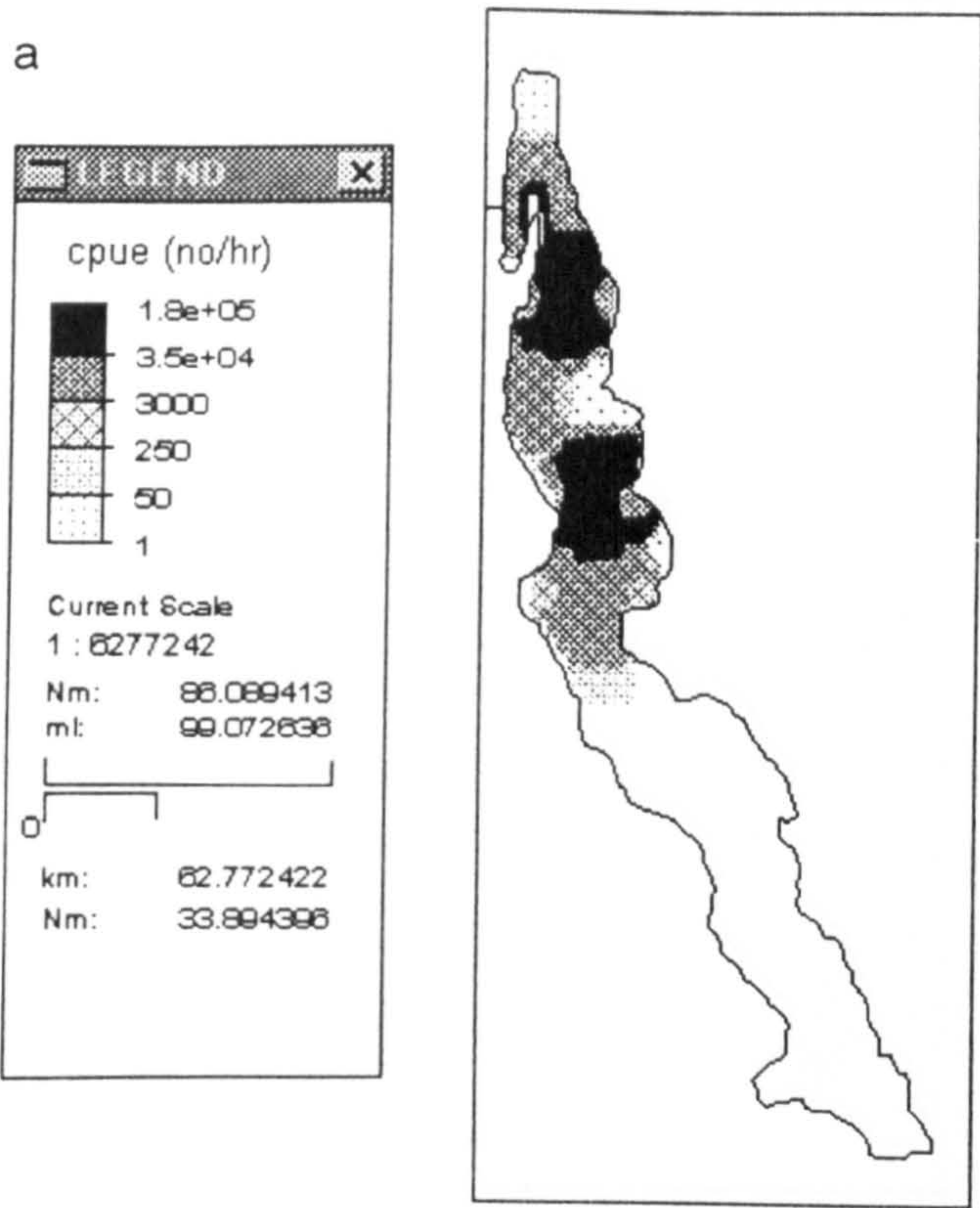


Figure 46. Pelagic trawl catch distribution of (a) young *S. tanganyicae* ( $TL < L_m$ ) and distribution of *S. tanganyicae* larvae (b) within 0-100 m water column in April 1996 survey. Catch per unit of effort (no/hr) and larval density (no/100 m<sup>3</sup>) are grouped in five levels shown in the 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 statute miles (mi).

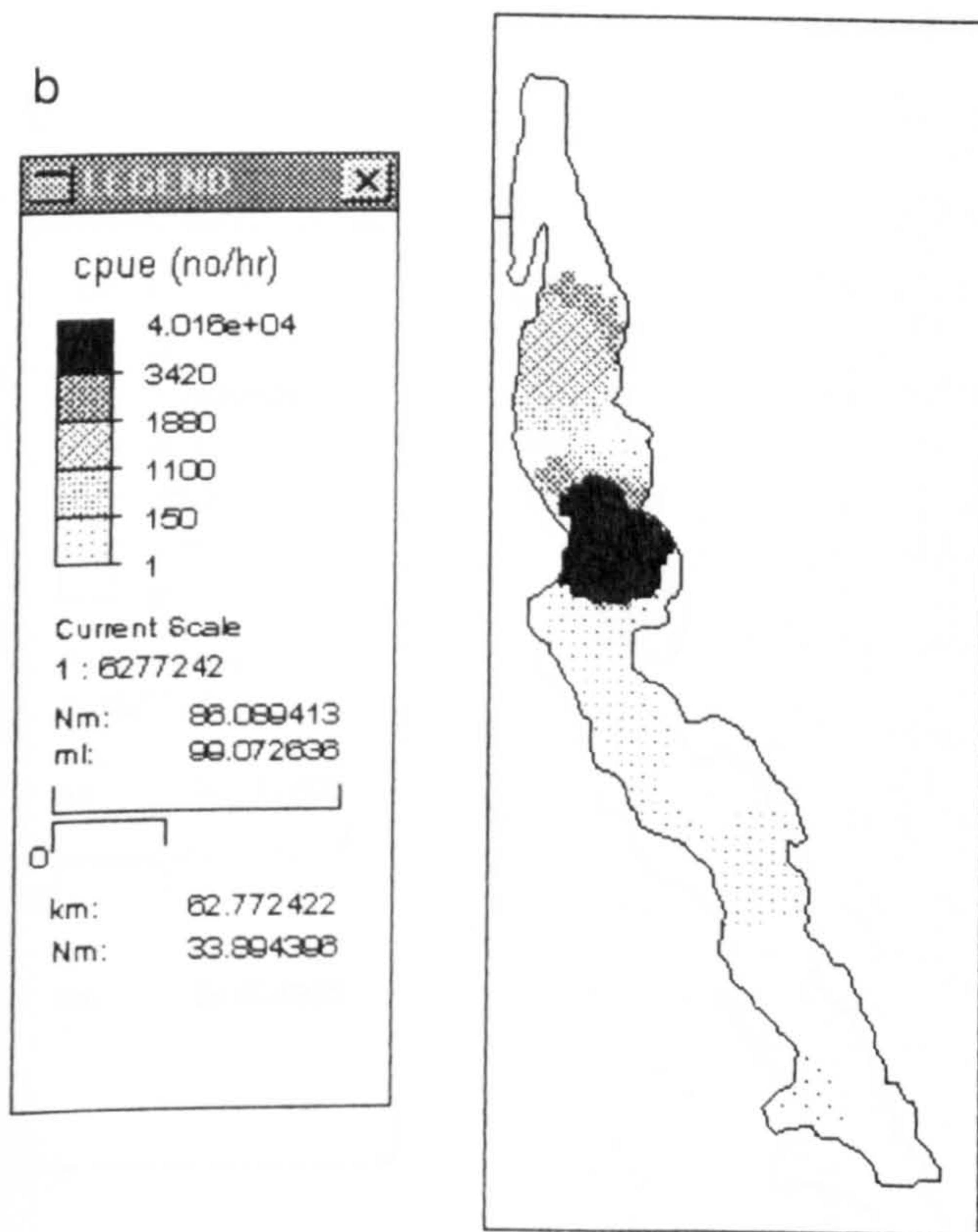
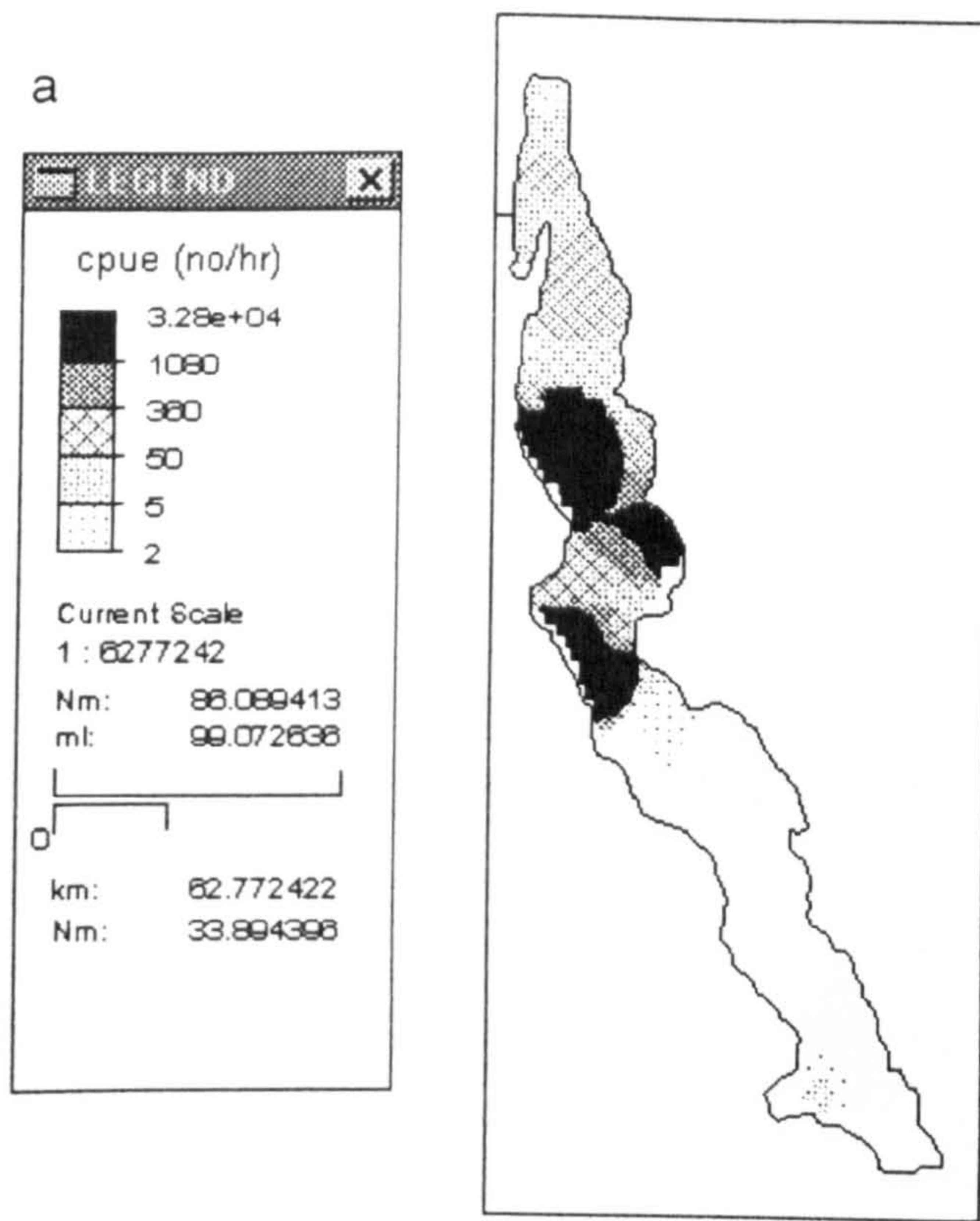


Figure 47. Pelagic trawl catch distribution of adult *S. tanganyicae* ( $TL > L_m$ ) in November-December 1997 (a) and February 1998 (b) survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern 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 statute miles (mi).

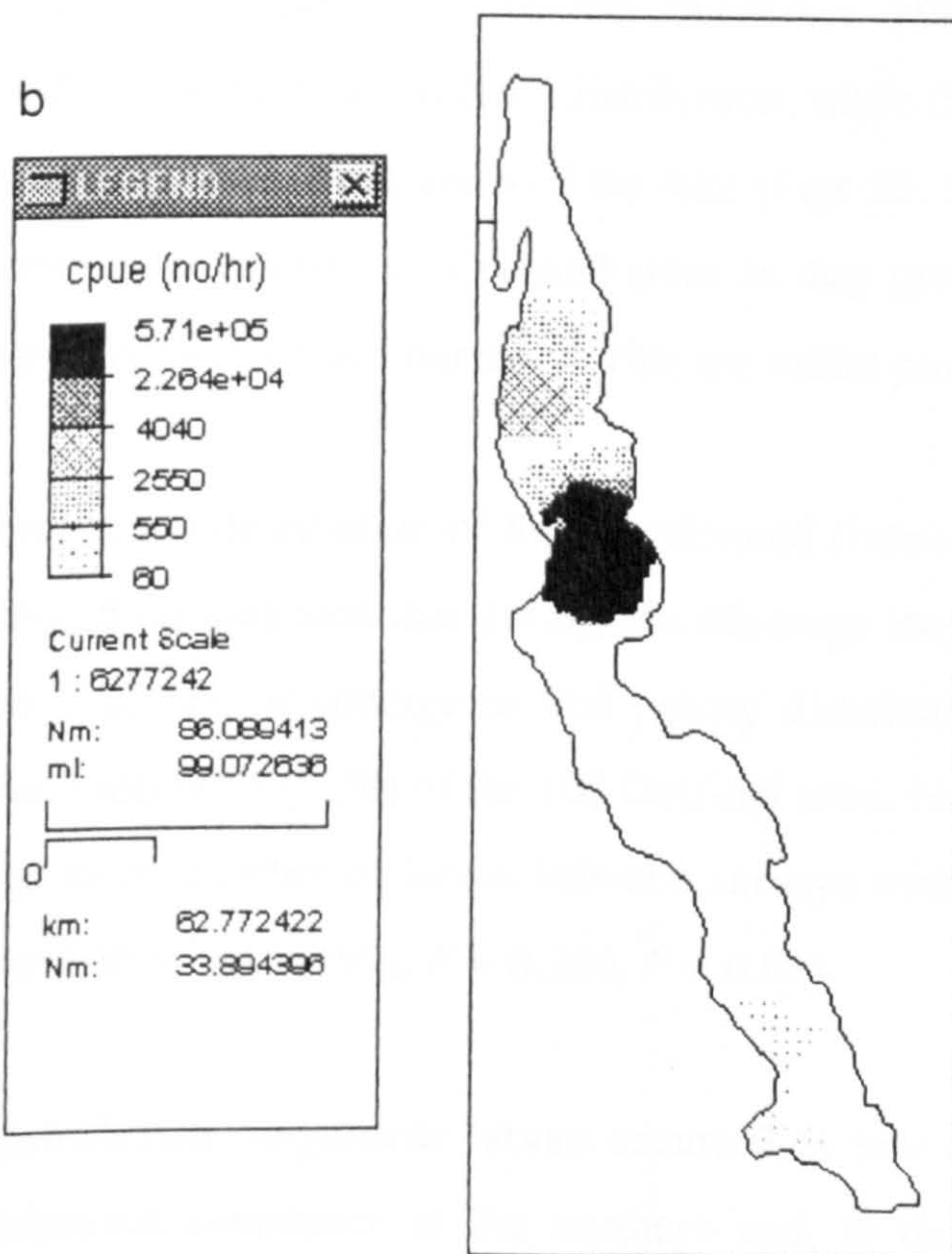
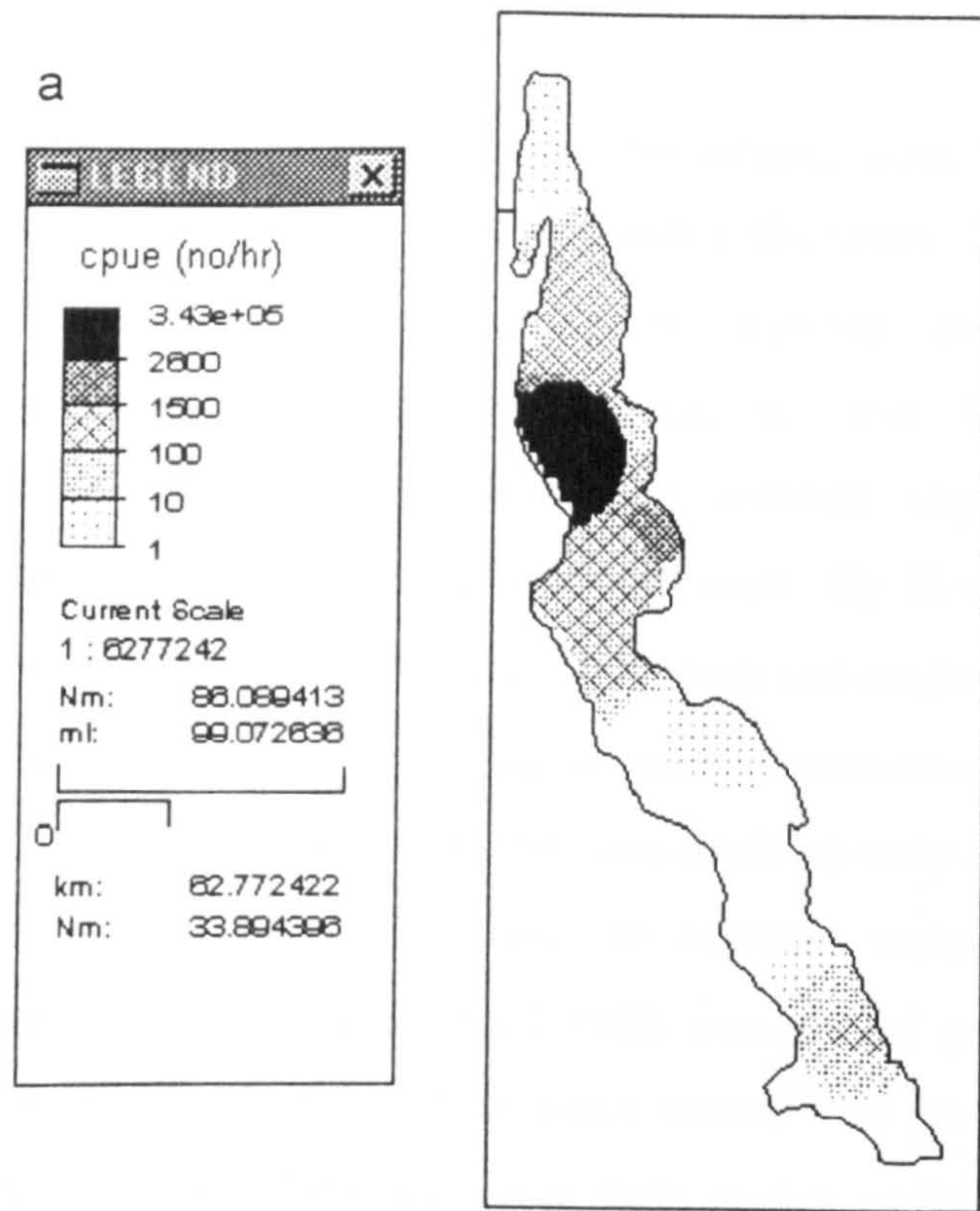


Figure 48. Pelagic trawl catch distribution of young *S. tanganyicae* ( $TL < L_m$ ) in November-December 1997 (a) and February (b) 1998 survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern 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 statute miles (mi).

*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 49 and 52). *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 50 and 52). 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 50, 51 and 52). 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. 53a) 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<sup>3</sup> (ANOVA,  $F = 0.296$ ,  $P = 0.88$ ).

*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 maximum absolute density (250 specimens per 100 m<sup>3</sup>) was recorded in the Kigoma sub-basin (Fig. 54). Peak larval abundance was recorded

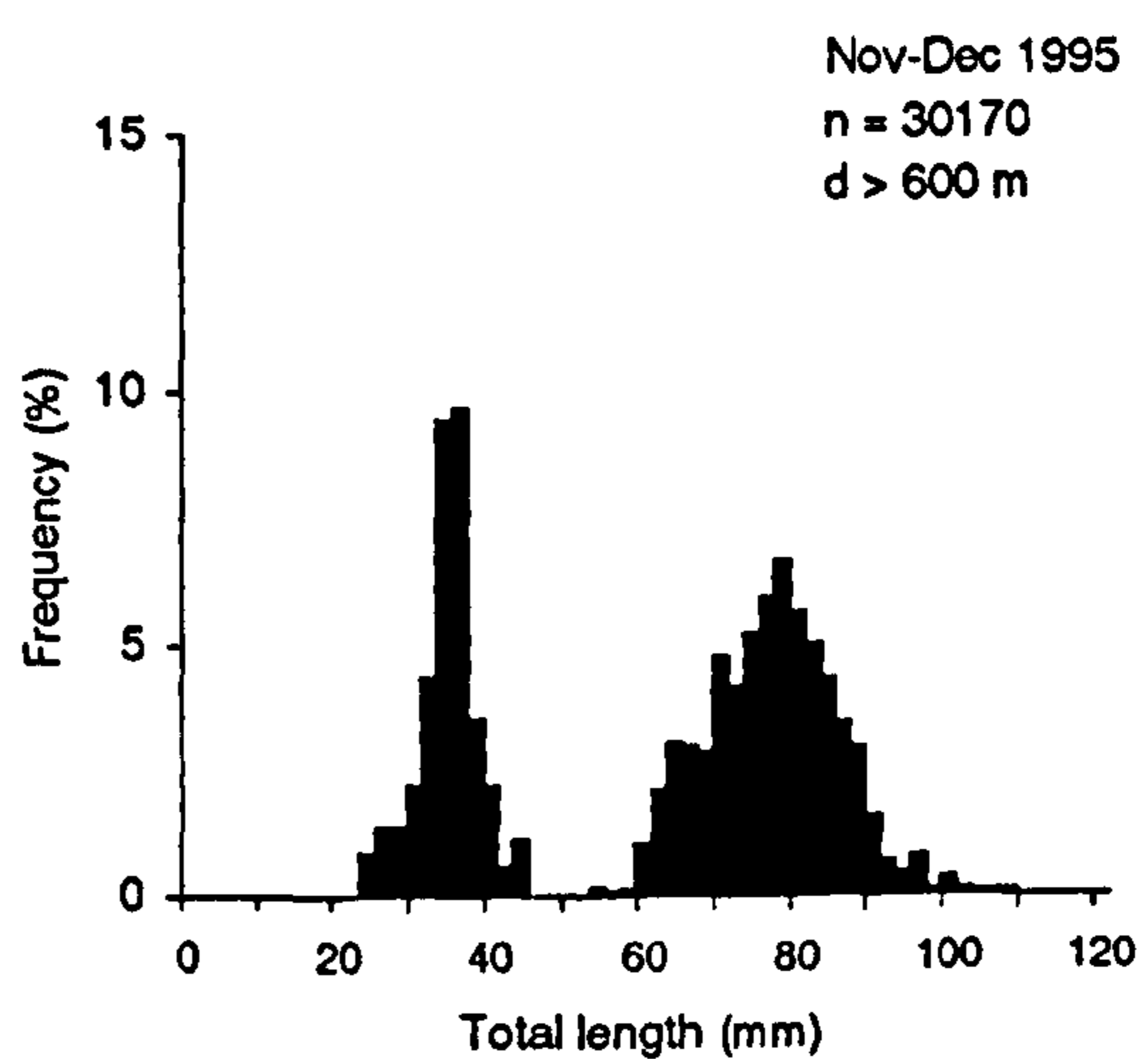
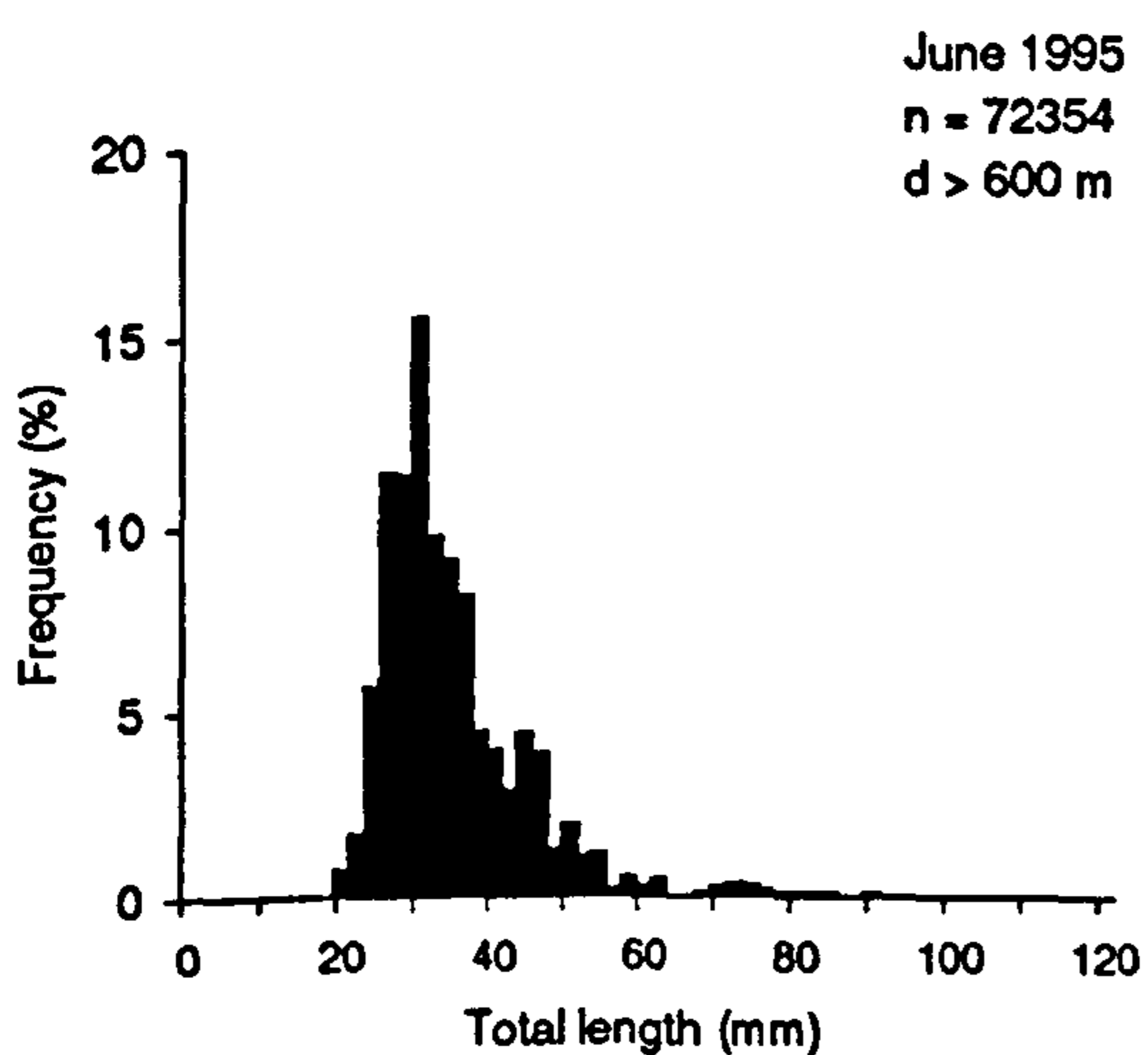
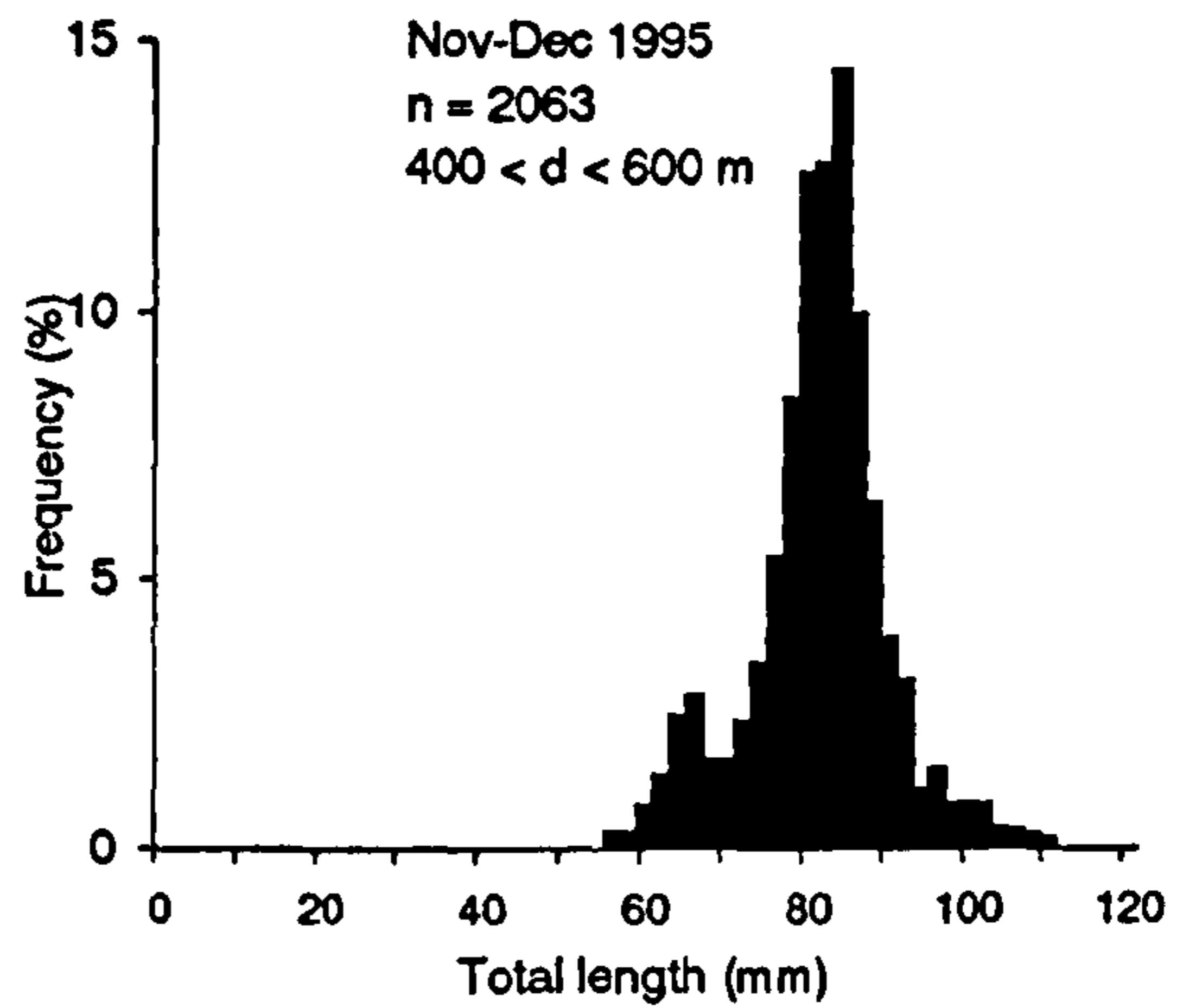
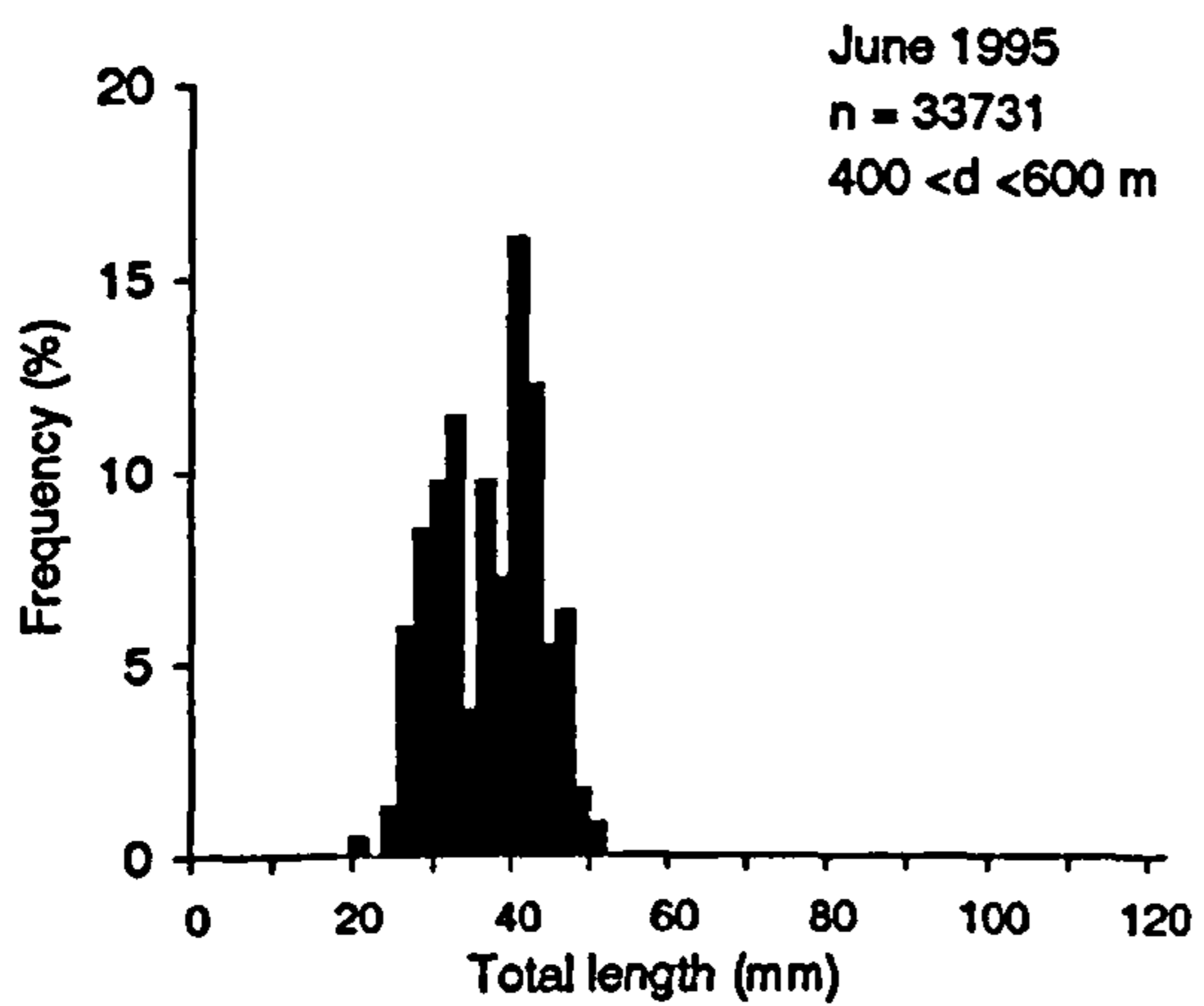
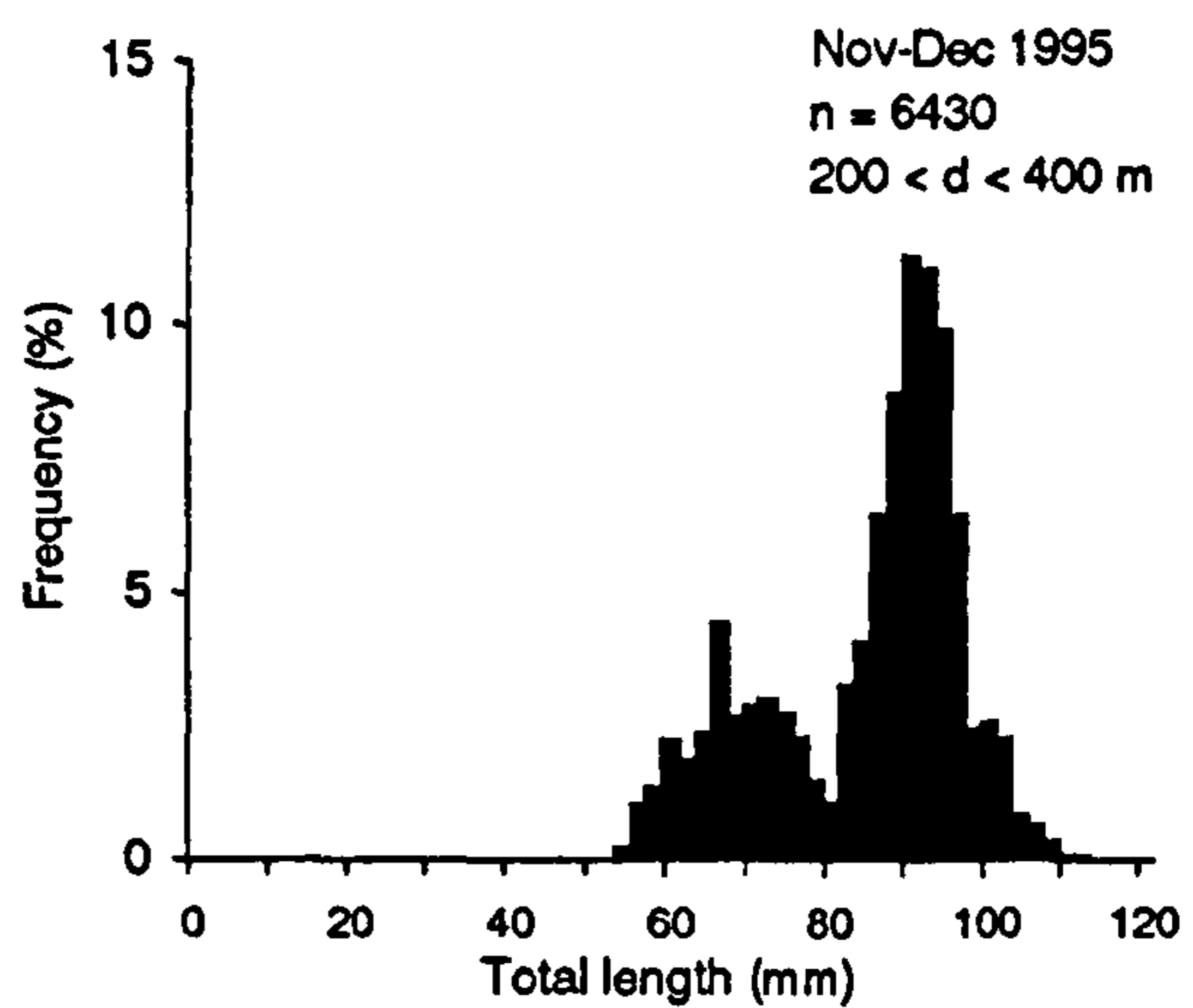
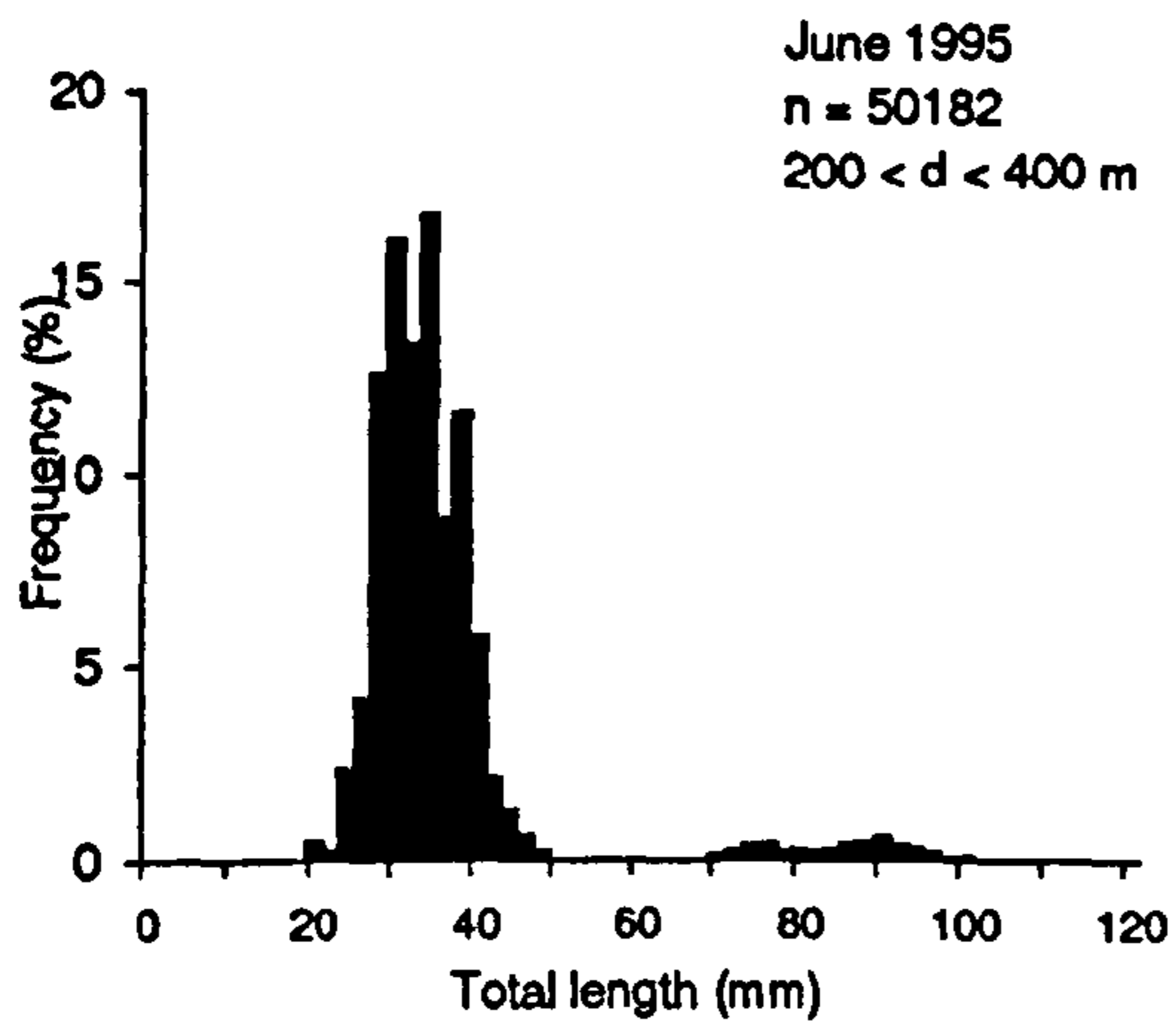
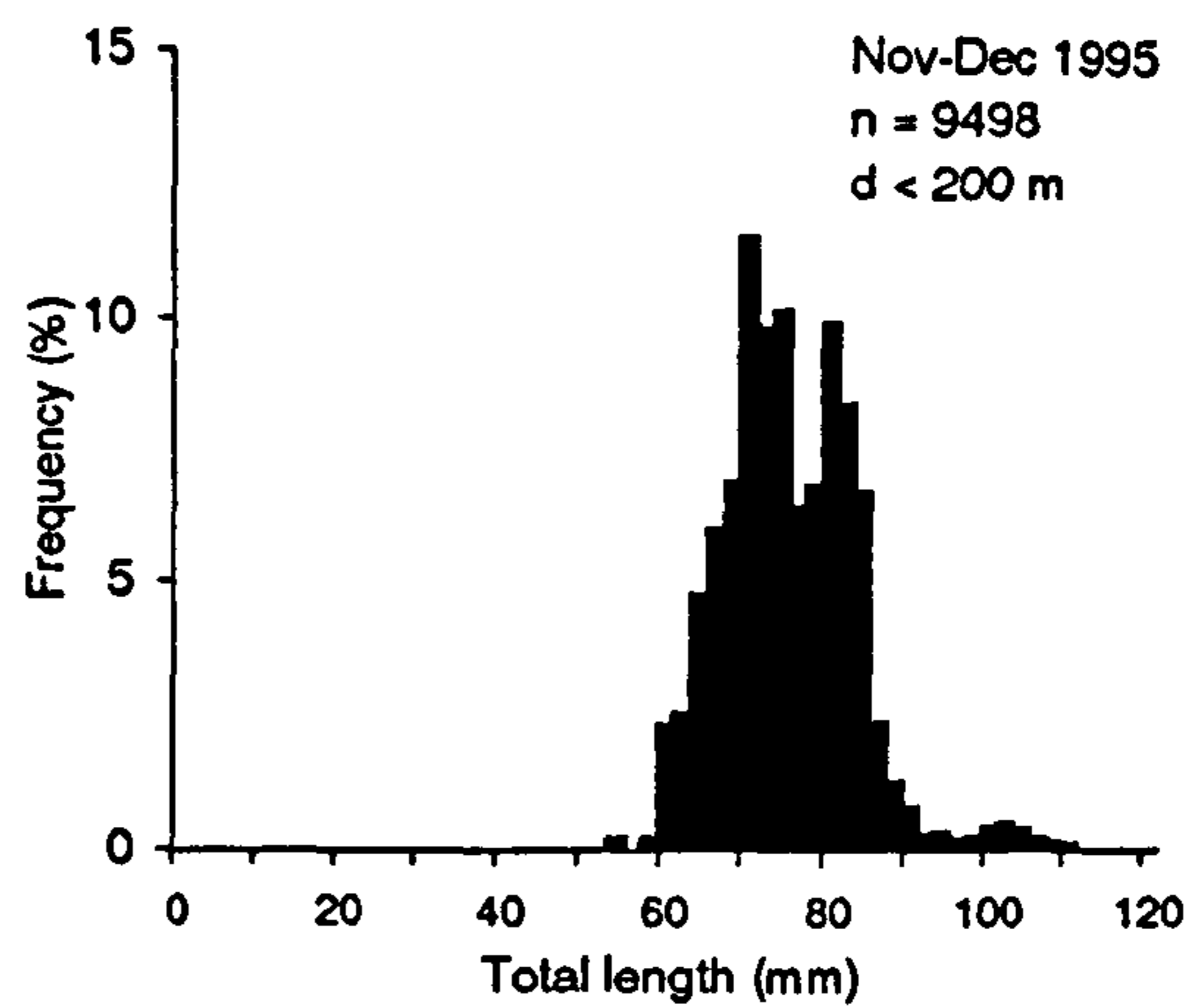
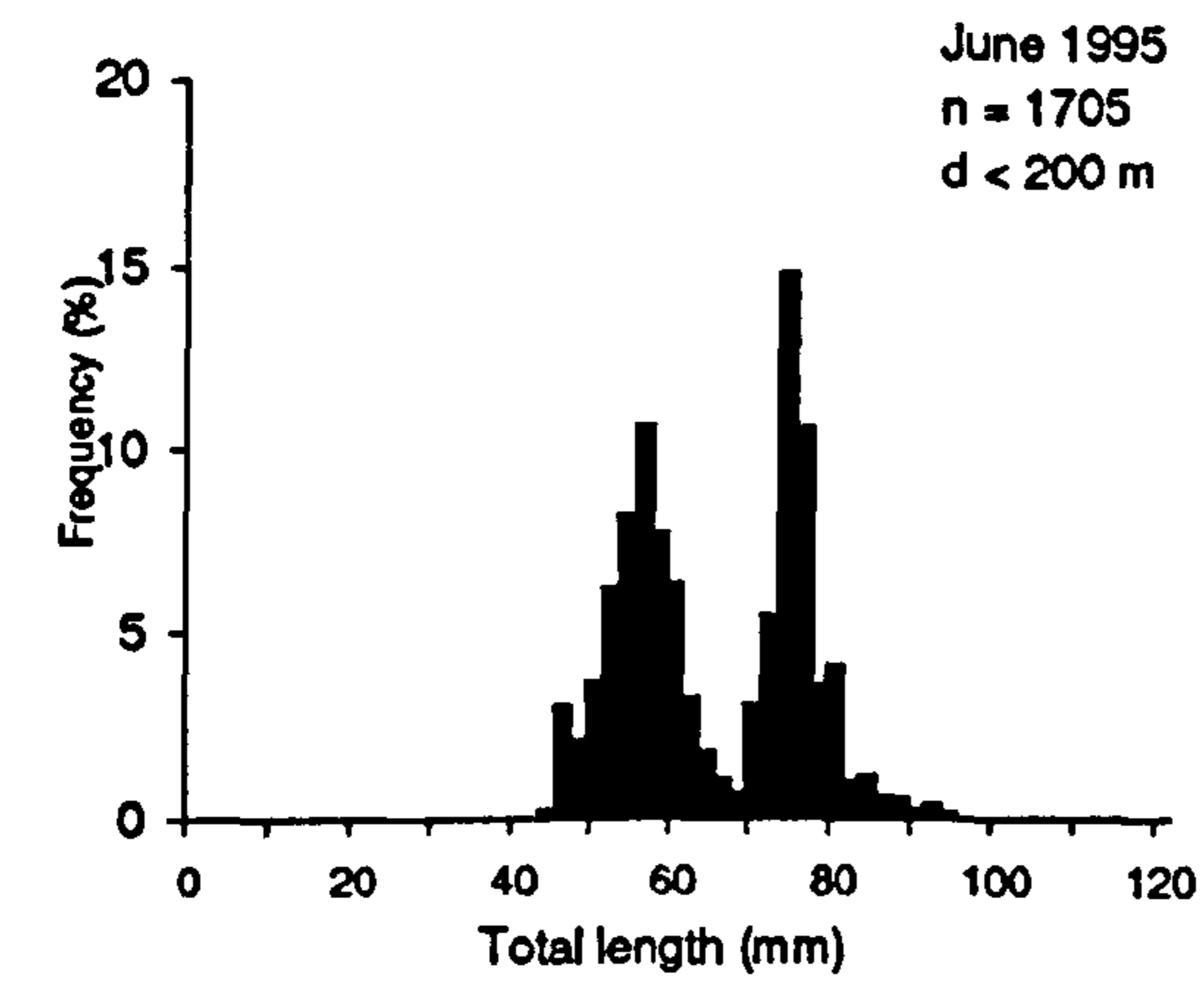


Figure 49. Size distribution of *S. tanganycae* by depth strata in June and November-December 1995. Bottom depth is indicated with d, n is the sample size.

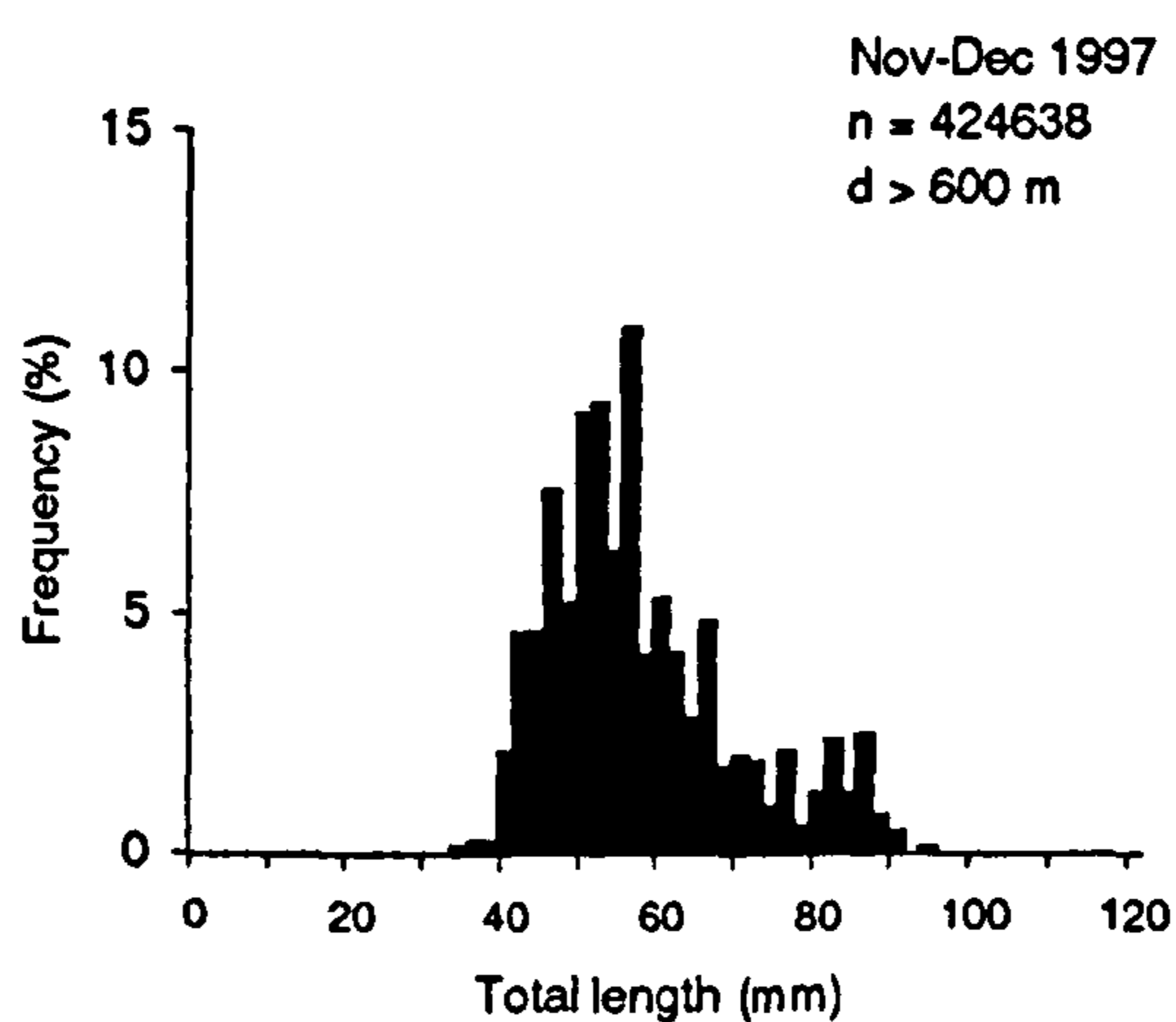
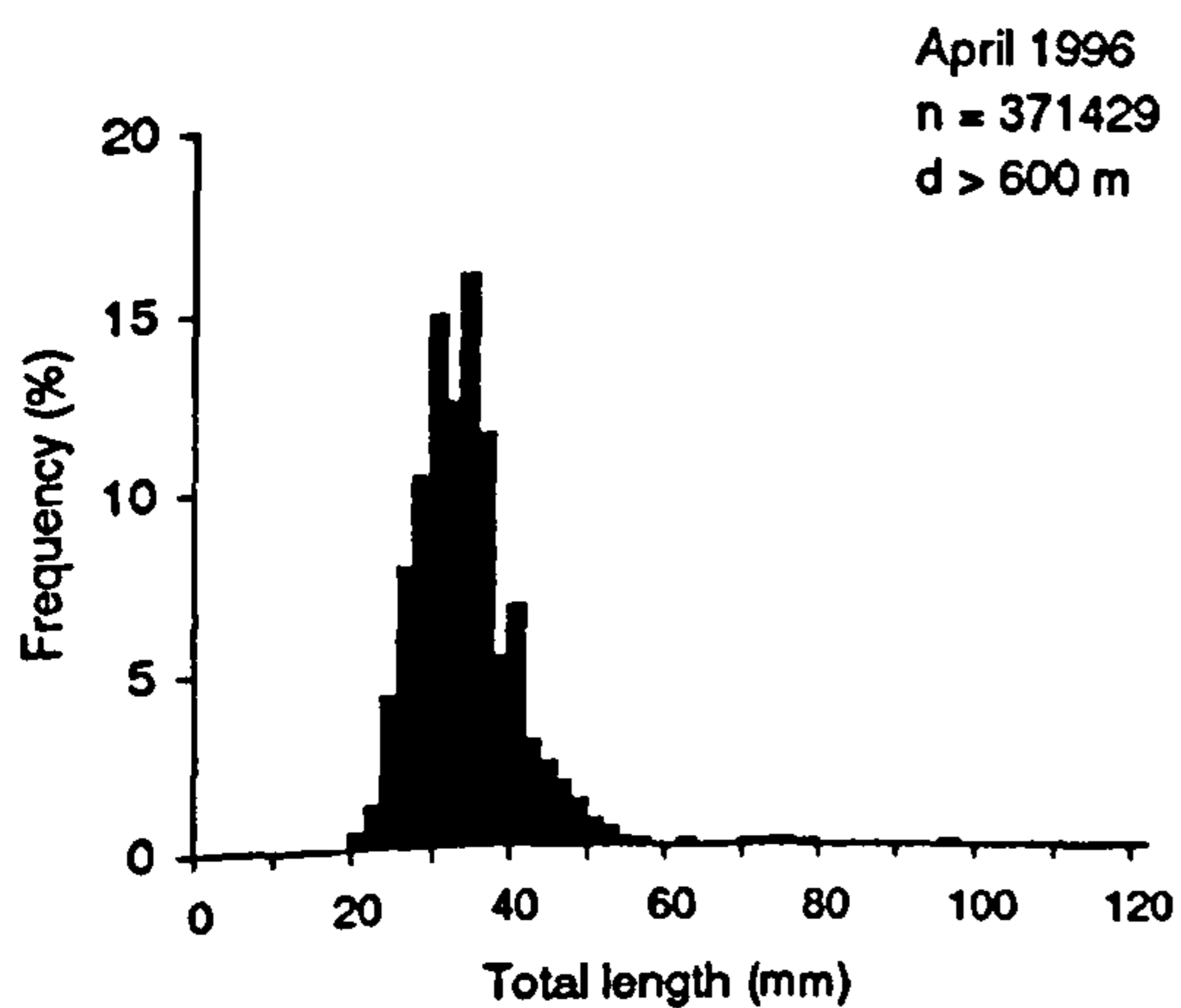
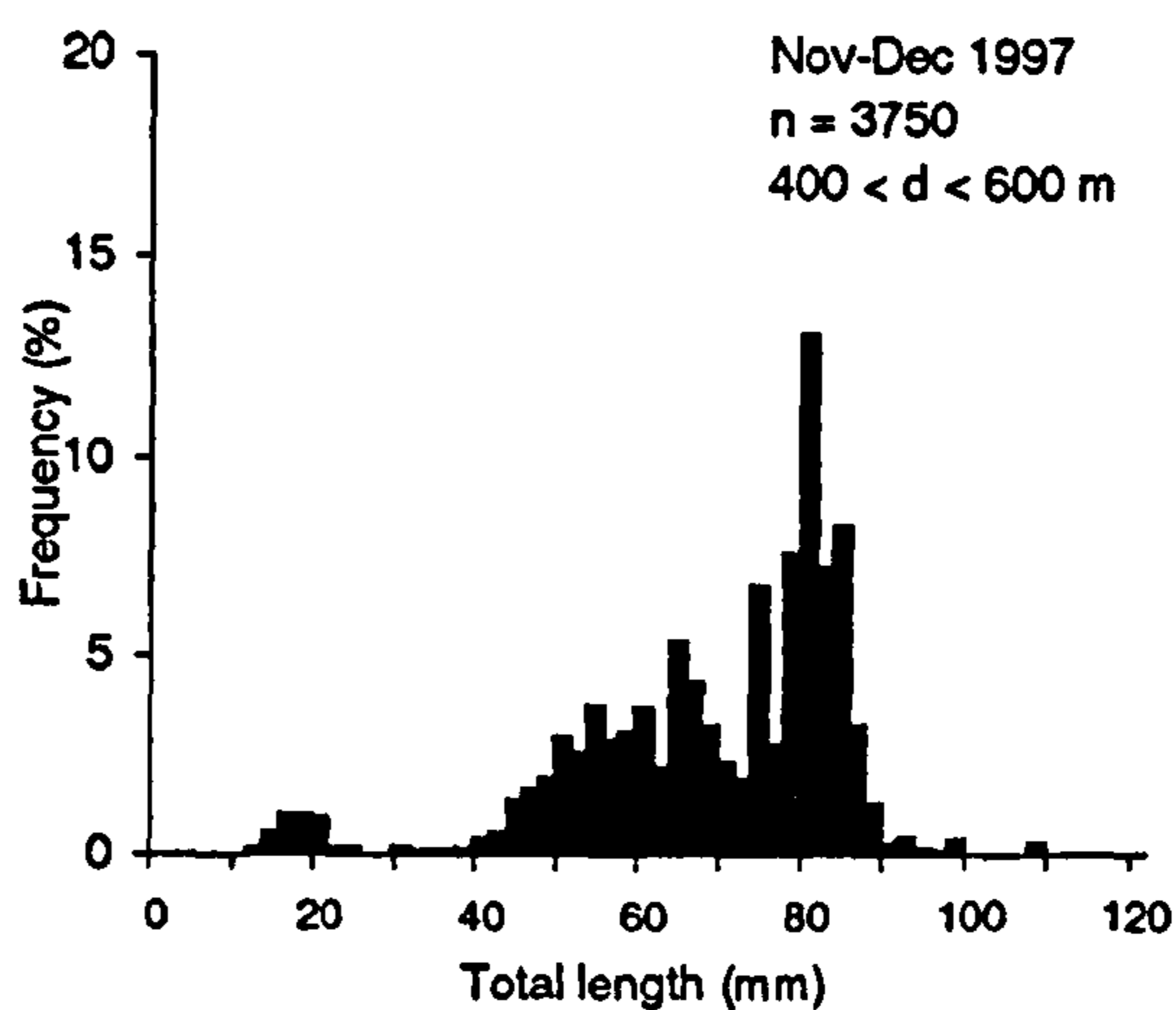
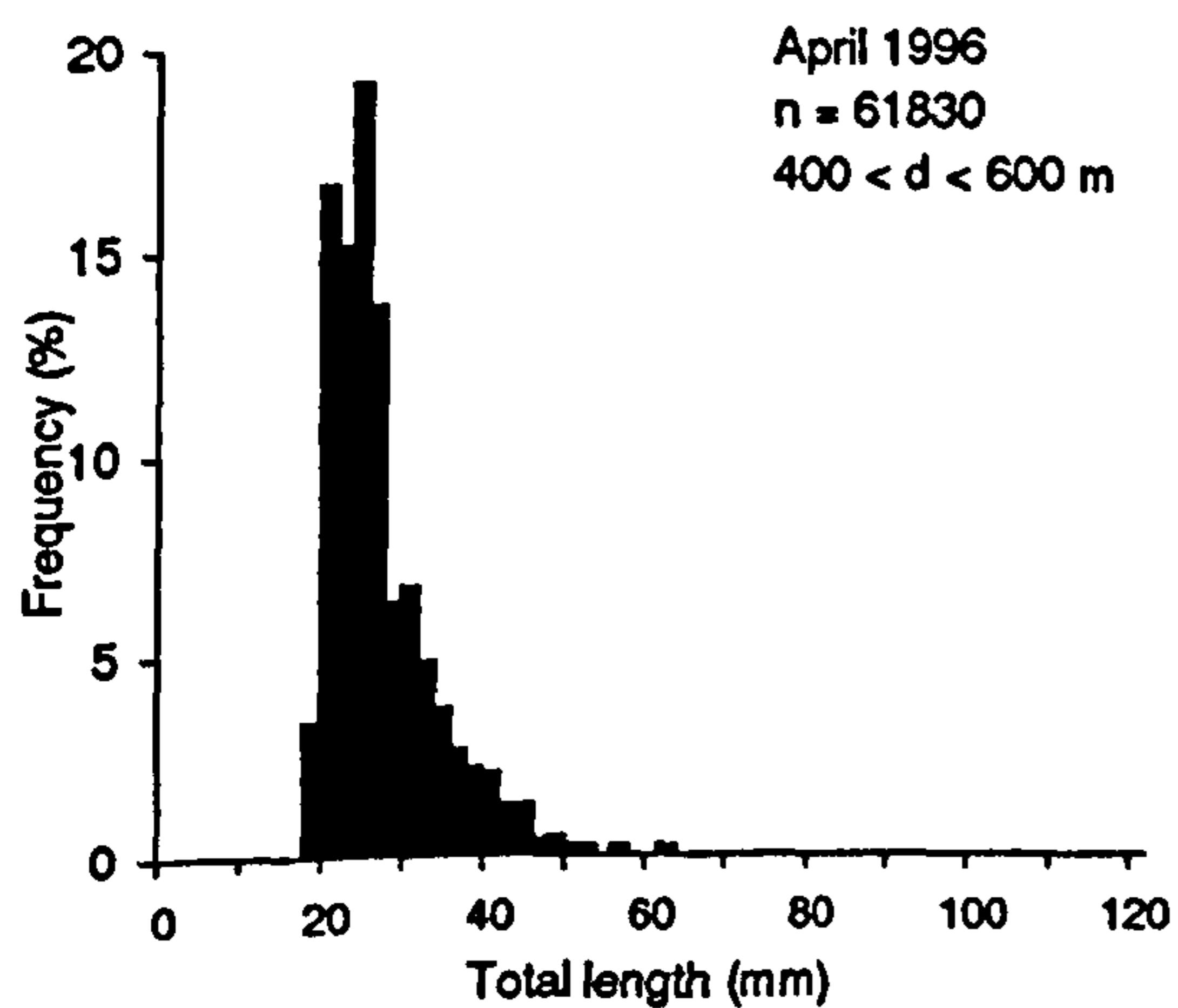
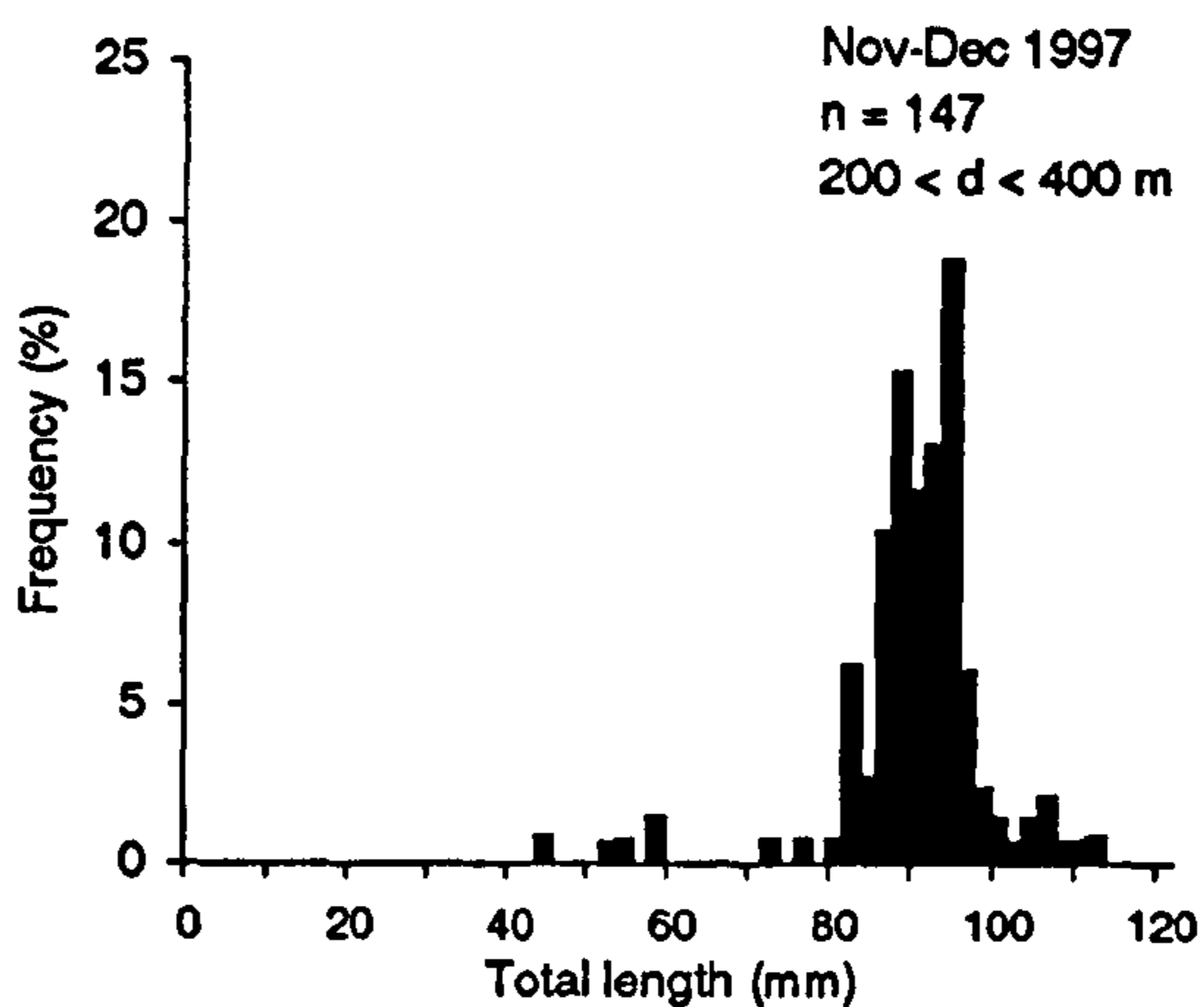
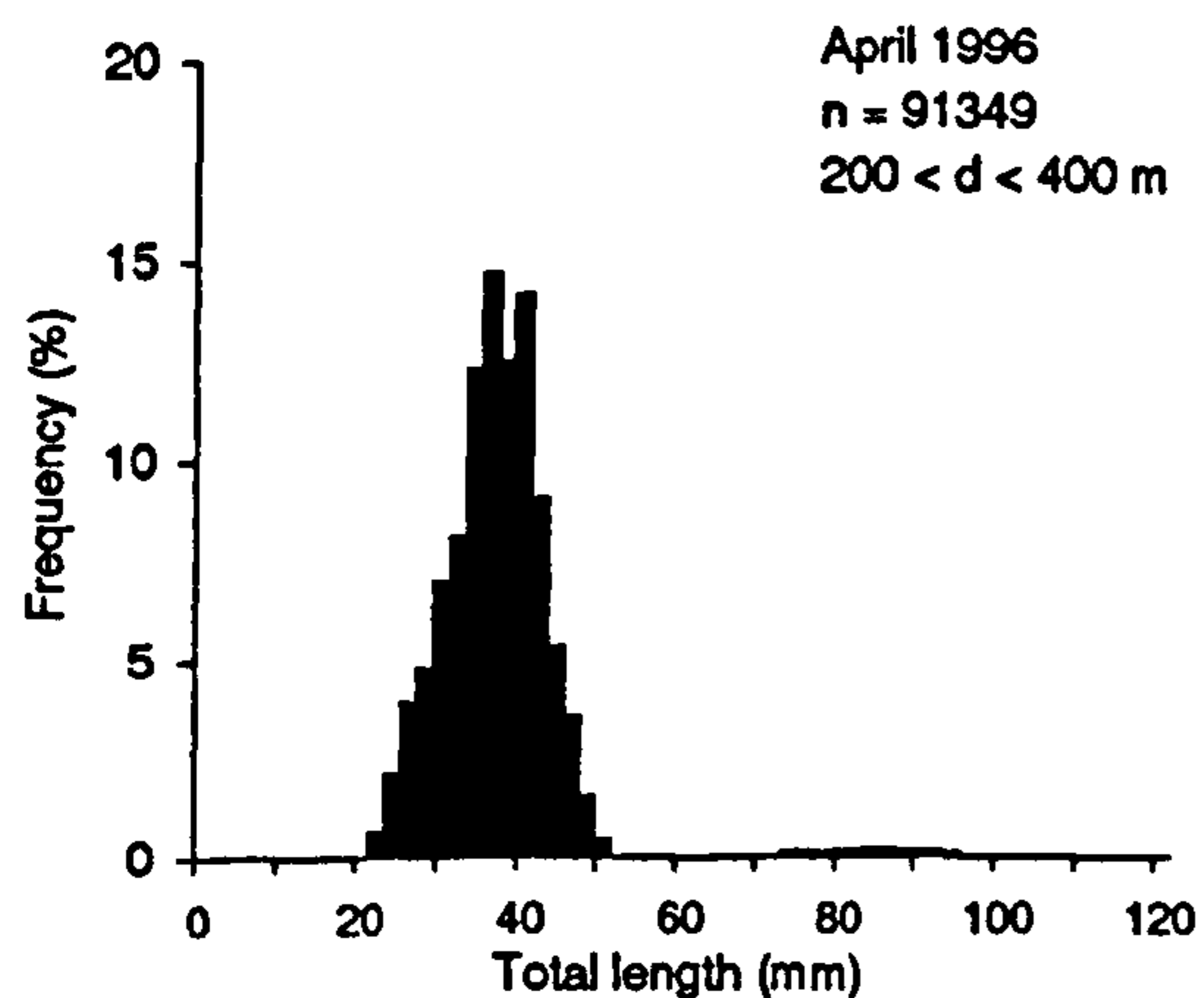
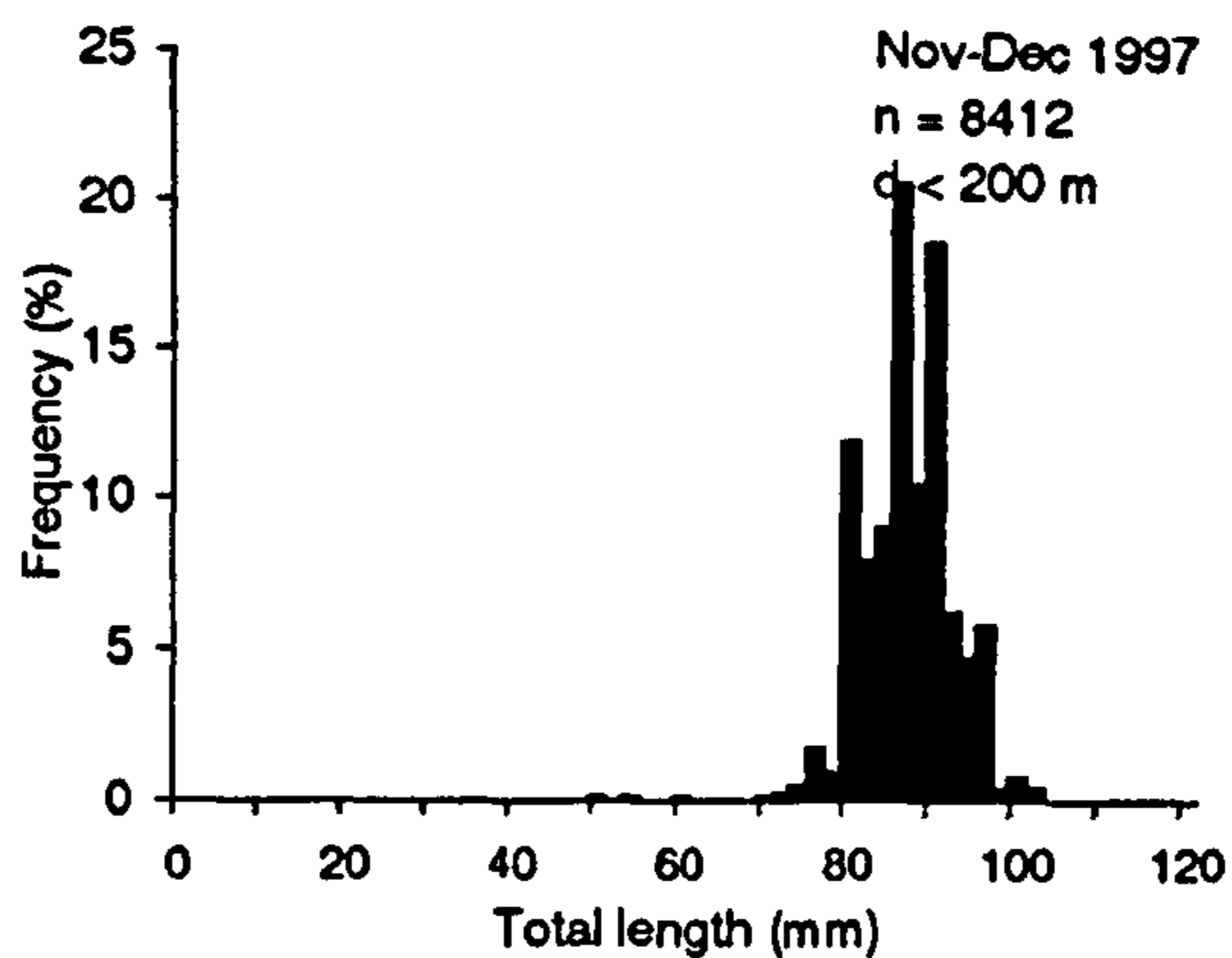
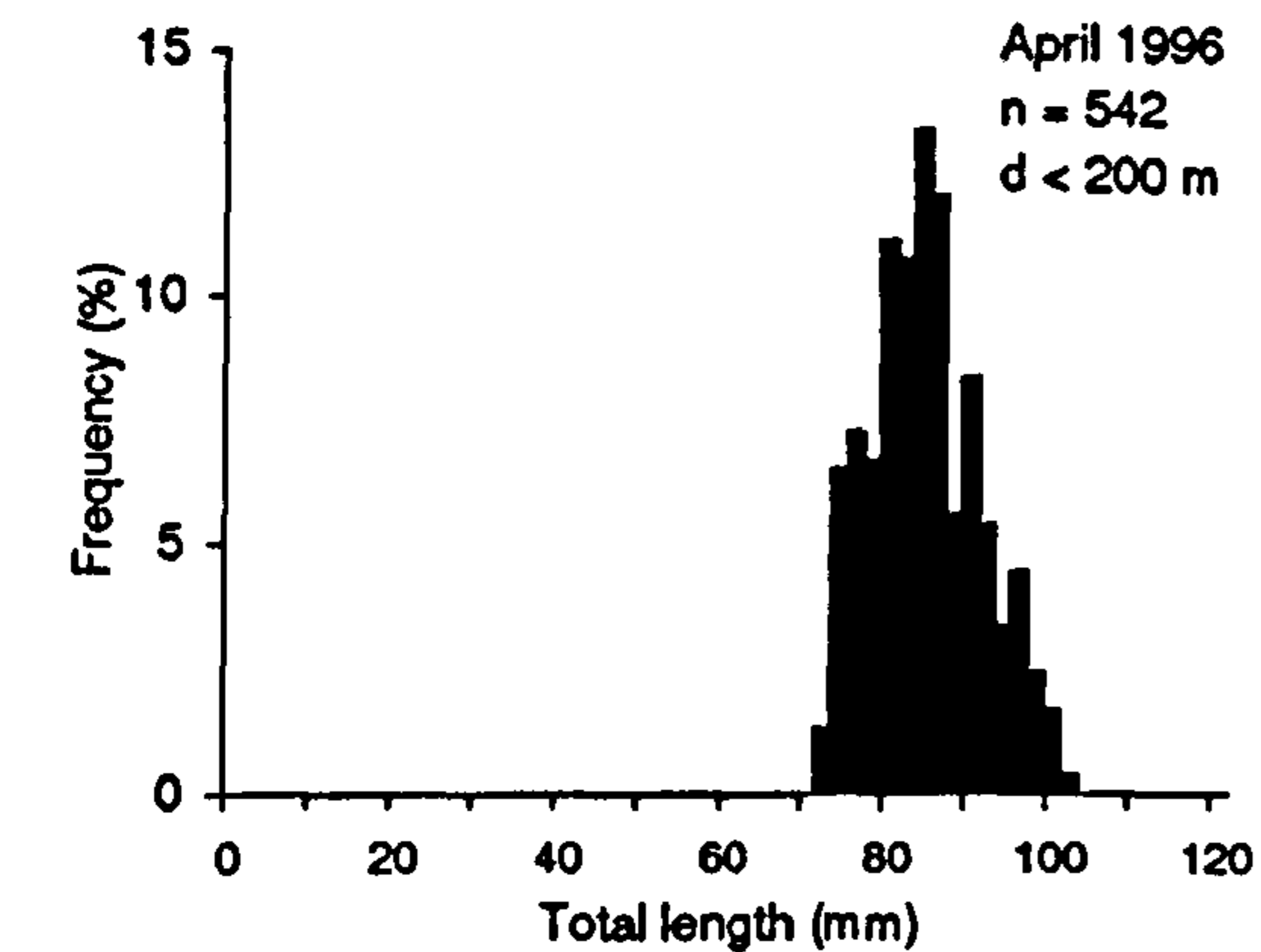


Figure 50. Size distribution of *S. tanganycae* by depth strata in April 1996 and November-December 1997. Bottom depth is indicated with d, n is the sample size.

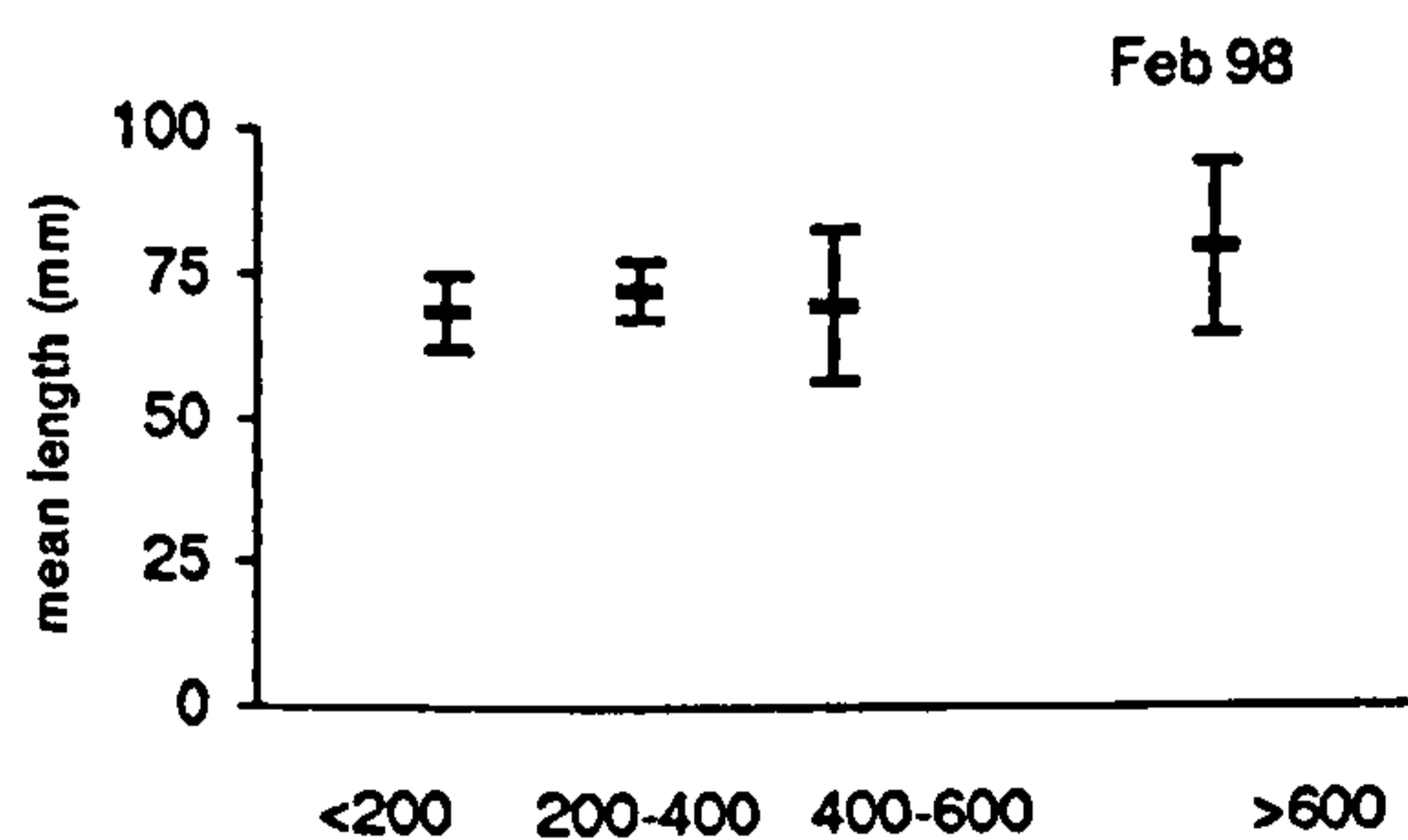
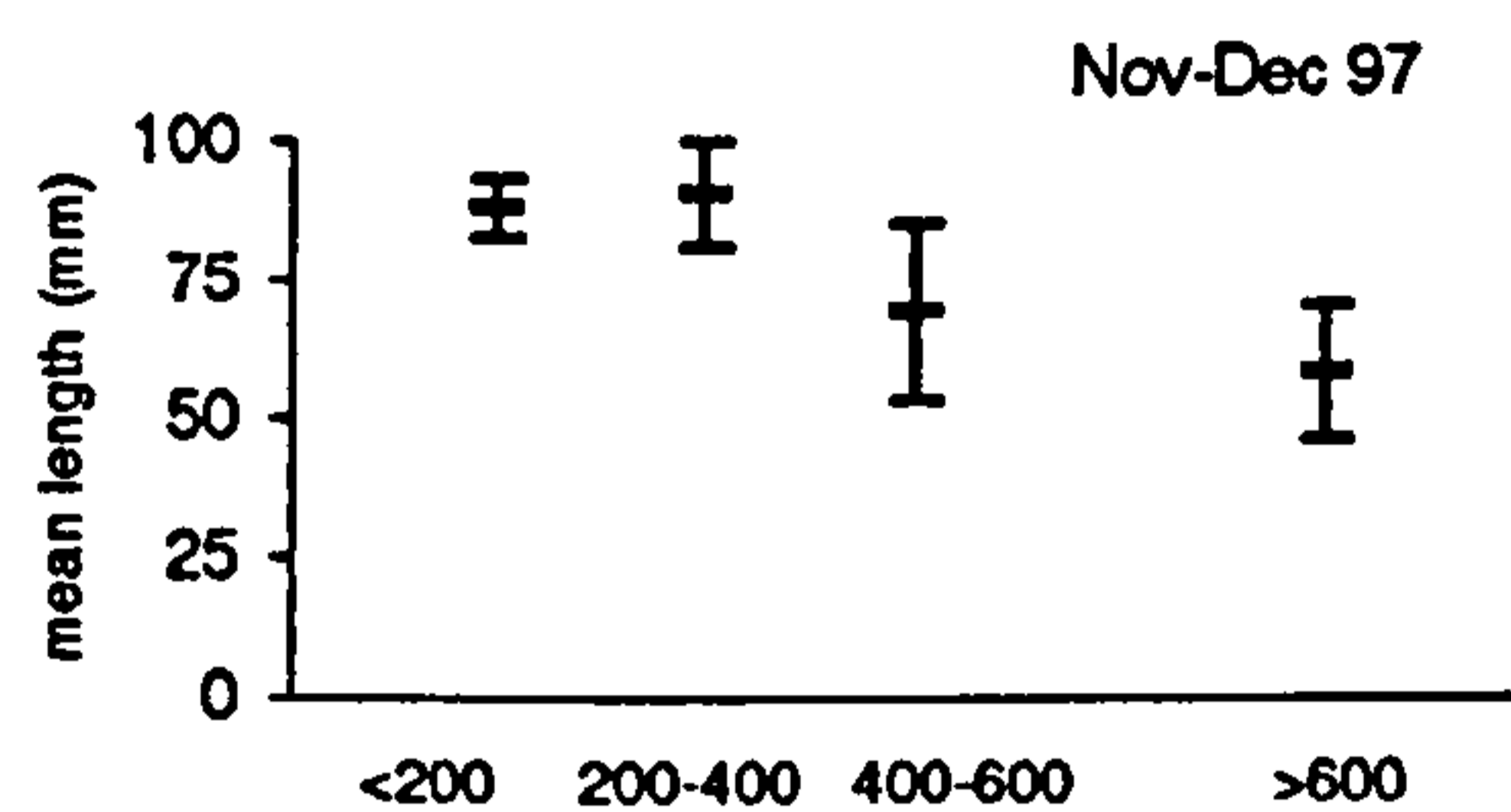
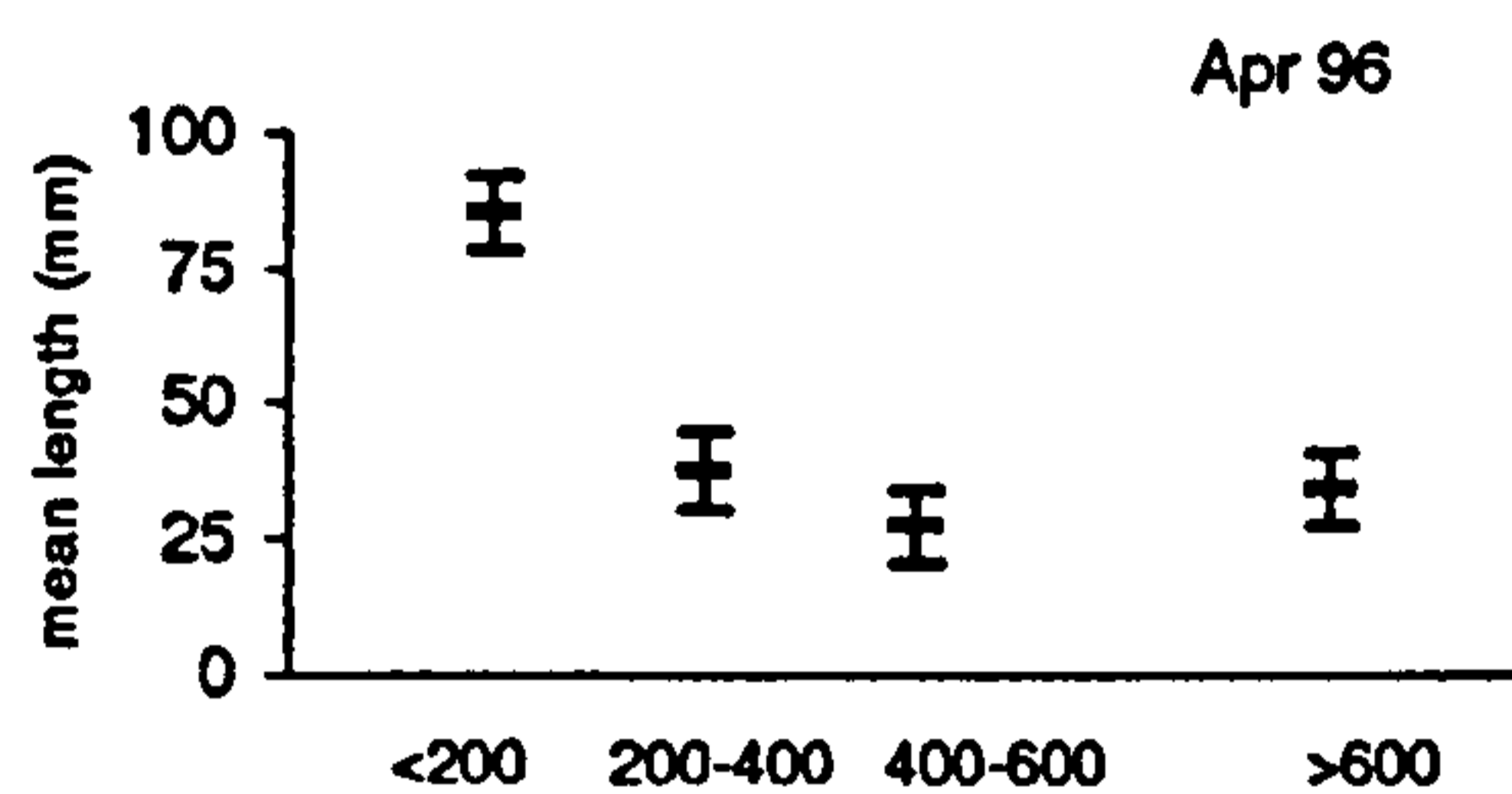
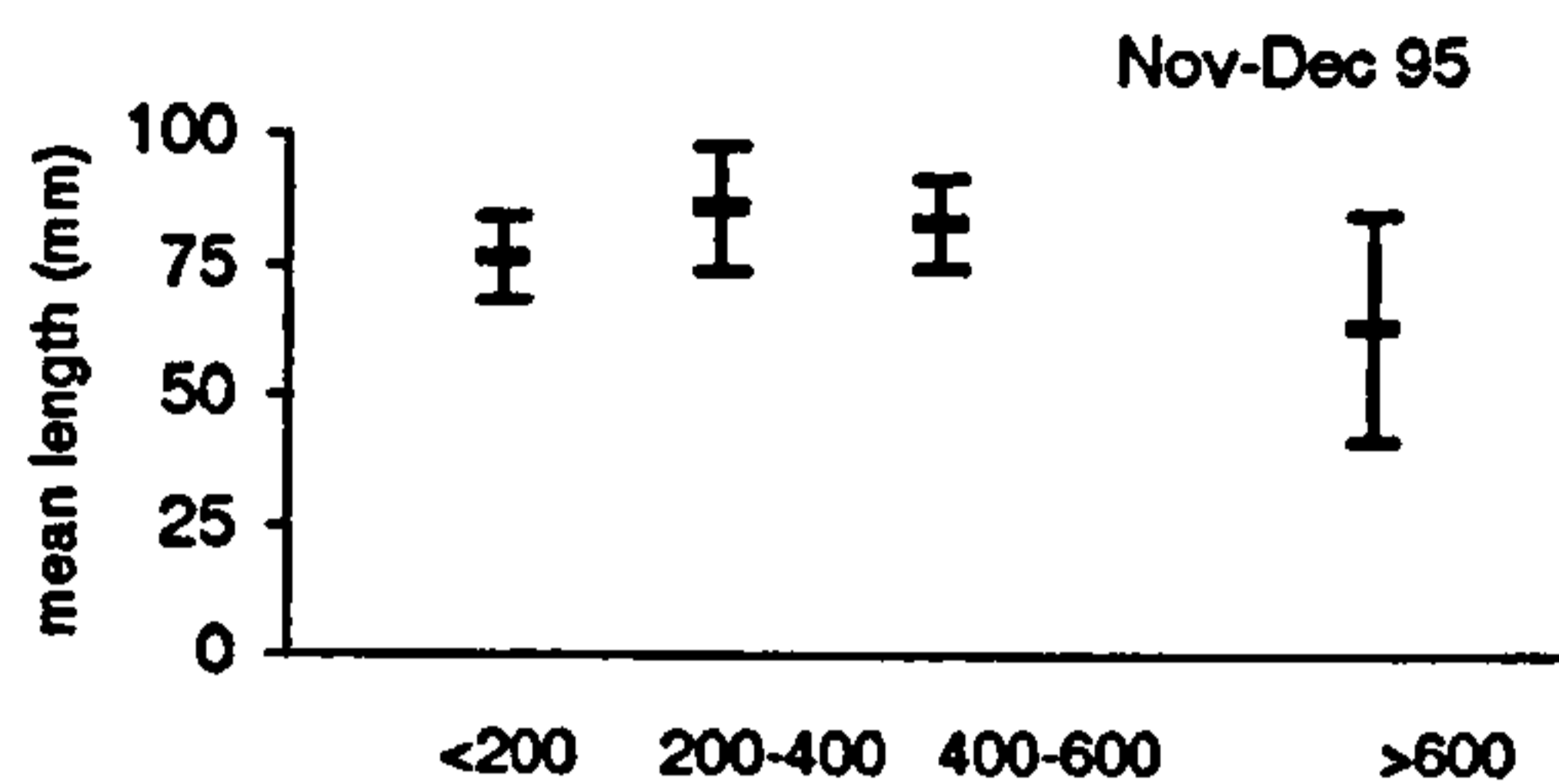
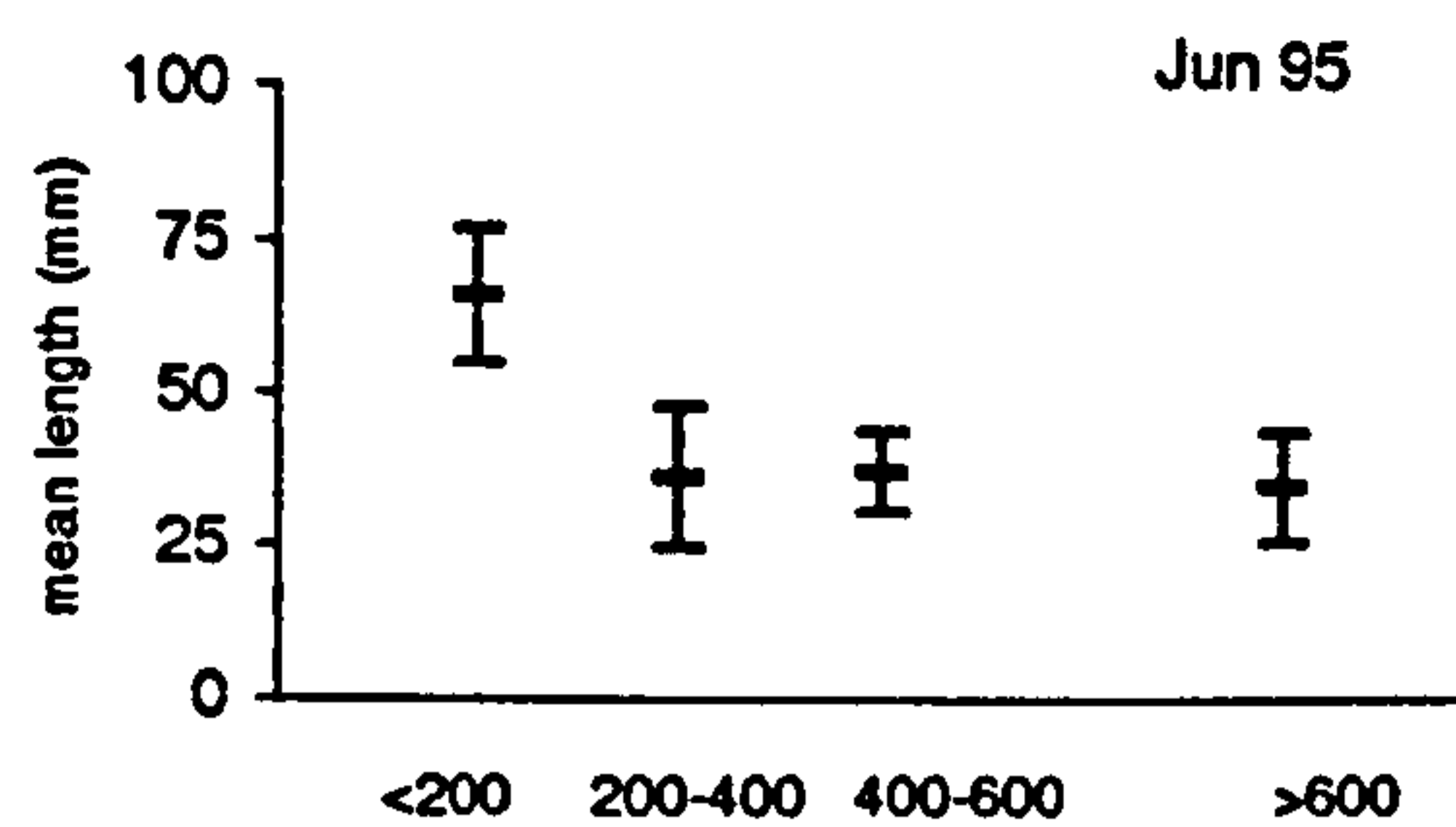
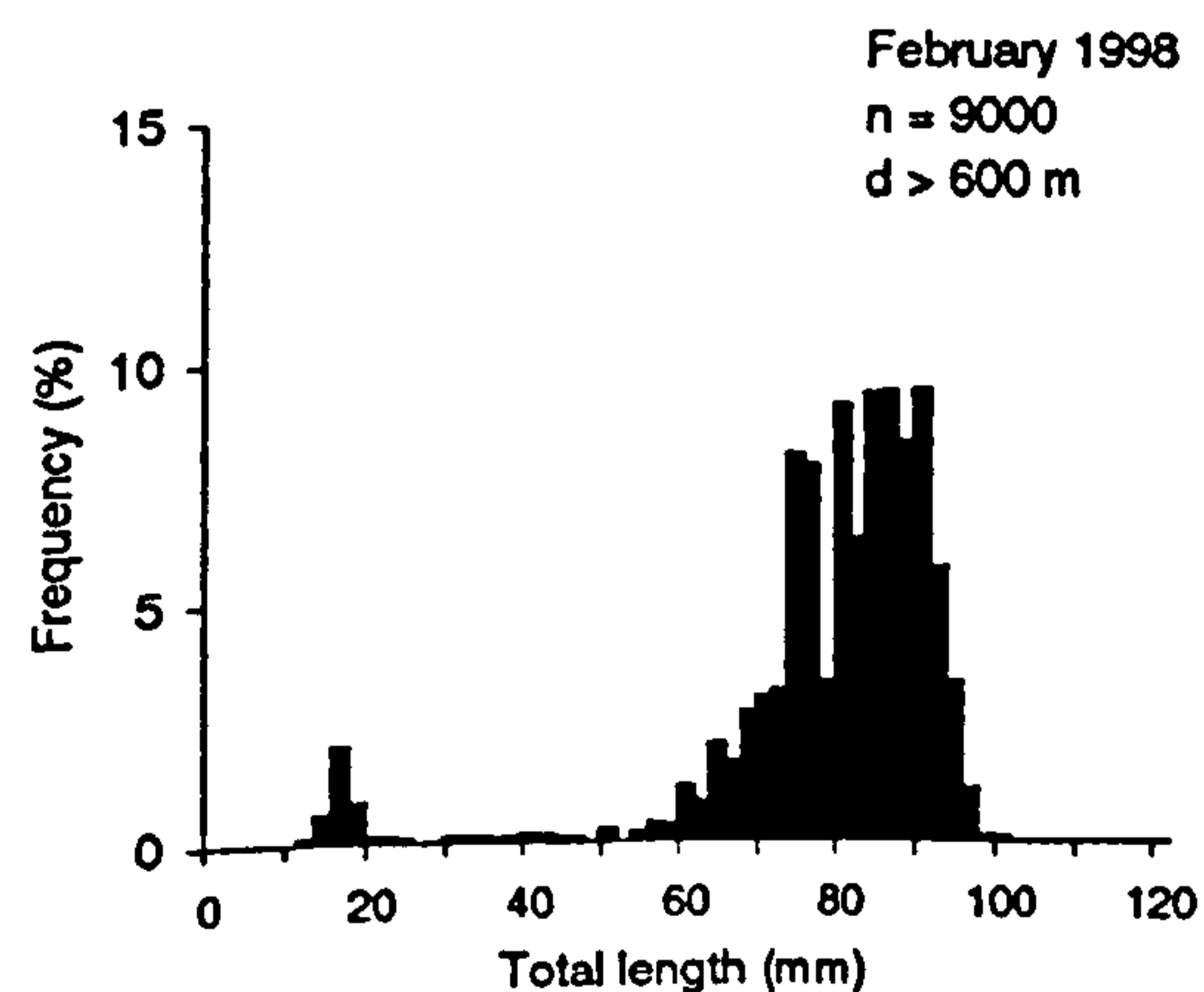
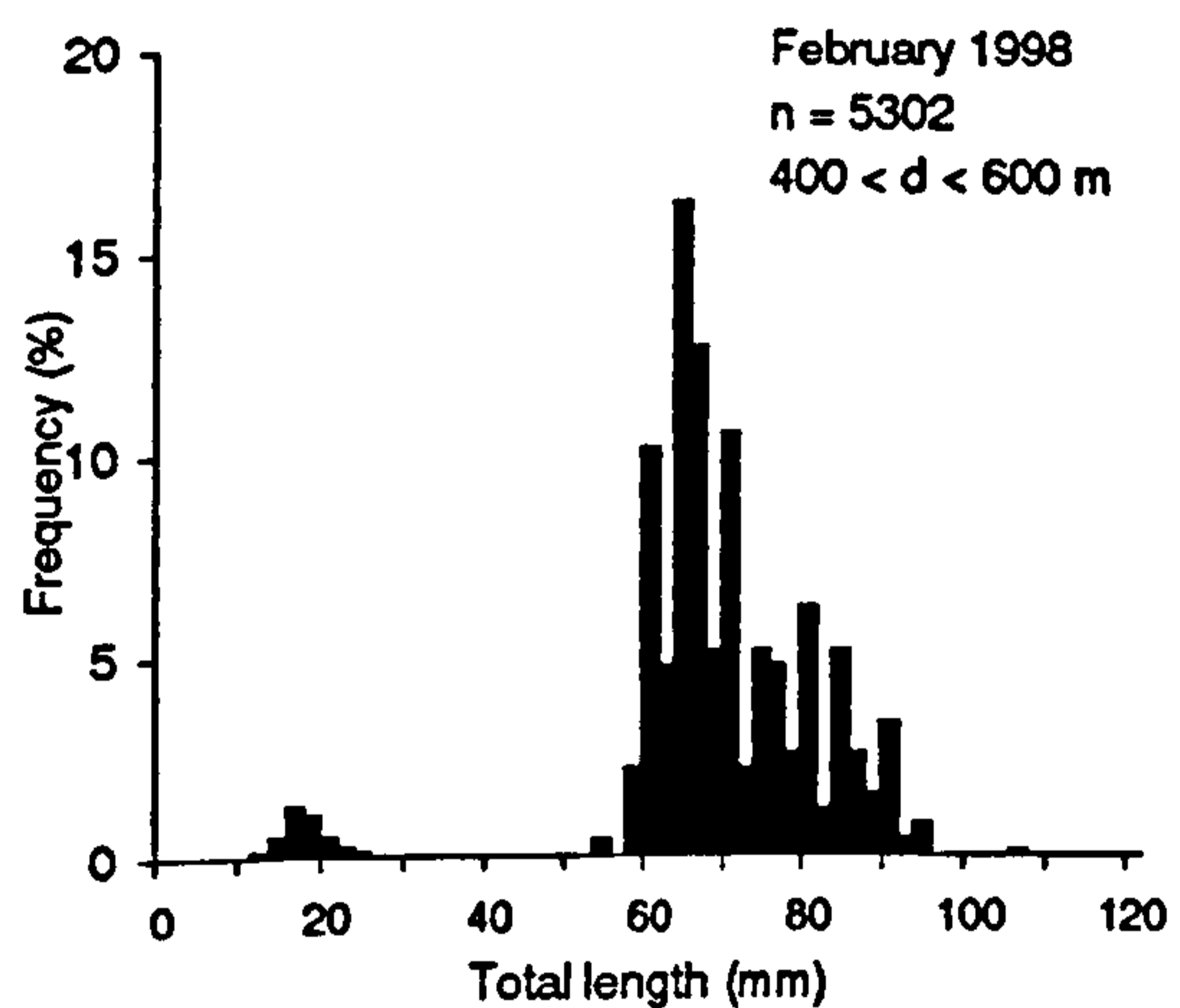
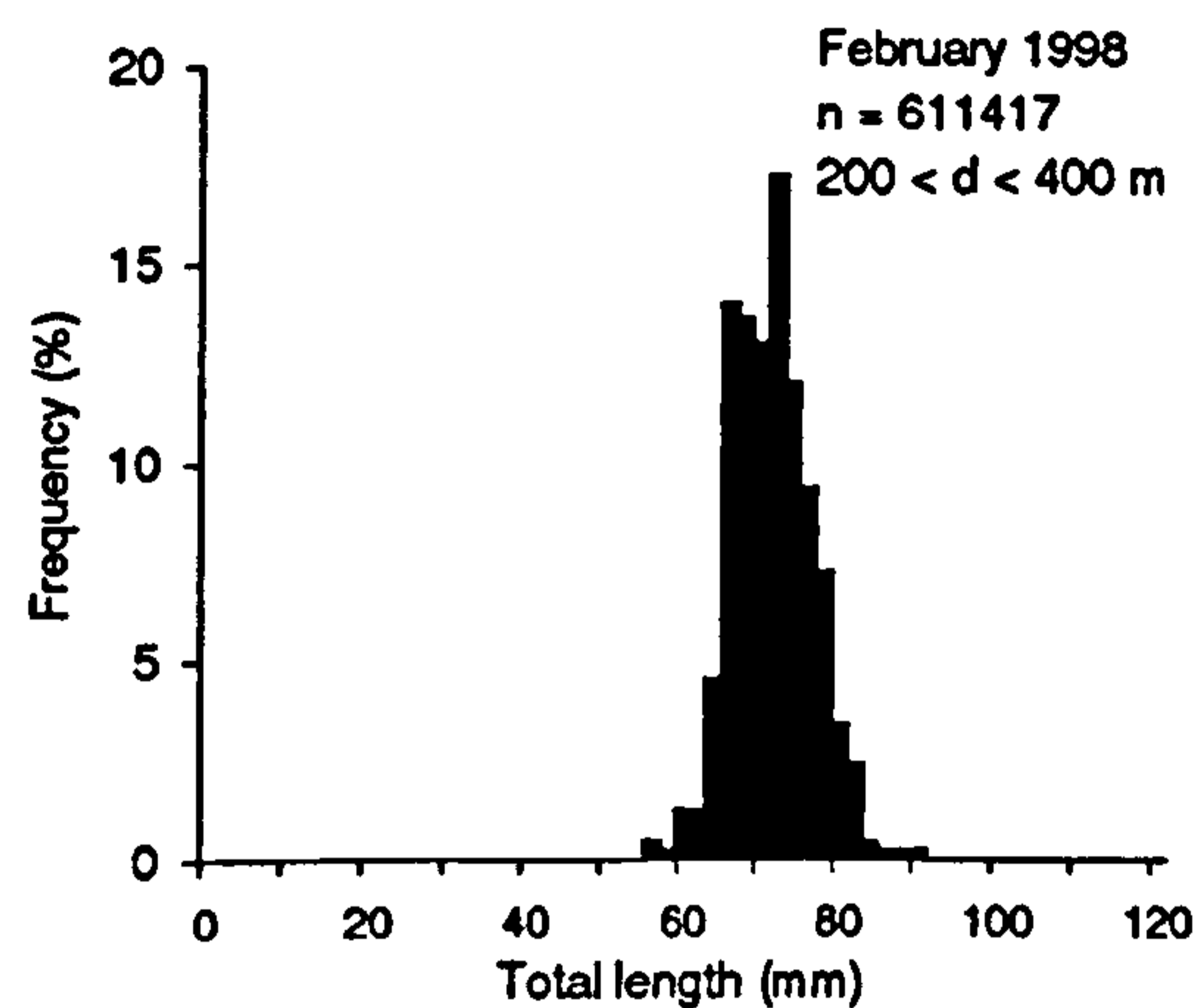
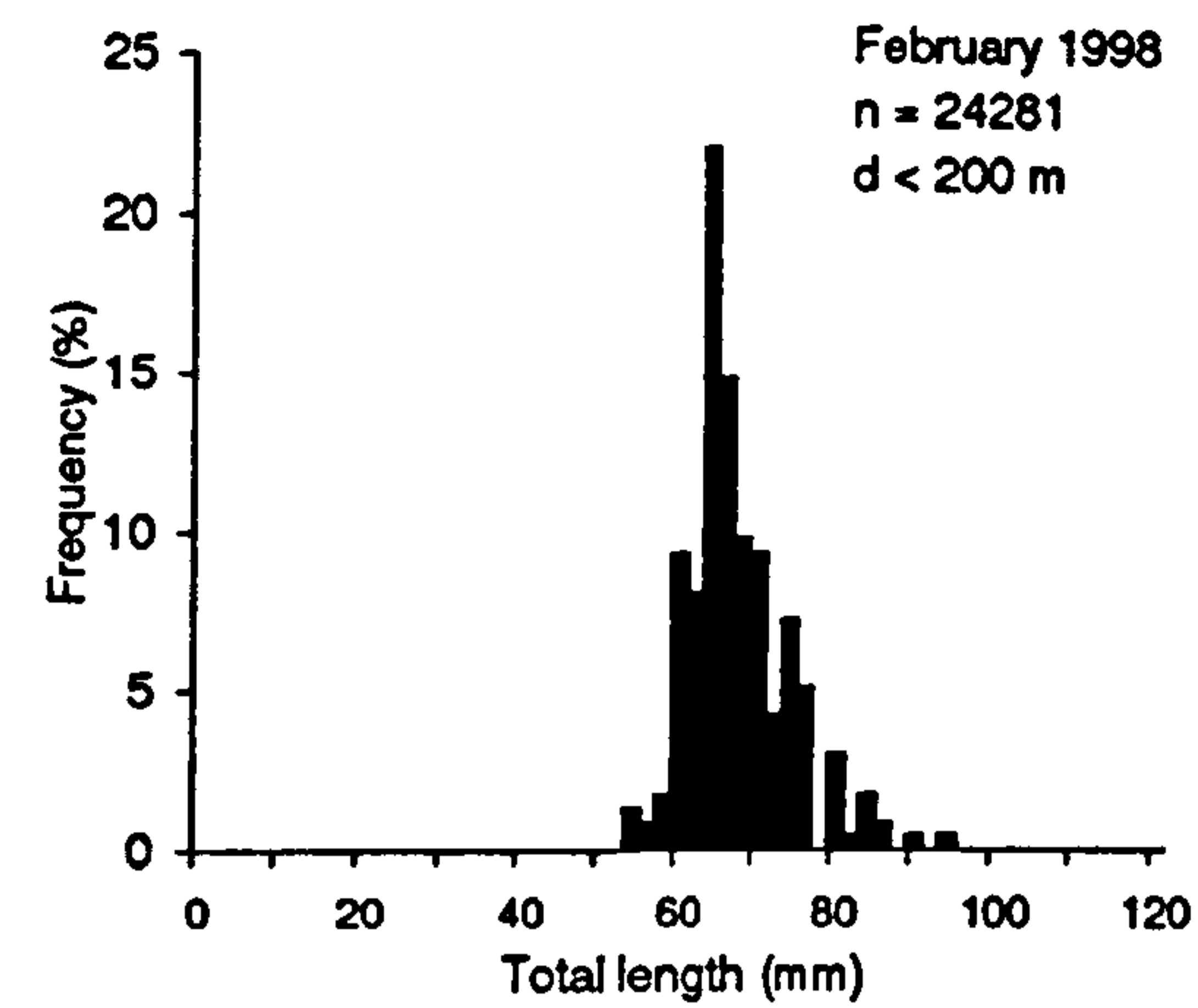


Figure 51. Size distribution of *S. tanganycae* by depth strata in February 1998. Bottom depth is indicated with d, n is the sample size.

Figure 52. Mean length of *S. tanganycae* in trawl catches from four bottom depth-defined zones (abscissa, m) during five surveys.



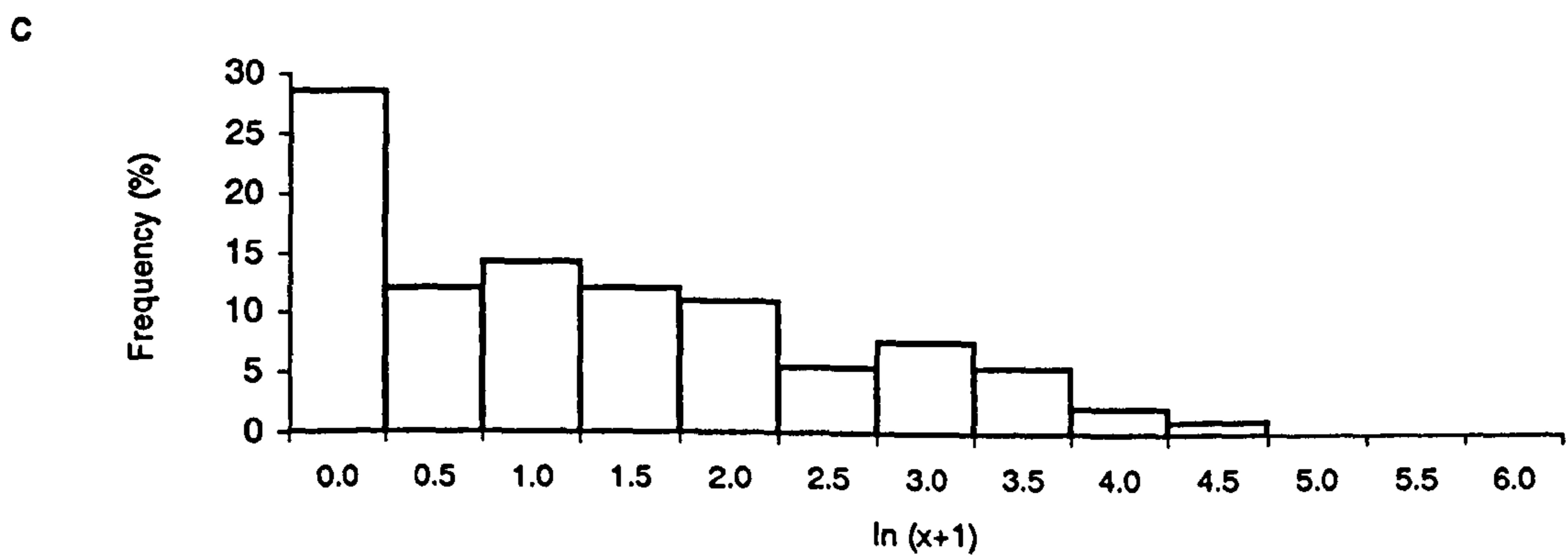
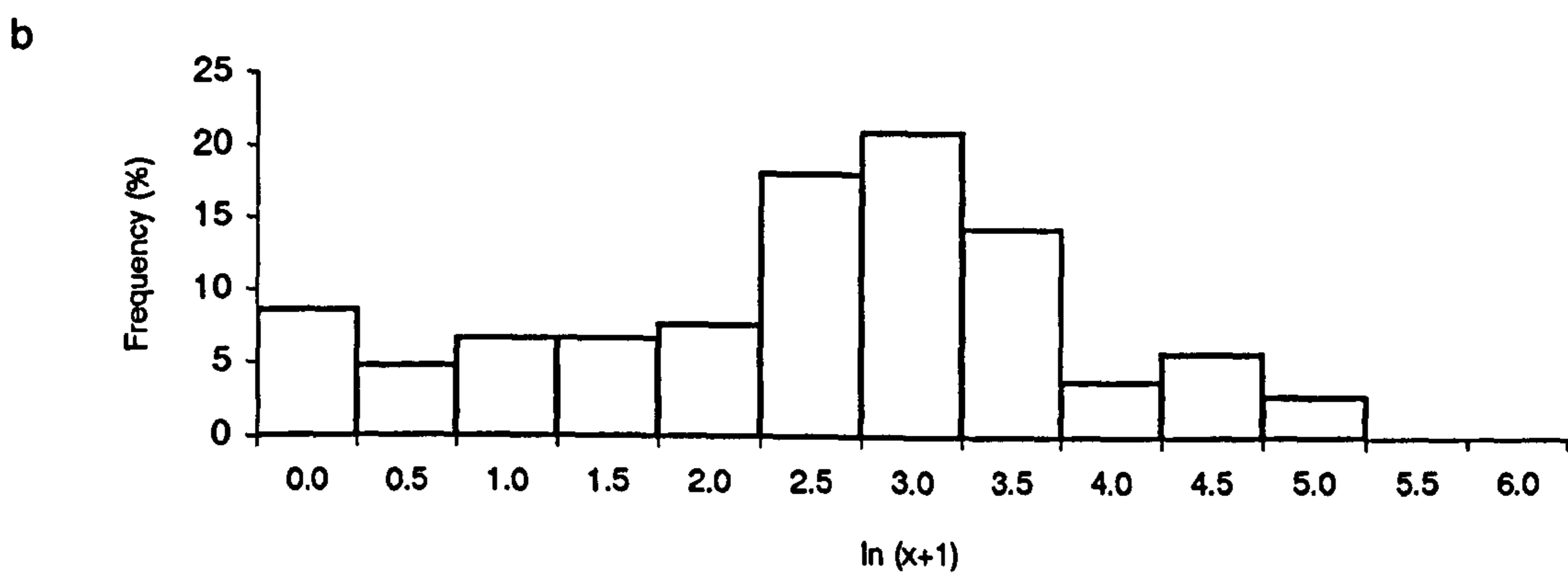
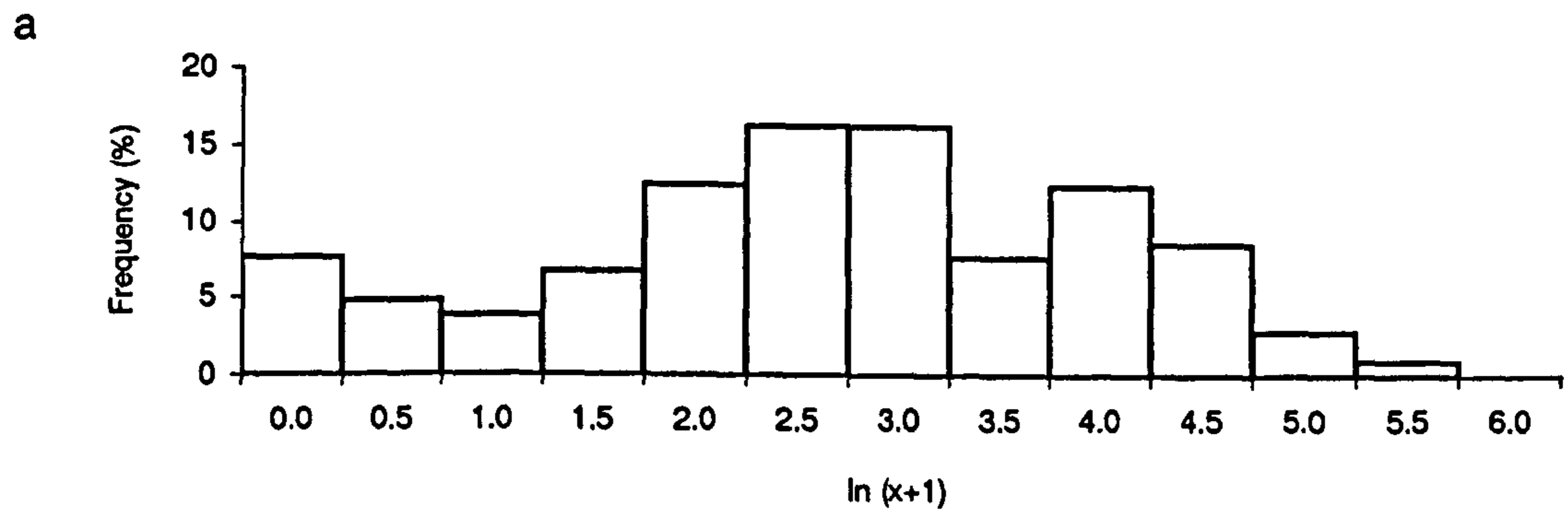


Figure 53. Frequency histograms of  $\ln(x+1)$  transformed number ( $n \times 100 \text{ m}^3$ ) of larvae in Gulf-net samples from all surveys. *Stolothrissa tanganycae*, a, *L. miodon*, b, *L. stappersii*, c.

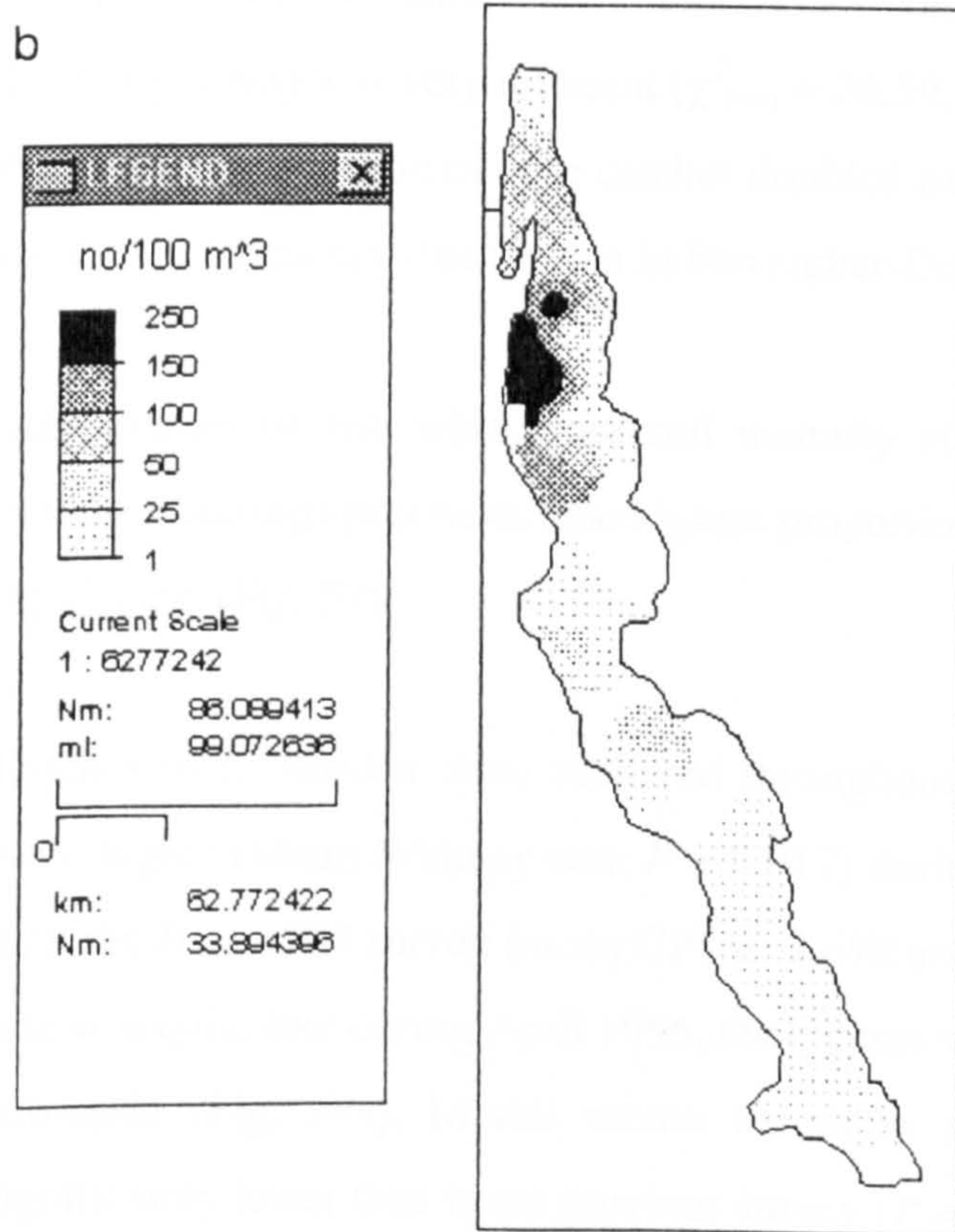
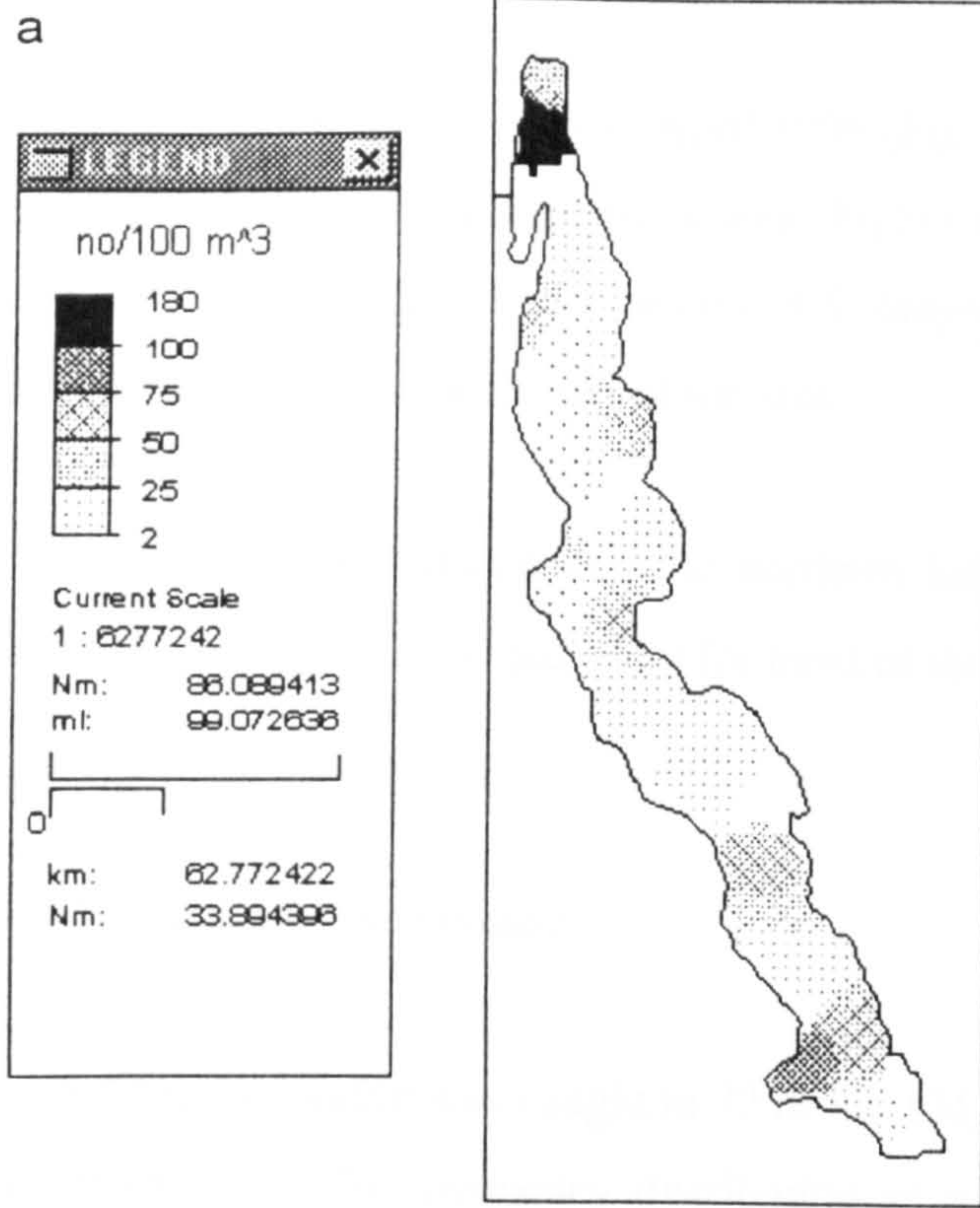


Figure 54. Distribution of *S. tanganyicae* larvae within 0-100 m water column in June (a) and November-December (b) 1995. Larval density (no/100 m<sup>3</sup>) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. 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 statute miles (ml).

in Kigoma and Kalemie areas in April 1996 (Fig. 46b). In November-December 1997 and February 1998 larval numbers were higher in the Kalemie sub-basins (Fig. 55). The data available on the distribution of *S. tanganyicae* 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. tanganyicae* was prevalent for most of its life cycle.

### 3.4.3 *Limnothrissa miodon*

*Limnothrissa miodon* was caught in 73 of the 131 hauls. Catch rates varied between 0 and 96 kg hr<sup>-1</sup>. The frequency distribution of catch rate (Fig. 56) between survey groups (June, November-December 1995 and November-December 1997 and February 1998) was very different ( $\chi^2_{[10]} = 26.39, P < 0.05$ ). 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. 57).

Catches of *L. miodon* were scattered throughout the lake (Fig. 58) 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<sup>-1</sup> respectively). Catch rate was quite low during April 1996, the highest values were obtained in the Kalemie sub-basin (Fig. 59a). In this month the mean survey CPUE was 2.021 kg hr<sup>-1</sup>, 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

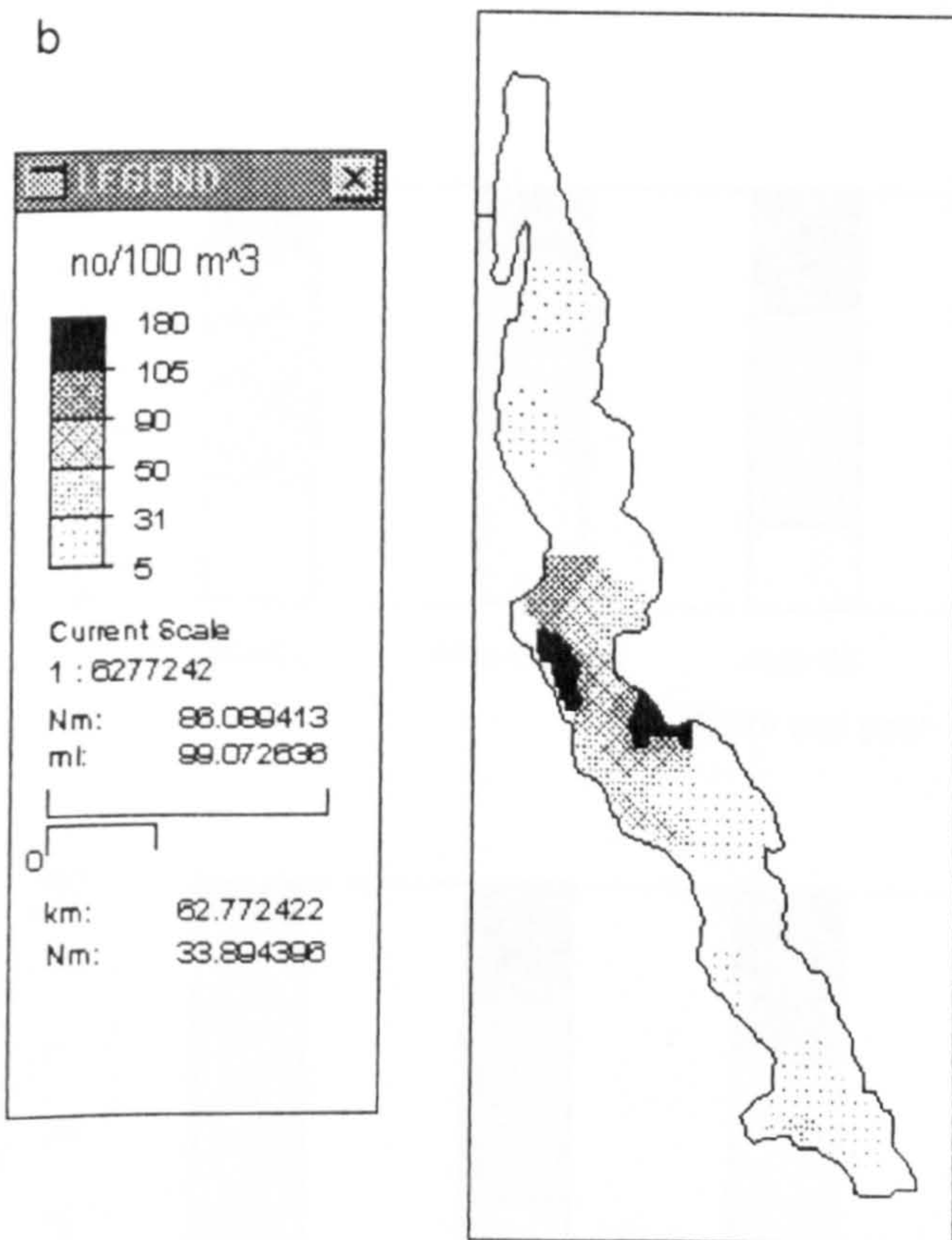
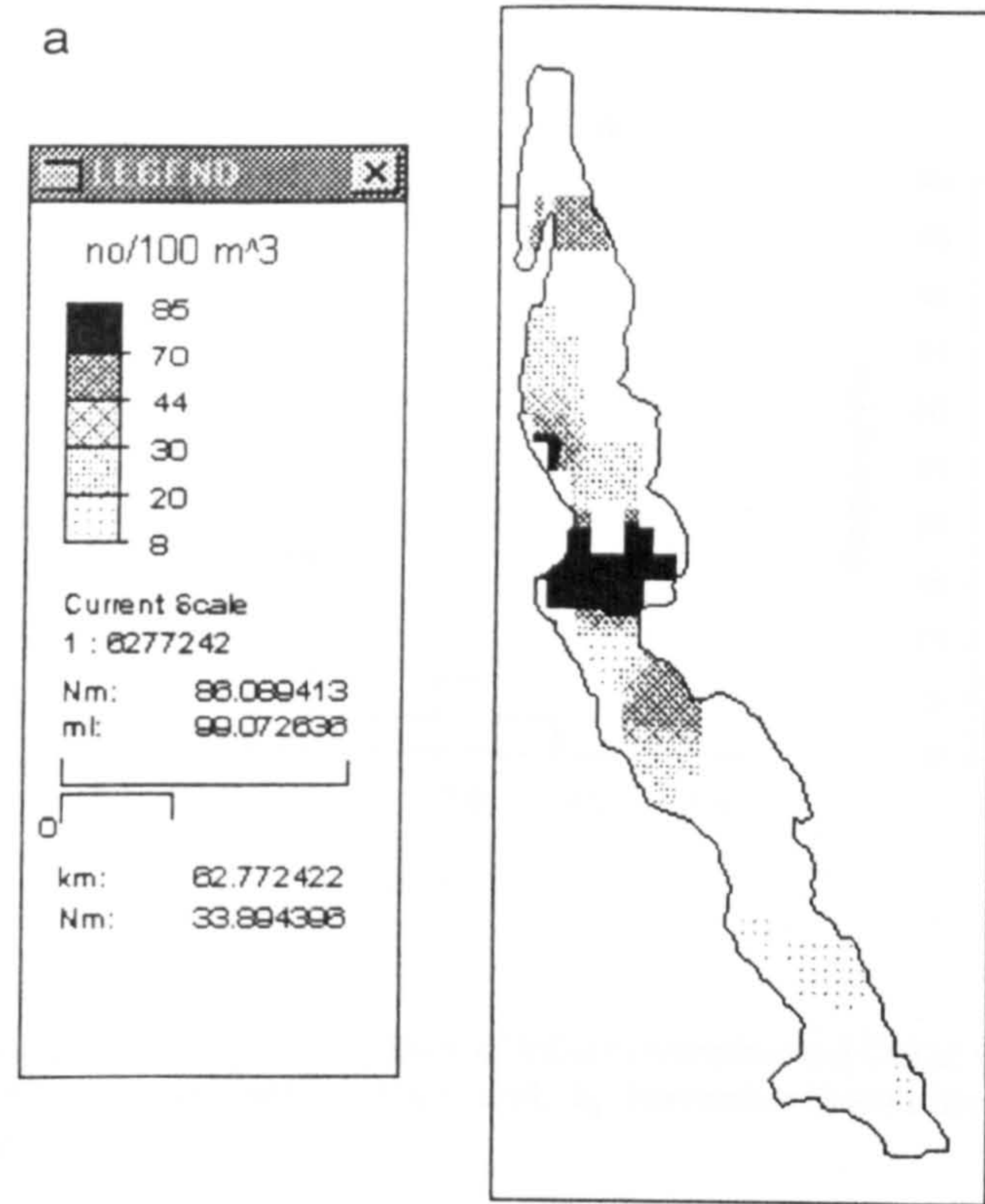


Figure 55. Distribution of *S. tanganyicae* larvae within 0-100 m water column in November-December 1997 (a) and February 1998 (b). Larval density (no/100 m<sup>3</sup>) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal 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 statute miles

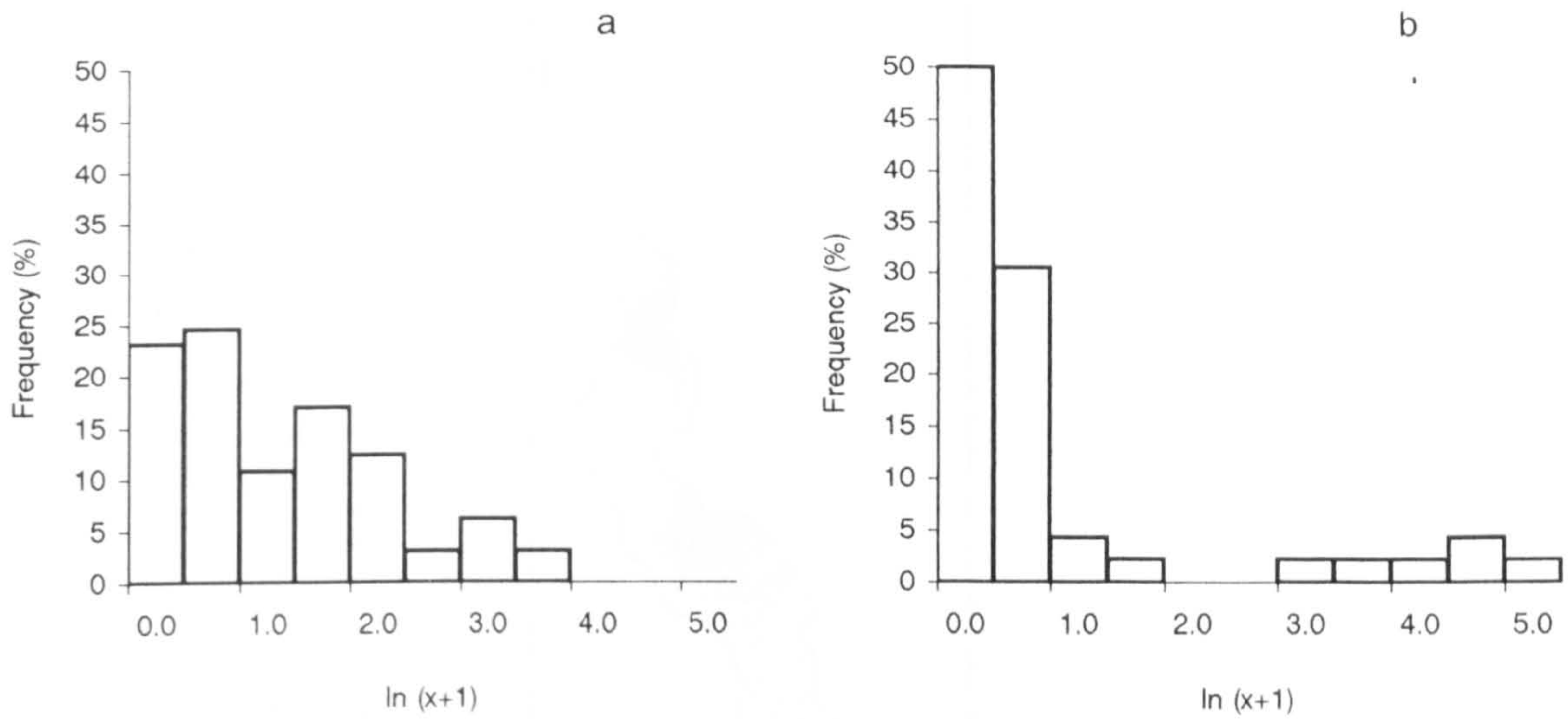


Figure 56. Frequency histograms of  $\ln(x+1)$  transformed CPUE values derived for *L. miodon* from, a, June and November-December 1995 and, b, November-December 1997 and February 1998 pelagic trawl surveys.

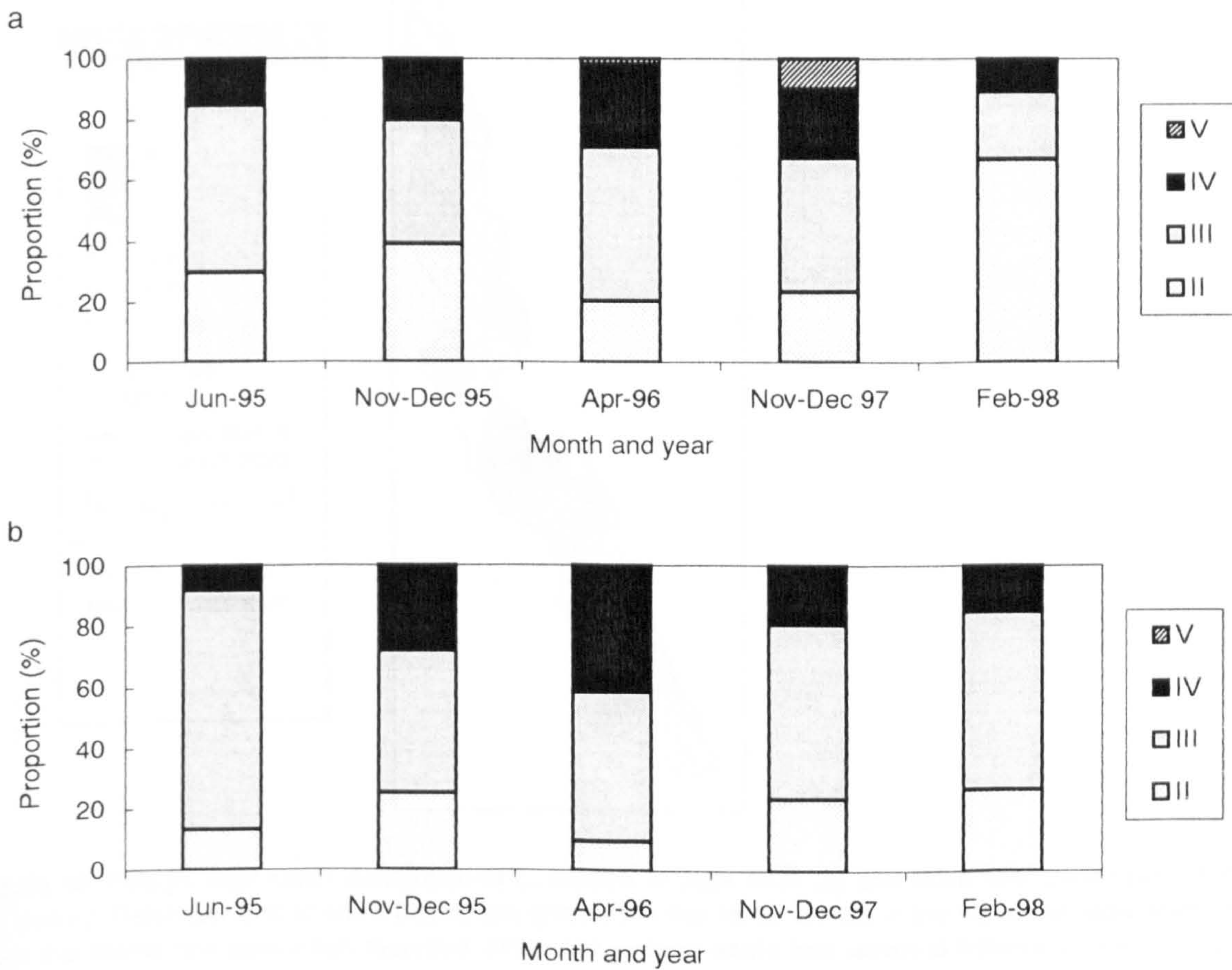
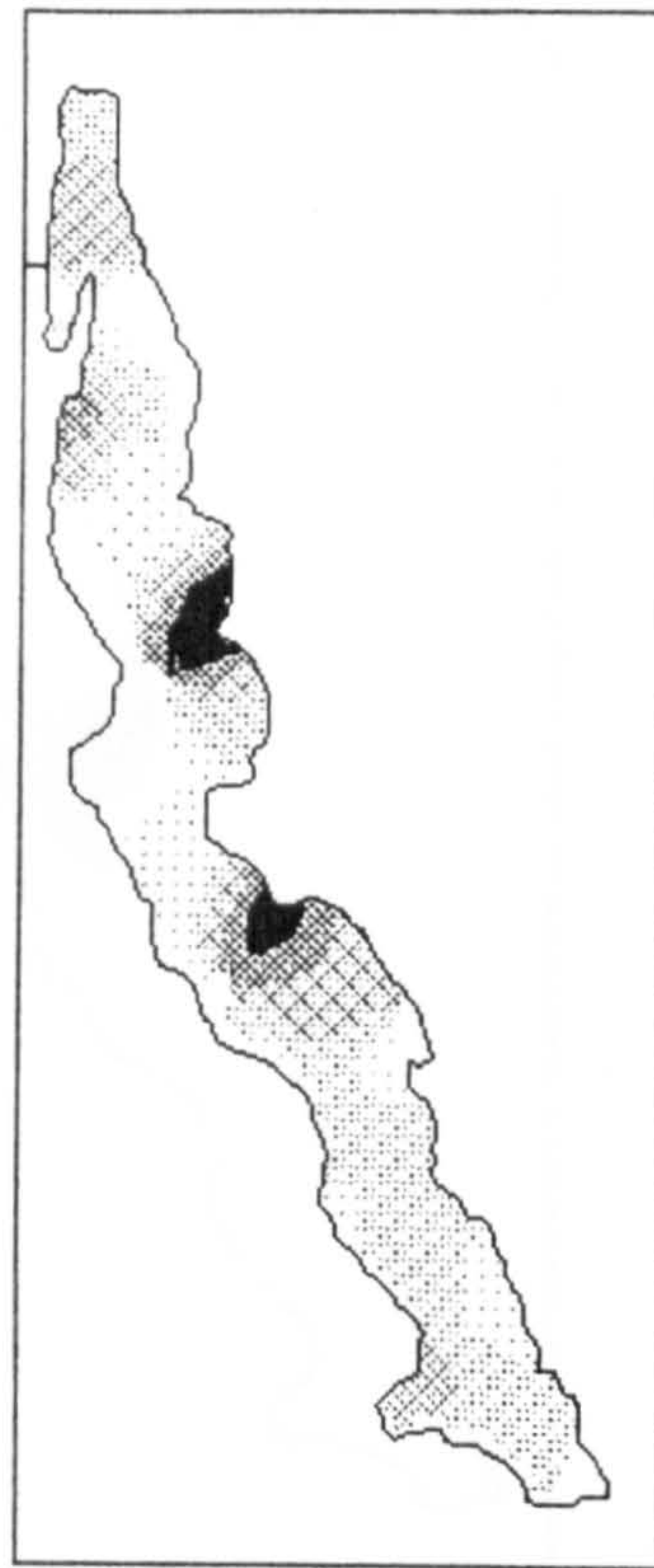
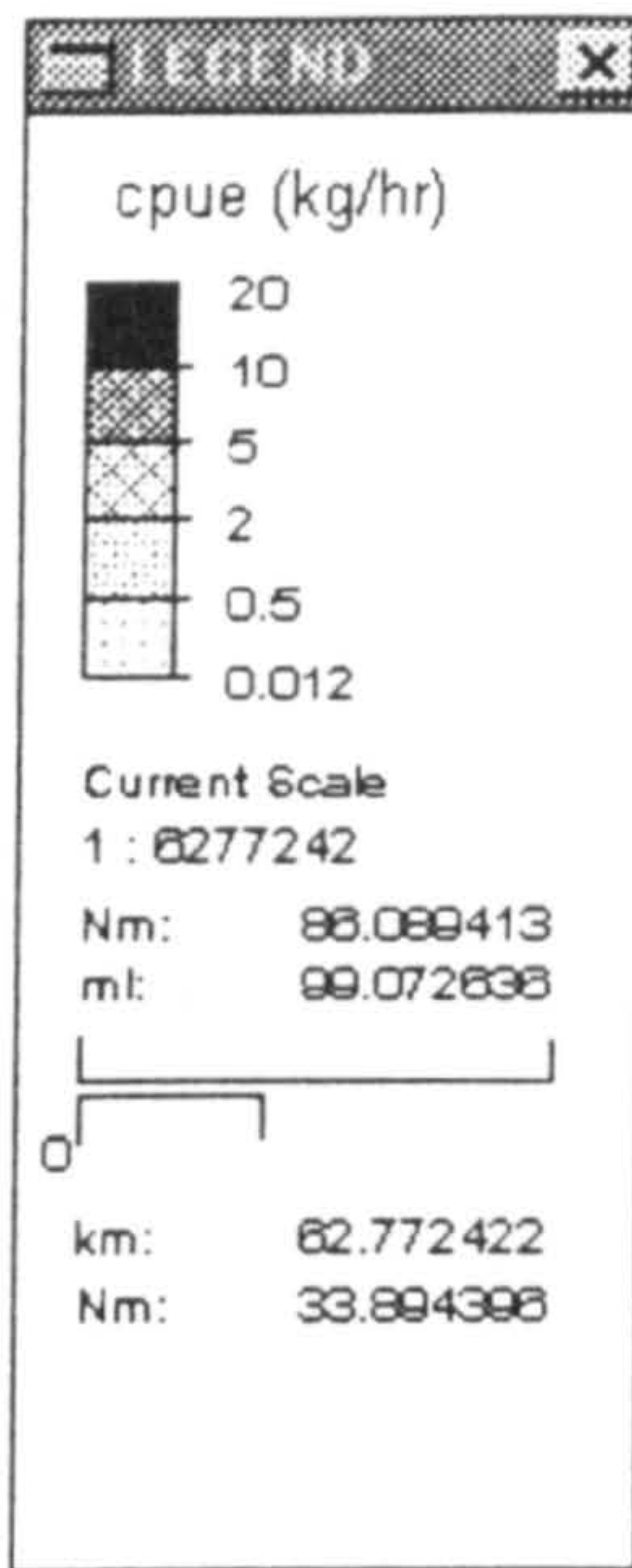


Figure 57. Maturity stages for *L. miodon* samples of females (a) and males (b) taken during lake-wide surveys in June (sample size,  $n=774$ ) and November-December ( $n=1080$ ) 1995, April 1996 ( $n=282$ ), November-December 1997 ( $n=453$ ) and February 1998 ( $n=251$ ).

a



b

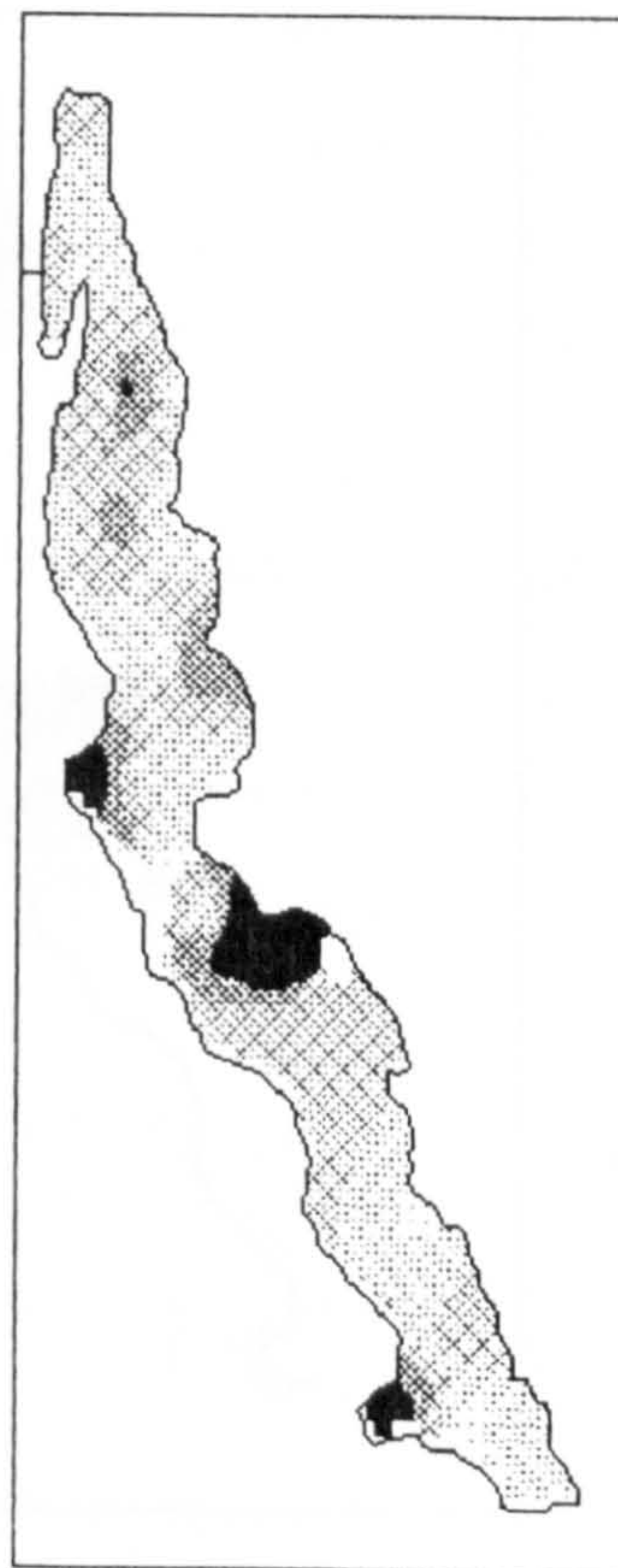
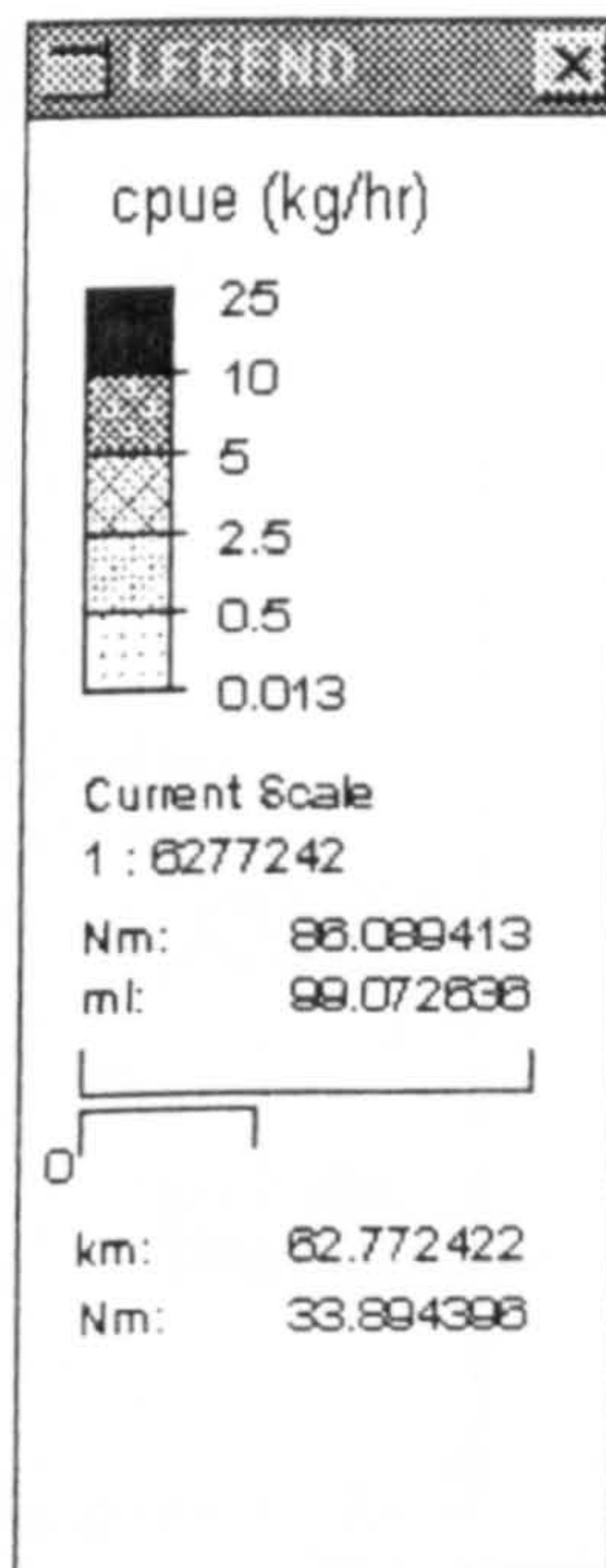


Figure 58. Pelagic trawl catch distribution of *L. midon* in June 1995 (a) and November-December 1995 (b) survey. Catch per unit of effort (kg/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. 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).

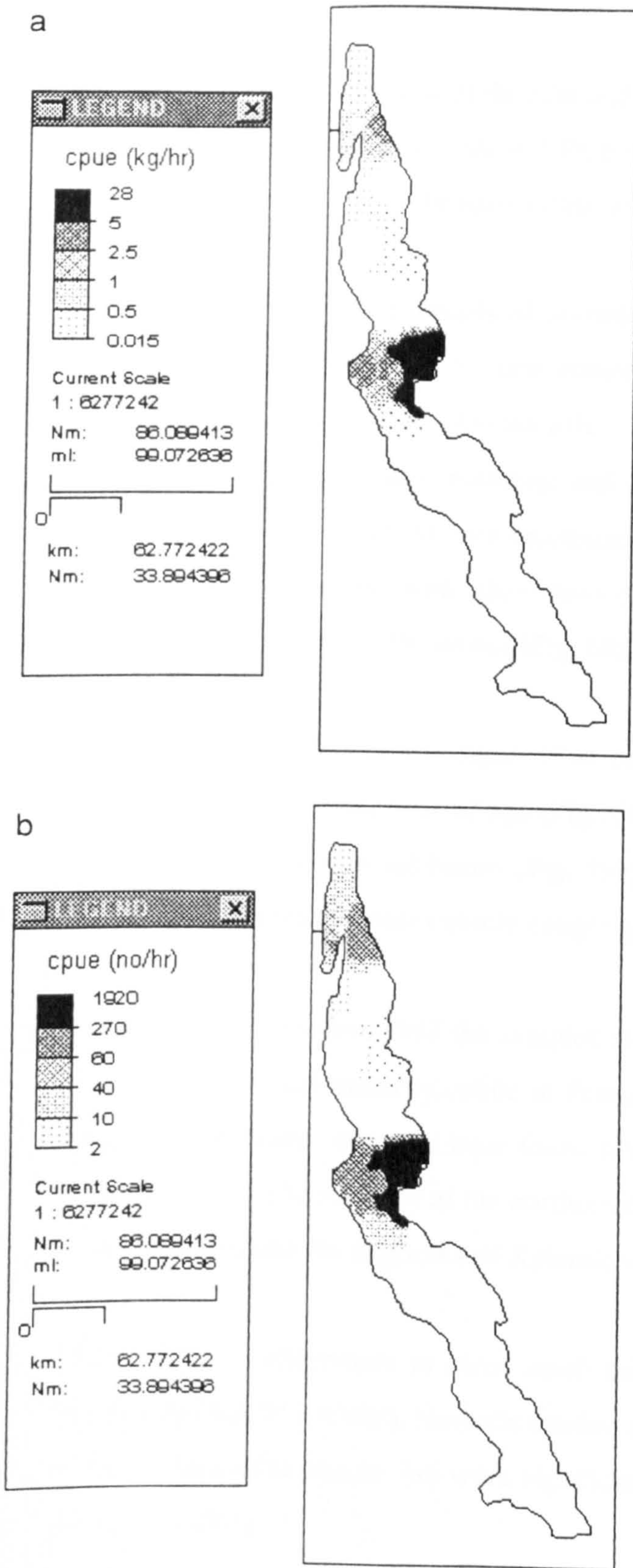


Figure 59. Pelagic trawl catch distribution (a) and number of adults ( $TL > L_m$ ) caught (b) of *L. miodon* in April 1996 survey. Catch per unit of effort (kg/hr) and number of adult fish (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. 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 statute miles (mi).

occurred in the northern end of the lake and the eastern area between the Kigoma and Kalemie sub-basins (Fig. 60). Mean CPUE was 0.231 and 14.683 kg hr<sup>-1</sup> 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. 61) 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. 62). Only maturing and mature fish were found in November-December 1995 (Fig. 62). Mature specimens (TL  $\geq$  L<sub>m</sub>; L<sub>m</sub> = 100 mm) were found to be quite localised in June, while they showed a more dispersed distribution and higher abundance in November-December (Fig. 63).

The size composition of the April 1996 catch was mainly composed of sexually mature fish of about one year of age (Fig. 64) sampled in the Rumonge and, mostly, in the (eastern) Kalemie sub-basins (Fig. 59b). Juveniles were rare in the most of the survey area and were almost entirely caught in the Rumonge area (Fig. 65a).

In November-December 1997 the sampled stock comprised mainly fish close to the attainment of sexual maturity, while in February 1998 only young *L. miodon* at an early stage of sexual maturity were found (Fig. 66). 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 67 and 68).

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. *Limnothrissa miodon* >125 mm total length composed 3.5% of the total



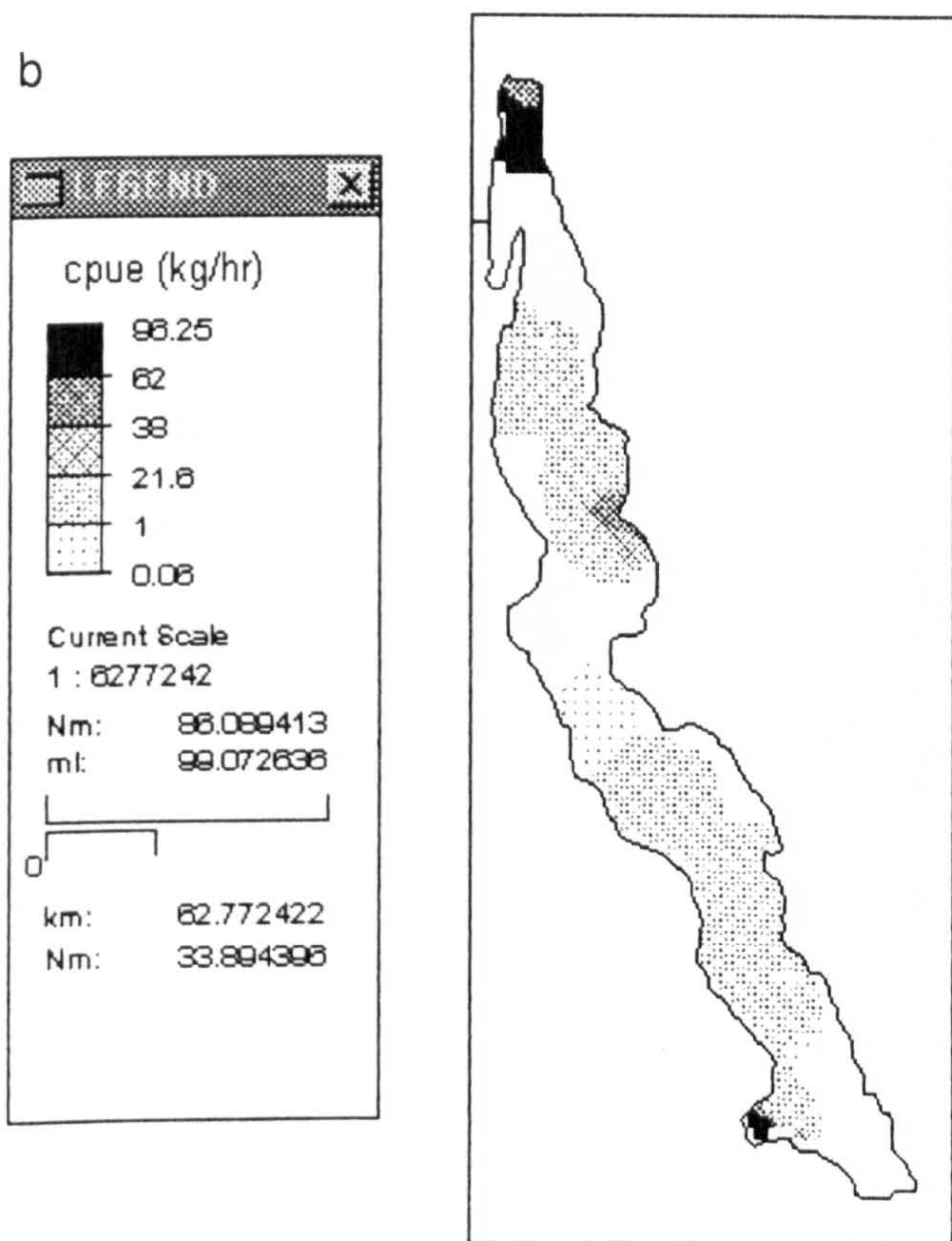
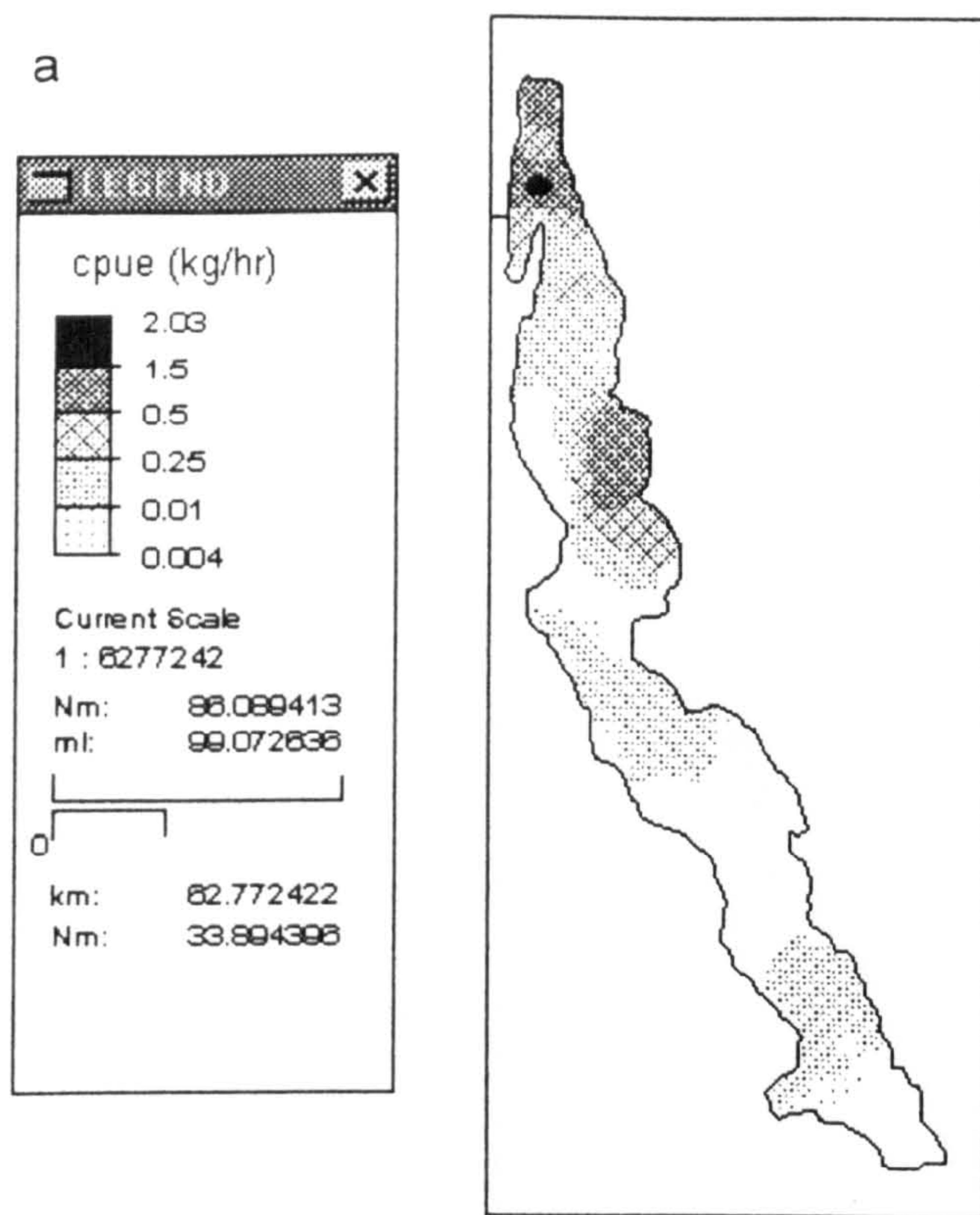


Figure 60. Pelagic trawl catch distribution of *L. miodon* in November-December 1997 (a) and February 1998 (b) survey. Catch per unit of effort (kg/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. 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 statute miles (ml).

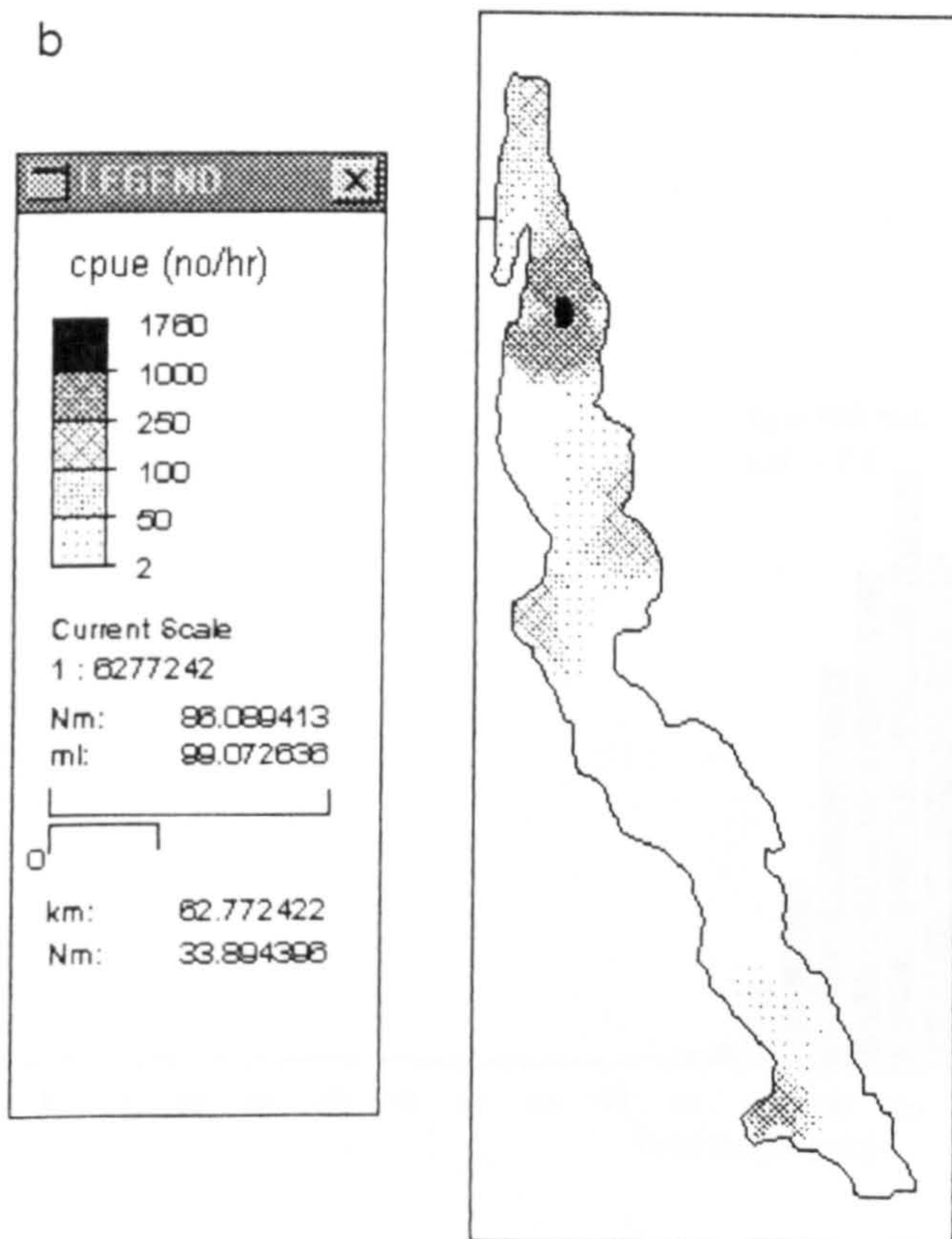
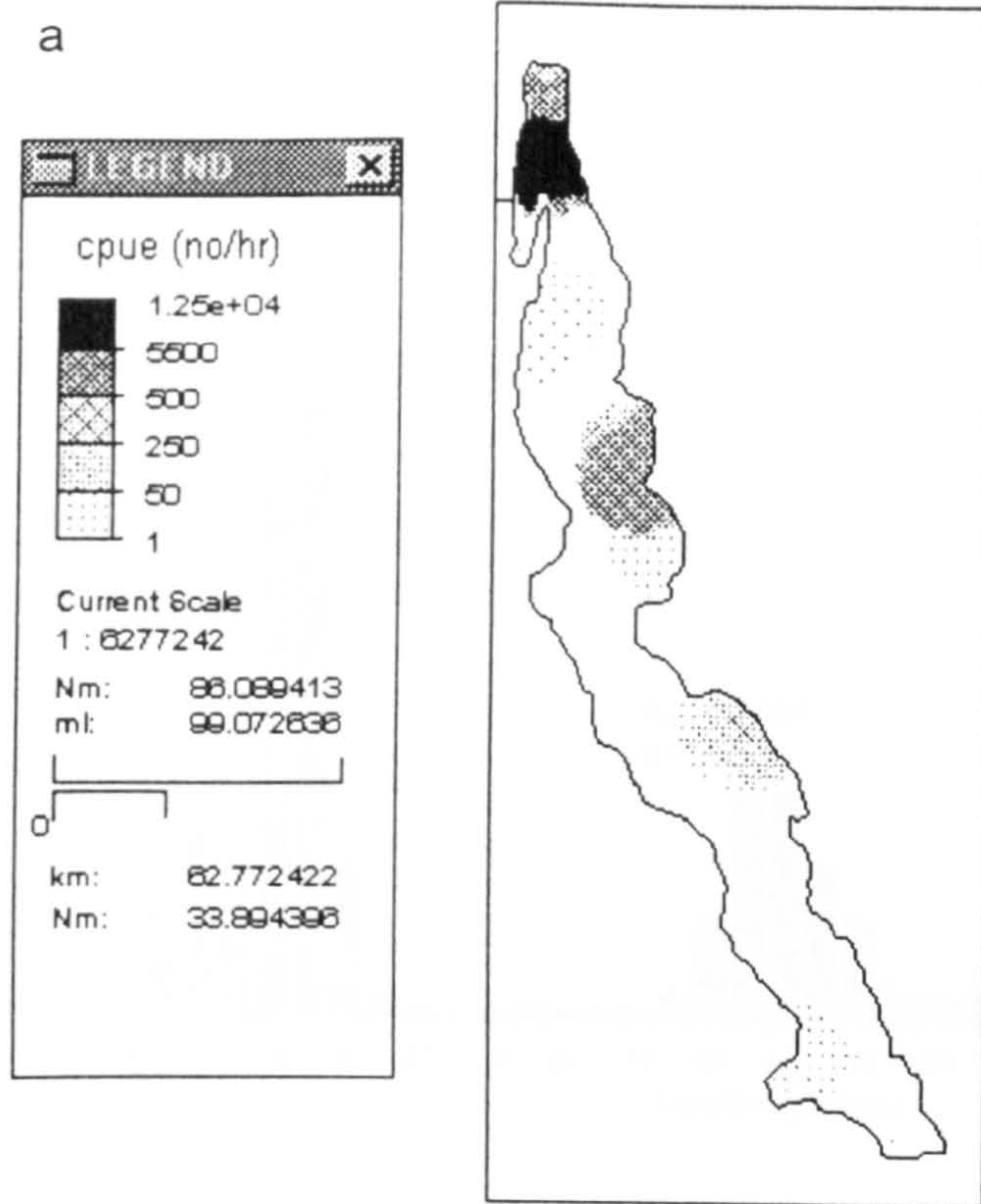


Figure 61. Pelagic trawl catch distribution of young *L. miodon* ( $TL < L_m$ ) in June 1995 (a) and November-December (b) 1995 survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has 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 statute miles (ml).

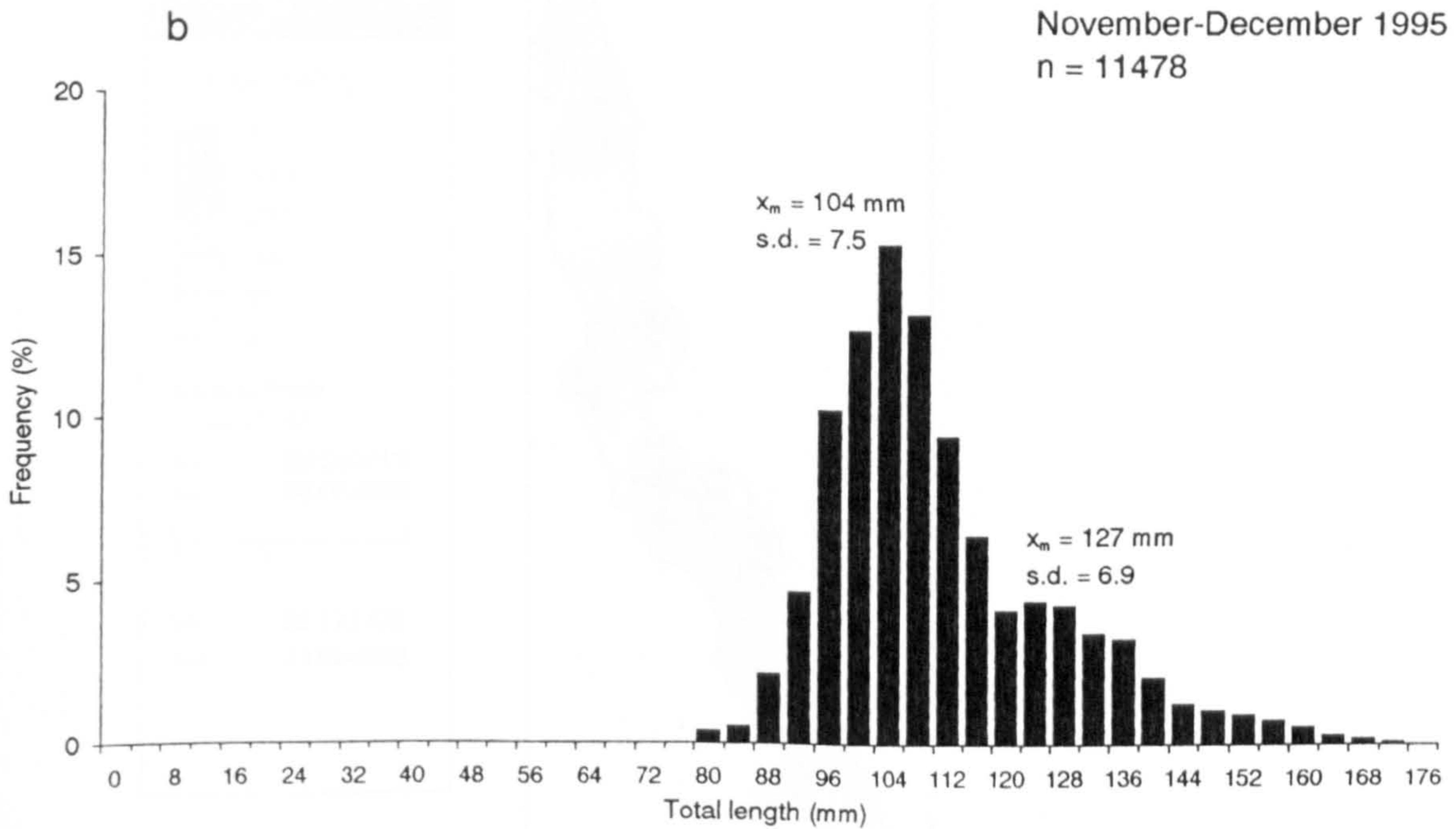
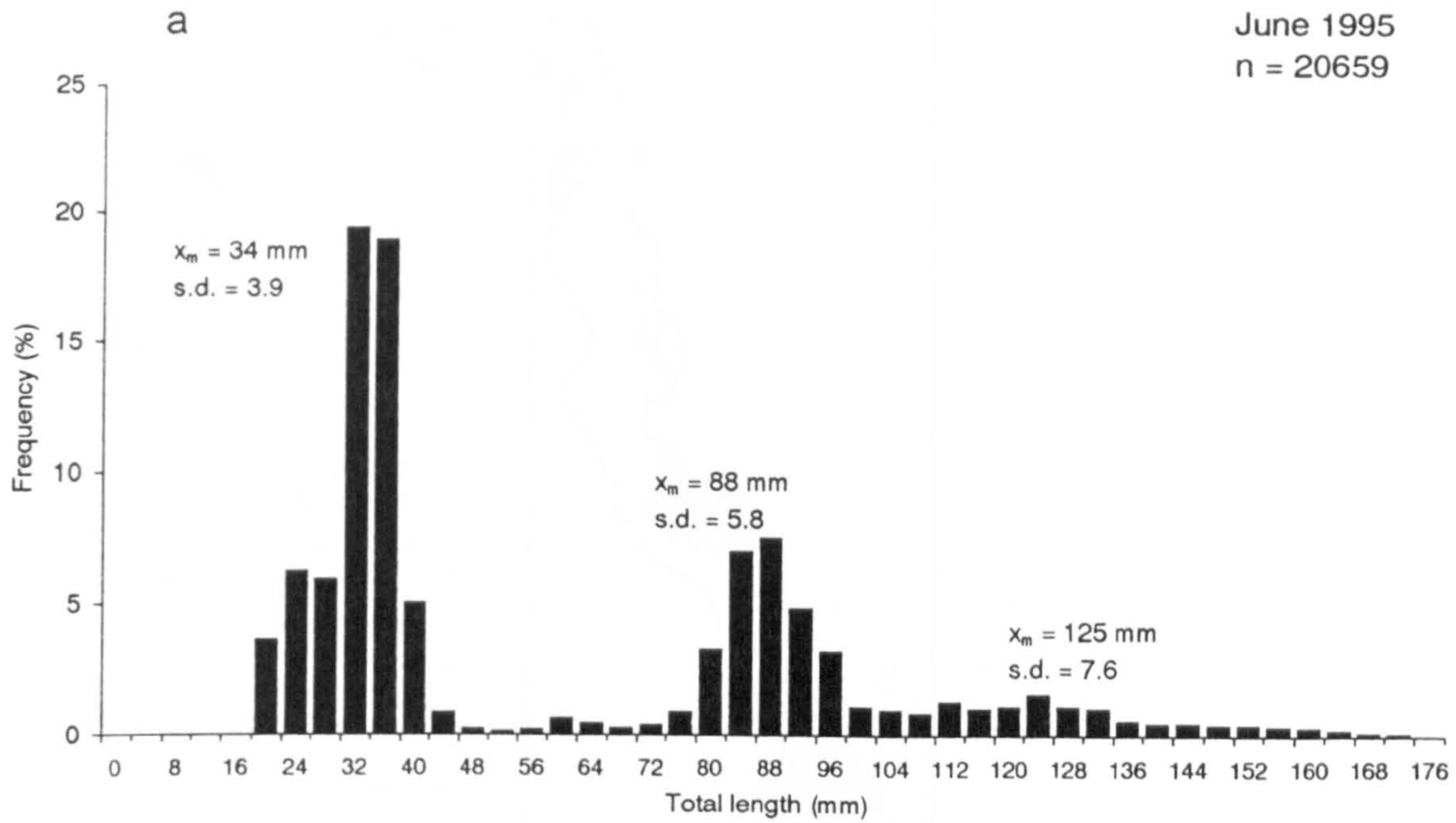


Figure 62. Size distribution of *L. miodon* for the whole lake from mid-water trawl surveys. **a**: June 1995 survey; **b**: November-December 1995 survey. N is the sample size,  $x_m$  and s.d. are the mean length and standard deviation of identified cohorts after Bhattacharya's decomposition of length distribution.

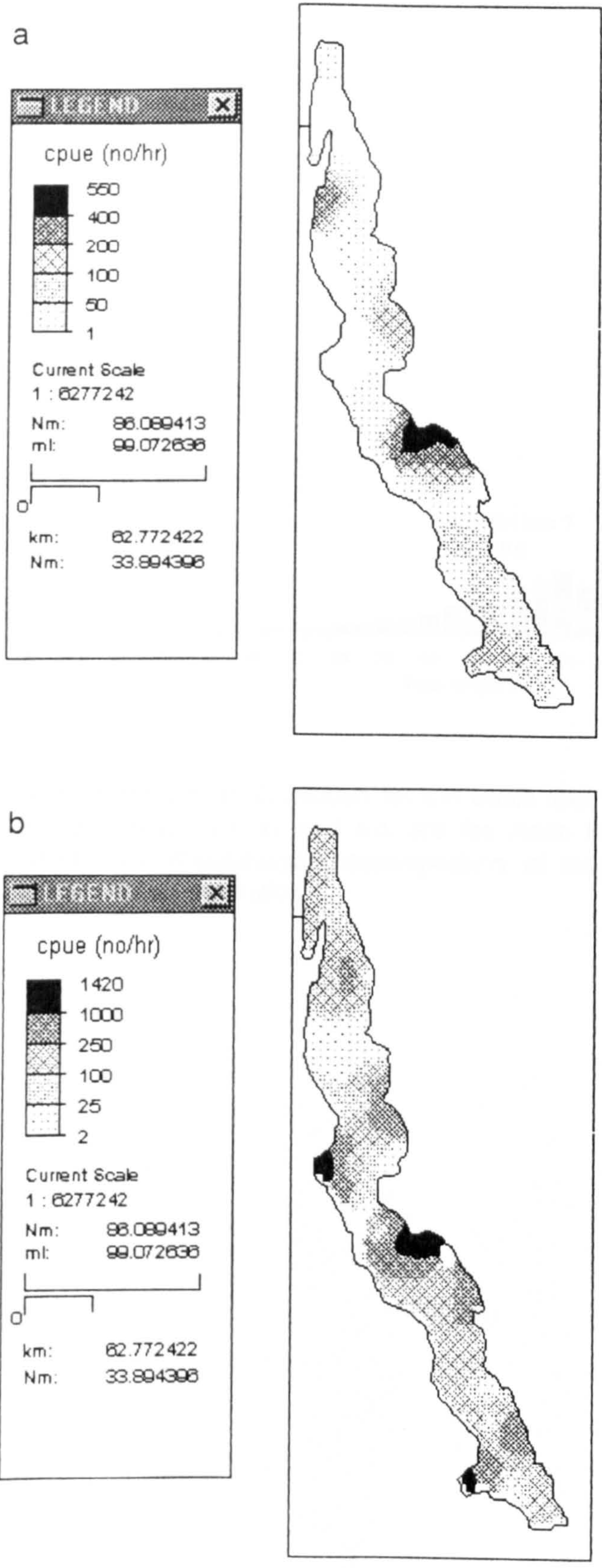


Figure 63. Pelagic trawl catch distribution of adult *L. miodon* ( $TL > L_m$ ) in June 1995 (a) and November-December 1995 (b) survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has 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).

April 1996  
n = 2907

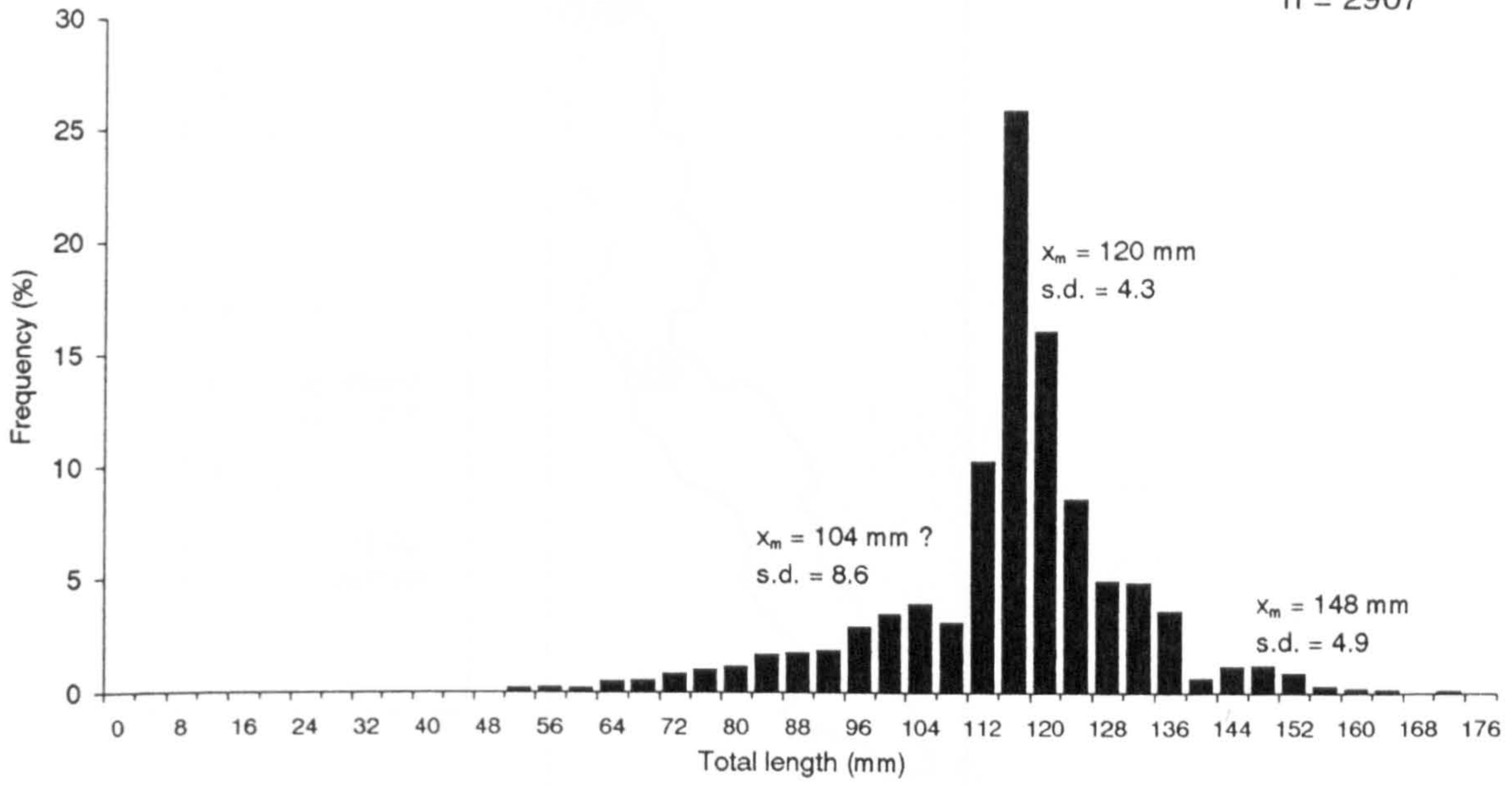


Figure 64. Size distribution of *L. miodon* for the whole lake from April 1996 mid-water trawl survey. N is the sample size,  $x_m$  and s.d. are the mean length and standard deviation of identified cohort after Bhattacharya's decomposition of length distribution. Question mark indicates uncertain cohort separation.

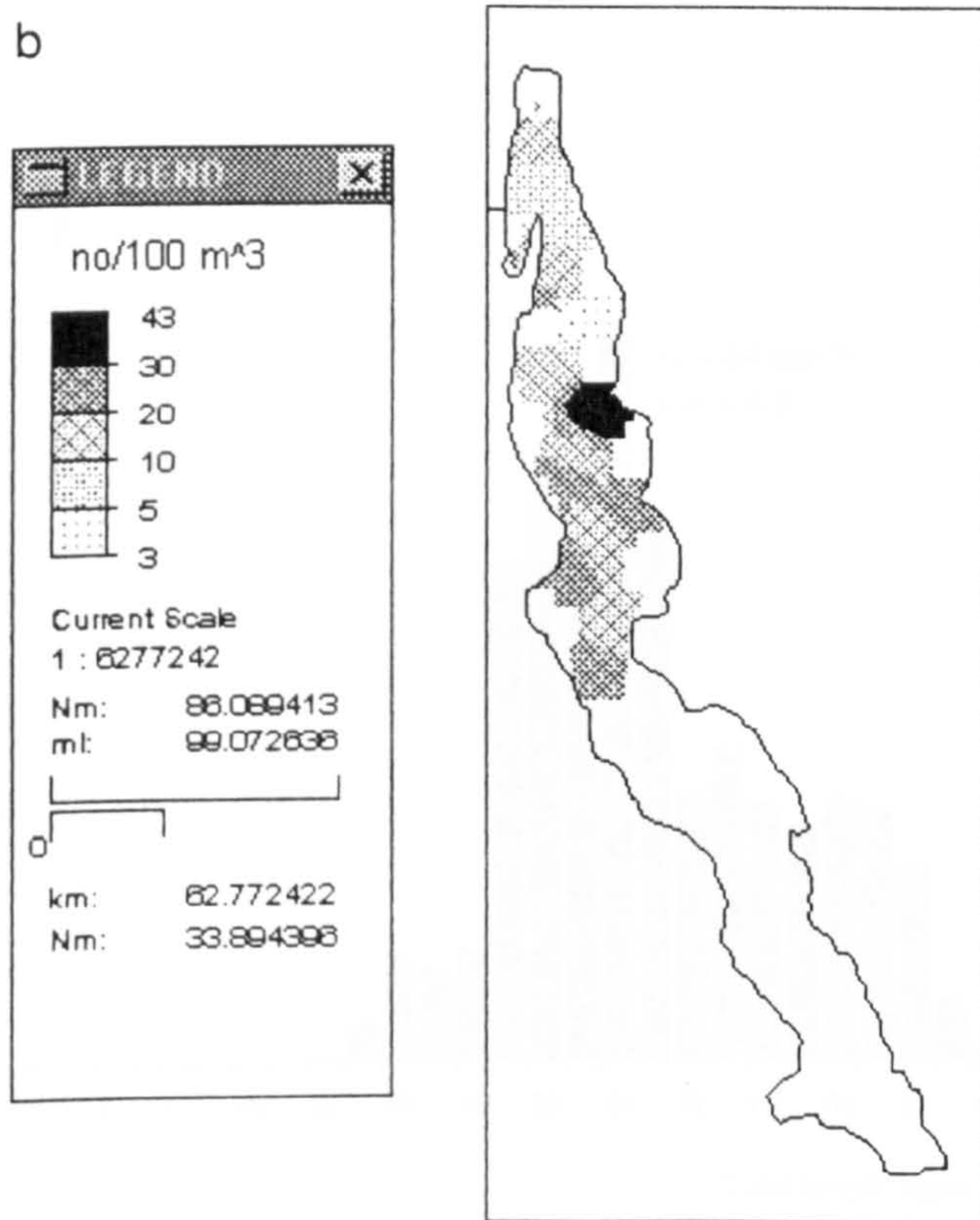
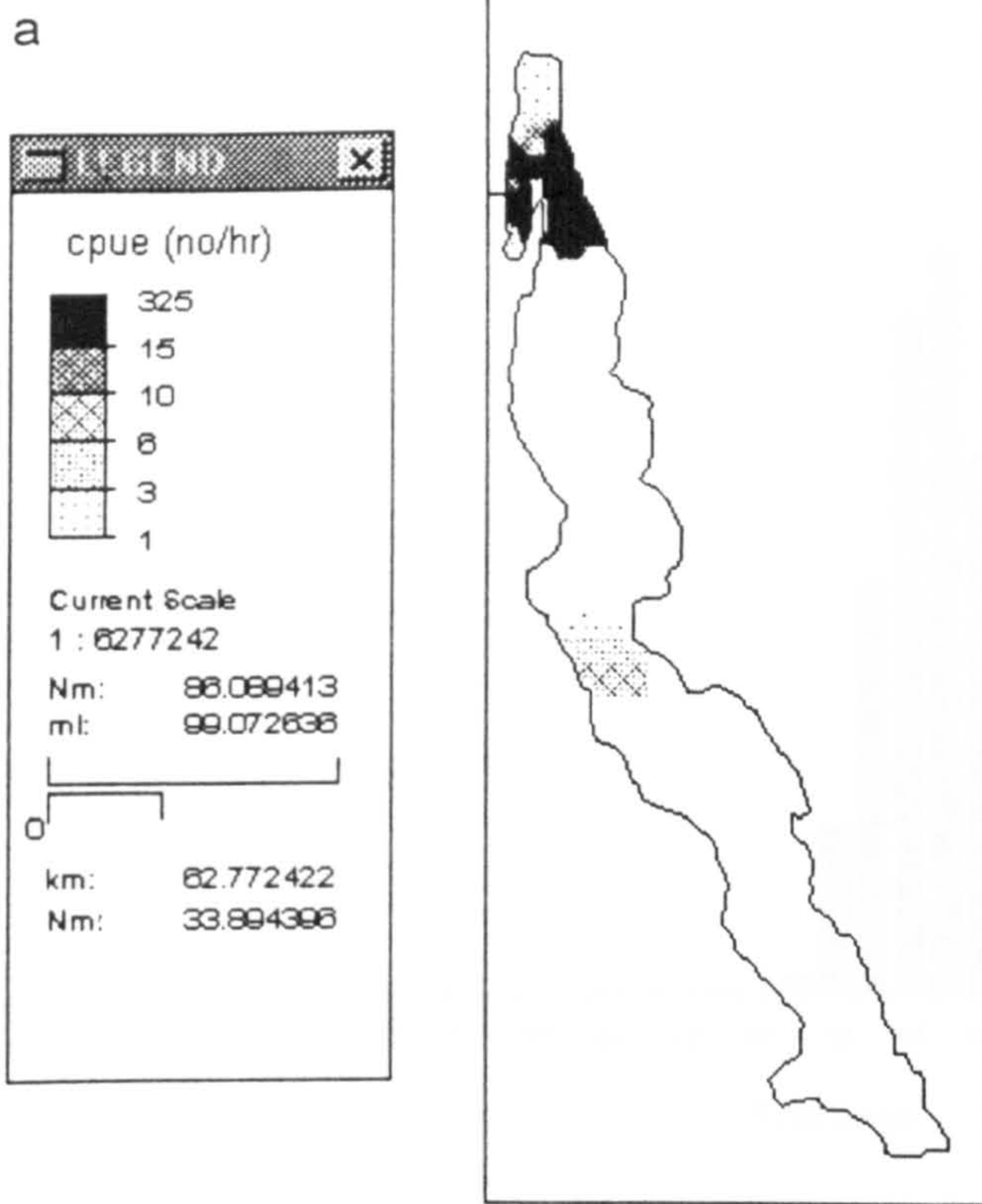


Figure 65. Pelagic trawl catch distribution of (a) young *L. miodon* ( $TL < L_m$ ) and distribution of *L. miodon* larvae (b) within 0-100 m water column in April 1996 survey. Catch per unit of effort (no/hr) and larval density (no/100 m<sup>3</sup>) are grouped in five levels shown in the legend window 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 statute miles (mi).

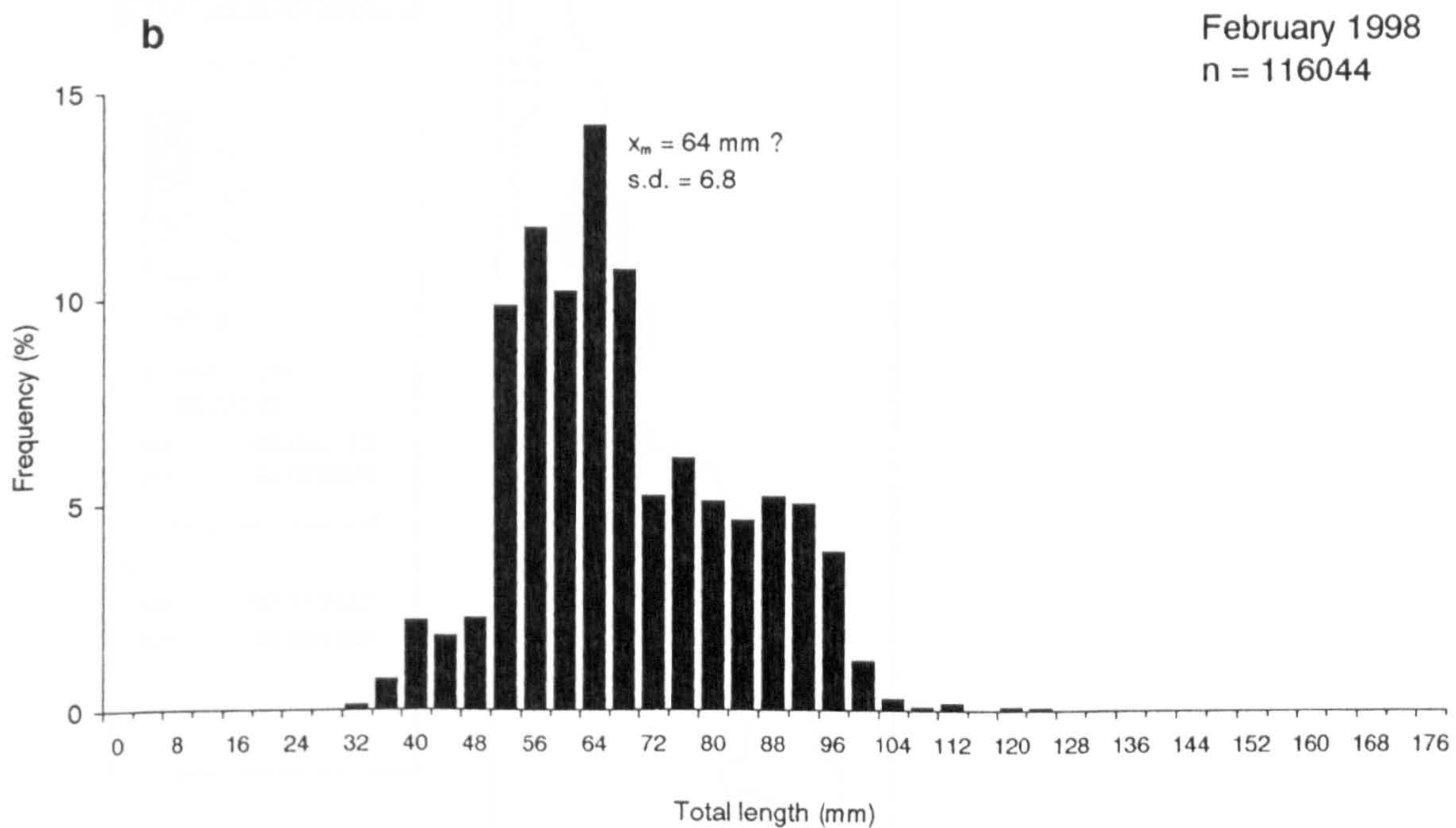
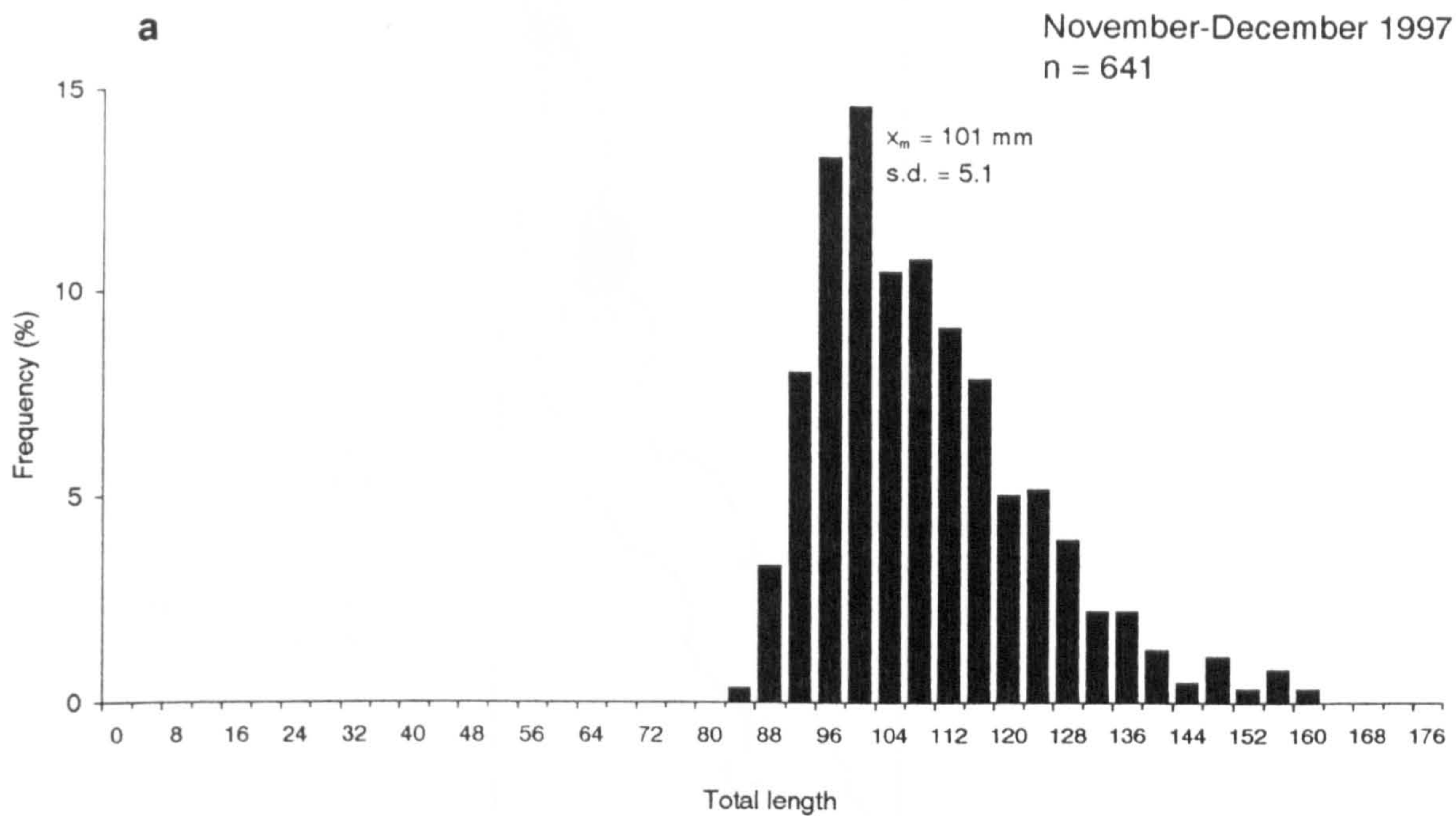


Figure 66. Size distribution of *L. miodon* for the whole lake from mid-water trawl surveys. a, November-December 1997 survey; b, February 1998 survey. N is the sample size,  $x_m$  and s.d. are the mean length and standard deviation of identified cohorts after Bhattacharya's decomposition of length distribution. Question mark indicates uncertain cohort separation.

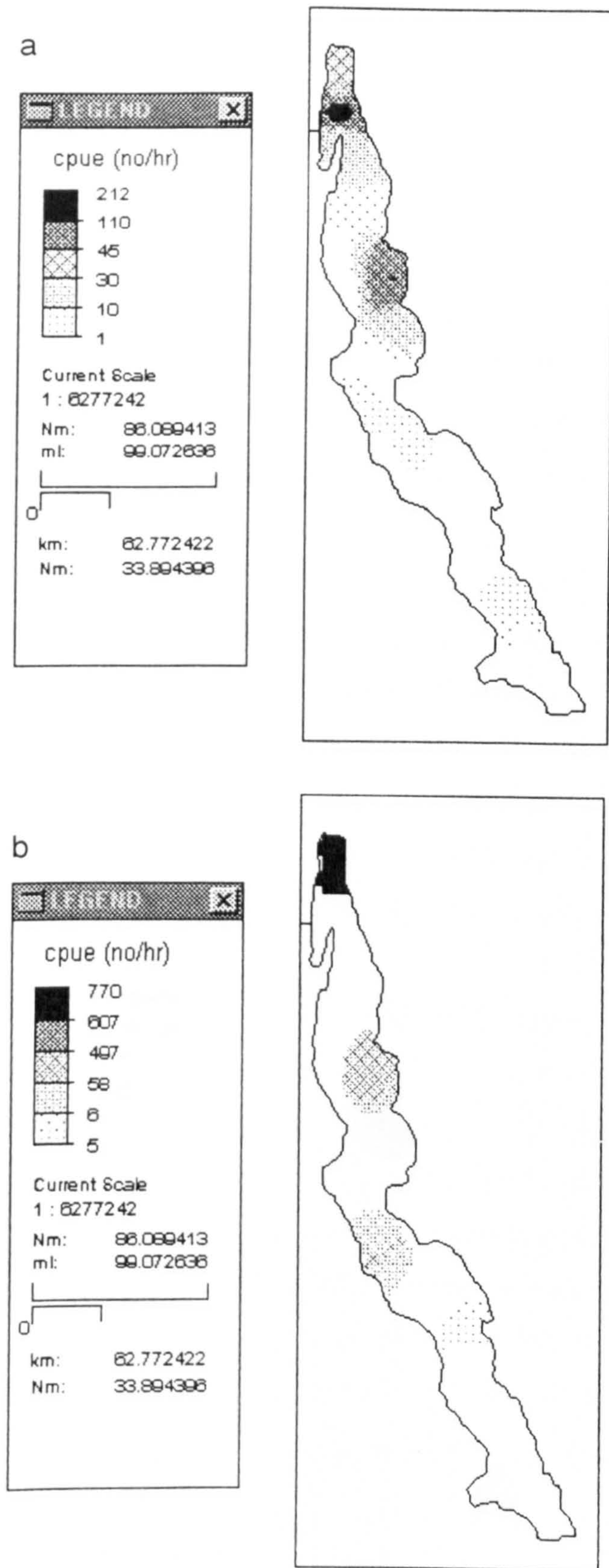
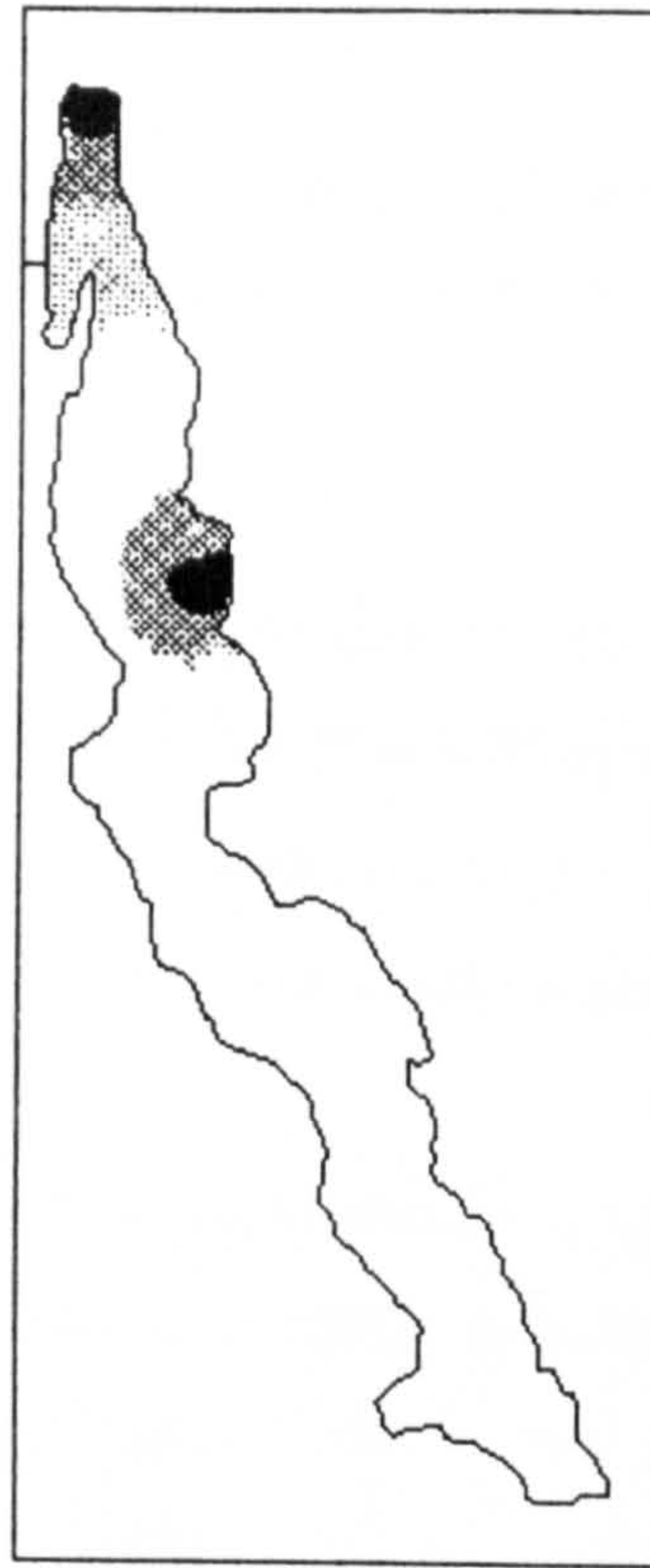
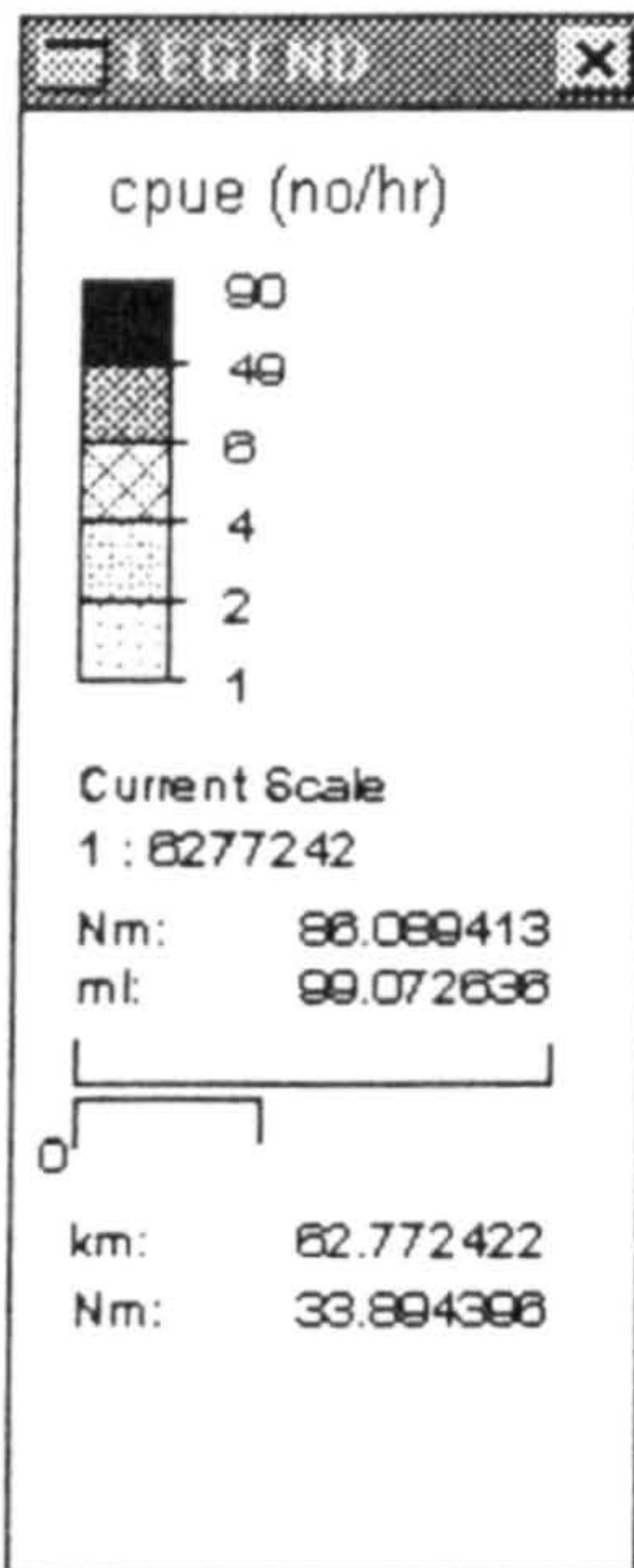


Figure 67. Pelagic trawl catch distribution of adult *L. miodon* ( $TL > L_m$ ) in November-December 1997 (a) and February 1998 (b) survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale 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 statute miles (mi).



a



b

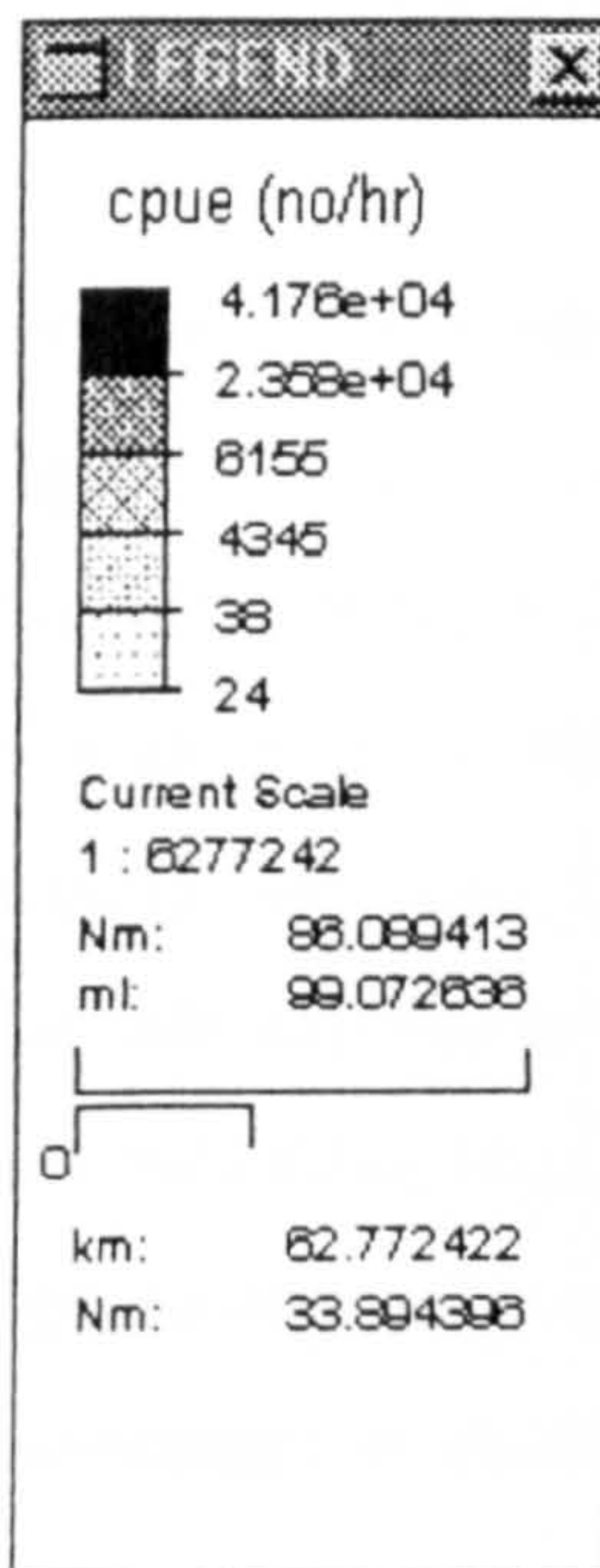


Figure 68. Pelagic trawl catch distribution of young *L. miodon* ( $TL < L_m$ ) in November-December 1997 (a) and February (b) 1998 survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale 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 statute miles (ml).

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 69, 70, 71 and 72). 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. 53b). The occurrence of larvae was common 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<sup>3</sup> 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 June and November-December 1995 surveys, *L. miodon* larval concentrations reached a maximum in the Bujumbura and Karonda areas (Fig. 73). In April 1996 the larval number was even lower and their number reached a maximum in the Kigoma and Kalemie sub-basins (Fig. 65b). 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. 74).

#### 3.4.4 *Lates stappersii*

*Lates stappersii* occurred in 86 of the 131 hauls and catch rates varied between 0 and 61 kg hr<sup>-1</sup>. 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.

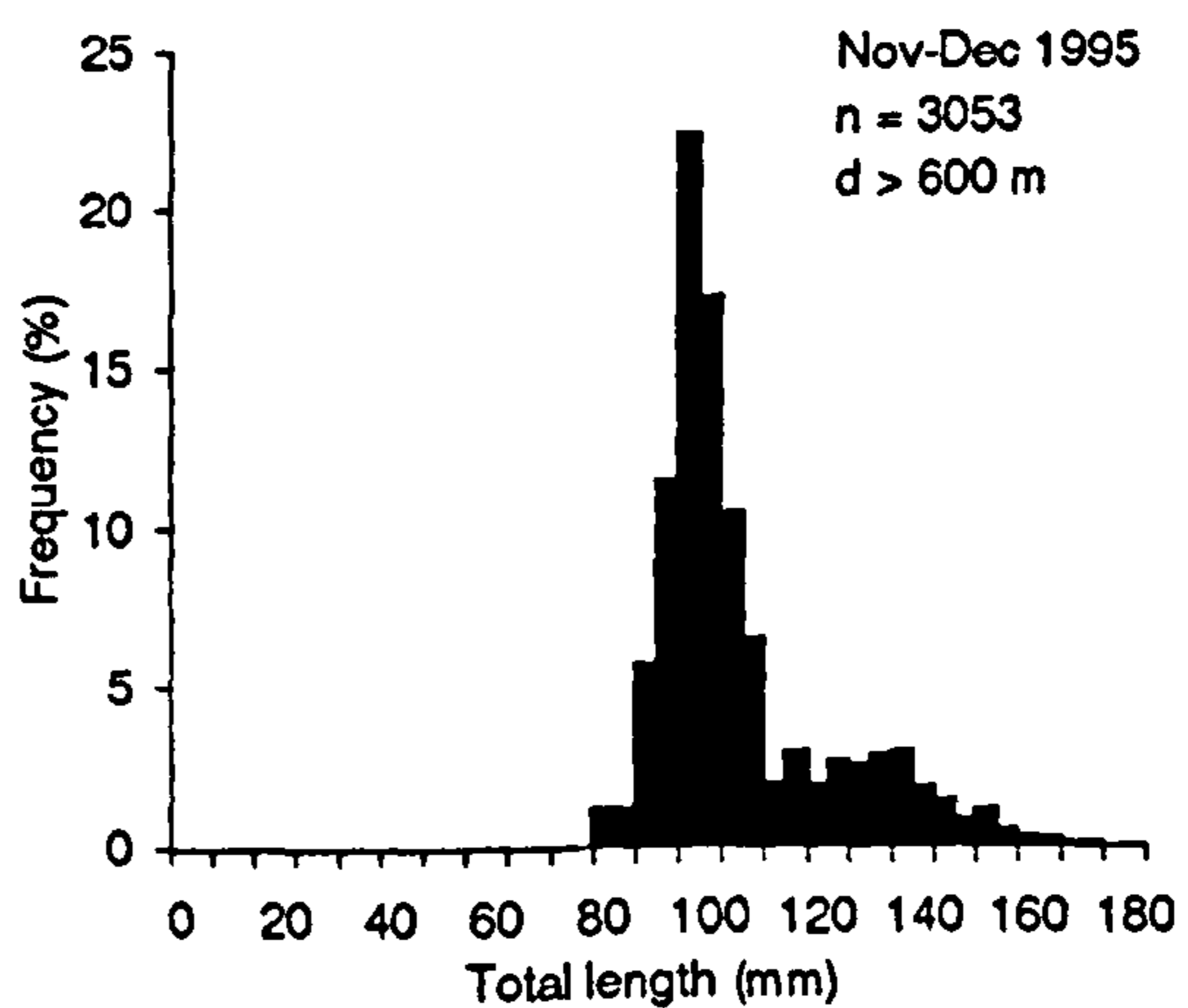
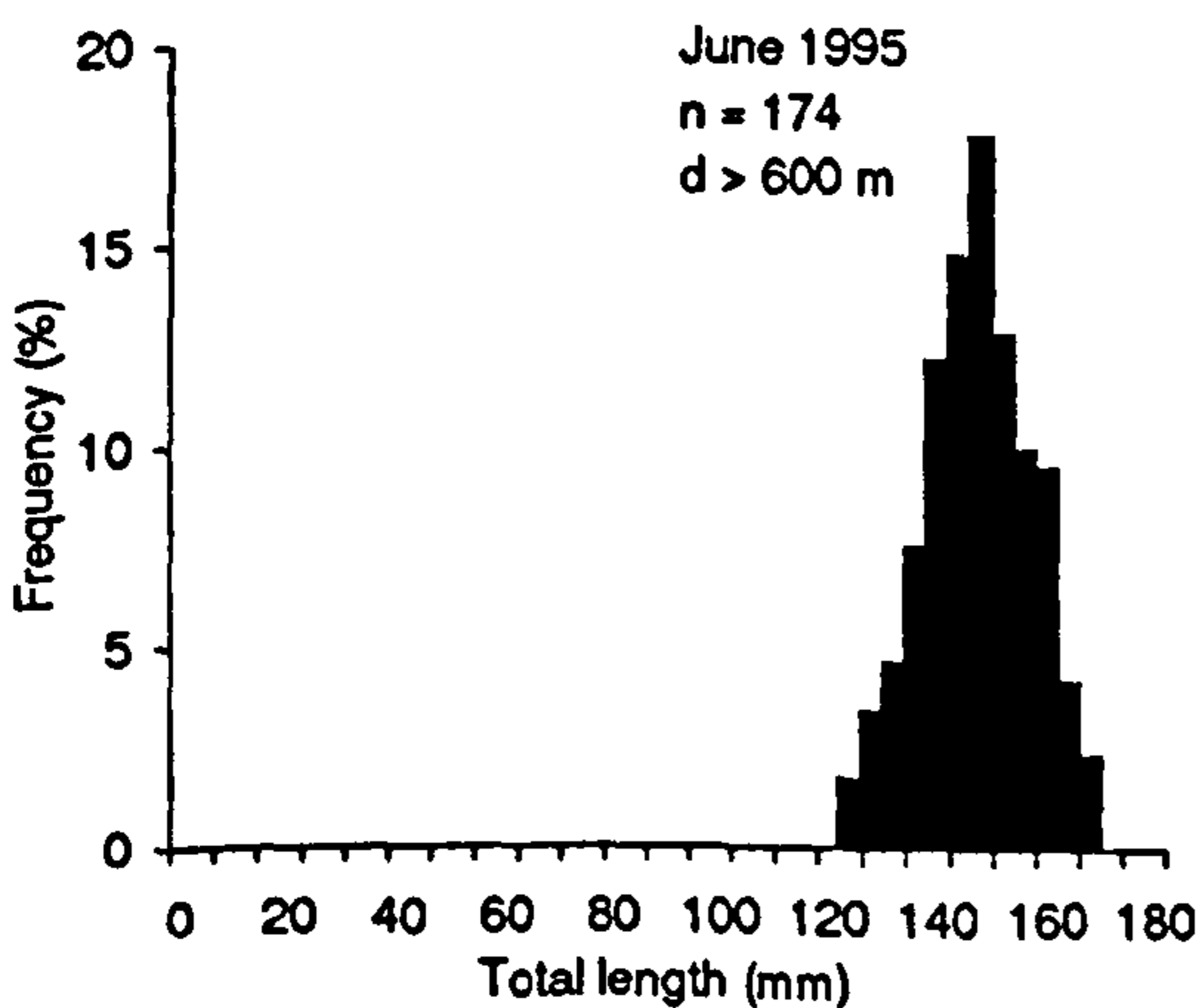
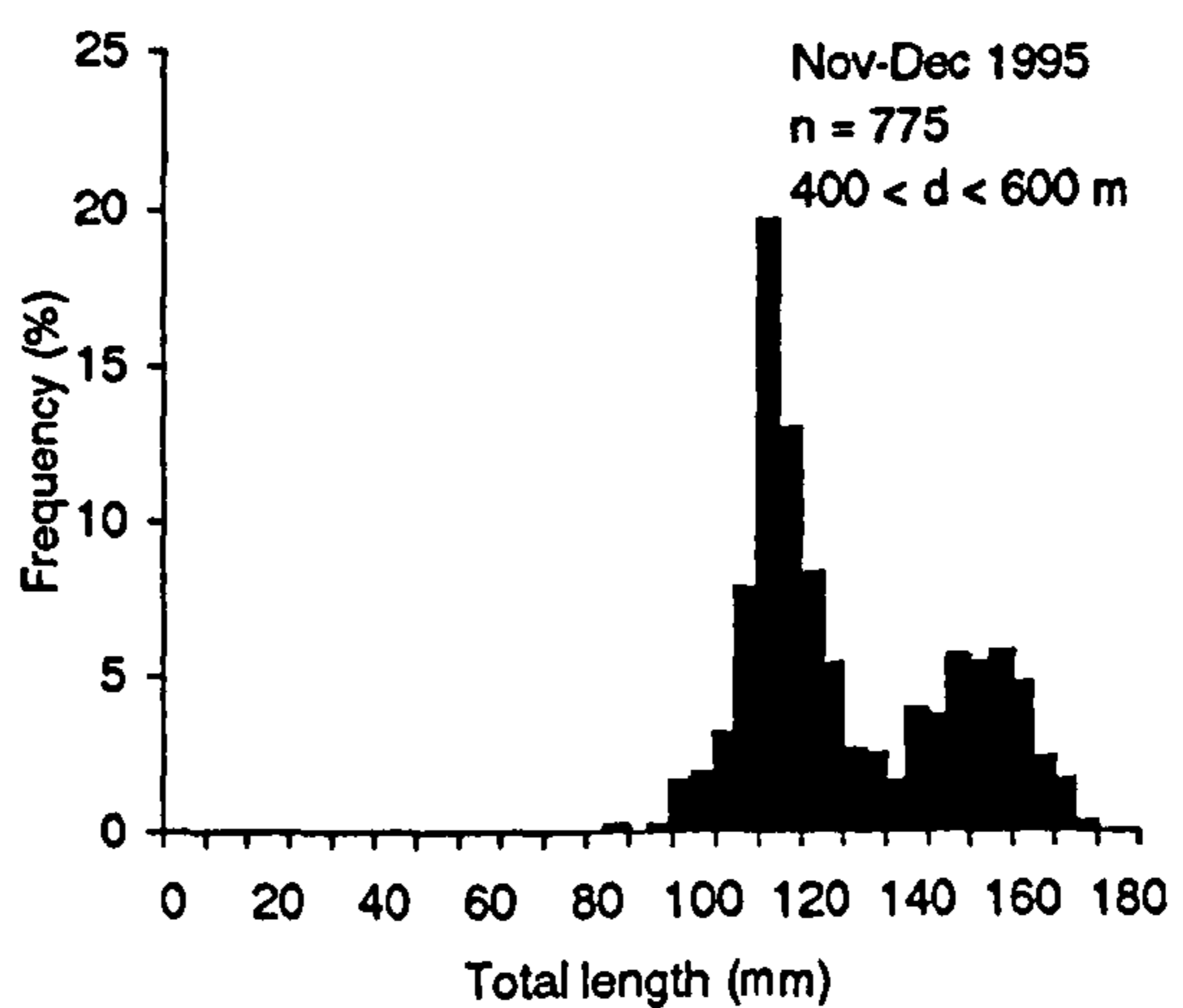
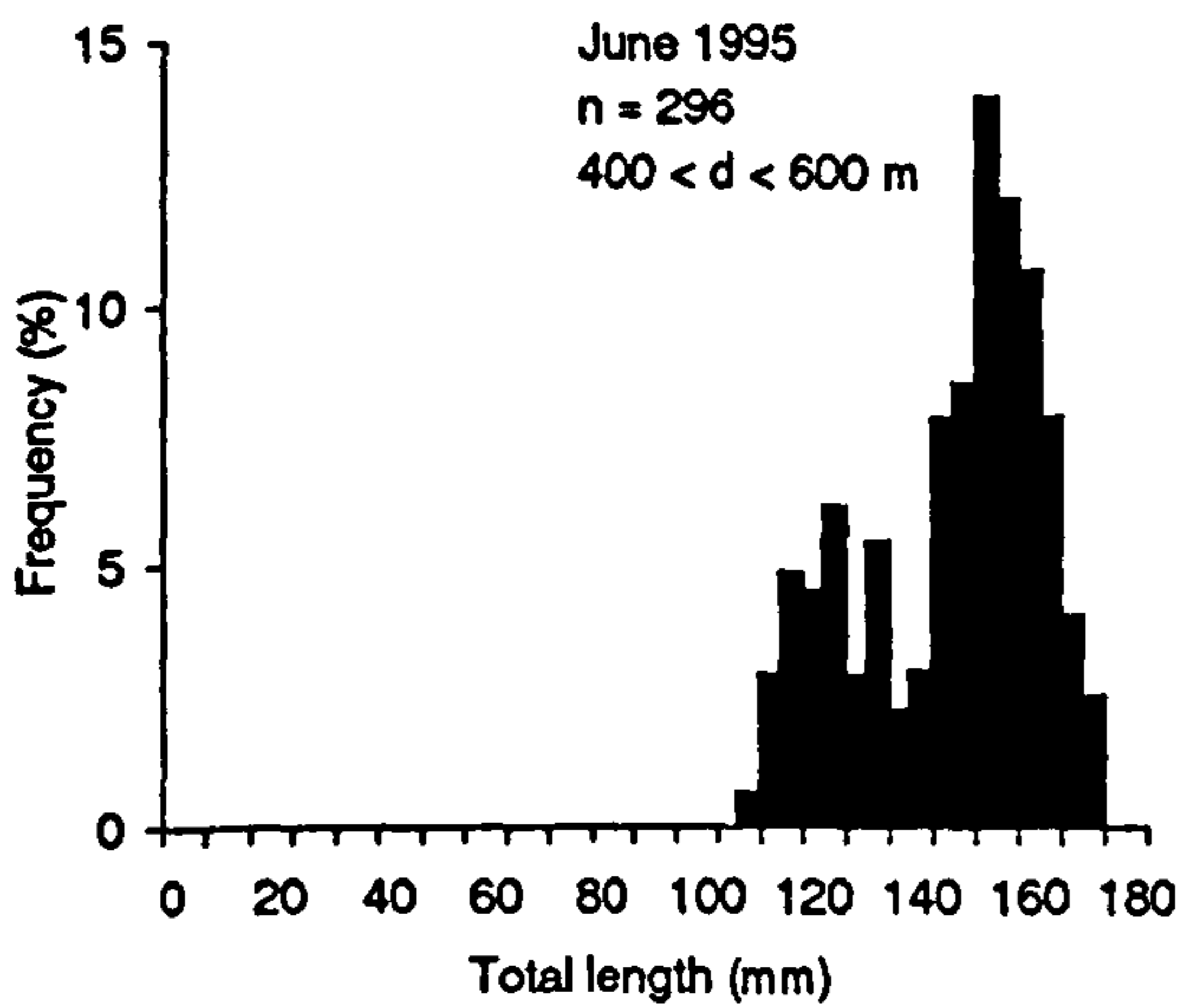
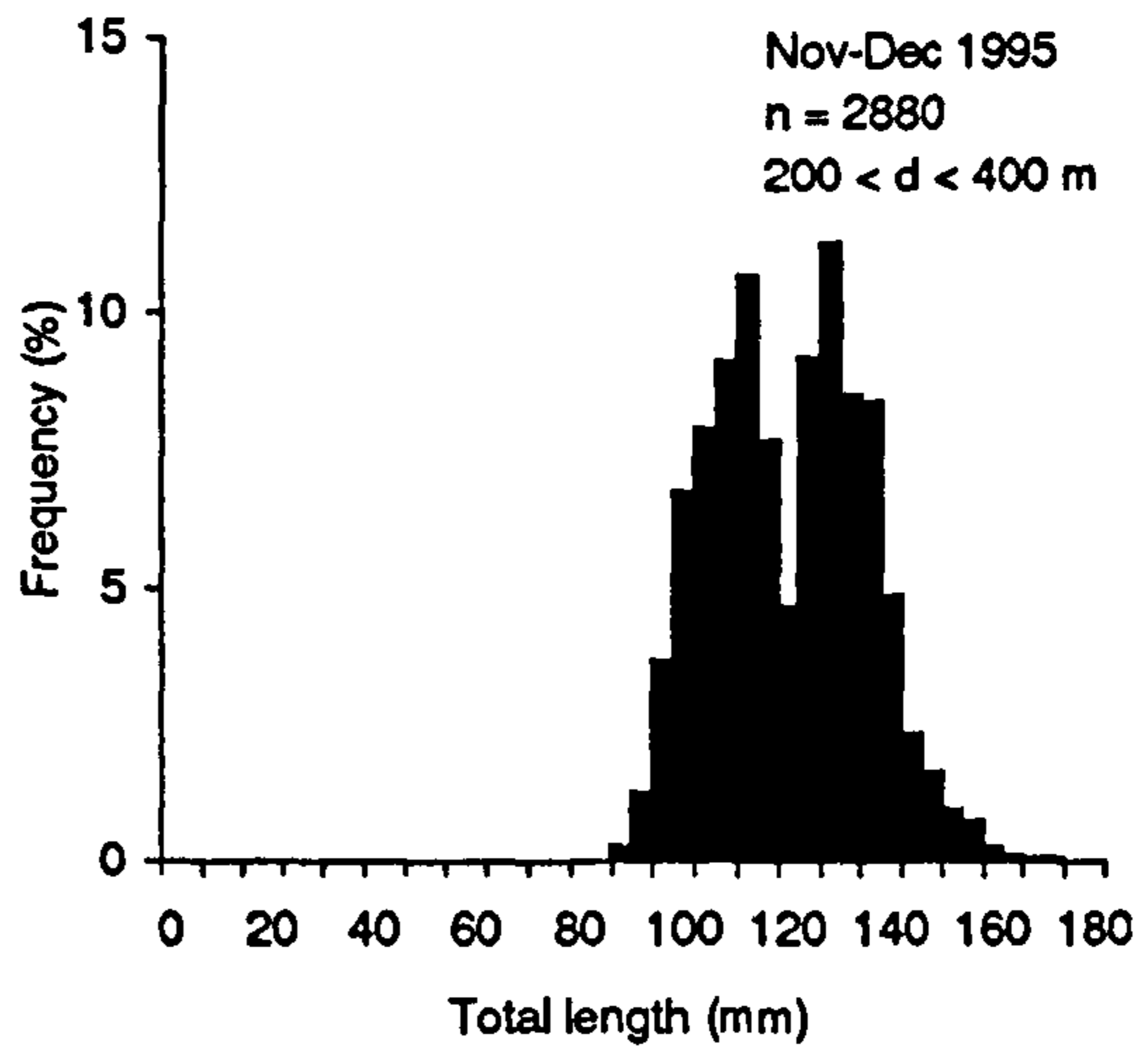
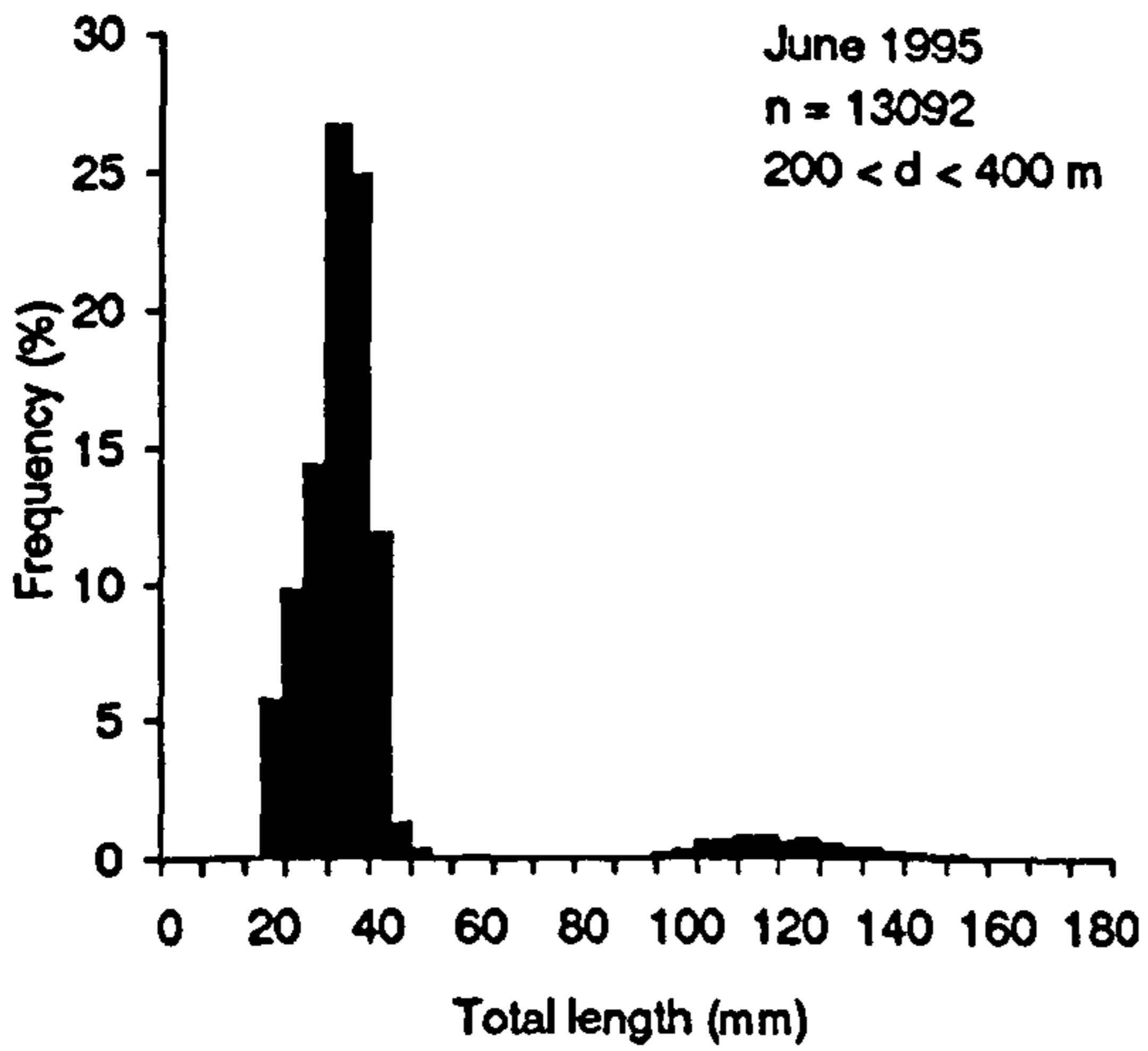
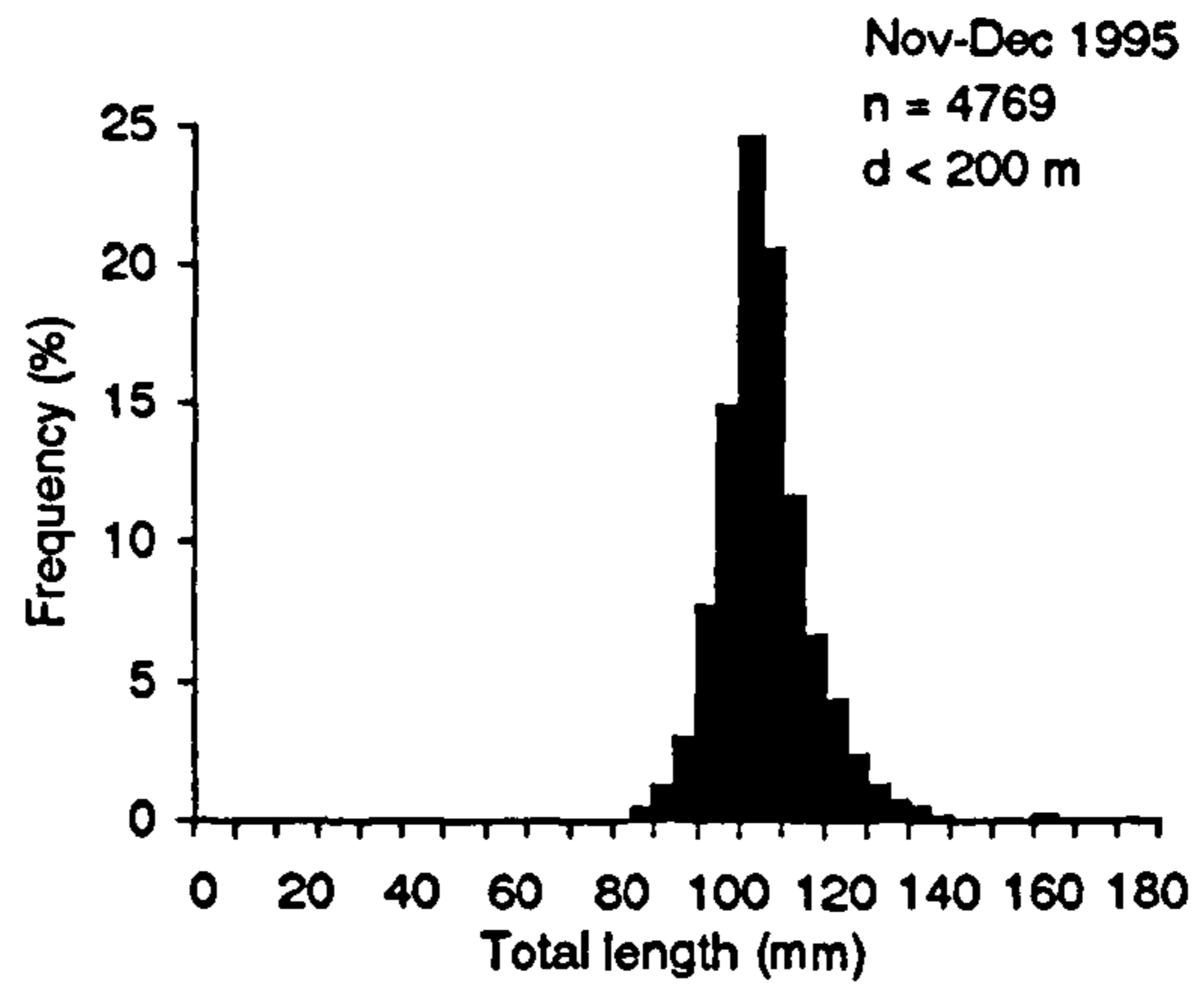
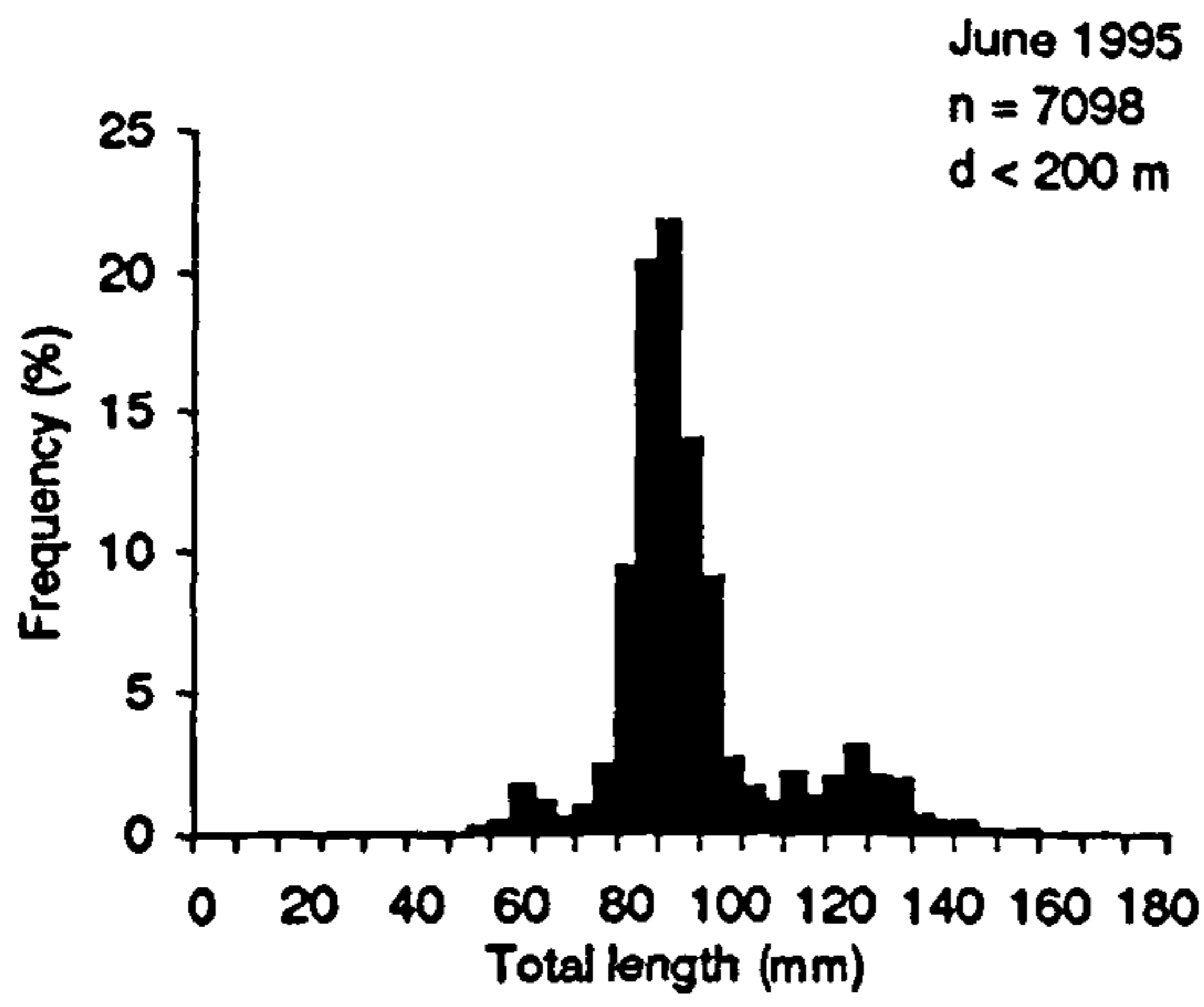


Figure 69. Size distribution of *L. miodon* by depth strata in June and November-December 1995. Bottom depth is indicated with d, n is the sample size.

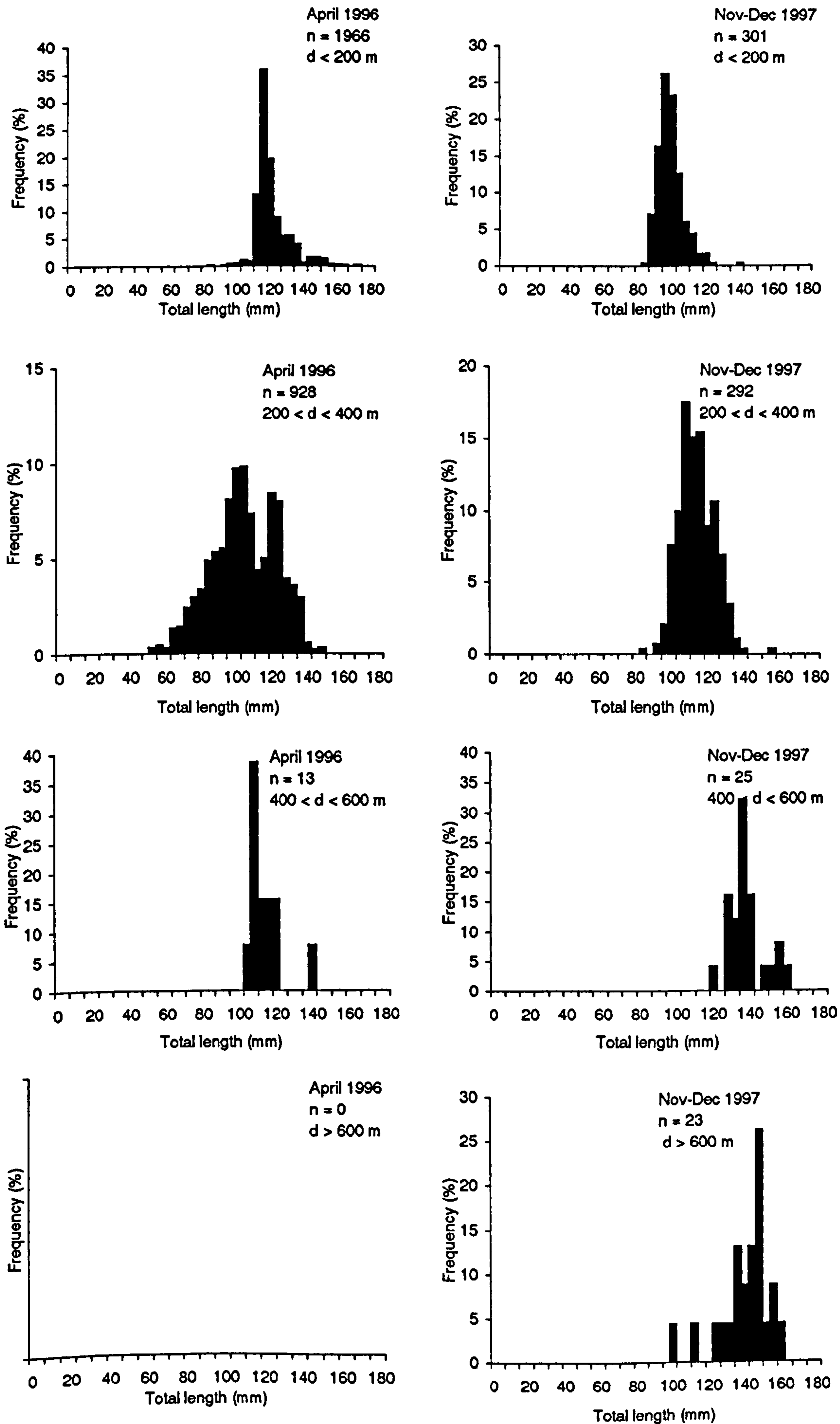


Figure 70. Size distribution of *L. miodon* by depth strata in April 1996 and November-December 1997. Bottom depth is indicated with d, n is the sample size.

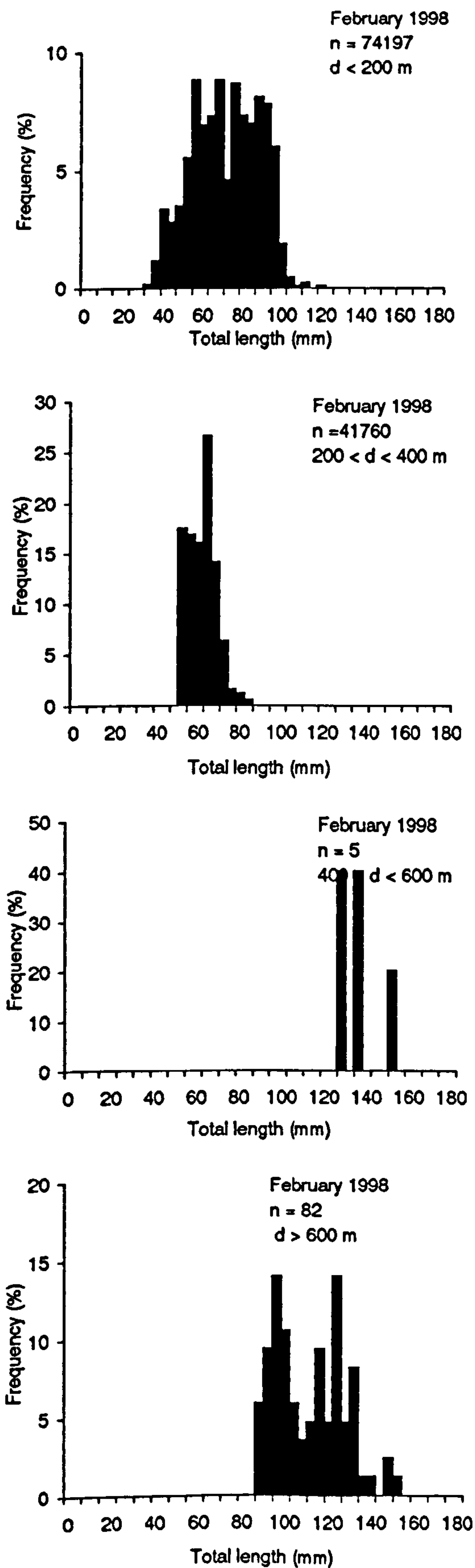


Figure 71. Size distribution of *L. miodon* by depth strata in February 1998. Bottom depth is indicated with d, n is the sample size.

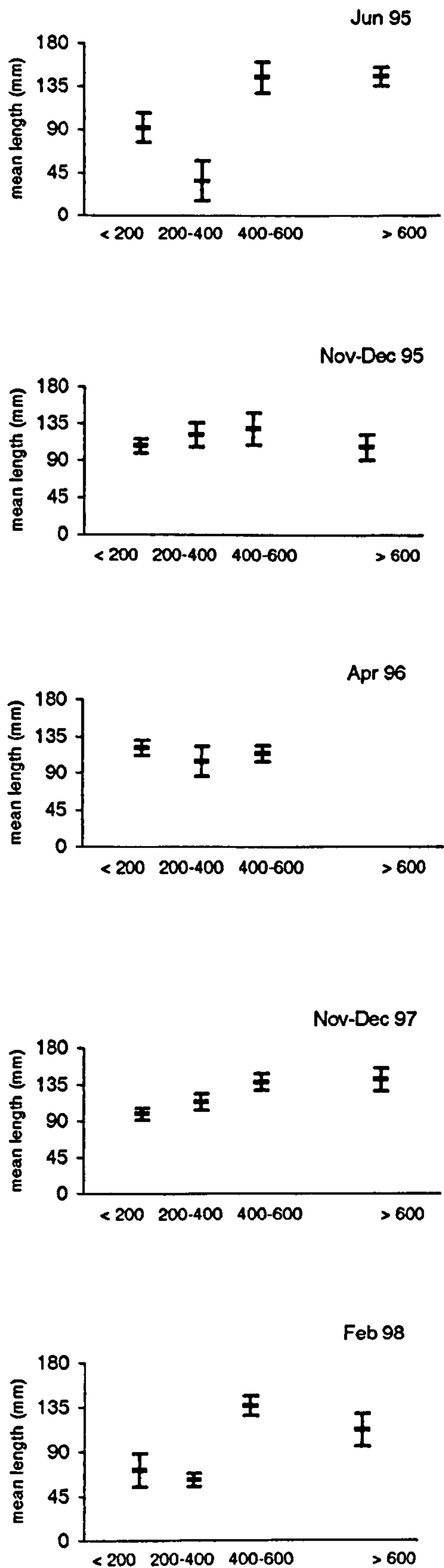


Figure 72. Mean length of *L. miodon* in trawl catches from four bottom depth-defined zones (abscissa, m) during five surveys.

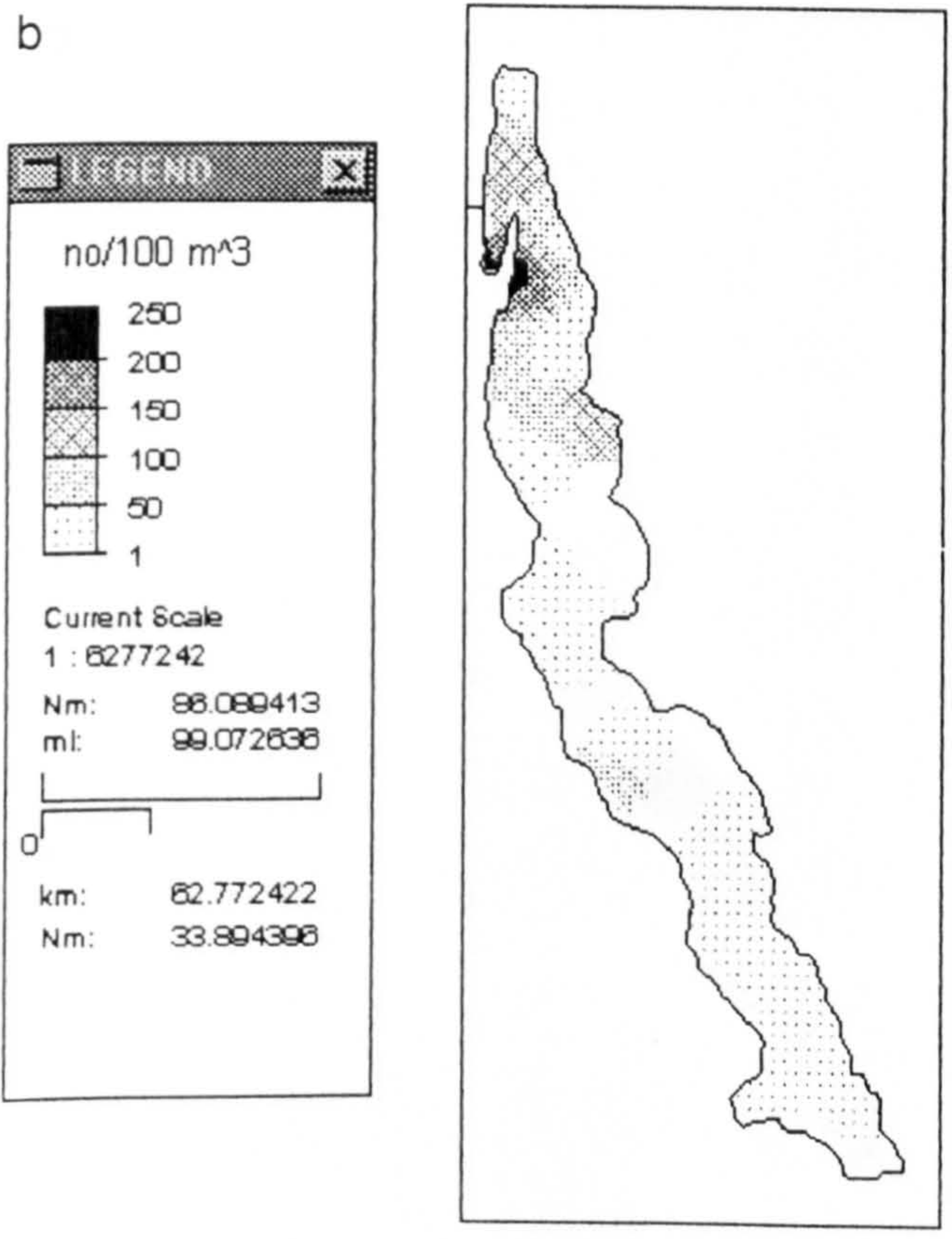
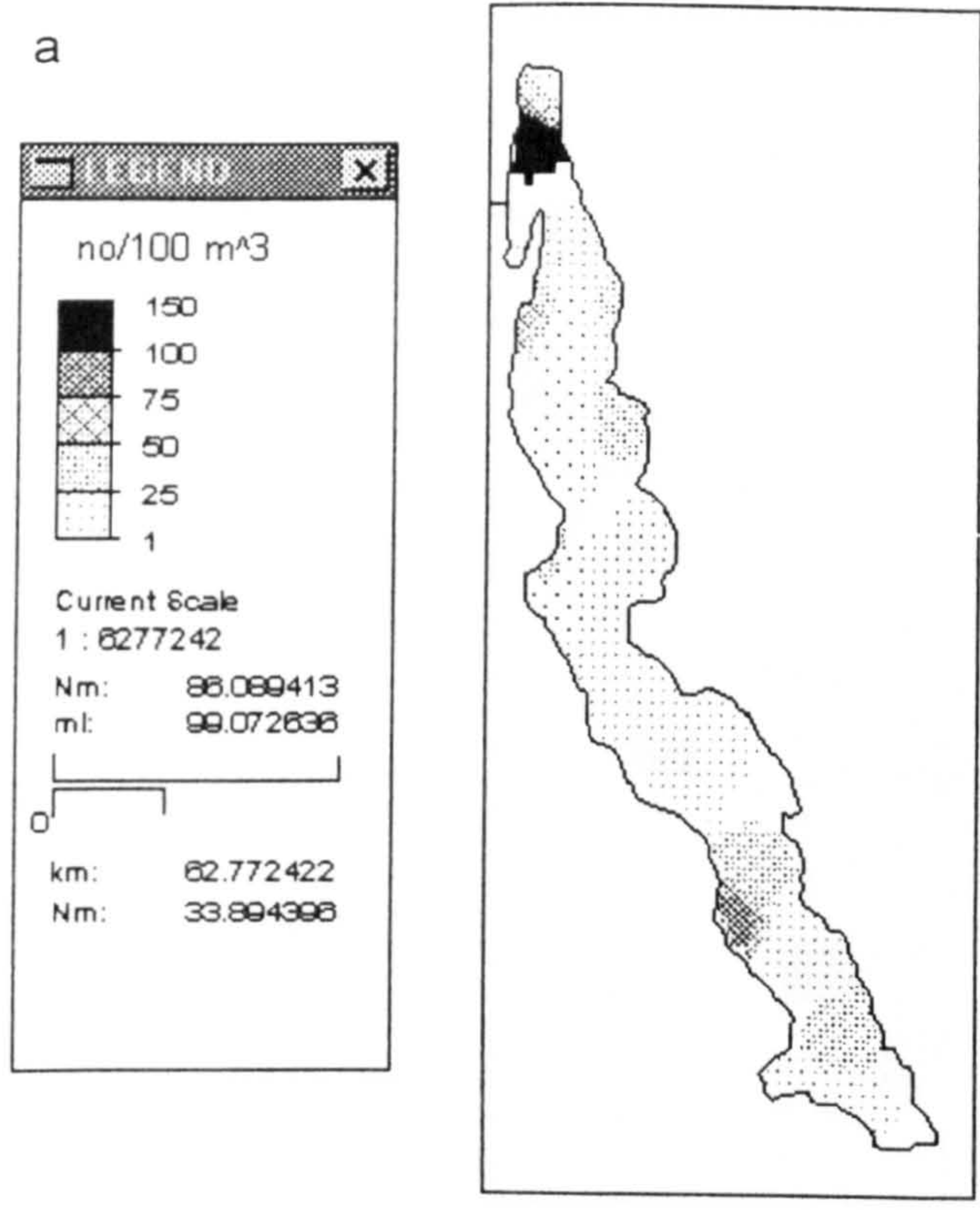


Figure 73. Distribution of *L. miodon* larvae within 0-100 m water column in June (a) and November-December (b) 1995. Larval density (no/100 m<sup>3</sup>) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. 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).

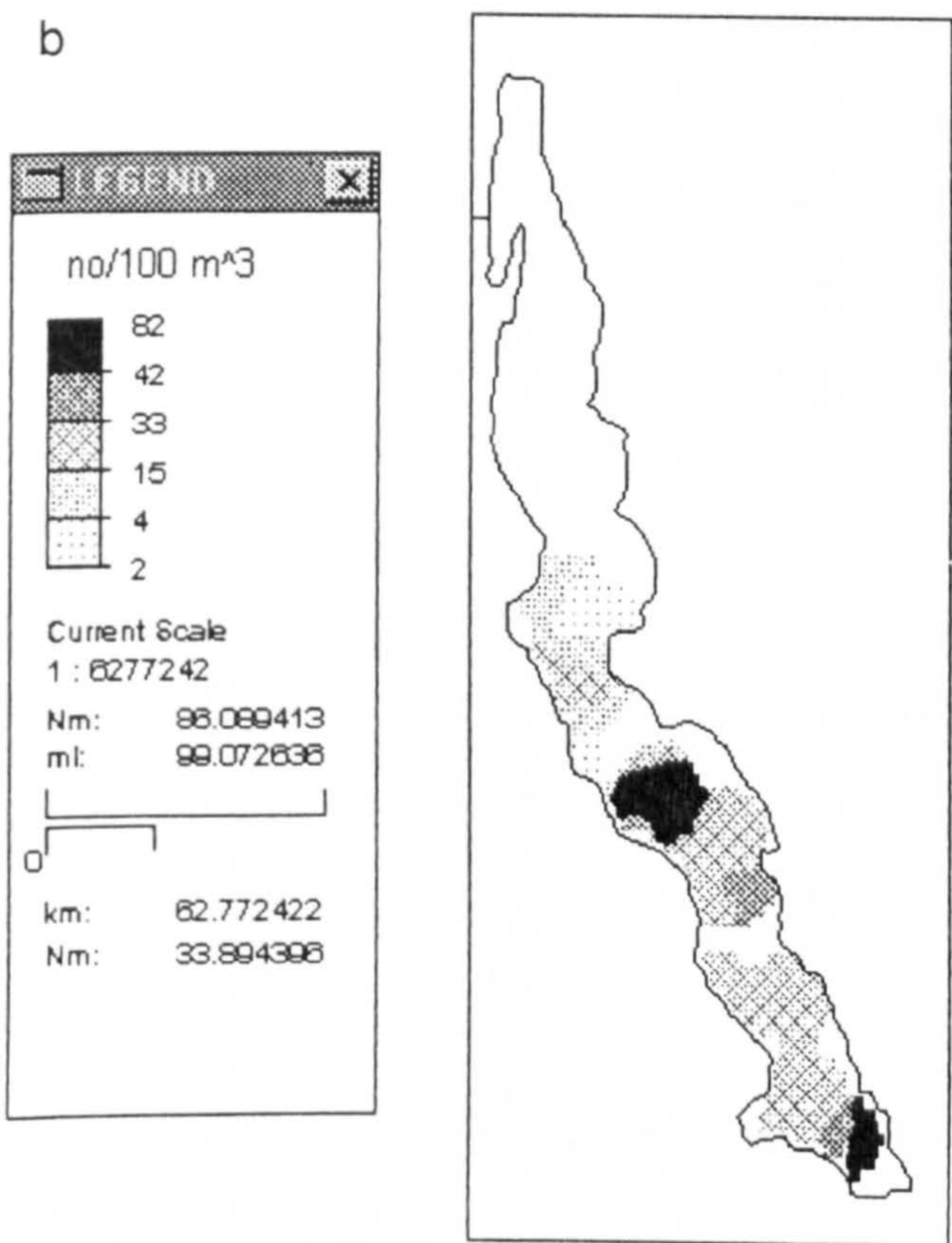
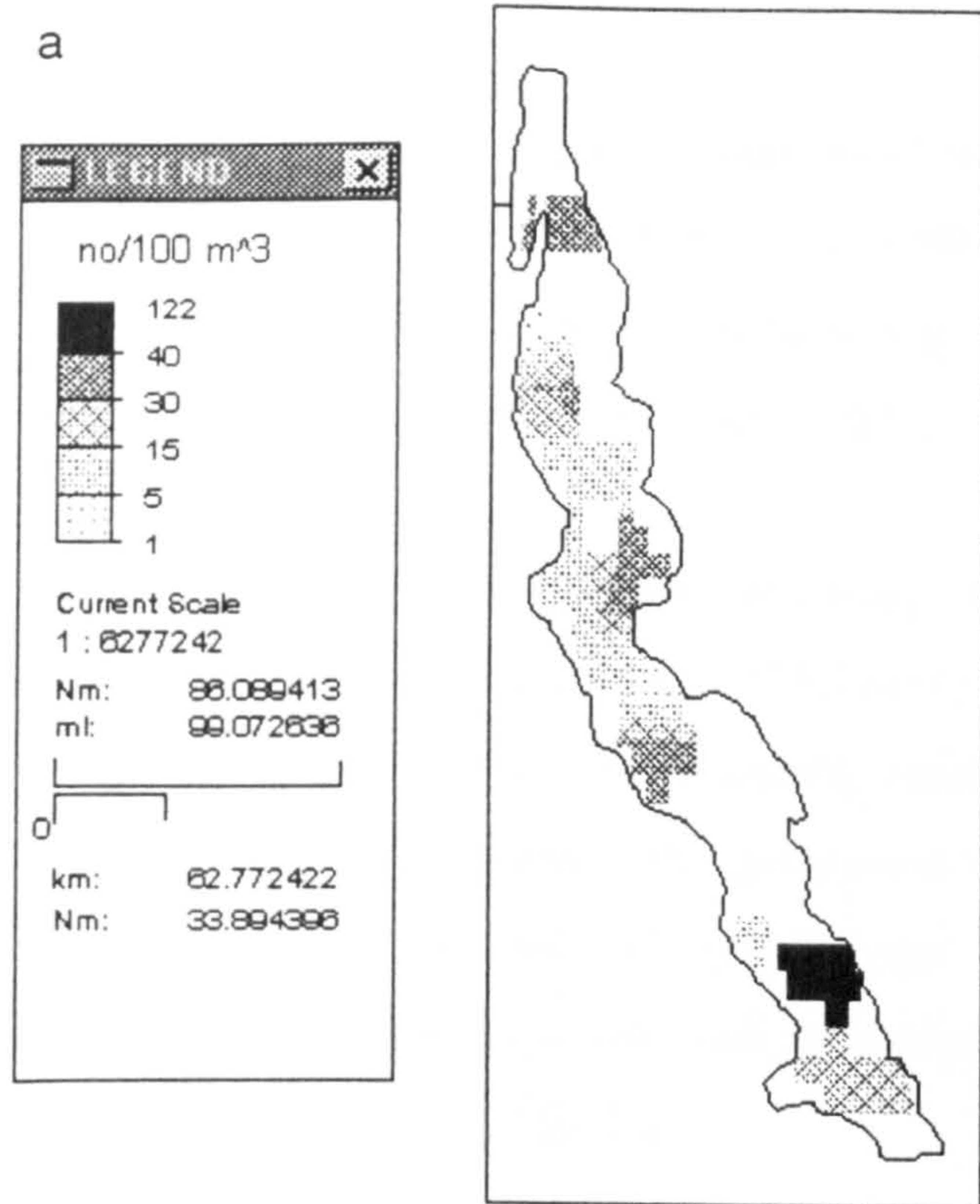


Figure 74. Distribution of *L. miodon* larvae within 0-100 m water column in November-December 1997 (a) and February 1998 (b). Larval density (no/100 m<sup>3</sup>) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. 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 statute miles

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. 75). The overall CPUE distribution was thus different from that obtained in 1995 ( $\chi^2_{[10]} = 38.40, P < 0.05$ ).

The sexual maturity composition of survey samples comprised mainly maturing females (stage II and III), except in February 1998 when the proportion of mature fish was the highest (Fig. 76). 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 latter month the proportion of mature males, as that of females, was the highest (Fig. 76).

*Lates stappersii* showed, in both 1995 surveys, a wide distribution occurring over the most of the lake (Fig. 77). 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<sup>-1</sup> 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. 78a). Mean CPUE (1.949 kg hr<sup>-1</sup>) was significantly lower than in the June and November-December 1995 surveys ( $P = 0.024$  and  $P = 0.011$  respectively).

CPUE of *L. stappersii* in November-December 1997 and February 1998 showed a more localised pattern (Fig. 79) 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



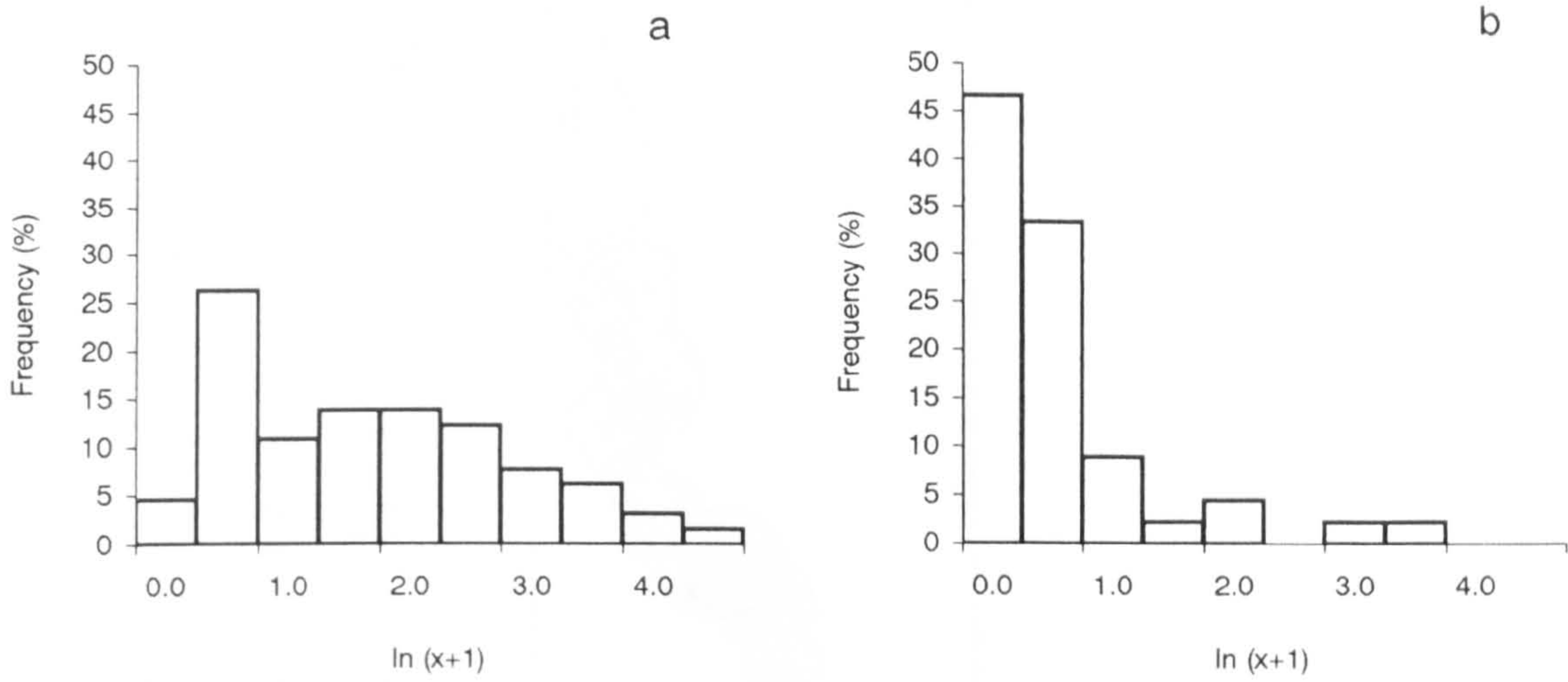


Figure 75. Frequency histograms of  $\ln(x+1)$  transformed CPUE values derived for *L. stappersii* from, a, June and November-December 1995 and, b, November-December 1997 and February 1998 pelagic trawl surveys.

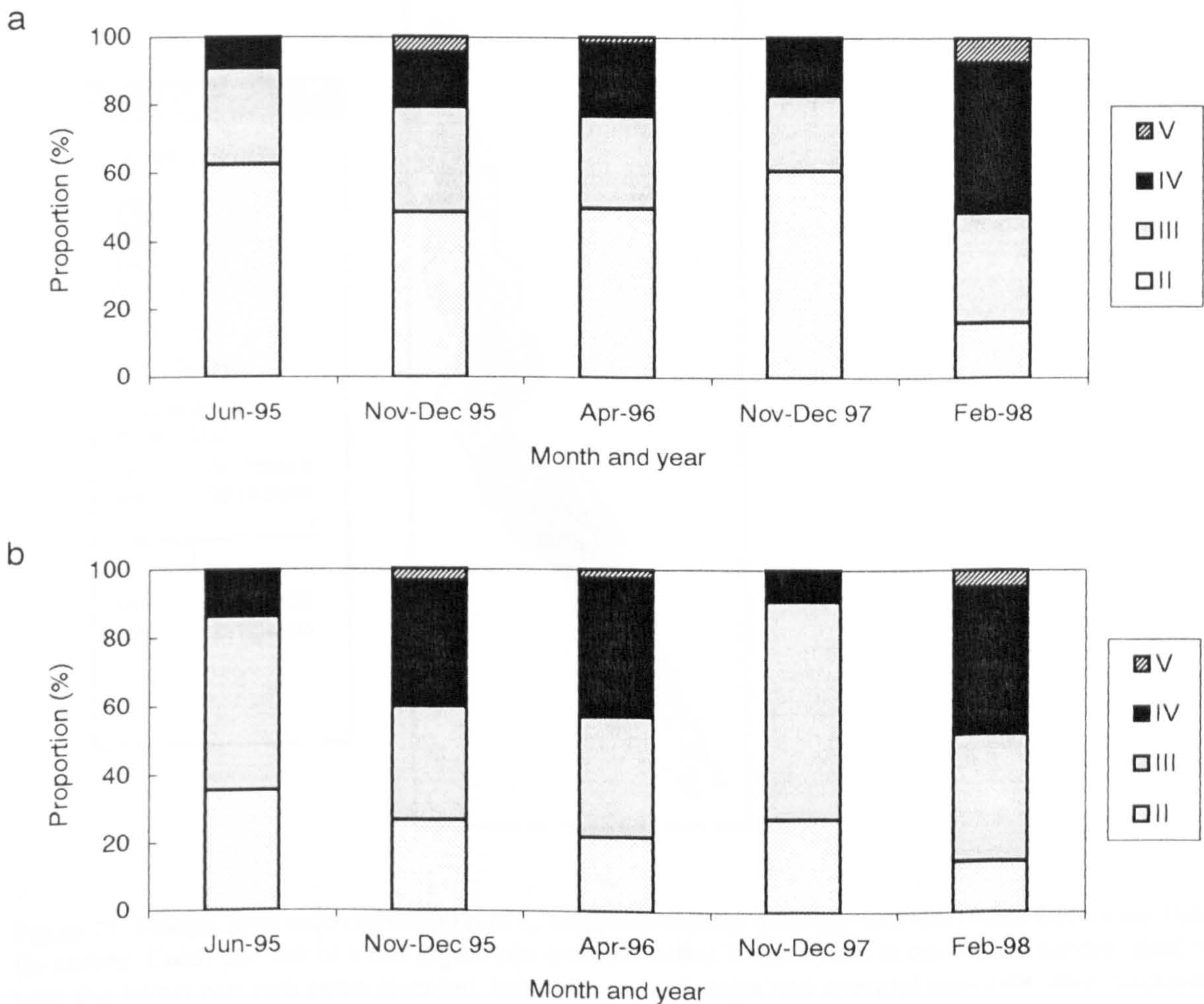


Figure 76. Maturity stages for *L. stappersii* samples of females (a) and males (b) taken during lake-wide surveys in June (sample size,  $n=671$ ) and November-December ( $n=861$ ) 1995, April 1996 ( $n=222$ ), November-December 1997 ( $n=63$ ) and February 1998 ( $n=310$ ).

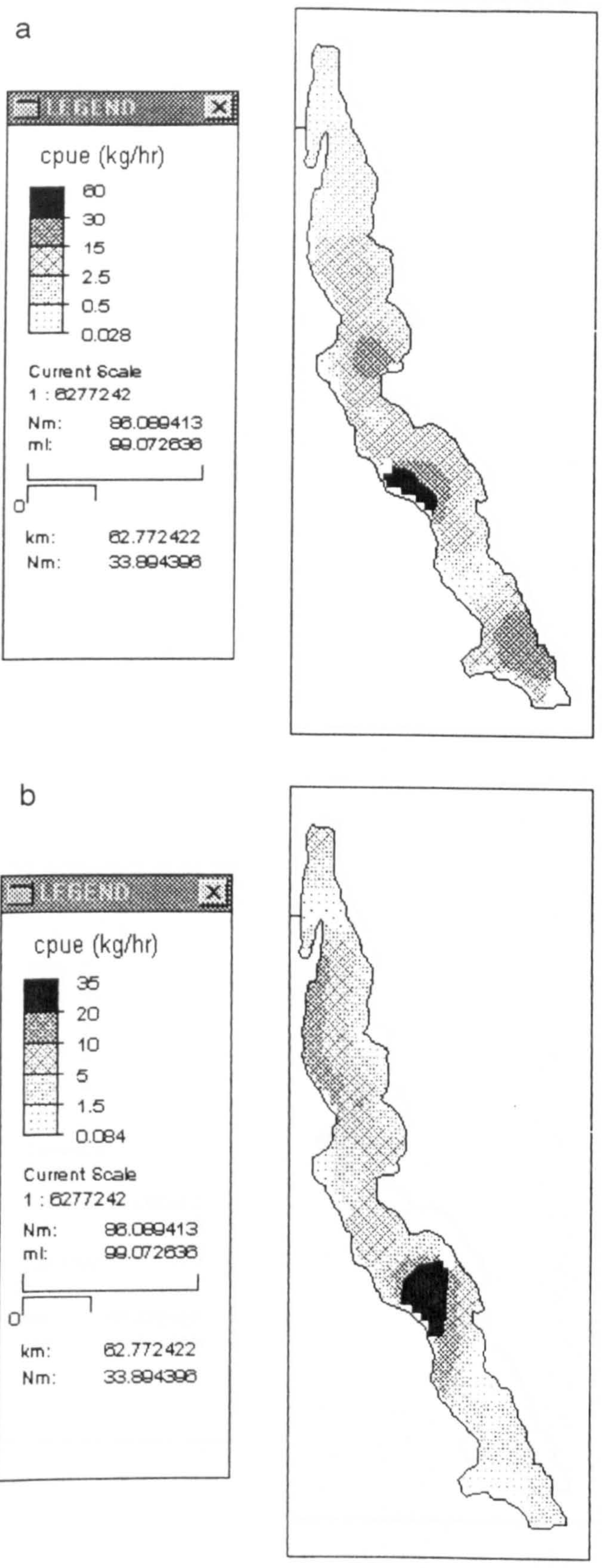
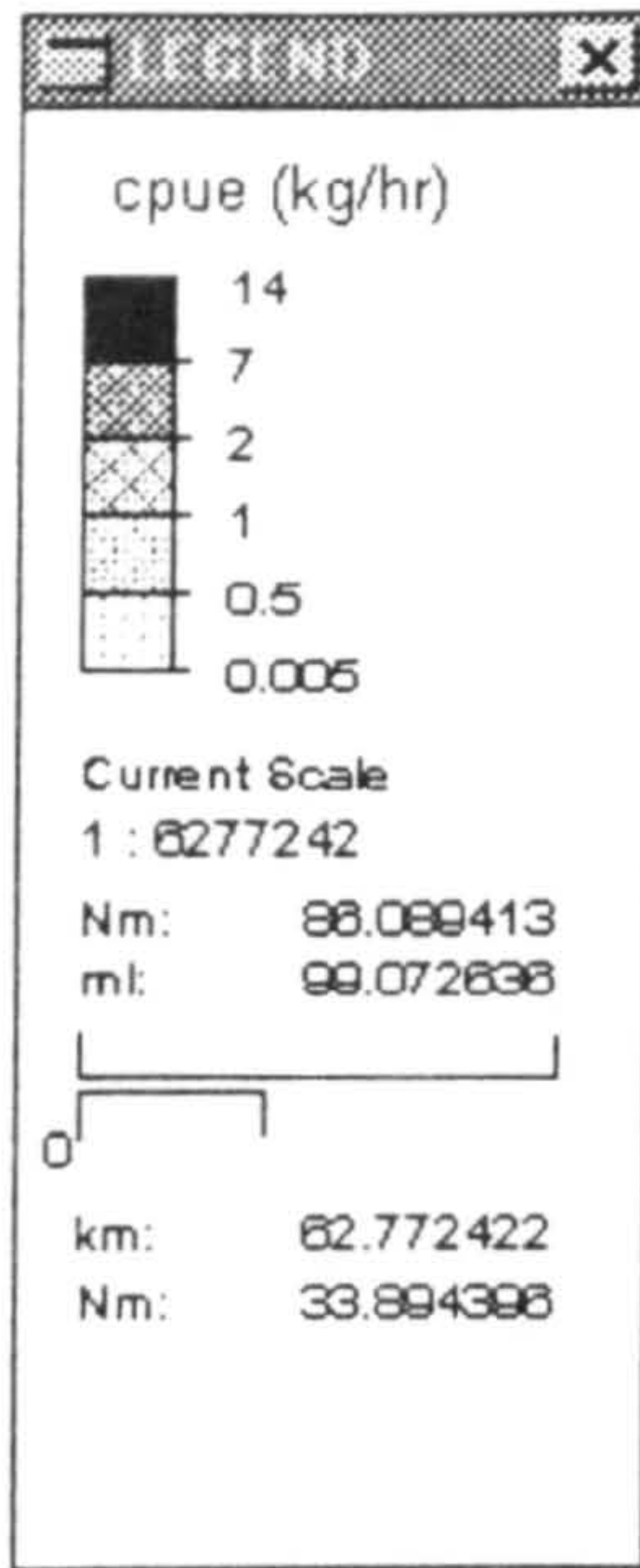


Figure 77. Pelagic trawl catch distribution of *L. stappersii* in June 1995 (a) and November-December 1995 (b) survey. Catch per unit of effort (kg/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statute miles (ml).

a



b

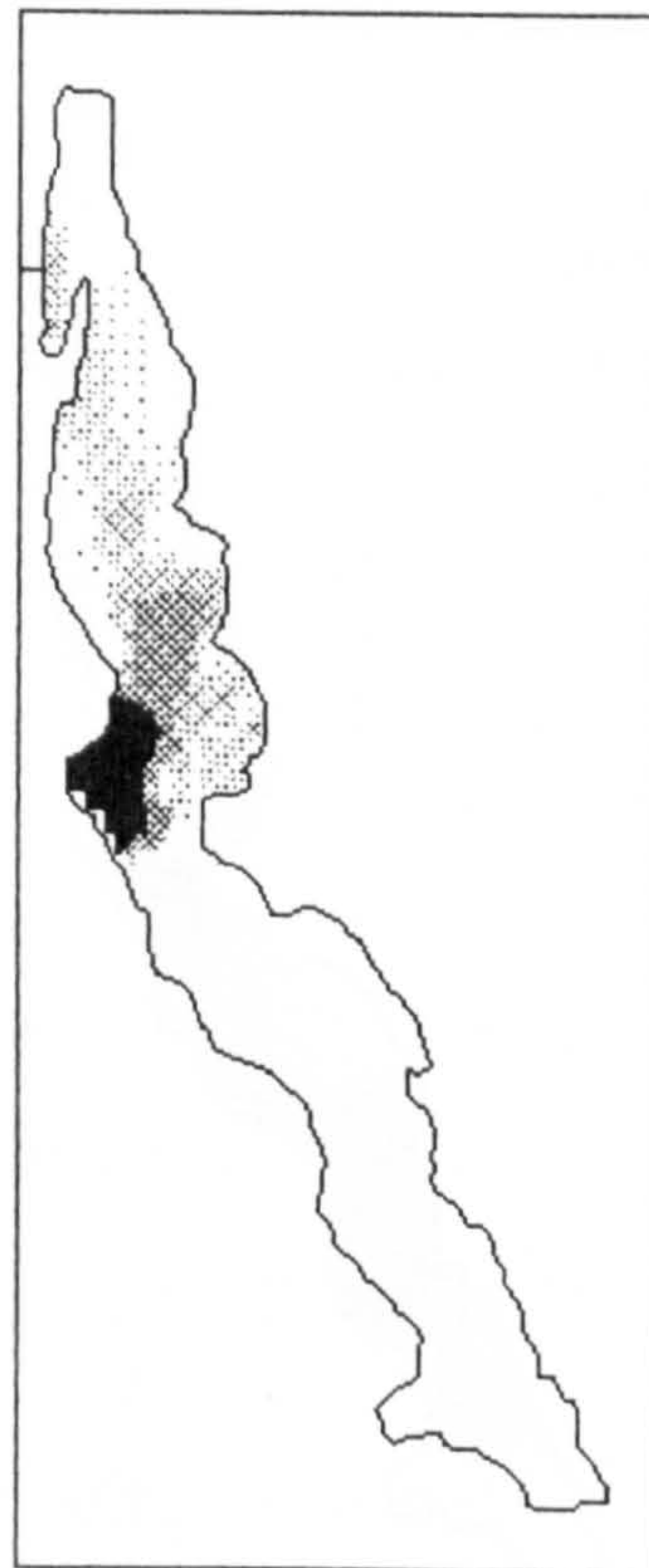
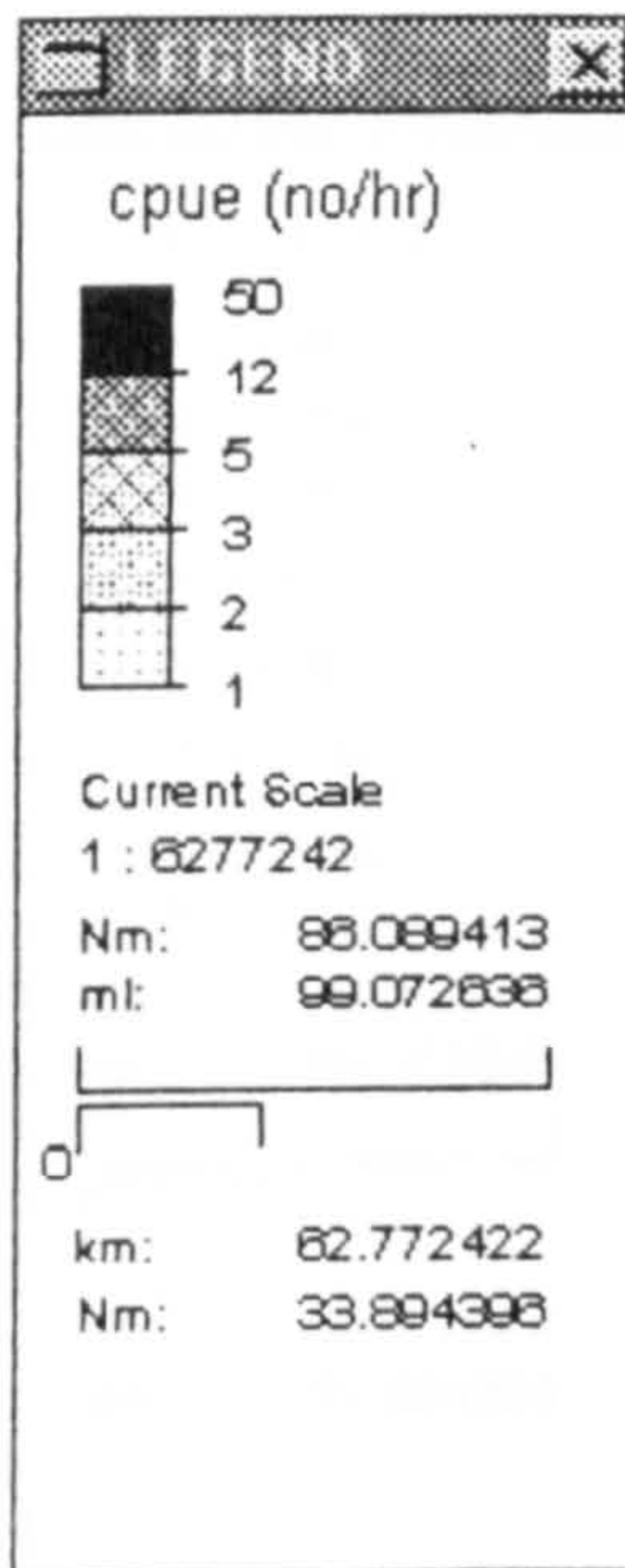


Figure 78. Pelagic trawl catch distribution (a) and number of adults ( $TL > L_m$ ) caught (b) of *L. stappersii* in April 1996 survey. Catch per unit of effort (kg/hr) and number of adult fish (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. 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 statute miles (ml).

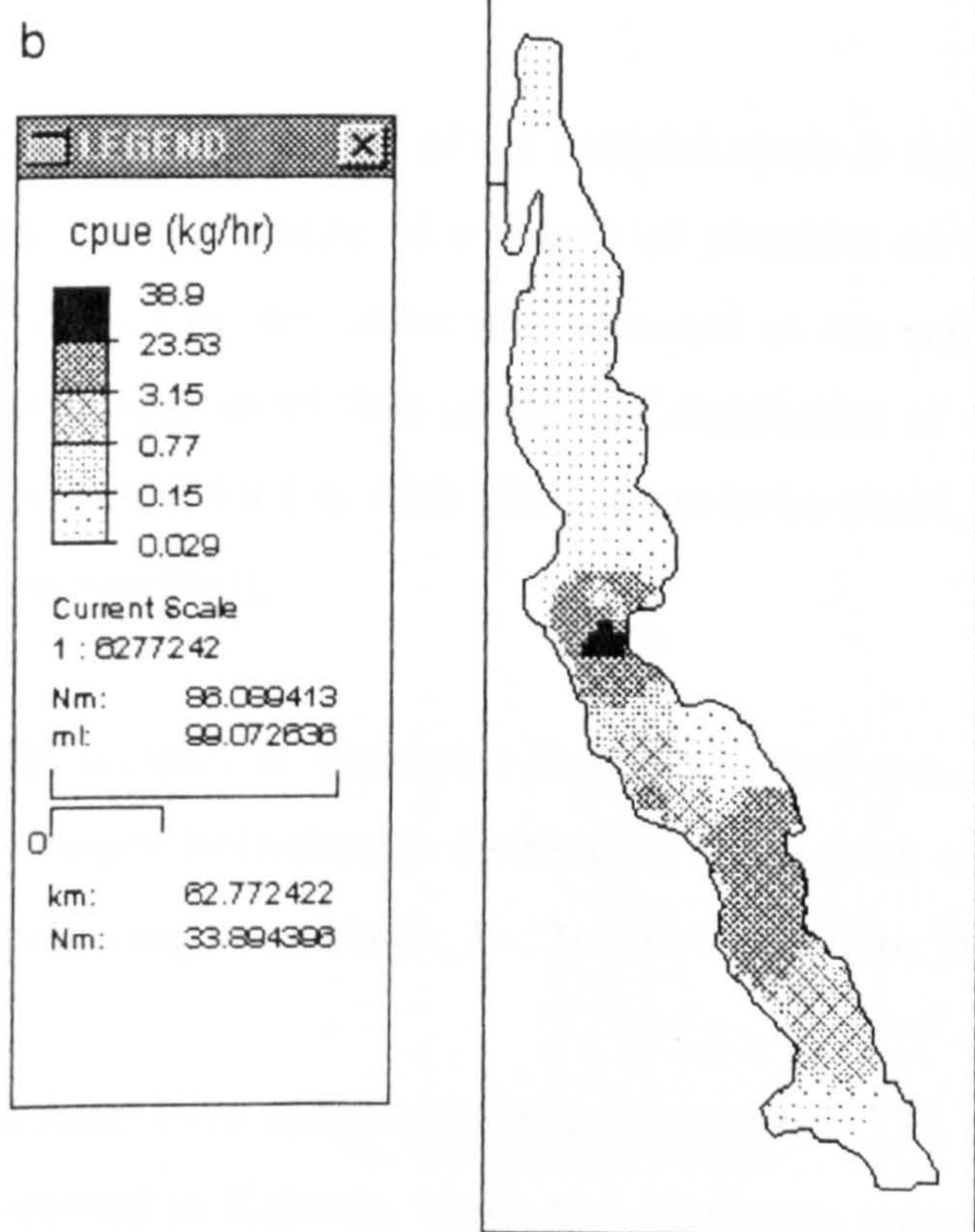
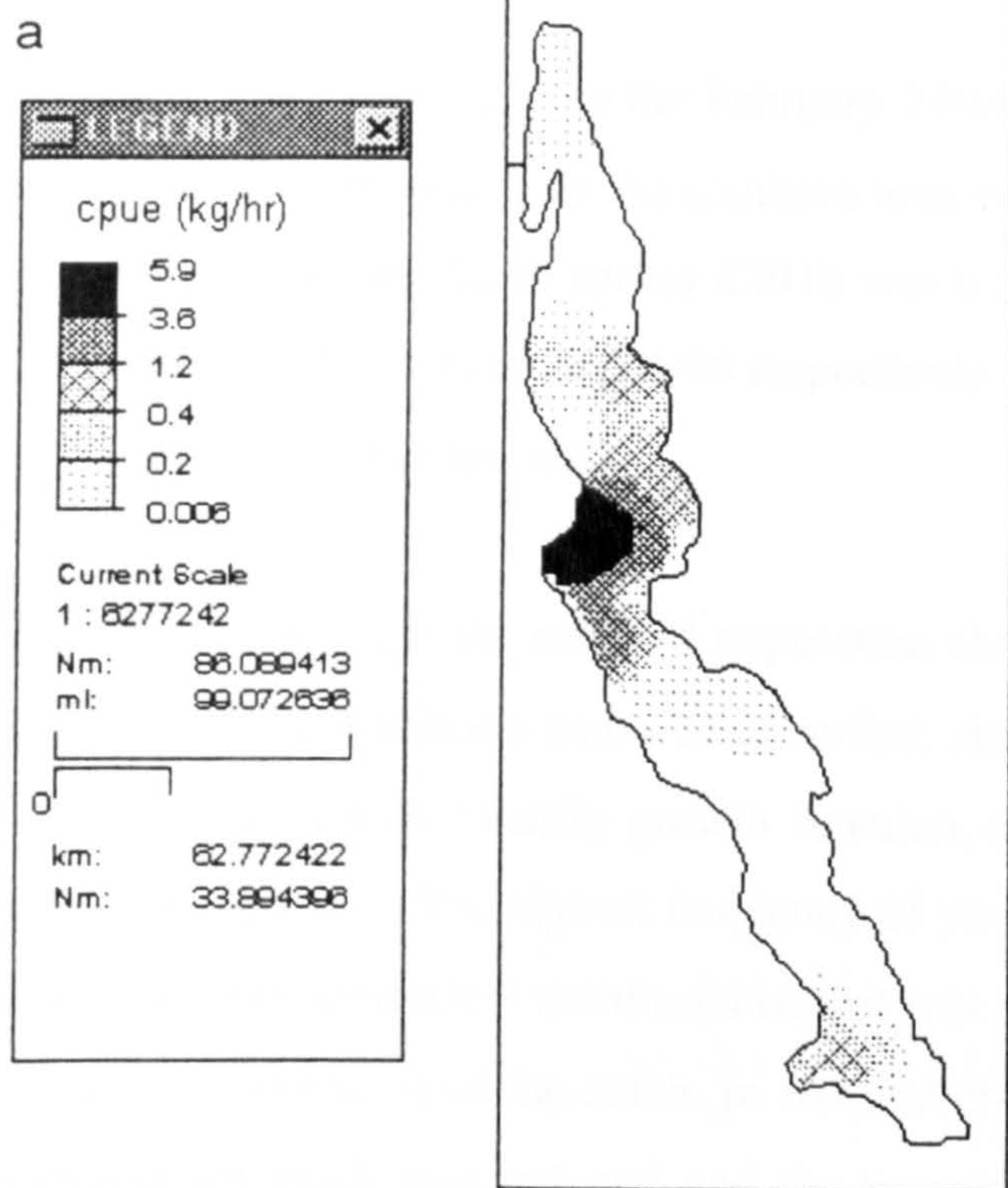


Figure 79. Pelagic trawl catch distribution of *L. stappersii* in November-December 1997 (a) and February 1998 (b) survey. Catch per unit of effort (kg/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. 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 statute miles (ml).

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<sup>-1</sup> 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. 80), where 3 to 4 cohorts could be identified. According to the growth pattern from the estimated von Bertalanffy growth function, 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. 81) 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. 82).

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. 83). 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. 84).

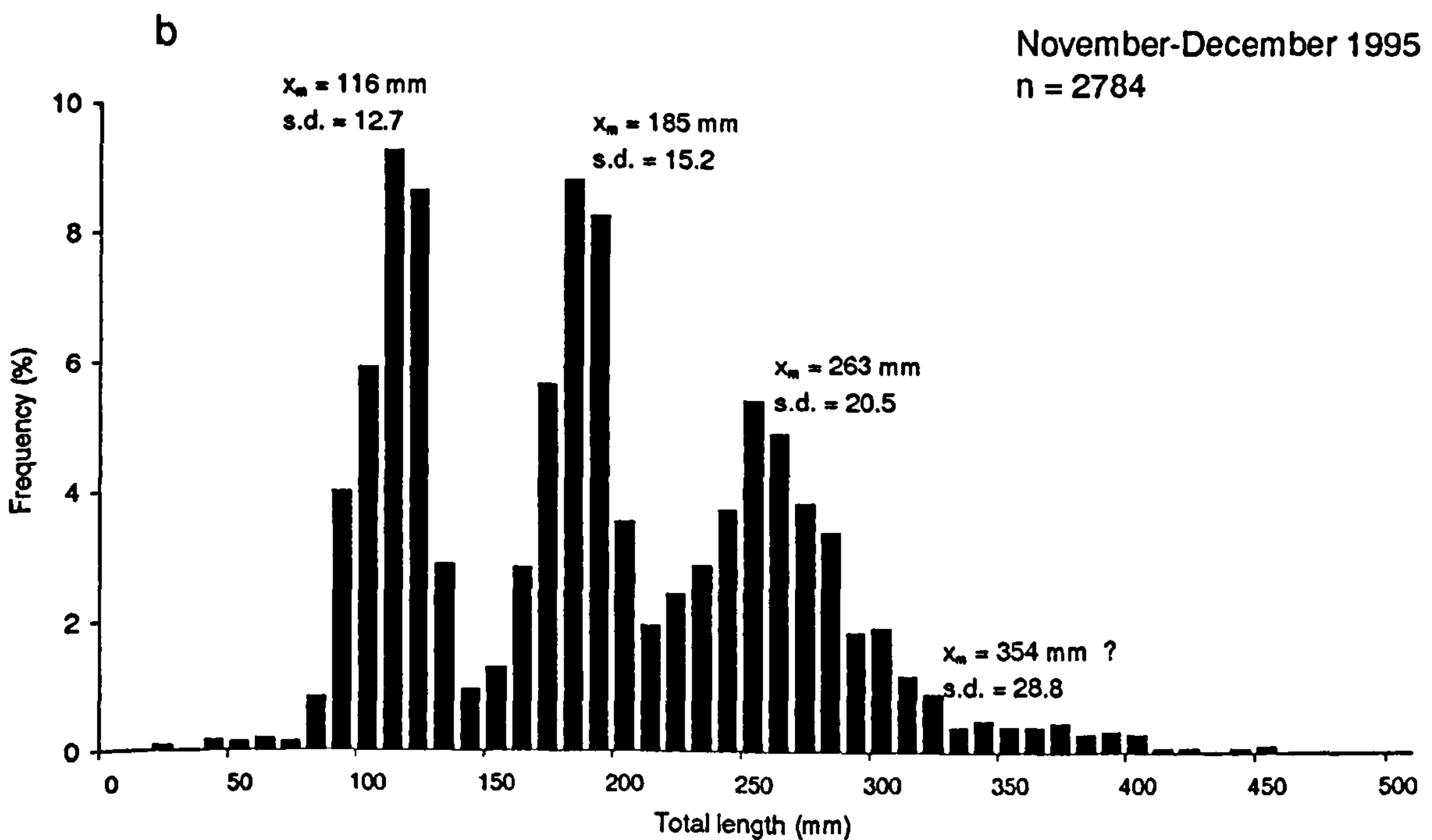
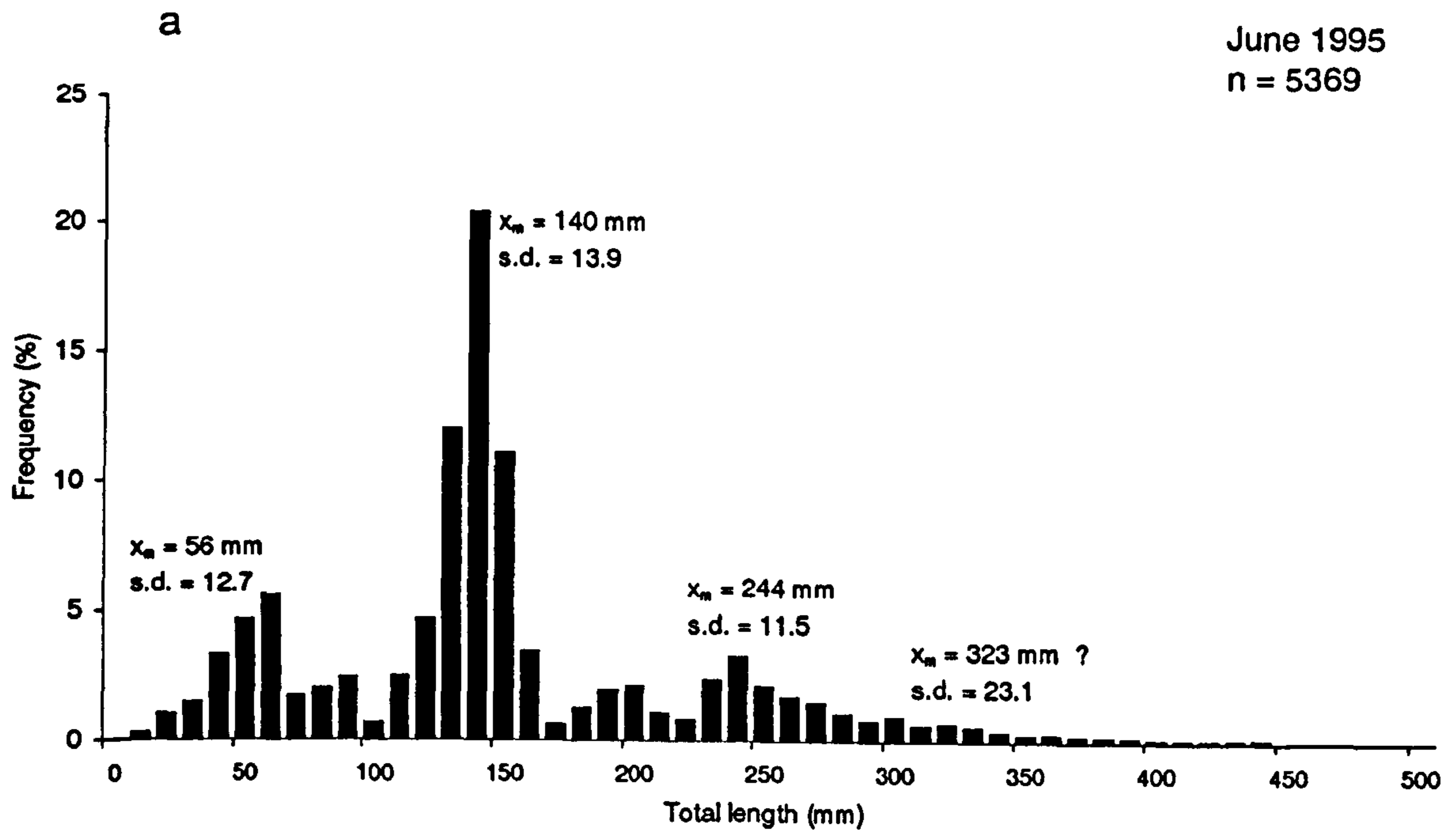


Figure 80. Size distribution of *L. stappersii* for the whole lake from mid-water trawl surveys. **a**: June 1995 survey; **b**: November-December 1995 survey. N is the sample size,  $x_m$  and s.d. are the mean length and standard deviation of identified cohorts after Bhattacharya's decomposition of length distribution. Question mark indicates uncertain cohort separation.

April 1996  
n = 1242

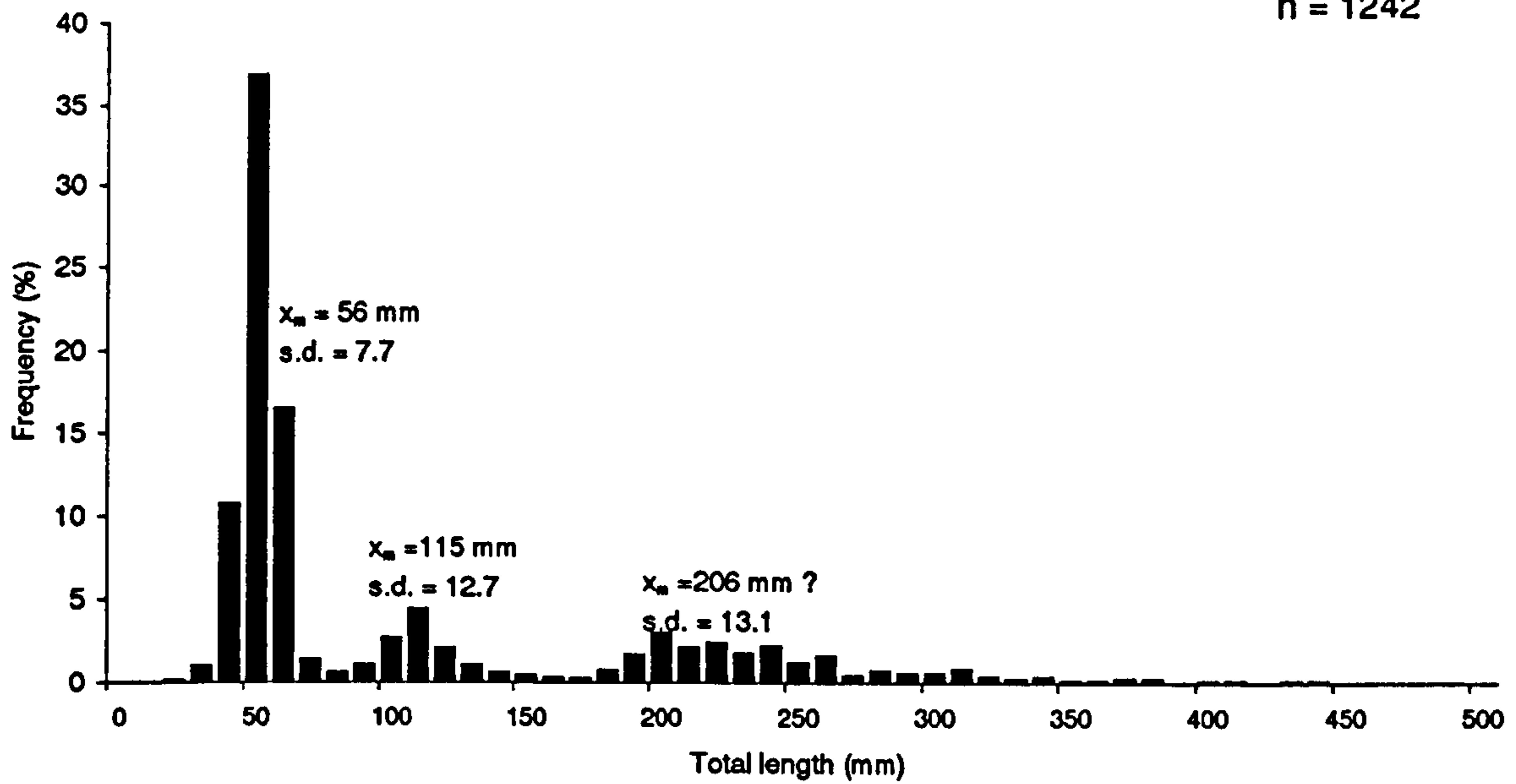


Figure 81. Size distribution of *L. stappersii* for the whole lake from April 1996 mid-water trawl survey. N is the sample size,  $x_m$  and s.d. are the mean length and standard deviation of identified cohort after Bhattacharya's decomposition of length distribution. Question mark indicates uncertain cohort separation.

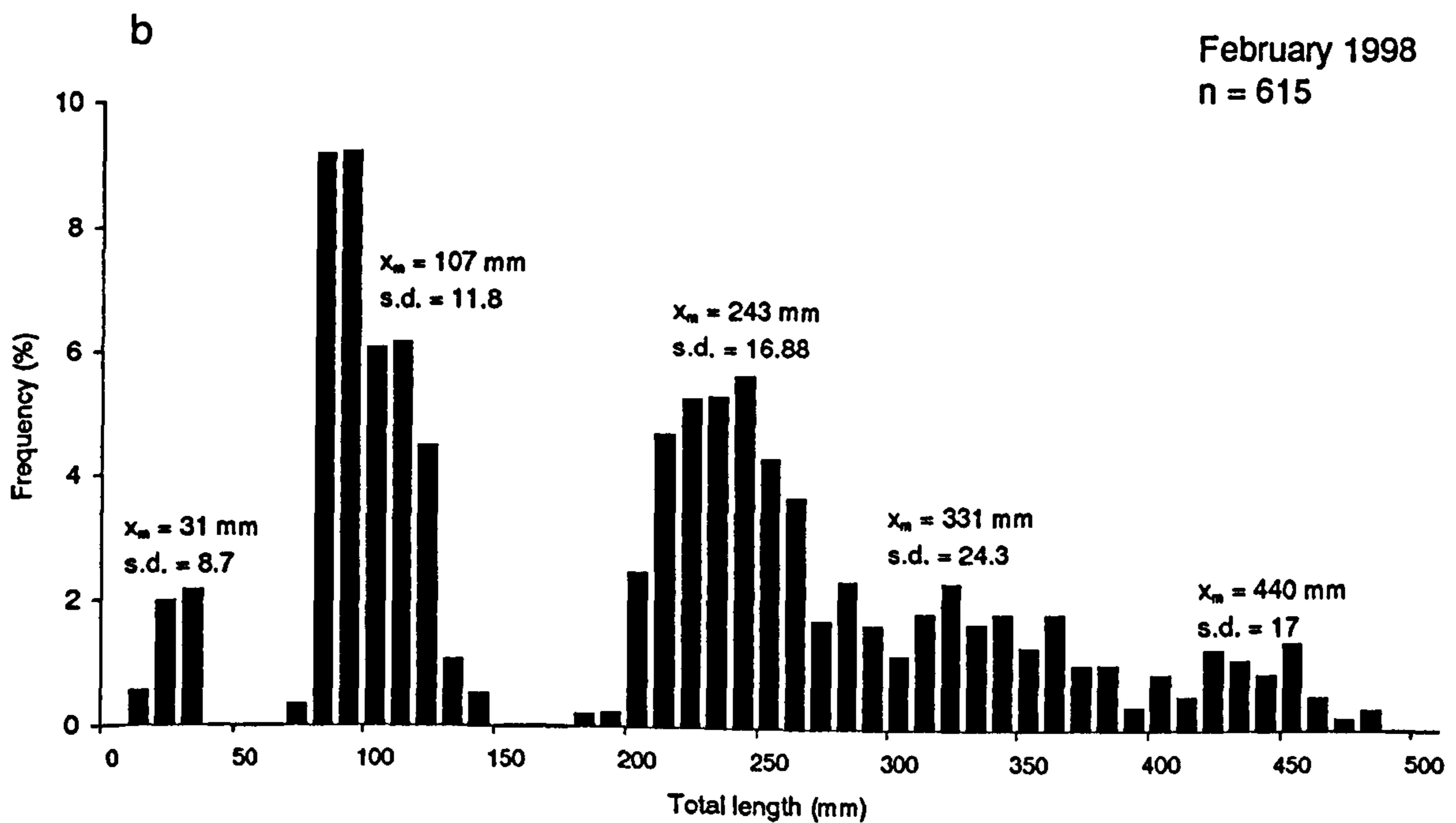
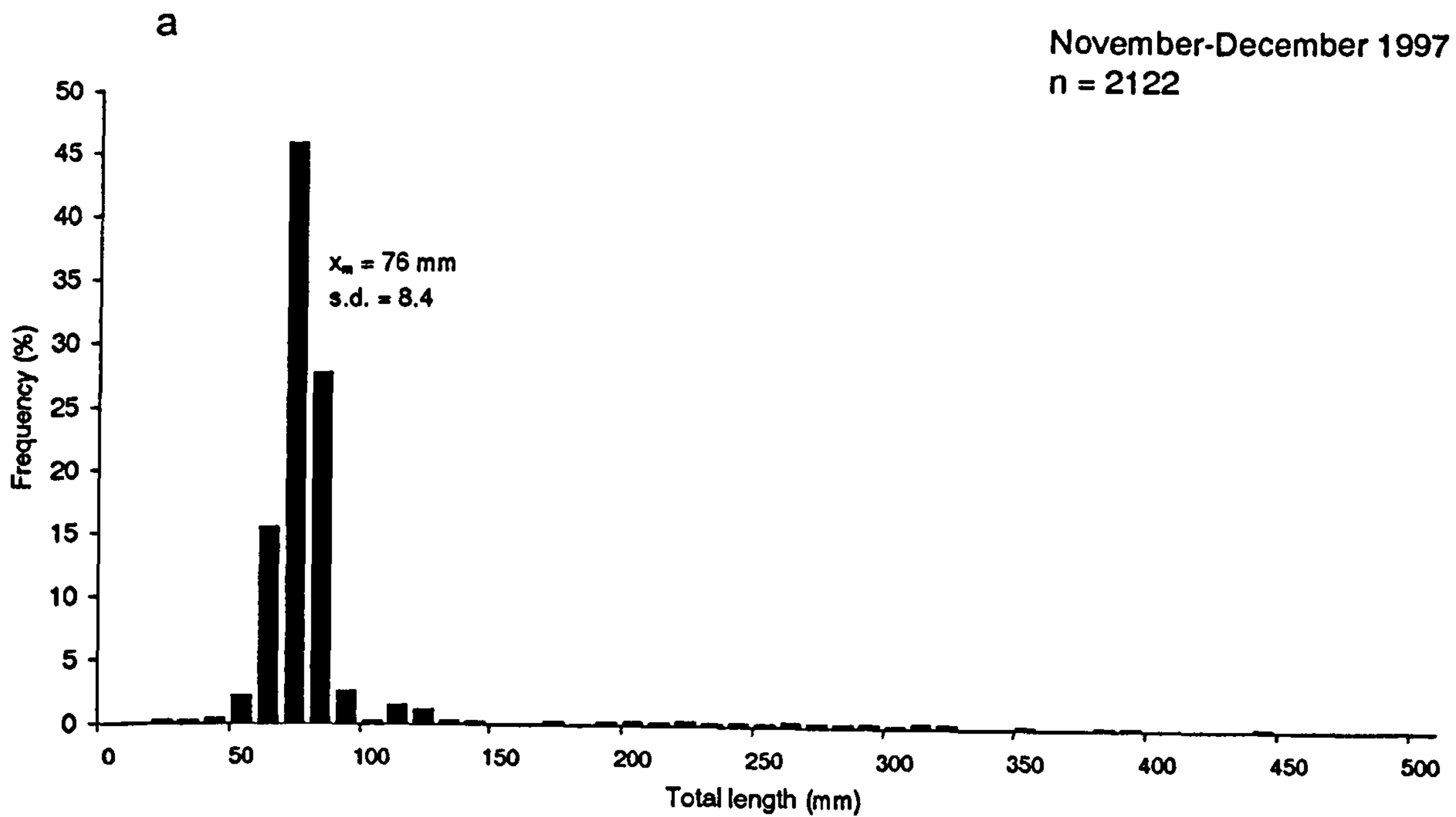


Figure 82. Size distribution of *L. stappersii* for the whole lake from mid-water trawl surveys. a: November-December 1997 survey; b: February 1998 survey. N is the sample size,  $x_m$  and s.d. are the mean length and standard deviation of identified cohorts after Bhattacharya's decomposition of length distribution.



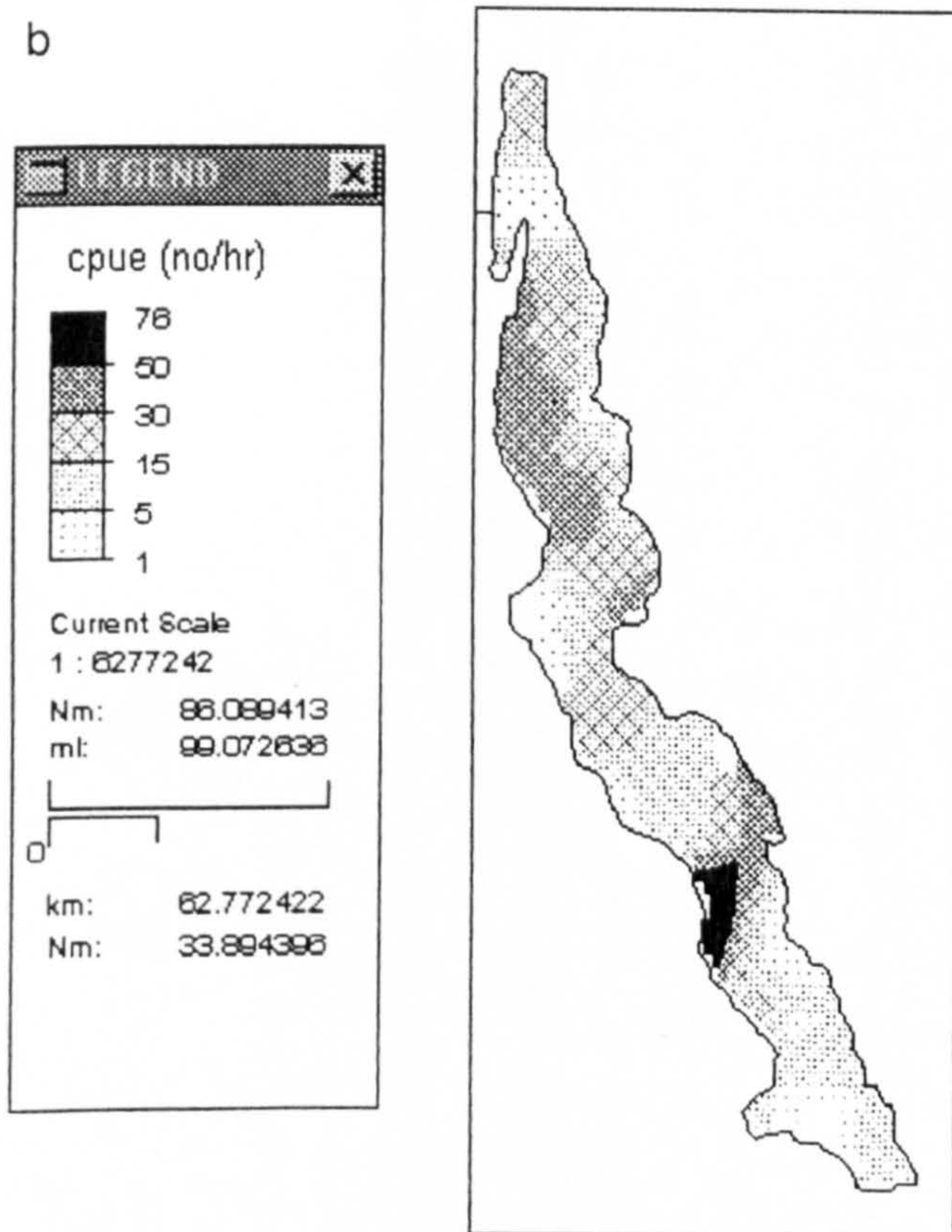
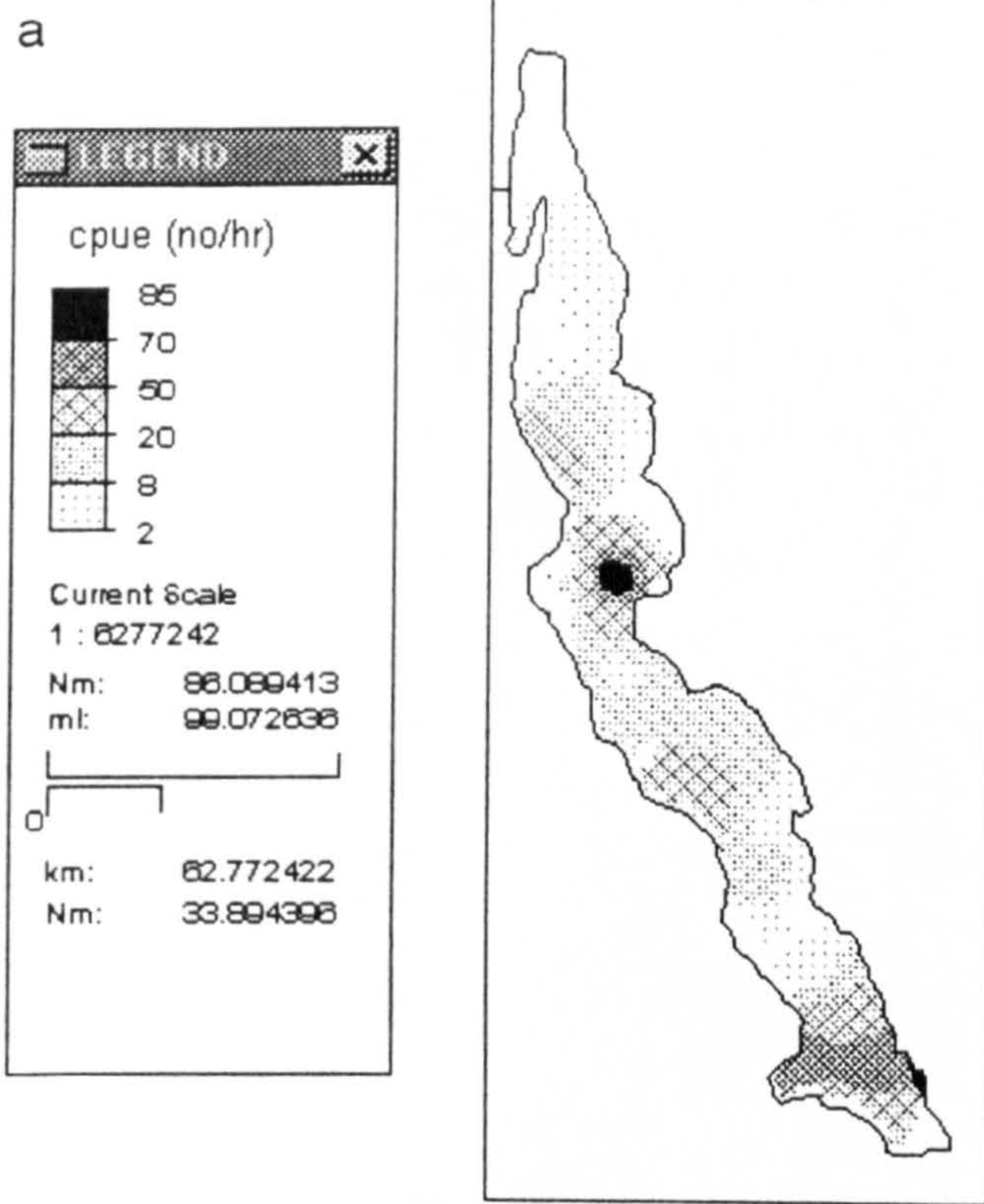


Figure 83. Pelagic trawl catch distribution of adult *L. stappersii* ( $TL > L_m$ ) in June 1995 (a) and November-December 1995 (b) survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale 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).

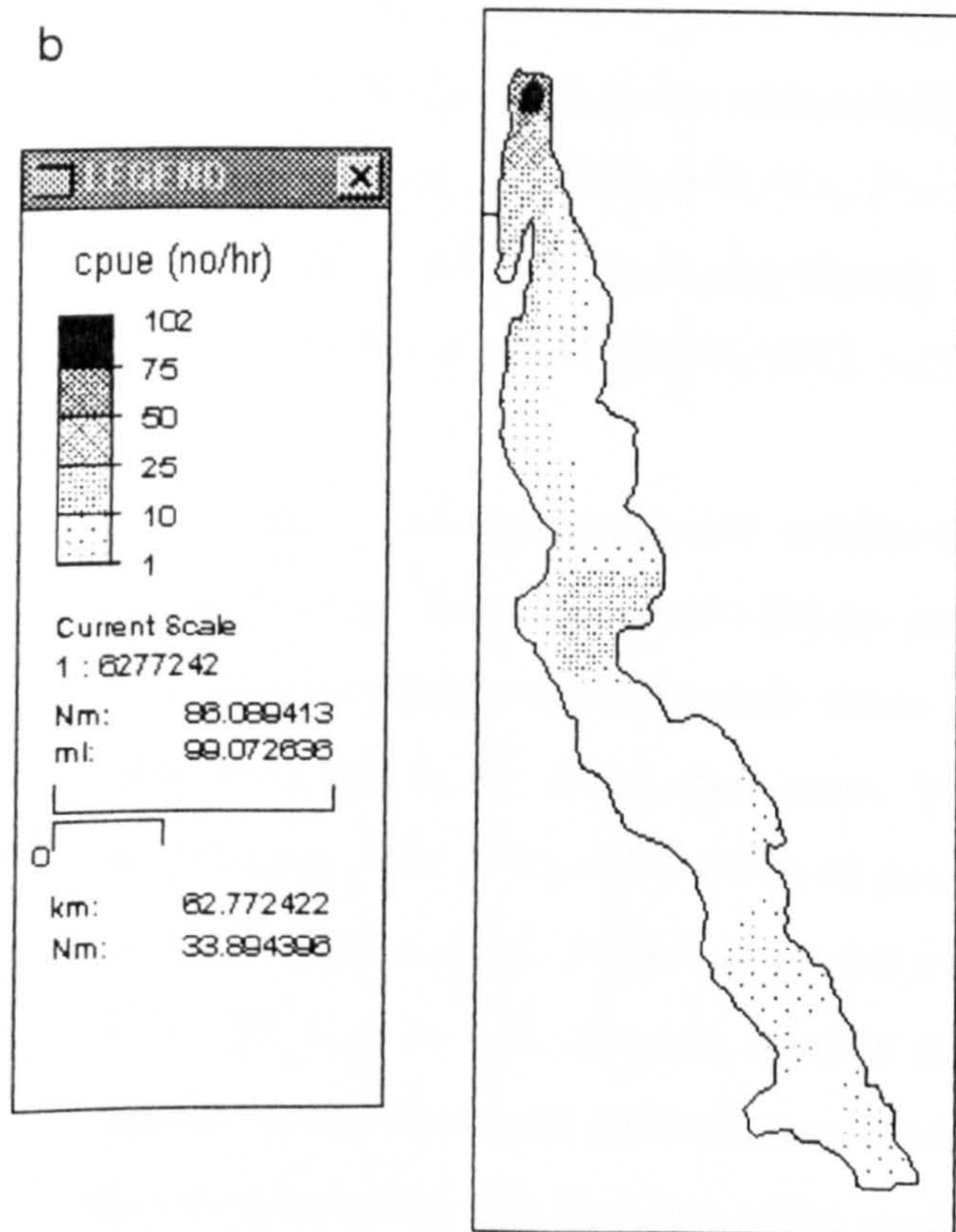
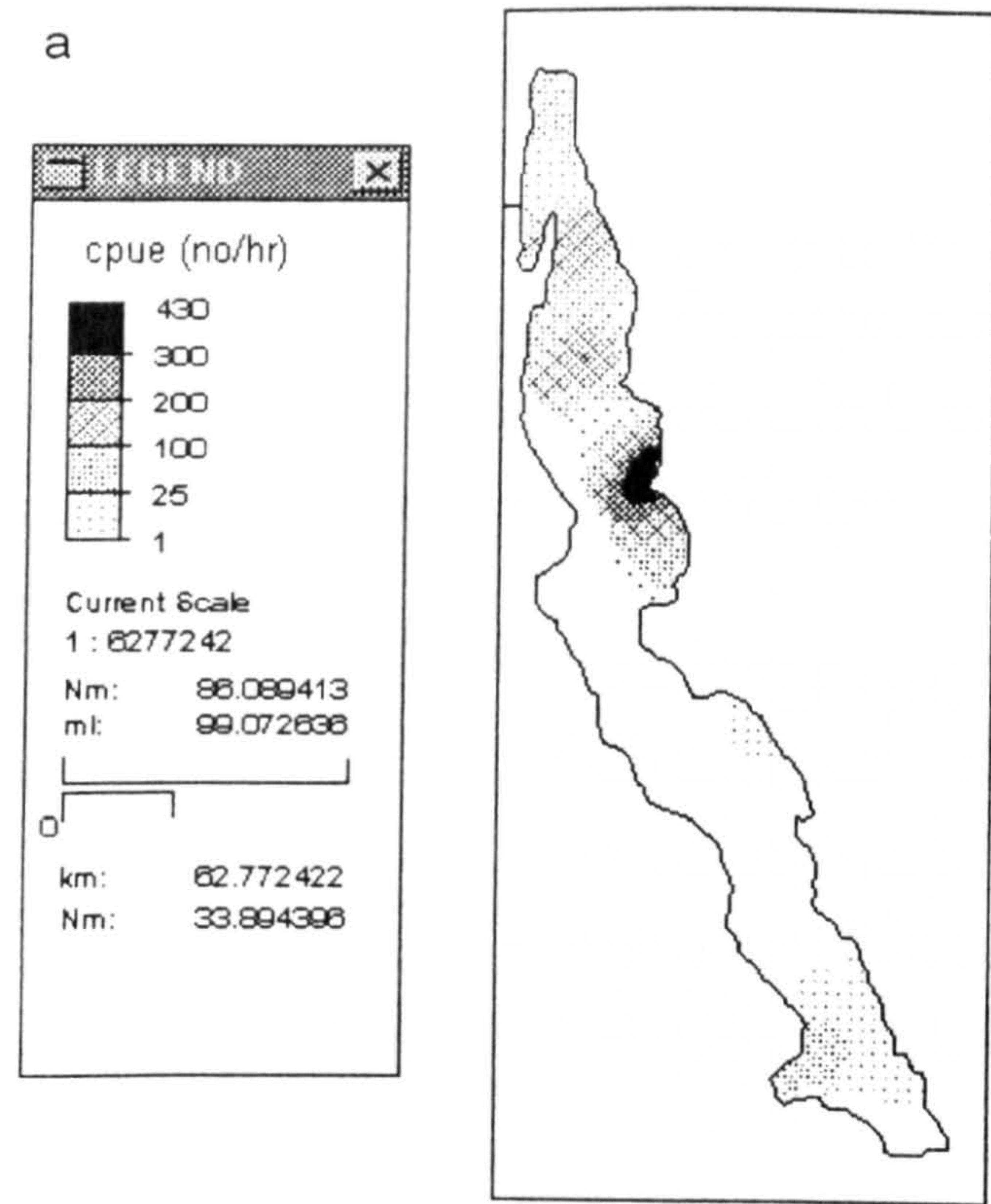


Figure 84. Pelagic trawl catch distribution of young *L. stappersii* (TL < 100 mm) in June 1995 (a) and November-December (b) 1995 survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale 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 statute miles (mi).

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. 78b). The juveniles, which at the time dominated the sampled stock, occurred in the northern area of the Kigoma sub-basin (Fig. 85).

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. 86). 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. 87).

*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 (Kruskall-Wallis 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 a 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 88, 89, 90 and 91).

*Lates stappersii* larvae were found in 65 of the 105 Gulf-net tows. The number of specimens per 100 m<sup>3</sup> of water varied from 0 to 96. The frequency distribution of the log-transformed number per sample was positively skewed because of the relative

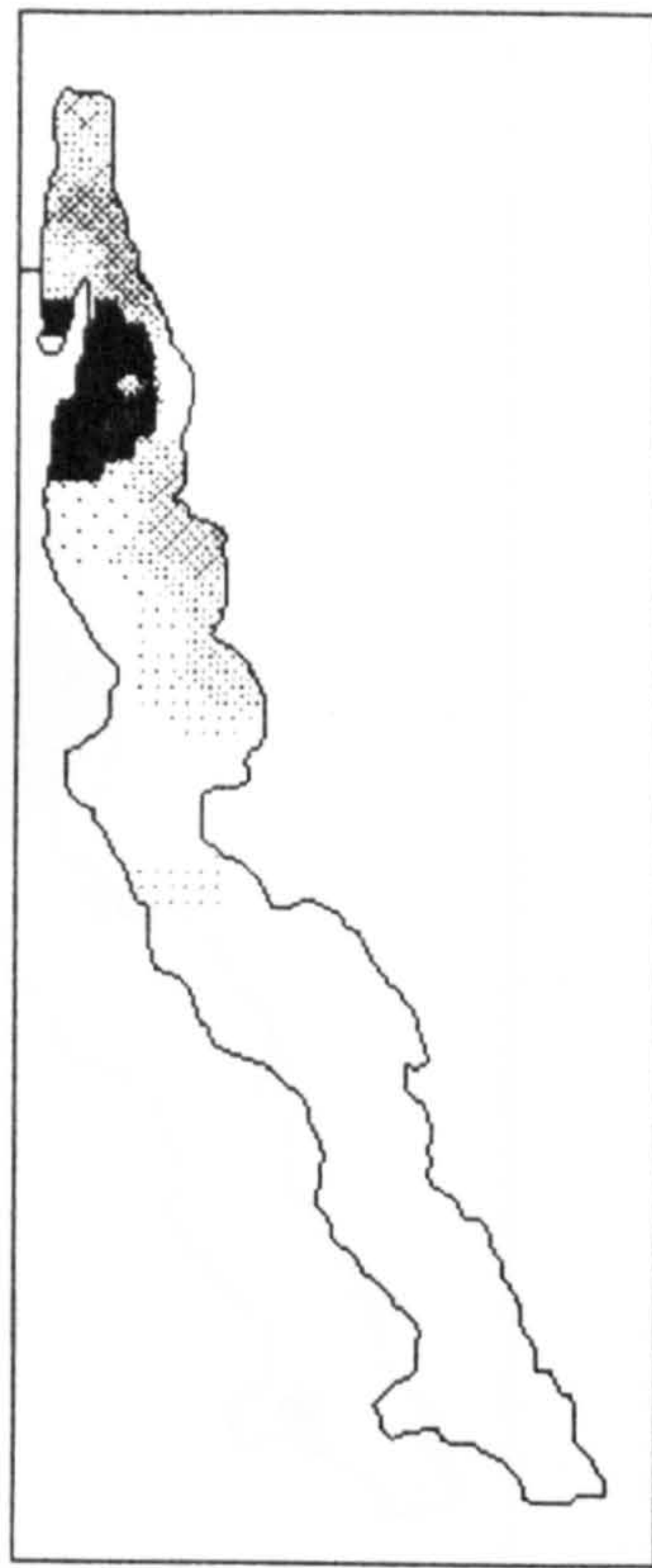
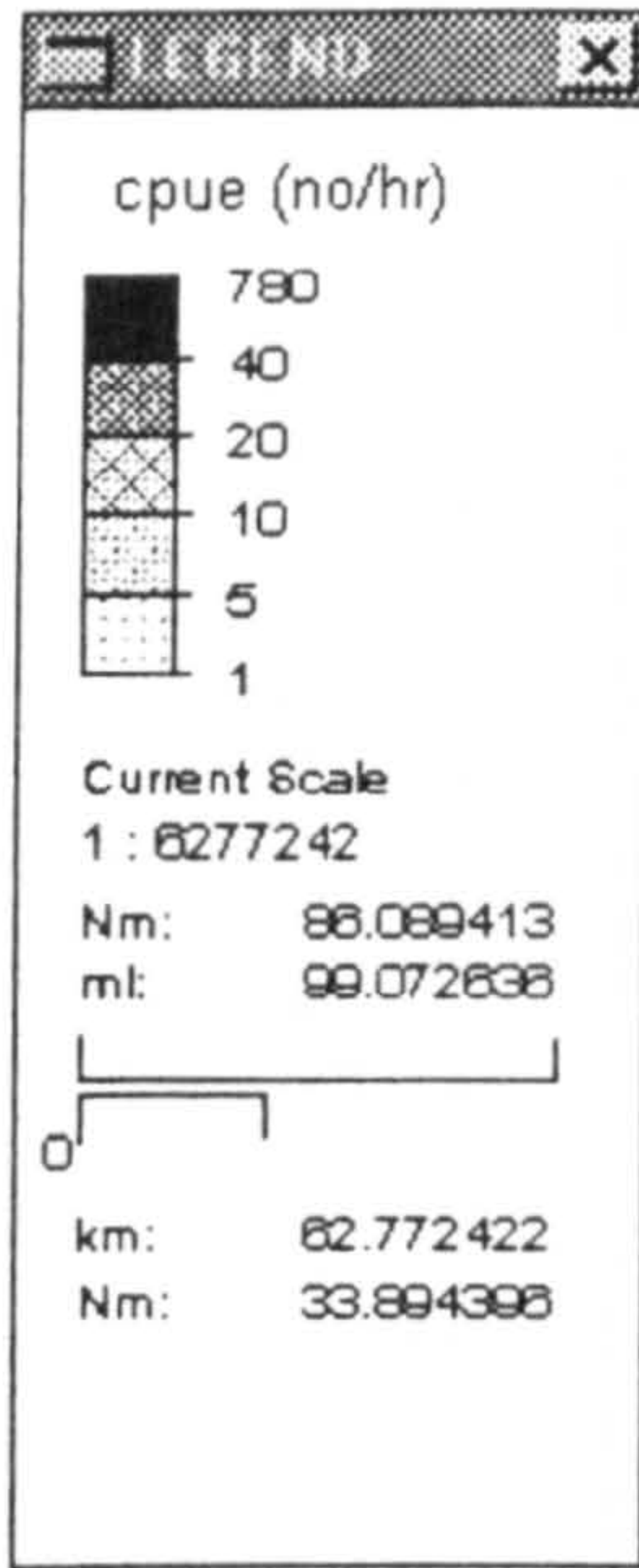


Figure 85. Pelagic trawl catch distribution of young *L. stappersii* (TL < 100 mm) in April 1996 survey. Catch per unit of effort (no/hr) is grouped in five levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale has unequal intervals**. Blank areas 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 (mi).

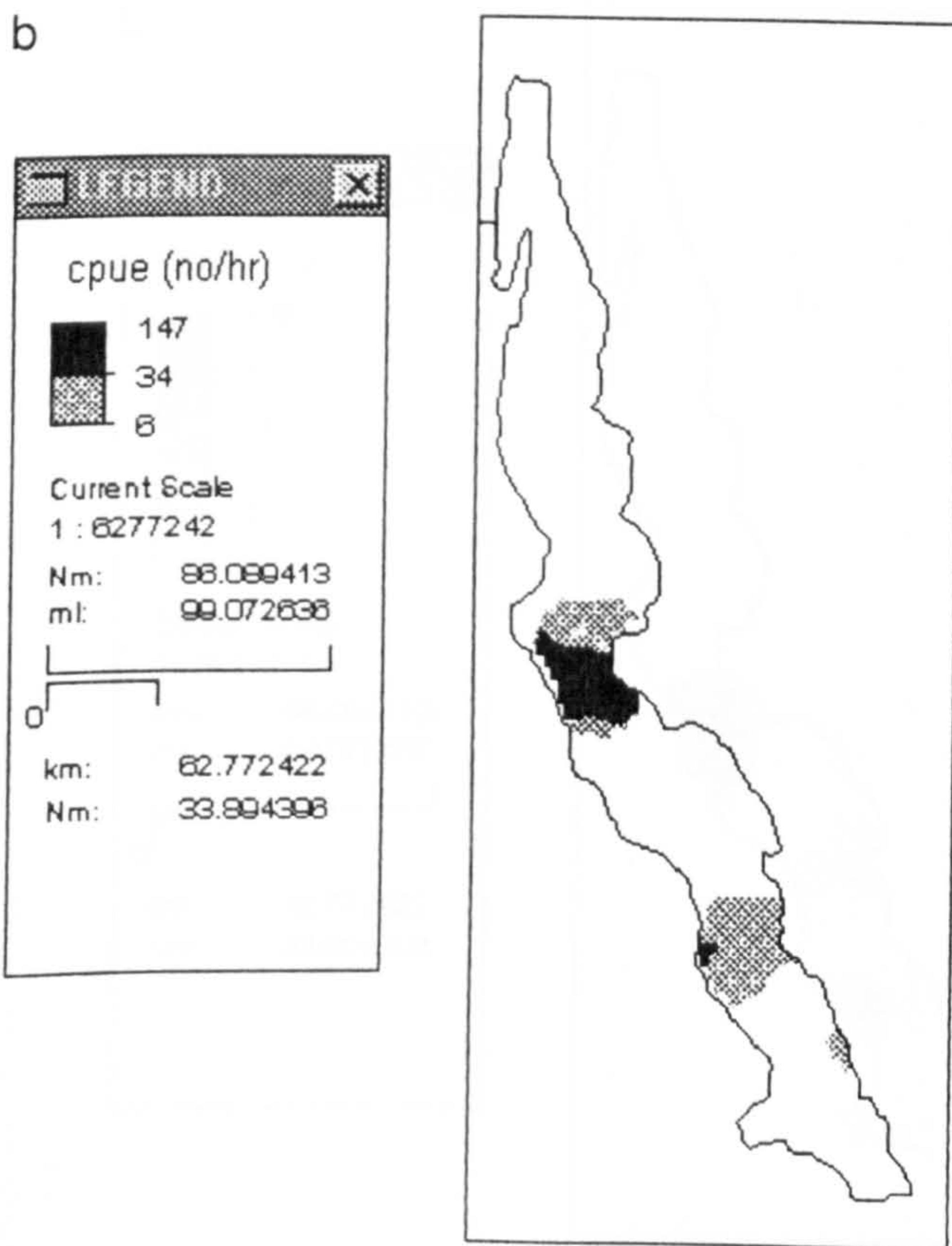
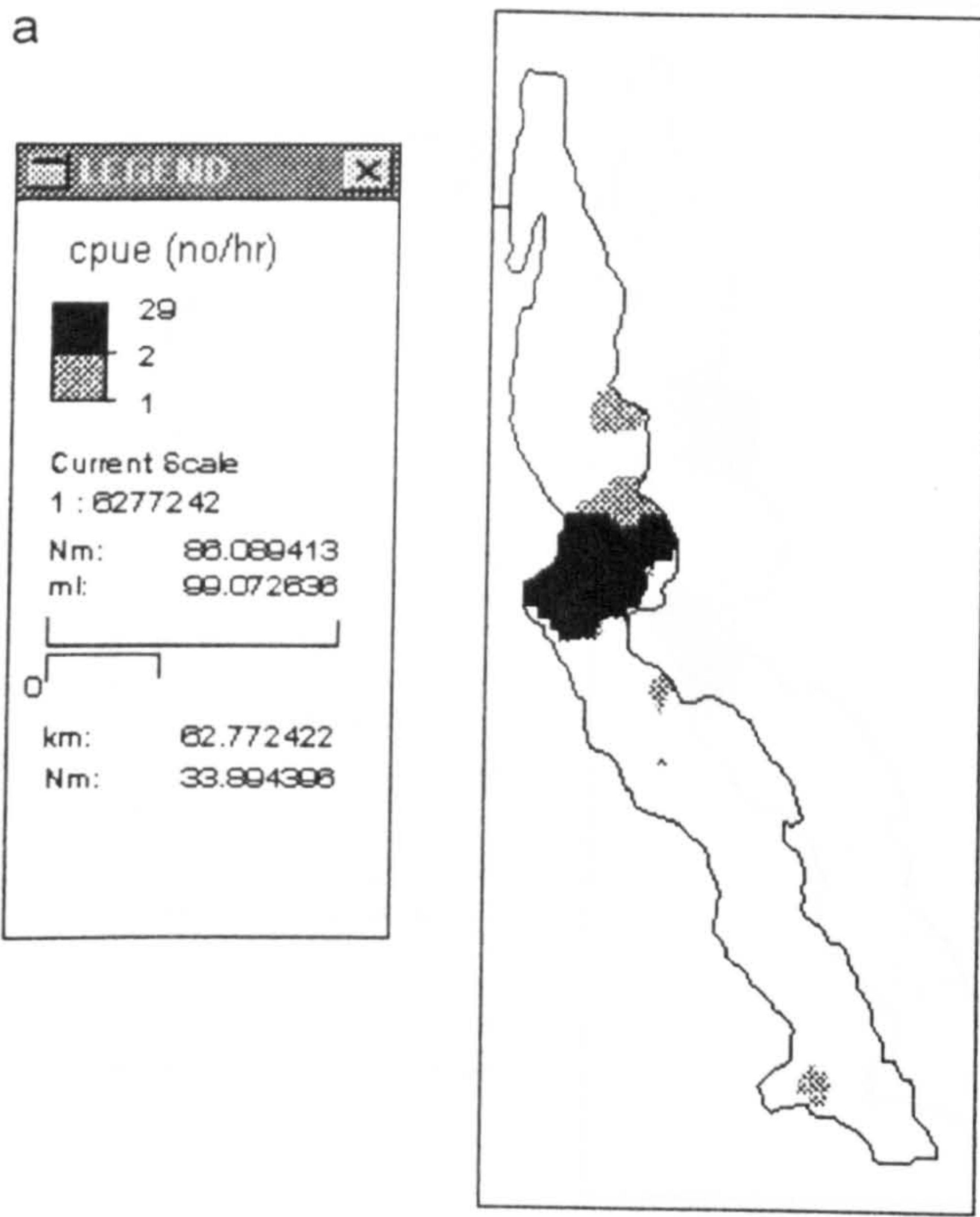
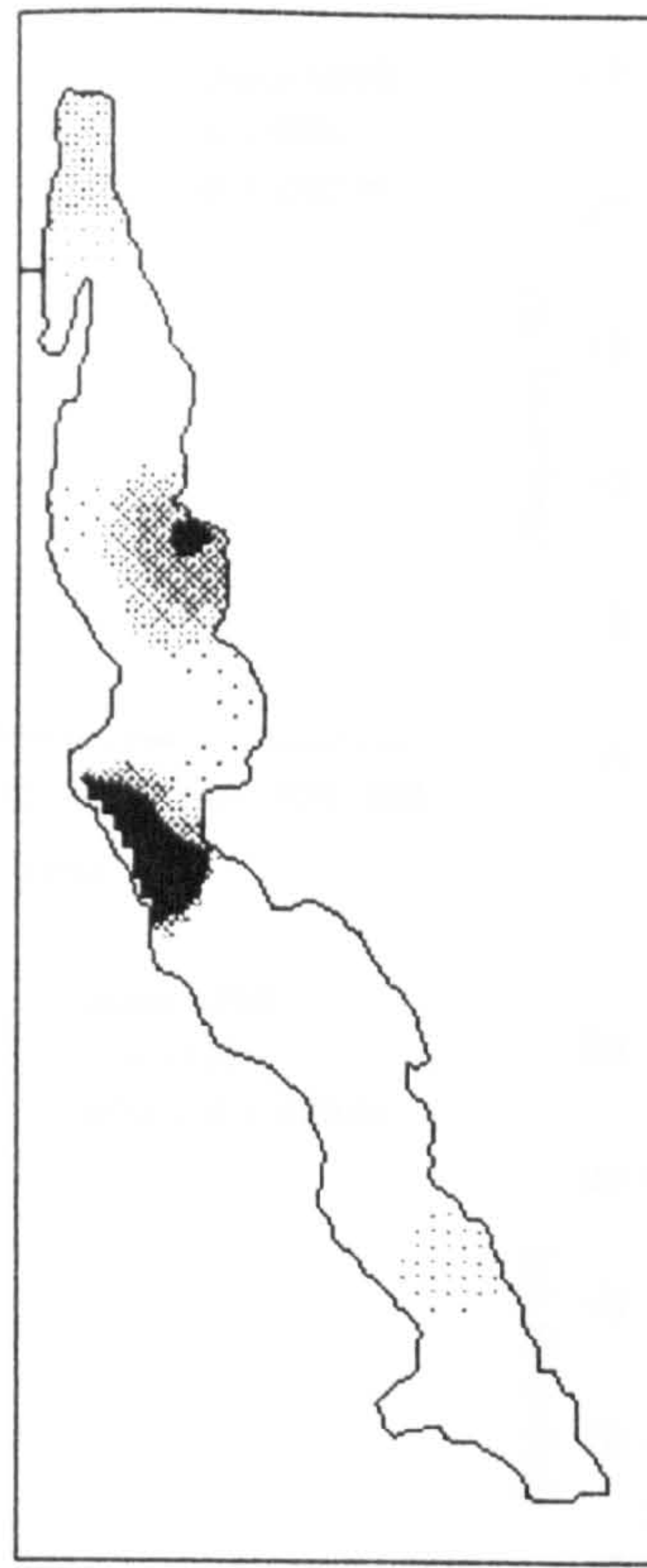
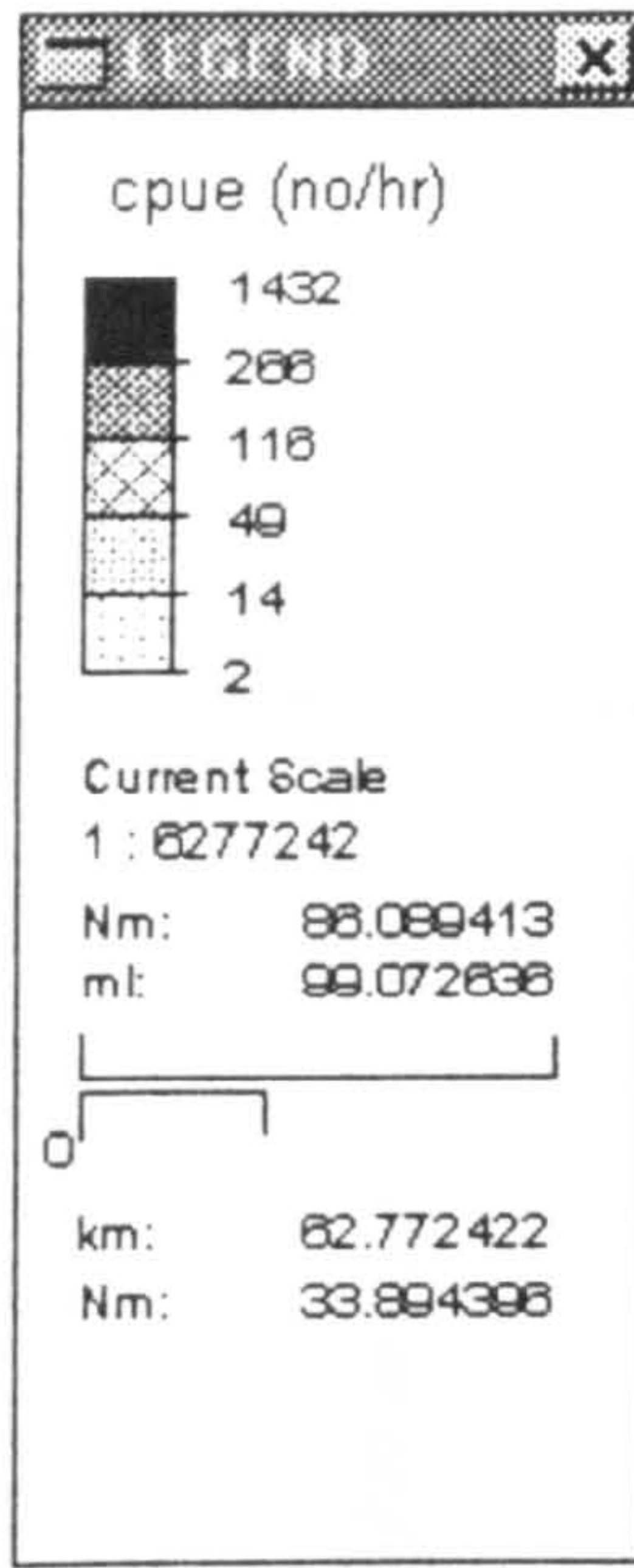


Figure 86. Pelagic trawl catch distribution of adult *L. stappersii* ( $TL > L_m$ ) in November-December 1997 (a) and February 1998 (b) survey. Catch per unit of effort (no/hr) are grouped in two levels shown in the legend window starting from the lowest non zero catch recorded. Note that **pattern scale 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 statute miles (ml).

a



b

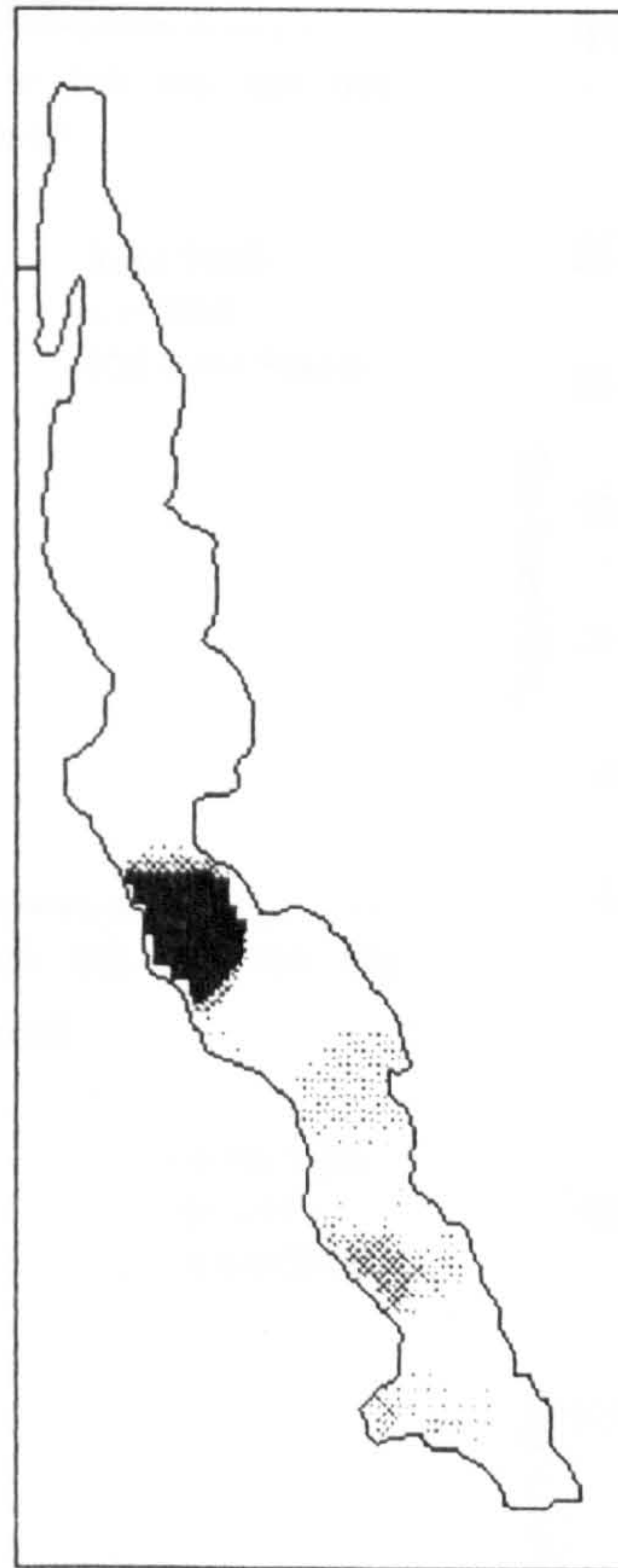
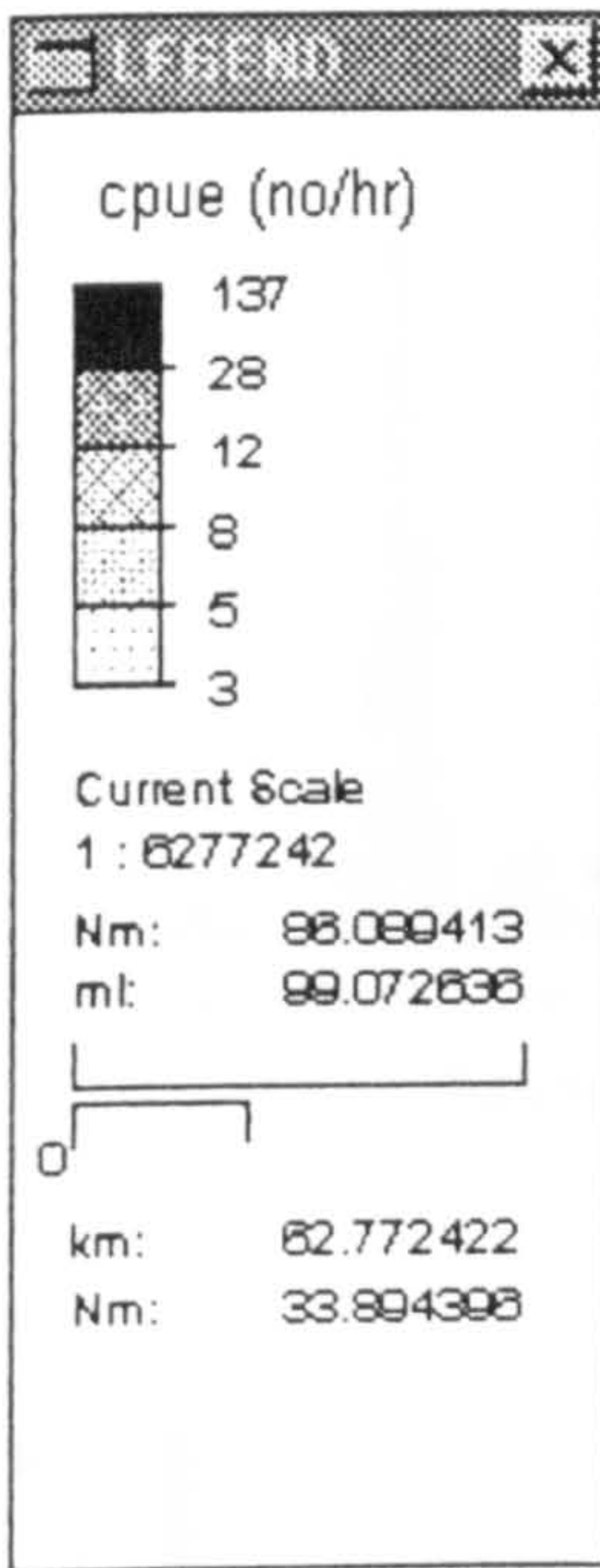


Figure 87. Pelagic trawl catch distribution of young *L. stappersii* (TL < 100 mm) in November-December 1997 (a) and February (b) 1998 survey. Catch per unit of effort (no/hr) are grouped in five levels shown in the legend window starting from the lowest catch recorded. Note that **pattern scale has unequal intervals**. Also displayed in the legend window is the current scale of the map in nautical miles (Nm), kilometers (km) and statute miles (mi).

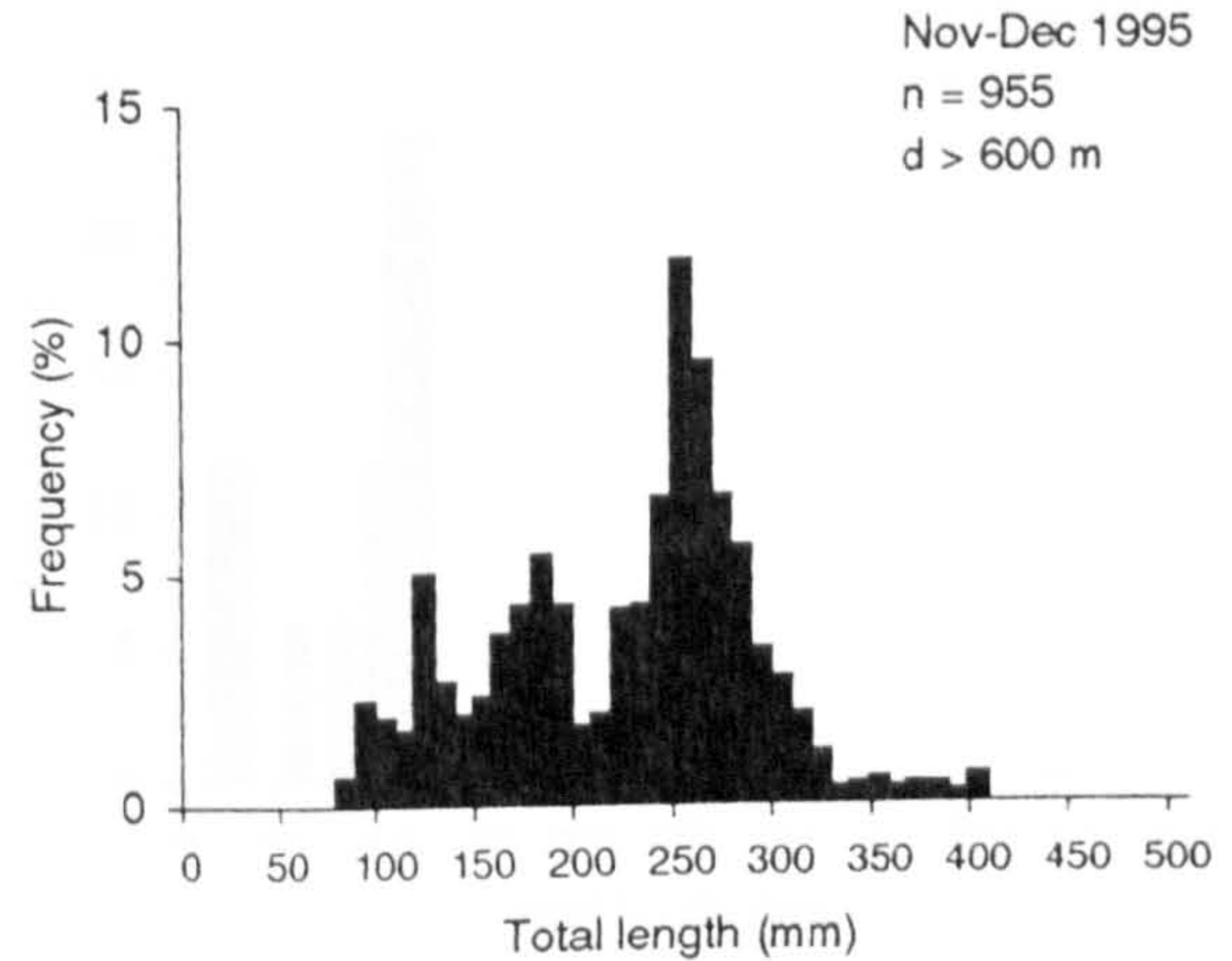
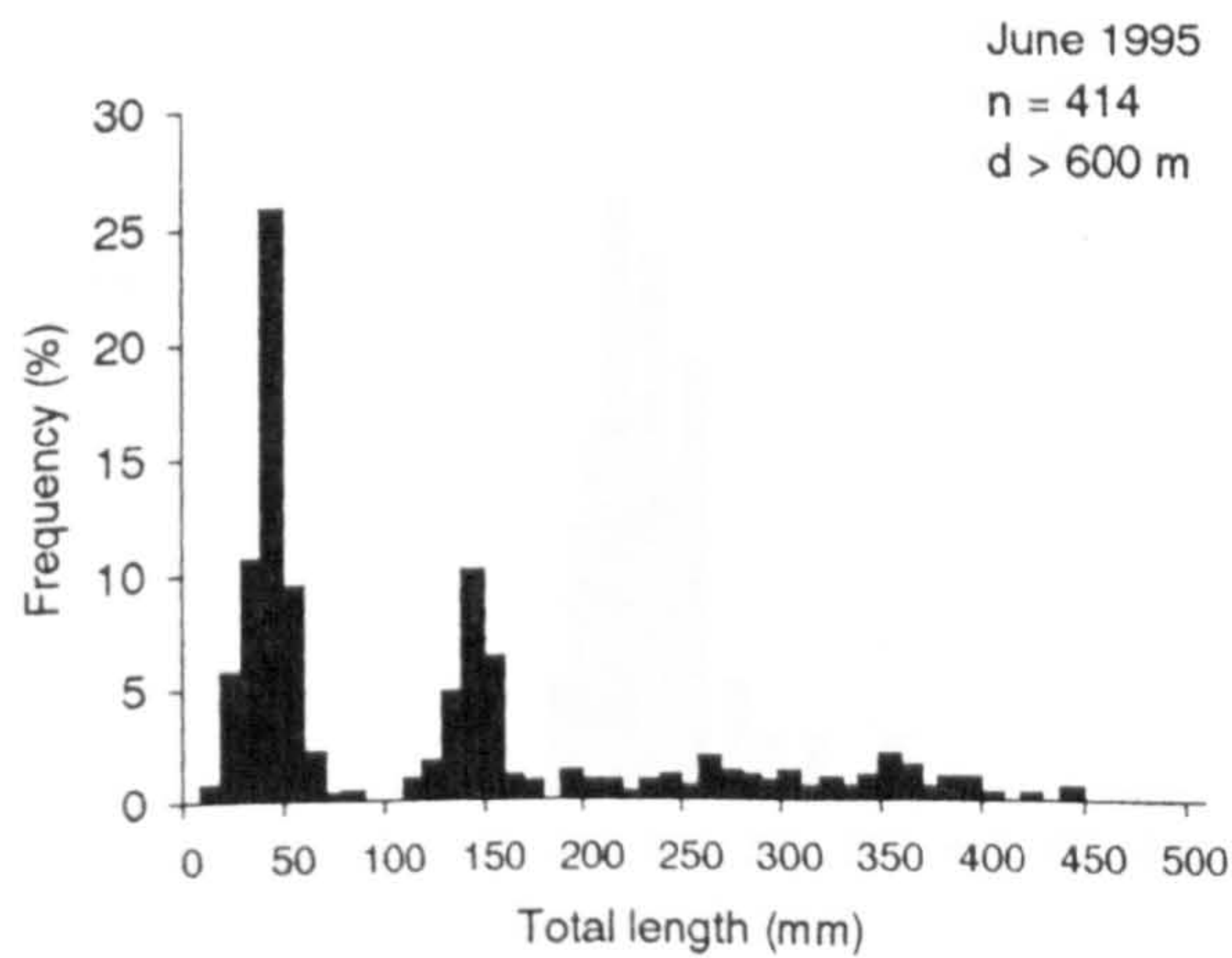
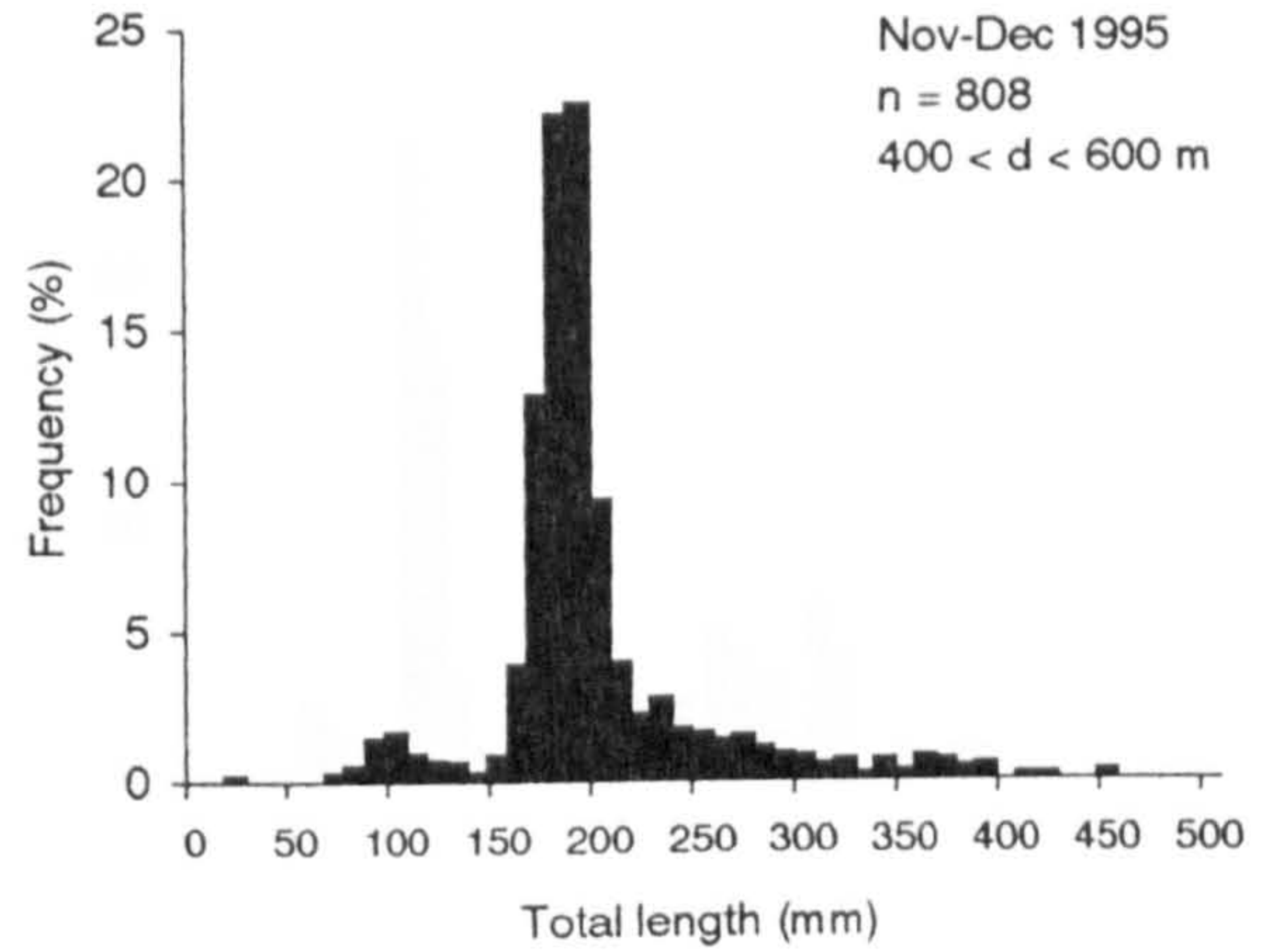
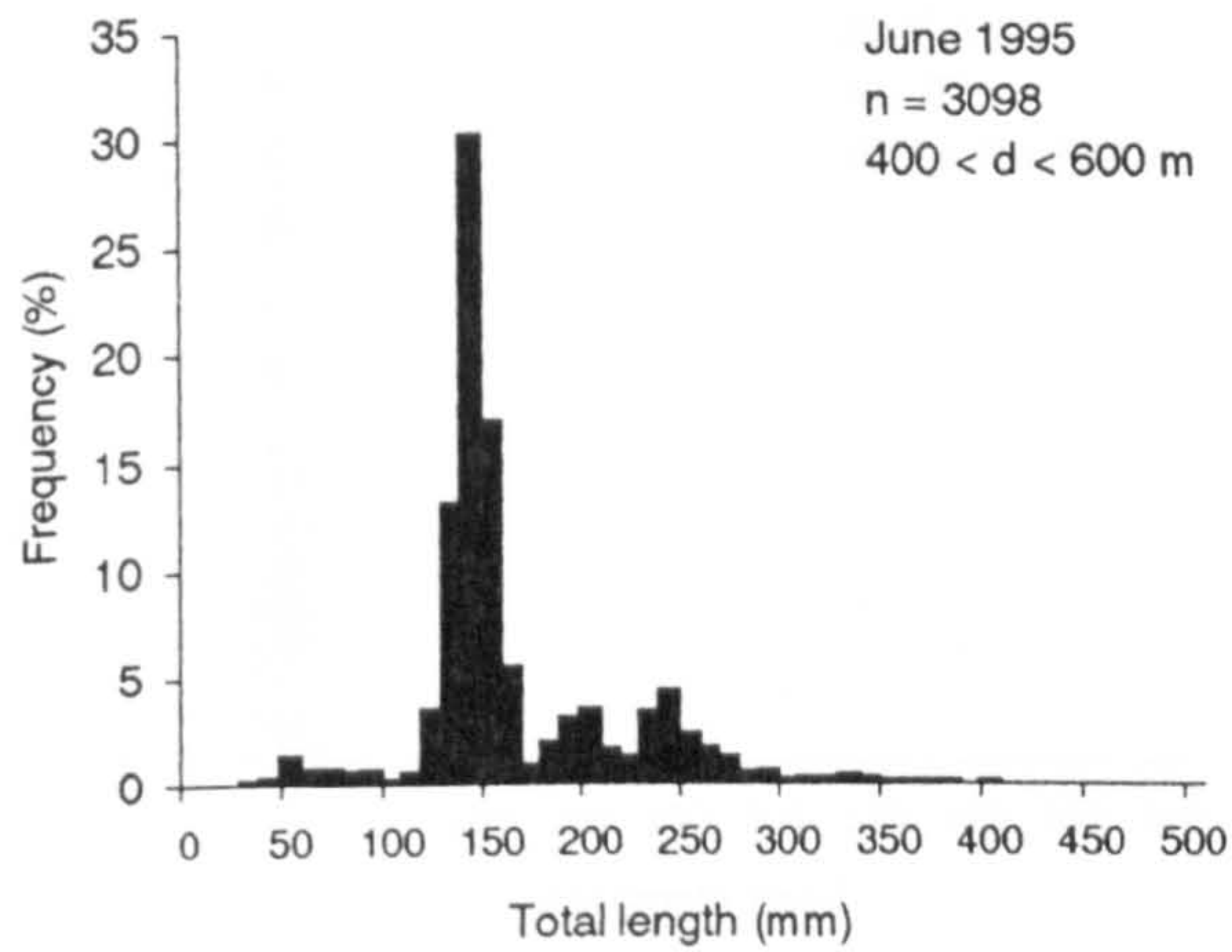
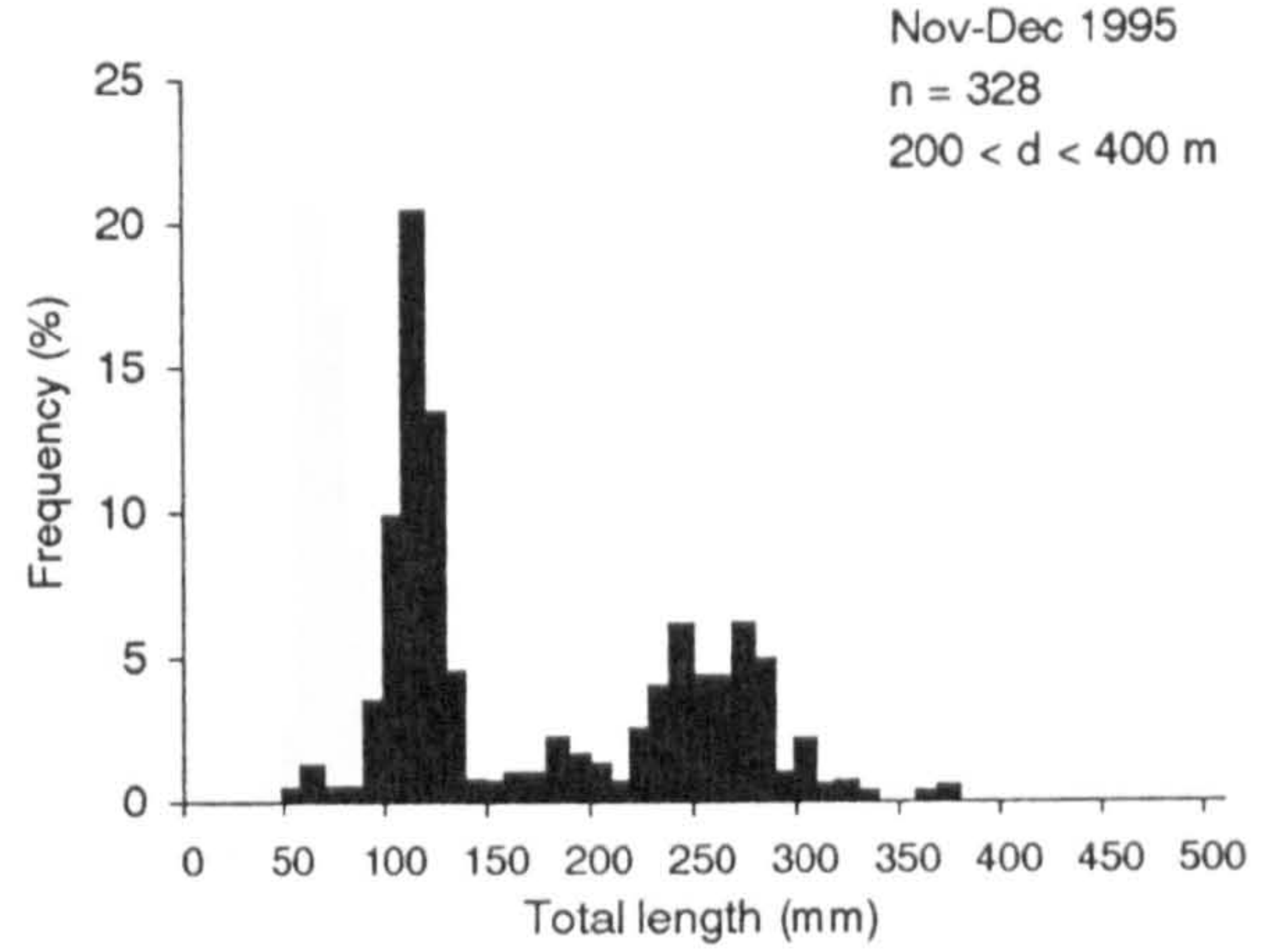
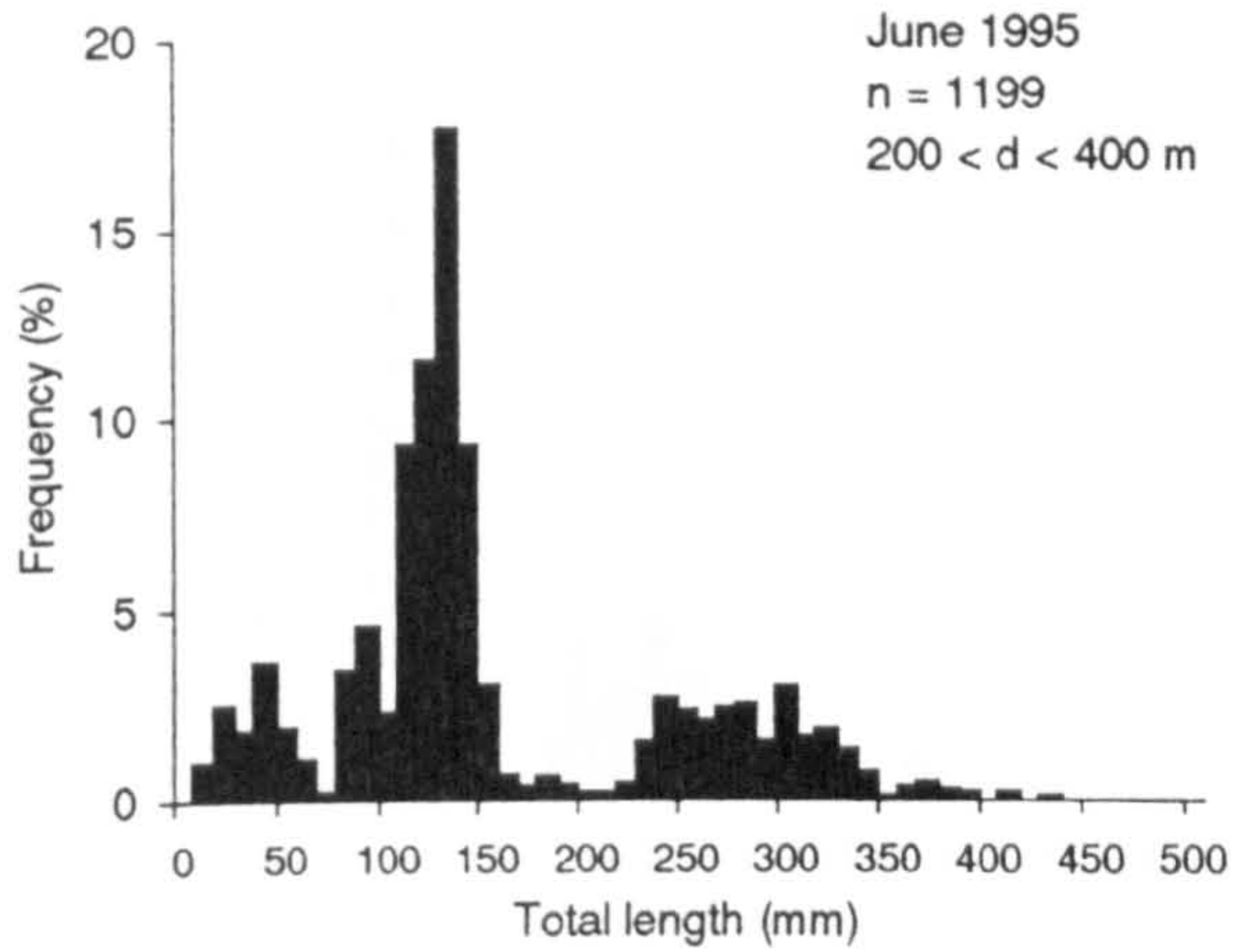
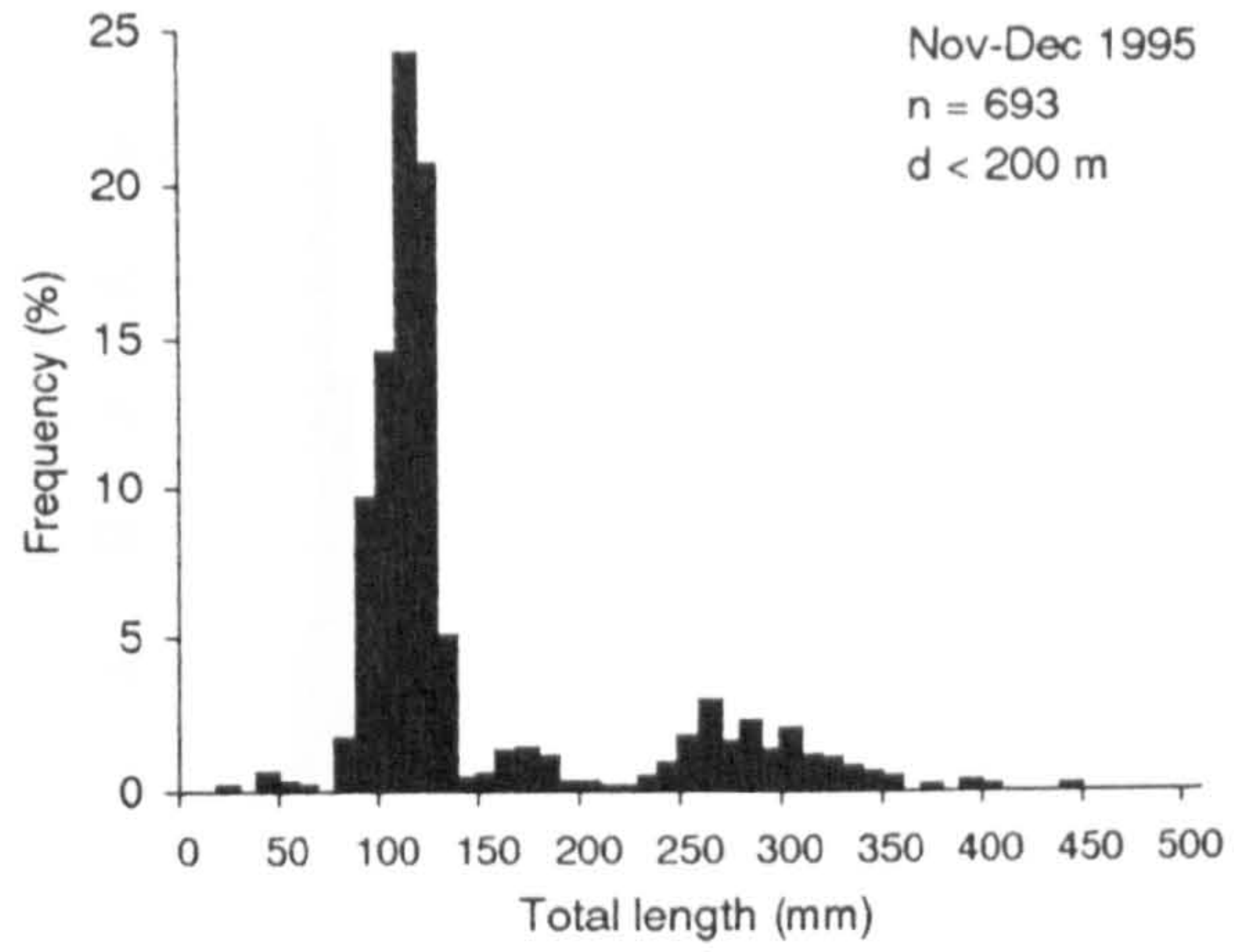
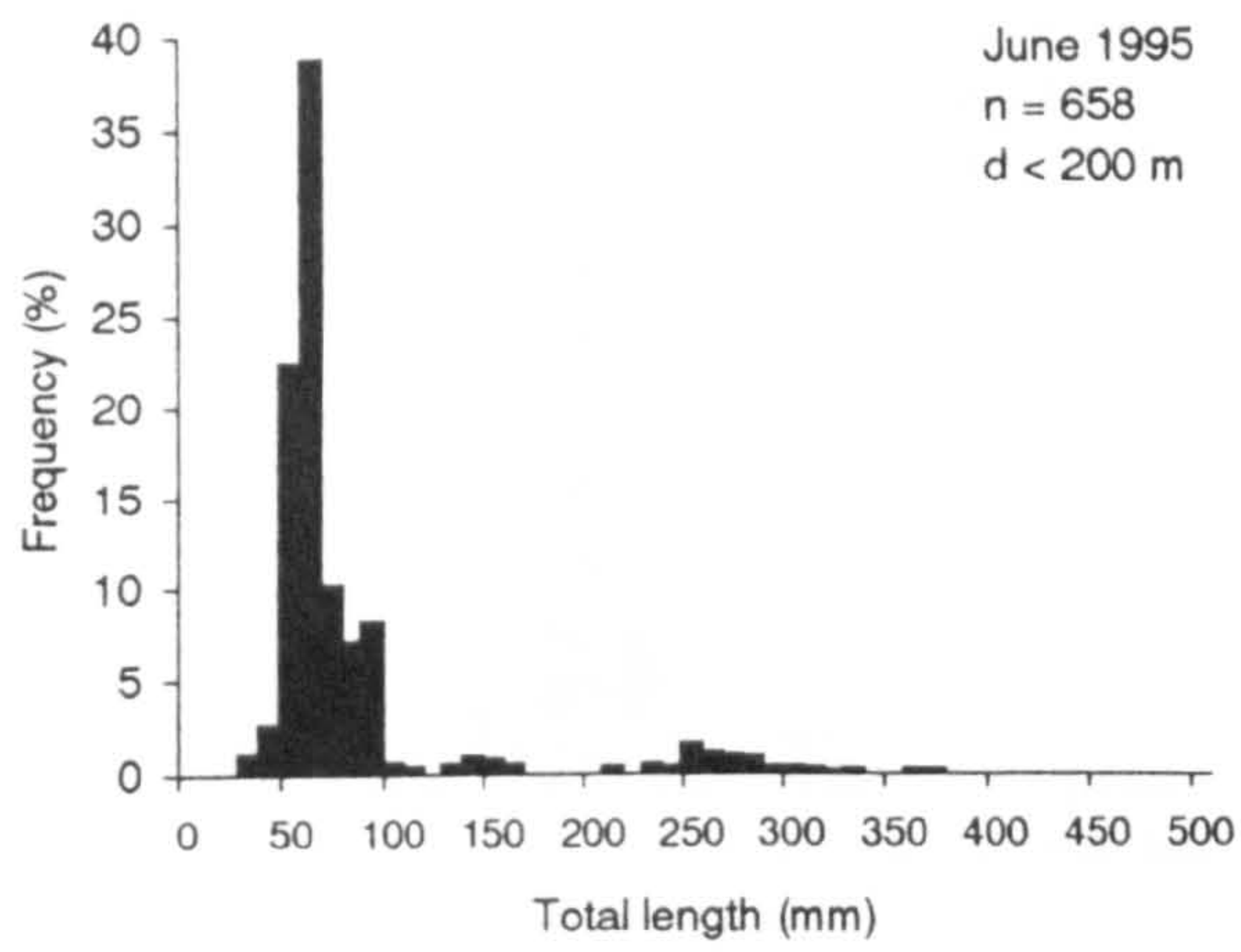


Figure 88. Size distribution of *L. stappersii* by depth strata in June and November-December 1995. Bottom depth is indicated with d, n is the sample size.

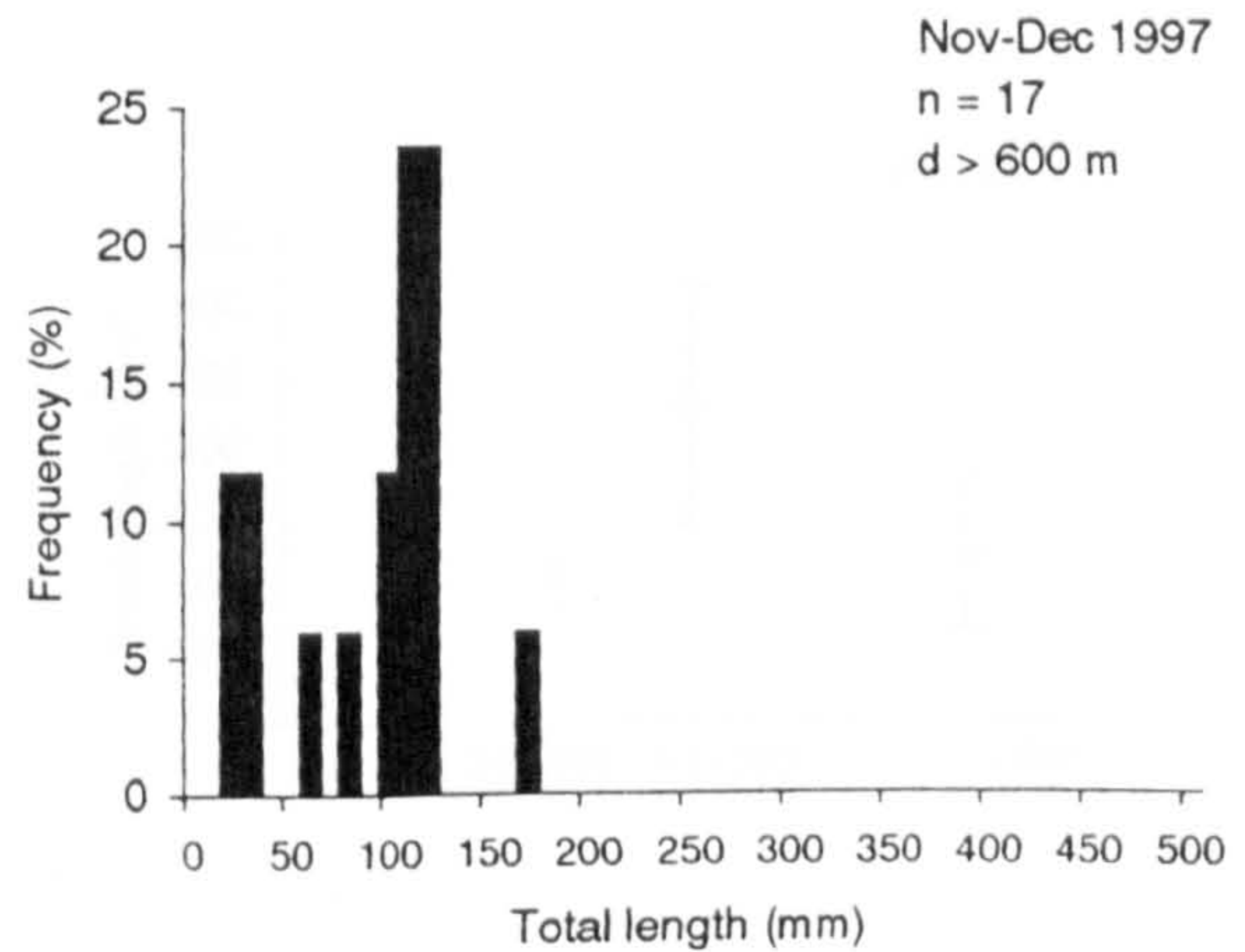
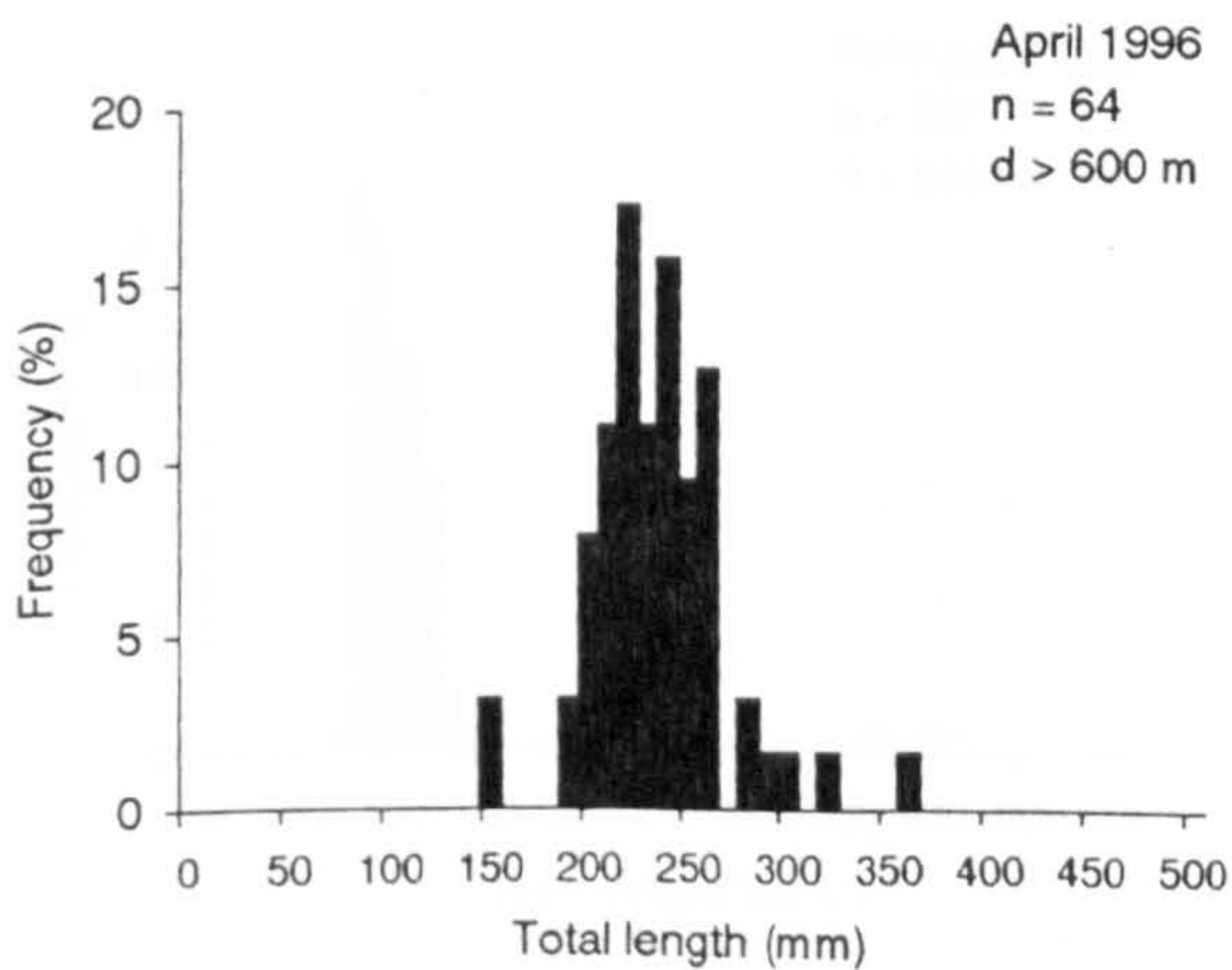
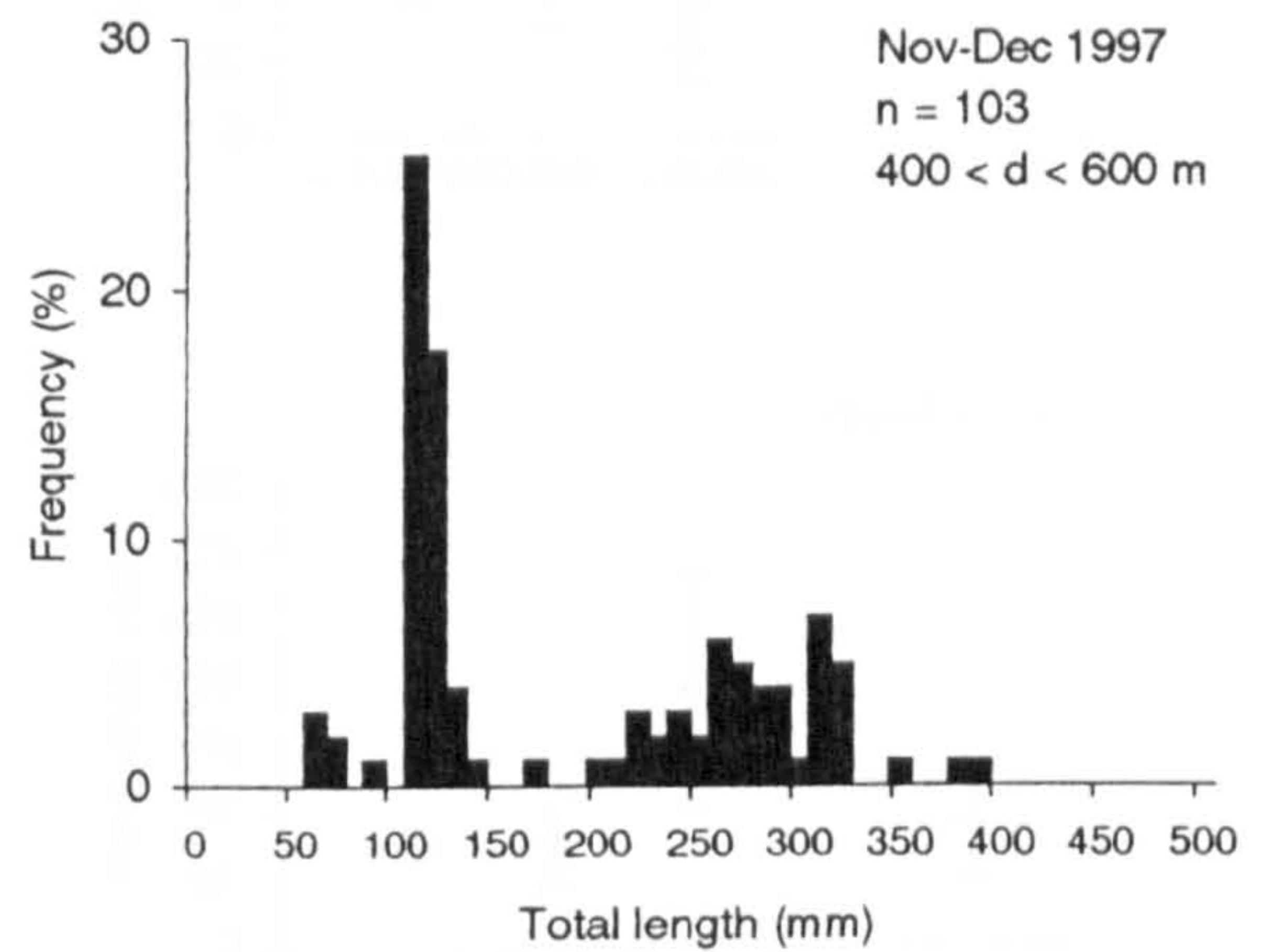
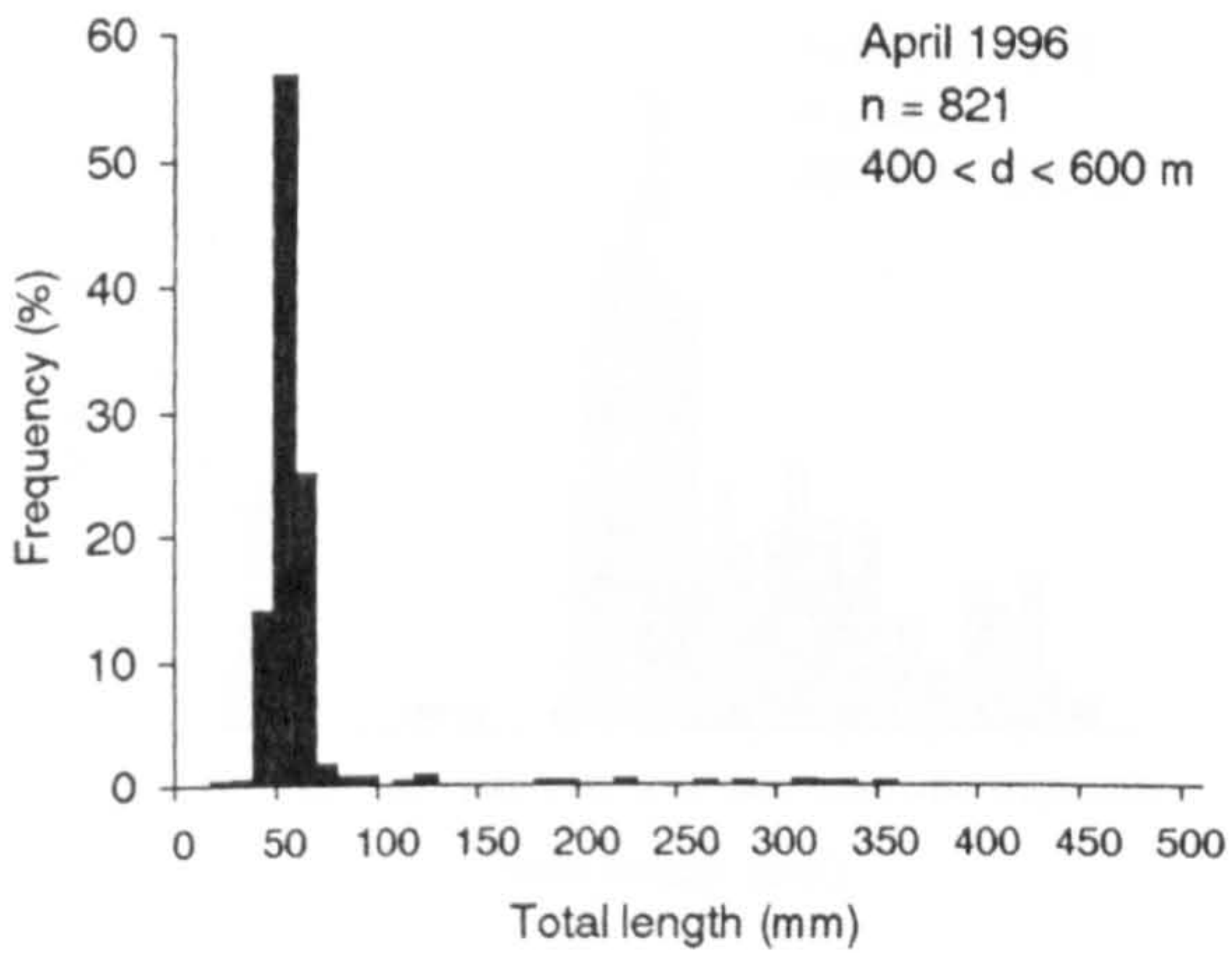
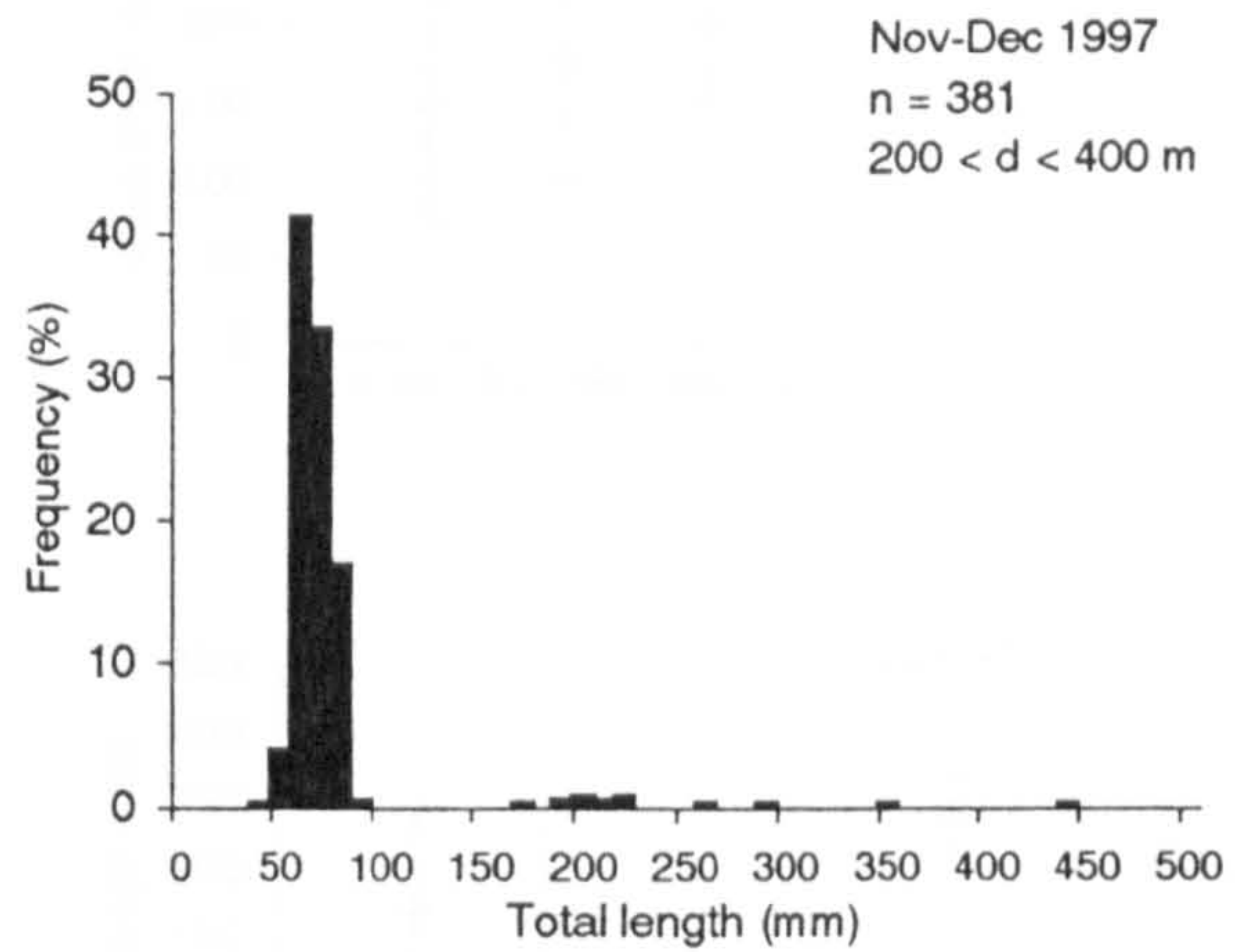
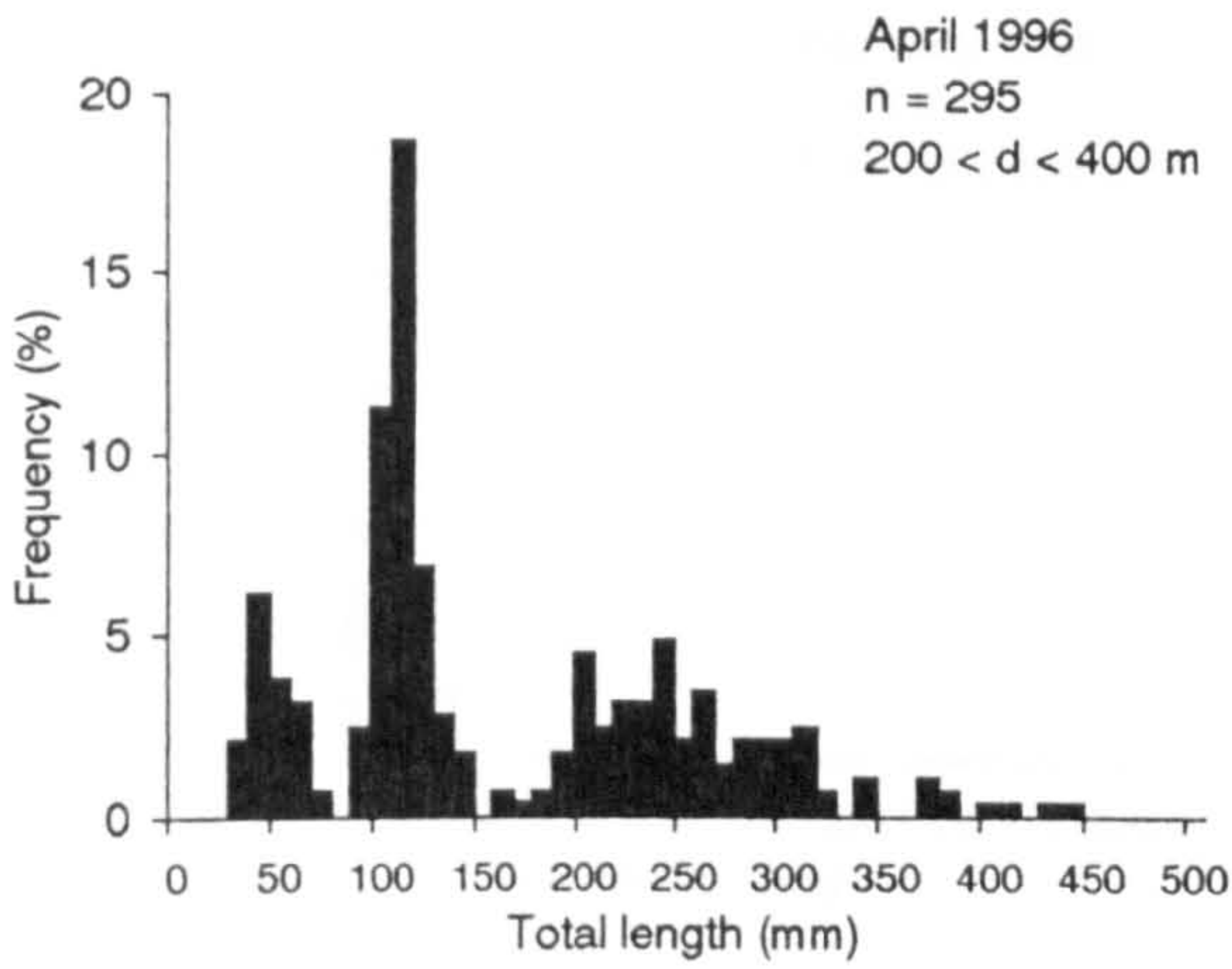
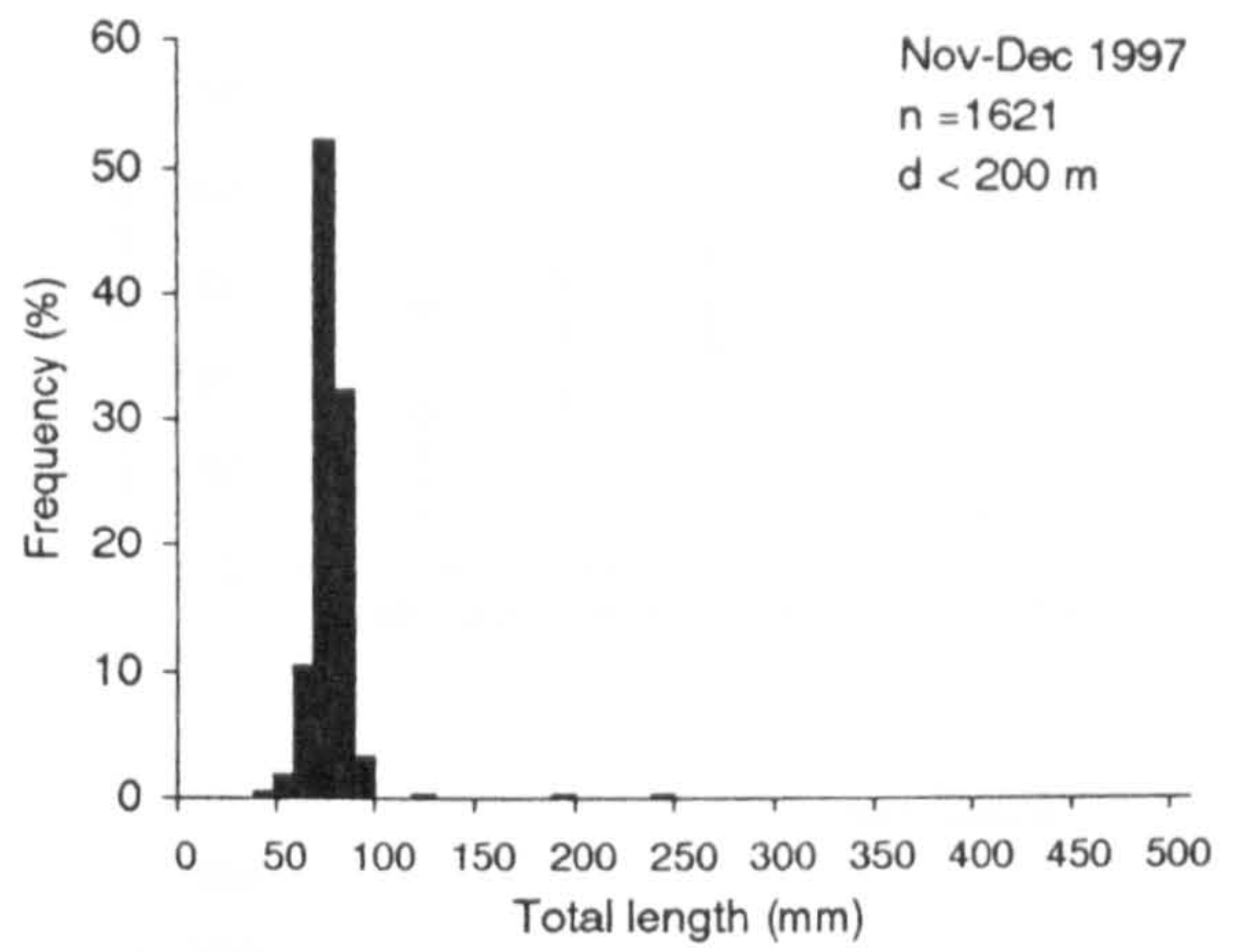
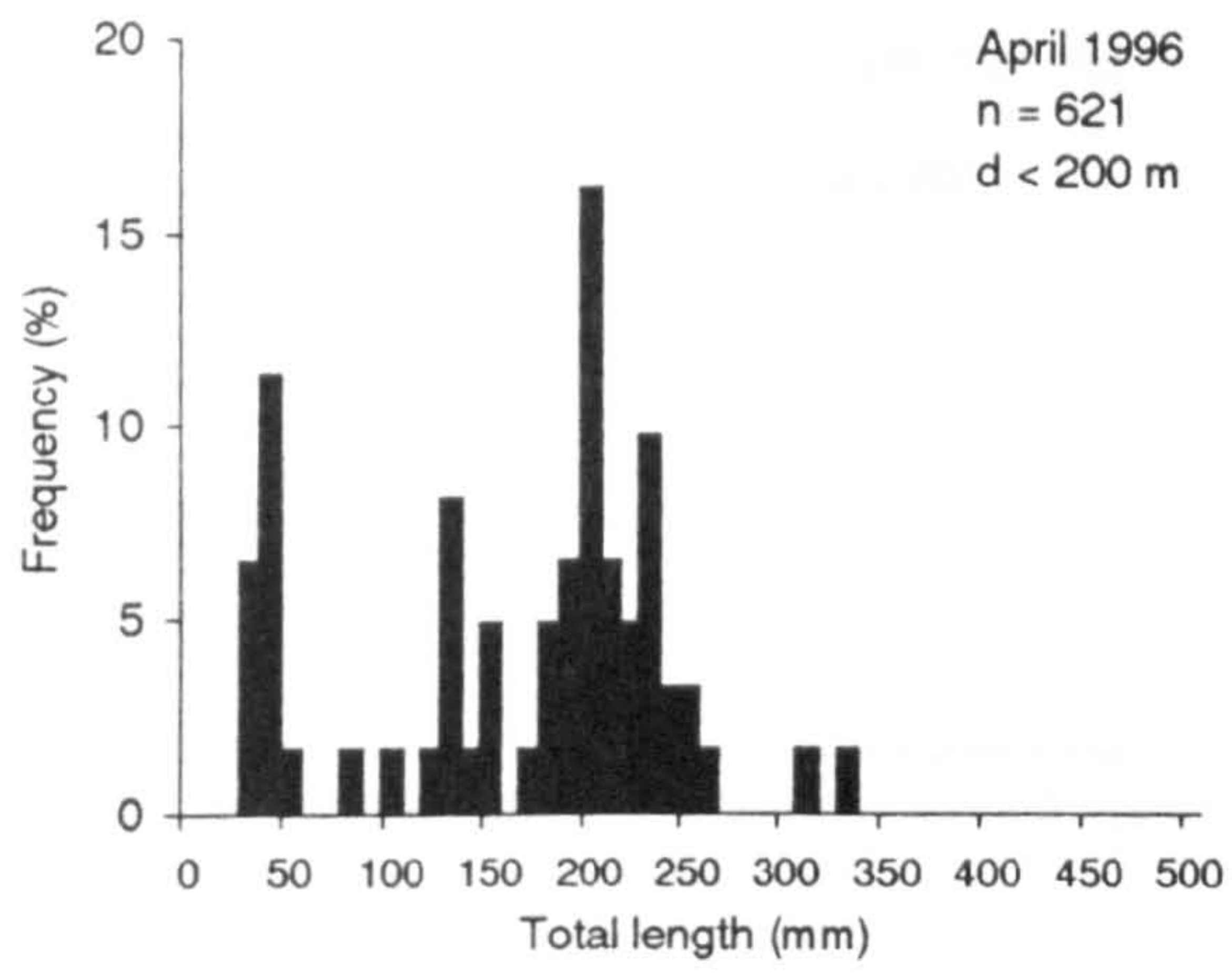


Figure 89. Size distribution of *L. stappersii* by depth strata in April 1996 and November-December 1997. Bottom depth is indicated with d, n is the sample size.



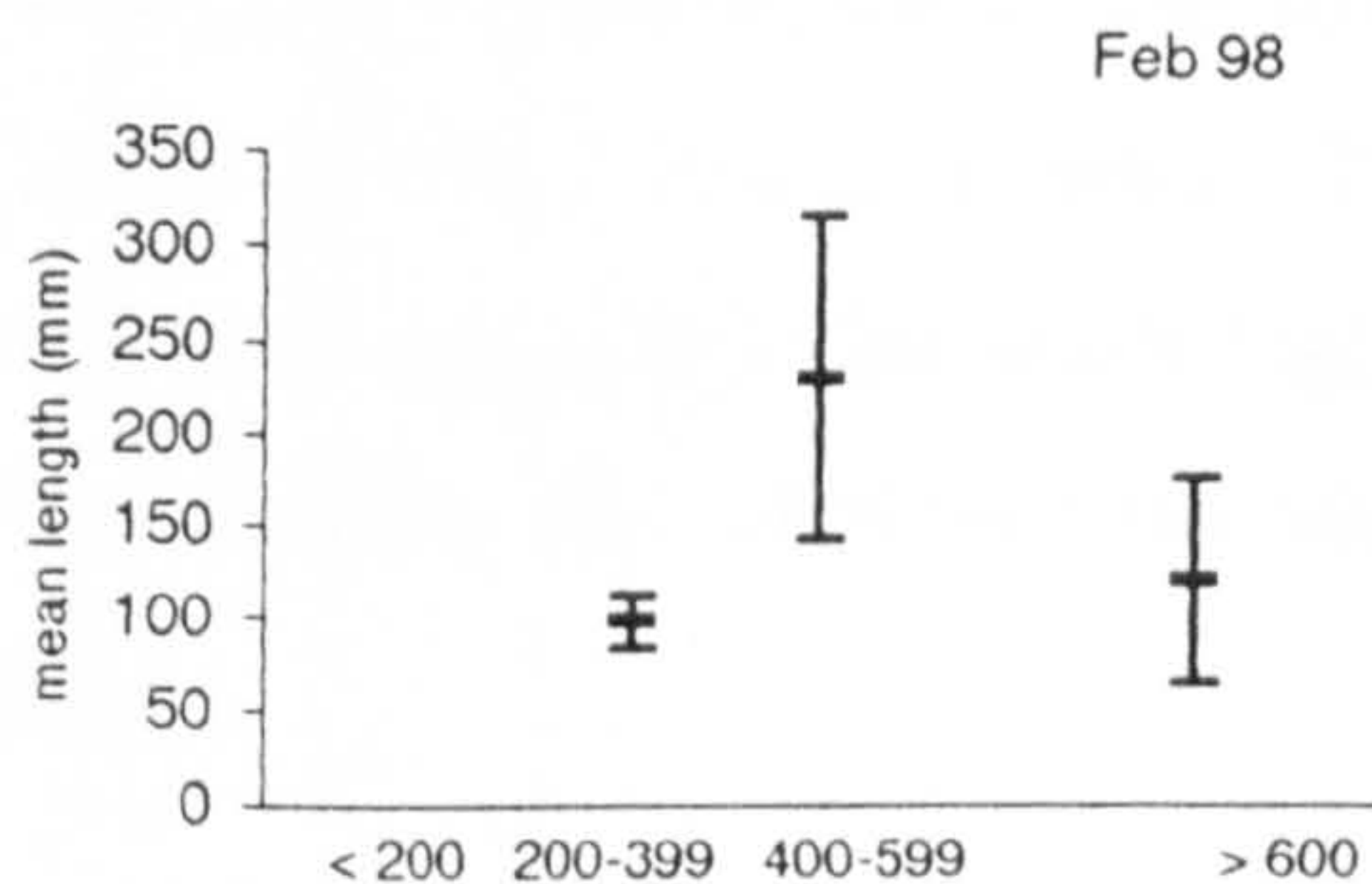
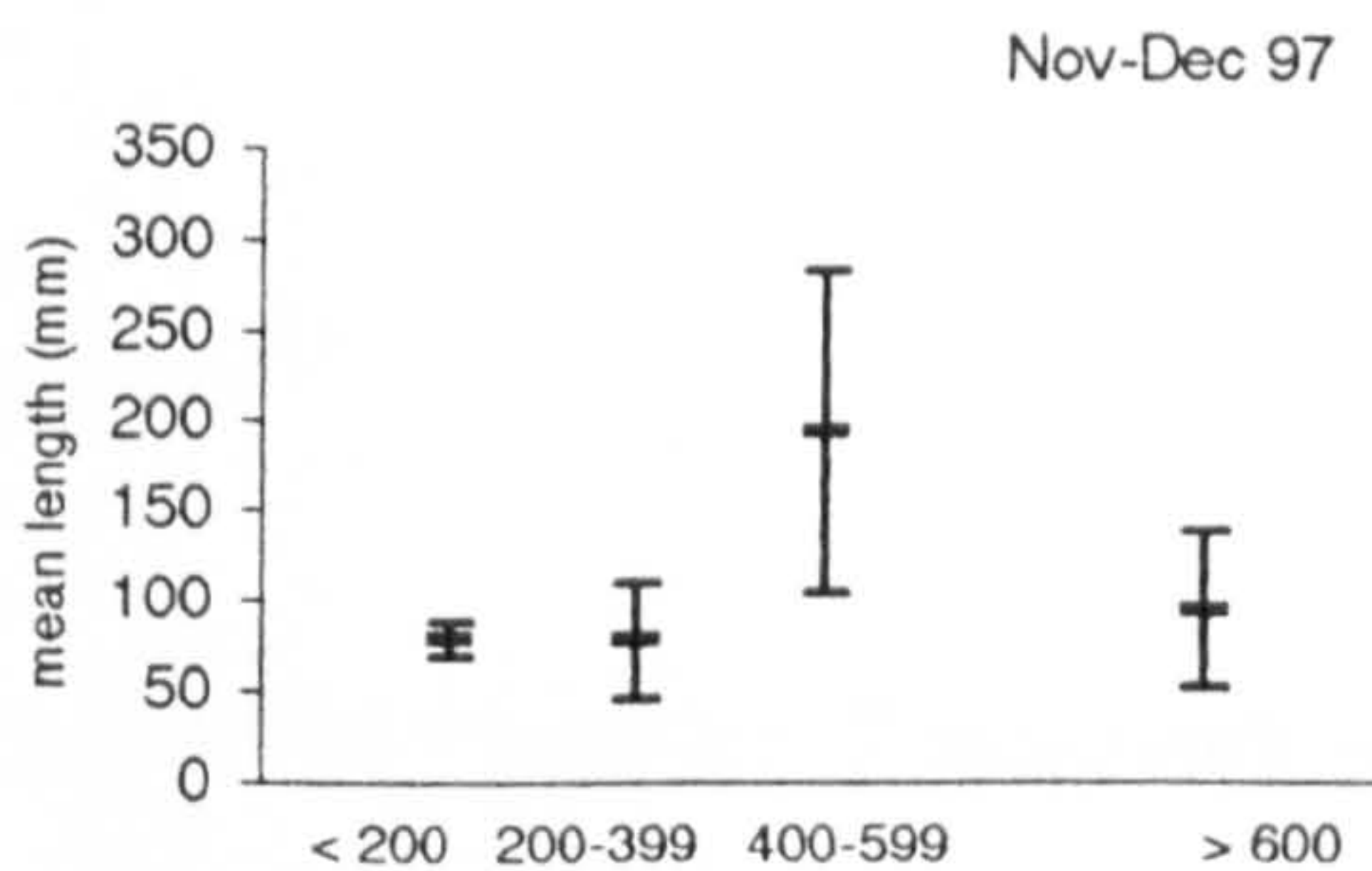
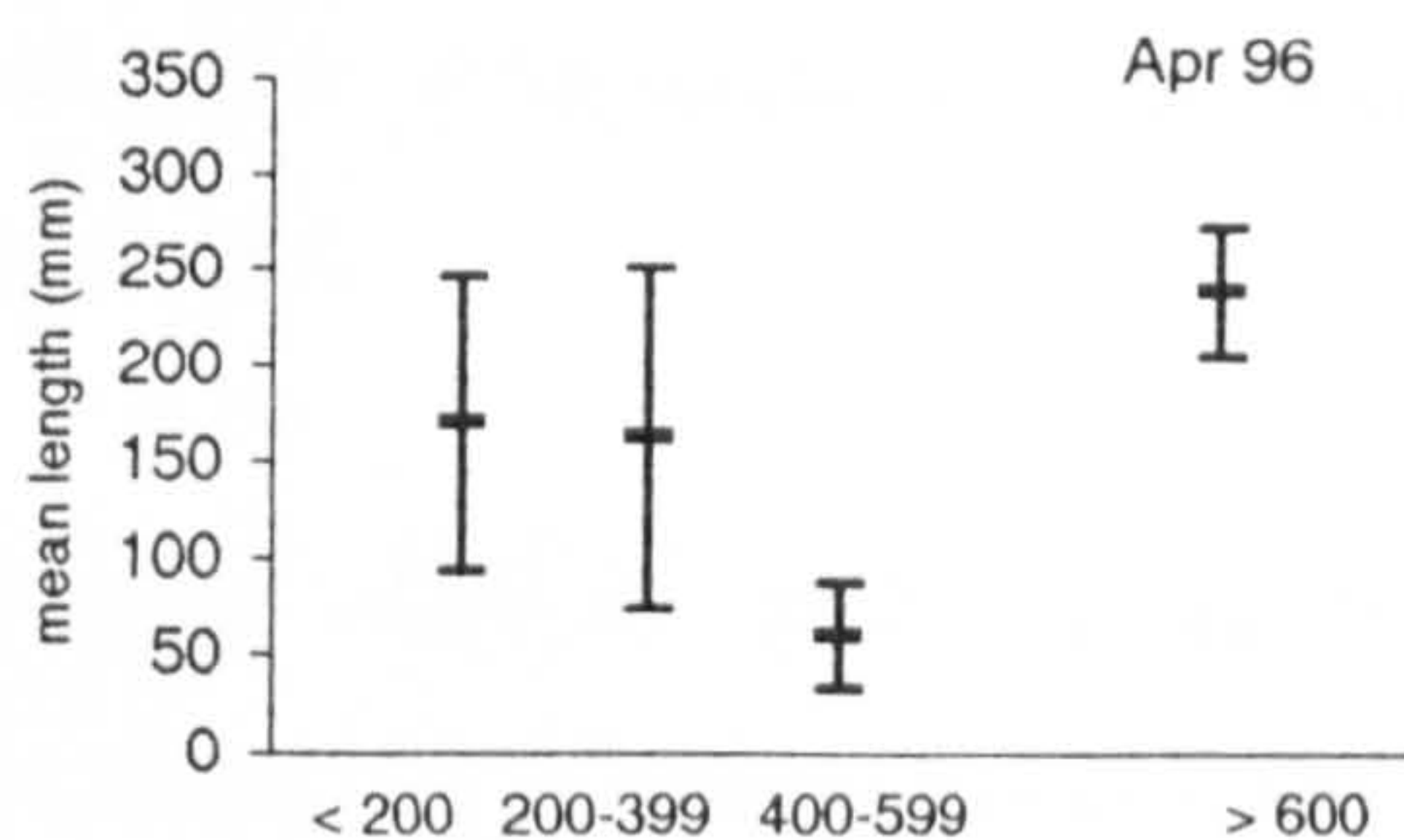
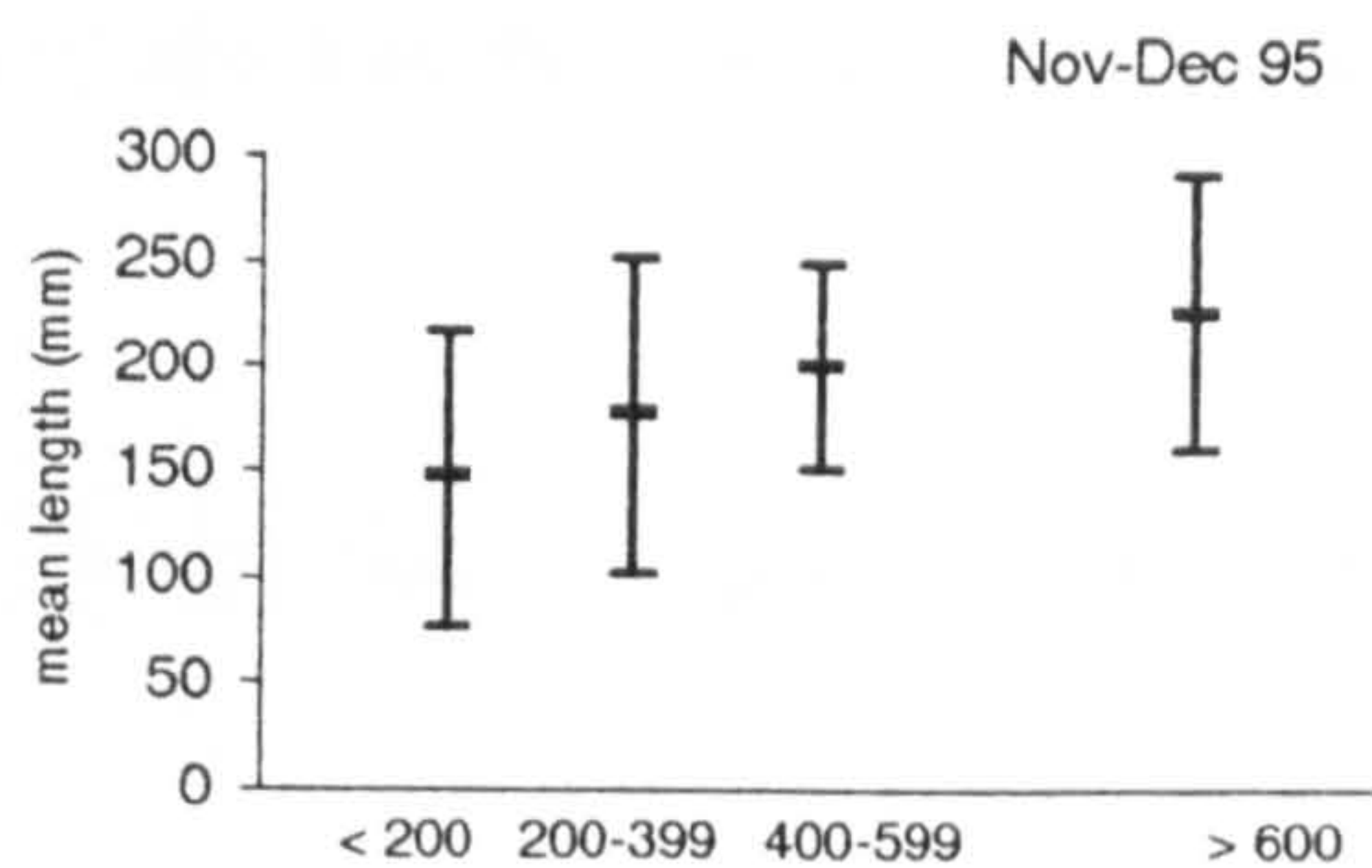
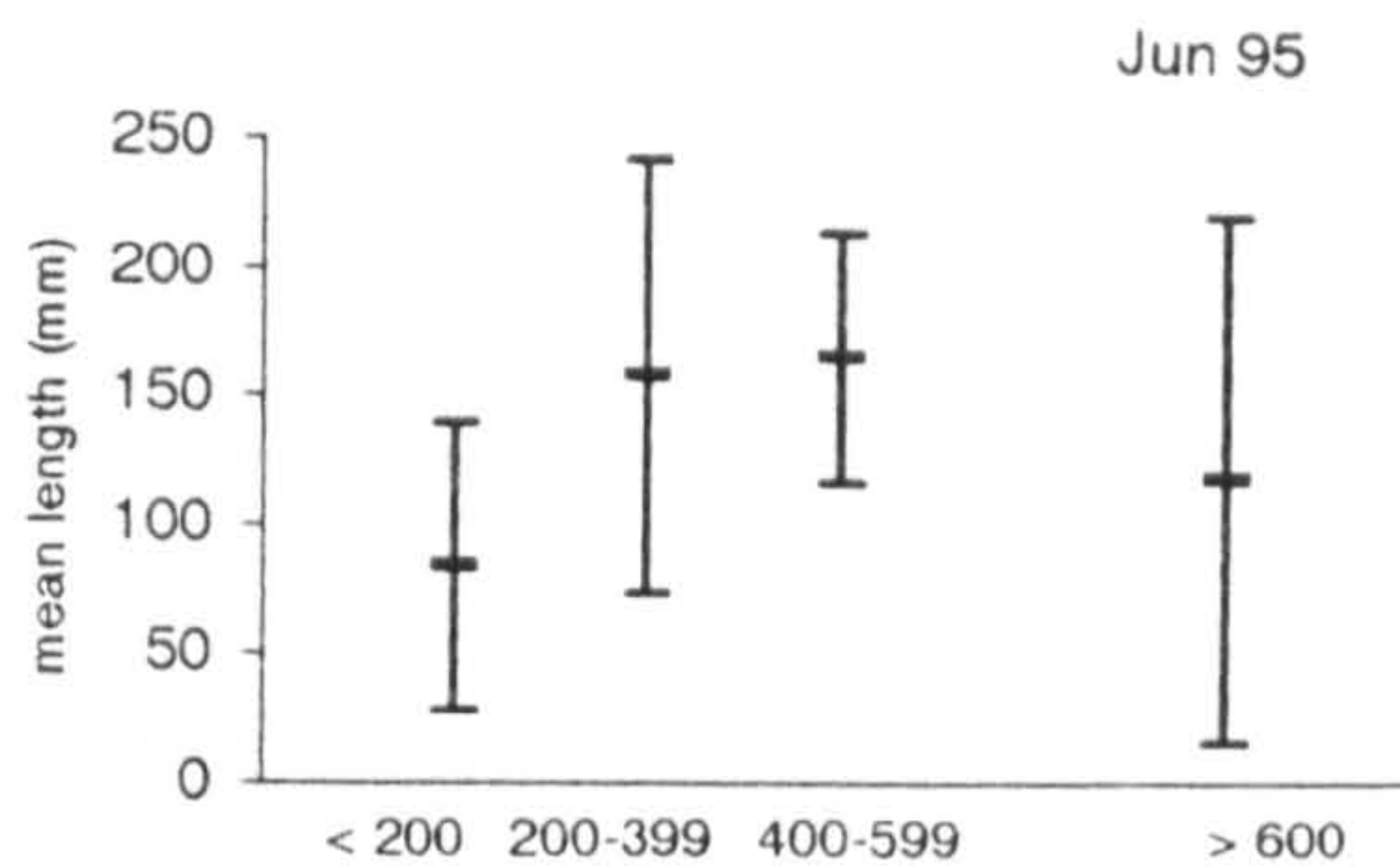
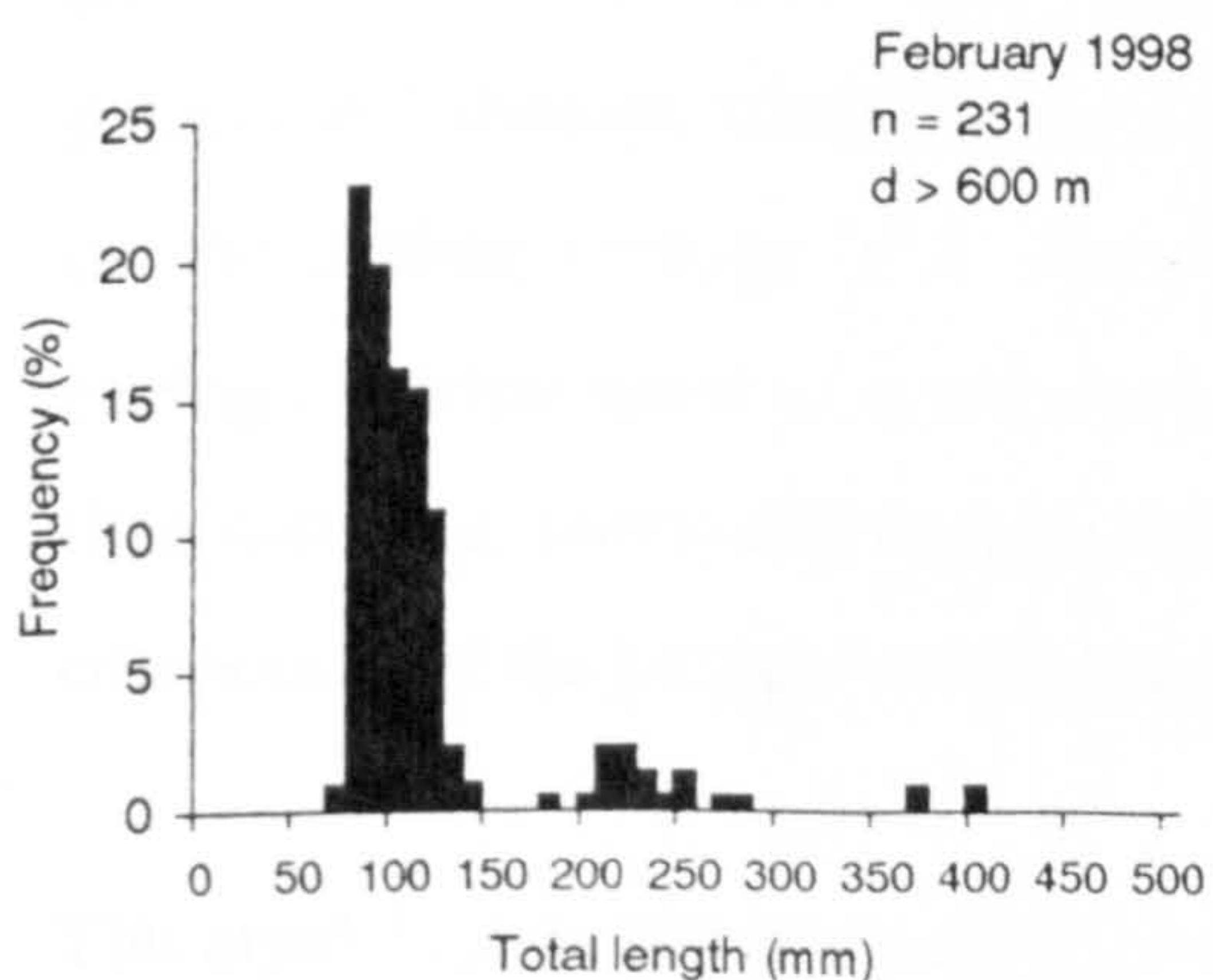
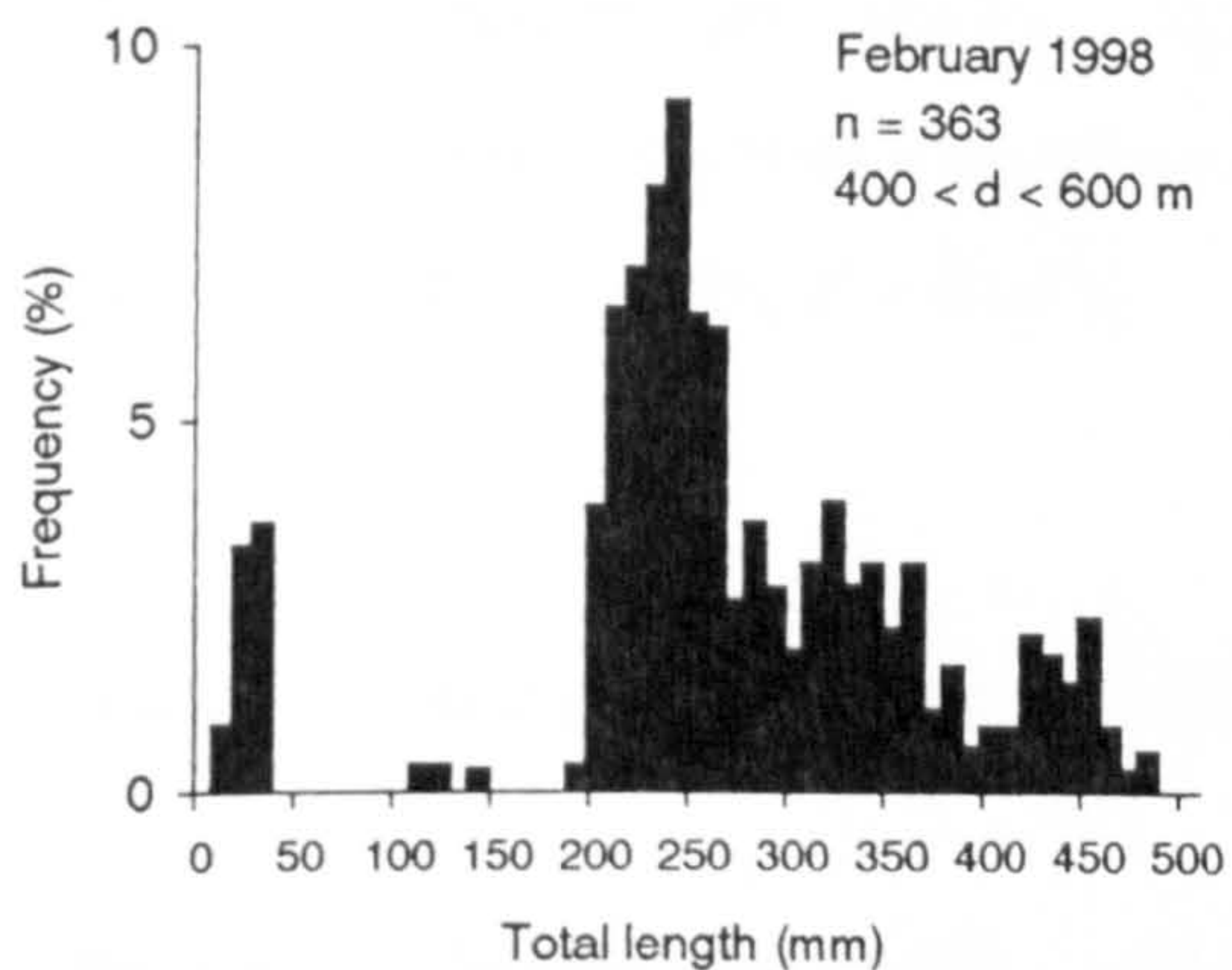
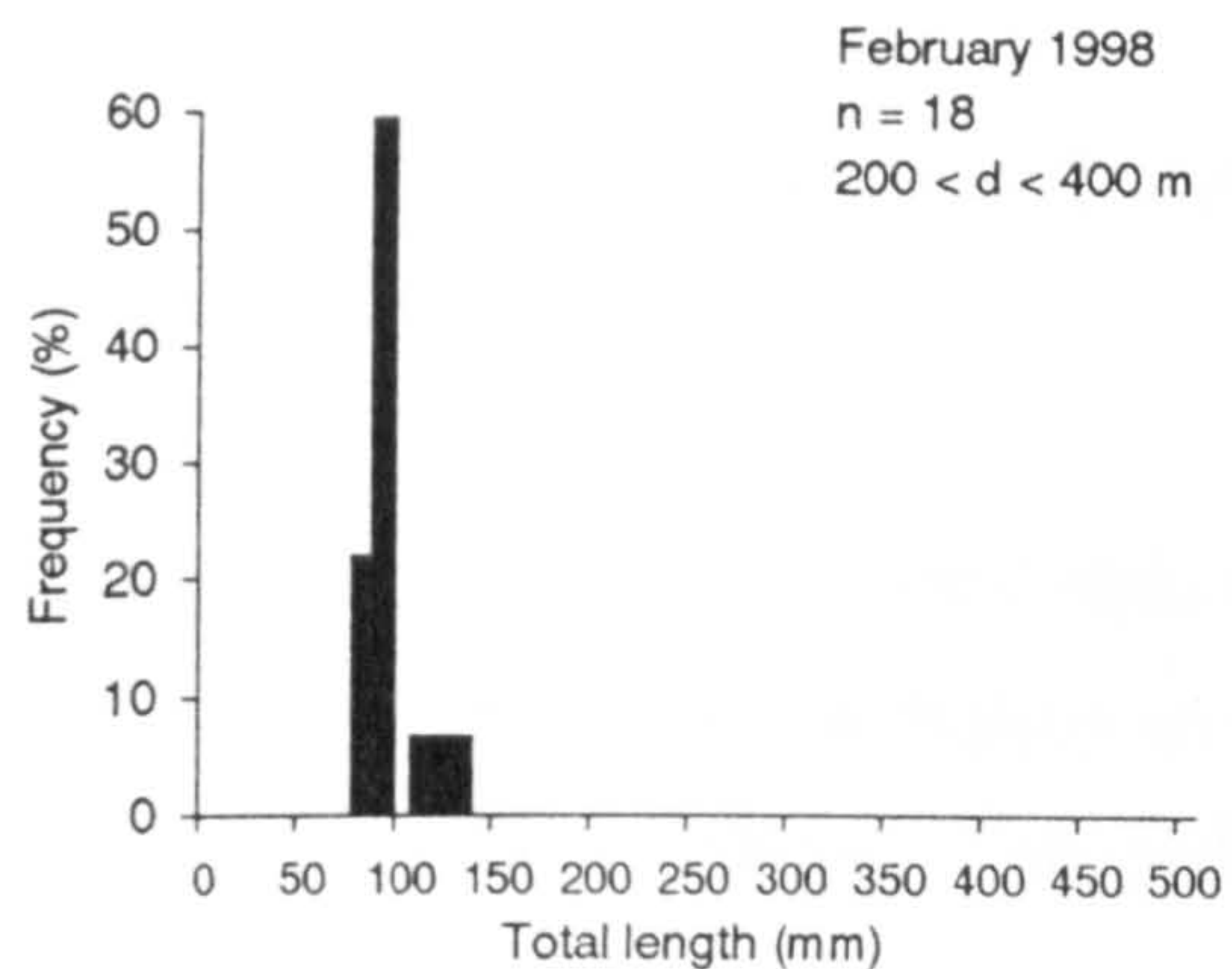
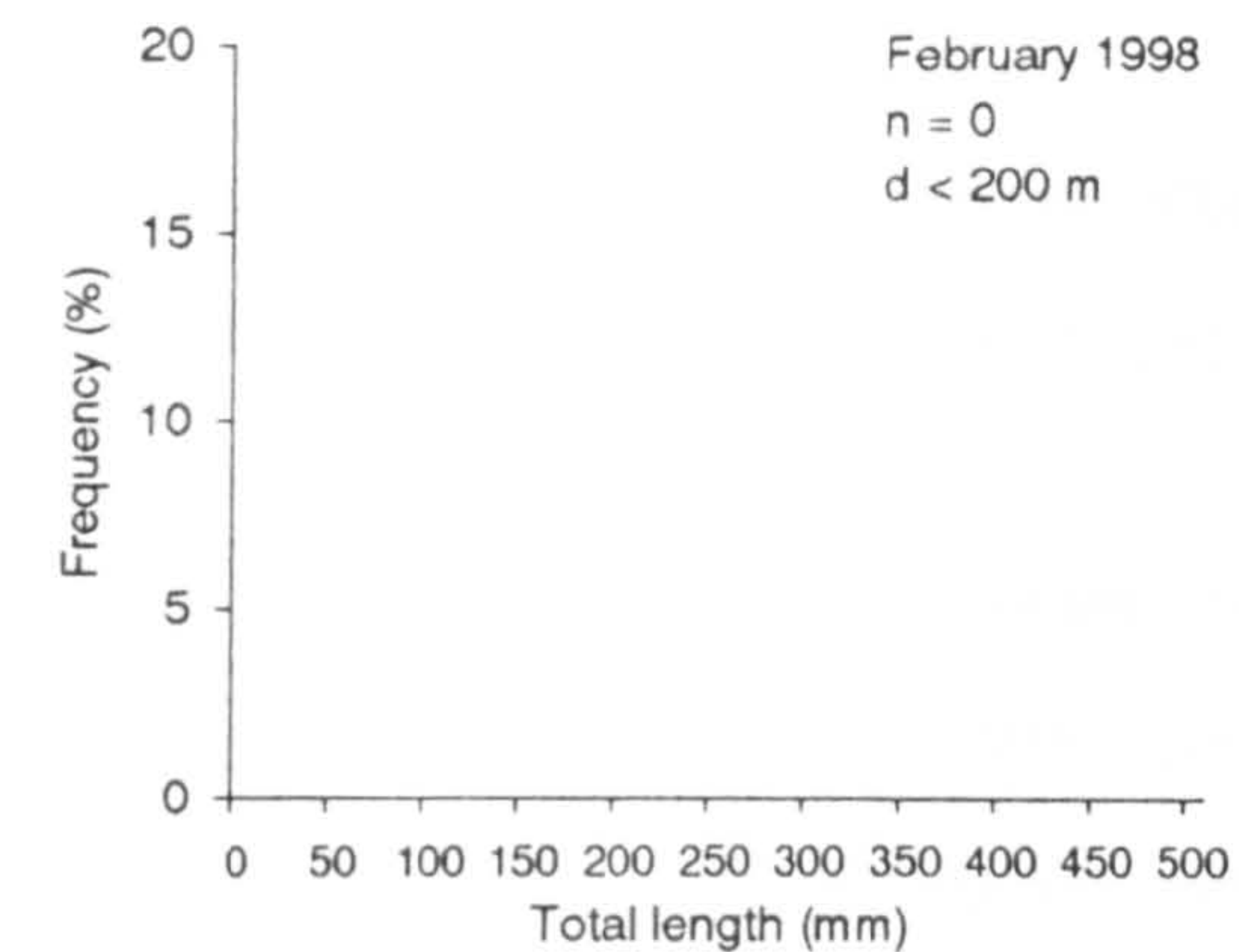


Figure 90. Size distribution of *L. stappersii* by depth strata in February 1998. Bottom depth is indicated with d, n is the sample size.

Figure 91. Mean length of *L. stappersii* in trawl catches from four bottom depth-defined zones (abscissa, m) during five surveys.

high occurrence of tows with no larvae (Fig. 53c). 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. 92).

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. 93). The highest density, and frequency in samples, of *L. stappersii* larvae occurred in February 1998 in the Moba sub-basin.

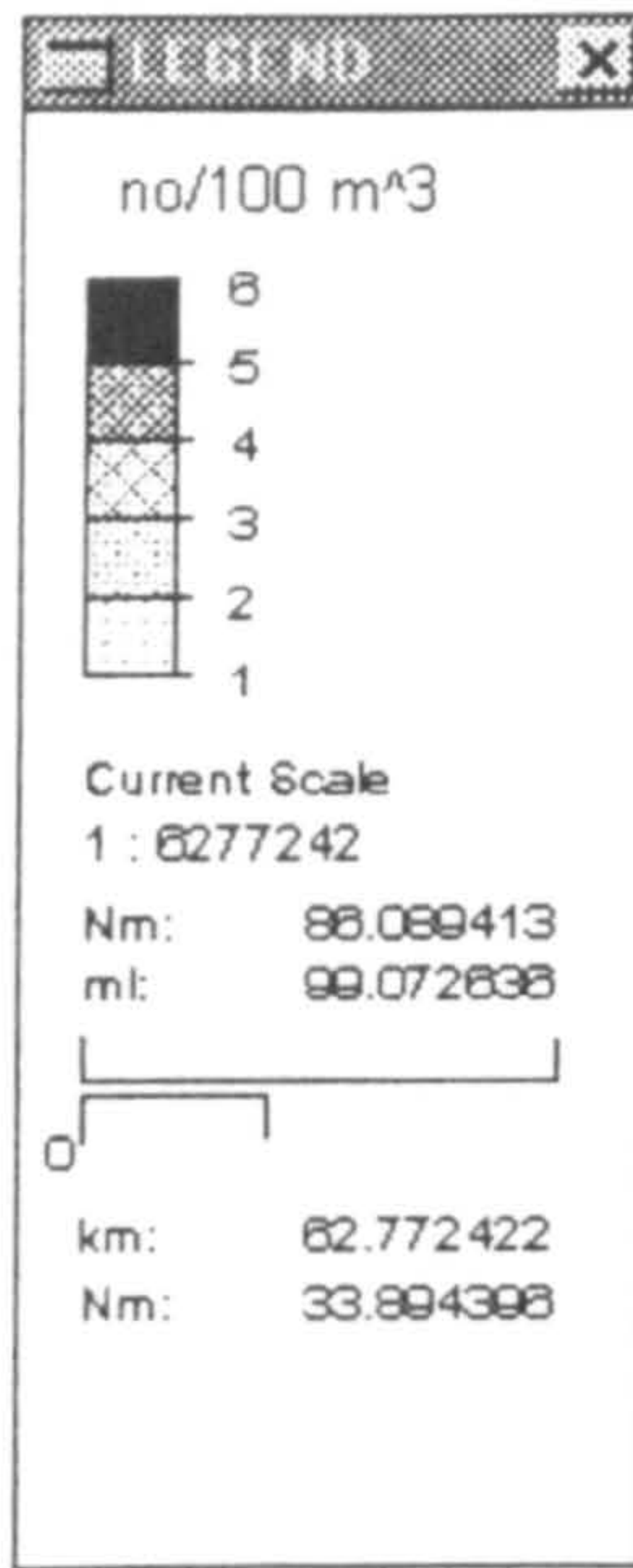
The mean number per 100 m<sup>3</sup> ranged from 1 (June 1995) to 30 (February 1998) individuals and there was a significant difference in the mean values between surveys (ANOVA,  $F = 20.336$ ,  $P < 0.001$ ).

#### 3.4.5 *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* (this work; 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<sup>3</sup> of water varied from 0 to 11212 and 32

a



b

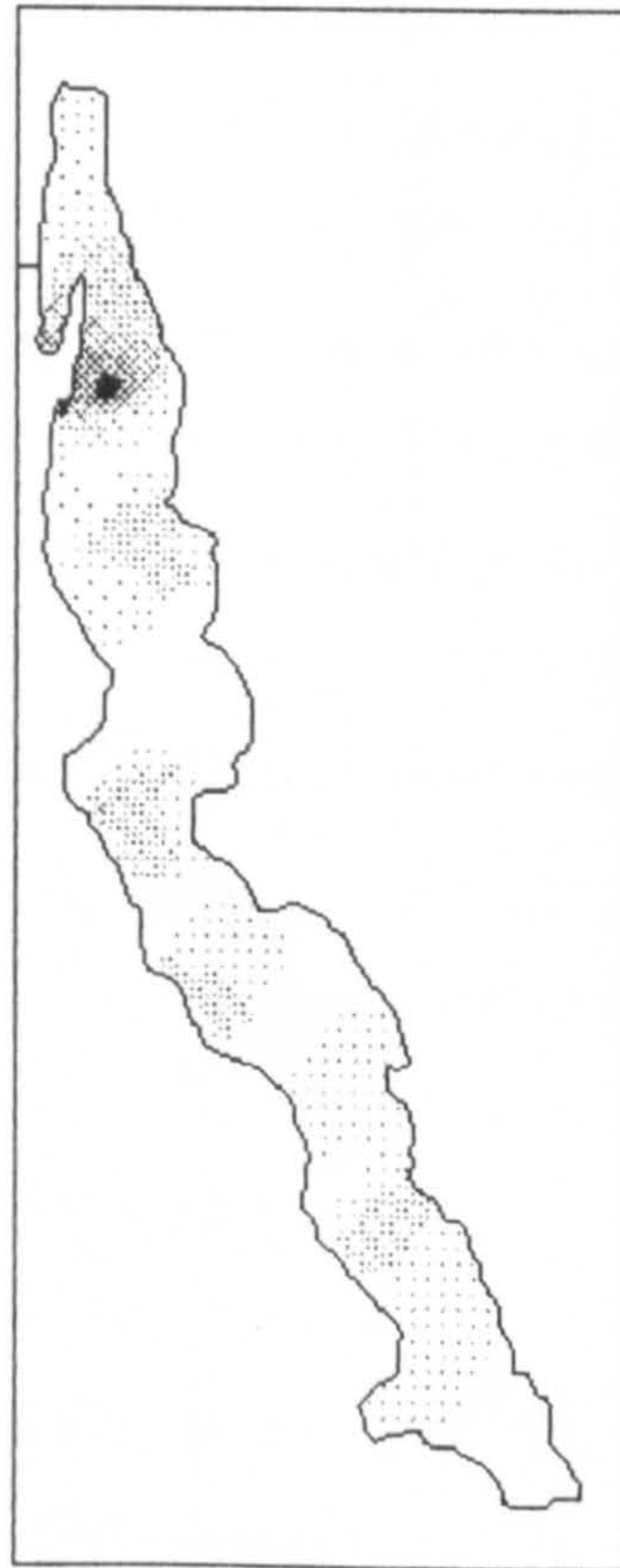
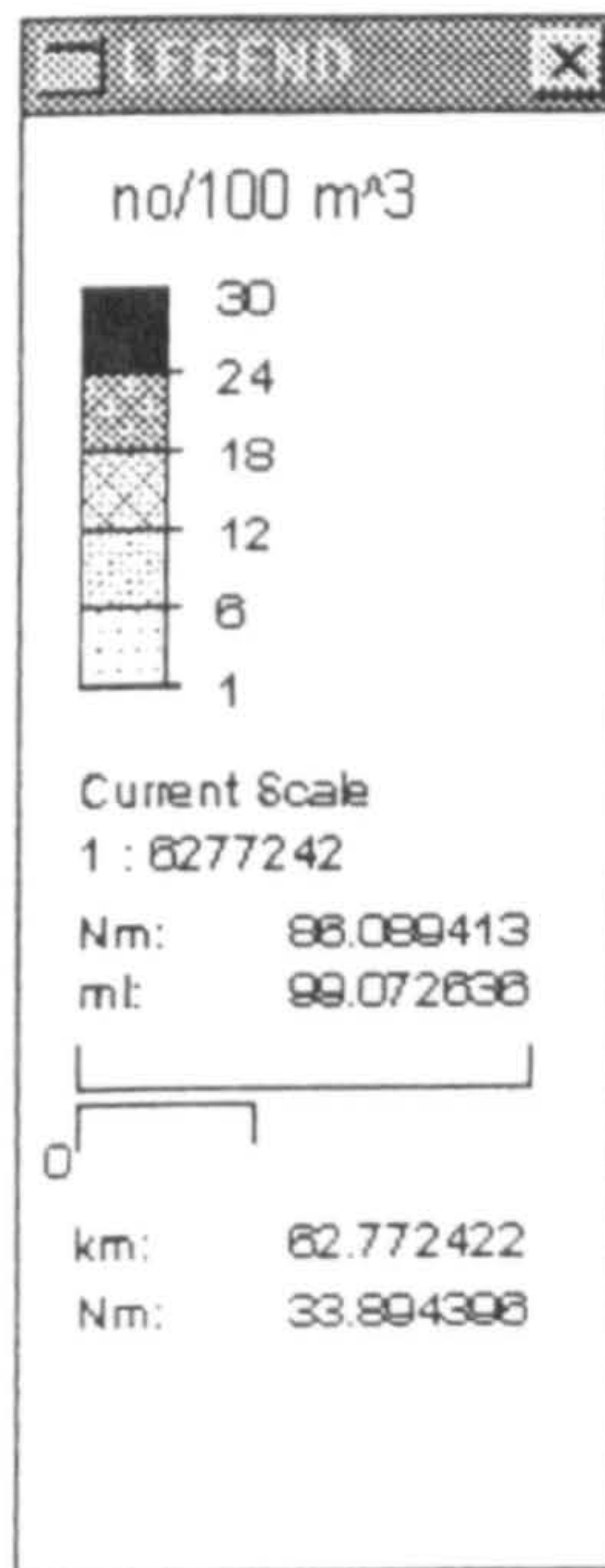
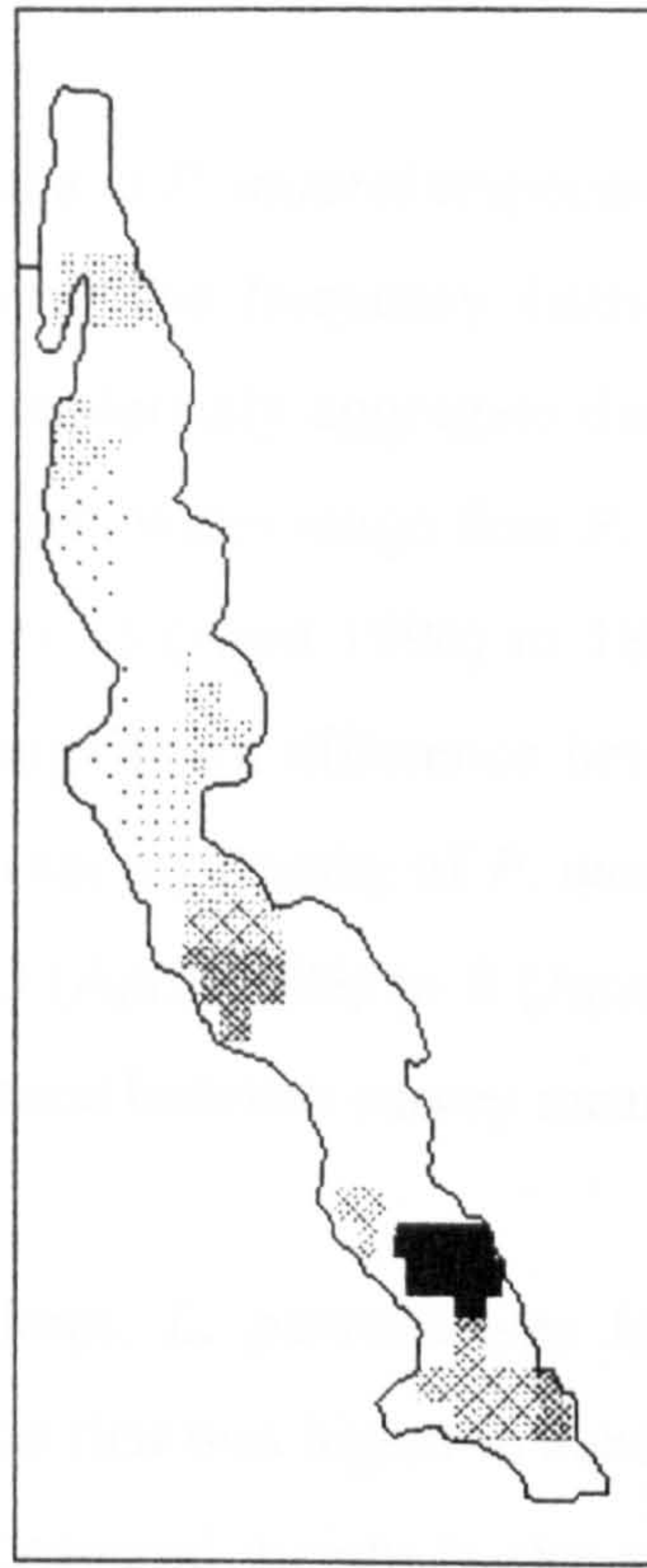
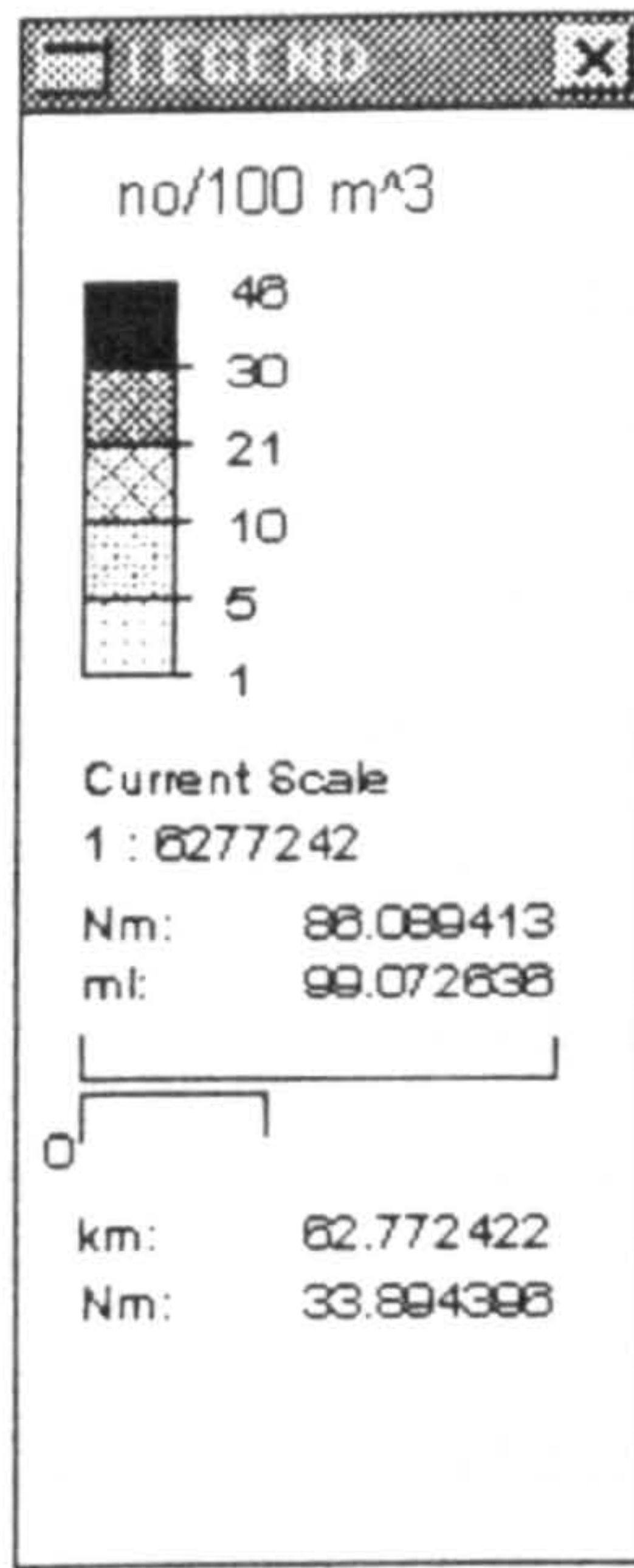


Figure 92. Distribution of *L. stappersii* larvae within 0-100 m water column in June (a) and November-December (b) 1995. Larval density (no/100 m<sup>3</sup>) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. 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 statute miles (mi).

a



b

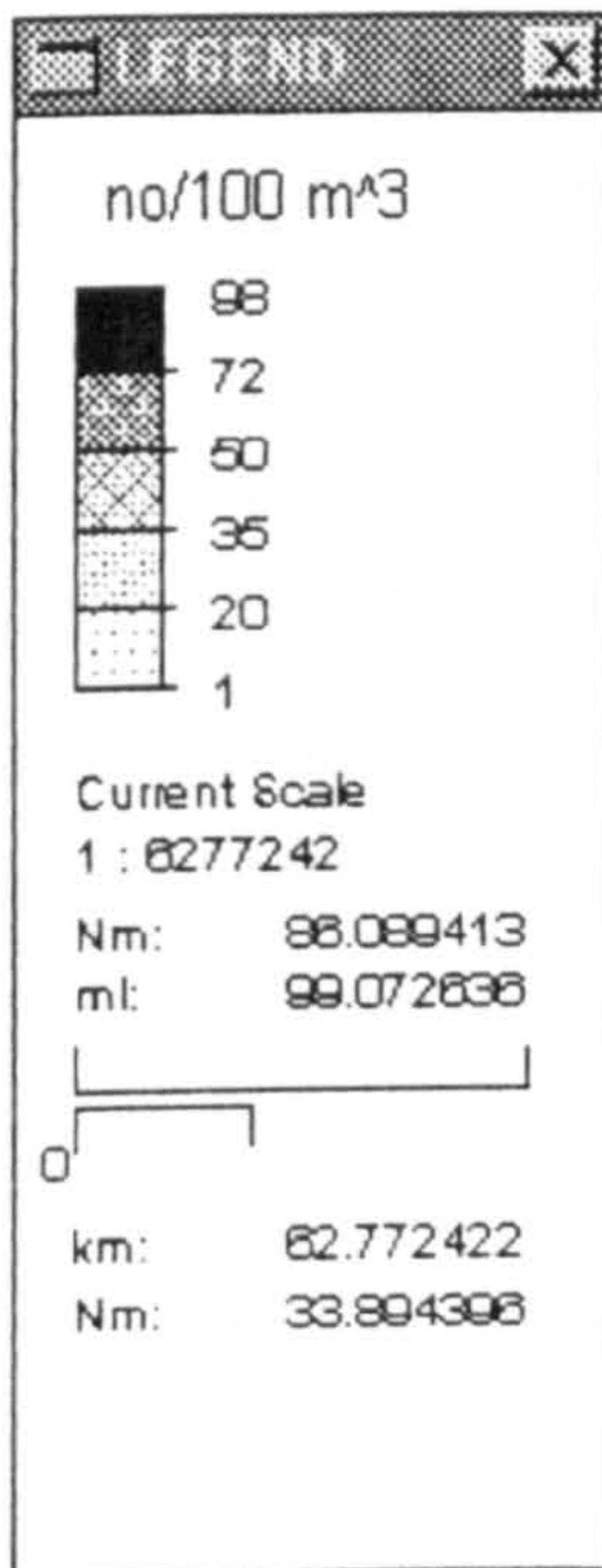


Figure 93. Distribution of *L. stappersii* larvae within 0-100 m water column in November-December 1997 (a) and February 1998 (b). Larval density (no/100 m<sup>3</sup>) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal 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 statute miles (ml).

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. 94). The mean number of *L. parvula* varied from 15 (April 1996) to 1896 x 100 m<sup>3</sup> (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<sup>3</sup> 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. 95). The distribution of *P. moorei* was throughout the lake, although higher densities, particularly in June 1995, were found in the southern half of the lake (Fig. 96). 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. 97). *Limnocaridina parvula* distribution in November-December 1997 and February 1998 confirmed the observed lake-wide pattern found in 1995. In both surveys this shrimp mainly occurred in the southern areas of the lake (Fig. 98). *Palaemon moorei* was found in low numbers, as in the previous surveys, and mainly occurred in the central regions of the lake (Fig. 99).

### 3.5 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 through pelagic trawling, Gulf-net sampling and stomach content analysis of *L. stappersii* caught in the trawl net. Also data collected during the 1993-95 sampling work at fixed stations around the lake were used.

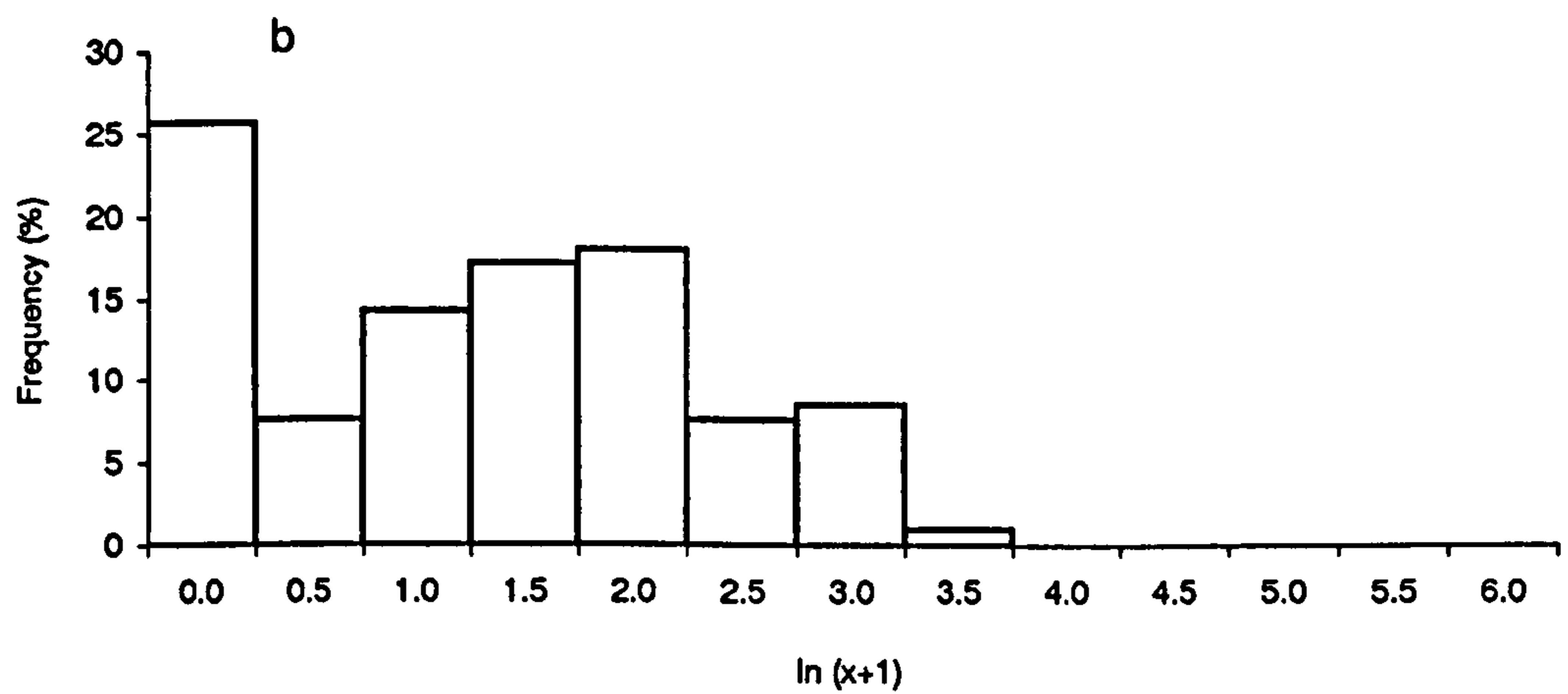
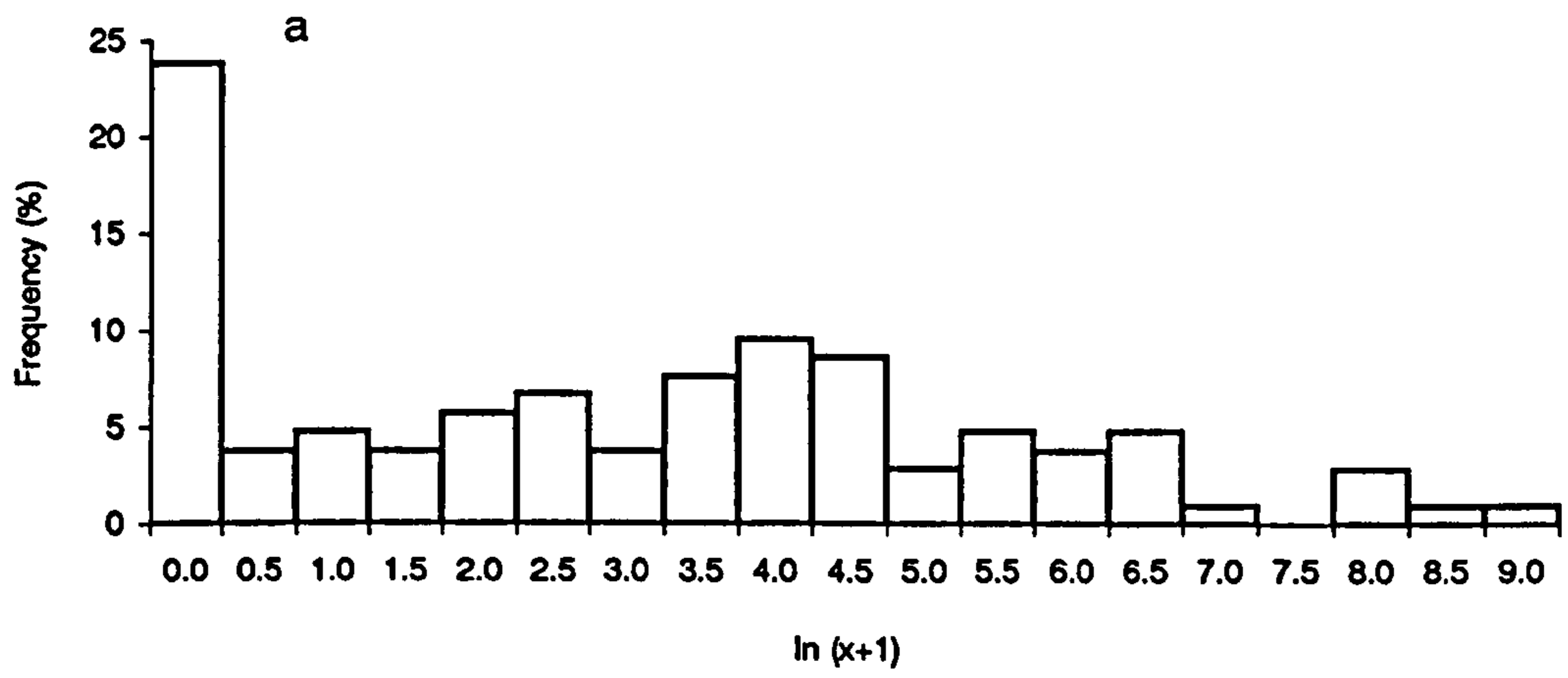


Figure 94. Frequency histograms of  $\ln(x+1)$  transformed number ( $n \times 100 \text{ m}^3$ ) of the shrimp *L. parvula*, a, and *P. moorei*, b, in Gulf-net samples from all surveys.

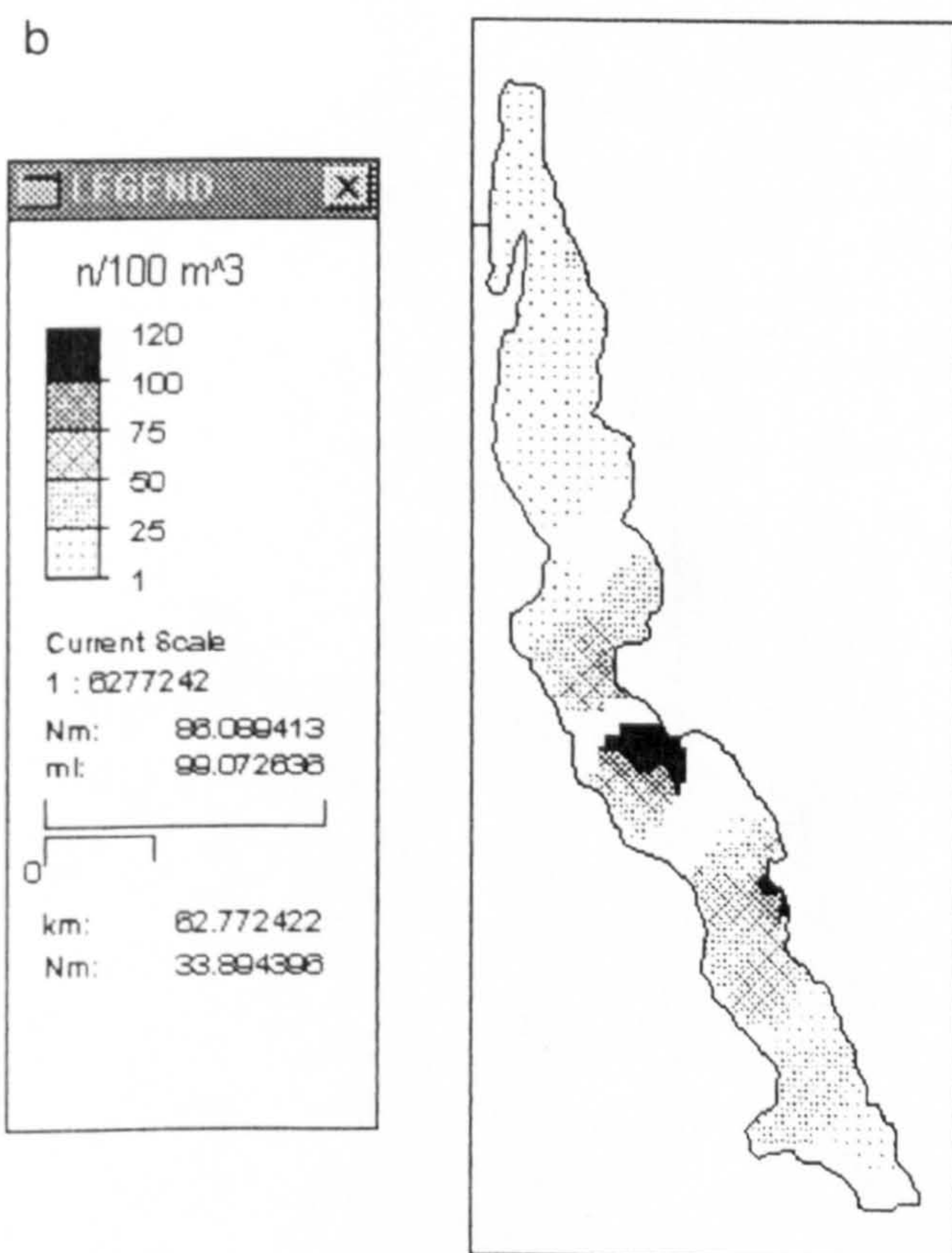
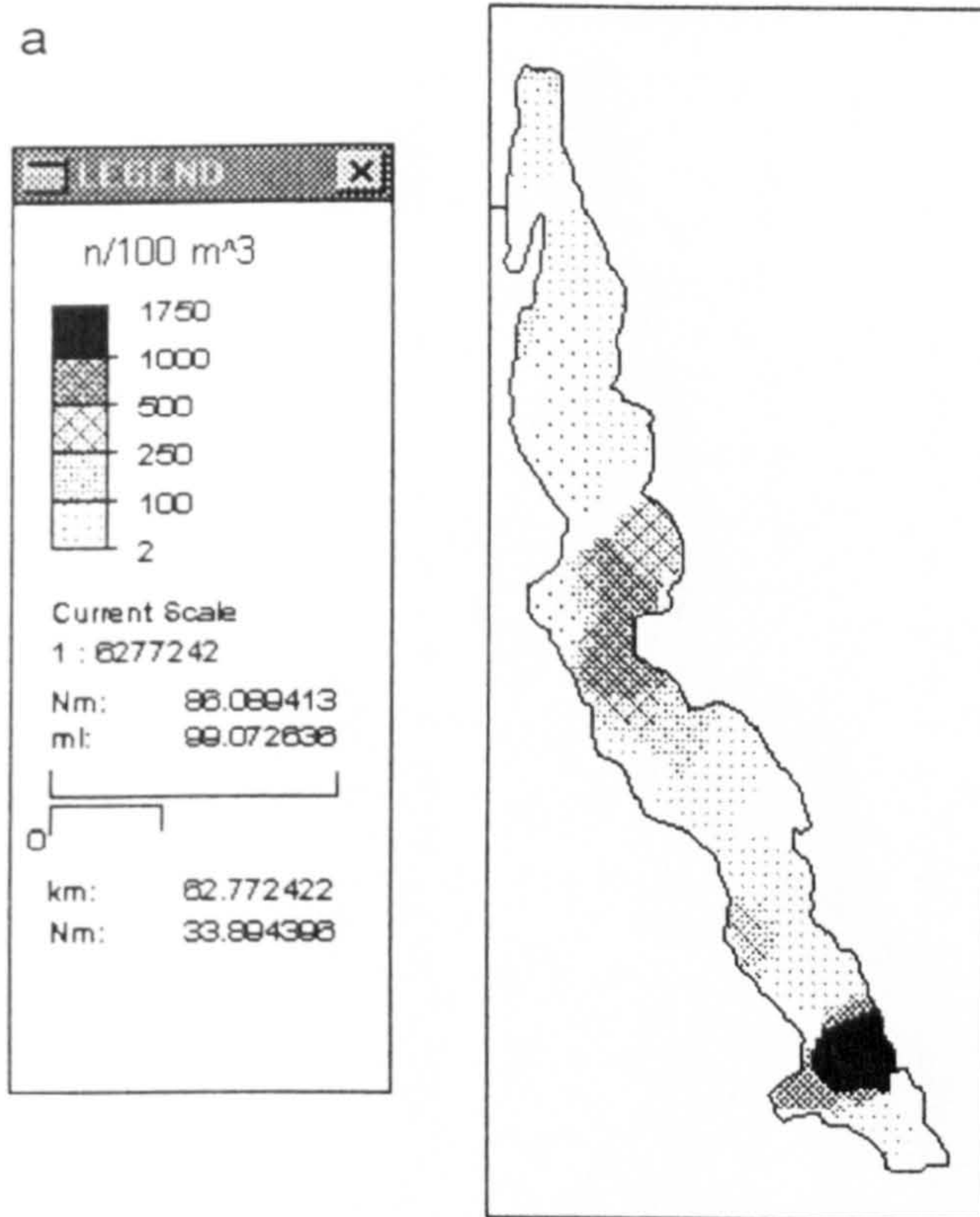


Figure 95. Distribution of *L. parvula* within 0-100 m water column from June (a) and November-December (b) 1995 surveys. Shrimp density ( $\text{no}/100 \text{ m}^3$ ) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal 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).

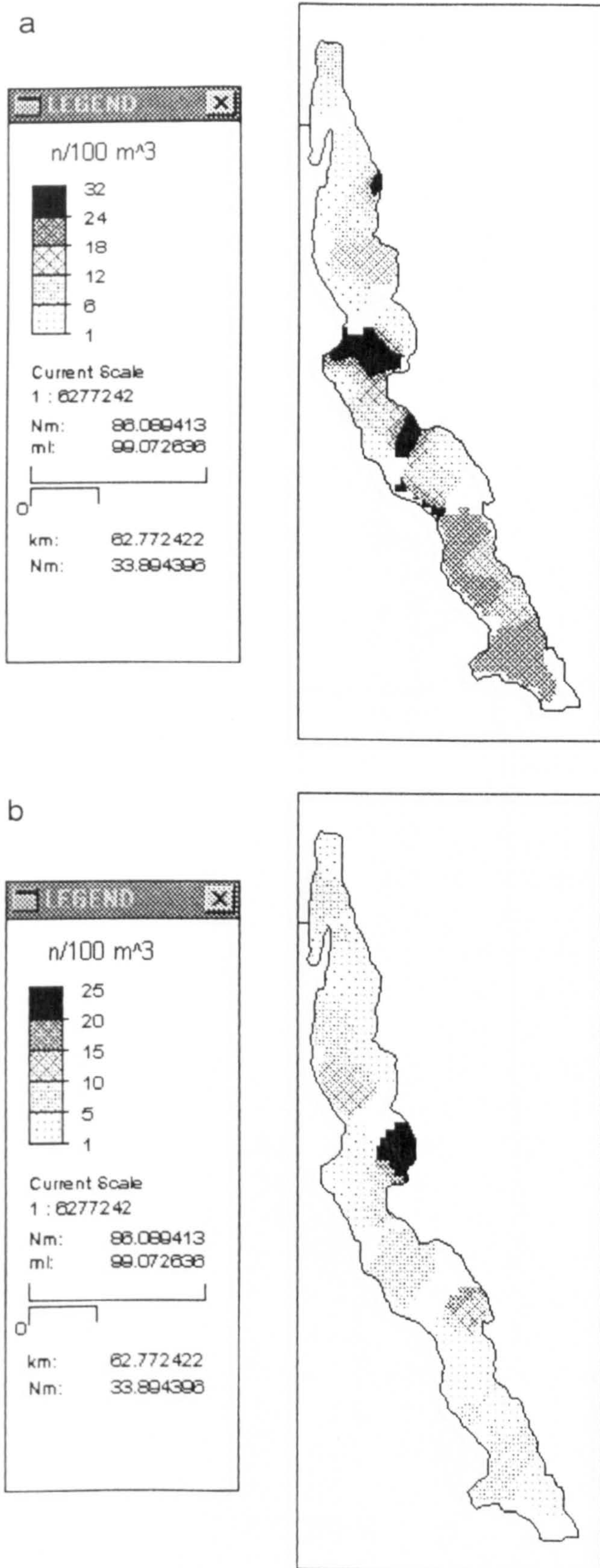


Figure 96. Distribution of *P. moorei* within 0-100 m water column from June (a) and November-December (b) 1995 surveys. Shrimp density (no/100 m<sup>3</sup>) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. 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).



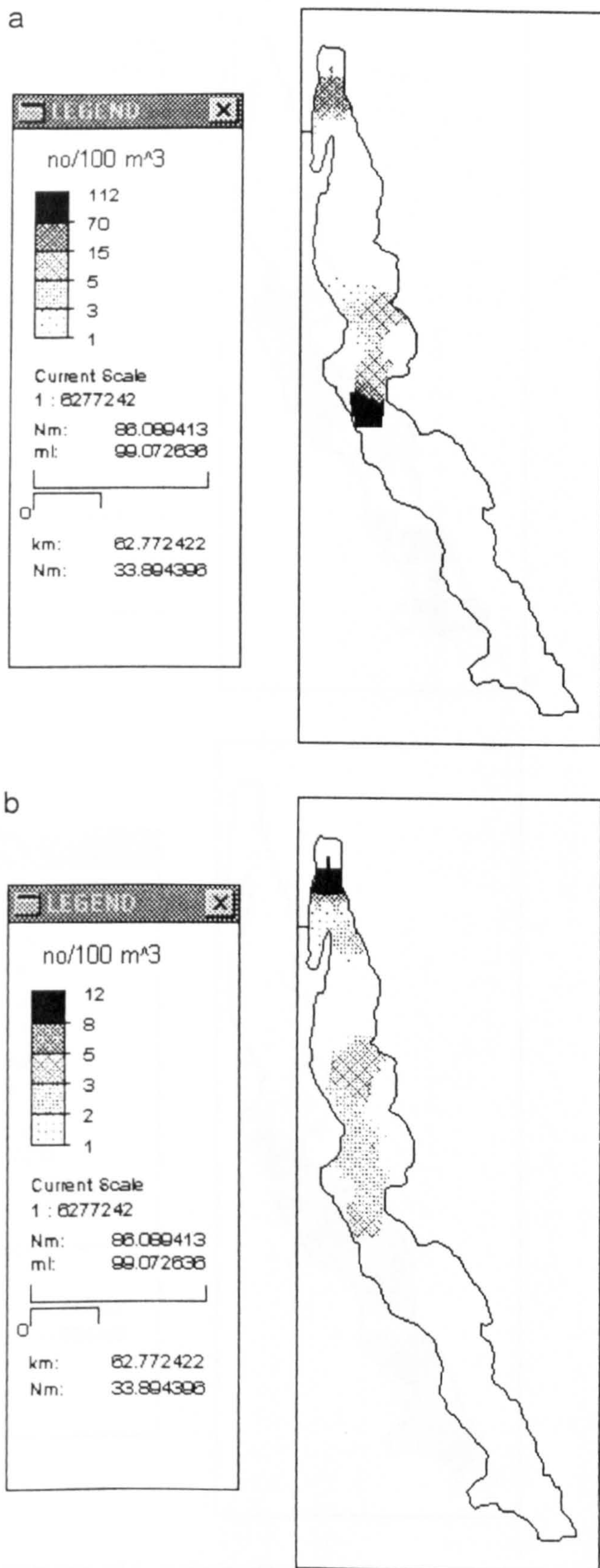
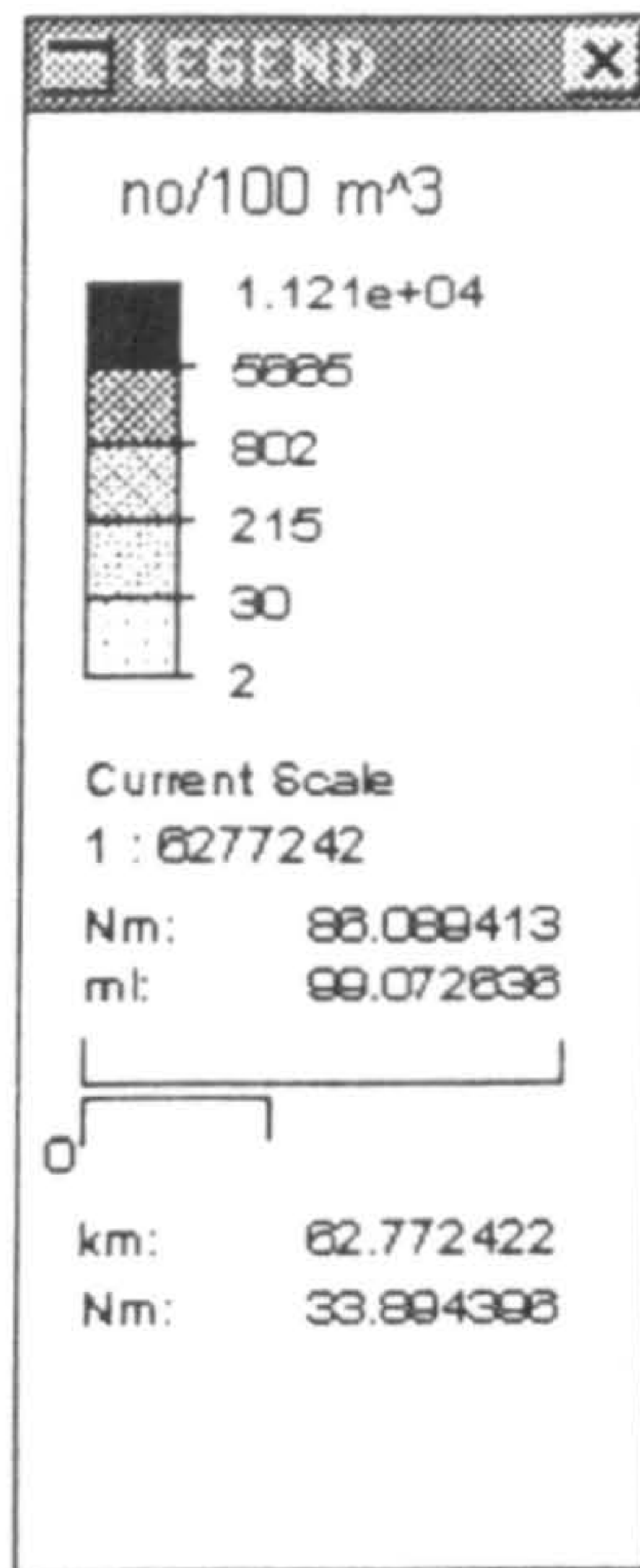


Figure 97. Distribution of *L. parvula* (a) and *P. moorei* (b) within 0-100 m water column from April 1996 survey. Shrimp density (no/100 m<sup>3</sup>) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal intervals**. Blank 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 statute miles (ml).

a



b

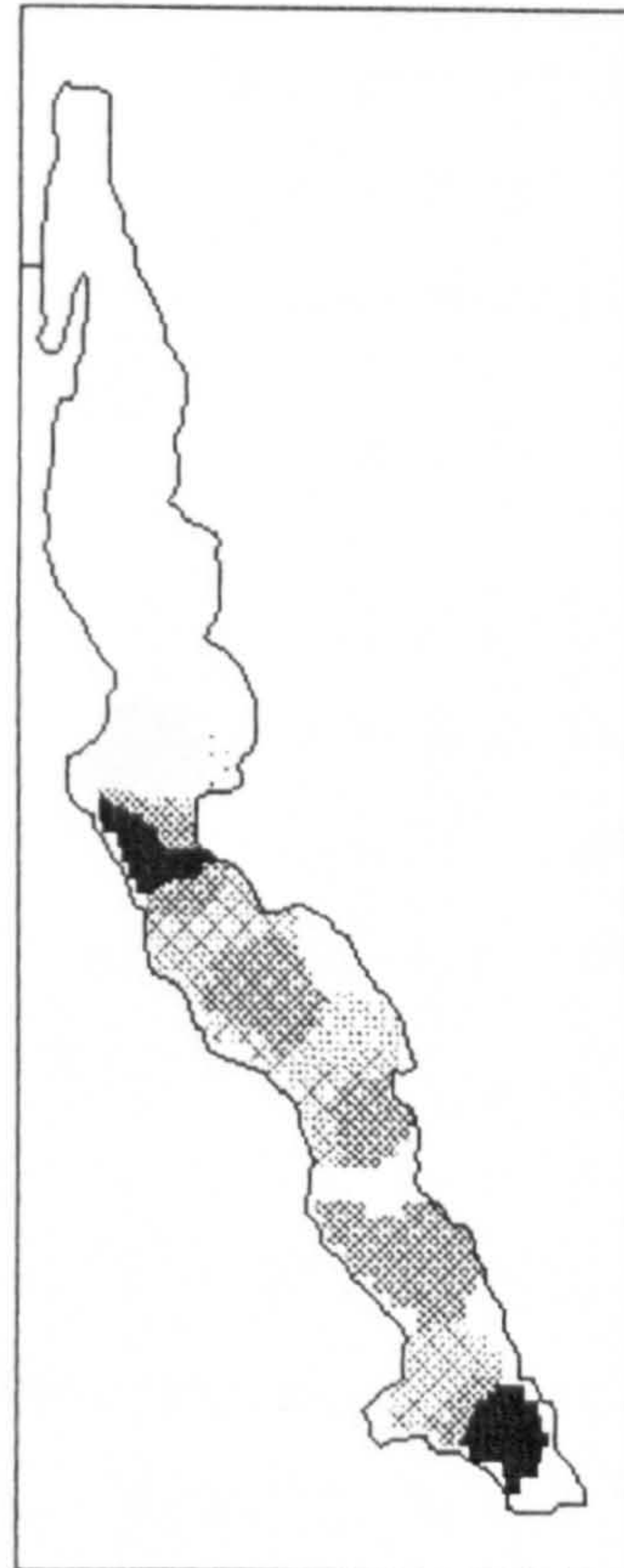
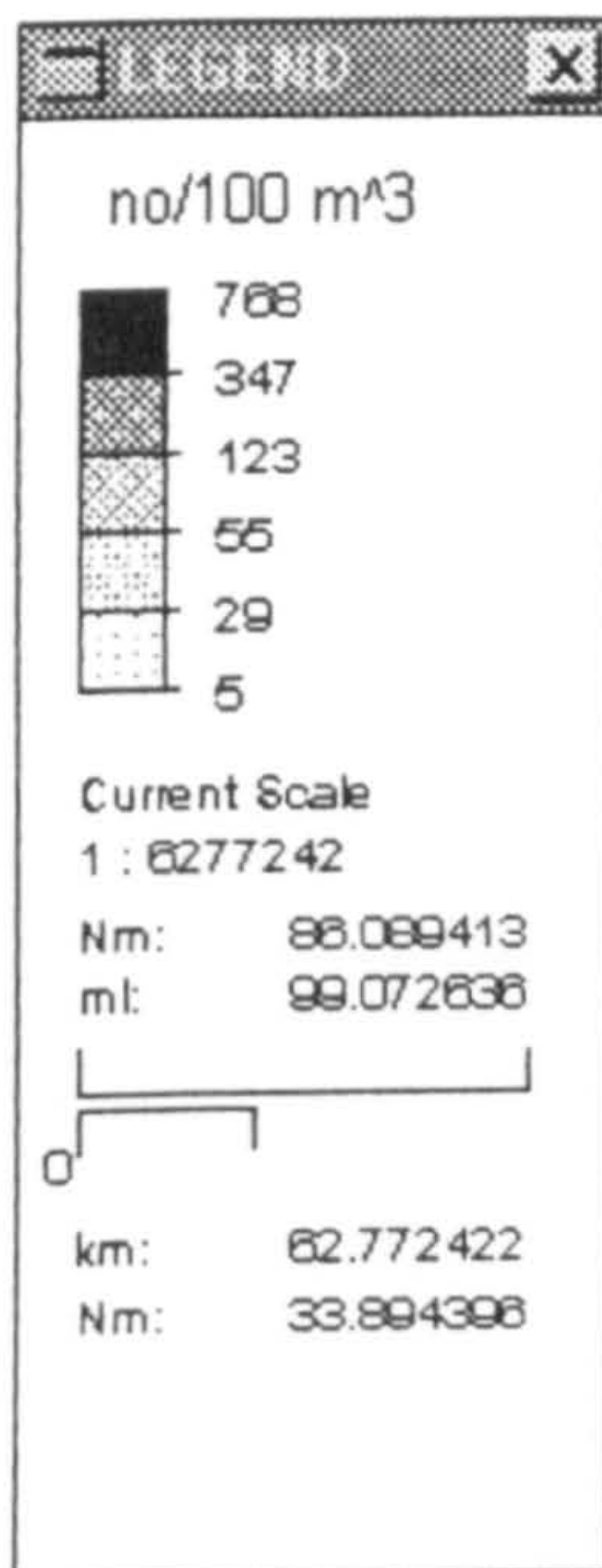


Figure 98. Distribution of *L. parvula* within 0-100 m water column from November-December (a) 1997 and February (b) 1998 surveys. Shrimp density (no/100 m<sup>3</sup>) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal 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 statute miles (ml).

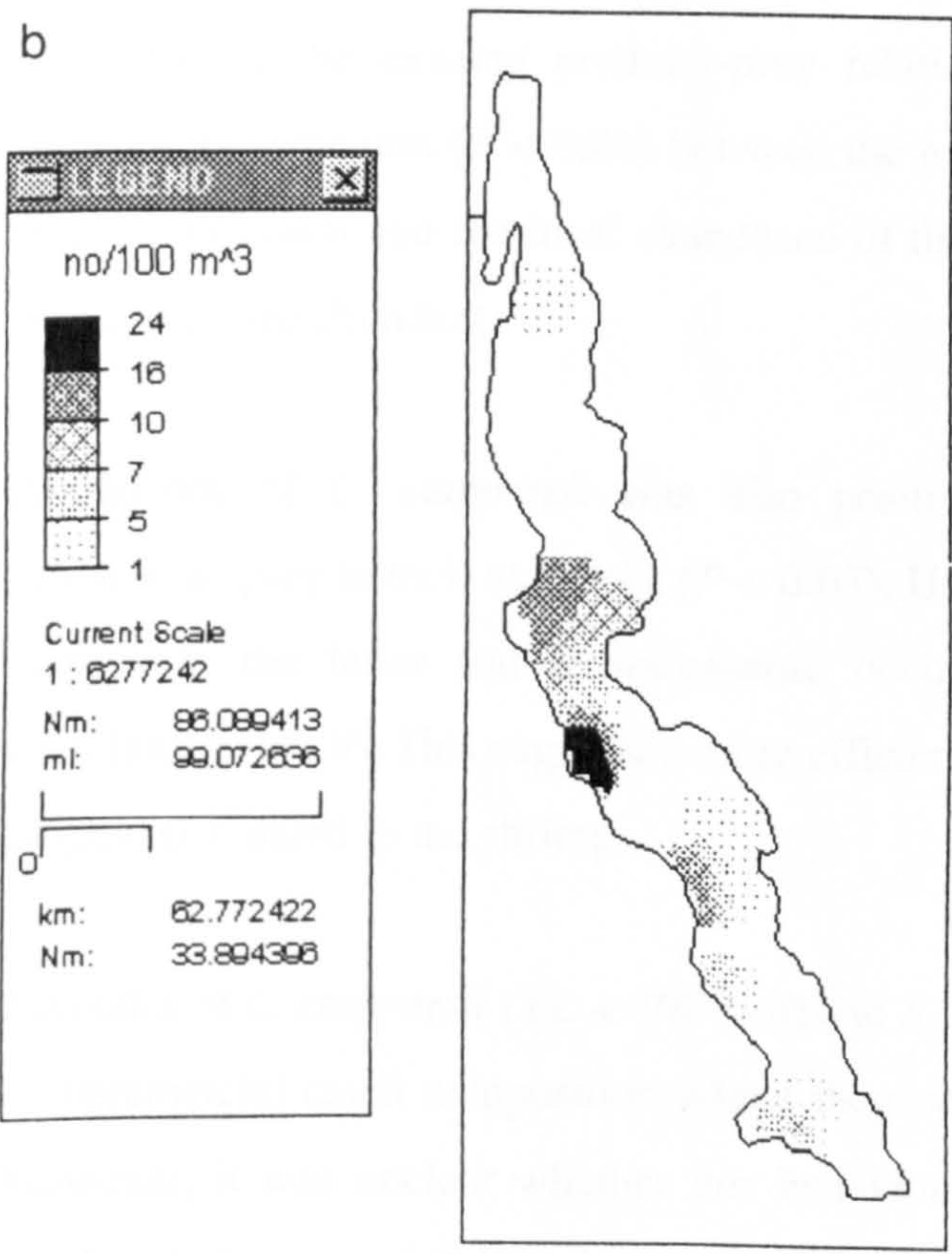
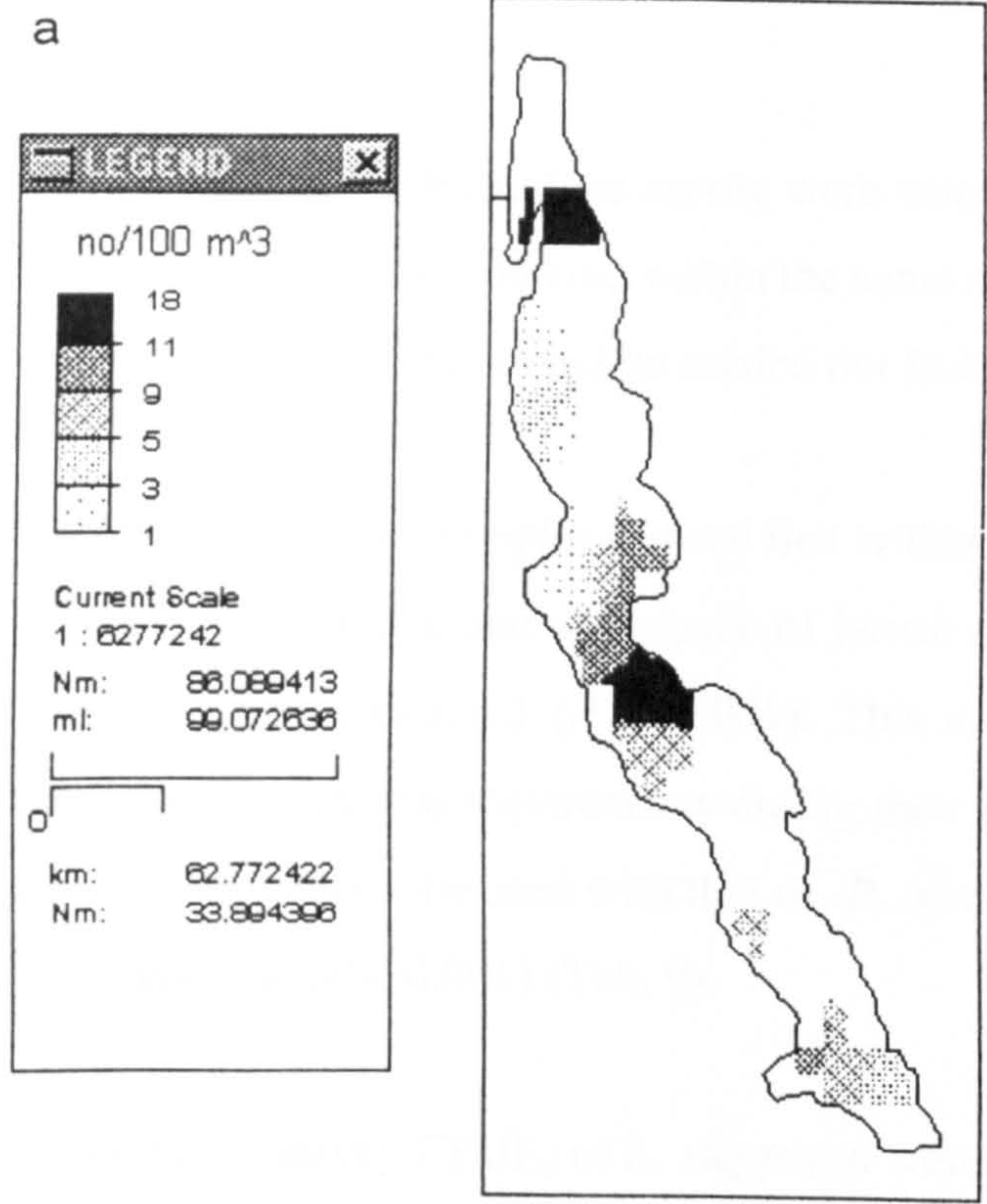


Figure 99. Distribution of *P. moorei* within 0-100 m water column from November-December (a) 1997 and February (b) 1998 surveys. Shrimp density (no/100 m<sup>3</sup>) is grouped in five levels shown in the legend window starting from the lowest number recorded. Note that **pattern scale has unequal 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).

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. tanganyicae* and *L. miodon* were strongly associated ( $P < 0.001$ ). This could suggest that both species have similar environmental requirements 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. tanganyicae* ( $P < 0.001$ ) (Tab. 9).

Catch rates (survey CPUE) of *L. stappersii* were positively correlated with *L. parvula* and *P. moorei* abundance ( $P < 0.01$  and  $P < 0.05$  respectively), and was probably indicative of the existing 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. 9): predators gather where prey are abundant.

Abundance of *L. stappersii* was also positively associated with number of *S. tanganyicae* prey in their stomachs ( $P < 0.05$ ). Unlike the case between shrimps and *L. stappersii*, the latter and *S. tanganyicae* occurrence in the environment was not correlated (Tab. 9). This suggests a more efficient predator avoidance capability of the clupeid compared to the shrimp.

Juveniles of *L. stappersii* (TL < 100 mm) and *S. tanganyicae* are believed, on the basis of commercial catch composition where they occur together, 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. tanganyicae*. Survey CPUE of young *L. stappersii* and *S. tanganyicae*, after logarithmic transformation, showed a high positive correlation ( $P < 0.001$ ; Tab. 9).

Table 9. Correlation coefficients between density ( $n/100\text{ m}^3$ ) 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: \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

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

The relation between mesozooplankton (copepods) and *S. tanganyicae* 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. tanganyicae* (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. tanganyicae*-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. tanganyicae* (CPUE) in the local fishing grounds and the number of copepods (no/m<sup>3</sup>). Catch per unit of effort of *S. tanganyicae* (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. tanganyicae* and copepod abundance are given in Figure 100 (copepod data from Kurki, 1996b). This showed the similarity in the abundance dynamics of the predator and its prey at Bujumbura and Kigoma (Figs 100a and 100b), while Mpulungu data (Fig. 100c) were affected by the initial high values and by the shorter time series available. Also, quantities of *S. tanganyicae* and *L. miodon* in fisheries statistical records are not reported separately but together within the clupeids commercial category.

The scatterplots of original data and the distribution of regression predicted values against residuals (Fig. 101) confirmed that while the correlation observed from Bujumbura and Kigoma data may be substantiated, the one from Mpulungu data should be discarded.

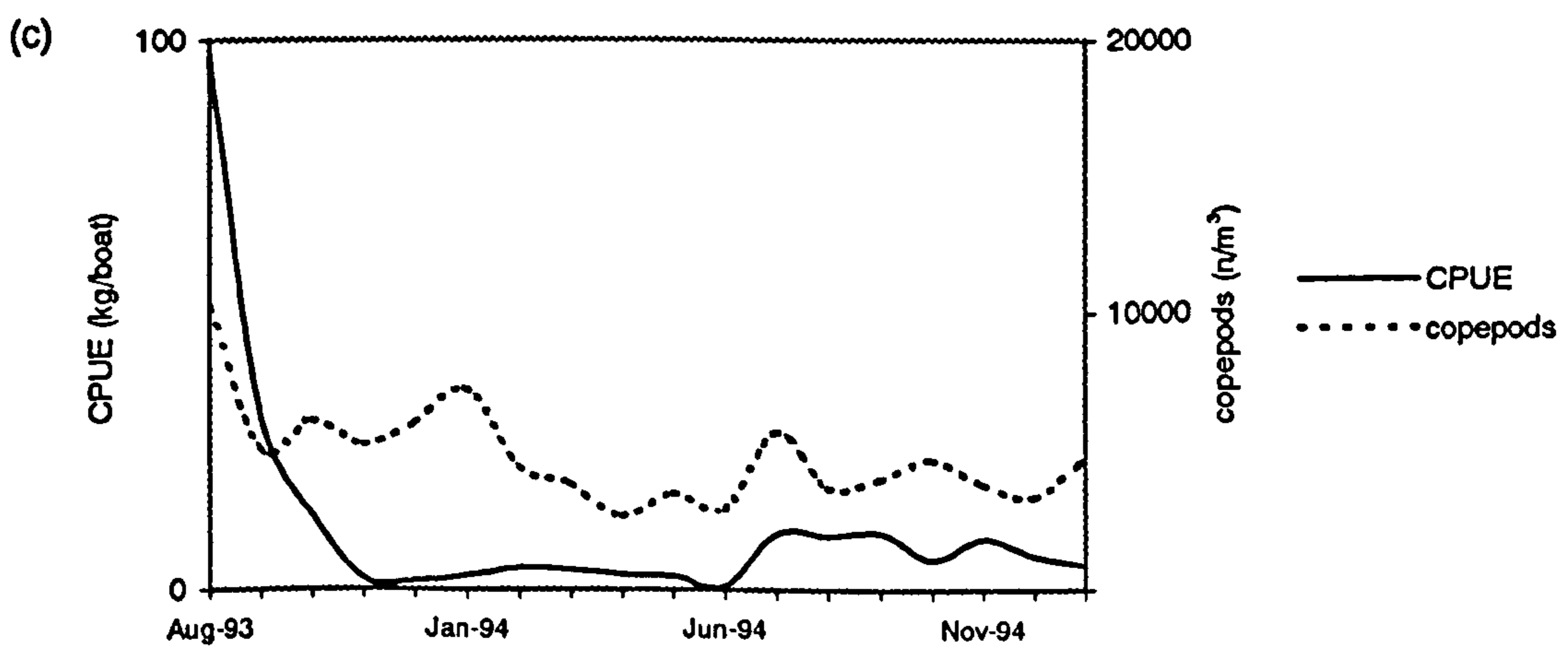
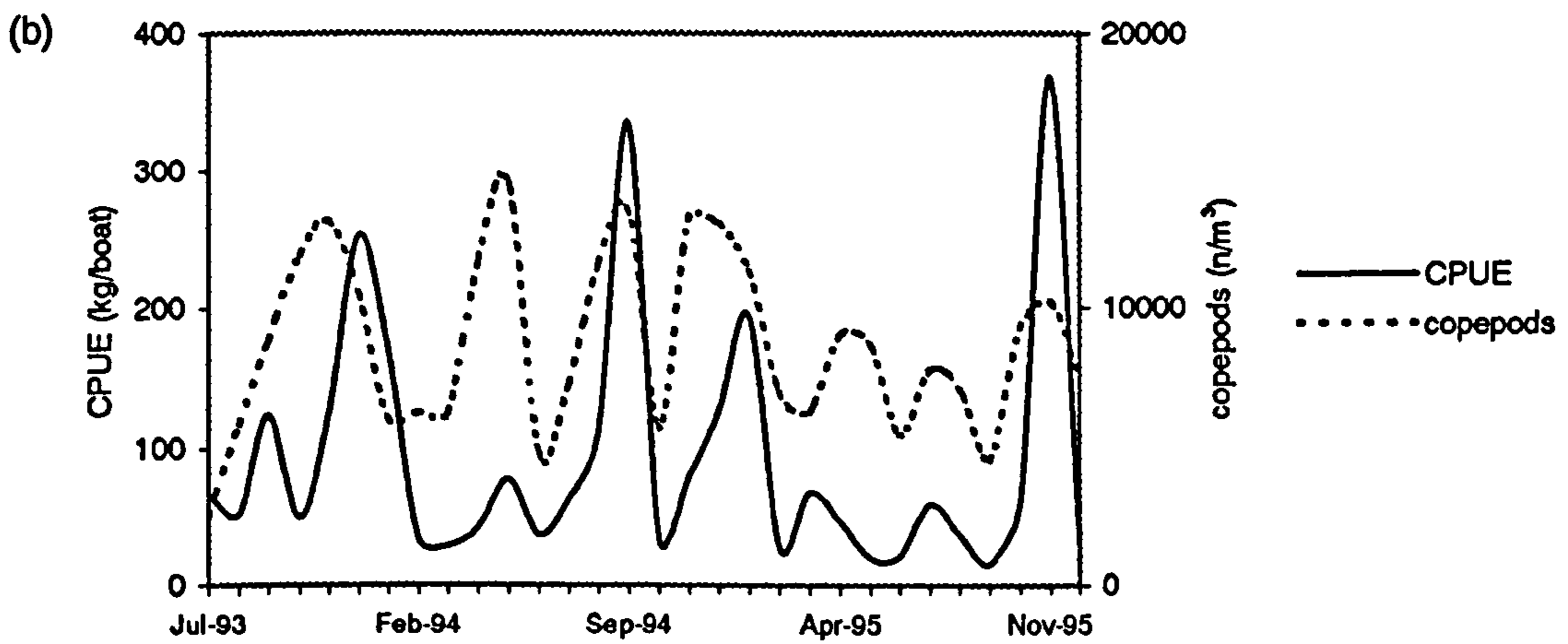
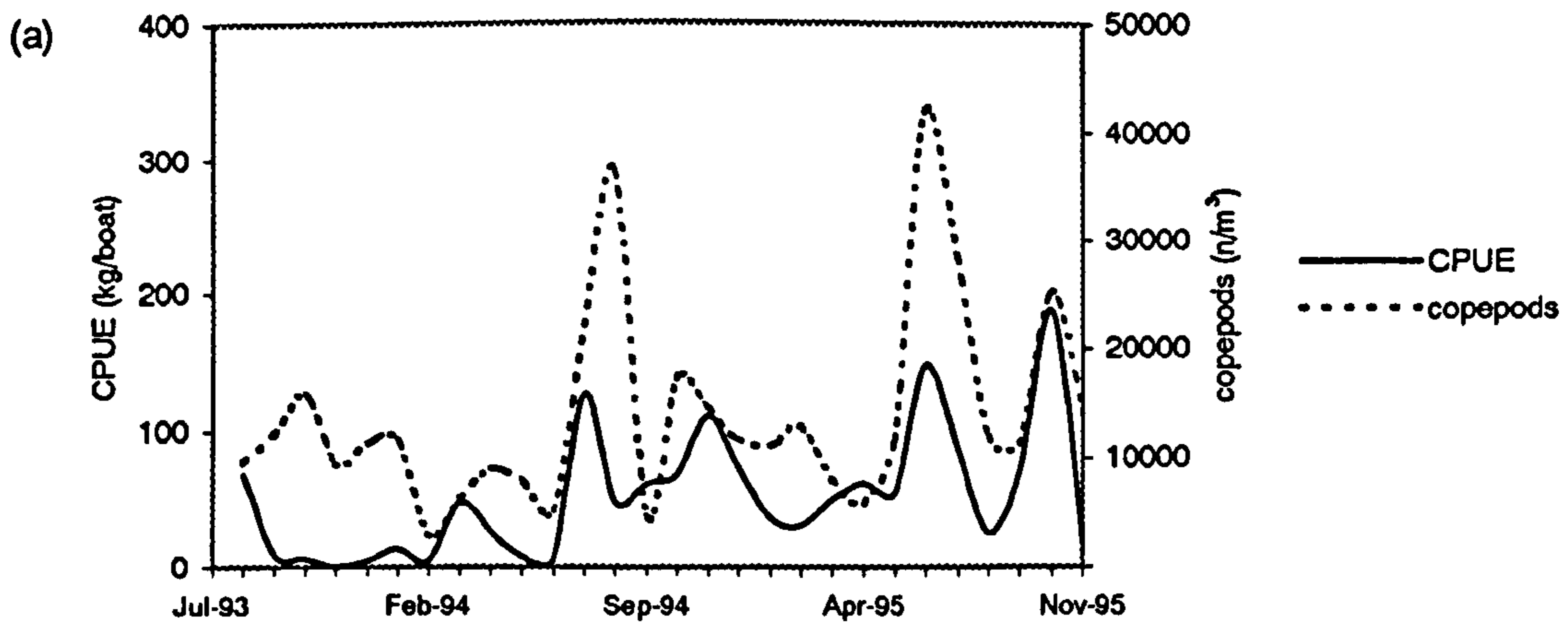


Figure 100. Monthly total number of copepods ( $n/m^3$ ) and mean CPUE (kg/boat) of *S.tanganicae* in Bujumbura (a), Kigoma (b) and mean CPUE of clupeids (both *S. tanganicae* and *L. miodon* unsorted) in Mpulungu (c).

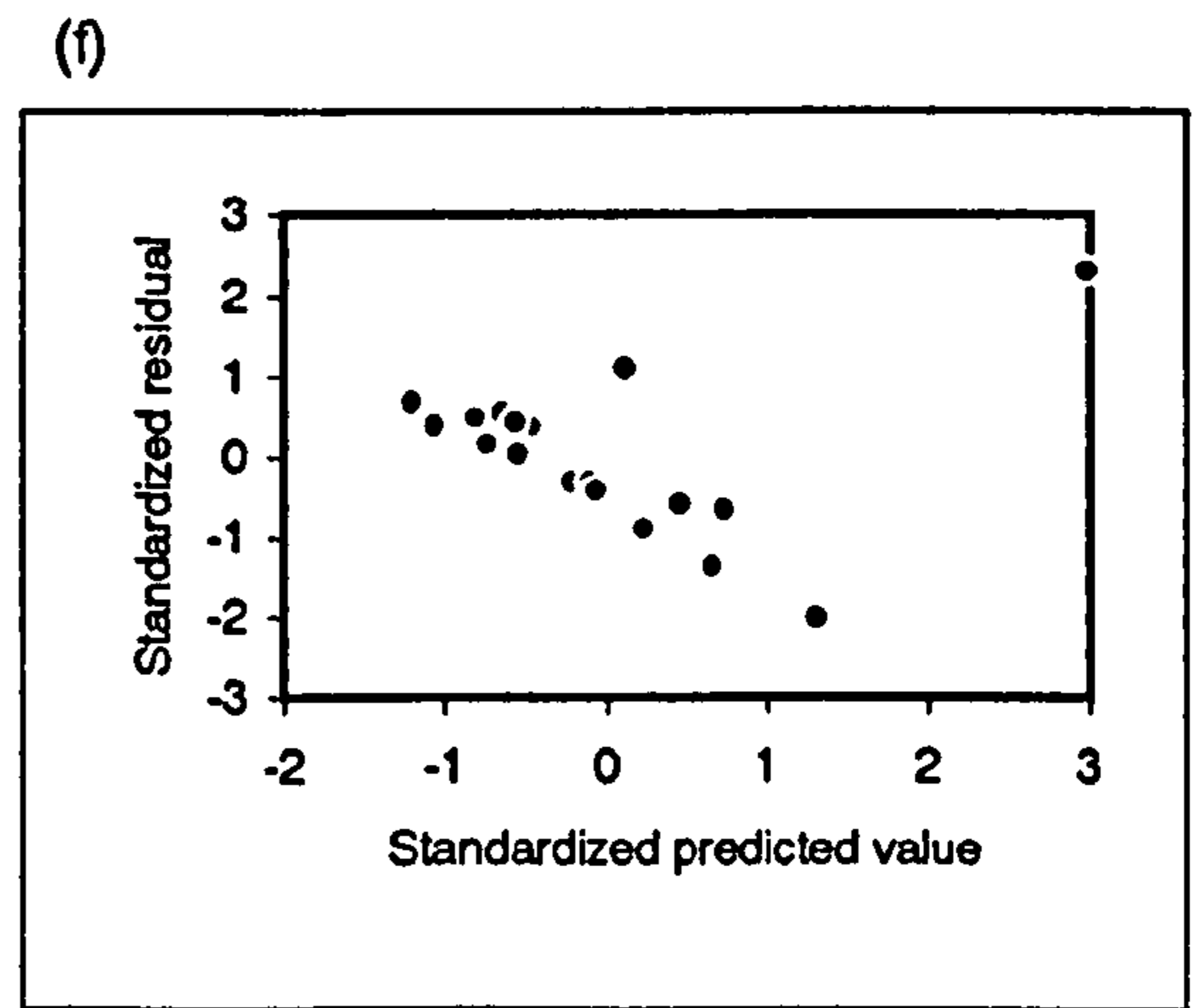
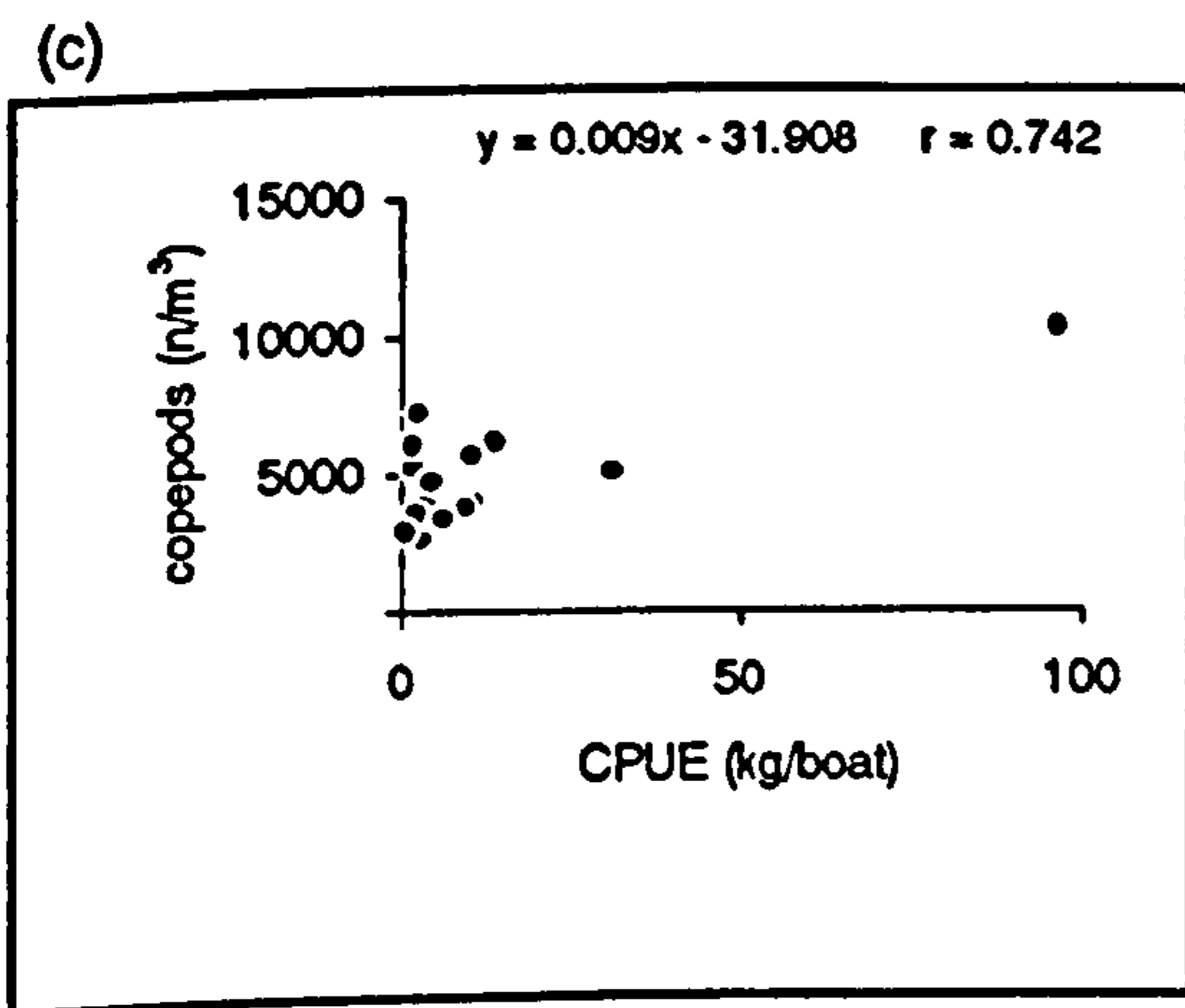
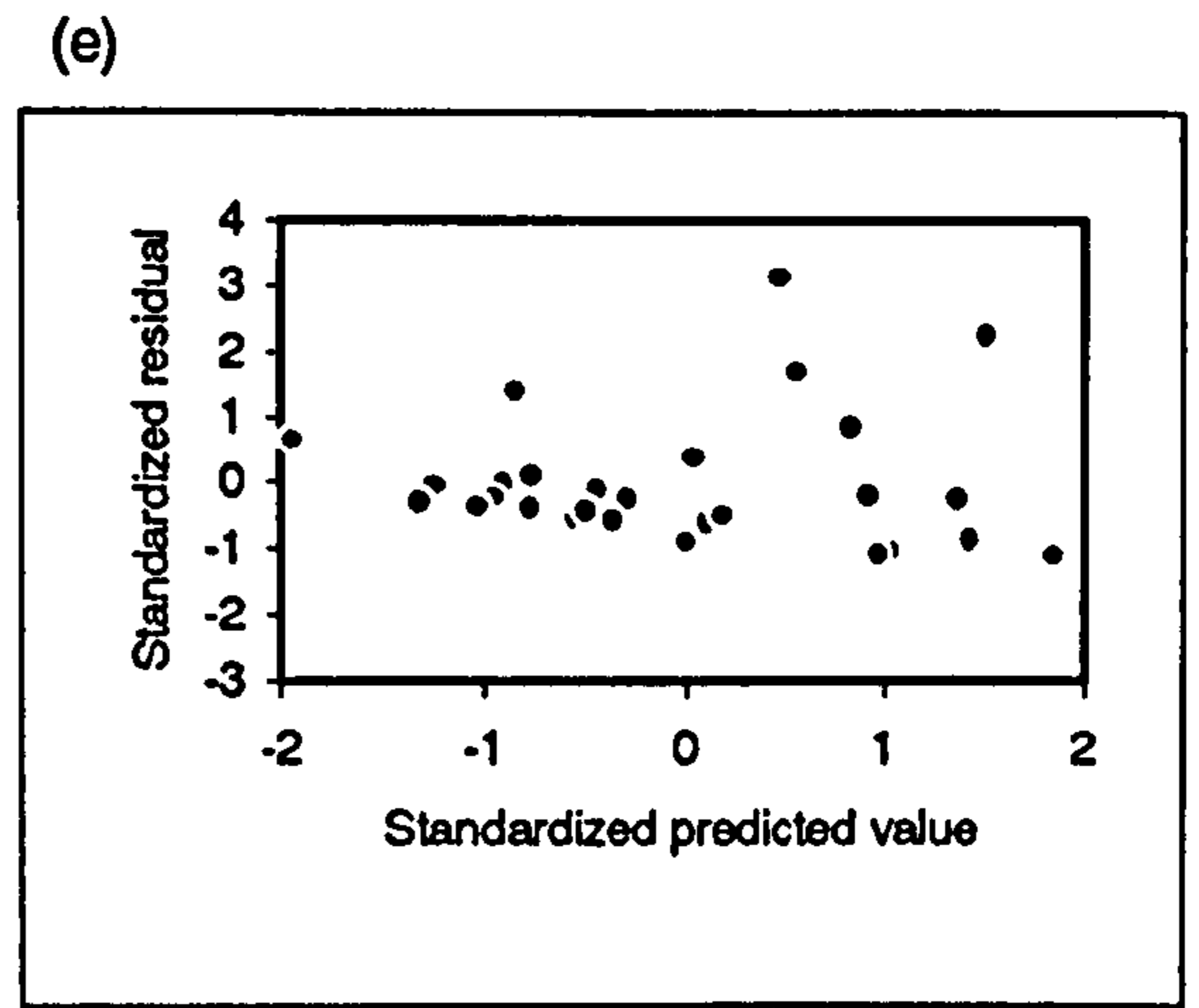
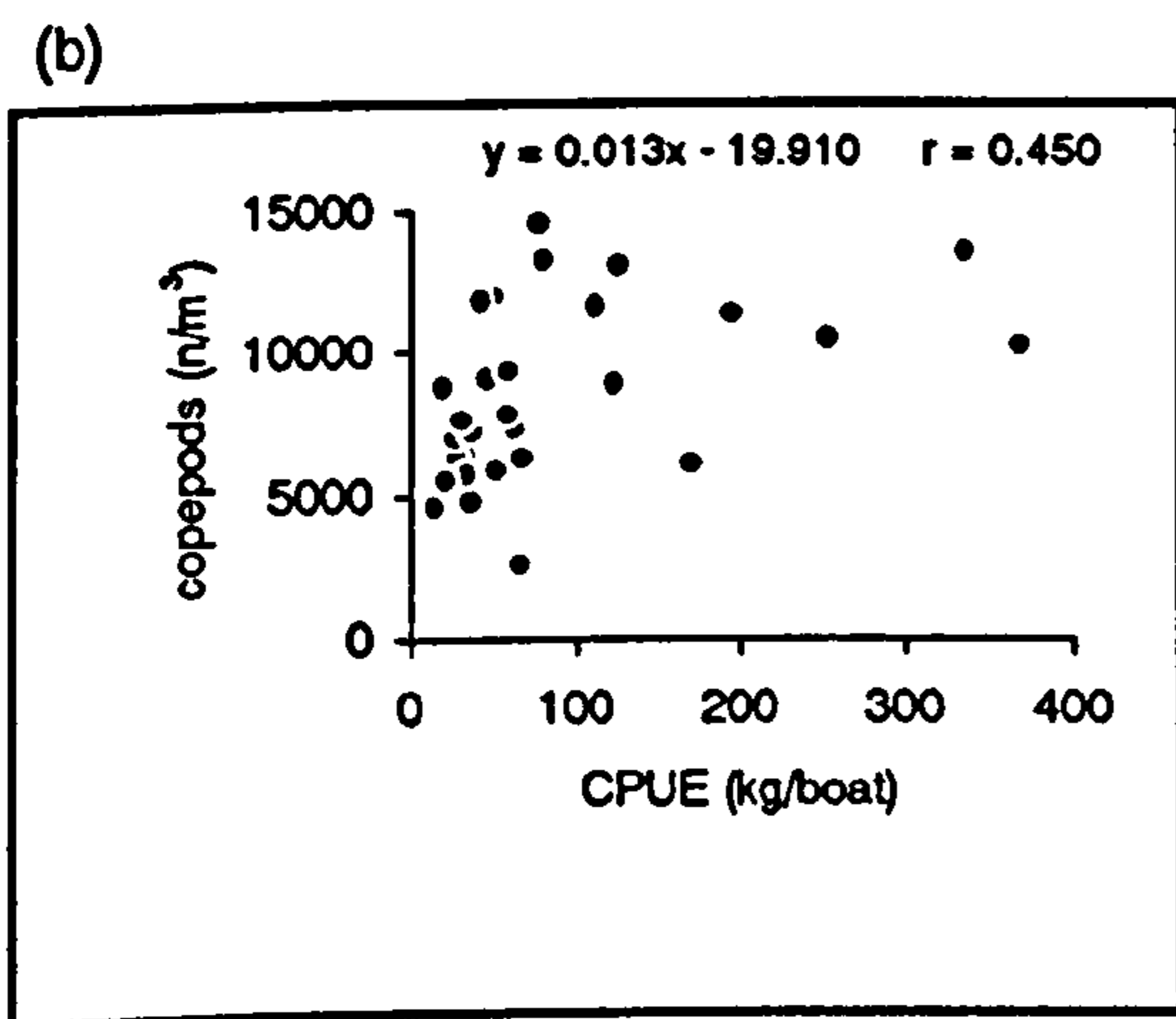
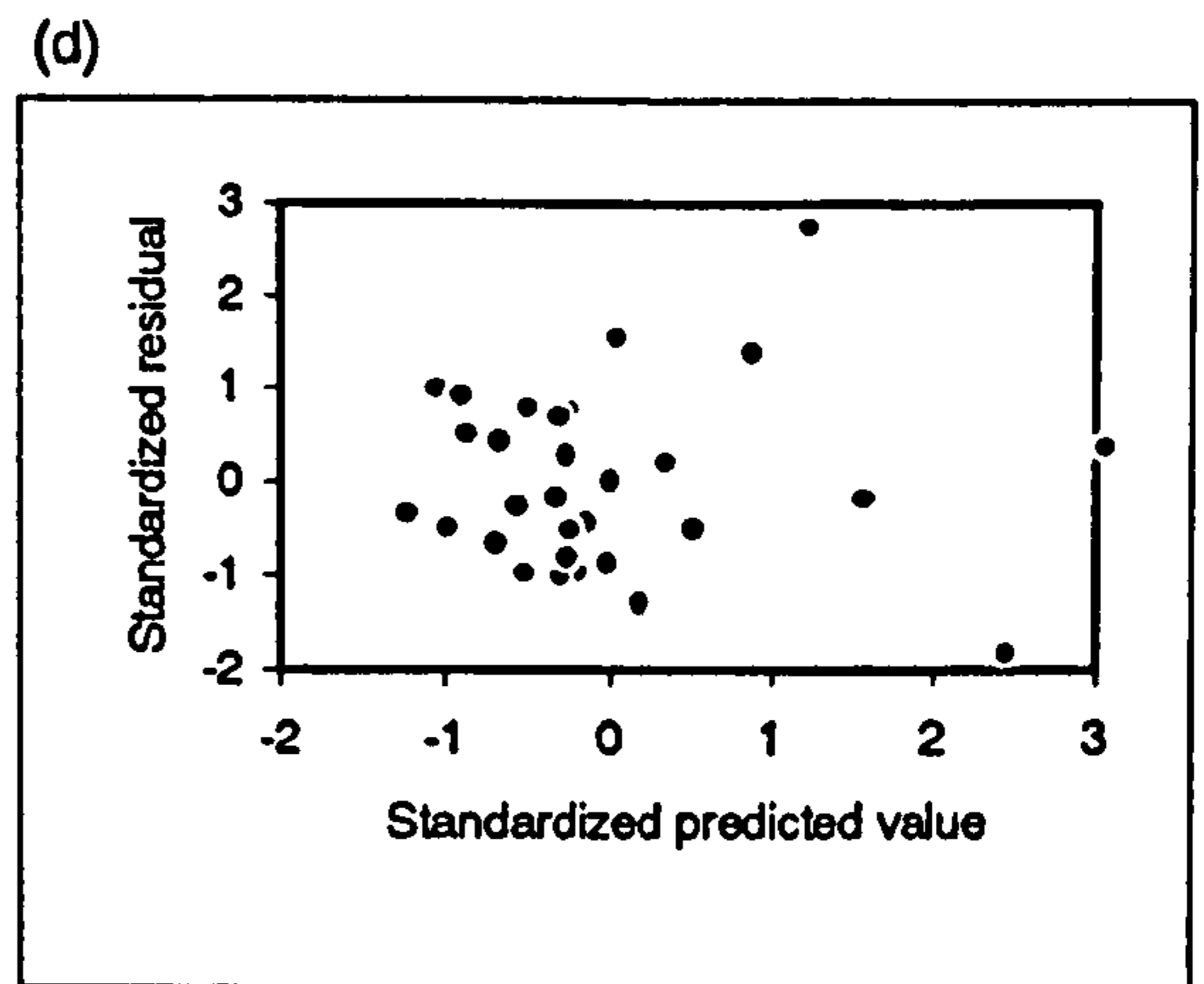
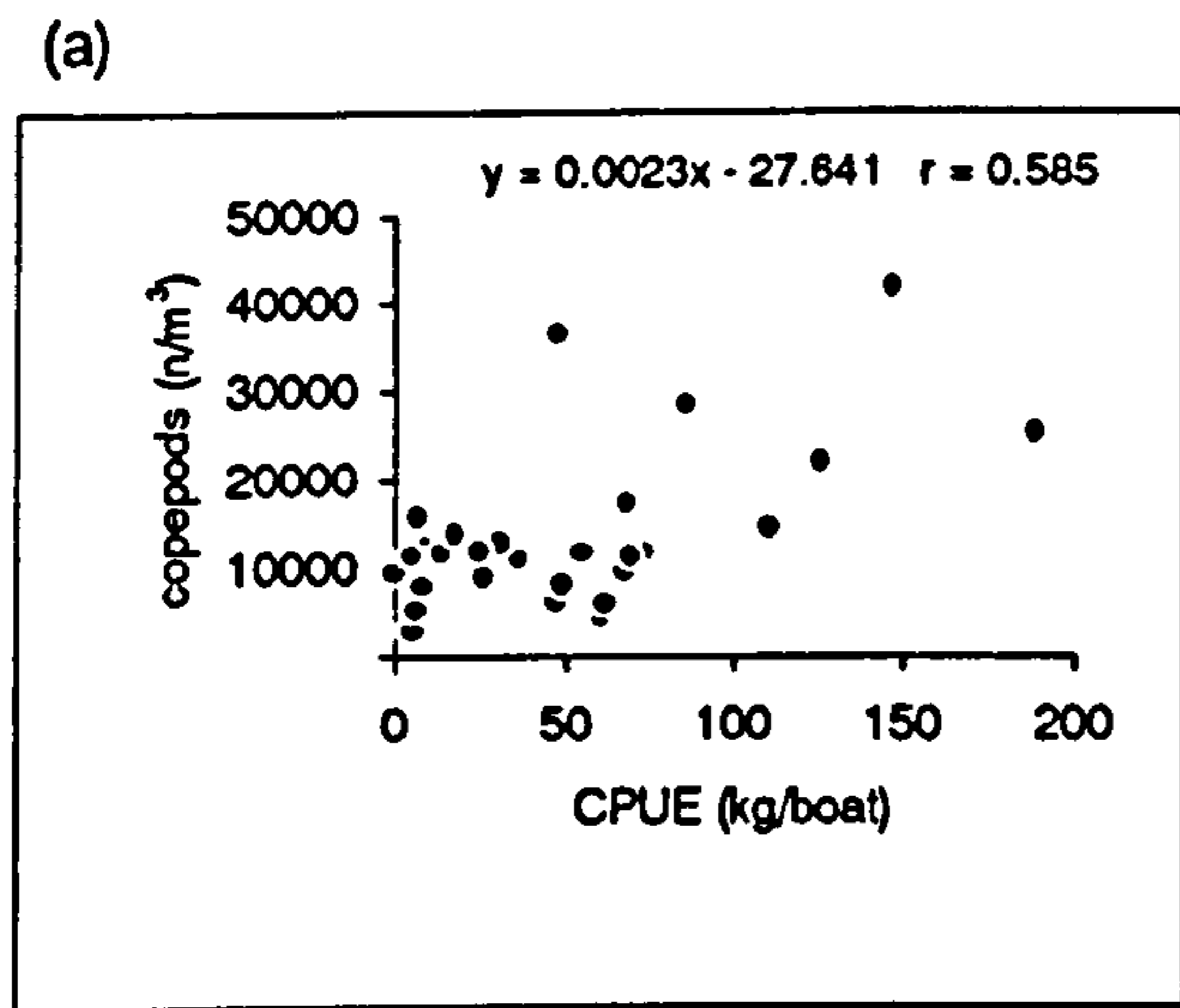


Figure 101. Scatterplot of monthly CPUE (kg/boat) and copepods number ( $n/m^3$ ), and scatterplot of regression predicted values against residuals from Bujumbura (a,d), Kigoma (b, e) and Mpulungu (c,f) data. *Stolothrissa tanganyicae* CPUE data have been used for Bujumbura and Kigoma. Clupeids CPUE (both *S. tanganyicae* and *L. miodon* unsorted) was used in Mpulungu.



### 3.6 Fishery exploitation

Simple biomass models outline the opposing effects of growth and mortality on the biomass of a typical *S. tanganyicae* cohort for the whole of the lake, and of *L. stappersii* cohorts in the Kigoma and Mpulungu areas. The weight of each individual increases through growth, and the number of fish in the cohort decreases through mortality. The biomass of the cohort therefore increases over time to reach a maximum before the cohort starts decaying. The *S. tanganyicae* cohort reaches maximum biomass at 5 months when the fish begin to be fully recruited to the fishery (Fig. 102). The *L. stappersii* cohort at Kigoma is exploited from 6 months (100 mm TL) but fishing mortality is low (Fig. 103). The *L. stappersii* stock at Mpulungu enters the exploited phase later at c. 18 months (230 mm TL) but fishing effort there is very intense resulting in a sharp biomass decline (Fig. 104).

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

This predictive model must be used with caution. Firstly, it is based on the unlikely assumption that there is no relationship between the size of the parental fish stock and its offspring. Secondly, the output of the yield-per-recruit analysis applies to equilibrium situations. It is rarely, if ever, true that fish stocks are at equilibrium (Hilborn and Walters, 1992), and particularly so for short-lived fish.

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

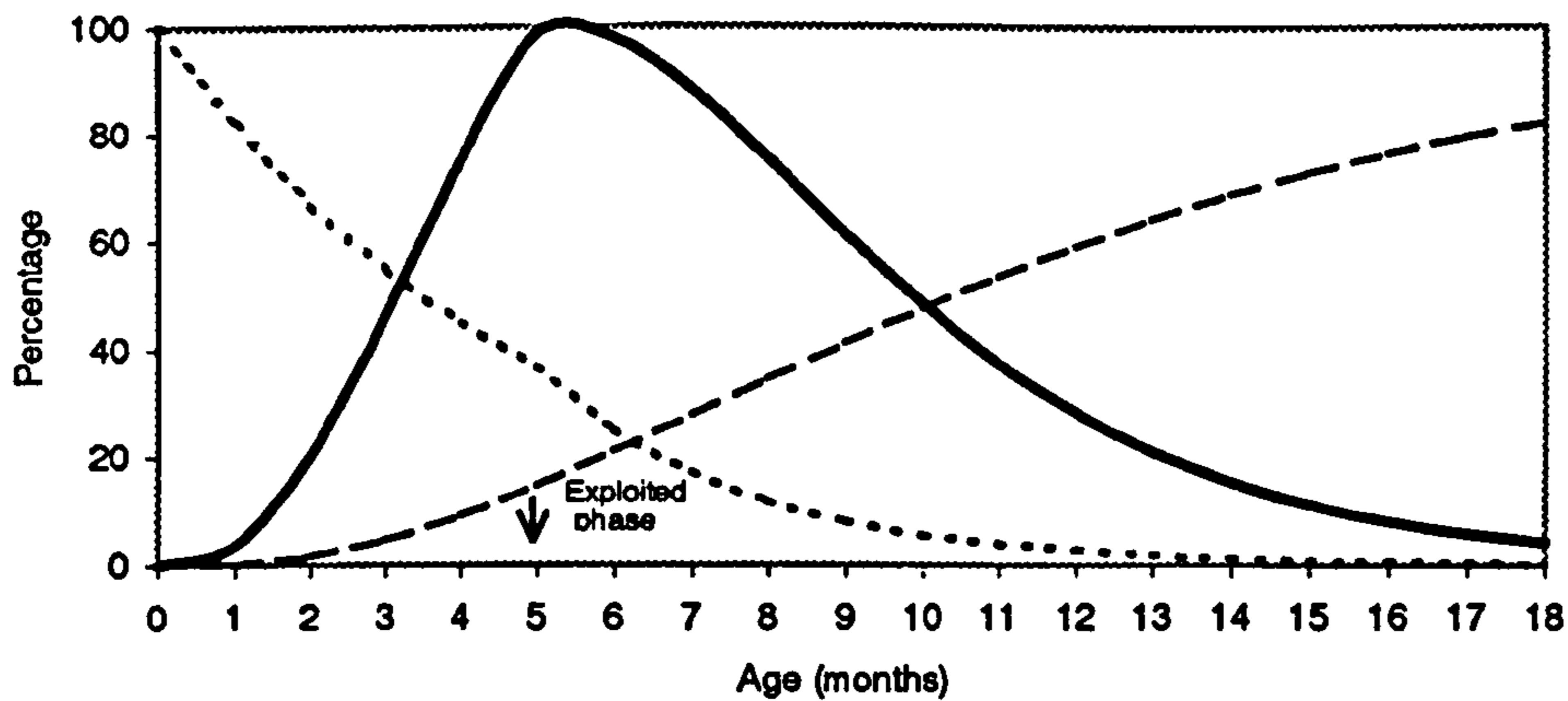


Figure 102. Relative numbers surviving (-----) and individual growth in weight (---), and cohort biomass (—), expressed as percentages of the maximum values against age for *S. tanganycae* (whole lake);  $L_{\infty} = 108 \text{ mm}$ ,  $K = 1.86 \text{ yr}^{-1}$ ,  $Z = 4.9 \text{ yr}^{-1}$ ,  $F = 2.16 \text{ yr}^{-1}$ ,  $W = 4.04^{-6} * TL^{3.11}$ .

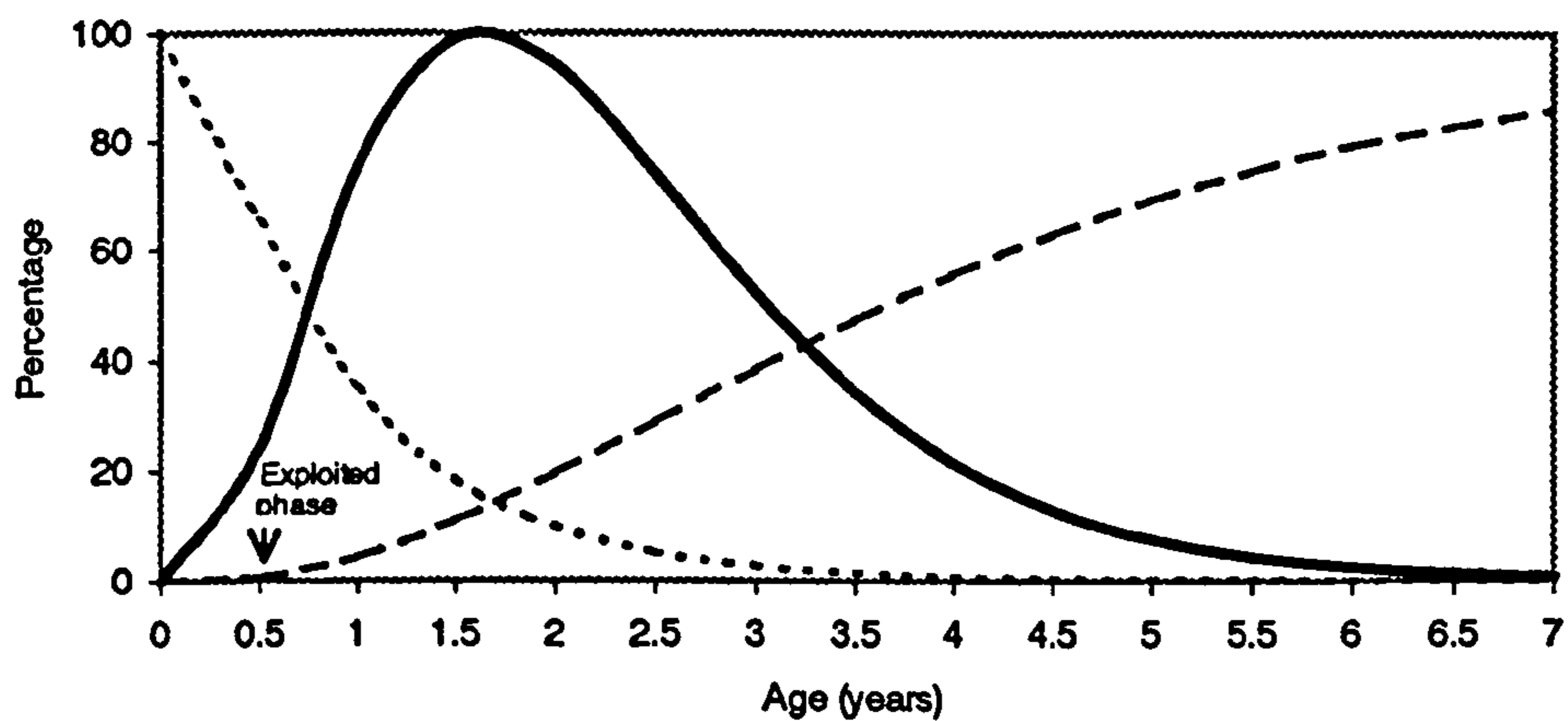


Figure 103. Relative numbers surviving (-----) and individual growth in weight (---), and cohort biomass (—), expressed as percentages of the maximum values against age for *L. stappersii* (Kigoma).  $L_{\infty} = 513 \text{ mm}$ ,  $K = 0.43 \text{ yr}^{-1}$ ,  $Z = 1.27 \text{ yr}^{-1}$ ,  $F = 0.42 \text{ yr}^{-1}$ ,  $W = 6.8^{-6} * TL^{2.99}$ .

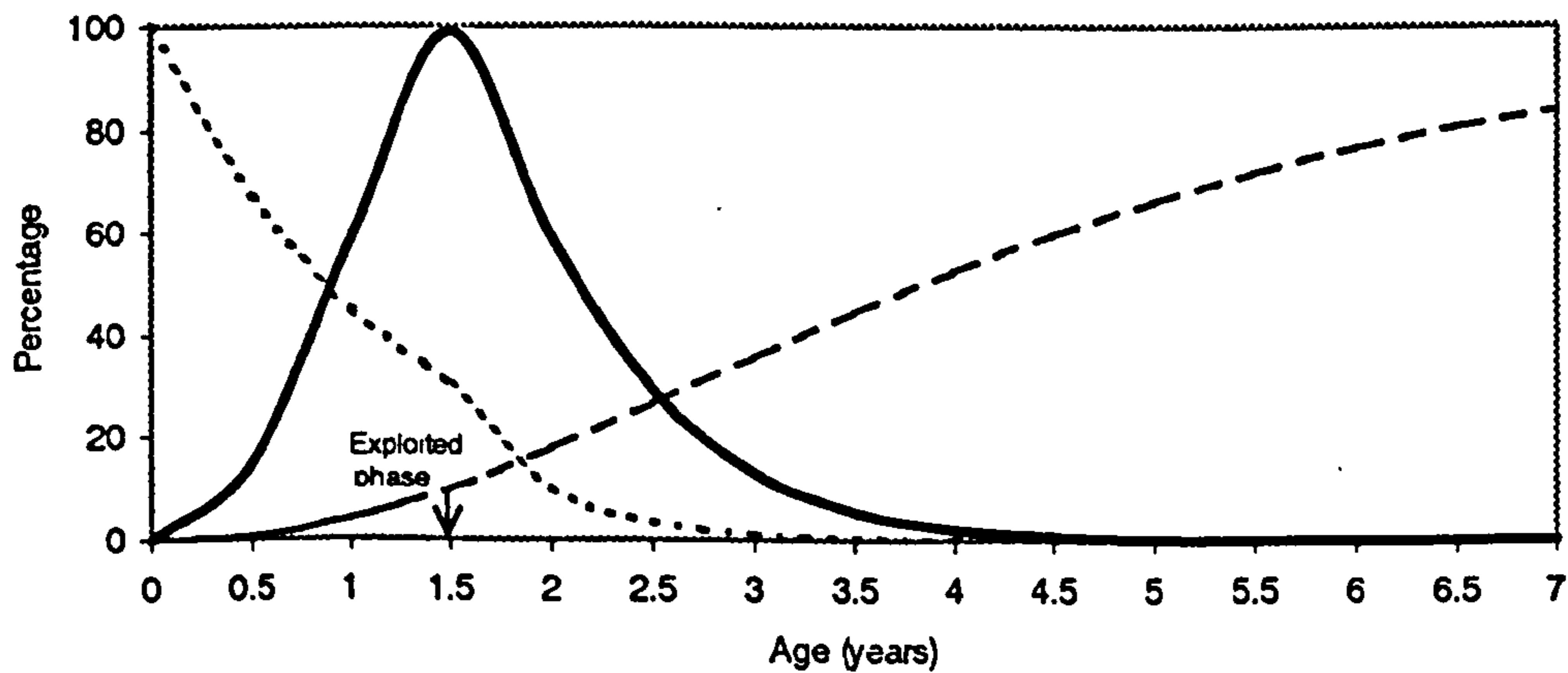


Figure 104. Relative numbers surviving (-----) and individual growth in weight (---), and cohort biomass (—), expressed as percentages of the maximum values against age for *L. stappersii* (Mpulungu).  $L_{\infty} = 520 \text{ mm}$ ,  $K = 0.41 \text{ yr}^{-1}$ ,  $Z = 2.23 \text{ yr}^{-1}$ ,  $F = 1.43 \text{ yr}^{-1}$ ,  $W = 6.8^{-6} * TL^{2.99}$ .

Despite  $L_c < L_m$  *S. tanganyicae* does not appear yet to be overexploited in the lake (Fig. 105). However, current rates of exploitation are close to  $E_{max}$  ( $E_{max}$  is the value of  $E$  associated with the highest  $Y'/R$  value for a given value of  $L_c$ ) and above the reference point<sup>1</sup> which reduces the relative biomass-per-recruit ( $B'/R$ ) to half its unfished level (when  $F$  or  $E = 0$ ) (Gulland, 1983).

No assessment can be made for *L. miodon*. The overestimation of  $Z$  determines unrealistically high  $F$  and, consequently,  $E$  rates. Relative  $Y'/R$  curves in Figure 106 are given only for the sake of comparison between the exploitation patterns in Bujumbura and Mpulungu which are characterised by different length at entry into the respective fisheries. As it can be expected, the very small length at entry into the beach seine fishery in the south has a marked negative impact on both yield and biomass.

The shape of the  $Y'/R$  curve of *L. stappersii* at Kigoma and Mpulungu (Fig. 107) highlights the effect of the different length at entry of the two fisheries. Currently, *L. stappersii* is lightly exploited in the Kigoma area, although the small  $L_c$  would make it easily vulnerable in the case of increased fishing mortality. The concentration of industrial fishing effort on adult *L. stappersii* in the south results in intensive exploitation and current  $E$  exceeds  $E_{max}$  corresponding to  $B'/R$  well below 50% of the unfished stock. This indicates that further increase of fishing effort (or  $F$ ) would not be sustainable.

There is some concern about the reliability of commercial fishery data from small pelagic shoaling species to represent the true population. The meaningfulness of commercial CPUE as a measure of the relative abundance of the stock can be misleading. Moreover, the high mobility of schooling species and the size-related structure of the schools may further reduce the quality of fishery-dependent information.

---

<sup>1</sup> Reference point defined *sensu* Caddy and Mahon (1995) as “a conventional value, derived from a technical analysis, which represents a state of the fishery or population, and whose characteristics are believed to be useful for the management of the unit stock”.

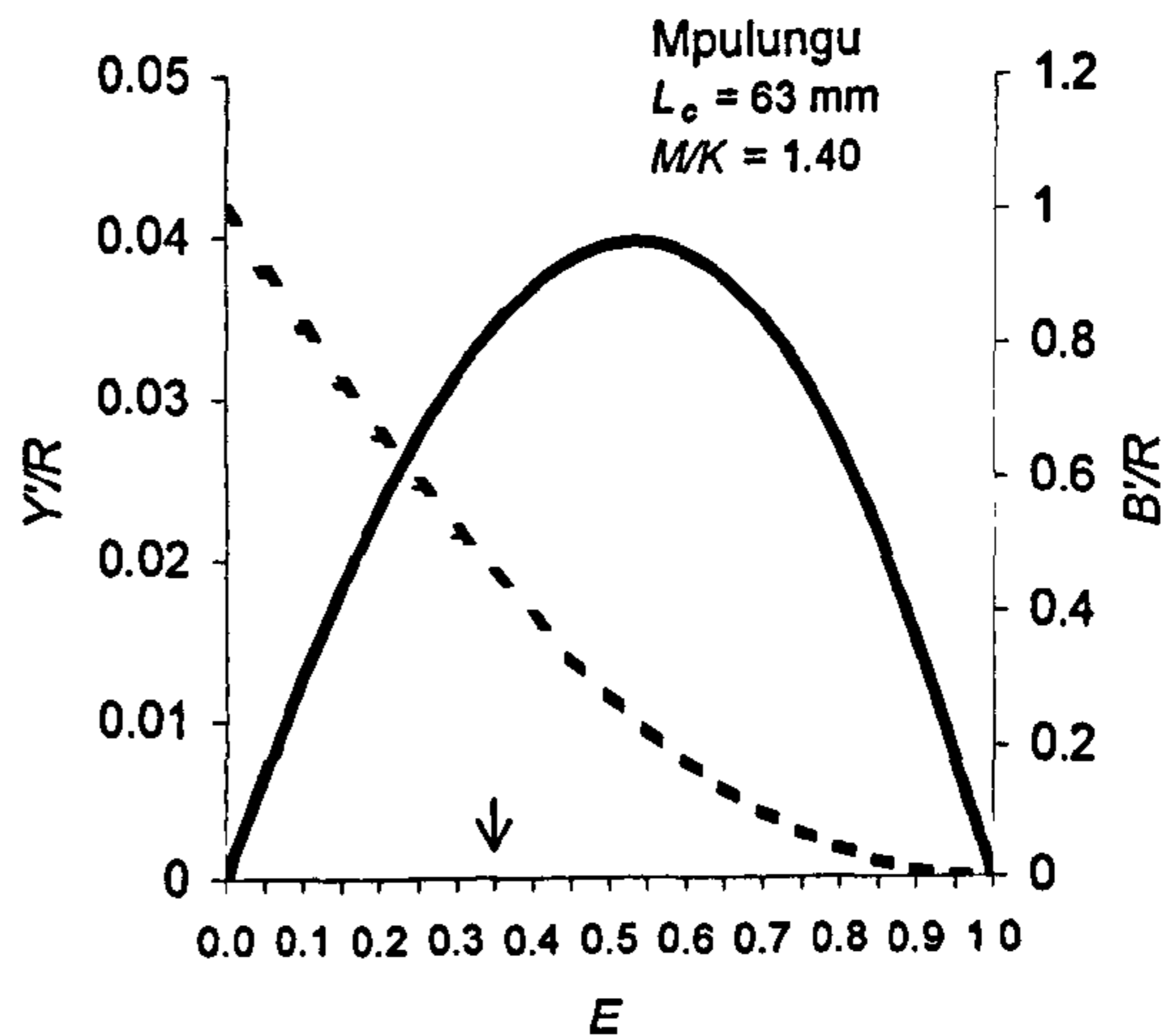
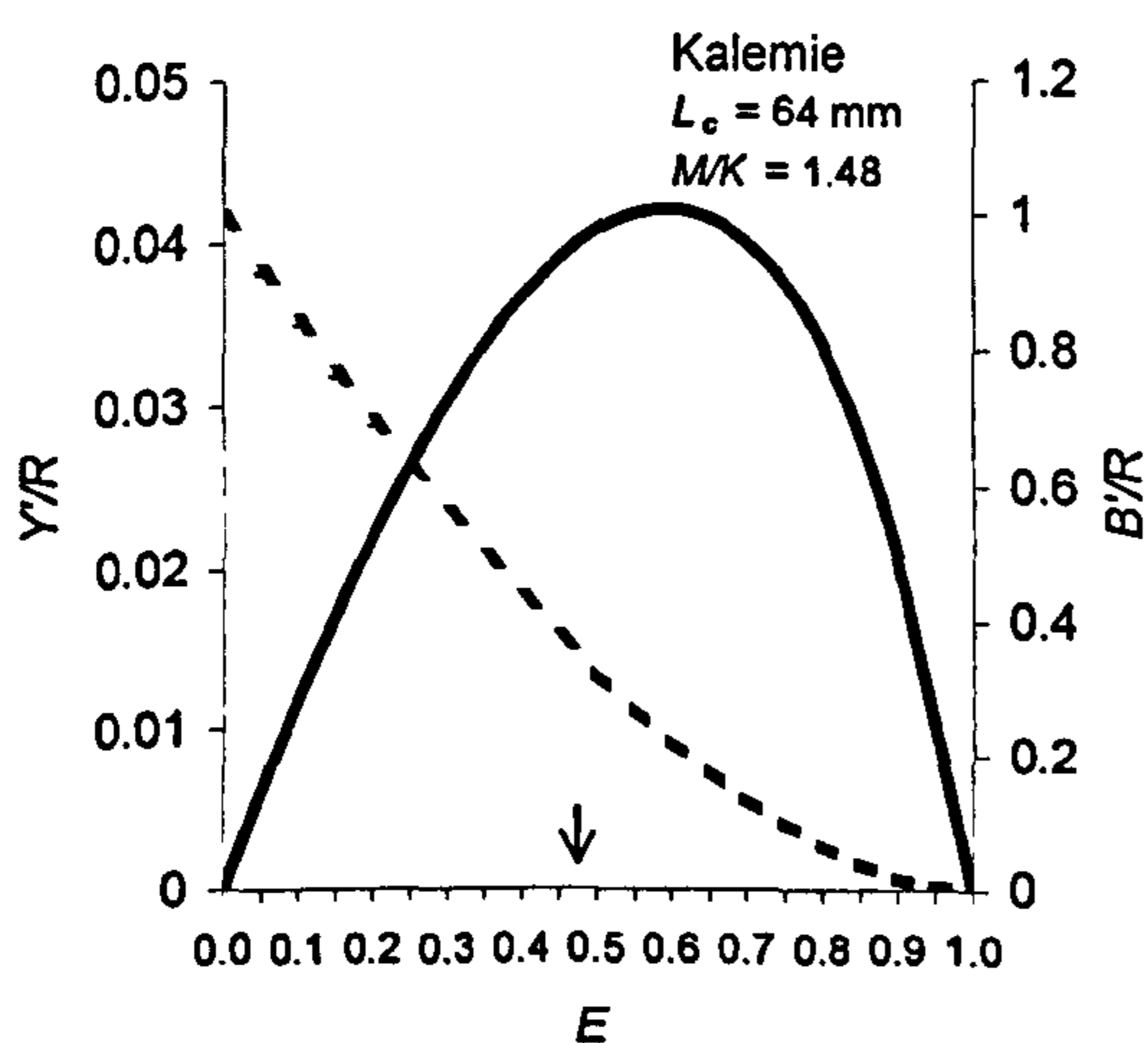
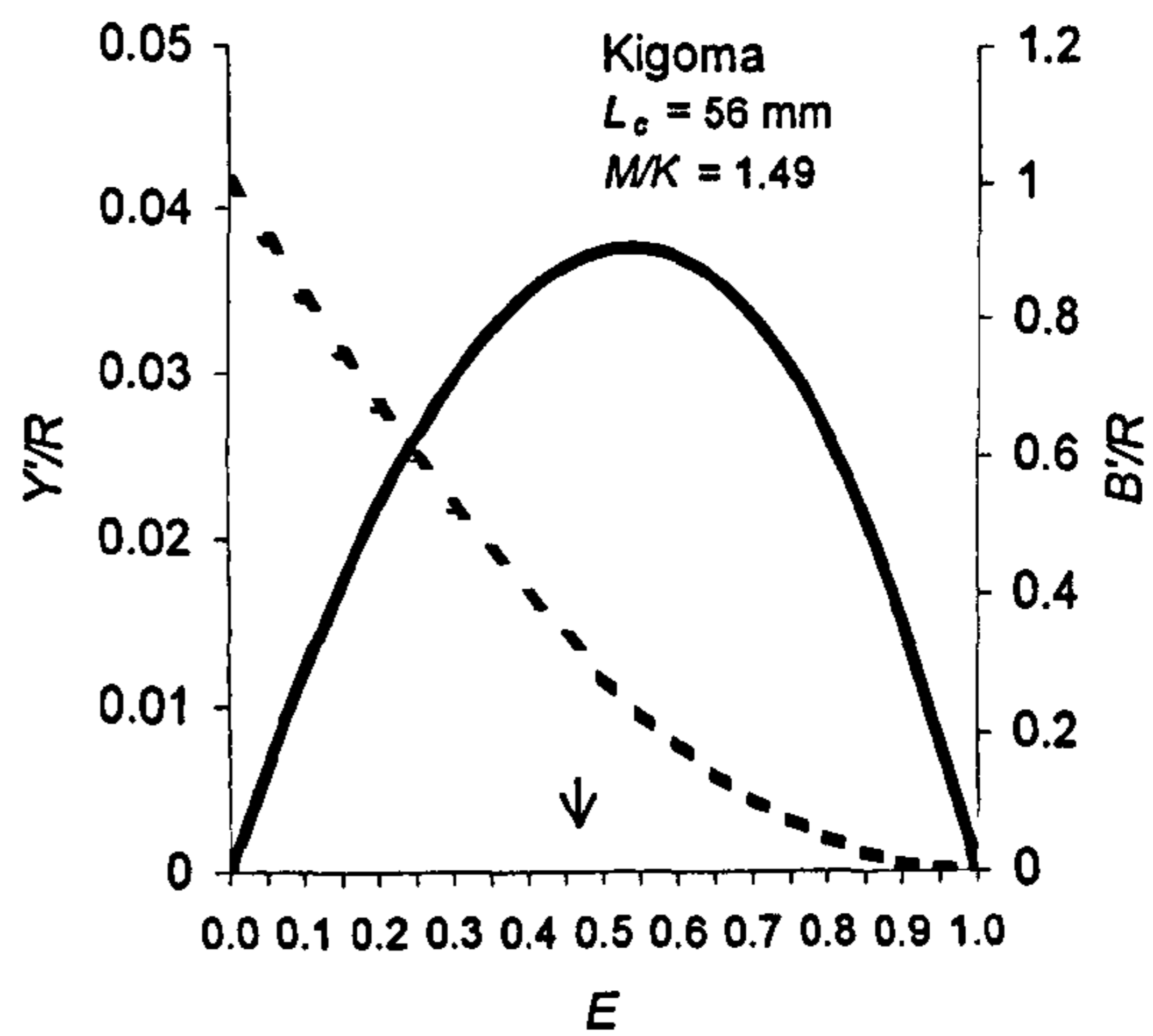
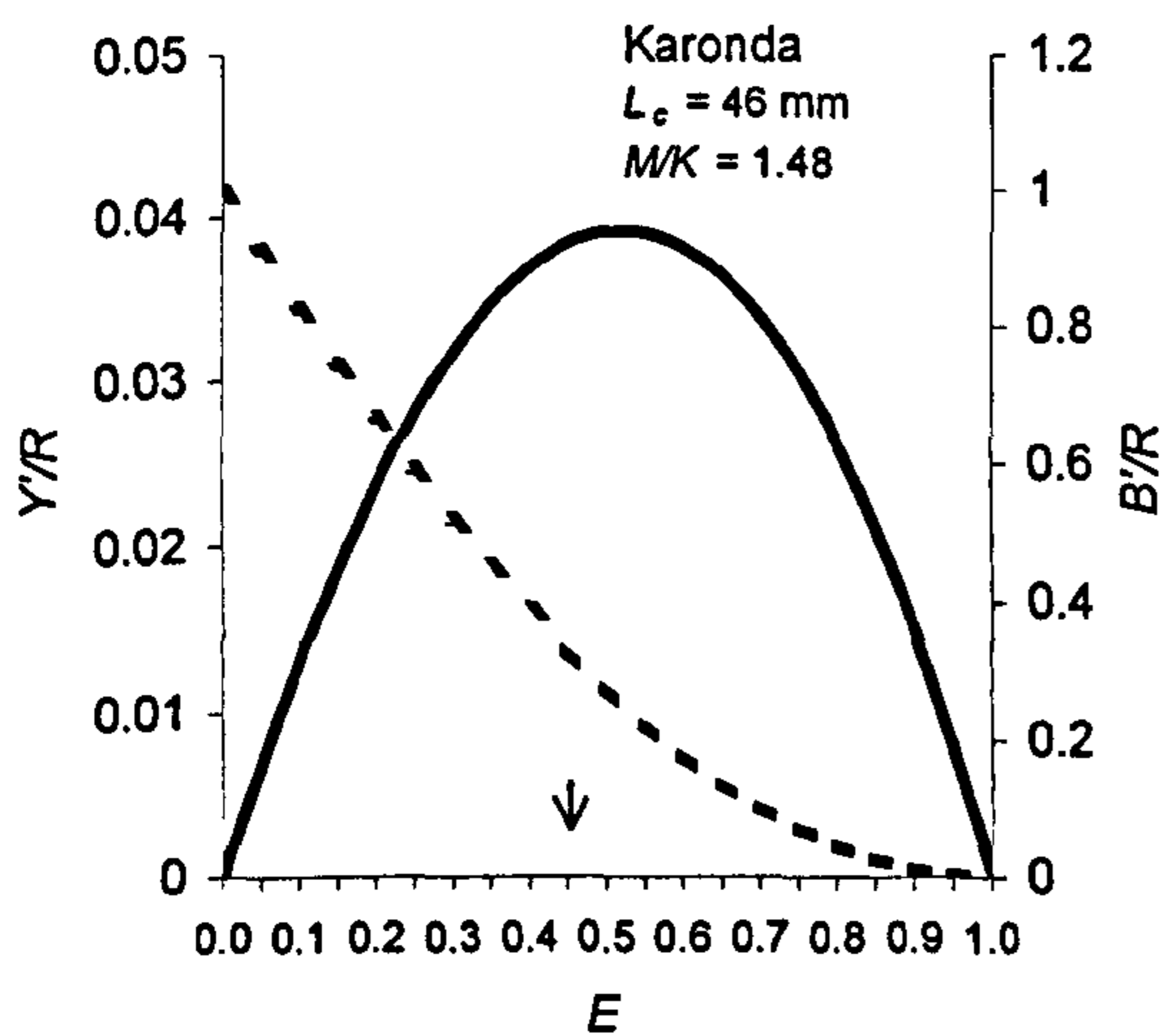
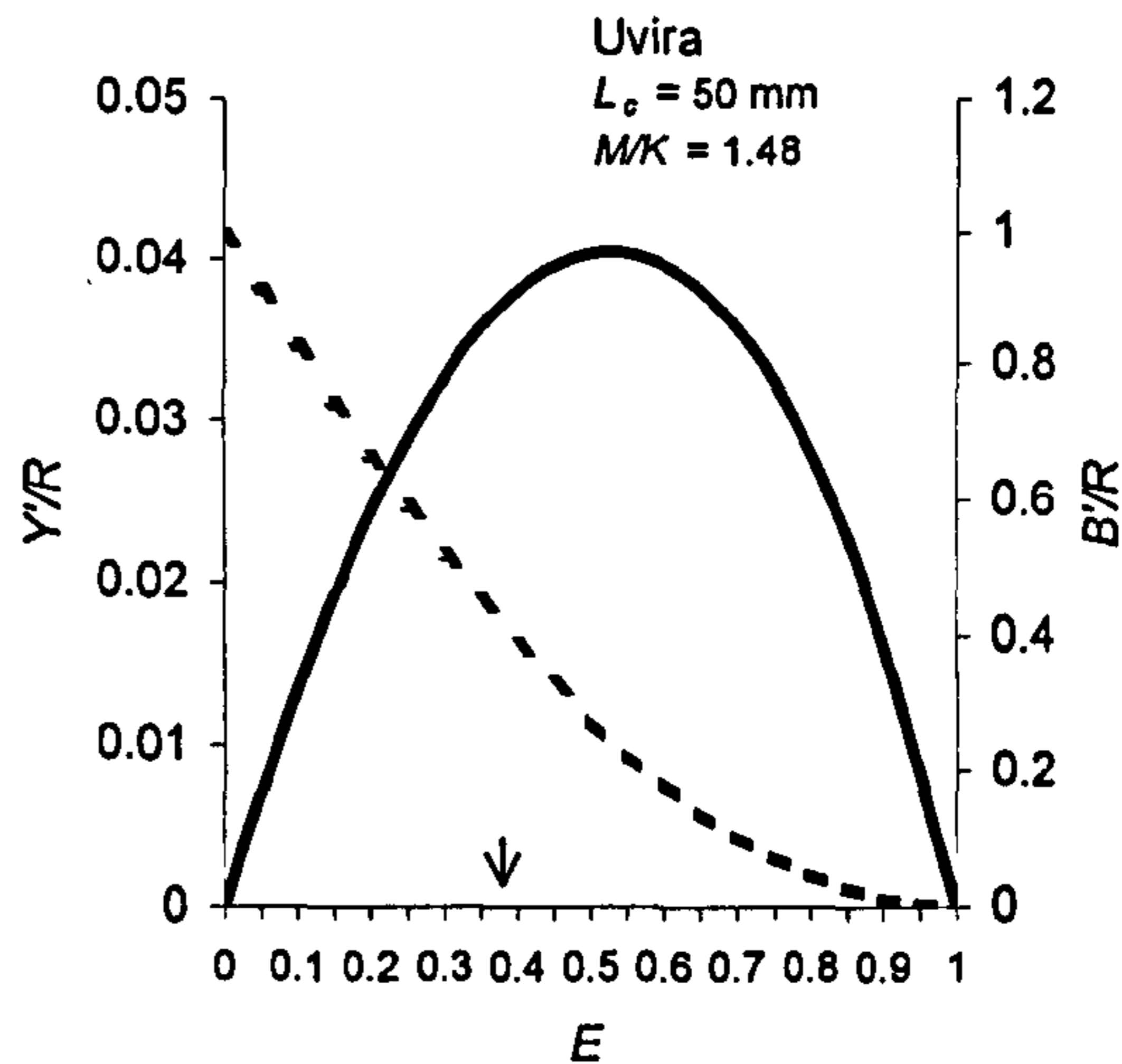
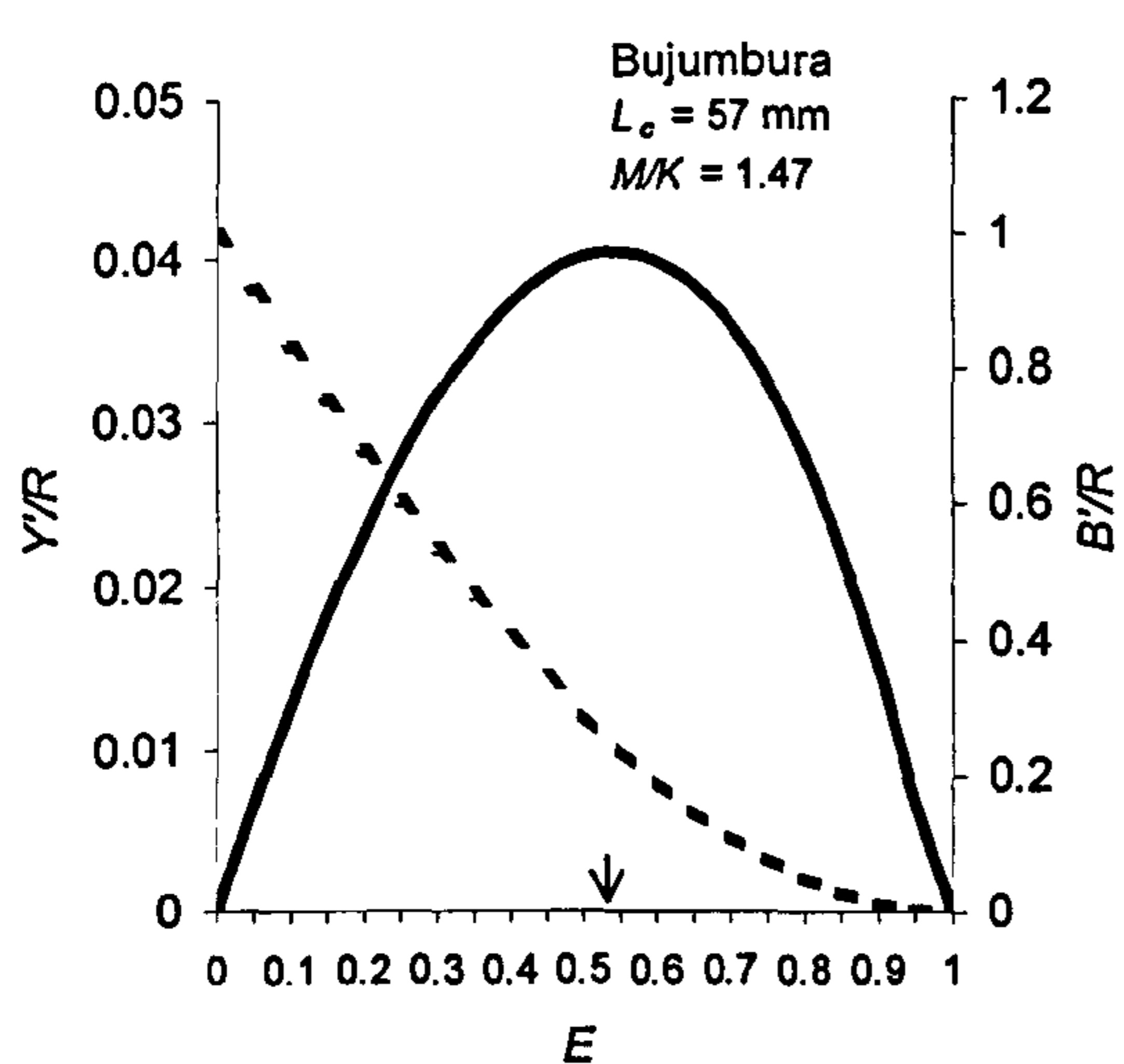


Figure 105. Relative yield-per-recruit ( $Y/R$ , solid line) and biomass-per-recruit ( $B/R$ , dotted line), expressed as a function of exploitation rate ( $E$ ), for *S. tanganycae* for different areas. Arrow indicates estimated current  $E$ .

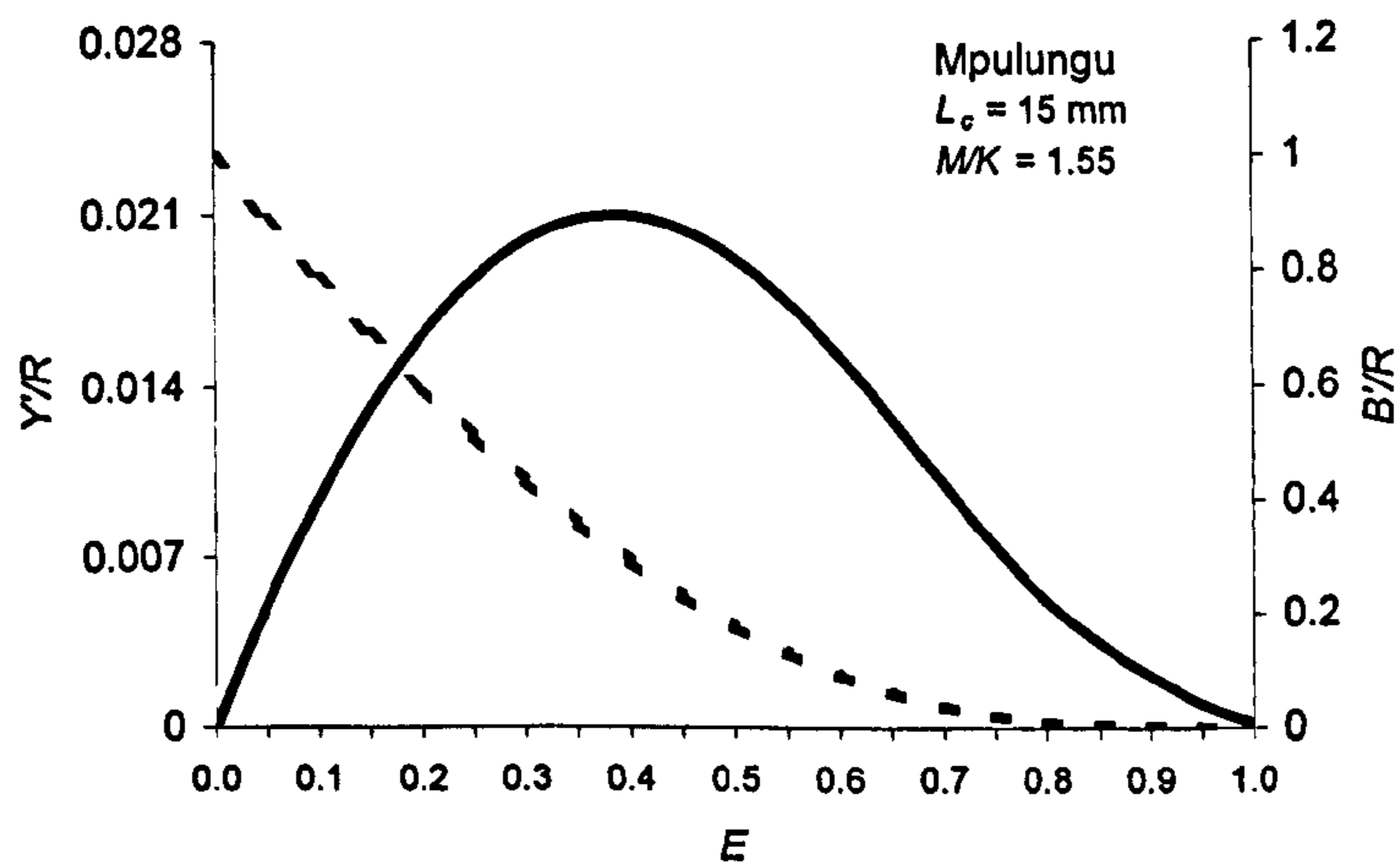
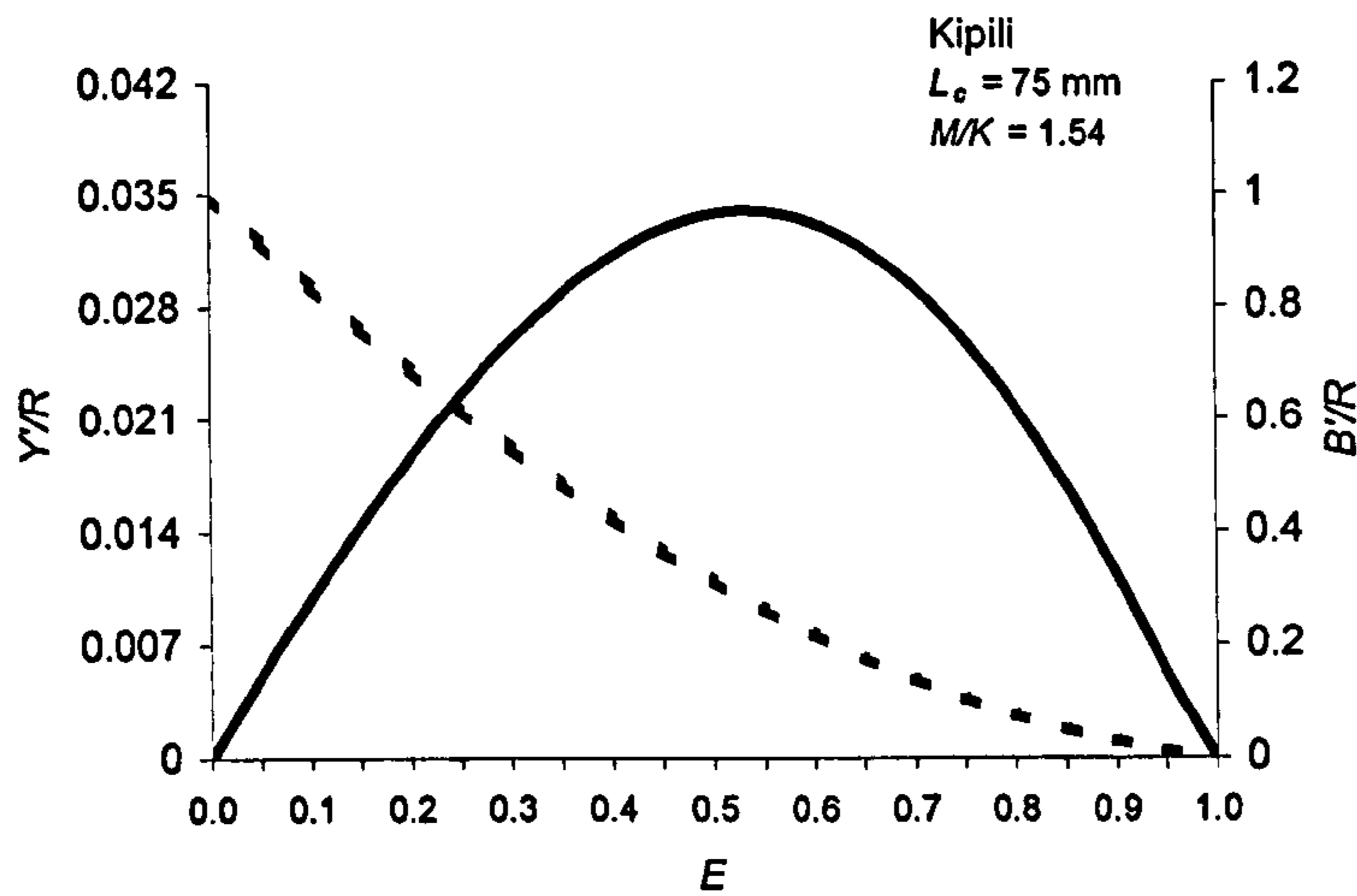
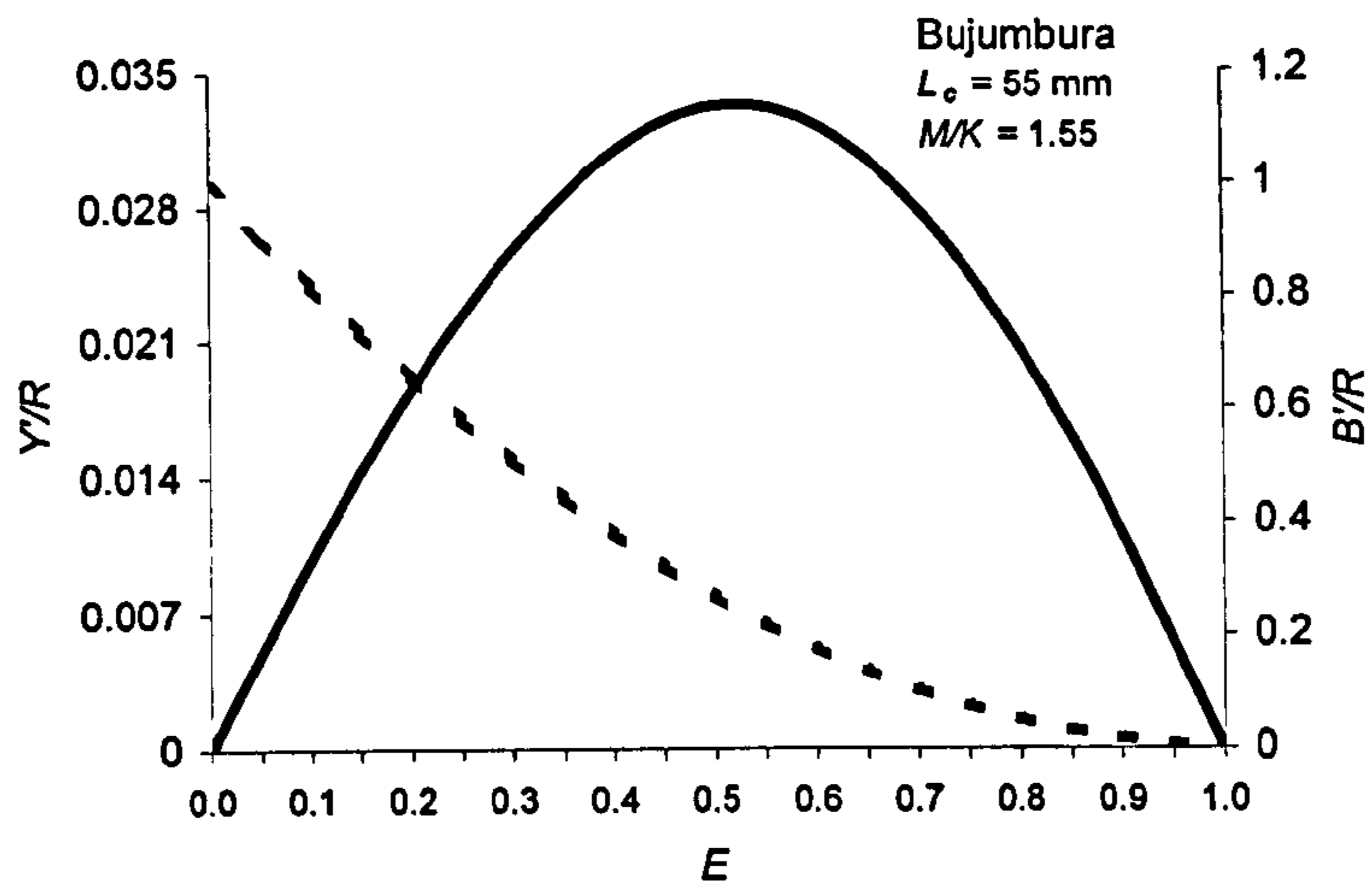


Figure 106. Relative yield-per-recruit ( $Y/R$ , solid line) and biomass per recruit ( $B/R$ , dotted line), expressed as a function of exploitation rate ( $E$ ), for *L. miodon* for different areas.

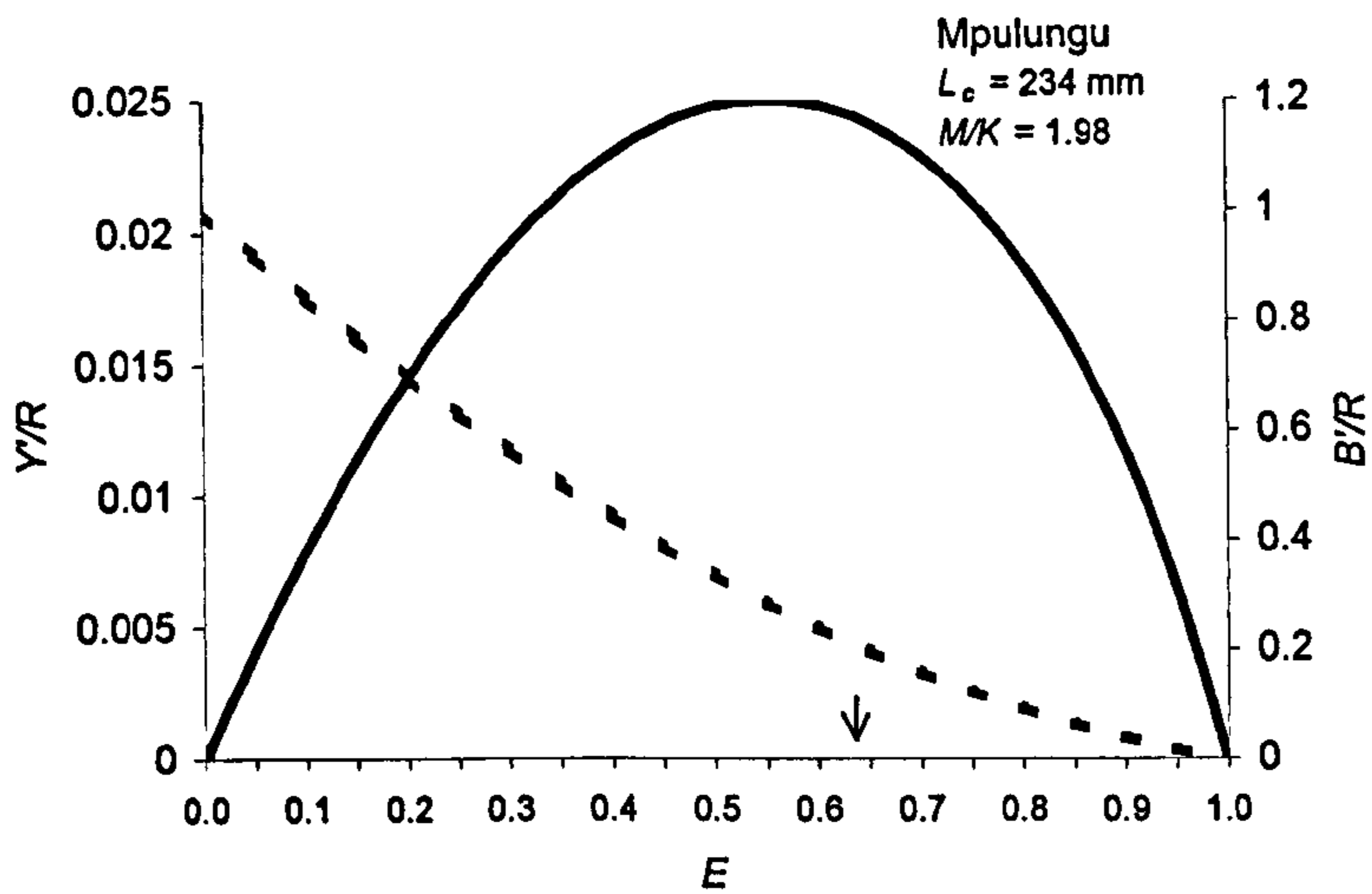
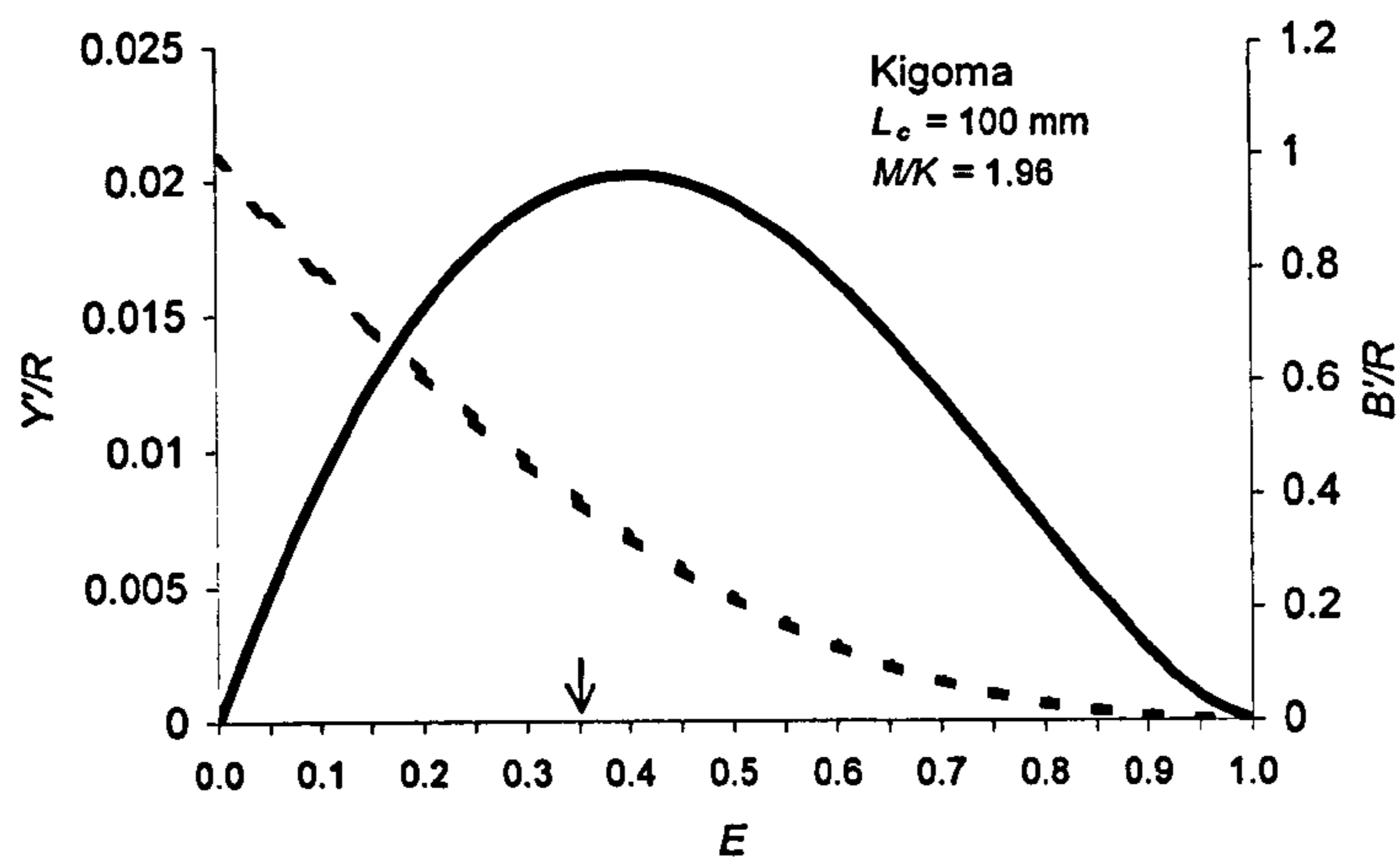


Figure 107. Relative yield-per-recruit ( $Y/R$ , solid line) and biomass-per-recruit ( $B/R$  dotted line), expressed as a function of exploitation rate ( $E$ ), for *L. stappersii* for different areas. Arrow indicates estimated current  $E$ .

The size distributions of fish caught during the June and November-December 1995 surveys in the area of Bujumbura-Uvira, Karonda, Kigoma, Mpulungu, Moba and Kalemie were compared with the size composition of the commercial catch in the same areas and periods. The Kolmogorov-Smirnov two-sample test was used to test the null hypothesis that the survey and commercial catch samples came from populations with the same distribution. A total of 22 L/F pairs (8 of *S. tanganyicae* and 7 of *L. miodon* and *L. stappersii*) could be compared. All *S. tanganyicae* size distributions were different ( $D > D_{.05}$ ;  $P = 0.05$ ) and only in one case *L. miodon* and *L. stappersii* length composition of survey and commercial catch was not significantly different ( $D < D_{.05}$ ) (Table 10). Overall, 91% of the total frequency distributions were (very) different between survey and commercial catch.

Although the comparison was not performed under strictly controlled conditions (e.g. time and sampling sites were approximate), the results suggested that, for all the three species, within the same area schools made by different size groups co-occurred and displayed highly dynamic movements.

Table 10. Kolmogorov-Smirnov two sample test for differences in distributions of two L/F samples of continuous observations. Length-frequency samples were from the area of Bujumbura-Uvira, Karonda, Kigoma, Mpulungu, Moba and Kalemie,  $D$  is the largest unsigned difference and  $D_{.05}$  is the critical value ( $P = 0.05$ ) for  $D$ .

<i>Stolothrissa tanganicae</i>	June 1995		November-December 1995	
	$D$	$D_{.05}$	$D$	$D_{.05}$
Bujumbura-Uvira	0.437	0.066	0.792	0.032
Karonda	0.999	0.029	0.049	0.033
Kigoma	0.777	0.025	0.277	0.032
Mpulungu			0.839	0.060
Kalemie			0.824	0.126
<i>Limnothrissa miodon</i>	June 1995		November-December 1995	
	$D$	$D_{.05}$	$D$	$D_{.05}$
Bujumbura-Uvira	0.979	0.03	0.103	0.151
Karonda				
Kigoma	0.430	0.389		
Mpulungu	0.990	0.106	1.000	0.103
Moba			1.000	0.076
Kalemie			0.845	0.130
<i>Lates stappersii</i>	June 1995		November-December 1995	
	$D$	$D_{.05}$	$D$	$D_{.05}$
Bujumbura-Uvira	0.516	0.144	0.896	0.177
Karonda	0.940	0.148		
Kigoma	0.800	0.096	0.104	0.174
Mpulungu	0.298	0.087	0.323	0.233



## 4. DISCUSSION

### 4.1 Life histories traits

Growth coefficients of the three species, estimated from the July 1993-June 1995 data, were similar to previously published estimates (Table 11). As far as the accuracy of length-based methods allows, there is no evidence of variations in the growth patterns within species between different parts of the lake. However, Pakkasmaa (1996) who studied the growth of *S. tanganyicae* and *L. miodon* from daily otolith increments, hypothesised that there were differences in growth rates in different parts of the lake, on the basis of differences in some otolith-fish size relationships between sampling stations.

A more accurate assessment of growth may be achieved from studying otolith daily growth rings. Fish ageing by such methods has been unsuccessful for *L. stappersii* (Kimura, 1991a), but may be feasible for the short-lived clupeids. In order to have alternative and independent age estimates for both clupeid species, an ageing study was carried out using the daily otolith increments. *Stolothrissa tanganyicae* and *L. miodon* otoliths were collected in 1994 at three landing sites (Bujumbura, Kigoma and Mpulungu) from the same stocks from which length data were obtained. Otoliths were also collected during the 1995 surveys. Fish and otolith length were strongly correlated, as was the relationship between fish length and otolith width (Pakkasmaa, 1996).

The results from ageing obtained by Pakkasmaa and Sarvala (1995) and Pakkasmaa (1996) were very consistent with growth estimates obtained by length based analyses. *Stolothrissa tanganyicae* of ca 60 mm were aged from otoliths as 150-160 days old and *L. miodon* of 60 and 100 mm as 120-160 and 250-350 days old respectively. Converting lengths from the average VBGF, estimated by length frequency distributions to relative age, the above lengths corresponded to 153 days for *S. tanganyicae* and 138 and 279 days for *L. miodon*.

*Stolothrissa tanganycae*

Area	Data collection	$L_{\infty}$ (mm)	Length meas.	$K$ annual	$\Phi'$	$Z$ annual	Source
Bujumbura	1972-76	93.8	FL	2.52	4.35	5.52	Roest, 1978
"	1972	92	TL	3.46	4.47	5.99	Moreau <i>et al.</i> , 1991
"	1974	100	TL	4.00	4.60	11.43	"
"	1974	90	TL	2.00	4.21		"
"	1980	107	TL	2.30	4.42	17.21	"
"	1981	100	TL	2.72	4.43	8.51	"
"	1982	101	TL	2.00	4.31	7.54	"
Uvira	1988	108	SL	1.90	4.35	9.23	Mulimbwa & Mannini, 1993
"	1988	109	SL	2.29	4.43		"
"	1987-89	106	SL	2.13	4.38		Mulimbwa & Shirakara, 1994
"	1993-95	104	TL	1.85	4.30	4.39	This study
Bujumbura	"	105	TL	1.89	4.32	6.10	"
Karonda	"	112	TL	1.77	4.35	4.79	"
Kigoma		90	FL	2.52	4.31	5.16	Chapman & van Well, 1978a
"	1993-95	105	TL	1.84	4.31	5.16	This study
Kalemie	1994-95	108	TL	1.80	4.32	5.05	"
Mpulungu	1962	91	TL	1.62	4.13	4.62	Moreau <i>et al.</i> , 1991
"		110		1.56	4.28		Pearce, 1985
"		112		1.56	4.29		"
"		116	FL	1.72	4.36		Kimura, 1991b*
"	1990	104	SL	1.87	4.31		Kimura, 1995*
"	1993-95	114	TL	2.00	4.41	4.33	This study
Whole lake	1995					4.56	This study

*Limnothrissa miodon*

Area	Data coll.	$L_{\infty}$ (mm)	Length meas.	$K$ annual	$\Phi'$	$Z$ annual	Source
Bujumbura	1974	165	TL	1.15	4.50	5.76	Moreau <i>et al.</i> , 1991
"	1980	161	TL	1.12	4.46	4.44	"
"	1981	172	TL	1.31	4.59	9.76	"
"	1982	172	TL	1.14	4.53	6.66	"
Uvira	1988	140	SL	1.19	4.37	4.67	Mulimbwa & Mannini, 1993
"	1987-1989	135	SL	1.15	4.32		Mulimbwa & Shirakara, 1994
Bujumbura	1993-95	180	TL	1.04	4.53	5.08	This study
Kigoma		175	TL	0.92	4.45		Ndugumbi <i>et al.</i> , 1976
Kipili	1993-95	180	TL	1.06	4.54	6.91	This study
Mpulungu		164		0.95	4.41	5.80	Pearce, 1985
"		178	FL	0.80	4.41		Kimura, 1991c*
"		156	FL	0.99	4.38		"
"	1990	155	SL	0.86	4.32		Kimura, 1995*
"	1993-95	182	TL	1.01	4.52	4.21	This study
Whole lake						3.13	This study

Table 11. Estimates of growth coefficients ( $L_{\infty}$ ,  $K$ ) and total mortality rates ( $Z$ ) for *S. tanganycae* and *L. miodon* from different L/F data sets and authors. El. refers to Elefan 1 method, Sources marked with asterisk means growth coefficients were obtained by otolith reading. Length meas. indicates whether fish length was measured as Total Length (TL), Fork Length (FL) or Standard Length (SL). For comparison  $L_{\infty}$  values originally expressed as FL and SL were converted to TL using the conversion coefficients given in Table 1. Whole lake area refers to  $Z$  estimate obtained through catch curve analysis applied to survey data and using the mean  $L_{\infty}$  and  $K$  from commercial catch data as input parameters.

<i>Lates stappersii</i>							
Area	Data collection	$L_{\infty}$ (mm)	Length meas.	$K$ annual	$\Phi'$	$Z$ annual	Source
Bujumbura	1973-80	470		0.40	4.95	1.78	Roest, 1988
"	1982	540	TL	0.42	5.09	1.95	Moreau & Nyakageni, 1992
"	"	535	TL	0.36	5.01		"
"	1983	580	TL	0.56	5.28	1.60	"
"	"	510	TL	0.35	4.96		"
Uvira	1988	462	SL (EI.)	0.46	4.99	2.16	Mulimbwa & Mannini, 1993
"	"	480	SL (SLCA)	0.38	4.94	2.02	"
Kigoma	1971-72	455	FL	0.25	4.71		Chapman & van Well, 1978b
"	1974-76	450	FL	0.40	4.91		"
"	1993-95	519	TL (EI.)	0.44	5.07	1.35	This study
"	"	506	TL (SLCA)	0.43	5.04	1.18	"
Kipili	"	550	TL (EI.)	0.41	5.09	2.33	"
"	"	550	TL (SLCA)	0.36	5.04	2.00	"
Mpulungu	1963-83	480		0.39	4.95	2.02	Pearce, 1985
"	1993-95	510	TL (EI.)	0.42	5.04	2.11	This study
"	"	530	TL (SLCA)	0.40	5.05	2.35	"
Whole lake						1.90	This study

Table 12. Estimates of growth coefficients ( $L_{\infty}$ ,  $K$ ) and total mortality rates ( $Z$ ) for *L. stappersii* from different L/F data sets and authors. EI. refers to Elefan 1 method, SLCA to Shepherd length composition analysis. Length meas. indicates whether fish length was measured as Total Length (TL), Fork Length (FL) or Standard Length (SL), for comparison  $L_{\infty}$  values originally expressed as FL and SL were converted to TL using the conversion coefficients given in Table 1. Whole lake area refers to  $Z$  estimate obtained through catch curve analysis applied to survey data and using the mean  $L_{\infty}$  and  $K$  from commercial catch data as input parameters.

Daily growth increment readings from otoliths can provide more reliable estimates of the age of young fish than length-based analysis (Beamish and McFarlane, 1983). This is because young fish are often under-represented in L/F samples due to gear selectivity. Consequently, the estimated growth curve is, for the young fish, only a backward projection on the time axis, which cannot describe accurately their growth. In the case of very large (and old) fish both methods yield the same uncertainty when ageing the largest specimens, i.e. large fish of the same size can have different ages or their otoliths may be difficult to analyse (Jones, 1992). Also ageing fish from otoliths is difficult under field conditions encountered in tropical areas. Length-based methods are easy to use and their careful application provides reliable information on the growth performance of exploited fish populations.

The constant sampling effort and the large number of fish sampled on a regular weekly basis at various sites around the lake, analysed in the present study to estimate the growth of *S. tanganyicae*, *L. miodon* and *L. stappersii*, and the similarity of the results with earlier studies (Table 11 and Fig. 108) indicate that estimates for each species are reliable. It can be observed that the growth performance of *L. miodon* lies between that of *S. tanganyicae* and *L. stappersii*. The auximetric grid in Figure 108 indicates the relationship between  $K$  and  $L_{\infty}$  for *S. tanganyicae*, *L. miodon* and *L. stappersii*. The points of each species group closely together in roughly elliptical areas. The  $\phi'$  ( $\phi' = \log_{10}K + 2\log_{10}L_{\infty}$ ) expresses the growth performance of a species, and is roughly constant for a given species despite changes in growth rates of different stocks (Pauly and Munro, 1984; Pauly, 1991). The differences between  $\phi'$  of species are relatively constant compared with those between growth parameters  $K$  and  $L_{\infty}$ . Differences in  $\phi'$  values may be interpreted as reflecting the differing life history and associated production capacity of the clupeid and centropomid species.

*Lates stappersii* is the most long-lived of the three species and displays the highest length increment rate which is, on average for the whole life-span, about 9 mm month<sup>-1</sup>, while that of the two clupeids is about 8 mm. The initial growth in length of *S. tanganyicae* and *L. miodon* during the first six months of life

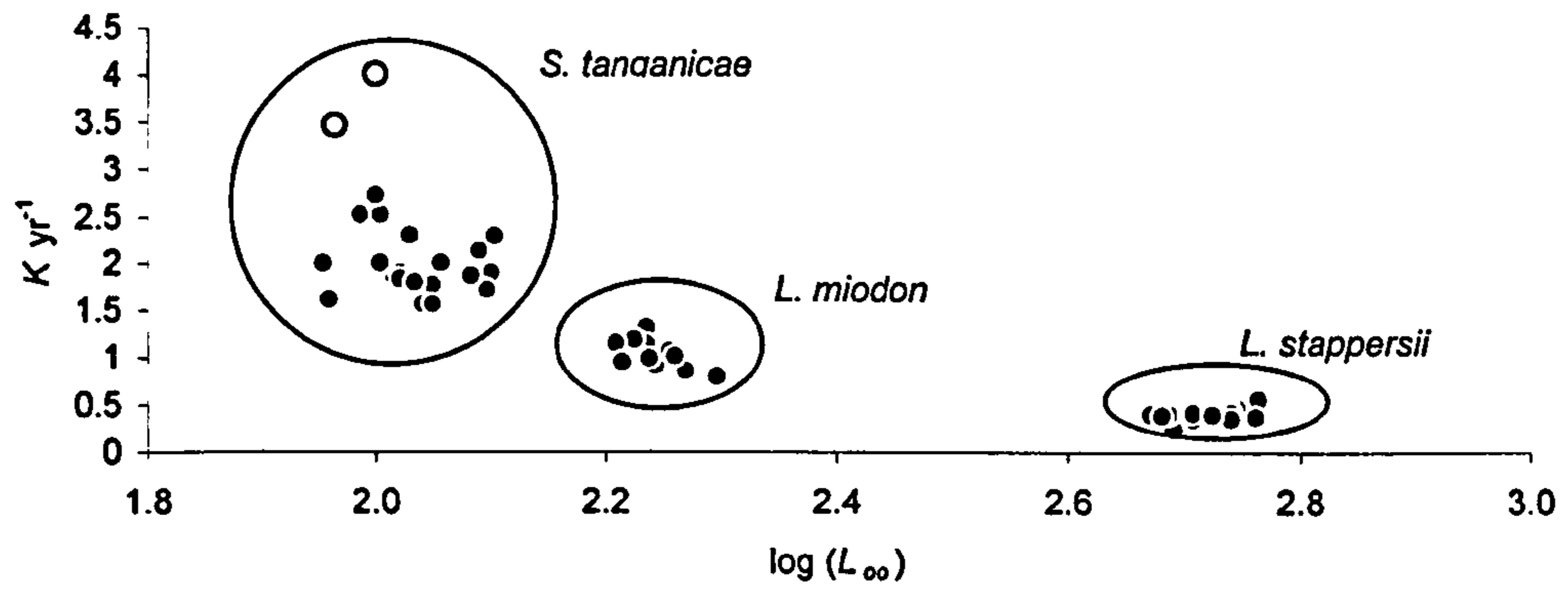


Figure 108. Auximetric plot of published growth parameters ( $K$  against  $\text{Log}(L_{\infty})$ ) of *S. tanaanicae*, *L. miodon*, *L. stappersii*. Data are from Table 11 and 12,  $L_{\infty}$  values originally given as standard length or fork length have been converted to total length using conversion parameters from Table 1. Open circles indicate probable overestimates.

was on average 10-12 mm month<sup>-1</sup> and that the young *L. stappersii* was about 14 mm month<sup>-1</sup>.

Tropical fish, and especially small pelagic species, are commonly believed to grow quicker than temperate fish. This generally accepted belief is not substantiated by growth comparisons (Edwards, 1984). The present results, and those from other authors, show that the growth rates of Lake Tanganyika clupeids are of the same magnitude typical of the clupeid group, on average 10-12 mm month<sup>-1</sup> during the first juvenile growth. *Stolothrissa tanganyicae* and *L. miodon* growth is not then faster than other similar fish species. Sarvala *et al.* (in press) found that their growth rate is low in comparison with that of some planktivorous fish in temperate-cool fresh-waters in the northern hemisphere. Edwards (1984) hypothesised that the lower growth rates in the tropics were due to higher maintenance metabolism and metabolic costs for reproduction, and available food sources may be more limiting.

The timing of clupeid reproduction as indicated by changes in the monthly GSI, does not show any obvious seasonality but a highly variable pattern, with four apparent peaks during the year in the case of *S. tanganyicae*, but no clear peaks in the case of *L. miodon*. To evaluate the seasonal allocation of reproductive output of the clupeids, a fecundity index correlated with an index of the spawning population abundance should be used. Even though mature fish always occur the spawning potential (e.g. egg production) is probably related to the dynamics of the spawning biomass (i.e. time when maximum number of mature fish are present). However, seasonal variation of GSI, which shows similar variability throughout the areas studied, would indicate that the reproductive process is continuous, although with varying intensity, throughout the year.

As a result of such dynamic reproductive strategies, knowledge on the timing of reproduction of Lake Tanganyika clupeids is not well defined within and between years (see Coulter, 1991b, for a review of results from previous authors). The reproductive process of *S. tanganyicae* 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; Pearce, 1985; Roest, 1977). Unlike most temperate clupeids which have a distinct spawning season and generally live for more than 2 years (Blaxter and Hunter, 1982), *S. tanganyicae* and *L. miodon* spawn almost continuously after becoming sexually mature and are short-lived (longevity of 1.5 and 2.5 yr, respectively).

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

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

It seems that, at least at Kigoma, *S. tanganyicae* is very efficient in exploiting a survival window, i.e. a period of high survival hypothesised by Alheit (1989) for small pelagics, which is open during the dry season (from June to September). In this period *S. tanganyicae* natural mortality could be reduced due to the low local abundance of adult *L. stappersii* (Coenen, 1995; FAO, 1978) and to increased primary and secondary production (and then food availability), which in turn is a consequence of the deepening thermocline and the vertical mixing of the water (Plisnier *et al.*, 1996). Production reaches a maximum around November (Hecky,

1991; Kurki, 1996b).

Survey findings suggest that although mature *S. tanganyicae* are always present, the spawning stock biomass reaches a maximum only in some periods (which probably lasts a few months), around the beginning of the year, while it is markedly reduced in the following months as a 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 relationship was found between larval northern anchovy (*Engraulis mordax* Girard) 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).

Survey results seem to support the hypothesis that the Lake Tanganyika *S. tanganyicae* fishery is sustained mostly by a single major cohort which is recruited during the dry season and makes the exploitable stock during the following wet season. Thus, even if reproduction never completely stops during the year, the combination of reproductive effort and larval survival shapes the recruitment into the exploitable stock of Lake Tanganyika clupeids.

Both *S. tanganyicae* and *L. miodon* have, on average within the year, two recruitment pulses. In the northern half of the lake the most important recruitment takes place during the dry season lasting until the onset of the wet season. For those fisheries based on *S. tanganyicae* this is the major recruitment upon which they will rely for about six months. It is during this period in the wet season that commercial catches are highest (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 these dynamics.

*Lates stappersii* reproduction follows a regular pattern, especially evident at Mpulungu, which takes place during the wet season. As expected for a relatively long-lived species, the seasonal reproductive period is fairly discrete and constant



between years (Chapman and van Well, 1978b; Ellis, 1978).

The size at which 50% of the fish reach sexual maturity and the  $L_m/L_\infty$  ratio provide an important insight on the life history of a species. Life history characteristics such as length at maturity, mortality rate and maximum length are interconnected (Peters, 1983; Calder, 1984) and may be linked to allocation of resources to reproduction. While a reduction in growth due to reproduction might increase the probability of death by maintaining the organism within a size range which makes it vulnerable to predation, the delay of reproduction has the advantage that a larger size and increased fecundity are achieved (Roff, 1992). Lake Tanganyika clupeids appear to have different strategies. Both *S. tanganyicae* and *L. miodon* reach  $L_m$  at the same age (8-9 months) but *S. tanganyicae* at this age has already completed about two third of its somatic growth while *L. miodon* only half.

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

The life history of *L. miodon* with the juvenile inshore phase enables the fish to elude *L. stappersii* and reduce predation pressure. Unlike *S. tanganyicae*, *L. miodon* is not a truly pelagic species and most of its first year of life takes place in shallow, inshore water thus avoiding *L. stappersii* predation. Although this species may be exposed to more diversified predation from others *Lates* species and piscivorous cichlids, the inshore environment has a richer source of potential prey than the pelagic zone. When *L. miodon* migrate offshore as adults they are too large for predation by *L. stappersii*.

The diet of *L. stappersii* has not previously been investigated at the same time in different areas or on lake-wide basis. The remarkable differences in the diet composition between the northern and southern halves of the lake indicate that the feeding ecology of *L. stappersii* depends on food availability rather than the age of the fish. Also, results show that *L. stappersii* is not entirely a piscivorous predator throughout its life. In both study areas fish prey become important in the diet of this predator well over the size of 100 mm previously observed (Ellis, 1978; FAO, 1978; Roest, 1992).

The southern sub-basins of the lake probably have a large shrimp population which may attract and sustain a resident, commercially-important, adult stock of *L. stappersii*, whose occurrence has led to the development of the most profitable industrial fishery of the lake. Clupeid prey, such as *L. miodon*, probably spend their early life in inshore waters which are not feeding grounds for *L. stappersii*, and *S. tanganyicae* abundance may be too low to make it an important prey item, either as larvae or adults.

Differences in meso- and macrozooplankton composition were reported by Kurki and Vuorinen (1995), Kurki (1996b) and Kurki *et al.* (in press). The abundance of pelagic copepods was found to be the lowest in the southern Mpulungu area. In this part of the lake shrimps predominate in the macrozooplankton community and their abundance was higher than in the north. How much this explains the present low abundance of *S. tanganyicae* in this area (Pearce, 1995; Plisnier, 1995) is difficult to assess. Certainly a high concentration of *L. stappersii* may have a substantial effect on the abundance of the *S. tanganyicae*.

Very large *L. miodon* (>125 mm), which occur mostly in open water, feed on both shrimps and *S. tanganyicae* (Ndugumbi *et al.*, 1976; Poll, 1953; pers. obs.), and thus occupy the same feeding niche as *L. stappersii*. It is likely that the presence of both *L. stappersii* and large *L. miodon* exerts a top-down control, through predation mortality, on *S. tanganyicae* effective enough to keep its abundance low at the southern end of the lake. Pearce (1995) noted that in the fishing areas of Mpulungu *L. stappersii* affects the abundance of *S. tanganyicae*, but not vice-versa. In this part of the lake shrimps are likely to be the most important prey of *L. stappersii* and play an important role to sustain the

local stock of this species. The size of the shrimp stock fluctuates during the year; when its abundance is low *L. stappersii* widens its diet composition to become similar to that displayed in northern areas. In Kigoma waters, where shrimp density appears to be lower than in the south, the food spectrum of *L. stappersii* is more heterogeneous, including other available prey.

A review of changes which have taken place from the 1960s within the pelagic fish community in the Mpulungu sub-basin is given by Pearce (1995). In 1989 this author carried out a study on the diet composition of *L. stappersii* in Mpulungu area. At that time *S. tanganyicae* was still an important component of the diet comprising, on a monthly basis, from 20% to 70% of the total food composition by weight (both larvae and adults). The remaining dietary component was mostly shrimp. From fishery statistics it appears that while *S. tanganyicae* abundance in the Mpulungu sub-basins has been drastically reduced over the last ten years this has not directly affected *L. stappersii*. In 1994 this species made up 96% of the total industrial catch in Zambia (Plisnier, 1995), however catch rates have decreased (Coenen, 1995). A major cause behind this decline is believed to be the seven fold rise of the industrial fishing effort (see section 4.4). In the present work it was observed that the fishing mortality on *L. stappersii* was higher in the southern areas of the lake. Fishing mortality may have more impact on *L. stappersii* in the south of the lake than the low density of clupeid prey which can be efficiently replaced in the diet by the abundant shrimps.

The importance of pelagic shrimps has been highlighted in this study. The magnitude and dynamics of the shrimp population needs to be assessed by appropriate investigations. In the past, considerable attention was paid to the *S. tanganyicae* and *L. stappersii* predator-prey relationship (Roest, 1988). However, predator-prey relationships appear to be more complicated as shrimps seem to play a major role in the food web.

## 4.2 Distribution

### 4.2.1 The *Stolothrissa tanganicae* stock

*Stolothrissa tanganicae* forms contagious aggregations during the juvenile and adult life stages. 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; 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 for a few decades and concentrated in a comparatively small and closed area, *S. tanganicae* has not declined.

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 tanganyicae* 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. tanganyicae* occur offshore but their occurrence increases from offshore towards the coast, thus it is likely (but yet to be fully proved) that the spawning grounds are along the continental shelf.

Contrary to the earlier statement on the inshore phase of young *S. tanganyicae* (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. Young *S. tanganyicae* 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 liftnet fishery. Fishing grounds of the former are normally more distant from the coast than those of the artisanal fishery.

*Stolothrissa tanganyicae* nursery grounds extend over the area of distribution 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. tanganyicae* 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. tanganyicae* larvae occur mostly offshore (Tshibangu and Kinoshita, 1995). The spatial distribution of *S. tanganyicae* 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. tanganyicae* 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 striking differences in the catch rate between the first (June, November-December 1995 and April 1996) and the second (November-December 1997 and February 1998) group of surveys have been introduced and discussed in the results section (par. 3.4.1). 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 (this will be verified once the acoustic survey results become available) then it could mean that *S. tanganyicae* 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. tanganyicae* as well. Murphy (1977) noted that this population behaviour is characteristic of clupeoid fishes, contributing to their susceptibility to overfishing.

Higher catchability with decreasing stock size have been reported in several pelagic stocks that have collapsed such as the California sardine (*Sardinops caeruleous*

Girard) (MacCall, 1976), the Atlantic menhaden (*Brevoortia tyrannus* Latrobe) (Schaaf, 1975, 1980), the Norwegian spring-spawning herring (*Clupea harengus* L.) (Ulltang, 1976, 1980), the South African pilchard (*Sardinops ocellatus* Jenyns) (Shelton and Armstrong, 1983) and the Peruvian anchoveta (*Engraulis ringens* Jenyns) (Csirke, 1989). In fisheries for pelagic species the catchability coefficient is inversely related to population size (Csirke, 1989). This is due to the shoaling habit and to the consequent vulnerability to acoustic detection and capture by modern fishing gear (Beverton, 1990). Commercial fishery CPUE may remain stable or even increase while pelagic or semi-demersal stocks approach collapse. The critical assumption that CPUE is proportional to stock abundance has been proved wrong following some dramatic fishery collapses such as that of the northern cod (*Gadus morhua* L.) off Newfoundland (Walters and Maguire, 1996).

It appears that stock of *S. tanganyicae* 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 mainly *S. tanganyicae*) in the northern end of the lake within two weeks in November 1973 yielded estimates of respectively 120000 and 260000 t (Johanesson, 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. tanganyicae*) move in daytime at rates as high as 68 m min<sup>-1</sup>. They tracked 68 schools and estimated a median movement rate of 10 m min<sup>-1</sup>.

The fast movements of *S. tanganyicae* schools are primarily determined by two factors: predation avoidance and search for food. Survey results do not show any significant positive association between *S. tanganyicae* and *L. stappersii* in the environment. *Stolothrissa tanganyicae* 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. tanganyicae* 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. tanganyicae* is very efficient at locating mesozooplankton 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. tanganyicae* moves into the area and becomes exposed to exploitation, as reflected by the increase of the local catch rates.

#### 4.2.2 The *Limnothrissa miodon* stock

The *L. miodon* stock is more evenly distributed over the lake than *S. tanganyicae* stock which is mostly confined within the northern half of the lake basin. The contribution of *L. miodon* to the liftnet and purse seine pelagic catches is smaller than that of *S. tanganyicae* and *L. stappersii*, while it dominates in the catch of the unselective 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 mosquito netting (Kihakwi and Chale, 1995). As they grow the young *L. miodon* move offshore and are successively recruited to the liftnet and purse seine fisheries. *Limnothrissa miodon* is probably a less specialised planktivorous feeder than *S. tanganyicae* which preys on the offshore zooplankton community (Matthes, 1967), while the former can feed on a wider food spectrum including the diversified inshore plankton community (de Iongh *et al.*, 1983). When energetic requirements increase, probably related to gonadal development, the fish migrate to offshore waters where they eat fish and shrimps. 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. tanganyicae* (Poll, 1953; Ndugumbi *et al.*, 1976; pers. obs.).



In Lake Kivu, where *L. miodon* was introduced, and is the only pelagic fish, large *L. miodon* display a cannibalistic behaviour preying inshore on juveniles (Reusens, 1987; de Iongh *et al.*, 1983). In Lake Tanganyika the natural fish prey of *L. miodon* is young *S. tanganyicae*, 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 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<sup>-1</sup> averaging 5.9 yr<sup>-1</sup>, 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<sup>-1</sup>.

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 contagiously 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.

#### 4.2.3 The *Lates stappersii* stock

*Lates stappersii* is known to be a fast, highly mobile fish capable of movement across the whole lake. 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 suggest 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 under-represented due to the low number of fish caught. *Lates stappersii* is a relatively long-lived species 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 a dramatic change in the fish population dynamics, it is possible that the efficiency of the fishing operations changed.

Juvenile and adult *L. stappersii* co-occur within a geographical area, even though young *L. stappersii* presence dwindles proceeding southward. However, 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.

Surprisingly there is little evidence of juveniles in the southern part of the lake even

though the abundance of *L. stappersii* seems in this region to be the highest of the lake. It may be that this size group was missed in the survey because of the low temporal frequency of sampling. However, catch of young *L. stappersii* was also rare in the commercial catch from the south which was continuously monitored during the three-year sampling period. It is possible that maturing and mature fish concentrate in the southern feeding grounds but spawning takes place further north. Notwithstanding *L. stappersii* larvae occur in the same areas where the rest of the stock is found and there is some evidence that spawning grounds of the species exist in the south of the lake 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. tanganyicae* 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 a southerly movement probably occurs.

There is no evidence of the existence of *L. stappersii* sub-populations in the lake. Results do not seem to indicate substantial differences between the lake areas. *Lates stappersii* is a highly mobile species and the individuals are 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, evidence of massive migrations has not yet been proven (Chapman, 1976; Chapman and van Well, 1978b). 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 liftnet 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. 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.

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 ( $Z = 1.2 \text{ yr}^{-1}$  and  $Z = 0.5 \text{ yr}^{-1}$  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.

During the 1980s *Lates stappersii* replaced *S. tanganycae* 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. 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.

#### 4.3 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. The present results show that the diet varies between the halves of the lake and that *L. stappersii* is not exclusively a fish predator. From the comparative analysis of *L. stappersii* feeding in the Kigoma and Mpulungu areas it shows that the diet composition is more heterogeneous, and *S. tanganyicae* is a principal prey item, at Kigoma, while in the south pelagic shrimps are an extremely important food item.

As stated before, there is not a simple predator-prey relation between *L. stappersii* and *S. tanganyicae*, 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. tanganyicae* abundance is low.

Predator-prey dynamics occurring on short time and small spatial scales are believed to play an important role in rapid changes in system state (Kitchell *et al.*, 1994). Predator avoidance mechanisms seem to be more efficient for *S. tanganyicae* (probably due to its 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. tanganyicae* 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. tanganyicae* 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 foraging behaviour as they grow.

A main factor which explains the rapid changes of *S. tanganyicae* 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. tanganyicae* stock to the fishery is strongly influenced by the timing and distribution, within local areas, of plankton abundance.

#### 4.4 Exploitation status and fisheries management implications

One of the most important features of any renewable natural resource such as fish, is productivity. This can be conveniently expressed as the production/biomass ratio ( $P/B$ ) of the species under exploitation. Production can be defined as the increase in

biomass of a species population over a given period of time (growth of new tissue and production of new offspring). When estimates of mean standing stock are available, total annual production is obtained simply by multiplying values for mean biomass and  $P/B$  ratio (Walters, 1977).

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

More uncertain is the  $P/B$  estimate for *L. miodon* because of biased  $Z$  estimates. Bias to estimate  $Z$  values has been reported due to fish migration (Mather *et al.*, 1974; Sousa, 1988). The migration of large *L. miodon* from fishing grounds to further offshore areas determines the overestimation of  $Z$ . The range of  $Z$  values available from the present study, as well as from previous research (Table 9), would indicate overestimated rates which do not match the expected longevity of 2.5 yr (Lévêque *et al.*, 1977). Mannini (1991) applied length cohort analysis to the *L. miodon* stock of Lake Kivu and obtained  $Z$  values not higher than  $2 \text{ yr}^{-1}$ , much lower than the value of  $9 \text{ yr}^{-1}$  obtained from catch curve analysis applied to the same data (Mannini, 1990). Total mortality from the catch curve analysis applied to June and November 1995 survey data for the whole of Lake Tanganyika was  $3 \text{ yr}^{-1}$ . This estimate is more realistic and less biased than those from commercial catch data. Therefore, the  $P/B$  of *L. miodon* can be reasonably expected to lie between 2 and 3. *Lates stappersii* is the most long-lived of the three species and has the lowest natural mortality resulting in the slowest turnover. A  $P/B$  of 1.5 can be regarded as representative for this species.

The  $P/B$  values of the three species indicate that annual total production can be higher (much higher for the two clupeids) than mean biomass. Coulter (1981) commented that in these circumstances "standing stock is a poor indicator of potential yield because production and mortality rates are so high and biomass fluctuates seasonally".

High total production of small pelagics explains how large standing stocks of long-lived predator species, i.e. *Lates* spp., in Lake Tanganyika and Victoria are sustained by planktivorous pelagic species with mean biomass much less than annual production (Mannini, 1992).

Coulter (1981) concluded his analysis on the lake Tanganyika pelagic community suggesting that predator biomass should be correlated with clupeid prey productivity rather than with clupeid biomass. Thus the potential fishery yield from small pelagic stock depends on their high production and on fishing mortality applied to their predators. It may seem that if natural predation decreases (e.g. increased fishing mortality) then the availability of the prey to fishery exploitation increases (Munro, 1983; Marten, 1979). However, there is no adequate evidence that ecosystems respond in such a straightforward manner (Larkin, 1979). Present knowledge of the predator-prey interactions and of their effects on multispecies fisheries is too weak for proper ecosystem management (Christensen, 1996).

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

When dealing with pelagic fish stocks with such characteristics a management target is to avoid exacerbating environmentally driven stock declines by irresponsible fishing. Stocks of shoaling fish should be managed with the objective to avoid stock-recruitment collapse by maintaining a stable spawning stock biomass above a determined (often poorly known) critical level (Beverton, 1990). The available information from pelagic and demersal fish stocks tentatively indicates that for small



pelagics a value of, at least, 40% of spawning per recruits (either in terms of biomass or eggs) can be a reference point for consistent stock replacement when the stock-recruitment relationship, and the stock size, are not known (Clark, 1991; Goodyear, 1993; Mace and Sissenwine, 1993; Caddy and Mahon, 1995).

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

The population dynamics of *S. tanganyicae* shows the typical characteristics, such as short life-span, and high mortality rate and turnover rate, that make it inherently prone to large fluctuations in the size of the population. Expansion or contraction of geographic range with increasing or decreasing population abundance is characteristic of clupeid species (MacCall, 1990). The reduced occurrence of *S. tanganyicae* 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. tanganyicae*, 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) 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, that is 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. tanganyicae* has the highest  $P/B$  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. tanganyicae* 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. tanganyicae* 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. tanganyicae*, 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). To date there is not enough 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 liftnet 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. Yield-per-recruit analysis indicates that *S. tanganyicae* is not yet overfished but current exploitation ( $E$ ) is close to  $E_{max}$ . 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. tanganyicae* below the length at maturity, which, for this species, is 78 mm. In other liftnet 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. tanganyicae* 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. tanganyicae* 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. tanganyicae* have been obtained from the present analysis and a mean value of 0.4 can be derived for the whole lake. This confirms that currently the *S. tanganyicae* stock is still, on a lake-wide basis, exploited within safe limits. If acoustic biomass estimates confirm the pattern of *S. tanganyicae* 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. tanganyicae* and *L. miodon* where juveniles spend the first months of their post-larval life are located in different areas. *Stolothrissa tanganyicae* 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 unselective beach seine fishery.

There is no evidence that late young and adult *L. miodon* are threatened by excessive fishing 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 unselective 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; Pauly *et al.*, 1998). Often it seems that a smaller, faster-growing species can take over the niche made vacant from another larger, slower-growing species (Dann, 1980). Long-lived, large *Lates* spp. 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 centropomids 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. 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,  $L_e = 235$  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 ( $E = 0.3$ ). Also the yield per recruit results confirm that excessive exploitation is taking place at the southern end. 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, perhaps the most important part, 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)

Nowadays the principle of “precautionary” approach to fisheries (FAO, 1995) starts to be widely recognised in the sector of aquatic renewable resources management. However, the general agreement on the precautionary principle in fisheries management requires management actions to be precautionary in practice too (Kirkwood and Smith, 1996). The aim of future management will be to prevent overfishing more than merely maximise (sustainable) fish yield or economic returns from fishing. This objective must be also integrated with the uneasy task of conserving the fishery and the fishing community as well. In many situations, especially in developing countries, the fishery management problem is tightly linked with socio-economic processes and changes at the national level. In small scale, artisanal fisheries, as are most of the Lake Tanganyika fisheries, the fish harvest is often the main income and, especially, the sole source of animal protein in the diet of local communities. The Lake Tanganyika fishery belongs to this typology and the fish resources are of tremendous importance to the population of this region which is also largely affected by socio-political and economic instability.

At the present stage of Lake Tanganyika fishery exploitation it is advisable to implement management action based on fishing effort control instead of on catch control (e.g. Total Allowable Catch, TAC). This approach will at least tend to keep the harvest rate stable, unless catchability increases sharply with decreased stock size, or with strong technological improvement of the effort. When stock size is not known, effort limitation is a better tactic than TAC quota control (Hilborn and Walters, 1992). This is particularly valid in the case of stocks of small pelagics which have natural fluctuations in size, where the best harvest policy, under risk-averse management, it is likely to be a fixed harvest rate strategy through effort control.

As previously discussed interannual fluctuations of, mainly, clupeid stock size can be expected, therefore fixed catch allocation will be detrimental at low stock size or will reduce the potential yield at high stock size. This means that to properly apply a TAC system the stock should be annually monitored, preferably through lake-wide fish resources appraisal surveys, and the information collected should be rapidly elaborated and disseminated, and the catch quota for the year quickly fixed. This is unfeasible on Lake Tanganyika. It would require scientific and management capability that currently are not available (and cannot be afforded) by the four riparian countries. Annual catch quotas need the most information and are the most expensive to implement. For instance, the current total catch should be estimated by sampling selected landing sites and raising to total landing. An estimate of effort (e.g. number of active fishing units) should also be made. Once estimated catch equals the TAC the fishery should stop. This procedure requires effective and expensive vessel and landing monitoring which would be almost impossible to establish around Lake Tanganyika. Effort limitations is easier to implement. Monitoring of fishing effort is still required but not routine sampling of the catch per landing. Effort control is less expensive and less prone to sources of error than TAC.

In the medium-long term perspective, 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, 1994).

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.

The international nature of Lake Tanganyika, and the mobility and uneven distribution of the pelagic fish resources, imply that fisheries policy issues will be mainly dealt with at government level. The patchy and dynamic distribution of the clupeid stocks does not facilitate community-based management as it does for other, more stable fish resources (e.g. demersal or benthic resources).

However, it would be advisable to augment the involvement of the local fishing communities in the fishery management process. Community-based fisheries management has the ultimate aim of linking fisheries to fish resources reducing fishery management costs. This would also encourage responsible fishing.

Also, the attitude of the fishing community does not seem to widely appreciate the concept of community based or co-management of the fish resources. In a recent socio-economic survey a rather dramatic difference emerged between fishing communities (from Zambia and some areas of Tanzania) who appreciate participatory approaches to fishery management, and those (from Burundi, D.R. Congo, rest of Tanzania) who favour that fishing regulations should be decided only by governments (Reynolds and Hanek, 1997). Participatory management is a critical tool to establish responsible fishing particularly in small scale, artisanal fisheries. The controversial attitude of the majority of Lake Tanganyika fishers towards participatory management of the lake fish resources needs to be given serious consideration and, possibly, changed since participatory management is a central tenet for responsible fishing.

Of more relevance to the lake's fisheries is that open access to commercial fishing should not be continued. An open access fishery management policy is unlikely to be precautionary in both principle and practice. License holding must be a legal requirement and, more importantly, must be enforced. Any 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).

## 5. CONCLUSIONS AND RECOMMENDATIONS

### 5.1 General conclusions

The commercial pelagic fisheries of Lake Tanganyika comprise three species, of which the most important are the clupeid *S. tanganyicae* and the centropomid *L. stappersii*. The other clupeid, *L. miodon*, is of secondary importance in the offshore catch. The pelagic fish community of the lake is very simple and consequently the offshore commercial 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 availability of food resources plays an important role in determining the occurrence of the catchable stocks of *S. tanganyicae* and *L. stappersii* in the lake. Contagious aggregation and highly patchy distribution characterise both *S. tanganyicae* and *L. miodon*, but are less pronounced for *L. stappersii*.

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

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

*Limnothrissa miodon* is more evenly distributed than *S. tanganyicae*. The two species have a different inshore-offshore, size-related distribution across the lake. Nursery grounds of the first are close to the shore while those of *S. tanganyicae* are in open, pelagic waters. With increase in size, *S. tanganyicae* 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 to be divided into northern

and southern components exploited by different fisheries at different levels.

The Lake Tanganyika ecosystem is not uniform along the north-south axis and quite remarkable spatial differences occur. There are, for example, considerable differences between northern and southern areas in fish distribution and feeding ecology. The fishery concentrates on clupeids in the north, on *L. stappersii* in the south and on both clupeids and the centropomid in the Kigoma area. Copepods are the main food of clupeids while shrimps are an important food of *L. stappersii*, particularly in the south.

The occurrence of *L. stappersii* is positively correlated with the abundance of pelagic shrimps. When *S. tanganyicae* is present at low abundance, *L. stappersii* exploit the shrimps. This is particularly the case in the south where shrimps appear to sustain the stock of *L. stappersii*. The occurrence of *S. tanganyicae* is linked to that of copepods with which there is a direct predator-prey relationship determining the local abundance pattern of the clupeid. In the past, considerable attention has been paid to the *L. stappersii* and *S. tanganyicae* predator-prey relationship. Such relationships appear to be more complicated than suggested in the past because of the relevance of the shrimp component in the feeding ecology of the predator.

The population dynamics of *S. tanganyicae* makes it a highly productive species which is quite resilient to exploitation. However, it is vulnerable to environmentally-induced recruitment failure which can quickly affect the size of the fishable stock. Effective assessment of *S. tanganyicae* is therefore difficult, and the risk of over-exploitation of this species is inherently high. *Lates stappersii* is a relatively long lived, opportunistic predator whose population is made up of several cohorts, which makes it less likely to experience recruitment failure.

On the basis of the appraisal of the current fisheries exploitation, it is advisable not to expand further the fishing effort at the northern end of the lake, where the lake's artisanal and industrial fisheries first developed, and indications of overexploitation have been observed. The unselective beach seining targeting *L. miodon* juveniles should be gradually phased out. The growth of the industrial fishing in the south of

the lake, where local overfishing is taking place, should be stopped or re-distribute further north to those areas where the *L. stappersii* stock experiences low exploitation. In view of the expected human population growth around the lake and of the consequent increase of fishing effort, it is imperative that open access to the lake pelagic fisheries is discontinued and regulated through a licensing system.

## 5.2 Future research and fishery management

The present work has pointed out the importance of fish research surveys on a lake-wide scale. However, the temporal frequency of the surveys executed so far is too low to properly follow the dynamics of the three target species, and particularly of the clupeid species. Ideally, future lake-wide surveys work should be carried out at least bimonthly for one year, thus allowing for accurate monitoring of cohort production.

*Lates stappersii* is believed to be a highly mobile species, migration patterns have been suggested but not proven. Frequent lake-wide surveys could verify such a hypothesis. Moreover, tagging experiments could be planned to track the movement of this species across the lake. Mark and recapture would also be useful to assess individual fish growth performance and, because otolith ageing is unfeasible for this species, this would allow validation of the growth estimates obtained from length-based methods.

While new information was gained on the feeding ecology of *L. stappersii*, the present knowledge on the diet of both clupeid species is rather approximate. Research projects on *S. tanganycae* and *L. miodon* feeding should be implemented at Bujumbura, Kigoma and Mpulungu where laboratory facilities are available.

The importance of the ecological role of the lake pelagic shrimps has been highlighted, yet information on pelagic fish larvae is still preliminary. The results of this work are from data collected during two time periods which are too far apart, and do not allow for an appropriate outline of the biological processes which characterise short-lived organism such as the pelagic shrimps, or the larval stages of fish. It is therefore important that future

studies on fish larvae and pelagic shrimps are carried out at the highest possible temporal sampling frequency in the areas of Bjumbura, Kigoma and Mpulungu.

Information about clupeid reproduction is unsatisfactory. Reproduction appears to be almost continuous throughout the year, but survey results show that the population is structured on few, well defined dominant cohorts. Whether this is due to marked seasonality of the reproductive process, or to egg and larval variable mortality within the year, has to be confirmed. Fecundity studies need to be carried out, and the patterns in reproductive potential should be assessed through appropriate indices based on the spawning biomass dynamics and egg production.

In consideration of the huge size of Lake Tanganyika and of its status as an international water body, future fishery research and management measures should be co-ordinated through a regional institution, the Lake Tanganyika Fisheries Organization (LTFO), with representatives from all countries. Fishery managers, scientists and representative of the fishing communities from the four riparian countries should be part of this organization, whose aim should be to harmonise all the activities related to the exploitation and conservation of the fish resources.

The activities of the LTFO should focus on sectors which need to be strengthened. For instance, fisheries statistics are fundamental to know the level of fishery yields from the lake. Currently each country has different systems, apart from the Democratic Republic of the Congo where there is no fishery statistics collection system. A database on the lake fishery productivity (catch and value) should be established based on common data collection and processing procedures.

Another field which needs to be improved is the legal infrastructure which should regulate the lake fisheries. Fishery regulations differ in the four countries and are normally poorly, if at all, enforced. Through the co-ordination of the supposed international organization for Lake Tanganyika, the corpus of national fishery legislations should be scrutinised, simplified and standardised in a single legal framework for the whole lake.

The international institution supervising the lake fisheries should also be in charge of the management of a geographic information system (GIS) for the lake. Nowadays GIS technology is easily available and relatively inexpensive. Geographic information systems are very effective tools to analyse data on natural resources and disseminate results. The lake fisheries GIS could be used to elaborate and display information on a variety of fishery-related topics such as: fish species dispersal, species composition in an area, distribution of fishing effort, restricted fishing zones.

Unless for specific purposes, scientific research on the pelagic fish resources of the lake should be carried out on a lake-wide basis. Research activities localised in small areas are of limited value when dealing with pelagic, highly dynamic fish stocks. Therefore, the scientific work throughout the lake should be organised according to identified priorities to fill the gaps in the scientific knowledge of the lake's ecosystem. Also, this would help to avoid duplication of research, optimising the use of the national, very limited, financial resources available for scientific investigations.

Finally, a possible Lake Tanganyika International Organization will have the ultimate aim of promoting world-wide the resources and assets of Lake Tanganyika to the general public, in the scientific community and, very important, in the donor community. The unique ecosystem of the lake, the level of its terrestrial and aquatic biodiversity, and the value of its fishery resources to the region make it a world heritage. The proper conservation and utilisation of the Lake Tanganyika is a commitment which goes beyond the responsibilities of the riparian states.

## REFERENCES

- Algaraja, K. (1984) Simple methods for estimation of parameters for assessing exploited fish stocks. *Indian J. Fish.* **31**, 177-208.
- Alheit, J. (1989) Comparative spawning biology of anchovies, sardines and sprats. *Rapp. P. -v. Reun. Cons. int. Explor. Mer*, **191**, 7-14.
- Allen, K.R., 1971. Relation between production and biomass. *J. Fish. Res. Bd Can.* **28**, 1573-1581.
- Allison, E.H., Patterson, G., Irvine, K., Thompson, A.B. and Menz, A. (1995a) The pelagic ecosystem. In: Menz, A. (Ed.) *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Nyassa*. Chatham, UK: Natural Resources Institute, pp. 351-367.
- Allison, E.H., Thompson, A.B., Ngatunga, B.P. and Irvine, K. (1995b) The diet and food consumption rates of the offshore fish. In: Menz, A. (Ed.) *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Nyassa*. Chatham, UK: Natural Resources Institute, pp. 233-278.
- Amstrong, M.J. and Shelton, P.A. (1990) Clupeoid life-history styles in variable environments. *Env. Biol. Fish.* **28**, 77-85.
- Anderson, A.M. (1961) Further observations concerning the proposed introduction of Nile perch into Lake Victoria. *E. Afr. Agric. J.* **26**, 195-201.
- Aro, E. (1993) Guidelines for sampling pelagic catches on Lake Tanganyika. Rome, FAO, GCP/RAF/271/FIN-FM/04, 25 pp.
- Ault, J.S. and Ehrhardt, N.M. (1991) Correction to the Beverton and Holt Z estimator for truncated catch length-frequency distributions. *Fishbyte*, **9**(1), 37-39.
- 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.
- Barel, C.D.N., Dorit, R., Greenwood, P.H., Fryer, G., Hughes, N., Jackson, P.B.N., Kawanabe, H., Lowe-McConnell, R.H., Ribbink, A.J., Trewavas, E., Witte, F. and Yamaoka, K. (1985) Destruction of fisheries in Africa's lakes. *Nature*, Lond., **315**, 19-20.
- Beadle, L.C. (1981) *The inland waters of tropical Africa. An introduction to tropical limnology*, 2nd edn. London: Longman. 475 pp.
- Beamish, R.J. and McFarlane, G.A. (1983) The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc.* **112**, 735-743.

- Beauchamp, R.S.A. (1955) The danger of overfishing existing stocks of *Tilapia* with particular reference to Lake Victoria and the Kavirondo Gulf. Rep. E. Afr. Freshwat. Fish. Res. Org., Jinja, Uganda, 30-34.
- Bell-Cross, G. and Bell-Cross, B. (1971) Introduction of *Limnothrissa miodon* and *Limnocaridina tanganyicae* from Lake Tanganyika in Lake Kariba. *Fish. Res. Bull. Zambia*, 5, 207-214.
- Benda, R.S. (1979) Analysis of catch data from 1968 to 1976 from nine fish landings in the Kenya waters of Lake Victoria. *J. Fish. Biol.* 15, 385-387.
- Benda, R.S. (1981) A comparison of bottom trawl catches rates in the Kenya waters of Lake Victoria. *J. Fish. Biol.* 18, 609-613.
- Bernacsek, G.M. and Lopes, S. (1984) Cahora Bassa (Mozambique). Rome, FAO, *CIFA Tech. Pap.* 10, 21-42.
- von Bertalanffy, L. (1938) A quantitative theory of organic growth. *Human Biol.* 10, 181-213.
- Beverton, R.J.H. (1990) Small marine pelagic fish and the threat of fishing; are they endangered? *J. Fish. Biol.* 37(Supplement A), 5-16.
- Beverton, R.J.H. and Holt, S.J. (1956) A review of methods for estimating mortality rates in exploited fish populations, with special references to sources of bias in catch sampling. *Rapp. P.-V. Réun. CIEM*, 140, 67-83.
- Beverton, R.J.H. and Holt, S.J. (1964) Table of yield functions for fishery management. Rome, FAO, *Fish. Tech. Pap.* 38, 49 pp.
- Beverton, R.J.H. and S.J. Holt, 1966. Manual of methods for fish stock assessment. Part II. Tables of yield function. Rome, FAO, *Fish. Biol. Tech. Pap.* 38, 67 pp.
- Bhattacharaya, 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., Bainbridge, R. and Rackham, O. (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* Xa. Chichester and New York: Academic Press, pp. 1-58.
- Blaxter, J.H.S. and Hunter, J.R. (1982) The biology of clupeoid fishes. *Adv. Mar. Biol.*, 20: 1-223.



- Bosma, E.M., Muhoza, S. and Zulu, I. (1998) The Gulfnet samples results of five cruises with the R/V *Tanganyika Explorer*. Rome, FAO, GCP/RAF/271/FIN-TD/March 1998, 26 pp
- Box, G.E.P. and Jenkins, G.M. (1976) *Time series analysis: forecasting and control*. San Francisco: Holden Day.
- Bruton, M.N. (1990) The conservation of fishes of Lake Victoria, Africa: an ecological perspective. *Env. Biol. Fishes*, **27**, 161-175
- Caddy, J.F. (1991) Death rates and time intervals: is there an alternative to the constant natural mortality axiom? *Rev. Fish Biol. Fisheries*, **1**, 108-138.
- Caddy, J.F. and Mahon, R. (1995) Reference points for fisheries management. Rome, FAO, *Fish. Tech. Pap.* **347**, pp. 83.
- Calder, W.A. (1984) *Size, Function and Life History*. Cambridge: Harvard University Press.
- Chapman, D.W. (1975) Characteristics of layers and schools of pelagic fish in Lake Tanganyika. Rome, 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. and van Well, P. (1978a) Growth and mortality of *Stolothrissa tanganyicae*. *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.
- Chapman, D.W., Rufli, H., van Well, P. and Ndugumbi, Z. (1976) Movements of pelagic fish in Lake Tanganyika. Rome, FAO, FI:DP/URT/71/012/35, 18 pp.
- Christensen, V. (1996) Managing fisheries involving predator and prey species. *Rev. Fish Biol. Fisheries*, **6**, 417-442.
- Clark, W.G. (1991) Groundfish exploitation rates based on life-history parameters. *Can. J. Fish. Aquat. Sci.* **48**, 734-750.
- Coenen, E.J. (1995) LTR's fisheries statistics subcomponent: March 1995 update of results for Lake Tanganyika. Rome, FAO, GCP/RAF/271/FIN-TD/32, 45 pp.
- Coenen, E., Hanek, G. and Kotilainen, P. (1993) Shoreline classification of Lake Tanganyika based on the results of an aerial frame survey (29.09.92 – 03.10.92). Rome, FAO, GCP/RAF/271/FIN-TD/10, 11 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. Rome, FAO, GCP/RAF/271/FIN-TD/80, 92 pp.
- Collart, A. (1958) Pêche artisanale et pêche industrielle au Lac Tanganyika. *Bull. Agric. Congo Belge*, 49(5), 1169-1268.
- Collart, A. (1960) L'introduction du *Stolothrissa tanganyicae* (Ndagala) au Lac Kivu. *Bull. Agric. Congo Belge*, 61, 975-985.
- Coulter, G.W. (1963) Hydrological changes in relation to biological production in southern Lake Tanganyika. *Limnology and Oceanography*, 8(4), 463-477.
- 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 stappersi* (Blgr.). *J. Fish Biol.* 9, 235-259.
- Coulter, G.W. (1981) Biomass, production and potential yield of the Lake Tanganyika pelagic fish community. *Trans. Amer. Fish. Soc.* 110, 325-335.
- Coulter, G.W. (Ed.) (1991a) *Lake Tanganyika and its life*. Natural History Museum Publications, Oxford: Oxford University Press. 354 pp.
- Coulter, G.W. (1991b) Pelagic fish. In: Coulter, G.W. (Ed.) *Lake Tanganyika and its life*. Natural History Museum Publications, Oxford: Oxford University Press, pp. 111-138.
- Coulter, G.W. and Spiegel, R.H. (1991) Hydrodynamics. In: Coulter, G.W. (Ed.) *Lake Tanganyika and its life*. Natural History Museum Publications, Oxford: Oxford University Press, pp. 49-75.
- Craig, J.F. (1997) A preliminary review of LTR scientific sampling programme. Rome, FAO, GCP/RAF/271/FIN-TD/74, 53 pp.
- Csirke, J. (1988) Small shoaling pelagic fish stocks. In: Gulland J.A. (Ed.) *Fish population dynamics: the implications for management*. Chichester: John Wiley and Sons Ltd. pp. 271-302.
- Csirke, J. (1989) Changes in the catchability coefficient in the Peruvian anchoveta (*Engraulis ringens*) fishery. In: Pauly, D. and Mendo, P. (Eds) *The peruvian upwelling ecosystem: dynamics and interactions*. ICLARM Conf. Proc. 18, pp. 207-219.
- Cushing, D.H. (1995) *Population production and regulation in the sea: a fisheries perspective*. Cambridge: Cambridge University Press. 354 pp.

- Dann, N. (1980) A review of replacement of depleted stocks by other species and the mechanisms underlying such replacements. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer*, 177, 405-421.
- Degens, E.T., von Horzen, R.P. and Wong, H.-K. (1971) Lake Tanganyika. Water chemistry, sediments, geological structure. *Naturwissenschaften*, 58(5): 229-241.
- 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.
- EAFFRO (1960) An. Rep. E. Afr. Freshwat. Fish. Res. Org. Jinja, Uganda, 48 pp.
- Edwards, R.R.C. (1984) Comparisons of growth in weight of temperate and tropical marine fish counterparts. *Can. J. Fish. aquat. Sci.* 41, 1381-1384.
- Ehrhardt, N.M. and Ault, J.S. (1992) Analysis of two length-based mortality models applied to bounded catch length frequencies. *Trans. Amer. Fish. Soc.* 121(1), 115-122.
- 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. Rome, FAO, FI:DP/URT/71/012, Tech. Rep. 1, 37 pp.
- FAO (1982) Biological studies on the pelagic ecosystem of Lake Malawi. Rome, FAO, FI:DP/MLW/75/109, Tech. Rep. 1, 176 pp.
- FAO (1995) Precautionary approach to fisheries. Part 1: Guidelines on the precautionary approach to capture fisheries and species introductions. Elaborated by the technical consultation on the precautionary approach to capture fisheries (including species introduction). Lysekil, Sweden, 6-13 June 1995 (A scientific meeting organized by the Government of Sweden in cooperation with FAO). Rome, FAO, *Fish. Tech. Pap.* 350, Part 1, 52 pp.
- Fryer, G. (1960) Concerning the proposed introduction of Nile perch into Lake Victoria. *E. Afr. Agric. J.* 25, 267-270.
- 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.
- Garrod, D.J. (1960) The fisheries of Lake Victoria. *E. Afr. Agric. For. J.* 26, 42-48.

- Goldschmidt, T., Witte, F. and Wanink, J.H. (1993) Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in the sub-littoral areas of Lake Victoria. *Conserv. Biol.* 7, 686-700.
- Goodyear, C.P. (1993) Spawning stock biomass per recruit in fisheries management: foundation and current use. In: Smith, S.J., Hunt, J.J. and Rivard, D. (Eds) Risk evaluation and biological reference points for fisheries management. *Can. Spec. Publ. Fish. Aquat. Sci.* 120, 67-81.
- Graham, M. (1929) *The Victoria Nyanza and its Fisheries*. London: Crown Agents for the Colonies. 255 pp.
- Graham, M. (1943) *The fish gate*. London: Faber & Faber.
- Gréboval, D.F. and Mannini, P. (1992) The fisheries of Lake Victoria: review of basic data. FAO, Rome, *RAF/87/099-WP/16/92*, 45 pp.
- Gulland, J.A. (1983) *Fish stock assessment: A manual of basic methods*. New York: John Wiley and Sons. 223 pp.
- Gulland, J.A. and Rosemberg, A.A. (1992) A review of length-based approaches to assessing fish stocks. Rome, FAO, *Fish. Tech. Pap.* 323, 100 pp.
- Gunderson, D.R. and Dygert, P.H. (1988) Reproductive effort as a predictor of natural mortality rate. *J. Cons. CIEM*, 44, 200-209.
- Hamblyn, E.L. (1960) The Nile perch project. A. Rep. E. Afr. Freshwat. Fish. Res. Org., Jinja, Uganda, 26-32.
- Hecky, R.E., (1991) The pelagic ecosystem. In: G.W. Coulter (Ed.). *Lake Tanganyika and its life*. Natural History Museum Publications, Oxford: Oxford University Press, pp. 90-110.
- Hecky, R.E. (1993) The eutrophication of Lake Victoria. *Verh. Int. Verein. Limnol.* 25, 39-48.
- Hecky, R.E., Fee, E.J., Kling, H.J. and Rudd, J.W. (1981) Relationship between primary production and fish production in Lake Tanganyika. *Trans. Am. Fish. Soc.* 110, 336-345.
- Henderson, H.F. (1976) Notes on *Luciolates* based on a study of length frequency diagrams from the ring-net fisheries on Lake Tanganyika; and notes on the large size of *Limnothrissa miodon* in the catches of the ring-net fishery in Tanzania. Rome, FAO, *FI:DP/URT/71/012/29*, 6 pp.
- Hilborn, R. and Walters, C.J. (1992) *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. London: Chapman & Hall. 570 pp.
- Hyslop, E.J. (1980) Stomach content analysis. A review of methods and their application. *J. Fish. Biol.* 17, 411-429.

- Huttula, T., Podsetchine, V., Kotilainen, P. and Mölsa, H. (1994) Hydrology of Lake Tanganyika. In: Kern-Hansen, Rosbjerg, D. and Thomsen, R. (Eds) (1994) Nordic Hydrological Conference, Tórshavn, Færøerne, 2-4 August 1994. København: NHP report 34, Koordineringskomitéen for Hydrologi I Nordem (KOHYNO), pp. 43-52.
- de Iongh, 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.
- Jackson, P.B.N. (1971) The African Great Lakes fisheries: past present and future. *Afr. J. Trop. Hydrobiol. Fish.* **1**, 35-49.
- 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. Rome, FAO, *EIFAC Tech. Pap.* **23**, Suppl. 1(1), 292-306.
- Jones, C.M. (1992) Development and application of the otolith increment technique. In: Stevenson, D.K. and Campana, S.E. (Eds) *Otolith microstructure examination and analysis. Can. Spec. Publ. Fish. Aquat. Sci.* **117**, 1-11.
- Junor, F.J.R. and Begg, G.W. (1971) A note on the successful introduction of *Limnothrissa miodon* the Lake Tanganyika sardine to Lake Kariba. *Newsl. Limnol. Soc. Sth Afric.* **16**, 8-14.
- 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, Rome, GCP/RAF/271/FIN-TD/30, 63-65.
- Kimura, S. (1991a) On the otoliths of *Lates stappersii*. In: Kawanabe, H. and Nagoshi, M. (Eds) *Ecological and limnological study on Lake Tanganyika and its adjacent regions*. **7**, 65.
- Kimura, S. (1991b) Growth of *Stolothrissa tanganyicae* estimated from daily otolith rings in southern Lake Tanganyika. In: Kawanabe, H. and Nagoshi, M. (Eds) *Ecological and limnological study on Lake Tanganyika and its adjacent regions*. **7**, 60-61.
- Kimura, S. (1991c) Growth of *Limnothrissa miodon* estimated from daily otolith rings in southern Lake Tanganyika. In: Kawanabe, H. and Nagoshi, M. (Eds) *Ecological and limnological study on Lake Tanganyika and its adjacent regions*, **7**, 62-64.
- Kimura, S. (1995) Growth of the clupeid fishes, *Stolothrissa tanganyicae* and *Limnothrissa miodon*, in the Zambian waters of Lake Tanganyika. *J. Fish. Biol.* **47**, 569-575.

- King, M. (1995) *Fisheries biology, assessment and management*. Oxford: Fishing News Books, Blackwell Science Ltd. 341 pp.
- Kinncar, P.R. and Gray, C.D. (1997) *SSPS for Windows*, 2nd edn. East Sussex: Psychology Press Ltd. 386 pp.
- Kirkwood, G.P. and Smith, A.D.M. (1996) Assessing the precautionary nature of fisheries management strategies. FAO, Precautionary approach to fisheries. Part 2: scientific papers. Prepared for the technical consultation on the precautionary approach to capture fisheries (including species introduction). Lysekil, Sweden, 6-13 June 1995 (A scientific meeting organized by the Government of Sweden in cooperation with FAO). Rome, FAO, *Fish. Tech. Pap.* 350, Part 2, pp. 141-158
- Kitchell, J.F., Eby, L.A., He, X., Schindler, D.E. and Wright, R.A. (1994) Predator-prey dynamics in an ecosystem context. *J. Fish. Biol.* 45 (Supplement A), 209-226.
- Kudhongania, A.W. and Chitamwebwa, D.B.R. (1995) Impact of environmental change, species introductions on the fish stocks of Lake Victoria. In: Pitcher, T.J. and Hart, P.J.B. (Eds) *The impact of species changes in African lakes*. London: Chapman & Hall, pp. 19-32.
- Kurki, H. (1993) Field notes on zooplankton. Rome, FAO, GCP/RAF/271/FIN-FM/09, 26 pp.
- Kurki, H. (1996a) Zooplankton sampling on board R/V *Tanganyika Explorer*. Rome, FAO, GCP/RAF/271/FIN-FM/20, 16 pp.
- Kurki, H. (1996b) The results of zooplankton sampling at three localities in Lake Tanganyika; July 1993 - December 1995. Rome, FAO, GCP/RAF/271/FIN-TD/51, 45 pp.
- Kurki, H. and Vuorinen, I. (1995) Zooplankton ecology of Lake Tanganyika. Report on the results of LTR's scientific sampling programme. Rome, FAO, GCP/RAF/271/FIN-TD/34, 29 pp.
- Kurki, H., Mannini, P., Vuorinen, I., Aro, E., Mölsä, H., Lindqvist, O.V. (1998) Macrozooplankton communities in Lake Tanganyika indicate food chain differences between the northern part and the main basins. *Hydrobiologia*, (in press).
- Larkin, P.A. (1979) Predator-prey relations in fishes: an overview of the theory. In: Clepper, H. (Ed.) *Predator-prey Systems in Fisheries Management*. Washington, DC: Sport Fisheries Inst. pp. 13-22.
- Lévêque, C., Durand, J.R. and Écoutin, J.M. (1977) Relations entre le rapport P/B et la longévité des organisme. *Cah. ORSTOM, ser. Hydrobiol.* 11, 17-31.

- Lindqvist, O.V. and Mikkola, H. (1989) Lake Tanganyika: review of limnology, stock assessment, biology of fish and fisheries. Prepared for the regional project for the management of fisheries, Lake Tanganyika. Rome, FAO, GCP/RAF/229/FIN, 51 pp.
- Lluch-Belda, D., Crawford, R.J.M., Kawasaki, T., MacCall, A.D., Parrish, R.H., Schwartzlose R.A. and Smith, P.E. (1989) World-wide fluctuations of sardine and anchovy stocks: the regime problem. *S. Afr. J. Mar. Sci.* **8**, 195-205.
- 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. (1976) Density dependence of catchability coefficient in the California Pacific sardine, *Sardinopsis sagax caerulea*, purse seine fishery. Calif. Coop. Oceanic Invest. Rep. **18**, 136-148.
- MacCall, A.D. (1990) *Dynamic geography of marine fish populations*. Seattle: University of Washington Press. 153 pp.
- Mace, P.M. and Sissenwine, M.P. (1993) How much spawning per recruit is enough? In: Smith, S.J., Hunt, J.J. and Rivard, D. (Eds) Risk evaluation and biological reference points for fisheries management. *Can. Spec. Publ. Fish. Aquat. Sci.* **120**, 101-118.
- Mambona, W.B.C. (1996) Enquête cadre simulatanée pour le Lac Tanganyika, Zaïre. Rome, FAO, GCP/RAF/271/FIN-TD/47, 100 pp.
- Mann, M.J. (1970) A resume of *Tilapia* fisheries of Lake Victoria up to the year 1960. E. Afr. Freshwat. Fish. Res. Org. Ann. Rep., 1969, Append. B. 21-27.
- 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). Rome, FAO, FI:DP/BDI/73/020/5, 1-58.
- Mannini, P. (1990) Paramètres de la population de *Limnothrissa miodon* du lac Kivu (1980 - 1989). Rome, FAO, RWA/87/012/Document de Travail (TR)/32, 41 pp.
- Mannini, P. (1991) Aspects de la dynamique et de l'aménagement du stock de *Limnothrissa miodon* du lac Kivu. Rome, FAO, RWA/87/012/Document de Travail (TR)/43, 21 pp.
- Mannini, P. (1992) Some characteristics of small pelagic species and possible affinities with the population of Lake Victoria *Rastrineobola argentea*. In: Mannini, P. (Ed.) The Lake Victoria Daga ( *Rastrineobola argentea* ). Report of the First Meeting of the Working Group on Lake Victoria *Rastrineobola argentea*, 9-11 December 1991, Kisumu, Kenya. Rome, FAO, RAF/87/099-TD/38/92, 62-79.

- Mannini, P. (1993) Field notes for Fish Biology. Rome, 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*. Rome, FAO, GCP/RAF/271/FIN-FM/19, 27pp.
- Mannini, P., Katonda, I., Kissaka, B. and Verburg, P. (1998) Feeding ecology of *Lates stappersii* in Lake Tanganyika. *Hydrobiologia*, (in press).
- Marten, G.G. (1979) Predator removal: effect on fisheries yields in Lake Victoria (East Africa). *Science*, **203**, 646-648.
- Marshall, B.E. (1984) Small pelagic fishes and fisheries in African inland waters. Rome, FAO, *CIFA Tech. Pap.* **14**, 25 pp.
- Mather, F.J., Mason, J.M. and Jones, A.C. (1974) Analysis of migrations and mortality of bluefin tuna, *Thunnus thynnus*, tagged in the Northwestern Atlantic Ocean. *U.S. Fish. Bull.* **72**(4), 900-914.
- Mathisen, O.A. (1975) Preliminary report on a mission (acoustic estimation) for the Lake Tanganyika Fisheries project. Rome, 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.
- Menz, A (Ed.) (1995) *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Nyassa*. Chatham, UK: Natural Resources Institute. 386 pp.
- Moreau, J., J. Munyandorero and Nyakageni, B. (1991) Evaluation des paramètres démographiques chez *Stolothrissa tanganyicae* and *Limnothrissa miodon* du Lac Tanganyika. *Verh. Internat. Verein. Limnol.* **24**, 2552-2558.
- Moreau, J. and B. Nyakageni, 1992. *Luciolates stappersii* in Lake Tanganyika. Demographical status and possible recent variations assessed by length frequency distributions. *Hydrobiologia*, **232**, 57-64.
- Mulimbwa, N. and Mannini, P. (1993) Demographic characteristics of *Stolothrissa tanganyicae*, *Limnothrissa miodon* and *Lates stappersii* in the northwestern (Zairian) waters of Lake Tanganyika. In: Marshall, B.E., and Mubamba, R. (Eds) Papers presented at the symposium on biology, stock assessment and exploitation of small pelagic fish species in the African great lakes region. Bujumbura, Burundi,



25-28 November 1992. Rome, FAO, *CIFA Occasional Paper*, 19, 176-195.

- Mulimbwa, N. and Shirakihara, K. (1994) Growth, recruitment and reproduction of sardines (*Stolothrissa tanganicae* and *Limnothrissa miodon*) in Northwestern Lake Tanganyika. *Tropics*, 4(1), 57-67.
- Munro, J.L. (1983) Biological and ecological characteristics of Caribbean reef fish. In: Munro, J.L. (Ed.) *Caribbean Coral Reef Fishery Resources*. ICLARM Stud. Rev. 7, 223-221.
- 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. Rome, FAO, FI:DP/URT/71/012/36, 15 pp.
- Ngomirakiza, M. and Haling, L. (1972) Développement de la pêche artisanale dans le eaux burundaises du Lac Tanganyika. Rome, FAO, CIFA Symposium 72/S9, 1-4.
- Okemwa, E.N. (1984) Potential fishery of Nile perch *Lates niloticus* Linne (Pisces: Centropomidae) in Nyanza Gulf of Lake Victoria, East Africa. *Hydrobiologia*, 108, 121-6.
- 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. Rome, FAO, GCP/RAF/271/FIN-TD/52, 97 pp.
- Paffen, P., Coenen, E., Bambara, S., Wa Bazolana, M., Lymo, E. and Lukesa, C. (1997) Synthesis of the 1995 simultaneous frame survey of Lake Tanganyika fisheries. Rome, FAO, GCP/RAF/271/FIN-TD/60, 35 pp.
- Pakkasma, S. (1996) Age and growth of the pelagic clupeids in Lake Tanganyika estimated from daily otolith increments. M. Sc. Thesis, University of Turku. 48 pp.
- Pakkasmaa, S. and Sarvala, J. (1995) Preliminary study and growth of the pelagic clupeids in Lake Tanganyika. Rome, FAO, GCP/RAF/271/FIN-TD/41, 29 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. (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. CIEM*, 39(2), 175-92.
- Pauly, D. (1983a) Some simple methods for the assessment of tropical fish stocks. Rome, 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), 17-19.
- 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. (1987) A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic invertebrates. In: Pauly, D and Morgan, G.R. (Eds) *Length-based methods in fisheries research*. ICLARM Conf. Proc. 13, 7-34.
- Pauly, D. (1991) Growth performances in fishes: rigorous description of patterns as a basis for understanding causal mechanism. *Aquabyte*, 4(3), 3-6.
- Pauly, D. (1994) Theory and practice of overfishing. In: Pauly, D. *On the sex of fish and the gender of scientists. Collected essays in fisheries science*. London: Chapman & Hall, pp. 89-103.
- Pauly, D. and David, N. (1981) ELEFAN I, a BASIC program for the objective extraction of growth parameters from length-frequency data. *Meeresforschung*, 28(4), 205-211.
- Pauly, D. and. Munro, J.L. (1984) Once more on the comparison of growth in fish and invertebrates. *Fishbyte*, 2(2), 21.
- Pauly, D. and Soriano, M.L. (1986) Some practical extensions to Beverton and Holt's relative yield-per-recruit model. In: Naclean, J.L., Dizon, L.B. and Hosillo, L.V. (Eds) *The First Asian Fisheries Forum*. Manila: Asian Fisheries Society, pp. 491-496.
- 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*. Rome, 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.
- Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.
- Peterson, I. and Wroblewski, S.J. (1984) Mortality rate of fishes in the pelagic ecosystem. *Can. J. Fish. Aquat. Sci.* 47, 1117-1120.
- 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.
- Pitcher, T.J. (1995) Species changes and fisheries in African lakes: outline of the issues. In: Pitcher, T.J. and Hart P.J.B. (Eds) *The impact of species changes in African lakes*. London: Chapman & Hall, pp. 1-18.
- Plisnier, P.D. (1995) Catch assessment survey in Zambian waters of Lake Tanganyika in 1994. Rome, FAO, GCP/RAF/271/FIN-TD/41, 26 pp.
- Plisnier, P.D., Langenberg, V., Mwape, L., Chitamwebwa, D., Tshibangu K. and Coenen, E. (1996) Limnological sampling during an annual cycle at three stations on Lake Tanganyika (1993-1994). Rome, FAO, GCP/RAF/271/FIN-TD/46, 136 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. Rome, FAO, GCP/RAF/271/FIN-TD/72, 39 pp.
- Poll, M. (1953) *Poissons non Cichlidae. Résultats scientifique de exploration hydrobiologique du Lac Tanganika (1945-47)*. Bruxelles: Institute Royal des Sciences Naturelles de Belgique, Vol III, fasc. 5A. 251 pp.
- Reusens, M. (1987) Programme de recherche halietique au Lac Kivu en particulier sur le *Limnothrissa miodon*. Rome, FAO, RWA/87/012, FAO, Doc. de Travail, 3, 114 pp.
- Reynolds, J.E. and Gréboval, D.F. (1988) Socio-economics effects of the evolution of Nile perch fisheries in Lake Victoria: a review. Rome, FAO, *CIFA Tech. Pap.* 17, 148 pp.

- Reynolds, J.E. and Hanek, G. (1997) Tanganyika fisheries and local stakeholders. An overview of the LTR lakewide socio-economic survey. Rome, FAO, GCP/RAF/271/FIN-TD/71, 70 pp.
- Reynolds, J.E., Gréboval, D.F. and Mannini, P. (1995) Thirty years on: the development of the Nile perch fishery in Lake Victoria. In: T.J. Pitcher, P.J.B. Hart (Eds), *The Impact of Species Changes in African Lakes*. London: Chapman & Hall, pp. 181-211.
- Ribbink, A.J. (1987) African lakes and their fishes: conservation scenarios and suggestions. *Env. Biol. Fishes*, **19**, 3-26.
- Rikhter, V.A. and Efanov, V.N. (1976) On one of the approaches to estimation of natural mortality of fish populations. ICNAF Res. Doc., 76/VI/8, 12 pp.
- Roest, F. (1977) *Stolothrissa tanganyicae*: population dynamics, biomass evolution and life history in the Burundi waters of Lake Tanganyika. Rome, FAO, *CIFA Occas.Pap.* **5**, 42-63.
- Roest, F. (1978) *Stolothrissa tanganyicae*: population dynamics, biomass evolution and life history in the Burundi waters of Lake Tanganyika. *CIFA Tech. Pap.* **5**, 42-62.
- Roest, F. (1988) Predator-prey relations in northern Lake Tanganyika and fluctuations in the pelagic fish stocks. In: Lewis, D. (Ed.) *Predator-prey relationships, population dynamics and fisheries productivities of large african lakes*. Rome, FAO, *CIFA Occas. Pap.* **15**, 104-129.
- Roest, F. (1992) The pelagic fisheries resources of Lake Tanganyika. *Mitt. Internat. Verein. Limnol.* **23**, 11-15.
- Roff, D. A. (1986) Predicting body size with life history models. *BioScience*, **36**, 316-323.
- Roff, D.A. (1992) *The evolution of life histories. Theory and Analysis*. London: Chapman & Hall. 535 pp.
- Sarvala, J., Salonen, K., Jarvinen, M., Aro, E., Huttula, T., Kotilainen, P., Kurki, H., Langerberg, V., Mannini, P., Peltonen, A., Plisnier, P.-D., Vuorinen, I., Mölsä, H., Lindqvist, O. V. (1998) Trophic structure of Lake Tanganyika revisited: carbon flows in the pelagic food web. *Hydrobiologia*, (in press).
- Schaff, W.E. (1975) Fish population models: potential and actual links to ecological models. In: Russel, C.F. (Ed.) *Ecological modelling in a resource management framework: the proceedings of a symposium*. Maryland: John Hopkins University Press, pp 211-239.
- Schaff, W.E. (1980) An analysis of the dynamic population response of Atlantic menhaden, *Brevoortia tyrannus*, to intensive fishery. *Rapp. P.-V. Réun. CIEM*, **177**, 243-251.

- Shannon, L.V., Crawford, R.J.M., Brundrit G.B. and Underhill, L.G. (1988) Responses of fish populations in the Benguela ecosystem to environmental change. *J. Cons. perm. int. Explor. Mer.* 45(1), 5-12.
- Shelton, P.A. and Armstrong, M.J. (1983) Variations in parent stock and recruitment of pilchard and anchovy population in the Southern Benguela system. In: Sharp, G.D. and Csirke, J. (Eds) *Proceedings of the Expert Consultation to examine changes in abundance and species composition of neritic fish resources*. San José, Costa Rica, 18-29 April 1983. Rome, FAO, *Fish. Rep.* 291, Vol. 3, pp 1113-1132.
- Shepherd, J.G. (1987) A weakly parametric method for estimating growth parameters from length composition data. In: Pauly, D. and Morgan, G. R. (Eds.) *Length-based methods in fisheries research*, ICLARM Conf. Proc. 13, 113-119.
- 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.
- Sokal, R.R. and Rohlf, F.J. (1981) *Biometry*, 2nd edn. New York: Freeman and Company. 859 pp.
- Sousa, M.I. (1988) Sources of bias in growth and mortality estimation of migratory pelagic fish stocks, with emphasis on *Decapterus russelli* (Carangidae) in Mozambique. Rome, FAO, *Fish. Rep.* 389, 288-307.
- Sparre, P. and Venema, S.C. (1992) Introduction to tropical fish stock assessment. Part I. Manual. Rome, FAO, *Fish. Tech. Pap.* 306.1, Rev. 1. 376 pp.
- Thompson, A.B. (1995) Fisheries potential. In: Menz, A. (Ed.) *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Nyassa*. Chatham, UK: Natural Resources Institute, pp. 369-3386.
- Tiercelin, J.J. and Mondeguer, A. (1991) The geology of the Tanganyika Trough. In: G.W. Coulter (Ed.) *Lake Tanganyika and its life*. Natural History Museum Publications, Oxford: Oxford University Press. pp. 7-48.
- Treasurer, J.W., Owen R. and Bowers, E. (1992) The population dynamics of pike, *Esox lucius*, and perch, *Perca fluviatilis*, in a simple predator-prey system. *Env. Biol. Fishes*, 34(1), 65-78.
- Tshibangu, K.K. and I. Kinoshita, 1995. Early life histories of two clupeids, *Limnothrissa miodon* and *Stolothrissa tanganyicae*, from Lake Tanganyika. *Japan. J. Ichthyol.*, 42(1), 81-87.
- Tuomainen, V., Mölsä, H., Parkkinen, J., Patomäki, L. and Lindqvist, O.V. (1997) The NOAA series' AVHRR radiometer's capability of revealing water features in Lake Tanganyika. FAO/FINNIDA Research for the Management of

- the Fisheries on Lake Tanganyika. FAO, GCP/RAF/271/FIN-TD/77, 39 pp.
- 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.
- Turner, G.F. (1995) Management, conservation and species changes of exploited fish stocks in Lake Malawi. In: T.J. Pitcher, P.J.B. Hart (Eds), *The Impact of Species Changes in African Lakes*. London: Chapman and Hall, pp. 365-395.
- Ulltang, O. (1976) Catch per unit of effort in the Norwegian purse seine fishery for Atlanto-Scandian (Norwegian spring spawning) herring. Rome, FAO, *Fish. Tech. Pap.* 155, 91-101.
- Ulltang, O. (1980) Factors affecting the reaction of pelagic fish stocks to exploitation and requiring a new approach to assessment and management. *Rapp. P.-V. Réun. CIEM*, 177, 489-504.
- Walters, T. F. (1977) Secondary production in inland waters. *Advance in Ecological Research*, 10, 91-164.
- Walters, C. and Maguire, J. (1996) Lessons for stock assessment from the northern cod collapse. *Rev. Fish Biol. and Fisheries*, 6, 125-137
- Wandera, S.B. (1990) The exploitation of small pelagic fishes of the great lakes of Africa with reference to the mukene (*Rastrineobola argentea*) fishery of the northern waters of Lake Victoria. In: Fisheries of the African Great Lakes. Research papers presented at the International Symposium on Resource Use and Conservation of the African Great Lakes. Bujumbura, 29 November – 2 December 1989. International Agricultural Centre, Wageningen, The Netherlands, Fisheries and Aquaculture Unit. Occasional Paper, 3, 67-74.
- Wanink, J.H. (1989) The ecology and fishery of dagaa, *Rastrineobola argentea* (Pellegrin) 1904. In: Fish Stocks and Fisheries in Lake Victoria (A handbook to the HEST/TAFIRI and FAO/DANIDA regional seminar, Mwanza, January/February 1989). Leiden, The Netherlands, Rep. Haplochromis Ecology Survey Team (HEST) and Tanzanian Fish. Res. Inst. (TAFIRI), pp. 53 (App. II).
- Wanink, J.H. (1991) Survival in a perturbed environment: the effects of Nile perch introduction on the zooplanktivorous fish community of Lake Victoria. In: Ravera, O. (Ed.) *Terrestrial and Aquatic Ecosystems: Perturbation and Recovery*. Chichester: Ellis Horwood, pp. 269-75.
- Welcomme, R.L. (1966) Recent changes in the stocks of Tilapia in Lake Victoria. *Nature, Lond.*, 212, 52-54.
- Welcomme, R.L. (1967) Observations on the biology of the introduced species of *Tilapia* in Lake Victoria. *Revue Zool. Bot. afr.* 76, 249-279.

- Witte, F. and Goudswaard, P.C. (1985) Aspects of the haplochromine fishery in southern Lake Victoria. Rome, FAO, *Fish. Rep.* **335**, 81-88.
- Witte, F., Goldschmidt, T., Wannik, J., van Oijen, M., Goudswaard, K., Witte-Mass, E. and Bouton, N. (1992) The destruction of an endemic species flock. Quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Env. Biol. Fishes*, **34**, 1-28.

Appendix 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 work 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	03°28,31	29°16,92	03°31,91	29°17,59	16/11/95	03°26,99	29°09,21	03°26,62	29°12,69	02/04/96	03°25,86	29°14,84	03°29,71	02°91,47
16/6/95	03°43,03	29°13,95	03°46,26	29°15,34	17/11/95	03°28,11	29°15,36	03°02,58	29°18,66	03/04/96	03°32,88	29°15,34	03°37,11	29°15,21
16/6/95	04°14,60	29°25,88	04°17,22	29°28,37	17/11/95	03°37,30	29°18,78	33°73,90	29°18,22	03/04/96	03°46,05	29°15,12	03°48,72	29°17,98
17/6/95	04°34,05	29°37,50	04°37,79	29°36,45	17/11/95	03°56,51	29°08,39	03°55,53	29°11,91	03/04/96	03°57,67	29°07,62	03°57,40	29°11,61
17/6/95	04°33,91	29°10,02	04°36,27	29°08,64	17/11/95	03°57,69	29°16,11	03°59,65	29°20,34	03/04/96	03°57,39	29°15,46	03°56,48	29°19,40
18/6/95	04°45,62	29°25,81	04°49,29	29°27,07	18/11/95	03°58,09	29°24,05	04°00,92	29°24,27	04/04/96	03°57,09	29°23,91	04°01,30	29°23,07
18/6/95	05°20,47	29°45,63	05°17,38	29°46,63	18/11/95	04°27,87	29°14,21	04°28,66	29°17,58	04/04/96	04°27,56	29°13,44	04°27,68	29°17,35
19/6/95	05°03,95	29°37,91	04°59,32	29°36,95	19/11/95	04°28,42	29°38,59	04°31,13	29°38,49	05/04/96	04°27,36	29°25,72	04°27,60	29°30,04
20/6/95	05°41,49	29°53,15	05°45,14	29°54,25	19/11/95	04°57,37	29°08,06	04°57,06	29°11,42	05/04/96	04°27,65	29°37,38	04°30,37	29°34,64
20/6/95	05°56,60	29°37,30	05°58,24	29°34,56	20/11/95	04°57,29	29°25,72	04°58,05	29°28,90	05/04/96	04°57,39	29°08,70	04°56,90	29°13,05
20/6/95	06°05,51	29°21,16	06°09,24	29°23,19	20/11/95	04°56,39	29°36,47	04°54,70	29°33,53	05/04/96	04°57,30	29°26,00	04°57,49	29°29,86
20/6/95	06°12,26	29°42,03	06°16,58	29°40,22	21/11/95	05°28,03	29°19,47	05°28,64	29°22,70	06/04/96	04°57,40	29°36,23	04°55,48	29°32,40
21/6/95	06°23,72	29°39,55	06°24,86	29°43,40	21/11/95	05°27,39	29°35,59	05°27,31	29°38,70	07/04/96	05°27,08	29°20,03	05°26,80	29°23,84
22/6/95	06°31,79	30°00,16	06°31,15	30°03,91	22/11/95	05°28,05	29°44,50	05°30,75	29°46,66	08/04/96	05°27,46	29°36,33	05°26,94	29°39,76
21/6/95	06°37,22	30°17,06	06°38,03	30°18,46	22/11/95	05°56,90	29°16,27	05°56,50	29°19,69	08/04/96	05°28,94	29°44,54	05°32,19	29°45,59
22/6/95	06°52,58	30°08,68	06°56,15	30°07,23	23/11/95	05°57,09	29°31,24	05°56,80	29°35,16	08/04/96	05°57,46	29°20,52	05°57,77	29°24,10
22/6/95	07°07,04	30°27,57	N/A	N/A	23/11/95	05°56,71	29°45,73	05°54,72	29°48,67	08/04/96	05°58,78	29°35,23	05°58,48	29°38,79
22/6/95	07°24,58	30°21,36	07°26,94	30°18,67	24/11/95	06°28,43	29°46,60	06°29,27	29°50,29	09/04/96	05°57,07	29°47,67	05°58,09	29°44,54
23/6/95	07°39,56	30°15,15	07°39,25	30°19,04	24/11/95	06°31,86	29°57,00	06°31,24	30°00,26	09/04/96	06°26,69	29°25,55	06°26,50	29°30,49
23/6/95	07°25,44	30°46,07	07°56,41	30°45,10	24/11/95	06°57,38	29°46,52	06°56,89	29°50,18					
23/6/95	08°04,88	30°51,11	N/A	N/A	25/11/95	06°57,68	30°05,61	06°58,44	30°09,45					
24/6/95	08°23,61	30°52,93	08°26,82	30°54,36	25/11/95	06°58,69	30°31,65	07°02,56	30°31,05					
25/6/95	08°32,97	30°50,11	08°30,73	30°47,73	25/11/95	07°27,53	30°40,16	07°27,53	30°17,44					
25/6/95	08°19,60	30°53,35	08°16,07	30°37,15	26/11/95	07°30,82	30°33,49	07°33,25	30°35,78					
26/6/95	07°51,57	30°37,75	07°48,42	30°37,40	26/11/95	07°78,74	30°26,65	08°00,92	30°30,20					
26/6/95	07°32,33	30°34,43	07°29,14	30°32,61	27/11/95	07°58,15	30°40,60	07°59,42	30°04,06					
27/6/95	07°05,18	29°59,50	07°03,36	29°56,65	27/11/95	08°00,75	30°50,87	08°03,89	30°52,07					
27/6/95	06°33,42	29°31,03	06°29,78	29°30,70	27/11/95	08°26,72	30°28,89	08°26,06	30°32,58					
28/6/95	05°51,37	29°21,35	05°48,52	29°23,50	28/11/95	08°27,50	30°51,09	08°27,37	30°54,99					
28/6/95	05°18,16	29°22,90	05°14,66	29°23,53	28/11/95	08°28,47	31°07,03	08°31,80	31°07,27					
29/6/95	05°04,23	29°29,80	50°29,39	29°29,87	29/11/95	07°38,40	30°38,38	07°41,09	30°40,34					
29/6/95	04°18,97	29°22,29	04°14,55	29°21,80	1/12/95	04°56,72	29°36,74	04°56,91	29°32,94					
					3/12/95	04°03,25	29°26,11	03°59,40	29°24,47					



Appendix 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	03°27,45	29°15,66	03°30,53	29°15,03	5/2/98	05°27,92	29°26,11	05°30,77	29°23,65
23/11/97	03°40,92	29°14,81	03°44,54	29°14,73	6/2/98	06°01,53	29°34,21	06°02,25	29°30,65
23/11/97	03°50,46	29°15,12	03°53,55	29°13,98	6/2/98	06°11,42	29°36,96	06°12,32	29°40,70
23/11/97	04°01,76	29°11,05	04°00,85	29°14,24	7/2/98	06°58,83	29°48,71	06°59,86	29°52,62
23/11/97	04°03,28	29°17,95	04°06,21	29°21,41	8/2/98	07°13,02	30°24,01	07°14,63	30°22,84
23/11/97	04°20,49	29°24,37	04°23,07	29°21,69	8/2/98	07°43,23	30°37,99	07°44,74	30°41,33
24/11/97	04°40,78	29°09,85	04°44,10	29°09,77	8/2/98	08°03,41	30°42,02	08°04,53	30°45,30
24/11/97	04°43,62	29°35,63	04°47,88	29°35,31	9/2/98	08°19,59	30°40,38	08°22,11	30°37,71
25/11/97	05°04,27	29°39,86	05°00,65	29°37,52	9/2/98	08°28,31	30°29,91	08°27,69	30°31,96
25/11/97	04°58,81	29°12,44	05°02,31	29°13,21	11/2/98	07°51,35	30°30,10	07°50,56	30°26,33
26/11/97	05°12,90	29°42,22	05°15,86	29°43,11	11/1/00	07°37,56	30°26,62	07°35,13	30°28,41
26/11/97	05°14,56	29°20,30	05°14,45	29°15,79	12/2/98	06°49,76	30°05,68	06°49,73	30°02,66
27/11/97	05°32,07	29°44,75	05°35,46	29°46,38	13/2/98	06°34,99	29°36,65	06°33,58	29°40,33
27/11/97	05°52,35	29°28,65	05°52,83	29°32,69	13/2/98	06°04,90	29°40,32	06°03,03	29°42,45
28/11/97	06°06,84	29°38,54	06°10,76	29°39,55	14/2/98	05°35,48	29°37,01	05°33,17	29°39,30
28/11/97	06°17,53	29°23,93	06°21,80	29°25,36	14/2/98	05°24,77	29°43,71	05°22,34	29°44,11
28/11/97	06°31,40	29°53,36	06°32,54	29°57,24	15/2/98	05°13,78	29°43,20	05°11,77	29°42,99
29/11/97	06°39,67	29°34,07	06°38,96	29°37,96	15/2/98	05°08,74	29°41,18	05°05,01	29°39,37
29/11/97	06°37,96	30°13,74	06°40,78	30°16,79	17/2/98	04°46,31	29°15,82	04°45,11	29°18,94
30/11/97	07°38,60	30°19,27	07°40,89	30°16,05	18/2/98	04°35,64	29°22,36	04°34,02	29°17,96
1/12/97	07°56,50	30°43,08	07°59,96	30°44,84	19/2/98	03°24,32	29°19,05	03°28,00	29°17,72
2/12/97	08°07,77	30°49,14	08°08,18	30°53,58	19/2/98	03°28,76	29°18,55	03°25,20	29°19,77
2/12/97	08°30,62	30°55,13	08°31,01	30°59,09					
4/12/97	08°23,50	30°39,37	08°24,82	30°35,00					
4/12/97	08°20,72	30°34,13	08°17,37	30°36,95					