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PRELIMINARY STUDY AND GROWTH OF THE PELAGIC CLUPEIDS IN LAKE TANGANYIKA ESTIMATED FROM DAILY OTOLITH INCREMENTS

by

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PREFACE

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

This project aims at the determination of the biological basis for fish production on Lake Tanganyika, in order to permit the formulation 0f a coherent lake—wide fisheries management policy for the four riparian States (Burundi, Tanzania, Zaïre and Zambia).

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

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1. INTRODUCTION

Sound fisheries management requires a good understanding of the population dynamics of the target fish species. To fulfill this requirement, it is necessary to find out the generation times, life span and rates of biomass and population growth. For the commercially important pelagic fish species of Lake Tanganyika, basic information for such analyses has been accumulated since July 1993 by the FAO/FINNIDA project "Research for the Management of the Fisheries on Lake Tanganyika". Catch samples have been collected weekly from several fixed stations around the lake (Aro and Mannini, 1995), and these data will be complemented with samples from representative experimental areal trawling using the *R/V Tanganyika Explorer*.

As the first step towards a comprehensive population analysis, von Bertalanffy growth parameters were estimated from these weekly catch samples for the period July 1993 – June 1994, using various programs for length frequency analysis (Aro and Mannini, 1995). The results obtained agreed fairly well with published growth estimates, all of which were also derived from length frequency distributions (recent examples Moreau *et al.*, 1991; Mambona Wa Bazolana and Fryd 1993; Mulimbwa and Mannini 1993; earlier data summarized by Coulter, 1991 and Marshall, 1993).

However, the length-frequency method has serious limitations; it involves the examination of a large number of samples at regular intervals and is applicable only to the youngest individuals (the first few months of short-living species). It is useful for species with a distinct breeding season, but if breeding is continuous, the information obtained is not perfectly reliable. Both of the pelagic clupeid species of Lake Tanganyika, *Limnothrissa miodon* and *Stolothrissa tanganicae*, have an extended breeding season (Aro and Mannini, 1995) and therefore the length-frequency method may not be very suitable for estimating their age. Differences in individual growth rates reduce the information obtained from length-frequency analysis. Furthermore, the technique can not be used to determine the age of an individual fish.

Therefore, and especially considering the variability of the size distributions evident in the data collected during the LTR project (Aro and Mannini, 1995), and in data published earlier (e.g. Moreau *et al.,* 1991), it would be desirable to check the length-based growth rate estimates through independent methods.

The most promising alternative seems to be age-determination by counting the daily growth increments which form under suitable conditions in the fish otoliths (Pannella, 1971; Campana and Neilson, 1986). In Lake Tanganyika, the pronounced diel migrations of crustacean zooplankton, combined with the stable light-dark photoperiod generate, regularly recurring diel variation in the feeding conditions of planktivorous fish. Therefore, there is good reason to expect fairly clear daily growth rings in the otoliths of the pelagic planktivore species *Limnothrissa miodon* and *Stolothrissa tanganicae*.

The counting of daily otolith increments has been successfully applied to the age-determination of *Limnothrissa miodon* in Lake Kariba (Chifamba, 1993; Mtsambiwa, 1993). Recently, Kimura (1991b, 1991c) has analysed growth increments in the otoliths of *Limnothrissa miodon* and *Stolothrissa tanganicae* from the southern end of Lake Tanganyika (Mpulungu), and verified their daily nature in the cichlid *Neolamprologus moorii* (Kimura 1991a). In contrast, the otolith rings of *Lates stappersii* were difficult to interpret and were not suitable for age determination (Kimura, 1993d). In the latter species, scale structure was also found to be unsuitable for age determination (B. Nyakageni, personal communication).

Against this background, the LTR project decided to organize a pilot study to assess the feasibility of using otolith microstructure for the age determination of the pelagic clupeids, *Limnothrissa miodon* and *Stolothrissa tanganicae*. The preliminary results of this investigation are reported here.

2. MATERIALS AND METHODS

The otoliths were collected by the local LTR and counterpart staff during the period August-September 1994 at three LTR-stations (Bujumbura, Kigoma and Mpulungu). Two otoliths (sagittae) from each fish were taken, washed in water, dried, and stored in plastic vials. There were 141 pairs of otoliths from Bujumbura (99 *L. miodon* and 42 *S. tanganicae*), 126 pairs from Kigoma (18 *L. miodon* and 108 *S. tanganicae*) and 113 pairs from Mpulungu (83 *L. miodon* and 30 *S. tanganicae*). Each vial contained the essential information about the sample: species, otolith number, fish length and date. Bujumbura samples also had information about wet weight, sex, maturity class and wet weight of the gonad. Some otoliths in the Bujumbura sample had not been properly dried before storage in the vials and were mouldy (5% of *Limnothrissa* and 7% of *Stolothrissa*).

Several methods can be used in making preparations from the otoliths (Secor *et al.,* 1992). Most researchers have used some clearing compound (e.g., glycerol, immersion oil, Euparal or Canada balsam) and then mounted the otoliths in a mounting medium (e.g., Euparal, thermoplastic cement or Spurr). For this investigation, Euparal, glycerol and immersion oil were mostly used as the clearing and mounting medium. Some experiments were made using other methods (hydrochloric acid [used by Chifamba, 1992], Aquamount or polyvinyl lactophenol), but they were not successful. The mounting medium had little effect on the quality of the otolith preparation; all media used did clear the otolith to some extent. Euparal was preferred because otoliths mounted in it can be stored for a long time. It did have some disadvantages; an irritating smell and a tendency to stiffen too quickly (which may have been due to the age of our Euparal). The complete drying takes days or weeks.

The length and width of each otolith were measured with an ocular micrometer. Otoliths were measured under an Olympus GWB BH-2 microscope at 100× magnification and the counting of the rings was carried out at 400× magnification. The counting area was the dorso-ventral axis from the centrum towards either lateral edge of the otolith (Kimura, 1991c).

In the smallest otoliths, i.e. in fishes under 60 mm total length, the rings were relatively easy to distinguish independent of the mounting medium. The bigger the fish, the thicker the otoliths were and thus the rings were difficult to see. The most difficult parts to interpret were the central primordia and the outer edges of the otolith where the rings were narrow. The time of the first increment formation varies from species to species. Increment formation can start before hatching, or at the beginning of external feeding. The exact date of first increment formation in our study species is not known. Because of resolution problems, counting was started from the first visible increment, which was not necessarily the first increment. Close to the outer edge, increments often appeared laterally compressed or disappeared completely from view. This is due to edge effects, which are caused by the refraction of transmitted light through the curved surface of the otolith edge (Neilson, 1992).

Some otoliths were ground to make the ring structure more clearly visible. The polishing procedure followed the techniques of Huuskonen and Karjalainen (1995). One otolith from each pair was mounted on a microscope slide with Epon and the mounting medium was allowed to polymerize for approximately 24 hours at 60°C. The otolith was ground close to the midplane with 1000 and 1200 abrasive grit paper and finished with polishing powder. A drop of glycerol was applied on the otolith before it was studied under a light microscope.

Initially, the purpose was to analyse the otoliths with a computer-aided system, that is, a video camera fitted to a microscope and connected to a personal computer. However, the PC program available was constructed for counting annuli from salmonid scales, and it appeared that daily growth increments in otoliths were much too dense to be analysed using this system. There were also problems with the resolution of the video image. Therefore, to keep to the timetable, the otolith reading for the present report was done manually.

3. RESULTS

Visual observations showed that the otoliths changed shape during development. In small specimens, the sagittae were almost circular, but as the fish grew older, they became, as the name indicates, arrow-shaped. There was no systematic difference between the right and left sagitta in shape or dimension. The largest otoliths usually had dentated edges. An analysis of covariance showed that in both *L. miodon* nor *S. tanganicae*, the regression coefficients of otolith width on otolith length did not differ between stations. In contrast, the mean widths adjusted for length did differ: in both species otoliths collected from Mpulungu were significantly wider relative to their length than those from the other stations (Figs. 1, 2). The intercepts of the linear regression were always significant, suggesting some curvilinearity (TABLE 1).

TABLE 1. Linear regressions of otolith width (OW) on otolith length (OL) in *Limnothrissa miodon* and *Stolothrissa tanganicae* at different sampling stations in August–September 1994
(OW = a ± b*OL; parameter values ± SD, coefficient of determination (r^2), number of observations (n) and the probability level (P) are given).

	a	b	r^2	n	P
L. miodon					
Bujumbura	0.116 ± 0.022	0.439 ± 0.011	0.956	73	<0.0001
Kigoma	0.276 ± 0.074	0.366 ± 0.033	0.889	17	<0.0001
Mpulungu	0.182 ± 0.022	0.432 ± 0.023	0.917	34	<0.0001
S. tanganicae					
Bujumbura	0.159 ± 0.027	0.378 ± 0.020	0.942	25	<0.0001
Kigoma	0.301 ± 0.054	0.290 ± 0.031	0.713	37	<0.0001
Mpulungu	0.381 ± 0.146	0.202 ± 0.152	0.307	6	0.2542

Total fish length and otolith length and width were strongly correlated at all stations (TABLE 2; Figs. 3–6). A linear relationship between otolith width/length and fish length would facilitate the back-calculation of the individual growth history from the otolith readings. However, the intercept of the linear regression was always significant, which indicates that the relation was actually curvilinear. A plot of the whole *L. miodon* data, comprising the widest length range, further suggests that the relationship may still be basically linear, but with its slope changing close to a fish length of about 40 mm (Figs. 3, 4). The ranges of fish length studied so far differ between stations, which makes comparisons between areas somewhat uncertain. However, preliminary covariance analyses indicated that (1) in *L. miodon*, regression coefficients of otolith width on fish length were significantly different between stations; (2) in *S. tanganicae*, the regression slopes did not differ between areas, but otoliths from Kigoma were significantly wider relative to fish length than those collected from the other stations. If interpreted according to Campana and Jones (1992), such differences may suggest slower growth of *S. tanganicae* off Kigoma than off Bujumbura or Mpulungu.

TABLE 2. Linear regressions of otolith length (OL) or width (OW) on fish length (FL) in *Limnothrissa miodon* and *Stolothrissa tanganicae* at different sampling stations (OL = a + b*FL or OW = a + b*FL; parameter values ± SD, coefficient of determination (r^2) and the number of observations (n) are given). All regressions were highly significant (P<0.0001), except those for *S. tanganicae* from Mpulungu that were nonsignificant.

	Otolith length			
	a	b	r^2	n
L. miodon				
Bujumbura	0.184 ± 0.041	0.019 ± 0.0004	0.964	73
Kigoma	0.555 ± 0.237	0.016 ± 0.002	0.769	17
Mpulungu	-0.073 ± 0.056	0.023 ± 0.001	0.913	34
S. tanganicae				
Bujumbura	0.029 ± 0.076	0.020 ± 0.001	0.930	25
Kigoma	0.324 ± 0.174	0.018 ± 0.002	0.632	40
Mpulungu	0.728 ± 0.361	0.004 ± 0.007	0.094	6

	Otolith width			
	a	b	r^2	n
L. miodon				
Bujumbura	0.179 ± 0.018	0.009 ± 0.0002	0.968	74
Kigoma	0.451 ± 0.087	0.006 ± 0.0008	0.774	18
Mpulungu	0.142 ± 0.031	0.010 ± 0.0007	0.870	34
S. tanganicae				
Bujumbura	0.179 ± 0.037	0.007 ± 0.0005	0.874	28
Kigoma	0.314 ± 0.056	0.006 ± 0.0007	0.687	37
Mpulungu	0.514 ± 0.135	0.001 ± 0.002	0.049	6

Daily growth increments from the whole otolith could be counted from only a few specimens (Fig. 7). The sagittae of a 20-mm *L. miodon* from Bujumbura seemed to have about 50 daily rings, and those of a 60-mm fish had around 130 rings. Most otoliths were so thick that the ring structure could not be distinguished through the whole otolith. The number of the rings was then estimated indirectly: the width of the rings was measured from the central part and from the outer part of the otolith, and otolith radius was divided by the mean increment width. The results obtained in this way are, however, more or less biased, because the increment width changes continuously with the fish growth rate. In many cases, at first the fish seemed to grow quite slowly, then the growth rate accelerated, to slow down again at a later age. Individual differences were, however, marked. The variability of growth may partly reflect genetic variation or partly result from differences in food (plankton) abundance.

Limnothrissa miodon from Bujumbura had a total length of 20 to 144 mm. The increment width in the central area of the otoliths varied from 1.47 to 4.17 µm (mean = 2.59 µm, n = 47; Fig. 8). Close to the outer edge, increment widths varied from 1.17 to 2.44 µm (mean = 1.82 µm, n = 23; Fig. 9). Calculated from the mean increment width of each individual, the otoliths of fish between 75 and 135 mm of total length contained 100–350 rings (Fig. 10).

The sampled specimens of *Stolothrissa tanganicae* from Bujumbura had a total length between 35 and 94 mm. The increment width in the central part of their otoliths varied from 1.67 to 2.5 µm (mean = 1.97 µm, n = 6). Calculated from this overall mean increment width, fish with a total length of 35–90 mm should have 120–240 otolith increments, while calculated from the mean individual increment widths, fish measuring 60–90-mm should have 130–270 rings (Fig. 11). Three individual fishes belonging to the length classes of 35–39, 40–44 and 55–59 mm had 145, 140 and 150 otolith increments, respectively.

The size range of fishes from Kigoma varied from 84 to 123 mm of total length for *L. miodon* and from 53 to 99 mm for total length for *S. tanganicae*. The otoliths were so large and thick and therefore non-transparent, that no increment information could be obtained from them (except for tentative counts for two specimens of *L. miodon*). Only the length and width of the otoliths were measured. If the average increment widths measured from Bujumbura are applied to *L. miodon* from Kigoma, the 84 to 123-mm fish should have 200–270 otolith increments (Fig. 12); similar calculations for *S. tanganicae* indicate 160–230 increments for the 53 to 99-mm range fish (Fig. 13).

The size range of *L. miodon* from Mpulungu waters was from 19 to 165 mm and that of *S. tanganicae* from 50 to 105 mm. However, as yet, only otoliths from fishes less than 60 mm long have been examined.

L. miodon from Mpulungu had increments from 1.13 to 2.79 µm wide in the central part of the otoliths (mean = 1.97 µm, n = 23; Fig. 14) and from 1.47 to 3.90 µm wide close to the outer edge of the otoliths (mean = 2.37 µm, n = 18; Fig. 15). The width of the central increments was uncorrelated with fish size. The width of the peripheral increments showed weak positive correlation with fish size, but this was due to two deviating data points. The smallest individuals had the broadest average increment width. A fish of 19 mm total length had 38 increments, which means an average increment width of 3.29 µm; another 21-mm fish had 48 increments, yielding a mean increment width of 3.13 µm. However, some small fish could have narrow increments too: a 21-mm fish had 100 increments, or a mean increment width of 1.85 µm. Calculations based on the mean increment width suggested that 20 to 60-mm fish should have 80–190 otolith increments (Fig. 16).

In *S. tanganicae* otoliths from Mpulungu, the increment width in the centre was from 1.46 to 2.03 µm (mean = 1.81 µm, n = 6) and close to the outer edge from 1.67 to 3.57 µm (mean = 2.44 µm, n = 3). A 55-mm long fish had approximately 160 increments, and another, a 57-mm fish also had 160 increments. Approximately 110 increments were counted in a 54-mm fish, but the very first increments were indistinguishable. According to the mean increment widths, the six 50 to 57-mm fish studied so far should have 110–170 otolith increments (Fig. 17).

4. DISCUSSION

4.1 Methodological aspects

The age of fishes is commonly determined by studying the growth increments in hard parts, scales, otoliths, opercular bones, vertebrae, cross-sections of dorsal or pectoral spines and fin rays. The chosen structure depends on fish species; in clupeids, the age determination is usually based on the otoliths. Primary growth increments are those formed on a daily basis; other increments can be formed at shorter intervals (subdaily increments) or longer intervals (e.g., lunar cycle). Annual increments formed in the bony structures are appropriate for determining the age of long-living species or fishes from temperate waters, but for short-living and tropical species primary growth increments must be used.

A growth increment in the otolith is a bipartite structure composed from an incremental zone and a discontinuous zone. The incremental or continuous zone is formed under active metabolism and is composed of an inorganic calcium compound, usually aragonite. Sometimes aragonite is replaced by other polymorphs, calcite or vaterite (Neilson, 1992; David and Grimes, 1994). Their occurrence is usually associated with otoliths with aberrant characteristics. The discontinuous zone is formed under low calcification and is composed of organic protein matrix.

Fish age determination from primary growth increments is based on several assumptions. The method requires that the ring formation begins at the same time in different individuals and that the rings form at a constant rate. The ring formation rate must be independent of fish growth rate. It has been verified that rings are also formed under starvation when the fish does not grow (e.g. Maillet and Checkley, 1989). Exceptions in ring formation can be predicted and modelled through the understanding of the ring formation process.

Since its original discovery by Pannella (1971), the daily character of otolith increment formation has been validated in several studies (e.g. Post and Prankevicius 1987 [*Perca flavescens*], Rey and Eckmann, 1989 [*Coregonus lavaretus*], Zhang and Runham, 1992a, 1992b [*Oreochromis niloticus*]; see also Geffen, 1992). However, in some cases extra rings may appear, the rings may form irregularly, or may be otherwise difficult to interpret correctly (Huuskonen and Karjalainen, 1993 [*Coregonus albula*], Thompson and Bulirani, 1993 [*Engraulicypris sardella* from Lake Malawi], Zhang and Runham, 1992c [*Oreochromis niloticus*]).

There is no hard evidence that the otolith increments counted in *L. miodon* or *S. tanganicae* were daily growth rings. However, considering the rhythmicity of the environment in Tanganyika, and published reports for other species and environments, the daily character of the rings seems very likely. A similar assumption was also made by Kimura (1991b, 1991c).

We expected that the otoliths of *L. miodon* and *S. tanganicae* could have been studied without any special preparation method, just under a light microscope. However, this was successful only for the smallest individuals (otoliths), because otoliths from larger fishes were too thick, thus making their transparency poor. Grinding of the otolith improves the image, but the grinding procedure is very time consuming and therefore has been tested for only about ten otoliths so far. For the largest otoliths, grinding should be done from both sides. Grinding of the larger otoliths is recommended in further studies of *Limnothrissa* and *Stolothrissa* otoliths.

The counts should be done routinely at least two or three times, but because the work is very time consuming and the period available was brief, usually only one count per otolith was possible (both otoliths from each fish were studied, if they were available). Verifying counts will be done later in 1995 after the first author has returned from Siena.

Counting of subdaily increments may cause errors in the results (Campana, 1992). Correct interpretation of daily and non-daily increments demands long experience, 380 pairs of otoliths are not enough. The primary growth increments in the otoliths of *Limnothrissa* and *Stolothrissa* were usually very narrow. The widest recorded increment widths were therefore doubtful; in these cases, the faintest increments may have been ignored during the otolith reading. Further work should utilize an oil immersion objective to attain higher magnification and resolution. According to Neilson (1992), increments less than 2 µm should be studied with scanning electron microscopy (SEM). However, Klink and Eckmann (1992) found that the use of SEM could not improve increment resolution; if there were unambiguous rings, they could be measured and counted with the light microscope. Regardless, SEM examination cannot become a routine method in Lake Tanganyika's case.

4.2 Growth rates

Our results indicated that the age of a 60-mm *L. miodon* might be 120–160 days, while a 100-mm fish might be 250–350 days old. In *S. tanganicae* a 60-mm fish might be 150–160 days old. The present data do not yet allow reliable comparisons between the different stations, and neither was it possible to fit a von Bertalanffy growth curve to compare with the growth estimates obtained using size-frequency methods (e.g. Aro and Mannini 1995). However, preliminary evaluations can be made. Our age estimate for the 60-mm *L. miodon* is within the range of previously published estimates based on length-frequency data, but close to the lower end of the range (Marshall, 1993). For the 60-mm *L. miodon*, our age estimates also agree with those of Kimura (1991c) obtained from otolith analysis, but for the 100-mm fish Kimura's figure suggests higher ages. For 60-mm *S. tanganicae*, Kimura (1991b) indicates an age of 140–160 days which agrees well with our age estimates. For 60-mm *S. tanganicae*, our growth rate estimates also resemble those of Moreau *et al.,* (1991). Thus, for young fish the length-based methods and otolith readings seem to give consistent results. Further otolith analyses will clarify the situation in older fish, and also elucidate possible between-station and between-season differences.

The correlation between otolith size and fish total length has also been observed in other studies, e.g. in white crappie *Pomoxis annularis* (Maceina and Betsill, 1987). Differences in otolith size in relation to fish length suggest that there may be significant differences in growth between stations. Otolith size and fish growth rate are, however, not necessarily correlated, as has been demonstrated for Arctic charr *Salvelinus alpinus* (Mosegaard *et al.,* 1986). If the wide scatter observed in the increment number – fish length relationship in Bujumbura is true, it indicates high variation in individual growth. The consistently different shape of otoliths in the Mpulungu samples in both species is interesting and may indicate genetic isolation of the pelagic fish populations at the southern end of the lake.

In samples from Mpulungu, in both species, the increment width was larger close to the outer edge. If true, this would indicate higher growth rate at an older age. In Bujumbura, the increment widths were narrower towards the edge, which should be the normal situation. The irregularities in the decrease of the width of the outermost increments with fish size may reflect growth differences between successive cohorts, but it remains to be shown whether the patterns observed are true.

5. CONCLUSIONS

Nowadays, otolith microstructure analysis is an important and accepted technology in fisheries biology, which can also be used in the future to get more information about the population dynamics of Lake Tanganyika clupeids. The age determination of young fish (length <60 mm) can be done by counting the increments in whole-mounted otoliths under an ordinary research microscope. For the ageing of larger (older) fish, however, special polishing of the otoliths is necessary, and this is laborious and time-consuming. Although age determination from the daily rings of otoliths probably cannot become a routine method for monitoring the age structure of the pelagic clupeid fish populations in Tanganyika, further comparisons should be made between the growth estimates obtained from the otolith analyses and from the length-frequency methods.

The present otolith samples were collected during the period August-September 1994. To get accurate information about the growth and age of *L. miodon* and *S. tanganicae*, samples should cover the whole year. Moreover, an analysis of a greater number of otoliths is needed for more reliable comparisons with other methods and earlier data. The present otolith samples will be re-examined during the summer 1995 for the M.Sc. thesis of the first author. In addition, we suggest that the otolith sampling be repeated in April 1995 at all three field stations, the otoliths analysed during June-August 1995, and the final report prepared for the International Symposium on Lake Tanganyika in September 1995.

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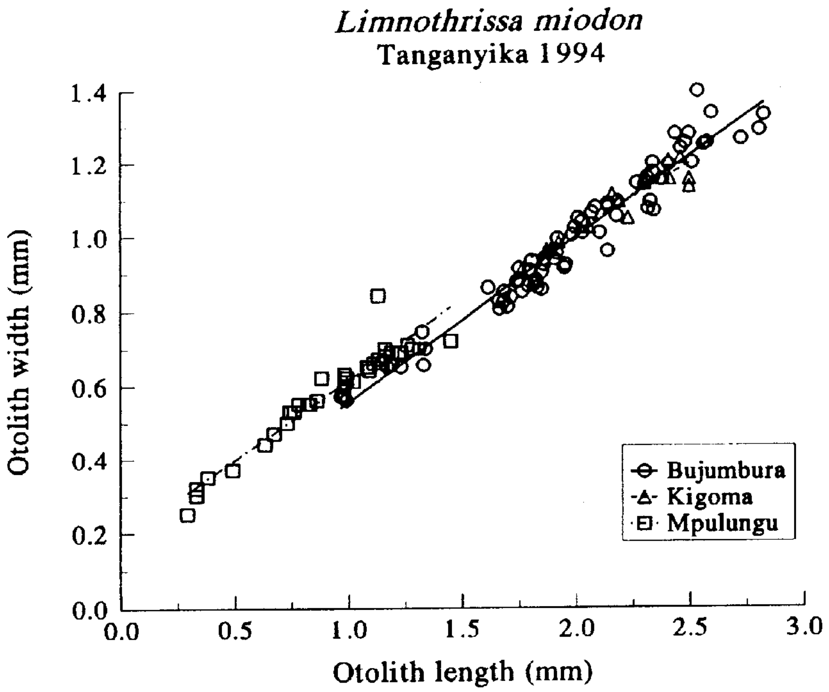

Fig. 1. Relationship between otolith width and otolith length of *Limnothrissa miodon* in different parts of Lake Tanganyika.

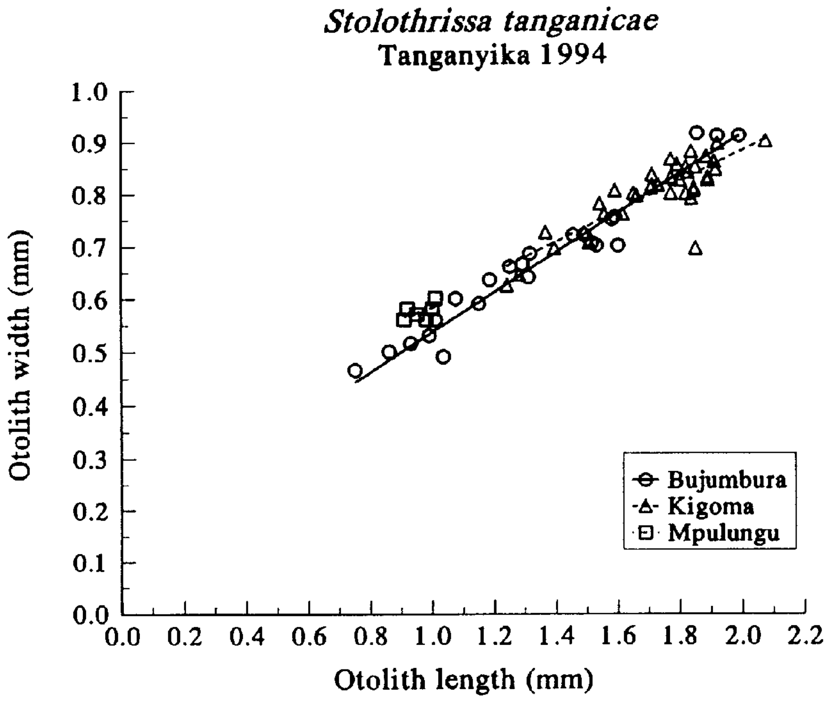

Fig. 2. Relationship between otolith width and otolith length of *Stolothrissa tanganicae* in different parts of Lake Tanganyika.

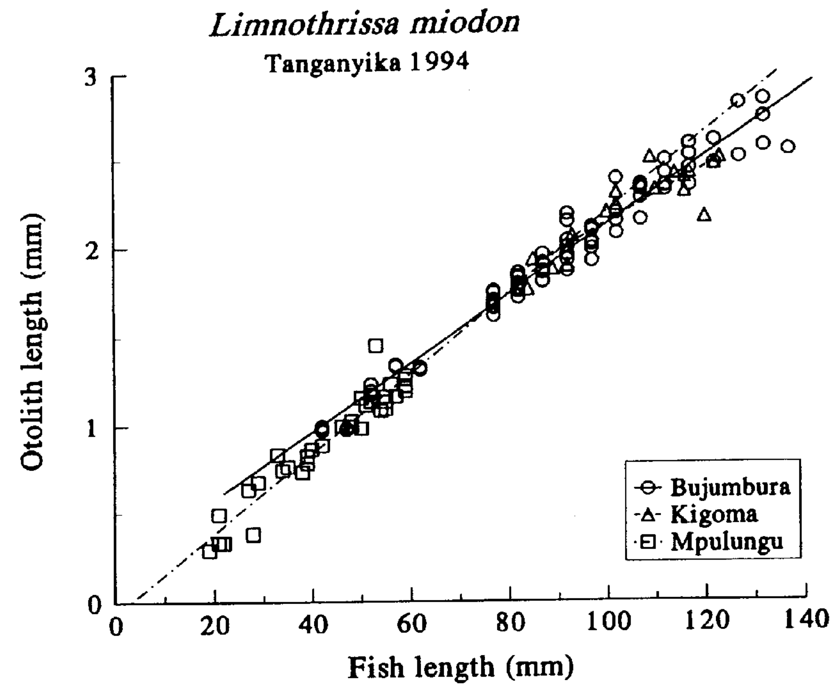

Fig. 3. Relationship between otolith length and fish length in *L. miodon* in different parts of Lake Tanganyika.

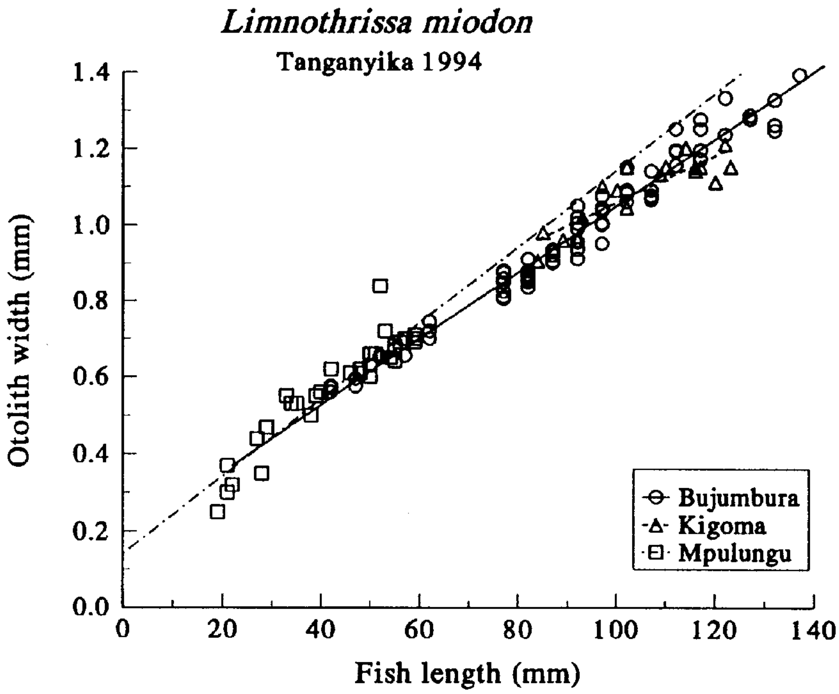

Fig. 4. Relationship between otolith width and fish length in *L. miodon* in different parts of Lake Tanganyika.

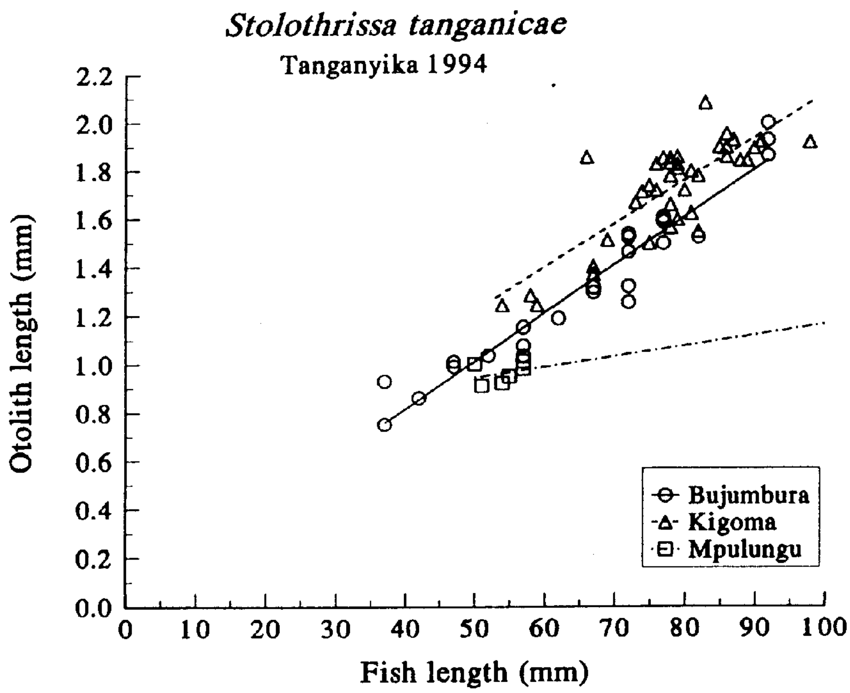

Fig. 5. Relationship between otolith length and fish length in *S. tanganicae* in different parts of Lake Tanganyika.

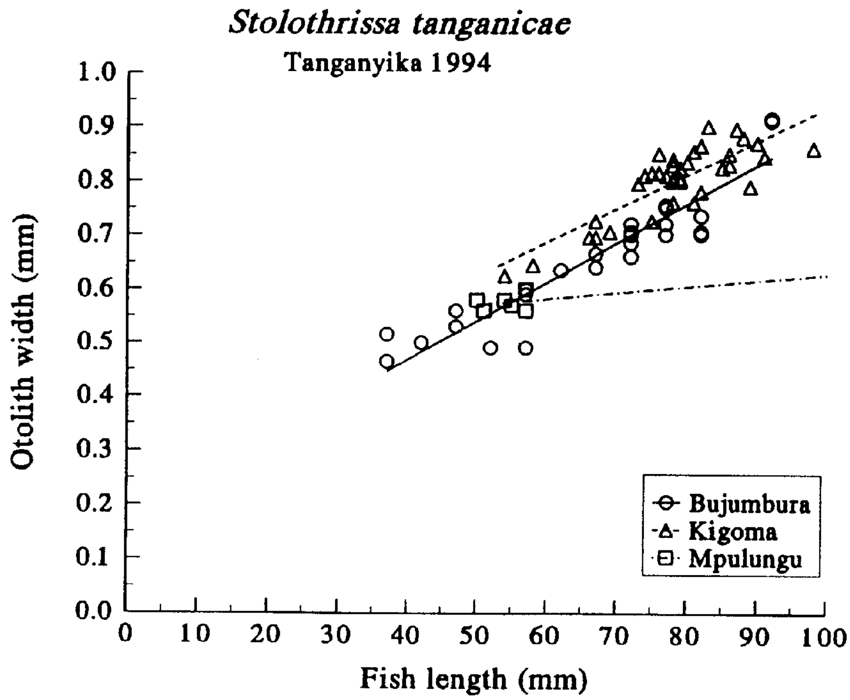

Fig. 6. Relationship between otolith width and fish length in *S. tanganicae* in different parts of Lake Tanganyika.

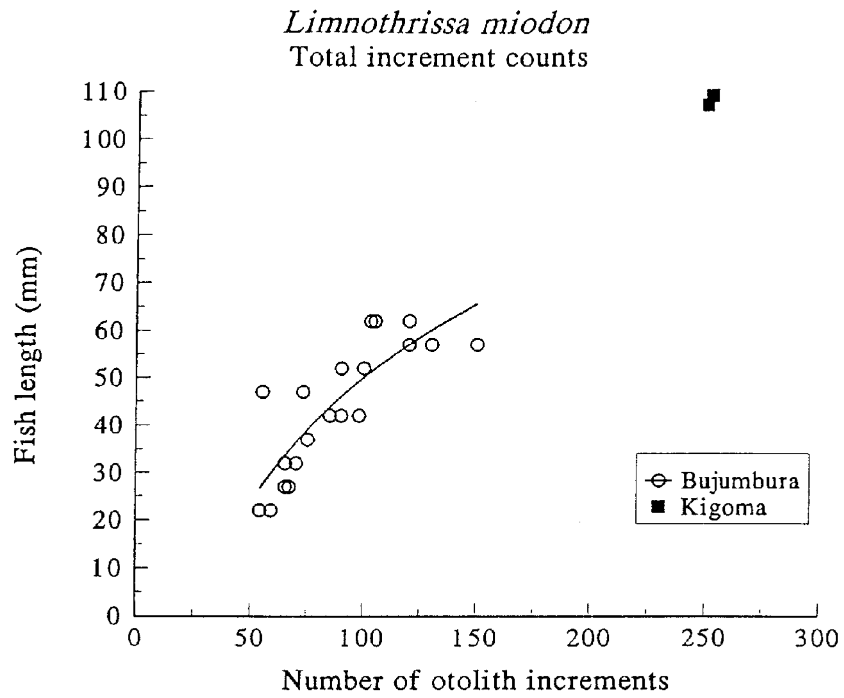

Fig. 7. Number of otolith increments *vs.* fish length in *L. miodon* based on total counts of increments.

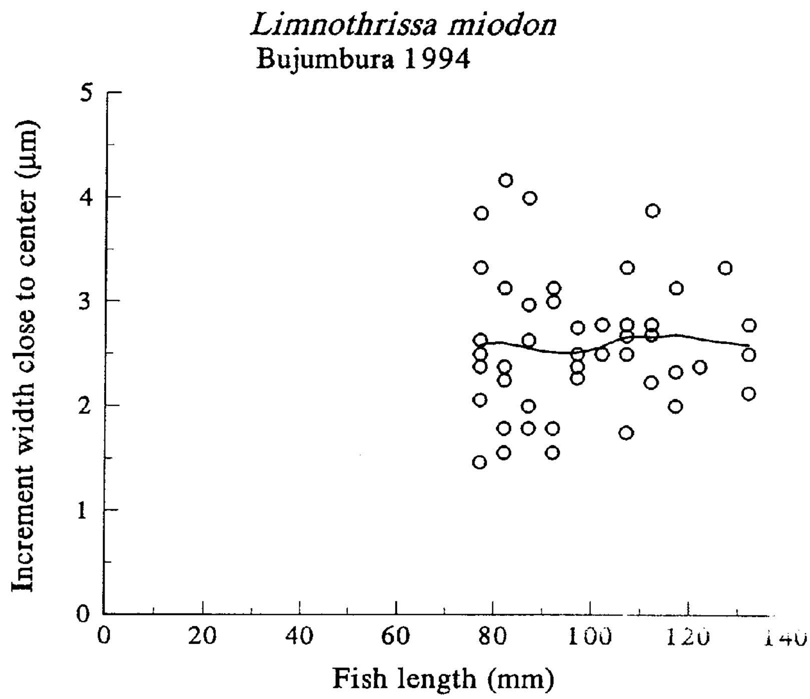

Fig. 8. Increment width close to the otolith focus relative to fish length in *L. miodon* from Bujumbura (curve produced by LOWESS regression).

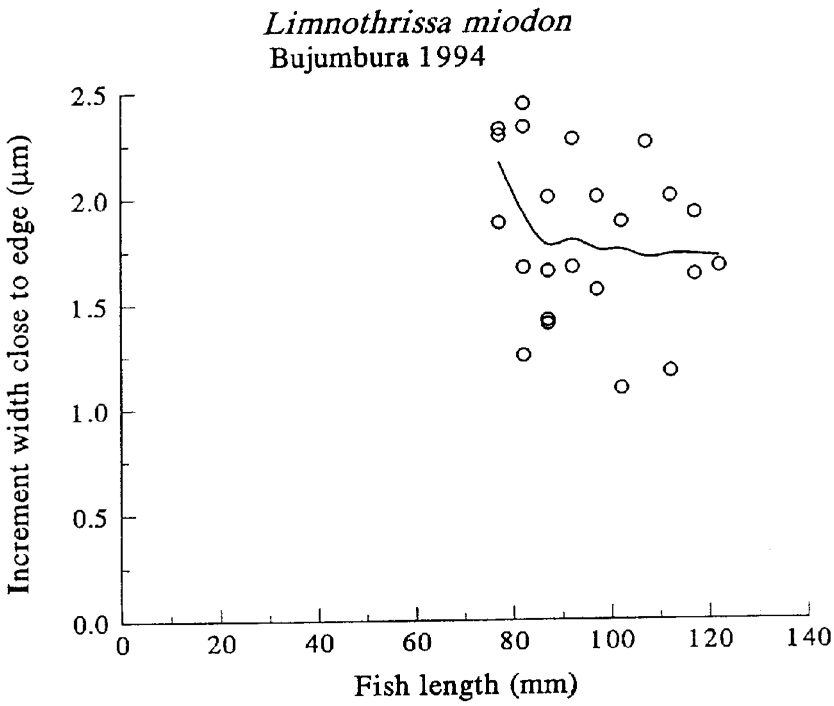

Fig. 9. Increment width close to the otolith edge relative to fish length in *L. miodon* from Bujumbura (curve produced by LOWESS regression).

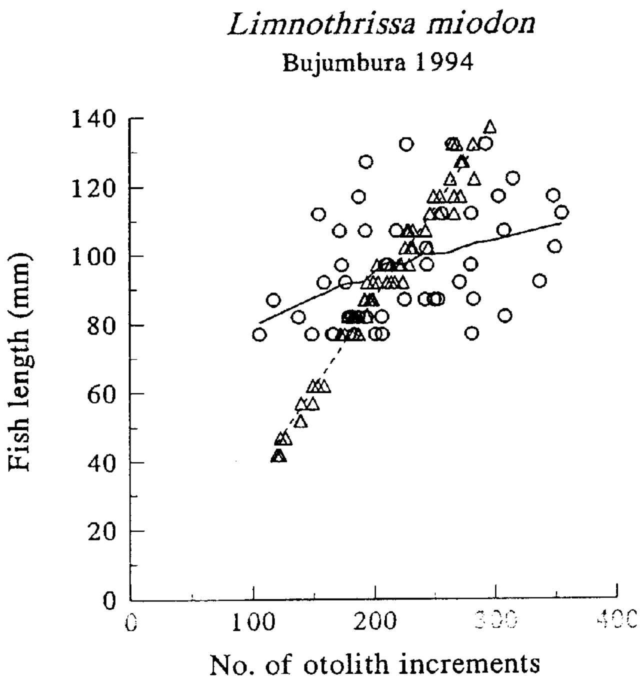

Fig. 10. Number of otolith increments *vs.* fish length in *L. miodon* from Bujumbura (circles based on individual mean increment width, triangles based on overall mean increment width).

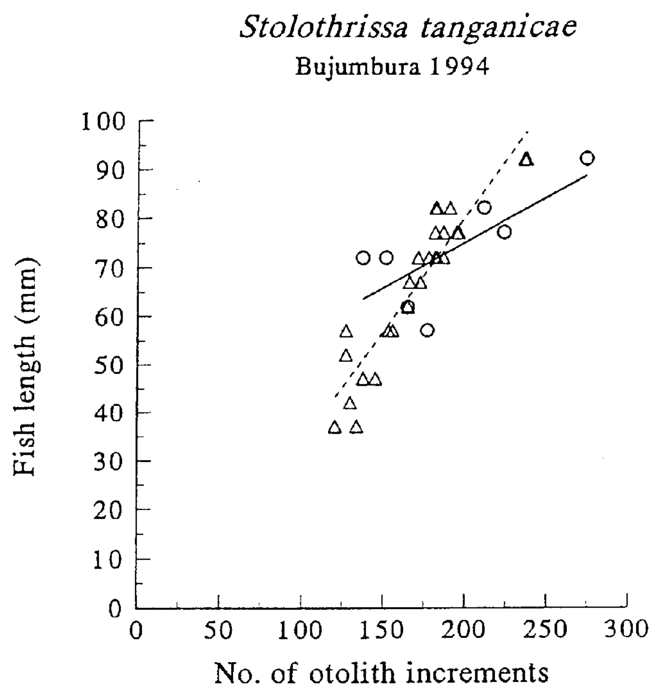

Fig. 11. Number of otolith increments *vs.* fish length in *S. tanganicae* from Bujumbura (circles based on individual mean increment width, triangles based on overall mean increment width).

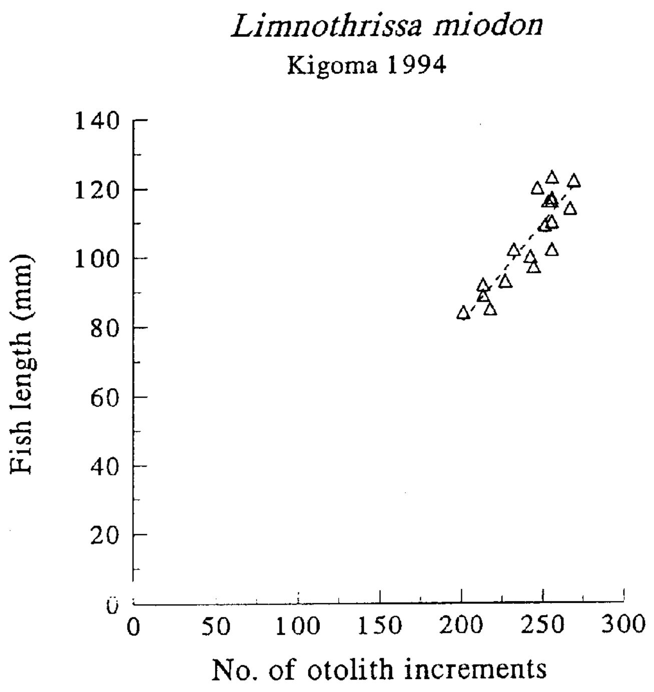

Fig. 12. Number of otolith increments *vs.* fish length in *L. miodon* from Kigoma (based on overall mean increment width).

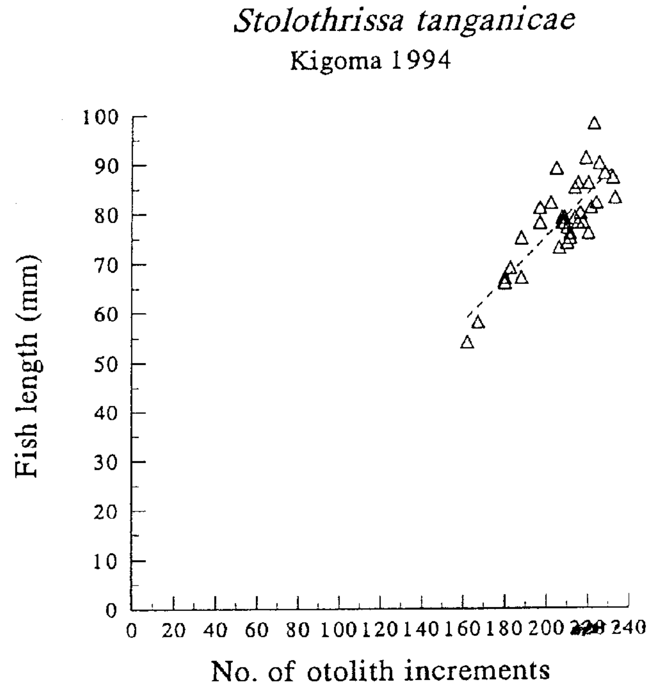

Fig. 13. Number of otolith increments *vs.* fish length in *S. tanganicae* from Kigoma (based on overall mean increment width).

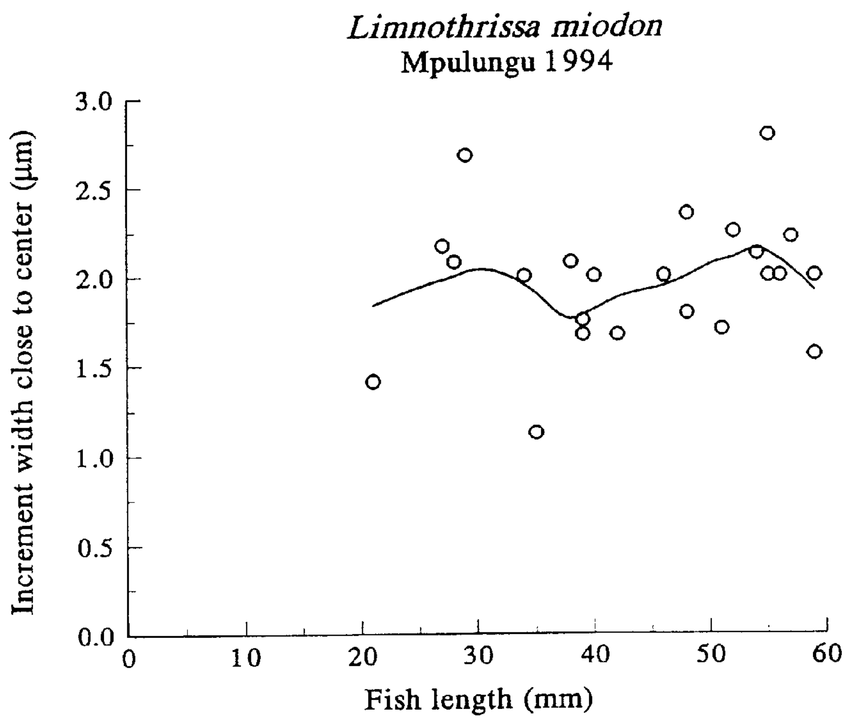

Fig. 14. Increment width close to the otolith focus relative to fish length in *L. miodon* from Mpulungu (curve produced by LOWESS regression).

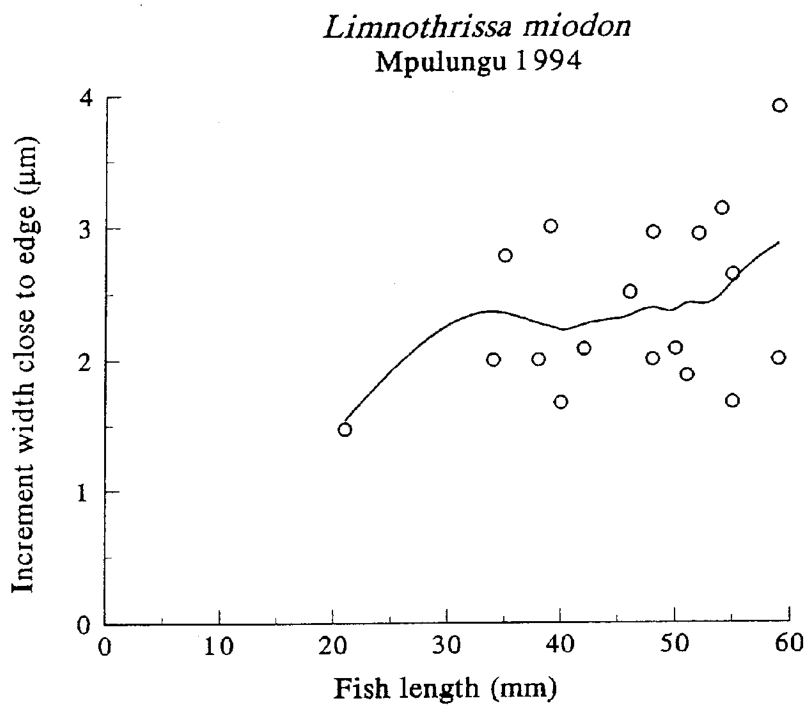

Fig. 15. Increment width close to the otolith edge relative to fish length in *L. miodon* from Mpulungu (curve produced by LOWESS regression).

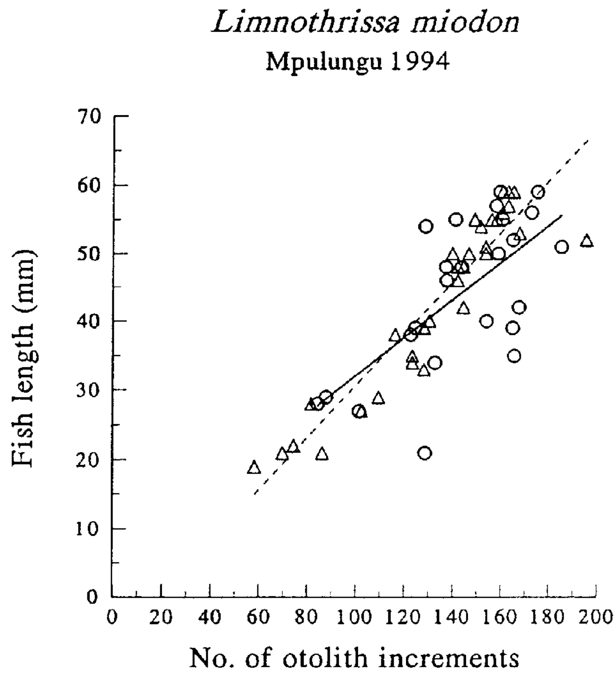

Fig. 16. Number of otolith increments *vs.* fish length in *L. miodon* from Mpulungu (circles based on individual mean increment width, triangles based on overall mean increment width).

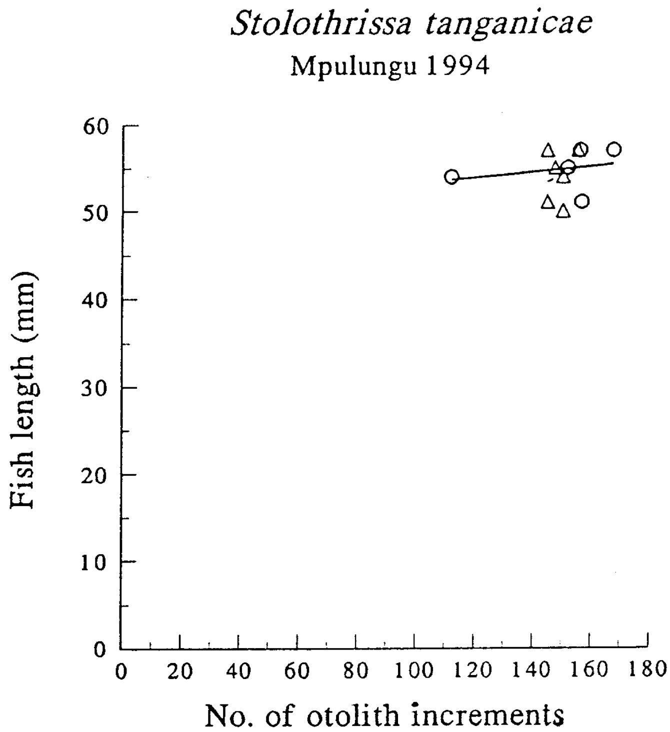

Fig. 17. Number of otolith increments *vs*. fish length in *S. tanganicae* from Bujumbura (circles based on individual mean increment width, triangles based on overall mean increment width).