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Biparental Mouthbrooding and Guarding in a Tanganyikan Cichlid *Haplotaxodon microlepis*

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Abstract Differences between parental roles of males and females in *Haplotaxodon microlepis* (Cichlidae) were investigated in Lake Tanganyika, and the early ontogeny and growth of the species were studied in the aquarium. Eggs were mouthbrooded by the female, and it is suggested that small larvae (<9 mm in total length) were also mouthbrooded by females though such samples were not collected. Above this size the larvae began to feed, and parents jointly performed mouthbrooding and guarding until the young grew to 25–30 mm, nearly 2 months after spawning. Males and females mouthbrooded to the same extent, but when a part of the brood was released, females mainly guarded the released brood and males took the mouthbrooding role. Differences in parental-care patterns between *H. microlepis* and other monogamous mouthbrooding cichlids are discussed.

Cichlid fishes exhibit either mouthbrooding or substrate-brooding (guarding) of eggs and fry, but there are also some species of intermediate types (Fryer and Iles, 1972; Keenleyside, 1979; Kuwamura, 1986). Among the approximately 170 species of cichlids in Lake Tanganyika (Poll, 1986), 6 species are known to perform prolonged biparental guarding after mouthbrooding: *Asprotilapia leptura*, *Haplotaxodon microlepis*, *Perissodus microlepis*, *Plecodus straeleni*, *Xenotilapia flavipinnis* and *X. longispinis* (Yanagisawa and Nshombo, 1983; Yanagisawa, 1985, 1986; Kuwamura, 1986). Differences in male-female parental roles have been studied in detail for *P. microlepis* (Yanagisawa and Nshombo, 1983; Yanagisawa, 1985) and *X. flavipinnis* (Yanagisawa, 1986), but little is known for other species.

In this paper, I describe the early ontogeny, growth and male-female parental roles of *H. microlepis*, and discuss differences in parental-care pattern between it and other monogamous mouthbrooders.

Study area, materials and methods

During the period from July to September of 1986, underwater observations and collections were conducted using SCUBA at Mbemba (3°36′S, 29°10′E), Zaire, northwest coast of Lake Tanganyika. A census line in an offshore rocky area was extended 130 m, parallel to the shore line, at the depth of 10 m. A large aggregation (>100 fish) of nonbrooding *H. microlepis* was found several meters above the bottom at a site on the line. Brooding fish occurred usually in pairs, sometimes singly but rarely in aggregation, at depths of 3–15 m in and around the rocky area.

In the vicinities of the census line, 14 brooding fish were collected by a screen net. They were tagged, measured in standard body length underwater, and released. A small part of the brood was sampled from each parent, and the total length of each brood was measured later in the laboratory. Tagged fish were censused at intervals of 2–5 days for more than a month. Their locations and whether they were mouthbrooding, guarding or nonbrooding were recorded along with the number and approximate total length of the fry released out of the parent's mouth.

For some brooding pairs, whether tagged or not, 10–20 min observations were occasionally made (N=20). The following data were recorded separately for the male and female: 1) range of movement, 2) whether or not they were mouthbrooding, 3) number and approximate total length of the fry if they were released, 4) number of attacks against conspecifics and other species, and 5) feeding behavior.

Twenty-three broods were collected with their parent(s), just after the above observations for untagged pairs or at the end of the study period for tagged pairs. During the collection, a part of the brood was often lost due to their fleeing or predation by other fishes. For parents, standard

length, body weight and gonad weight were measured, and sex and stomach contents were examined. For broods, total length was measured, total number counted, and gut contents examined.

Fifty eggs, which were collected from a mouth of a parent, were put into a tank of 1 liter and incubated with aeration for 40 days. The water was changed every day. After hatching, fry were given dry commercial food (Tetramin powder) once or twice per day. Two to four individuals were sampled every day for the first 2 weeks and every 2 to 9 days afterward. Their total length was measured and the developmental stages and gut contents were observed microscopically. Water temperature in the aquarium ranged from 23 to 26°C, while that at the depth of 10 m along the census line was 25–26°C.

Results

Early ontogeny and growth. Neither spawning nor courtship of *H. microlepis* was seen during the observation hours (0930–1500). However, eggs collected from the mouths of two parents at 1123 and 1410 were in the early cleavage phase, and it was assumed that they were spawned in the early morning of the days of collection. A part of the eggs of the latter was reared in a tank without the parent, and the early ontogeny and growth were recorded (Figs. 1, 2).

The eggs were elliptical, 2.4 mm long and 1.8 mm in diameter. On the 2nd day the embryo appeared, extending nearly half of the circumference of the yolk. In the early morning of the 4th day, larvae of 4.6–4.8 mm TL (total length) hatched (Fig. 2A). These larvae had a large yolk sac and lay on their lateral side on the bottom. The optic cups with lens and the auditory vesicles with two pairs of otoliths were clearly observed. The notochord slightly flexed upward. The mouth was not open. Melanophores were present only on the surface of the yolk sac. The larvae had three pairs of head glands, which function as adhesive organs in substrate-brooding cichlids (Fryer and Iles, 1972; Peters and Berns, 1982).

On the next day of hatching, pectoral fin buds appeared. The mouth opened 2 days after hatching (6.5–6.7 mm TL; Fig. 2B). Melanophores had appeared on the head and the retina of the eye, and also a few in the trunk. Five days

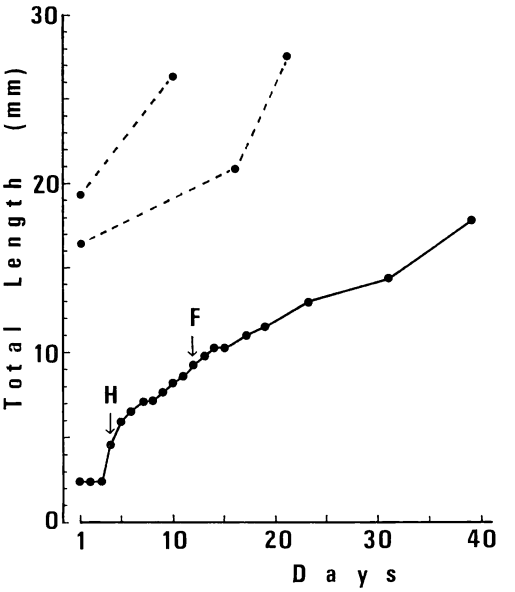

Fig. 1. Growth of the young of *Haplotaxodon microlepis* in the aquarium (solid line) and in nature (broken lines). H: Hatching occurred. F: Feeding was first observed.

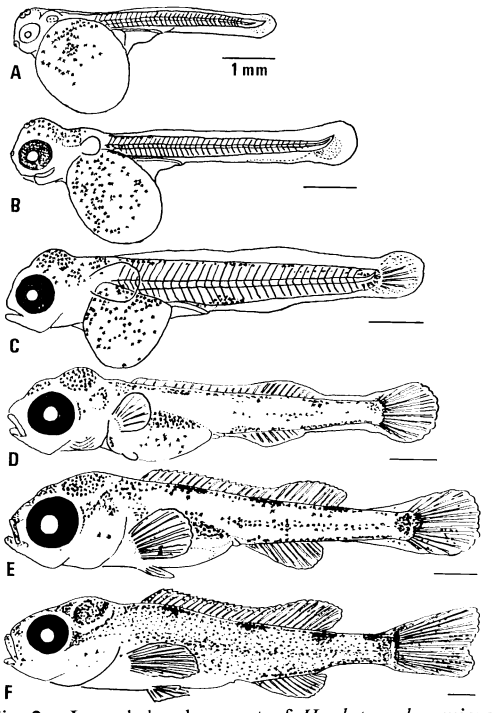

Fig. 2. Larval development of *Haplotaxodon microlepis* in the aquarium. A, newly hatched larva, 4.8 mm in total length; B, 2 days after hatching, 6.5 mm; C, 5 days, 7.7 mm; D, 8 days, 9.2 mm; E, 13 days, 10.9 mm; F, 35 days, 17.9 mm.

after hatching (7.7–7.8 mm TL; Fig. 2C), caudal fin rays partly differentiated and the larvae began to swim occasionally near the surface. The part of the fin-fold comprising the future dorsal and anal fins somewhat bulged. The retina of the eye became darker and melanophores also increased on the head and along the dorsal and ventral surface of the trunk.

Eight days after hatching (9.2–9.5 mm TL; Fig. 2D), the pelvic fin buds appeared, and the pectoral, dorsal, anal and caudal fin rays were partly differentiated. Melanophores appeared also on the lateral side of the trunk. The yolk sac became small, both jaws had well developed, and the larvae began to feed on Tetramin. All the larvae were actively swimming near the surface in the daytime and resting on the bottom during the night.

All fins developed and the yolk was almost absorbed 13 days after hatching (10.9–11.1 mm TL; Fig. 2E). The juvenile attained 17.6–18.2 mm TL 35 days after hatching (Fig. 2F). Melanophores considerably increased both on the body and fins, and four dark bands were apparent along the dorsal side. The growth rate after hatching was 0.38 mm/day.

Growth of juveniles was recorded for two broods in nature (Fig. 1). They grew from 16.4 to 27.6 mm TL (mean, N=10) in 20 days (growth rate=0.56 mm/day), and from 19.4 to 26.4 mm TL in 9 days (0.77 mm/day). As the parental care continued until the juvenile grew to 25–30 mm TL (see Table 1 and below), the duration of parental care is estimated to be 50–60 days.

Methods of parental care. Brood size was approximately 100–200, though only partial broods were collected for most of the 23 broods (Table 1). Eggs were mouthbrooded by the female in one of the two cases examined, while in the other case the sex of the parent, which was found alone, was not determined since it was tagged and released

Table 1. Total length and number of young mouthbrooded or guarded in each brood of *Haplotaxodon microlepis*. ?: The parent was not found. >: Only a part of the brood was counted. +: Present but not counted. a–e: Broods mixed with 11 (20.7–21.7 mmTL, a), 3 (21.3–21.7 mm, b), 1 (20.5 mm, c) and 1 (21.4 mm, d) conspecific juveniles, or with an aggregation of juveniles of *Perissodus microlepis* (e).

Total length (mm)	Mouthbrooded		Released and guarded	Total number
	by ♀	by ♂		
2.4 (egg)	99	0	0	99
9.3– 9.7	0	>65	0	>65
9.7–10.1	>40	?	0	>40
9.9–10.3	0	>4	0	>4
14.4–15.1	+	50	0	>50
15.8–16.2	120[a]	81[b]	0	201
16.0–17.5	25	+	0	>25
16.6–18.5	0	100	0	100
17.2–19.3	88	?	0	>88
17.4–18.6	16[c]	?	0	>16
17.8–18.5	+	102	0	>102
18.0–19.0	55	?	0	>55
18.6–20.0	?	>53	0	>53
18.8–20.0	>17	+	0	>17
19.0–20.1	32	?	0	>32
20.4–21.0	0	+	25	>25
20.4–21.7	>40	0	0	>40
20.8–21.4	19	?	0	>19
23.0–24.8	51	77	0	128
24.1–25.6	>24	11	+	>35
25.3–27.0	0	>7	+	>7
25.7–26.8	32	20[d]	0	52
25.6–29.6	0	0	>20[e]	>20

but not found again. Larvae smaller than 9.3 mm TL were not collected. After this size, the female and/or male parent(s) exhibited mouthbrooding until the fry reached 25–30 mm TL. Fry larger than 9–10 mm TL were sometimes found outside the parents' mouths, being guarded by the parents. This occurred more often as the fry grew larger (Table 1). The released fry formed an aggregation a few meters above the bottom, feeding on plankton. The smallest larvae (9.3–9.7 mm TL) collected had empty guts; larger ones, however contained copepods in their stomachs. Larvae apparently begin to feed after attaining 9–10 mm TL, which is consistent with the aquarium observation.

Three broods in the parent mouths were found to contain several conspecific juveniles of obviously different body size (Table 1). Aggregations of juveniles larger than 25–30 mm TL were independent of parents and often mixed with aggregations of juvenile *Perissodus microlepis*, all being guarded by the latter's parents. The methods of intra- and interspecific mixing of broods were not observed in the present study, but it may be assumed that parents bring their young in mouths to put under the care of another brooding parent, as was confirmed in *P. microlepis* (Yanagisawa, 1985).

Of the 14 brooding fish tagged, 9 were observed again. Five were found only at the sites at which they were tagged. The other four were found only once, about a month after tagging, 30–40 m away from the original sites. At the time of tagging, the young brooded by the first five fish were 16–22 mm TL, while those of the latter four were smaller, 9–15 mm TL. The broods of undiscovered tagged fish (N=5) were also small: eggs or 9–15 mm TL. This suggests that brooding pairs are mobile when their young are small, and afterwards become site-attached. Untagged mouthbrooding fish were sometimes found in mid-water 3–10 m above the bottom, either in pairs or singly. When they were tracked, they often fled for more than 30 m and were soon lost. Probably these were brooding smaller young, and this might be the reason why very small larvae (<9 mm TL) were not collected in the present study.

Differentiation of male-female parental roles. Both parents were usually found together while

Table 2. Difference in behavior of the male and female in brooding pairs of *Haplotaxodon microlepis*. ♯ The time when the fish was found within 5 m from the possible fry-releasing site. * These species were observed to prey upon the fry of *H. microlepis* during the collection of their parents. a–d: Significant differences were found between the left and right of the symbols. a, $P<0.01$ and b, $P<0.05$, Wilcoxon's signed rank test; c, $P=0.016$, Fisher's exact probability test; d, $P<0.05$, Mann-Whitney's U test.

	Fry not released (160 min, N=13)		Fry (partly) released (127 min, N=7)	
	Female	Male	Female	Male
Present time♯: min (%)	133 (83.1) a	94 (58.8)	124 (97.6) b	62 (48.8)
Mouthbrooding time: min (%)	112 (84.2)	80 (85.1)	29 (23.4) c	62 (100.0)
No. of attacks (per 10 min)	26 (2.0)	9 (1.0)	36 (2.9) d	1 (0.2)
Attacked species				
*Haplotaxodon microlepis**	4	2	10	1
*Perissodus microlepis**	6	2	14	0
*Lepidiolamprologus elongatus**	3	1	2	0
*L. attenuatus**	1	0	1	0
L. cunningtoni	1	0	0	0
Cyathopharynx furcifer	1	0	0	0
Lamprologus callipterus	1	0	0	0
Neolamprologus brichardi	1	0	0	0
Ophthalmotilapia nasutus	0	0	1	0
Paracyprichromis nigripinnis	0	0	1	0
Petrochromis famula	1	0	0	0
Plecodus straeleni	0	1	0	0
Unidentified spp.	7	3	7	0

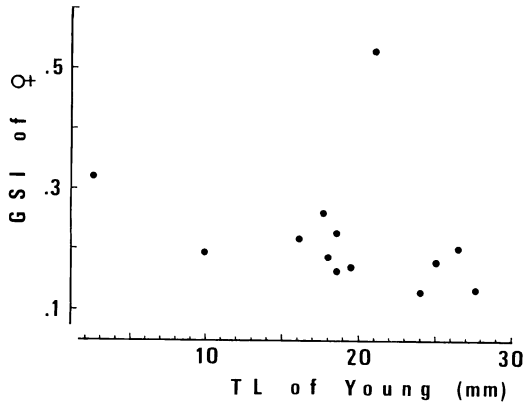

Fig. 3. Gonosomatic index (GSI) of brooding females in relation to the total length (TL) of their offspring. ($y=0.303-0.004x$; $r=-0.264$, $N=13$, $P>0.2$).

brooding (e.g. 70% of the 23 broods; Table 1). In each pair the male was always larger than the female: the average standard length (±SE and range) was 168.5±5.0 mm (140–186, N=11) for brooding males and 150.3±4.3 mm (115–171, N=11) for females. Body color did not differ between sexes, but mouthbrooding parents often had a black head and pale body, while non-mouthbrooding fish had a black longitudinal line on a pale body.

Behaviors of parents, whose young were larger than 14 mm TL, were observed for 10–20 min (N=20), and are summarized in Table 2. When a part of a brood was released, the female was usually situated near the brood, and the male was a few meters away, often moving around more than 5 m. Females were more site-attached than males even when no fry were released. Mouthbrooding time did not differ between males and females when no fry were released, but when part of the brood was released, males more frequently mouthbrooded than females (Table 2). Both males and females, whether mouthbrooding or not, attacked various kinds of cichlid fishes at 1–2 m from either the released brood or, when no fry were released, the possible releasing site. When some fry were released, females exhibited attacks more frequently than males. *H. microlepis*, *P. microlepis* and *Lepidiolamprologus elongatus* were more often attacked than other species; these were potential predators on the released fry (Table 2).

Parents were not observed feeding near the (possible) fry-releasing sites. However, some brooding fish (2/8 females and 1/6 males) collected in the morning had full stomachs. Diets consisted of shrimp and ephemerae. All specimens (8 brooding and 3 nonbrooding fish) collected in the afternoon had empty stomachs. In spite of feeding more or less during the brooding period, the gonosomatic index (GSI=100×(Gonad weight)/(Body weight)) of females did not increase during the period (Fig. 3). One specimen showed relatively high value of GSI (0.535), but the oocytes in the ovary were less than 2 mm in diameter and were immature.

Discussion

The Tanganyikan cichlid *Haplotaxodon microlepis* exhibited biparental mouthbrooding and guarding. Joint mouthbrooding by the male and female has not been reported in any other cichlids of the lake (Kuwamura, 1986), although in some African cichlids, such as *Sarotherodon* spp., biparental mouthbrooding occurs from the egg stage (Trewavas, 1983) and in some American

Table 3. Some comparisons of the early ontogeny and parental care between *Haplotaxodon microlepis* (present study) and *Perissodus microlepis* (Yanagisawa and Nshombo, 1983).

	H. microlepis	*P. microlepis*
Female size	115–171 mm SL	72–86 mm SL
Clutch size	100–200	171
Eggs	2.4×1.8 mm	1.7×1.2 mm
↕ Mouthbrooding	by ♀ (?)	by ♀
Newly released larvae	9–10 mm TL	6.5 mm TL
(age after spawning)	(11 days)	(9–11 days)
↕ Mouthbrooding	by ♀ & ♂ (mainly ♂)	rarely by ♀ or ♂
↕ Guarding	by ♀ & ♂ (mainly ♀)	by ♀ & ♂ (mainly ♀)
Largest juveniles cared	25–30 mm TL	25–31 mm SL
(age after spawning)	(50–60 days)	(45–60 days)

cichlids from the larval stage after guarding the eggs (Reid and Atz, 1958; Timms and Keenleyside, 1975; Keenleyside, 1979). It was not determined in the present study which sex mouthbroods small larvae (<9 mm TL) as such specimens were not collected, but females seem to play the role because 1) eggs were mouthbrooded by the female, and 2) the larvae might not be released from the parent's mouth until they grow larger than 9 mm TL since they began to feed only after this size.

Morphological studies have suggested that *Haplotaxodon* is closely related to *Perissodus*, both belonging to the Tribe Perissodini (Poll, 1986). The parental-care pattern and early ontogeny of *H. microlepis* also had many similarities to those of *P. microlepis* (Yanagisawa and Nshombo, 1983; Table 3). The clutch size is almost equal, though the female body size of *H. microlepis* is considerably larger than that of *P. microlepis* and egg size is also larger in the former. Small larvae of both species have head glands, which are well developed in substrate-brooding cichlids rather than in mouthbrooders (Fryer and Iles, 1972; Peters and Berns, 1982). The period of maternal mouthbrooding of eggs and small larvae is about 10 days in both species. The total length of the newly released larvae is much larger in *H. microlepis* (>9 mm) than in *P. microlepis* (6.5 mm), but the developmental stages of both are almost equal (compare Fig. 2D of the present paper and Fig. 2B of Mihigo, 1986). Total periods of parental care are nearly two months in both species, though the maximum size of the juvenile under care is somewhat smaller in *H. microlepis* (Table 3). Intra- and interspecific mixing of broods also occurs in both species (Yanagisawa, 1985; Yanagisawa and Nshombo, pers. comm.).

During the latter period of parental care, *P. microlepis* performs biparental guarding, the female playing a leading role (Yanagisawa and Nshombo, 1983), and mouthbrooding takes place on rare occasions (Yanagisawa, 1985). The female of *H. microlepis* also plays a leading role in guarding, but both parents frequently exhibit mouthbrooding until the juveniles become independent. Males of *P. microlepis* sometimes desert their mates and broods (Yanagisawa and Nshombo, 1983), but such desertion was not seen in *H. microlepis* during the present study. Thus, males of *H. microlepis* contribute in parental care, at least by mouthbrooding, more than those of *P. microlepis*.

In another monogamous mouthbrooder of Lake Tanganyika, *Xenotilapia flavipinnis*, males contribute much more in parental care (Yanagisawa, 1986). That is, though females mouthbrood eggs and small larvae, males later take over the mouthbrooding role, and then juveniles are guarded by both parents, mainly by the male. During the guarding period, females are engaged more frequently in feeding and consequently are likely to increase their reproductive rates. Because the species is serially monogamous, the active participation of the male in parental care is also advantageous to him, as it increases his reproductive success (Yanagisawa, 1986). Increase of gonosomatic index of females, as occurs in *X. flavipinnis* (Yanagisawa, 1986), however, was not observed during the brooding period of *H. microlepis*. This may be due to a seasonal change of breeding activity in *H. microlepis* (Nshombo, pers. comm.) as the present data were collected only during August and September. However, it is more likely that it is related to the difference between the two species in the degree of the male participation in parental care. At present, it is not known whether *H. microlepis* are serially monogamous, and further studies on the continuity of pair bond are needed to understand the differentiation of male-female parental roles in this species.

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タンガニイカ湖のカワスズメ *Haplotaxodon microlepis* における両親による子の見張りと口内保育

桑村哲生

Haplotaxodon microlepis の子の保護における雌雄の役割分担を潜水調査し，仔稚魚の発育を水槽飼育により明らかにした．卵は雌が口内保育していた．全長 9 mm 以下の仔魚は採集されなかったが，これらも雌親が口内保育していると推察された．これより大きな仔魚は摂餌を開始し，以後，全長 25–30 mm (産卵の約 2 ケ月後) まで両親により見張りまたは口内保育されていた．口から放出された仔稚魚の群れは主に雌によって保護され，一方雄は口内保育をより頻繁に行った．両親による見張りと口内保育を行う他のカワスズメ科魚類と比較して，雌雄の役割分担について考察した．

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