# Growth parameters of the clupeids *Limnothrissa miodon* and *Stolothrissa tanganicae* in northern Lake Tanganyika (Bujumbura sub-basin).

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**SUMMARY**

The analysis of growth parameters in fish stocks, such as the asymptotic length ($L_\infty$) and the curvature parameter (K) is crucial for the estimation of production rates and total mortality rates in fisheries management. Here, we estimated the growth parameters of the clupeids *Limnothrissa miodon* and *Stolothrissa tanganicae* in the northern part of Lake Tanganyika (Bujumbura sub-basin). Both species are important targets of pelagic fisheries, but the available estimates are based on scarce size frequency data, and rarely on size as a function of age data. We provide new estimates of $L_\infty$ and K based on size as a function of age data, with age inferred from otolith weight. Furthermore, we reanalyze several length frequency datasets using more sophisticated statistical procedures, and test if growth parameters estimated by length frequency analysis are consistent with those obtained based on size as a function of age. We found that length frequency analysis consistently underestimates $L_\infty$ and overestimates K as compared to length-at-age data. We recommend that length-at-age data should be obtained at a much broader spatial and temporal scale than currently available to advance our understanding of the growth dynamics of the two sardine species. This will improve the assessment of stock productivity and biomass of Lake Tanganyika's pelagic fisheries, as well as the level of fishing pressure that can be sustained.

Key words: growth, size frequency analysis, daily increments of otoliths, *Stolothrissa tanganicae*, *Limnothrissa miodon*, Lake Tanganyika, Bujumbura sub – basin

## INTRODUCTION

Lake Tanganyika is about 10 million years old (Cohen *et al.* 1993) and is the second deepest and the fifth largest freshwater body in the world (Langenberg, 2008). So far, 1200 animal and plant species have been identified in this lake, ranking among the most diverse lake ecosystems in the world. Among the main groups in this lake, fishes show a high degree of biodiversity (Cohen *et al.* 1993; Van Steenberge *et al.* 2011). Lake Tanganyika's pelagic fisheries is a major source of food and economic activity of the human population living around the lake. These fish feed 12.5 million people in the areas adjacent to Lake Tanganyika (Mölsä et al. 1999; LTA 2022). Two small-sized clupeids, *Stolothrissa tanganicae* and *Limnothrissa miodon*, commonly known as "freshwater sardines", along with the latid perch *Lates stappersii*, account for 60% to 90% of the total commercial catch in the pelagic environment (Mölsä et *al.* 1999). In the mid-1990s, annual harvests from Lake Tanganyika were estimated to range between 165 000-200 000 tons, quantities that translate into annual revenues of tens of millions of US dollars (Mölsä et *al.* 1999).

As for other African Great Lakes, the lack of a long-term monitoring programme for Lake Tanganyika feeds uncertainty about the status of the lake and its pelagic fish stocks (Plisnier et al. 2022). Fisheries statistics published from the North of Lake Tanganyika suggest that annual catch rates (measured as catch per unit effort; CPUE) have been declining since the early 1980s (Mulimbwa 2006; Mulimbwa 2020; LTA Secretariat, 2012; Mushagalusa et al. 2015; Okito et al. 2017; Van der Knaap et al. 2014). The declines have been attributed to excessive fishing pressure and the use of illegal fishing gear (Mulimbwa 2006; Mulimbwa 2020; LTA Secretariat, 2012; Mushagalusa et al. 2015; Okito et al. 2017; Van der Knaap et al. 2014), as well as to global warming (Plisnier, 1997; O'Reilly et al. 2003; Verburg et al. 2003). However, overfishing can only be assessed based on declines in the total annual catch, of which no reliable data exist (Van der Knaap et al. 2014). Interestingly, while fisheries stakeholders in the North of the Lake do indicate a noticeable decrease in fish abundance and size, they do not attribute the problems in the fisheries to overfishing (De Keyzer et al. 2020). Yet another recent study found that CPUE has been stable in the North of Lake Tanganyika since 1993 (Sarvala & Mulimbwa 2023), indicating that not all fisheries statistics show the same trend. The impact of the effects of global warming on the pelagic fisheries has been questioned as well (Sarvala et al. 2006a, Sarvala et al. 2006b; Sarvala & Mulimbwa 2023). These uncertainties confirm that better fisheries monitoring is required to more accurately forecast fishing yields, assess fisheries potential, and understand the impact of fishing activities (Kolding et al. 2019).

One cornerstone of adequate fisheries management concerns the analysis of growth. Growth parameters such as the asymptotic length ($L_\infty$) and the curvature parameter (K) form the basis for the estimation of production rates (recruitment, natural mortality, and fishing mortality) and total mortality rates, which together enable the prediction of fishing yields (Beverton & Hold 1957). $L_\infty$ and K can either be determined based on changes in length frequency distributions over time (lengt-frequency analysis; LFA) or based on length as a function of age data (length-at-age analyis; LAA). LFA has the advantage that size data are easy to obtain. However, the method requires frequent catch data to identify subsequent cohorts and track their modal

growth progression. In environments and species with multiple periods of reproduction throughout the year, multiple overlapping cohorts and multimodal size frequency distributions may complicate cohort identification. Here, LAA might be more powerful. A commonly used technique for age determination in fish involves counting natural growth rings on the otoliths (Beamish & McFarlane 1983). In several tropical fishes, the diurnal transition from light to dark leaves a mark on the otoliths, and these daily increments can be used to estimate fish age in days (Kaningini, 1995; Kumura, 1995; Chifamba 2019). This method is suitable for tropical environments where the temperature is almost constant throughout the year. While counting daily otolith rings can be time consuming, otolith radius and otolith weight tend to correlate well with the number of daily increments and are therefore also suitable to establish length-age relationships (Lou et al. 2005).

In this study, we estimated growth parameters for *S. tanganicae* and *L. miodon*. Various studies have gained useful insights in the biology of both clupeids, including their evolutionary origin (Milec et al. 2022), population genetic structure (De Keyzer et al. 2019; Junker et al. 2020), position in the food web (Sarvala et al. 1999; Ehrenfels et al. 2023), parasites (Kmentová et al. 2020), reproductive biology (Mulimbwa et al. 2014a; Mulimbwa et al. 2022), and responses to limnological changes (Kimirei & Mgaya, 2007; Plisnier et al. 2009; Mulimbwa et al. 2014b). While *S. tanganicae* is fully pelagic, *L. miodon* makes more use of the littoral areas, including for reproduction and as nursery grounds (Mulimbwa et al. 2022). Both fishes are the target of artisanal fisheries in the pelagic, but in shallow littoral waters, juveniles of *L. miodon* are also subject to the low selectivity of beach seines (Mölsä *et al.* 2002). Basic information for fisheries management, such as age at maturity and size at maturity are available for both species, although there are no in-depth studies assessing the variability in those parameters. In addition, the data are patchy in both time and space. Age at maturity is usually estimated at 8.5 months corresponding to a total length of 78 mm for females and 77 mm for males in *S. tanganicae*, and at 8.6 months corresponding to a total length of 101 mm for females and 95 2mm for males in *L. miodon* (Mannini 1998). Growth parameters have been obtained for both species as well (Chapman & van Well, 1978; Roest, 1978; Coulter, 1991; Moreau et al. 1991; Mulimbwa & Shirakihara, 1994; Kimura 1995; Ahonen 2001; Mulimbwa 2006). Most studies have inferred growth parameters using LFA on length–frequency distributions from catch data. The few exceptions using LAA include Kimura (1991b, c), Kimura (1995) and Ahonen (2001). Especially in *S. tanganicae*, the most abundant cohort is often the one recruited during the dry season (Mulimbwa et al. 2014b). Yet, multiple partially overlapping cohorts do occur in both species, and pose the aforementioned challenge of cohort delineation for the assessment of growth.

To meet the need for more accurate growth data for the two clupeid fishes, we provide new estimates of $L_\infty$ and K based on length-at-age data, with age inferred from otolith weight. Furthermore, we reanalyze three published datasets with length frequency data using more advanced statistical procedures, and test if growth parameters estimated by size frequency analysis are consistent with those obtained based on length-at-age data.

## MATERIAL AND METHODS

*Study design*

This study combines datasets from different surveys on the two clupeids that were all conducted in the northern end of Lake Tanganyika (03° 28’ S, 29° 17’ E; Figure 1) in the Bujumbura sub-basin. We included (1) length frequency data for the period 1987-1989 from Mulimbwa and Shirakihara (1994), (2) length frequency data for the period 1999-2001 from Mulimbwa (2006), (3) length as a function of age data for the period 2004-2005 from Mulimbwa et al. (2014b), and length frequency data for the period 2007-2008 from Mulimbwa et al. (2014b) (Table 1). Sampling and data collection procedures for each data type are described in more detail below.

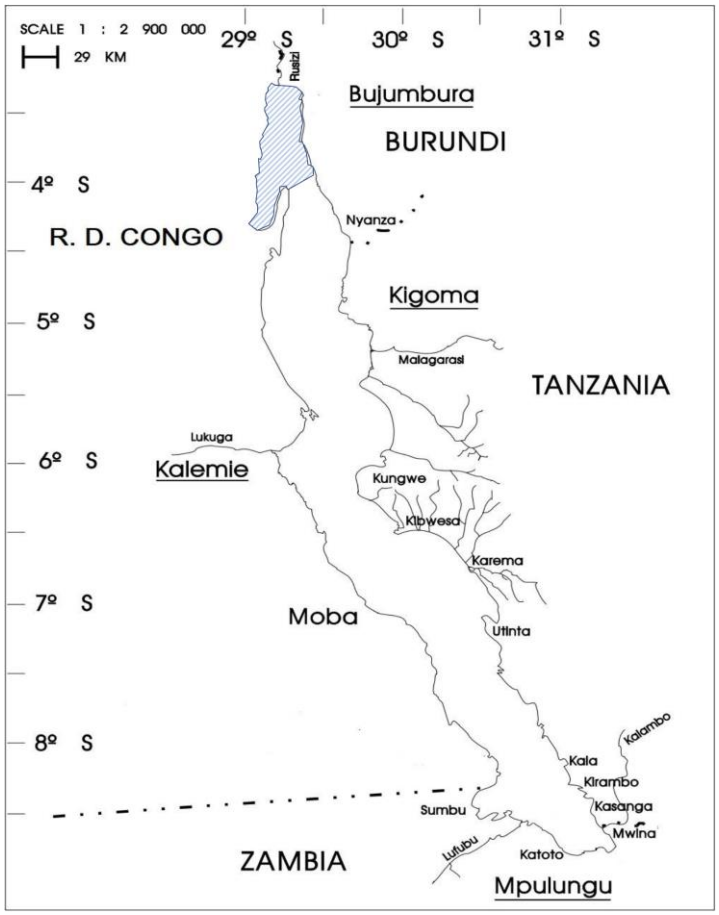


**Figure 1.** Geographic position of Lake Tanganyika bordered by DR Congo, Burundi, Tanzania and Zambia. The shaded area marks the Bujumbura sub-basin.

As *S. tanganicae* is entirely pelagic, all data for this species originate from samples collected in the pelagic environment. In contrast, *L. miodon* occurs in the pelagic environment as well as in littoral areas of the lake. The data for *L. miodon* were obtained from both the littoral and the pelagic in 1987 – 1988 and in 1999 – 2001, while in 2004 – 2005 and in 2007-2008 the species was only sampled in the pelagic.

Because the available length frequency data (1987-1989, 1999-2001, and 2007-2008) and length at age data (2004-2005) originated from different survey periods, our study design is not optimal to compare growth parameters based on the two data types. Nevertheless, since the length-at-age survey period is embedded within the two decades spanning the three length frequency surveys, it should still be possible to distinguish effects of data type from temporal patterns, especially when temporal variation is minor.

**Table 1.** Overview of datasets used in this study for the analysis of growth parameters including survey period, total sample size (N), data type (LF: length frequency data; LA: length-at-age data), published estimates of $L_\infty$ (TL in cm) and K, and reference. NA indicates that no information is available from the original publications. Estimates of $L_\infty$ marked with an asterisk are converted from SL to TL following Mannini *et al.* (1996).

| **Survey period (months)** | **N** | **Data type** | $L_\infty$ | **K** | **Reference** |
|---|---|---|---|---|---|
| | | *S. tanganicae* | | | |
| Nov 1987 - Apr 1989 (18) | 24,167 | LF | 12.34* | 2.14 | Mulimbwa & Shirakihara 1994 |
| May 1999 - Nov 2001 (30) | 84,503 | LF | 11.70 | 2.6 | Mulimbwa 2006 |
| 2004 - 2005 | 260 | LA | NA | NA | Mulimbwa et al. 2014b |
| Feb 2007 - May 2008 (16) | NA | LF | NA | NA | Mulimbwa et al. 2014b |
| | | *L. miodon* | | | |
| Nov 1987 - Apr 1989 (18) | 3,834 | LF | 16.12* | 1.15 | Mulimbwa & Shirakihara 1994 |
| May 1999 - Nov 2001 (27) | 12,272 | LF | 17.90 | 0.74 | Mulimbwa 2006 |
| 2004 - 2005 | 244 | LA | NA | NA | Mulimbwa et al. 2014b |
| Feb 2007 - May 2008 (16) | NA | LF | NA | NA | Mulimbwa et al. 2014b |

*Length-at-age data*

Briefly, 260 specimens of *S. tanganicae* and 244 specimens of *L. miodon* were collected in the pelagic from the study area in 2004-2005 (Table 1). First, the total length (TL) of each specimen was measured to the nearest mm, and otoliths were extracted and dried at room temperature at the CRH laboratory in Uvira (DR Congo). Subsequently, the otoliths were weighed with a microbalance (µg; dry weight at 20°C) at the University of Turku (Finland). Finally, the age of these fish was estimated using the relationship between otolith dry weight (ODW) in µg and age in days based on counts of daily rings following the formula age = (ODW + a)/b, where a = 99.4, b = 2.42 for *S. tanganicae* and a = 120.8, b = 2.53 for *L. miodon* (Ahonen 2001).

*Length frequency data*

For all three studies, samples were taken from artisanal fishing units using lift nets with a mesh size of 4.4 mm (knot to knot) in the upper four-fifths of the net and 3.3 mm (knot to knot) for the rest of the net. The samples were collected twice a week during the investigation period. After collection, samples were sorted by species at the CRH laboratory in Uvira (DR Congo). Their total lengths (TL) were determined to the nearest mm, and the specimens were grouped into size classes of 2 mm for *S. tanganicae*, and 4 mm for *L. miodon*, in 1999-2001 and 2007-

2008. The data from 1987-1989 were collected in 5 mm classes for both species. Total sample sizes for each period are shown in Table 1.

For 1987 – 1988, the original data from Mulimbwa and Shirakihara (1994) could not be retrieved from the authors. Instead, we digitized the length frequency plots in Mulimbwa and Shirakihara (1994) (Fig. 2 for *S. tanganicae*; Fig. 4 for *L. miodon*) using WebPlotDigitizer version 4.6 (Rohatgi 2022). Since length in this study was measured in mm as standard length (SL), size classes were converted to total length (TL) in mm following the formula TL = a + (b * SL), where a = 0.8729, b = 1.1562 for *S. tanganicae* and a = 1.6658, b = 1.1873 for *L. miodon* (Mannini *et al.* 1996).

*Data analysis*

1) Length-at-age analysis

A Von Bertalanffy growth function (VBGF) was fitted to the otolith derived length-age data, and its parameters $L_\infty$ (cm) and K ($year^{-1}$) were determined using the non-linear least squares method, available within the function "growth_length_age()" in the TropFishR package (Mildenberg et al. 2017).

2) Length frequency analysis

The growth parameters to fit a VBGF to length frequency data have historically been estimated using several methods (e.g. the Power-Wetherall or Ford-Walford method), most of which have been questioned for containing intrinsic biases from different sources (Schwamborn 2018). However, recent improvements to ELEFAN (electronic length frequency analysis, Pauly & David 1981), the most used method for fitting a growth curve to length frequency data, foreshadow a promising new path for length-based studies of aquatic populations. These advancements include the estimation of both $L_\infty$ and K with fewer assumptions than previous models (Taylor & Mildenberg 2017), as well as the calculation of their associated uncertainty using bootstrapping (Schwamborn et al. 2019). We applied these new methods using the TropFishR and fishboot packages in R (Mildenberg et al. 2017; Taylor & Mildenberg 2017; Schwamborn et al. 2019) with the parameters shown in Table 2.

ELEFAN relies on attributing different scores to the different length bins, depending on how much each bin deviates from a moving average across a user-defined number of length bins. This was done by grouping the size classes into 0.8 cm bin sizes, and a moving average of 5-7 size classes (Table 2), depending on the size of the smallest cohort, following the general rule of thumb (Taylor & Mildenberg 2017). Afterwards, a score is given to different growth curves, depending on whether they intersect with positively or negatively scored length bins (Gayanilo & Pauly 1997). The curve with the highest score is considered the best fitting curve to the data. Finding the best fitting curve can be computationally costly, and only recently two optimization approaches ("simulated annealing" and "genetic algorithm") have been implemented for growth function fitting in R (Taylor & Mildenberg 2017; Mildenberg et al. 2017). Both

optimization approaches can find high-scoring solutions, but because several models often score high, different solutions can be reached depending on initial settings, which end up being an intrinsic source of bias. To overcome this limitation, bootstrapping methodology can be applied, fitting a big number of growth curves with similar scoring solutions, and finally calculating the uncertainty of the mean value of the estimations (Schwamborn et al. 2019). We estimated $L_\infty$ and K of both species from length frequency data by bootstrapping both algorithms, using the package "fishboot" in R (Schwamborn et al. 2019), and we report the probability distribution of the estimations. The total parameter space considered ranged from 1 to 10 for K for both species (Table 2). For $L_\infty$, we considered values from 8 cm to 12 cm for *S. tanganicae*, and from 8 to 16 cm for *L. miodon* (Table 2). Here, the upper values are above the maximum total length reported for each species in Fishbase (*S. tanganicae*: 10 cm SL ~ 11.65 cm TL; *L. miodon*: 17 cm SL ~ 20.35 TL; Froese & Pauly 2017). We manually set a maximum age to each species (Table 2; 18 months for *S. tanganicae* and 30 months for *L. miodon*; Mannini et al. 1996), which is a key step for the calculation of the growth parameters in this method.

**Table 2.** Parameters used in the VBGF fitting using ELEFAN bootstrapping in each of the three surveys based on length frequency data. GA: Genetic algorithm; SA: Simulated annealing; MA: moving average; $L_\infty$: length at infinity; K: annual growth coefficient; t_anchor: peak spawning month; nresamp: number of permutations.

| Species | Algorithm | Parameter (unit) | 1987-1988 | 1999-2001 | 2007-2008 |
|---|---|---|---|---|---|
| *S. tanganicae* | GA, SA | MA (bins) | 5 | 7 | 5 |
| | | $L_\infty$(cm) | 6-12 | 6-12 | 6-12 |
| | | K (year$^{-1}$) | 1-10 | 1-10 | 1-10 |
| | | t_anchor (year) | 0-1 | 0-1 | 0-1 |
| | | nresamp | 400 | 400 | 400 |
| | | Agemax (year) | 18/12 | 18/12 | 18/12 |
| | | bin_size (cm) | 0.8 | 0. 8 | 0. 8 |
| *L. miodon* | GA, SA | MA (bins) | 5 | 7 | 7 |
| | | $L_\infty$(cm) | 8-22 | 8-22 | 8-22 |
| | | K (year$^{-1}$) | 1-10 | 1-10 | 1-10 |
| | | t_anchor (year) | 0-1 | 0-1 | 0-1 |
| | | nresamp | 400 | 400 | 400 |
| | | Agemax (year) | 30/12 | 30/12 | 30/12 |
| | | bin_size (cm) | 0. 8 | 0. 8 | 0. 8 |

3) Consistency between methods

To assess the consistency between length-at-age-based and size frequency-based methods, the agreement of growth parameters ($L_\infty$ and K) between different sampling periods was tested using the 95 % confidence intervals based on LAA or 95 % credibility intervals based on LFA.

## RESULTS

*S. tanganicae*

Length categories of the length frequency data across time periods ranged between 2.1 and 11.1 cm TL. Recruitment was continuous throughout the year, as indicated by small individuals (2.0 - 4.0 cm) appearing all year round in the length frequency data of the three survey periods. Length-at-age data comprised individuals ranging between 3.3 cm and 10.6 mm for TL, and between 56 and 372 days in age. The length distribution of the length frequency data and the length-at-age data was comparable (Figure 2).

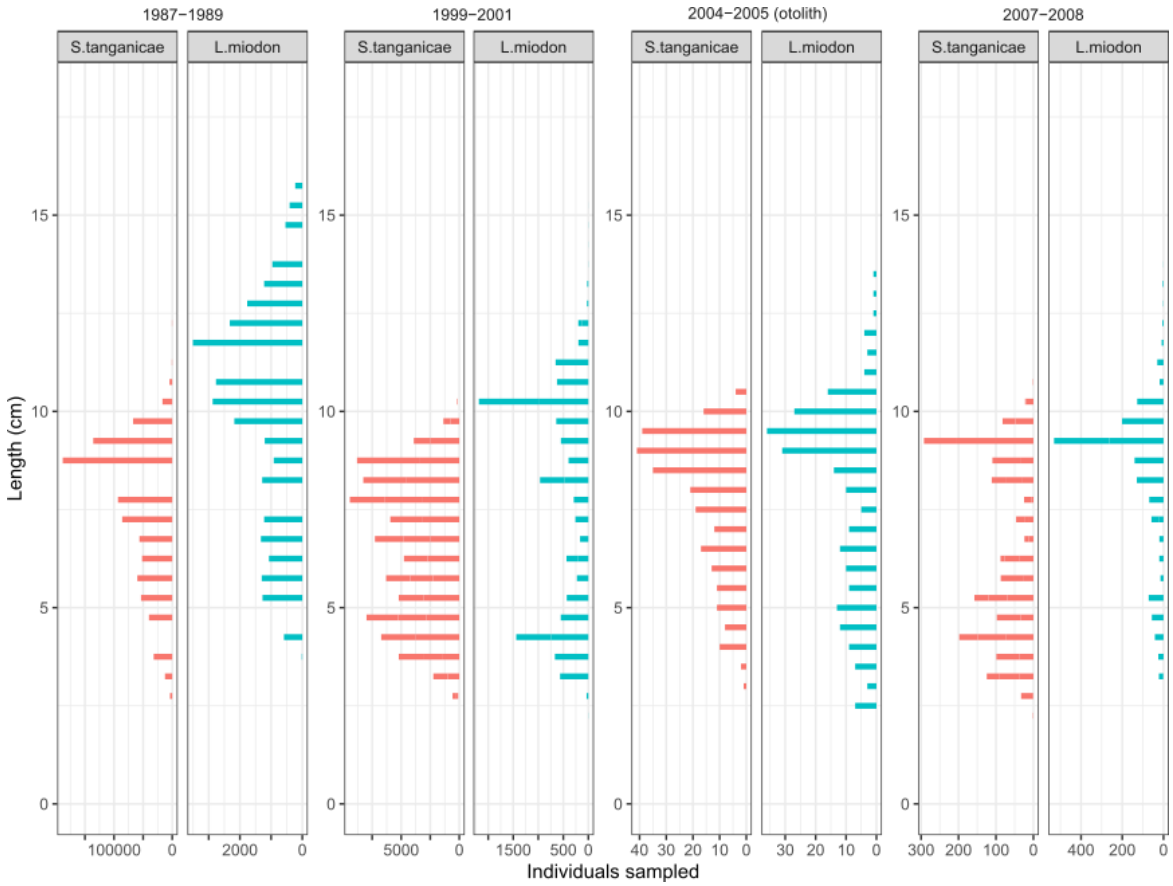


**Figure 2.** Total length distribution (cm) for both species and the four survey periods.

Based on length-frequency data analysis (LFA), estimates of $L_\infty$ (range: 8.67 - 9.56 cm) were consistent between estimation methods with narrow confidence intervals, and showed substantially lower values in 1987-1989 and 1999-2001 than in 2007-2008 (Table 3; Supplementary Figure 1). In contrast, the annual K (range: 4.35 - 7.87) showed very high uncertainty which led to an overlap in confidence intervals between most study periods and estimation methods (Table 3). Based on the length-at-age data (LAA) from 2004-2005, we obtained an estimate of 10.64 cm for $L_\infty$ and 3.18 for K (Table 3). Credibility intervals indicated that all estimates of $L_\infty$ and most estimates of K were respectively significantly lower and higher for LFA than for LAA. According to the LAA curve, *S. tanganicae* grows rapidly during

the first five months of its life and growth becomes almost constant after ten months (Figure 3; Figure 4; Supplementary Figure 2).

**Table 3**. Growth parameters of clupeids (*S. tanganicae*, *L. miodon*) estimated for different time periods and using different estimation procedures for length frequency analysis (LFA) and length-at-age analysis (LAA). Estimation methods include two optimization approaches in the case of LFA (SA: ELEFAN with simulated annealing; GA: ELEFAN using genetic algorithm), and the non-linear least-squares method (LSM) in the case of LAA. $L_\infty$: asymptotic total length (cm), K: annual growth coefficient. CI: Bayesian credibility intervals (in the case of LFA) or confidence intervals (in the case of LAA).

| **Survey period** | **Analysis** | **Estimation** | $L_\infty$ **[95% CI]** | **K [95% CI]** |
|---|---|---|---|---|
| | | *S. tanganicae* | | |
| 1987-1989 | LFA | GA | 8.78 [8.60-8.88] | 4.96 [3.84-6.94] |
| | | SA | 8.80 [8.32-9.10] | 4.35 [3.25-9.78] |
| 1999-2001 | LFA | GA | 8.67 [8.47-8.80] | 7.86 [6.81-8.79] |
| | | SA | 8.72 [8.18-8.83] | 7.87 [6.4-9.87] |
| 2004-2005 | LAA | LSM | 10.64 [10.32-11.05] | 3.18 [2.76-3.63] |
| 2007-2008 | LFA | GA | 9.41 [9.20-9.60] | 6.64 [3.72-9.35] |
| | | SA | 9.56 [9.02-9.64] | 5.98 [3.61-9.91] |
| | | *L. miodon* | | |
| 1987-1989 | LFA | GA | 11.53 [11.17-11.76] | 3.35 [2.96-4.55] |
| | | SA | 11.41 [11.12-11.80] | 3.97 [2.72-6.10] |
| 1999-2001 | LFA | GA | 10.99 [10.67-11.28] | 2.22 [1.63-2.87] |
| | | SA | 11.10 [10.56-11.36] | 2.13 [1.41-3.01] |
| 2004-2005 | LAA | LSM | 12.82 [12.18-13.64] | 1.73 [1.47-2.01] |
| 2007-2008 | LFA | GA | 9.61 [9.26-9.70] | 3.30 [2.44-9.84] |
| | | SA | 9.61 [8.89-9.87] | 3.65 [2.09-10.17] |

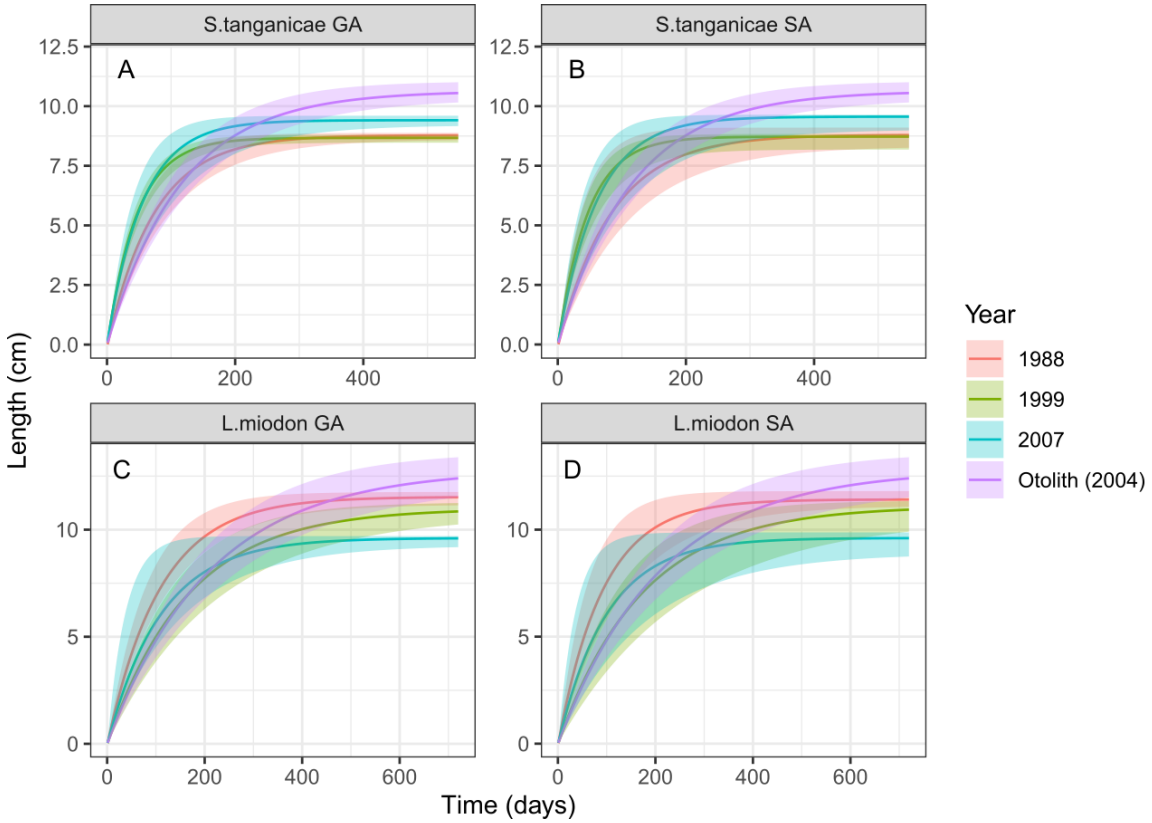


**Figure 3.** VBGF estimated from length frequency data of 1987-1988, 1999-2001 and 2007-2008 for (A) *Limnothrissa miodon* with Genetic Algorithm; (B) *Limnothrissa miodon* with Simulated Annealing; (C) *Stolothrissa tanganicae* with Genetic Algorithm; and (D) *Stolothrissa tanganicae* with Simulated Annealing. Each plot is superimposed with VBGF estimates from otolith-derived length at age data of 2004-2005.

*L. miodon*

Length categories of the length-frequency data across time periods ranged between 2.4 and 15.2 cm TL. Recruitment occurred less frequently throughout the year than in *S. tanganicae*, as small individuals (2-6 cm) were less frequent across the three survey periods. Length-at-age data comprised individuals ranging between 2.5 cm and 13.6 cm for TL, and between 62 and 571 days in age. In 1987-1989, the sampled individuals were markedly larger than in other years (Figure 2).

Based on length-frequency data, estimates of $L_\infty$ (range: 9.61 - 11.53 cm) were consistent across estimation methods, but values for 2007-2008 were substantially lower than for the other survey periods (Table 3; Supplementary Figure 1). Ranging between 2.13 and 3.97, the annual K was more consistent across the three LFA survey periods and estimation methods than estimations for *S. tanganicae*, although the uncertainty was generally also high (Table 3). Based on the length-at-age data from 2004-2005, we obtained an estimate of 12.82 cm for $L_\infty$ and 1.73 for K (Table 3). As for *S. tanganicae*, credibility intervals indicated that all estimates of $L_\infty$ and most estimates of K were respectively significantly lower and higher for LFA than for LAA. According to the LAA curve, *L. miodon* grows rapidly during the first ten months of

its life and growth becomes almost constant after 18 months (Figure 3; Figure 4; Supplementary Figure 2).

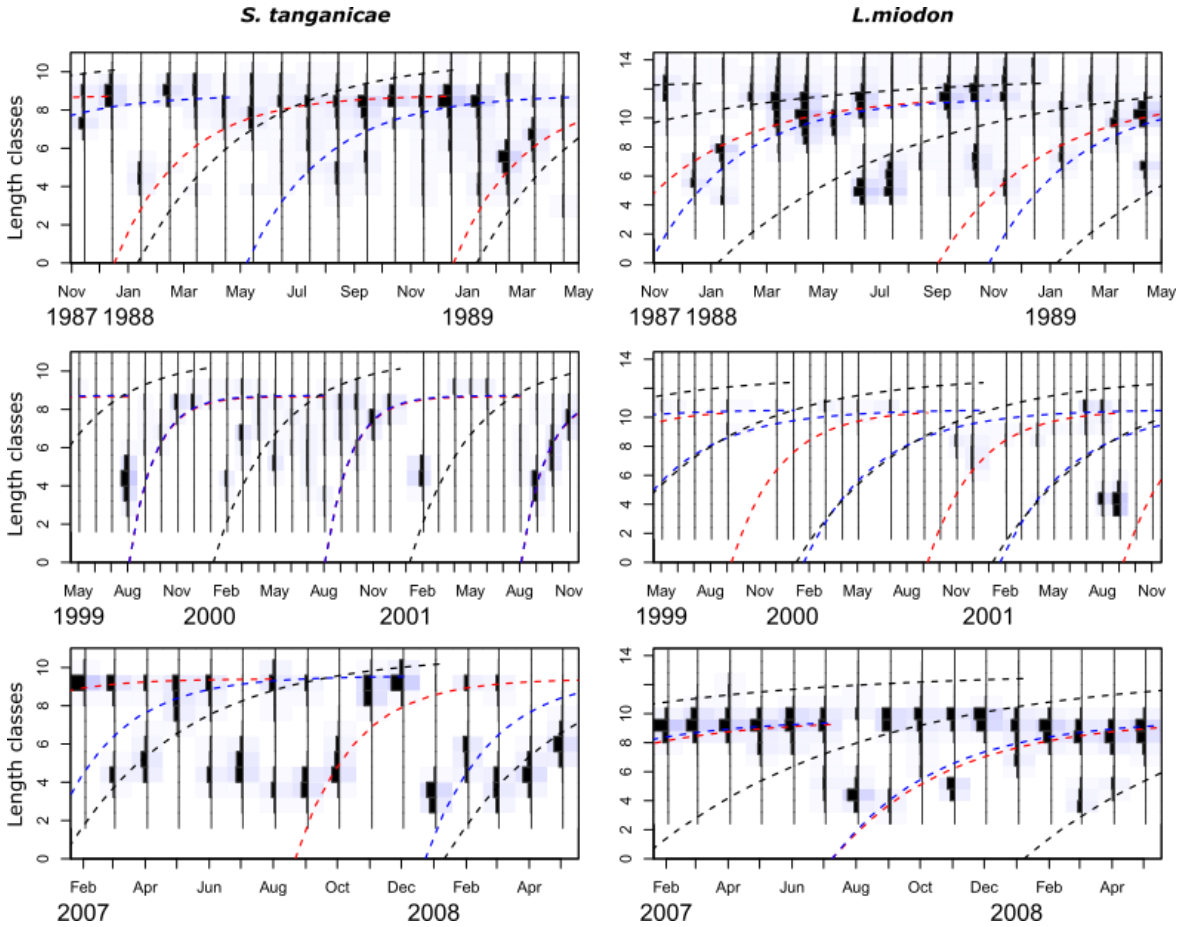


**Figure 4.** Length frequency data and corresponding Von Bertalanffy growth curves for the three survey periods for *Stolothrissa tanganicae* (A, B, C) and *Limnothrissa miodon* (D, E, F). The red and blue dashed lines mark growth curves estimated with the genetic algorithm and the simulated annealing algorithm, respectively. For comparison, the growth curves estimated from length-at-age data are superimposed (green dashed line). The length frequency data are plotted in dark blue, and blue shades reflect the frequency of each length class..

## DISCUSSION

The objective of this study was to examine the growth patterns of *S. tanganicae* and *L. miodon* in the North part of Lake Tanganyika. We compared growth estimates derived from length frequency data and length-at-age data, collected over different survey periods. This comparison informs us about the accuracy of size frequency-based estimation methods for growth parameters, and the necessity of complementing fisheries management with more complete life history information using age-based data. We consistently found lower estimates of $L_\infty$ and higher estimates of K for length frequency data than for length at age data, in both species. Below we discuss the reliability of this result, and its implications for the management of the artisanal fisheries.

Because length frequency and length at age data were collected in different survey periods, estimation procedure and survey period are confounded in our study, and therefore do not allow us to directly compare the results. Nevertheless, because the differences in estimates between the two procedures largely exceed the differences between survey periods within LFA, it is unlikely that temporal variation alone can account for the observed differences between the two methods. It is indeed more likely that the disparities between data types and estimation methods stem from methodological nuances that influence the estimation of growth parameters. Otolith-based methods are believed to provide accurate estimations of age, which together with direct measurements of length, should provide accurate growth curves (Schwamborn et al. 2023). Ahonen (2001) demonstrated that the age of the two sardine species can be reliably estimated from otolith dry weight (Pearson correlation between otolith dry weight and age based on counts of daily otolith rings: $r^2 = 0.88$ for *S. tanganicae*; $r^2 = 0.96$ for *L. miodon*). While this relationship was established using individuals from the central part of Lake Tanganyika (Kigoma, Malagarasi and Kipili; Ahonen 2001), we applied it here to individuals from the North of Lake. Nevertheless, this should yield acceptable results, and overall, the accuracy of our LAA-based estimates likely exceeds the accuracy of our LFA-based estimates.

In general, LFA is highly sensitive to sampling bias, and particularly to the lack of large, old individuals, which leads to biased estimations under high fishing pressure (Schwamborn 2018; Schwamborn et al. 2019; Wang et al. 2021). Other sources of sampling bias include the concentration of fishing efforts on commercially valuable areas, and differences in fishing gears and methods. These potential issues with LFA likely apply to the two Lake Tanganyika sardines, as notified previously by Mulimbwa & Shirakihara (1994). In the present study, the discrepancy between LFA-based and LAA-based estimates suggest that the largest individuals are missing in the length-frequency data of both species. The length-frequency data further indicated that the upper size range of *L. miodon* declined substantially with time. Yet, representative sampling for size is particularly challenging in *L. miodon* because large, mature individuals are more commonly observed in littoral areas than in the pelagic zone, so the sampling effort in each area can directly affect the results (Mulimbwa & Shirakihara 1994; Mulimbwa et al. 2022). Since no *L. miodon* were collected in the littoral areas during the most recent survey periods (2004-2005 and 2007-2008), it remains unclear if the reduction of the bigger size classes and the decrease in LFA-based estimates of $L_\infty$ over time is due to fishing pressure or due to sampling bias. Ideally then, changes in growth parameters should be investigated using length-at-age data. Our LAA-based estimates of $L_\infty$ for both *S. tanganicae* and *L. miodon* from catches in 2004-2005 were substantially lower than the LAA-based estimate for both species from catches in 1990 by Kimura (1995) (Figure 5). However, both studies were conducted at opposite ends of the lake, and spatial variation in environmental conditions may also affect growth trajectories. Overall, better data are required to confirm the possibility of fisheries-induced trends.

Another source of inaccuracy of LFA is the aggregation of individuals into length bins, which has the potential to obscure the age structure within each bin (Taylor & Mildenberger 2017; Schwamborn, 2018). This can manifest as well in lower $L_\infty$ values and higher K values,

particularly with bigger bin sizes (Wang et al. 2020). However, a recent study directly comparing LFA and LAA in lane snapper (*Lutjanus synagris*) found no difference in $L_\infty$ and K between the two methods (Schwamborn et al. 2023). Interestingly, from the single other length-at-age data available for the two Lake Tanganyika sardines, Kimura (1995) concluded that the growth parameters obtained from length-at-age data (based on daily counts of otolith rings) generally agreed with those previously estimated from analyses of length–frequency distributions. However, close inspection of Kimura's (1995) results reveals that the author's otolith-based estimates for $L_\infty$ almost always exceeded the estimates for $L_\infty$ from length-frequency studies, and *vice versa* for K, and thus seemed to be subject to the same bias we report here.

Yet, both our LAA-based and LFA-based estimates for the growth trajectory of the two sardine species from the North of Lake Tanganyika also substantially deviated from estimates of previous studies (Table 1; Figure 5). This includes both LAA-based and LFA-based studies from various regions of Lake Tanganyika (Figure 5), but also the length frequency datasets from the North of Lake Tanganyika for which we re-estimated the growth parameters (Figure 5; Table 1; Mulimbwa & Shirakihara 1994; Mulimbwa 2006). Almost all studies reported significantly larger values of $L_\infty$, and therefore lower values of K than the present study (Figure 5). This was true for both species, although the discrepancy for K between previous studies and the present study was more pronounced in *S. tanganicae*, while the discrepancy for $L_\infty$ was more pronounced in *L. miodon* (Figure 5). For the LFA-based estimates, this discrepancy could be explained by the fact that previous studies are largely based on outdated methods such as the Ford-Walford plot, which are known to generate inaccurate results (Schwamborn 2018). Indeed, the improved ELEFAN methods we used here are based on fewer assumptions and allow for screening a large range of parameter values, which should lead to more accurate and easily reproducible results (Mildenberger et al. 2017; Schwamborn et al. 2019). Still, the subjective choice of suitable parameter space for $L_\infty$ can often result in biased results with narrow confidence intervals (Schwamborn et al. 2023). For this reason, we opted for upper parameter limits above the maximum length reported in Fishbase for each species, which should result in unbiased estimations with realistic uncertainty estimates. Despite these improved estimation procedures, some of our LFA-based estimates, especially for K, come with very high uncertainty, which may indicate that the quality of the available length frequency data is insufficient to achieve robust conclusions. This leaves little room for scientific advice beyond improving monitoring efforts to obtain better and more accurate growth parameters based on LFA.

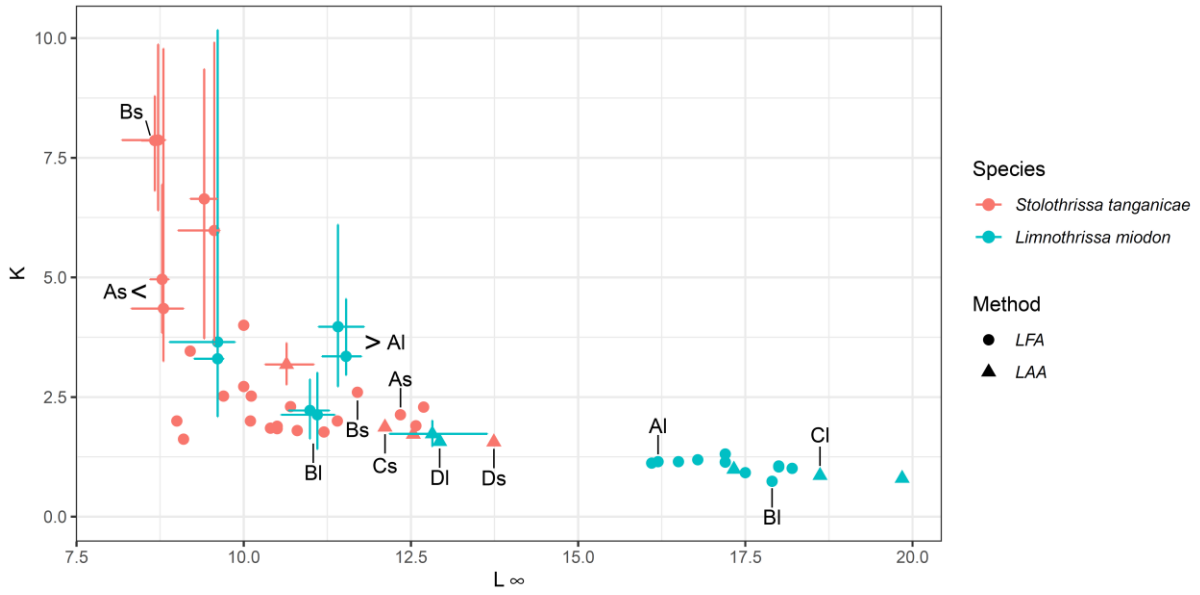


**Figure 5.** Plots of the annual growth coefficient (K) against asymptotic total length ($L_\infty$ in cm) for *S. tanganicae* (red) and *L. miodon* (blue) based on LFA (circles) or LAA (triangles). Data points with error bars (95 % confidence intervals) are from Table 3. Data points without error bars are derived from the overview provided by Table 9 and Figure 47 in Mannini et al. (1996), in addition to estimates by Ahonen (2001) and Mulimbwa (2006). Labeled data points are based on LFA data by Mulimbwa & Shirakihara (1994) (As: *S. tanganicae*; Al: *L. miodon*), LFA data by Mulimbwa (2006) (Bs: *S. tanganicae*; Bl: *L. miodon*), LAA data by Kimura (1995) (Cs: *S. tanganicae*; Cl: *L. miodon*), and LAA data by Ahonen (2001) (Ds: *S. tanganicae*; Dl: *L. miodon*).

*Conclusions and implications for fisheries management*

The lower $L_\infty$ and higher K values obtained with LFA could significantly impact the estimation of important population parameters for fisheries management. Notably, underestimating the asymptotic length can bias the perception of the maximum size that a species can attain, potentially affecting assessments of stock health and overall biomass. For instance, fisheries managers may ignore the protection of larger, older individuals that exceed the estimated asymptotic length and that contribute disproportionately to reproduction and overall population resilience (Birkeland & Dayton 2005). Conversely, overestimating the growth constant can influence predictions of population productivity and the determination of sustainable fishing quotas. Overestimating K could therefore result in overly optimistic assessments of the population's growth potential and the level of fishing pressure that can be sustained.

Our study underscores the need for future research aimed at advancing our understanding of growth dynamics and their implications for the pelagic fisheries of Lake Tanganyika. We recommend that length-at-age data are obtained at a much broader spatial and temporal scale than is currently available. However, as length frequency data can be more easily collected, such data will remain our primary source of information and should continue to be obtained. Furthermore, both length frequency data and length-at-age data should be collected for the

same study periods to refine our comprehension of the discrepancies between the two methods. In addition, it is important that all samples in a time series come from the same landing site and fishing area to rule out that changes in length frequencies over time are due to sampling bias. Overall, inaccuracies in growth parameter estimations might inadvertently lead to unsustainable exploitation levels, compromising the long-term viability of the fishery and cascading into ecological imbalances. As we have shown, it is straightforward to reanalyze existing length frequency data whenever the original data can be retrieved, but it is also possible to regenerate the data after digitizing published length frequency plots.

## ACKNOWLEDGEMENTS

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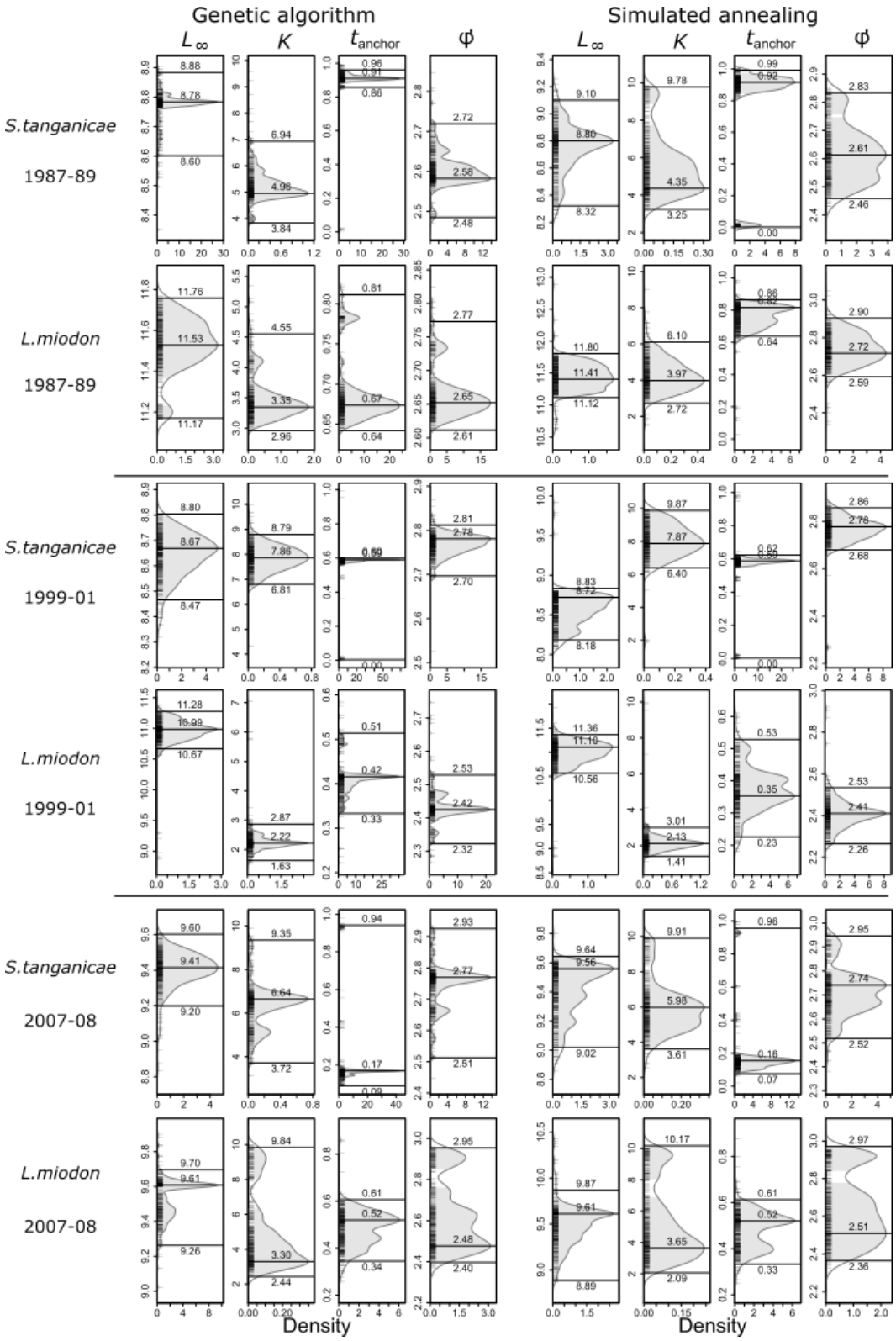
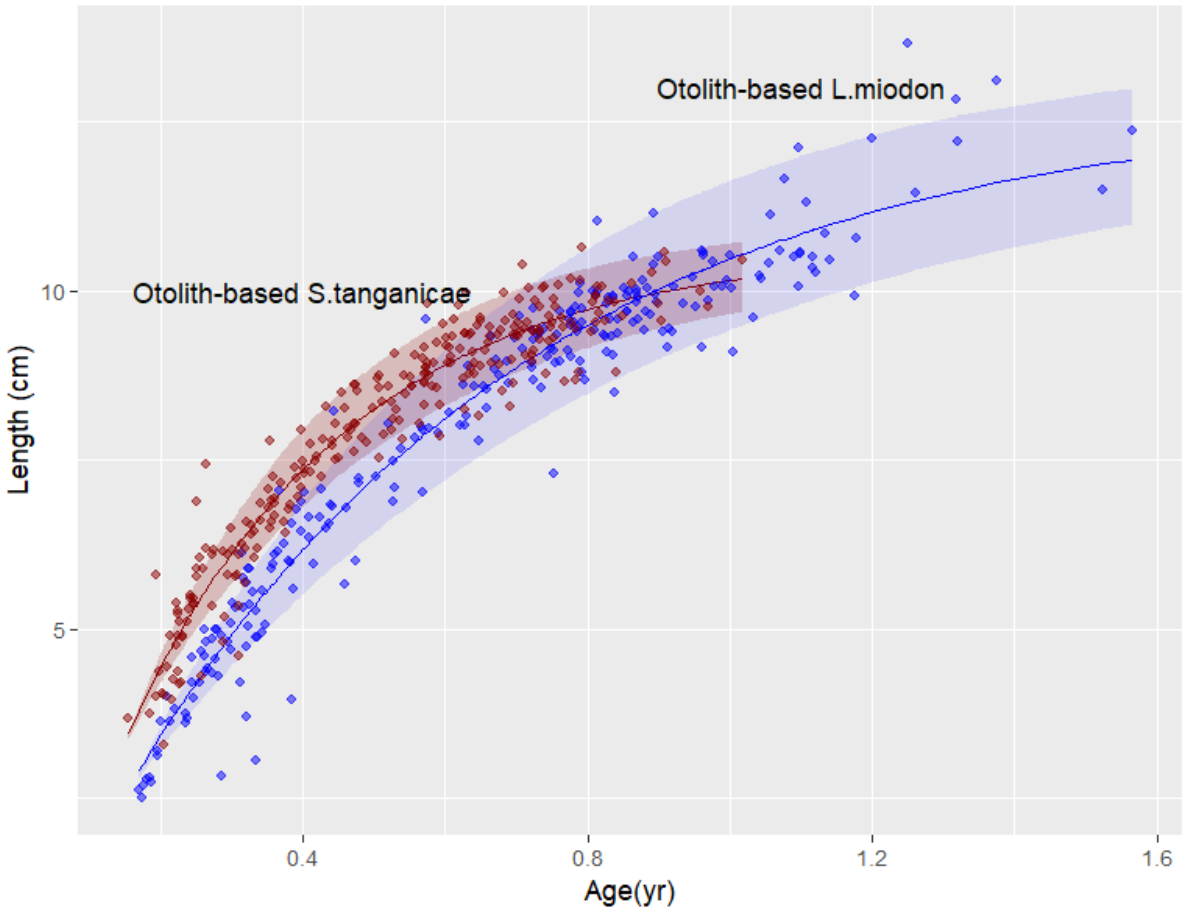
## SUPPLEMENTARY FIGURES




**Supplementary Figure 1.** Probability distribution of estimated parameters using genetic and simulated annealing algorithms for *Stolothrissa tanganicae* and *Limnothrissa miodon* in each study period.




**Supplementary Figure 2.** Von Bertalanffy growth functions (VBGF) for *Stolothrissa tanganicae* and *Limnothrissa miodon*, estimated from otolith-derived length-age relationships.