

DISTRIBUTION, ABUNDANCE AND PARENTAL CARE OF THE GENUS *LAMPROLOGUS* (CICHLIDAE) IN LAKE TANGANYIKA¹⁾

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ABSTRACT Distribution, abundance and parental care of the genus *Lamprologus*—*L. brichardi*, *L. compressiceps*, *L. elongatus*, *L. furcifer*, *L. leleupi*, *L. lemairei*, *L. modestus*, *L. savoryi*, *L. toae* and *L. tretocephalus*—inhabiting the rocky shore in Lake Tanganyika, were observed underwater by SCUBA diving from July to November 1981. Each species shows a substratum preference as for feeding, spawning and parental care. They have breeding territory on a small limited area, and the distributions never overlap. The parental care is divided into three types in relation to their mating types: monogamy, polygyny and colonial breeding. The fry distribution according to their development under parental care is divided into two patterns of expansion: the horizontal and the vertical.

INTRODUCTION

The genus *Lamprologus* is the common and dominant fish in the littoral zone of Lake Tanganyika, and shows a remarkable endemism. All the species are substratum spawners and the parents protect their offspring in a small limited area. General distribution of the fish in the lake was reported by Brichard (1978), but their microdistribution and abundance in the littoral zone were not described fully in any papers. This study is to describe the microdistribution, abundance, and features of parental care of 10 species of the genus *Lamprologus* inhabiting the rocky shore. The investigation was carried out as a part of the joint research on ecology and limnology of Lake Tanganyika by Zairan and Japanese scientists.

STUDY AREAS AND METHODS

The present study was done in a quadrat settled on the rocky shore bottom for Luhanga, along the shore line which is located on the north-western coast of Lake Tanganyika, from July to November 1981. The quadrat of 20 × 20 m² covered the bottom from the shore line down to the depth of 12 m (Fig. 1). It was further divided into 100 small quadrats (2 × 2 m²), and they were numbered according to their positions. For example, the first number of the small quadrat 7–8 indicates the 7th on the longitudinal row from the southern side of the large quadrat, and the second number, the 8th on the transverse row from the shore.

The details of geographical features of the bottom are important for the analysis of the characteristics of the fish distribution. The bottom gently deepens from the shore line for about 8 m offshore (flat area), but becomes steeper further on (steep area). The depths at the points of 8 m and 20 m offshore are 3 m and 12 m respectively.

The underwater observation of the fish distribution, abundance and parental care was done by SCUBA diving. Individual numbers and body length of the fish measured underwater were recorded on a plastic section paper. Parental care was observed in the rocky areas both in and outside the quadrat.

Out of the 13 species of the genus *Lamprologus* inhabiting the shores, the following 10 species were intensively observed: *L. brichardi*, *L. compressiceps*, *L. elongatus*, *L. furcifer*, *L. leleupi*, *L. lemairei*, *L. modestus*, *L. savoryi*, *L. toae* and *L. tretocephalus*.

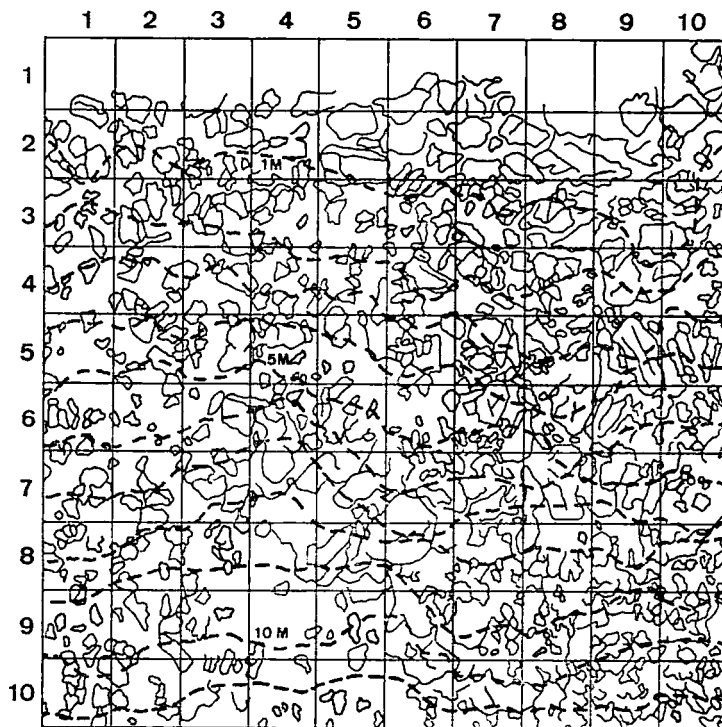


Fig. 1. Bathymetric map of quadrat. Fathom and substratum.

RESULTS

1. Eggs and Fry under Parental Care and Breeding Grounds

Spawning and breeding ground of each species in the rocky shore is shown schematically in Fig. 2. The grounds of *L. compressiceps* and *L. leleupi* were found neither in the quadrat nor anywhere around it. According to Brichard (1978), adults of both fishes become increasingly common from the depth of 10 m. This suggests that their spawning and breeding grounds are in a deeper area out of the quadrat.

Although *L. modestus* is not shown in Fig. 2, it is one of the most common and ubiquitous in the lake. There the fish are seen over both sand and rock, though they usually live in flat sandy areas. In order to spawn 100–300 eggs, a female, propped against a stone, burrows a deep tunnel. The tunnel has two entrances less than $4 \times 15 \text{ cm}^2$. The 36 nests observed ranged at the depth of 2 to 12 m, but most of them were found on sandy bottoms at the depth between 2 to 5 m. An average depth of the location of the 36 nests was 3.8 m. The fry are watched over by a female. Sometimes a male visits the nest. One dominant male usually visits several nests, each of which is protected by a female. The growing fry are able to expand their area horizontally protected by the female. The fry are distributed uniformly at regular intervals of 5–10 cm in the breeding ground of about 1 m^2 , because they are aggressive amongst each other.

L. brichardi is the most gregarious of all the species of *Lamprologus* in the lake. Mating occurs among the rubble rock and crevices (in the rock) at the depth of 3 to 12 m (Fig. 2). The

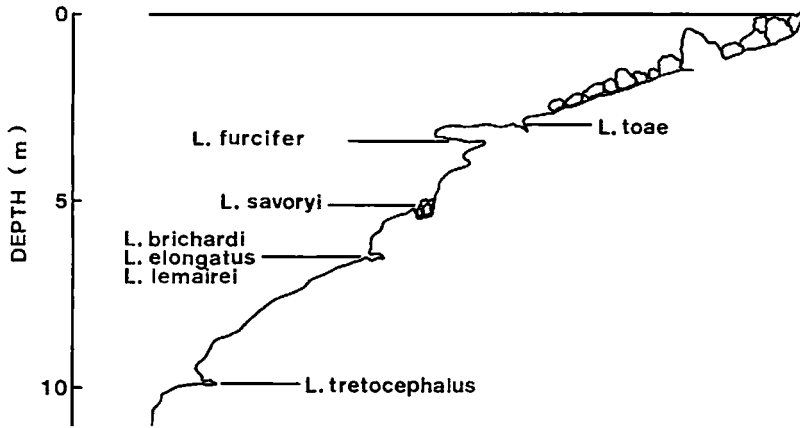


Fig. 2. Schematic spawning and breeding ground of each species in rocky shore.

fry are often kept under guard by several adults in a kind of communal nursery. Spawning behaviour and spawning place are the same as those in an aquarium already reported by Coeckelbergs (1974) and Lange (1974).

L. elongatus spawn 1000–1500 eggs usually in the crevices in the rock, but sometimes the eggs are laid between boulders at the depth of 3 to 10 m (Fig. 2). The eggs hatch out 3 days after spawning, and the larvae are carried to another small crevice in the mouth of their mother female. Both parents protect the eggs and the fry for about 12 weeks. Twenty-three nests in and out of the quadrat were observed. Their distribution ranged at the depth between 3 and 12 m (5.4 m in average): most of them concentrated at the depth of 3 to 5 m. The female usually stays close to the nest protecting the fry, while the male hovers 1 to 3 m above the nest, never getting far from the nest. Because of their large size, the parents protect their fry very successfully until they reach about 3 cm in body length and disperse. The growing fry, protected by the parents, gradually expand their area, 2–3 m above the bottom.

L. furcifer is a peculiar species with special habitats in the lake. It is never found anywhere other than against vertical or overhanging big rock slabs, usually in dark places. Under them the eggs are spawned on the slab, and 3–22 fry are protected only by a female as those of *L. modestus*. The 14 nests observed were distributed at the depth between 2 and 9 m (5.6 m in average), most of them concentrating at the depth of 3 to 5 m. The eggs and fry are protected by the female staying in the central part of the territorial area (less than 1 m²). Both the female and the fry cling to the slab most of the time. The fry are distributed uniformly at regular intervals of 5–10 cm in the area under protection of the female, because they also are very aggressive among each other. When the fry grow over 2.5 cm in body length, they disperse toward the fringe of the breeding ground. The parents produce new offspring right just after or at the same time their dispersion.

A female of *L. lemairei* lays eggs in a rock crevice which is situated on a steep slope. Two nests observed were located at the depth of 3 m and 8 m respectively. The postlarvae with 4 black vertical broad stripes on the trunk are taken care of by the parents. The female stays near the mouth of the nest, and the male watches over them from 1–2 m away.

L. savoryi spawns and breeds in dark recesses of rock rubble and boulders at the depth of 3–10 m. However the eggs were not observed in the study area. Several fry usually hide in the recesses and are watched over by both parents in breeding territory (about 2000 cm²) near the nest until they grow to about 3 cm in body length.

L. toae spawn 200–300 eggs and breed their fry on the slightly-sloping rock bottom at the depth of 2 to 6 m. The 34 nests observed were distributed at the depth between 2 and 5 m (3.2 m in average). Just after the eggs hatch, the prolarvae are transferred from the flat rock surface on which the eggs were laid to nearby small rock recess in the mouths of parents. Both parents strongly protect the fry in the breeding territory (less than 1 m²) never allowing any other fishes to invade until the fry become over 2 cm in body length. As green algae grow thickly on the rock, the breeding ground can be found easily. When the fry grow to about 2.5 cm in body length, they disperse around the nest.

L. tretocephalus spawn 200–300 eggs in the crevices of the rock or in a tunnel dug under the boulders 5 to 10 m below the surface of the water. Most of the 22 nests concentrated at the depth of 8 to 10 m (8 m in average). The eggs and the fry are guarded by both parents. The female stays close to the mouth of the tunnel, and the male hovers about 50 cm above the nest. When guarding the fry, the parents aggressively attack all other fishes including ones of the same species. The fry were protected in a remarkably restricted area (about 1 m²) for 20 weeks until they become over 3 cm in body length.

2. Distribution and Abundance

Six underwater observations of distribution and abundance were carried out in the quadrat from August to October 1981. The counted numbers of each species in the quadrat is shown in Table 1.

The stages of each species were divided as follows according to their breeding behaviour and morphological observations: fry with a body length of less than 3 cm under parental care; subadult with a body length between fry and adult; and adult more than 5 cm in *L. toae* and

Table 1. Abundance of each species of the genus *Lamprologus* per 400 m². Figures in the parentheses show the numbers of breeding adults.

Date	<i>L. fuscifer</i>				<i>L. toae</i>			
	Fry	Subadult	Adult	Total	Fry	Subadult	Adult	Total
Aug. 4	46	0	12 (6)	58	—	1	11 (6)	12
18	28	5	11 (2)	44	135	6	8 (8)	149
Sep. 8	41	8	13 (6)	62	33	1	10 (8)	44
Oct. 1	39	2	11 (5)	52	131	2	12 (8)	145
14	49	9	14 (6)	12	150	2	11 (8)	163
29	45	21	12 (4)	78	76	2	10 (6)	88

Date	<i>L. elongatus</i>			<i>L. modestus</i>			<i>L. tretocephalus</i>		
	Subadult	Adult	Total	Subadult	Adult	Total	Subadult	Adult	Total
Aug. 4	4	15 (4)	19	0	5 (1)	5	2	9 (6)	11
18	6	11 (6)	17	5	8 (0)	13	2	14 (10)	16
Sep. 8	18	5 (5)	23	9	8 (1)	17	8	8 (5)	16
Oct. 1	21	8 (6)	29	6	5 (0)	11	6	16 (3)	22
14	17	5 (4)	22	13	11 (0)	24	8	11 (5)	20
29	60	7 (2)	67	15	12 (1)	27	17	9 (2)	26

Date	<i>L. compressiceps</i>	<i>L. leleupi</i>	<i>L. lemairei</i>	<i>L. savoryi</i>
Aug. 4	10	16	6	21
18	15	43	1	49
Sep. 8	12	42	7	80
Oct. 1	12	34	5	50
Oct. 1	12	34	5	50
14	16	37	10	70
29	10	55	5	91

L. modestus, more than 6 cm in *L. tretocephalus*, more than 7 cm in *L. furcifer* and more than 8 cm in *L. elongatus*.

As *L. brichardi* was very abundant compared with other species, it was impossible to estimate the exact number in every observation period. According to the observation on the 1st of October the number of adults was roughly estimated at more than 2000 in the quadrat. It is the most abundant of all the species.

In order to estimate the number, *L. furcifer* and *L. toae* were divided into three stages, namely, fry, subadult, and adult; *L. elongatus*, *L. modestus* and *L. tretocephalus* two stages, subadult and adult. As for *L. elongatus*, *L. modestus*, and *L. tretocephalus*, Table 1 does not show the numbers of their fry, for they were too abundant to count exactly (under water) during the short period. As for *L. compressiceps*, *L. leleupi*, *L. lemairei* and *L. savoryi*, all the individuals with a length of more than 3 cm were counted. No distinction of developmental stages was made because the individuals of less than 3 cm were rarely found. The counted individuals seemed to be either subadults or adults.

The number of fry and adults were stable during the observations, but the number of subadults progressively increased, except in *L. toae*. It is likely that the increment depended on the recruitment of new subadults because their spawning was prosperous during the early period of underwater observation. Their spawning gradually declined thereafter.

The distribution of each species in the quadrat is shown in Fig. 3. It should be noted that virtually no individuals of the all species of *Lamprologus* live in a shallow area at the depth of less than 1 m, which is occupied mostly by algal feeders. The clear boundary of the distributions exists at the depth of 1 m at the transverse row between transverse nos. 2 and 3.

L. brichardi, being the most dominant species in the quadrat, inhabited a flat area at the depth of more than 3 m, and had a higher density at the depth from 8 to 10 m. This fish likes rubbled bottoms better than rocky ones in the steep area.

L. compressiceps is distributed in the rubbled area more than 1 m below the water surface and keeps away from the rocky area. This fish, however, extensively migrates in the quadrat without staying in a special microhabitat.

L. elongatus prefers as spawning place the rocky bottom more than 3 m below the water surface in the steep area. The main breeding ground and adult habitat are at the depth of 4 to 9 m. Subadults with a body length of more than 4 cm lives mainly in the flat area at the depth of 1 to 3 m. The distribution of adults is markedly limited to the substratum.

As *L. furcifer* has a preference for vertical or overhanging big rock slabs and the microhabitat is limited in the rocky area. The distribution becomes contiguous even in rocky area. In the quadrat, the big rock slabs range at the depth of 2 to 8 m. Therefore their distribution is concentrated in this area. The breeding grounds were observed at the small quadrats 6-4, 9-4, 4-5, 9-5, 9-6, 8-7, 6-8, and 10-8, but the breeding and non-breeding adults were in a high density at transverse row nos 4 (at the depth of 3 m) and 5 (4 m). The subadults gradually disperse around the breeding ground, so the high density of the subadults is observed between transverse row nos 4 and 7.

L. leleupi shows the peak density at the transverse row no 4. Main habitat of this fish ranges between 1 and 7 m below the water surface, except on the sandy bottom (the small quadrats 3-8, 4-8, 4-9, and 5-9).

L. lemairei has low density. There were only subadults in the quadrat. The characteristic of the distribution is not clear, but the subadults seem to prefer the rubbled bottoms. During the observations around the quadrat the adults chose the crevices on the rock wall as breeding ground.

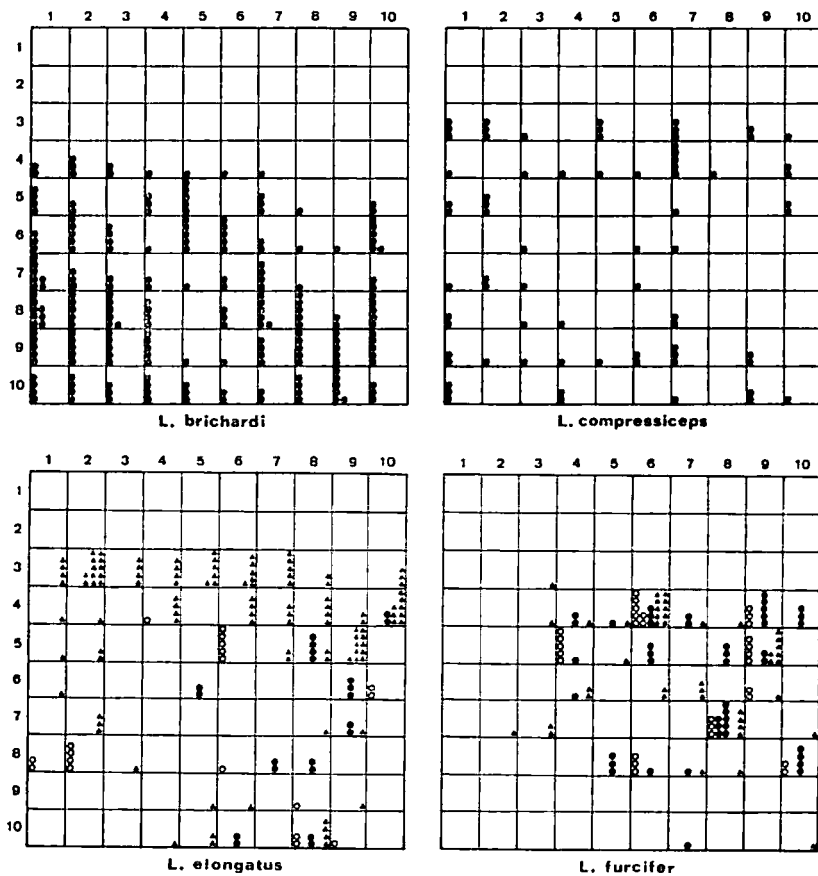
L. modestus prefer the sandy bottom to rocky areas, especially for breeding. In the quad-

rat, the breeding was found in the small quadrats 2-6, 4-7, and 4-8 on sandy bottom. Non-breeding adults hover not only above the sandy bottom but also above the rocky bottom. Subadults with a body length of more than 3 cm, gradually disperse around the breeding ground. The adults and subadults were abundant between the transverse row no 5 (4 m in depth) and 8 (8 m).

L. savoryi of all the stages live among the rock rubble. The distribution is contiguous in the quadrat as *L. furcifer* concentrates in the place where the rock rubble are abundant, e.g. 2-4, 3-4, 5-4, 1-6, 8-6, 3-8, 6-8, 10-8, 5-10, and 6-10.

L. toae is a rock-dweller living in the flat area. The adults and subadults were observed on the flat rock substratum between the transverse row no 3 (at the depth of 2 m) and 6 (5 m). The peak density was at the transverse row no 4, which is the boundary between the flat and the steep areas. The breeding was often found around the boundary. The subadults with a body length of more than 3 cm disperse around the breeding ground, but they do not go away.

L. tretocephalus is also a rock dweller living in the steep slope at the depth of more than 3 m. Breeding grounds were observed on a rocky area at the depth between 8 and 10 m. The adults showed the highest density on the slope at the depth of more than 8 m, while the subadults preferred the shallow area. The subadults, therefore, might have dispersed toward the shallow area from the breeding ground after becoming independent of parental care.



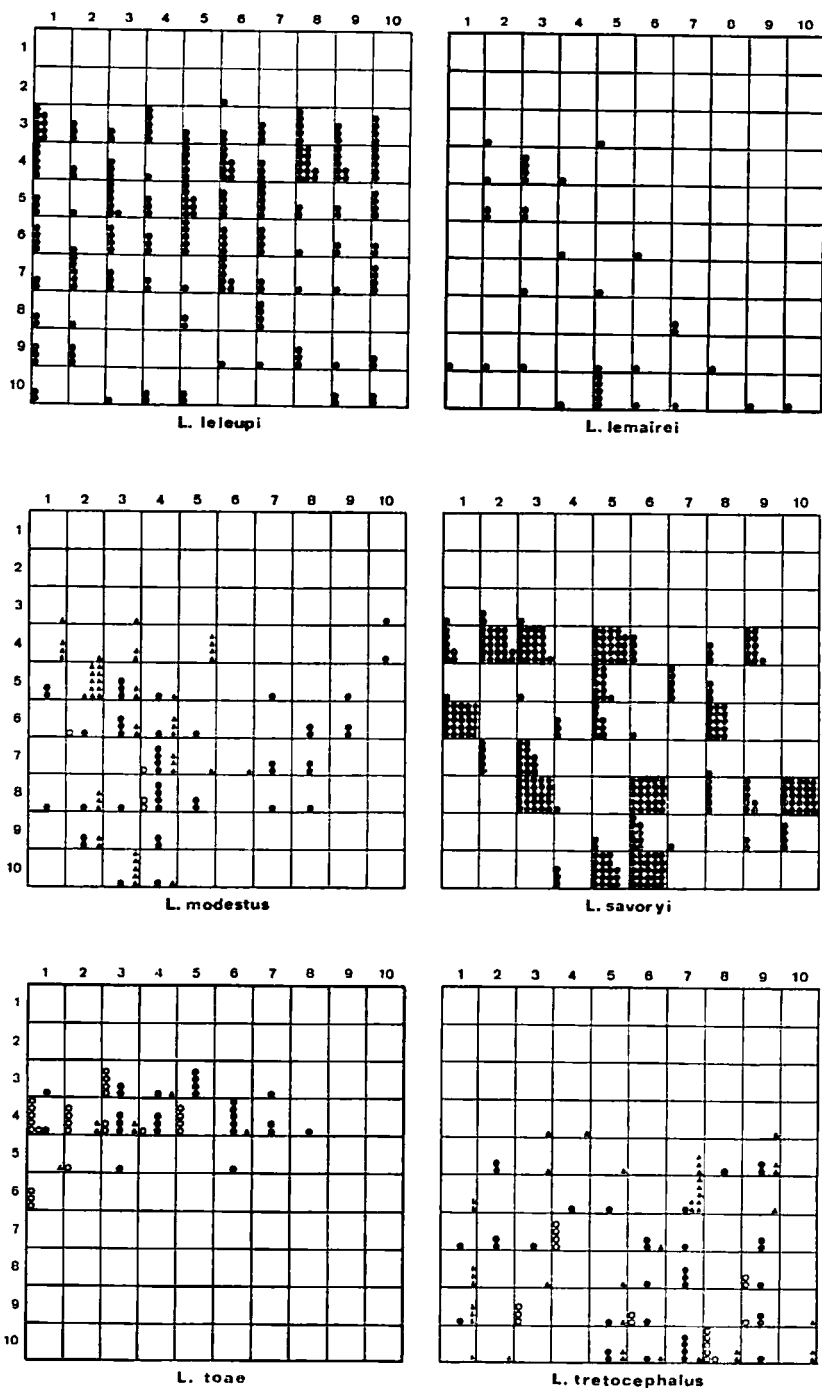


Fig. 3. Distributions of subadults (triangles), adults (solid circles) and breeding adults (open circles) in a quadrat settled on the rocky shore. Each symbol shows one individual, but in *L. brichardi* one symbol it equals 10 individuals, and an open circle shows a pair (female and male) except in *L. furcifer* and *L. modestus*.

CONCLUSION AND DISCUSSION

The habitat segregation is clearly found among the fishes in the rocky shore of Lake Tanganyika.

First, the segregation is observed between the algal feeding fishes and the carnivorous fishes. The carnivorous genus *Lamprologus* was not found in the area less than 1 m below the water surface, in which many species of algal feeder are predominate. The area is occupied by the following algal feeding fishes: *Eretmodes cyanostictus*, *Petrochromis polyodon*, *Pseudosimochromis curvifrons*, *Simochromis diorama*, *Tanganicodus irsacae*, *Tropheus moorei*, etc. (Takamura, 1982). According to Kawanabe (1981) and Takamura (1982), *P. polyodon* and *T. moorei* are dominant, protecting their feeding territory in the shallow area. The density of algal feeding fishes is very high in this area. Therefore all the species of the genus *Lamprologus* are unable to get in the area.

Secondly, each species of the genus *Lamprologus* shows a habitat preference for the rocky shore. There is a little overlap in the distribution of each species in the small quadrat mentioned above. It is said that the ecological requirements of each species are distinctly different. Especially their spawning and breeding sites never overlap.

All the species have a breeding territory on the substratum and protect their fry for about three months. Various modes of parental care are found in the genus *Lamprologus*. The parental care is divided into three types in relation to their mating types as follows:

1. By both parents (monogamy)—*L. elongatus*, *L. lemairei*, *L. savoryi*, *L. toae*, and *L. tretocephalus*
2. By only one female: male patrols several nests protected by a female (polygyny)—*L. fuscifer* and *L. modestus*
3. By several adults (colovial breeding)—*L. brichardi*

Such types as polyandry and the parental care by only one male were not found in the genus.

The distribution of the fry under parental care is different according to each species. The distribution can be divided into two patterns: the horizontal and the three dimensional expansions of the fry distributions according to their development. All the species except *L. elongatus* belong to the former and *L. elongatus* belongs to the latter. All the fry, however, line down on the bottom around the spawning and breeding around, when they are in danger of an attack of enemies.

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