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Early Life Histories of Two Clupeids, *Limnothrissa miodon* and *Stolothrissa tanganicae*, from Lake Tanganyika

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Abstract The early life histories of *Limnothrissa miodon* and *Stolothrissa tanganicae*, clupeids endemic to Lake Tanganyika, were researched in Uvira waters (Zaire), northern part of the lake, from May to July 1988. Larvae of both species have morphological characteristics in common with marine Clupeidae. *L. miodon* can be distinguished from *S. tanganicae* not only by the melanophore pattern along the ventral margin of the gut, but also by the eye shape and morphological proportions (HL/SL and snout length/HL). Both larvae initially have elliptical eyes, which gradually become round with growth in *L. miodon*, but which remain narrow in postflexion larvae of *S. tanganicae*. Larvae of both species aggregated near the surface at the night, but descended into waters deeper than 50 m during the day. *L. miodon* larvae were predominant near the shore, immigrating toward sandy shores with growth, whereas *S. tanganicae* larvae were more abundant offshore, where they remained throughout their life history.

Clupeidae is represented by 27 species in African fresh waters. Two of these, *Limnothrissa miodon* and *Stolothrissa tanganicae* (both Pellonulinae), endemic to Lake Tanganyika (Poll, 1953; Whitehead, 1985), where they occupy the pelagic zone and are locally called ndakala or carpenter and economically important, being the main protein resources for the people of the surrounding region (Coulter, 1991b).

Annual fluctuations in catch of these species have been explained as predator (centropomids)-prey (clupeids) interactions (Coulter, 1970). While the interval of the fluctuation cycles may be predicted, the amplitude cannot (Coulter, 1970). A number of workers have investigated spawning of Tanganyika pelagic fishes (Poll, 1953; Matthes, 1967; Coulter, 1970; Ellis, 1971; Roest, 1977; Chapman and van Well, 1978; Pearce, 1985), but little work has been done on the early life histories of these fishes. Some morphological descriptions of the clupeid larvae have been made and the discernible differences between the body forms of the two species noted (Poll, 1953). However, the latter's descriptions are insufficient for identification, especially of small larvae.

Since 1987, early life history studies of the pelagic fishes in northern waters of Lake Tanganyika (Fig. 1) have been continuously conducted. The purposes of this paper are to describe and distinguish the larvae of the two clupeid species, and to summarize their distribution.

Materials and Methods

The stations forming a transect at right angles to the coast at Uvira (Fig. 1, open circles) were sampled for larval fish in May and July 1988, using a conical plankton net (1 m mouth-diameter; 0.3 mm mesh-aperture). Day and night collections by discrete-depth, horizontal tows with the same net were carried out at 0, 25 and 50 m depths of St. 7 (Fig. 1, double circle) on May 16-17. Surface collections were conducted with the same net from St. 1 to St. 10 at night on July 9.

At stations from Kavimvira to Makobola (Fig. 1, solid circles), collections of chiefly juvenile inshore fishes were made with a small seine net on July 29 and 30 according to the procedure of Senta and Kinoshita (1985). The seine used and collection method were described in Kinoshita (1986).

All specimens were fixed in 10% formalin in the field, and transfered to 80% ethanol, sorted and measured in the laboratory. The larval descriptions were based on these samples.

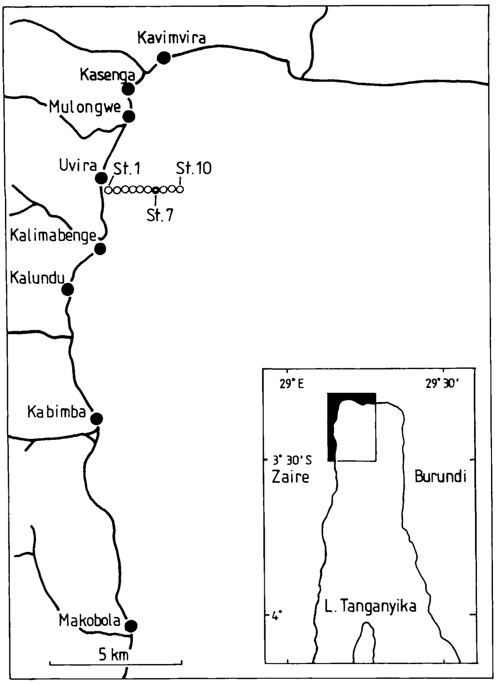

Fig. 1. Northern part of Lake Tanganyika showing stations where larval and juvenile fishes were collected. Stations indicated with open circles (Sts. 1–10) were surveyed with a larva net (1 m mouth diameter, 4 m long and 0.3 mm mesh-aperture) in May and July 1988. At St. 7 (double circle), discrete-depth (0, 25 and 50 m) horizontal tows were carried out with the same net on May 16–17, 1988. At stations indicated with solid circles (from Kavimvira to Makobola), collections along shores were made with a small seine (1×4 m, 1 mm mesh) on July 29 and 30, 1988.

Results

Description of larvae

Developmental stages of *Limnothrissa miodon* and *Stolothrissa tanganicae* are illustrated in Figures 2 and 3, respectively. Their ontogenies fundamentally resembled those of a variety of marine clupeids (Uchida, 1958; Jones et al., 1978; Bensam, 1986, 1987; Matarese et al., 1989). Bodies are elongated, each with a small head, a long straight gut, a well posteriorly-placed anus and few melanophores, in the larvae of both species.

L. miodon.—The snout-anus distance is 78–79% SL throughout the larval period. Total myomeres number 38 in larvae under 9 mm SL and 42 in those over 10 mm SL. The depressed head has relatively narrow eyes with ventral choroid tissue in larvae under 9 mm SL. Eyes become round and choroid tissue gradually disappear with growth (Fig. 2A–C). In larvae under 7 mm SL, the position of the pectoral fin is low; dorsal and caudal anlagen are present (Fig. 2A). The anal fin is apparent at 8.5 mm SL, myomeres between the dorsal and anal anlagen numbering five (Fig. 2B). Fin rays begin to form earlier in the dorsal than in the anal fin, but both fins are complete by about 12 mm SL (Fig. 2B, C). Notochord flexion begins at 6–7 mm SL being completed at 9–10 mm SL. The pelvic bud is present in larvae over 12 mm SL, with the rays being completed at about 15 mm SL (Fig. 2D, E). Some of gills are exposed posterior to the operculum in larvae of about 9 mm SL.

Single rows of melanophores are found ventrally on the gut at about 6 mm SL, and two rows dorsolaterally on the fore- and midgut at 8–9 mm SL (Fig. 2A, B). Melanophores are also distributed along the anal fin base, dorsal and ventral margins of the caudal peduncle, on the dorsal and caudal fins (Fig. 2C, D), and internally on the lateral surface of the head in larvae over 11 mm SL (Fig. 2E).

S. tanganicae.—The snout-anus distance is initially 75% SL, subsequently stabilising at 81–83% SL throughout the remaining larval period. Total myomeres number 41–43. Larvae have a depressed head and very narrow eyes with ventral choroid tissue. The choroid tissue disappear gradually with growth, but eyes retain the elliptical shape throughout the larval period (Fig. 3). Larvae under 6 mm SL lack fins, except for the pectoral fin placed low on the body (Fig. 3A). Dorsal and anal anlagen are present in larvae of 7 mm SL. There are three or four myomeres between the termination of the dorsal fin and the origin of the anal anlage. Fin rays develop earlier in the dorsal than in the anal fins, but are almost complete in both fins of 10–11 mm SL larvae (Fig. 3C). The caudal anlage begins to develop, pushing up the notochord tip at about 6 mm SL. Notochord flexion is completed in larvae of 9 mm SL. The pectoral fin rays begin to develop at about 12 mm SL, the pelvic bud also being present. The pectoral and pelvic fin rays are completed at 13.5 mm SL (Fig. 3D, E). Some gills are exposed posterior to the operculum in larvae of 7 mm SL.

No melanophores are found on the body, except on eyes, in larvae under 12 mm SL (Fig. 3A–C). At

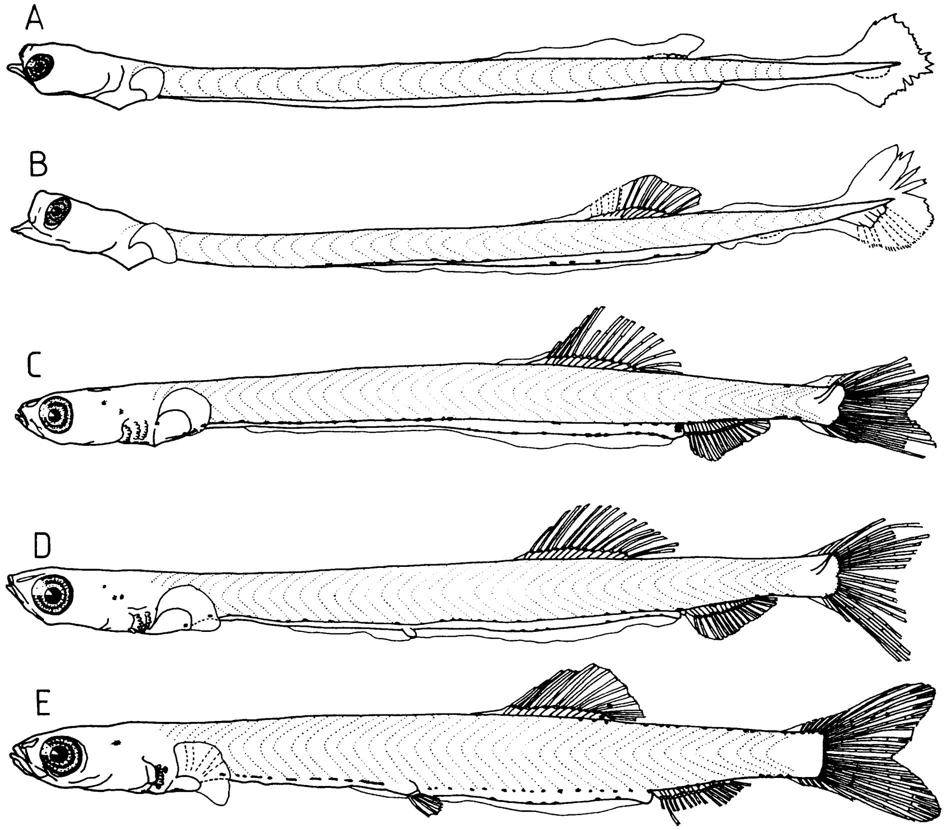

Fig. 2. Developmental stages of *Limnothrissa miodon* from the northern part of Lake Tanganyika. A) 6.3 mm SL preflexion larva; B) 8.5 mm SL flexion larva; C) 11.2 mm SL postflexion larva; D) 12.6 mm SL postflexion larva; E) 14.7 mm SL postflexion larva.

12 mm SL, a single row of melanophores occurs ventrally on the isthmus and caudal peduncle. In addition, two rows of melanophores appear dorsolaterally on the fore- and midgut (Fig. 3D, E).

Discrimination between two clupeids.—Although there seemed to be little difference in larval morphology between *L. miodon* and *S. tanganicae*, the two species could be distinguished by examination of melanophores, as indicated by Poll (1953). In *L. miodon*, melanophores were found along the gut in 6 mm SL larvae, and along the isthmus and ventral peduncle at 8.5 mm SL, whereas in *S. tanganicae*, melanophores were first observed anterodorsally along the gut in larvae over 12 mm SL (Figs. 2A, B and 3D). In *L. miodon*, melanophores on the dorsal margin of the body and caudal fin appeared in larvae over 11 mm SL, but were absent throughout the larval period of *S. tanganicae* (Figs. 2C–E and 3E). Discrimination between the two species on the basis of melanophores was not possible for larvae under 5 mm SL. The latter could be separated owing to differences in the eye shape and relative size of the head and snout between two species. Both the head and snout were longer and the eyes distinctly narrower in *S. tanganicae* than in *L. miodon* (Table 1).

Distribution

Vertical distribution.—The larvae of both species were mainly distributed in water deeper than 25 m during the first daytime observation (Fig. 4). They were concentrated near the surface during the night, increasing their densities in the 25 m layer at twilight. They descended to depths greater than 50 m during the second daytime observation.

Horizontal distribution.—Since both species tended to aggregate near the surface at night, surface collections at this time were conducted to determine the

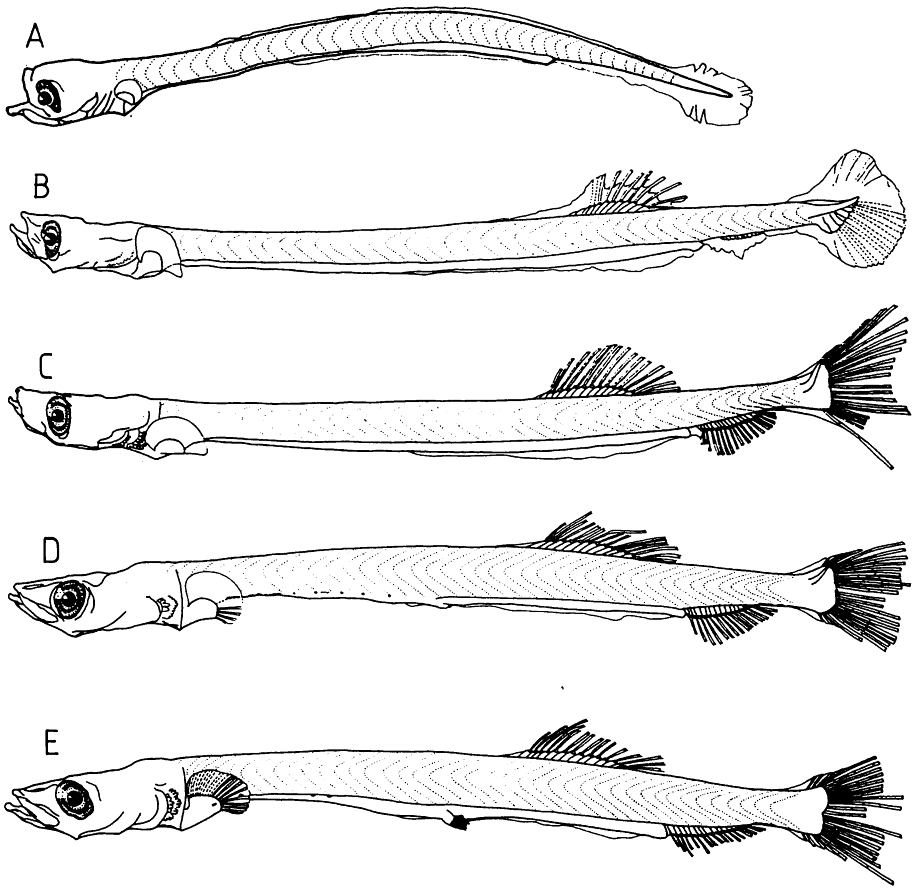

Fig. 3. Developmental stages of *Stolothrissa tanganicae* from the northern part of Lake Tanganyika. A) 3.9 mm SL preflexion larva; B) 8.2 mm SL flexion larva; C) 10.7 mm SL postflexion larva; D) 12.1 mm SL postflexion larva; E) 13.5 mm SL postflexion larva.

horizontal distribution of larvae. *L. miodon* larvae were predominant near the shore (0.3 km offshore), while *S. tanganicae* larvae tended to be abundant over 3 km offshore (Fig. 5).

Occurrence along shores.—Abundant larvae and juveniles of *L. miodon* occurred along the shores of sandy beaches, but *S. tanganicae* were not captured in this habitat (Table 2). Rocky shores at Kalundu (A), Kabimba and Makobola seldom yielded either species (Table 2).

Table 1. Comparison of morphological proportions (%) of larval *Limnothrissa miodon* and *Stolothrissa tanganicae* from Lake Tanganyika

	L. miodon (*n* = 19; 6.0–8.7 mm SL)		*S. tanganicae* (*n* = 20; 5.4–8.7 mm SL)	
	Range	Mean±SD	Range	Mean±SD
Short/Long axis of eye diameter	78.1–90.1	81.6±4.4	54.6–66.7	62.0±4.3
Head length/SL	10.0–13.3	11.8±0.9	13.9–15.9	15.1±0.6
Snout length/Head length	8.9–13.2	11.1±1.3	14.3–27.8	19.4±3.3

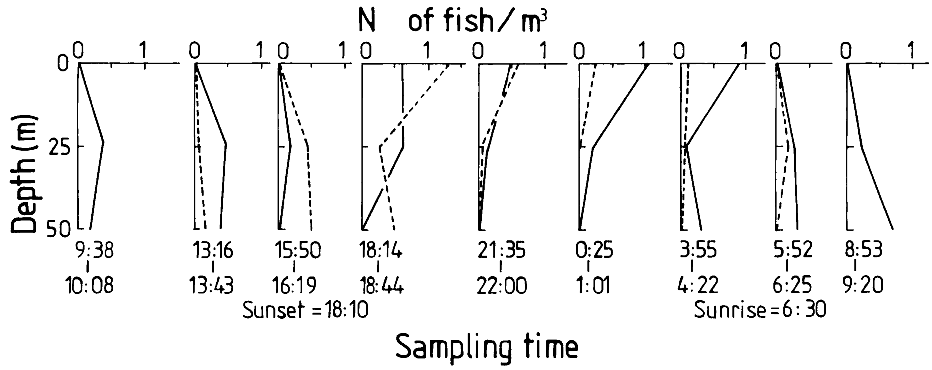

Fig. 4. Diel changes in vertical distribution of clupeid larvae at St. 7, off Uvira, on May 16–17, 1988. Solid and broken lines represent *Limnothrissa miodon* and *Stolothrissa tanganicae*, respectively.

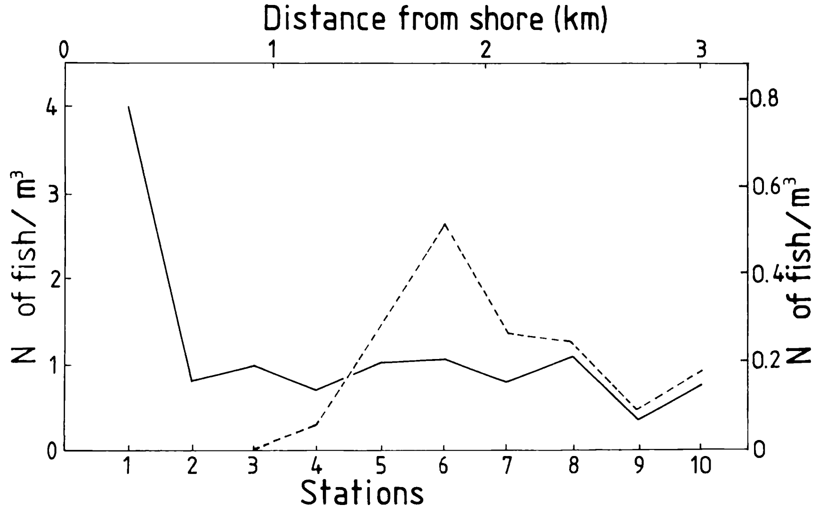

Fig. 5. Horizontal distribution of clupeid larvae in the surface layer off Uvira at 20:45–22:30 on July 9, 1988. Symbols are same as of Figure 4. The left and right scales show density of *Limnothrissa miodon* and *Stolothrissa tanganicae*, respectively.

Table 2. Number per haul of larvae and juveniles of *Limnothrissa miodon* and *Stolothrissa tanganicae* collected with a small seine net (1×4 m; 1 mm mesh) at nine shore sites on the northern part of Lake Tanganyika (see Fig. 1) on July 29 and 30, 1988

Sites	Shore form	*L. miodon*	*S. tanganicae*
Kavimvira	Beach	1.5	0
Kasenga	Beach	202.3	0
Mulongwe	Beach	2.0	0
Uvira	Beach	3.3	0
Kalimabenge	Beach	29.7	0
Kalundu (A)	Rocks	0.3	0
Kalundu (B)	Beach	116.7	0
Kabimba	Rocks	0	0
Makobola	Rocks	0	0

Discussion

The eyes of clupeid larvae from Lake Tanganyika are conspicuous for their shape, being elliptical rather than rounded, the latter being normal in marine clupeid larvae (Figs. 2A, B and 3). Fish larvae with elliptical eyes are generally found in groups inhabiting the mid-depths of oceans, for example, Anguilliformes, Salmoniformes and Myctophiformes (Okiyama, 1988). Weihs and Moser (1981) suggested that narrow eyes are a special adaptation for finding food deep waters characterized by low food density. The large volume of deep water in Lake Tanganyika, the second deepest lake in the world, may have influenced the evolution of this eye type. Eyes gradually became round with growth in *Limnothrissa miodon* (Fig. 2C–E), but remained elliptical until the postflexion period (over 14 mm SL) in *Stolothrissa tanganicae* (Fig. 3E). Significantly juvenile *L. miodon* were abundant, but *S. tanganicae* absent, along lake shore, indicating that immigration to the nearshore with growth occurs in *L. miodon*, but not in *S. tanganicae.* The difference in eye shape between the two species seemed to be related to the different horizontal distribution of the two species, i.e. eyes of *L. miodon*, which migrates to the nearshore, are elliptical for a short period only during larval development, whereas those of *S. tanganicae*, which continues to inhabit pelagic zones, remain elliptical.

The difference between day- and nighttime vertical distribution of both species larvae suggested diel vertical migration. Poll (1953) and Coulter (1961) also recognized this tendency in these larvae. Similar migration patterns have been observed in larvae of the herring *Clupea harengus*, anchovies *Engraulis japonica* and *E. mordax*, and yellowtail flounder *Limanda ferruginea* (Ida, 1972; Seliverstov, 1974; Hunter and Sanches, 1976; Smith et al., 1978). Diel vertical migrations are also undertaken by adult of Tanganyika clupeids, whose staple food (copepod larvae and adults) is concentrated near the surface in the evening (van Meel, 1954; Chapman, 1976). Thus a simple uniform diel vertical movement is undertaken by the pelagic zone fauna in Lake Tanganyika. Diel migration of the larval clupeids also seemed to be advantageous for feeding on copepod larvae having the same behavioral mode.

Coulter (1991a) noted the presence of larval and juvenile *L. miodon* in shallow waters, suggesting that the species utilized shallow waters as nurseries. Considering the scarcity of *L. miodon* along the rocky shores, their nurseries may be limited to sandy beaches (Table 2). In contrast, *S. tanganicae* larvae appeared to remain distributed in pelagic waters until the adult period.

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タンガニイカ湖産ニシン科魚類2種, *Limnothrissa miodon* および *Stolothrissa tanganicae* の初期生活史

Kalala K. Tshibangu・木下　泉

タンガニイカ湖北端に位置するウビラ（ザイール国）において，本湖固有種のニシン科魚類である *Limnothrissa miodon* と *Stolothrissa tanganicae* の初期生活史を 1988 年 5 月から 7 月にかけて調査した．両種の形態は海産ニシン科仔魚のものとほぼ一致し，消化管下面に沿う黒色素胞，頭長の体長比，吻長の頭長比および眼の形の違いによって，両種は明瞭に識別できた．特記すべきは両種にみられた楕円形の眼であるが，*L. miodon* では成長と共に眼は丸くなったのに対し，*S. tanganicae* では仔魚期を通じて楕円形が保たれた．両種仔魚とも，昼間は 50 m 以深に降下したが，夜間は表層近くに集積する傾向を示した．水平的には，*L. miodon* は沿岸に，*S. tanganicae* はより沖合に多い傾向にあった．*L. miodon* の成長した仔稚魚は砂浜の汀線付近に接岸して分布していたが，*S. tanganicae* は仔稚魚期を通して比較的沖合水域に分布していた．

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