Environmental Biology of Fishes **39**: 59–72, 1994.
© 1994 *Kluwer Academic Publishers. Printed in the Netherlands.*

Foraging behavior of the scale-eater *Plecodus straeleni* (Cichlidae, Teleostei) in Lake Tanganyika, Africa

Muderhwa Nshombo
Centre de Recherche en Sciences Naturelles/Uvira du Zaire, B.P. 254, Bujumbura, Burundi
Address for correspondence: c/o Yasunobo Yanagisawa, Department of Biology, Ehime University, 2–5 Bunkyo-cho, Matsuyama, 790 Japan

Received 10.5.1991 Accepted 25.5.1993

Key words: Lepidophagy, Hunting technique, Time budgets, Prey preference, Variable behavior, Sexual dichromatism, Cichlid fish

Synopsis

Sixty-nine individuals of *Plecodus straeleni* were followed for 1 h each in the field with the aid of SCUBA, and time budgets, hunting techniques and prey selection were investigated in relation to sex and body size. The time of cruising in midwater and on the substrate amounted to 3/4 of the total time. The rest of the time was mainly spent on five hunting techniques named pursuing, waiting, mingling, aiming and stealthy approaching. Pursuing (following a flying prey at high speed) was frequently used by adults, especially males, mainly to attack the spiny eel *Afromastacembelus moorii*. Waiting (keeping motionless on the substrate, waiting for a known prey) was used by some adult females when they tried to steal eggs of the mouthbrooder *Cyathopharynx furcifer* on the bower and by adult males when they targeted an eel having hidden under a rock. Mingling (mixing in a school of prey to attack school members) was a favorite tactic of subadults to attack plankton-feeders. Aiming (directing the head to a target fish for a moment) commonly occurred when both adults and subadults attacked solitary fishes. In stealthy approaching, the scale-eater approached an unwary prey from behind or sideway. Attacks by these hunting techniques amounted to 97% of the total attacks, which were made on 38 cichlid species and 7 non-cichlid species. Hunting techniques and prey preference varied not only with sex and size but even among consexuals of similar sizes. A number of individuals successively attacked only one or a few prey species in 1 h. Food specialization among individuals was attributed to their learning of the behavior and life style of preferred prey species.

Introduction

Lepidophagy or scale-eating is known from at least 17 genera of fresh-water fishes (Sazima 1983). It is onone of the most specialized feeding habits (Roberts 1970, Fryer & Iles 1972, Major 1973, Whitfield & Blaber 1978, Sazima 1983), although the external morphological specialization is minimal except for modified teeth and asymmetry of mouth-opening (Liem & Stewart 1976, Hori 1988). Scale-eaters use a variety of hunting techniques including ambush using a cover, stealthy approach and aggressive mimicry (Sazima 1983).

In Lake Tanganyika more than 170 endemic species of cichlid fishes exhibit a tremendous diversity of feeding habits (Poll 1956, Fryer & Iles 1972, Brichard 1978, Yamaoka 1982, 1983, Takamura 1983, 1984, Hori 1983, 1988). Of them, 6 in 2 genera are scale-eaters (Liem & Stewart 1976, Nshombo et al. 1985). *Plecodus straeleni* and *Perissodus microlopis*

are the most common scale-eaters and coexist in shallow rocky habitats. Body sizes of the two species are similar but the former has a deeper body (see Brichard 1978). They are claimed to use slightly different hunting tactics: *P. straeleni* dashes upon a prey fish after having more closely approached it than *P. microlepis* (Hori 1988). In my field observation, however, I noticed that their foraging behavior varied greatly even within a population. In *P. straeleni*, hunting techniques differed between the sexes corresponding to their color difference (Yanagisawa et al. 1990). The most remarkable difference was seen in the egg-eating habit: only females spent a lot of time cruising near the bowers of the cichlid fish *Cyathopharynx furcifer* to get eggs laid on the bower (Nshombo 1991). In *P. microlepis*, 4 color morphs were recognized among adults and their hunting techniques differed from one another (Nshombo unpublished).

This paper shows the time budgets of *P. straeleni* in the natural habitat and describes their hunting techniques and prey selection in relation to the sexes and body sizes based on observations for 1 h per individual. Special emphasis is put on individual variation in hunting.

Study area and methods

Field observations were conducted at Pemba on the northwest coast of Lake Tanganyika during April-November 1987, April-September 1988 and November 1989-January 1990, with the aid of SCUBA. The bottom at Pemba slopes steeply toward the depths, following a gentle slope of 50–70 m from the shoreline to a point about 8 m deep. I observed 69 solitary individuals of *P. straeleni* (50–130 mm in standard length) from a distance of 2–5 m for 1 h each and recorded a sequence of their behavior on plastic paper. The observation time was between 0900 and 1530 hours. Individuals with dark blue vertical bands on a pale background were regarded as males and those with beige vertical bands on a darkish background as females, although the latter may have included a small number of males (Yanagisawa et al. 1990). The body size was estimated visually, and individuals larger than 95 and 85 mm SL were considered adults for males and females, respectively. Cruising more than and less than 50 cm above the substrate was referred to as midwater-cruising and substrate-cruising, respectively.

Cruising routes were traced on a map for 1 h for 5 individuals and for 2 h for another individual. To locate their positions exactly, a 60 × 70 m quadrat divided into 10 m grids (3–30 m deeo), a 200 m line (5 m deep) and a 100 m line (10 m deep) were used.

To measure the diversity of prey species attacked by one scale-eater, Simpson's index of concentration.

$$\Sigma\Pi^2 = \sum_{i=1}^{s} (n_i/N)^2,$$

was used, where n_i is the number of attacks upon prey species i and N the number of total attacks. To compare the prey similarity between and within sex and size classes, the similarity index,

$$C_{\Pi} = 2 \sum_{i=1}^{s} n1_i \cdot n2_i/(\Sigma\Pi 1^2)N_1 N_2 \ (0 \le C \le 1)$$

$$\Sigma\Pi 1^2 = \sum_{i=1}^{s} (n1_i)^2, \ \Sigma\Pi 2^2 = \sum_{i=1}^{s} (n2)^2/N2^2,$$

was used, where $n1_i$ and $n2_i$ are the numbers of attacks upon prey species i by two classes (or two indi-

Table 1. Time budget (in percent) by *Plecodus straeleni* in different sex and size classes.

Sex and size classes	No. of 1 h observations	Cruising		Hunting techniques				Others
		midwater	substrate	pursuing	waiting	mingling	aiming	
Adult male	10	24.0	51.0	3.9	9.7	5.6	4.1	1.7
Adult female	20	13.6	63.0	2.0	9.2	5.2	6.3	0.7
Subadult male	18	3.9	75.1	1.4	2.2	13.6	3.0	0.8
Subadult female	21	10.7	69.9	1.4	4.3	3.7	9.0	1.0

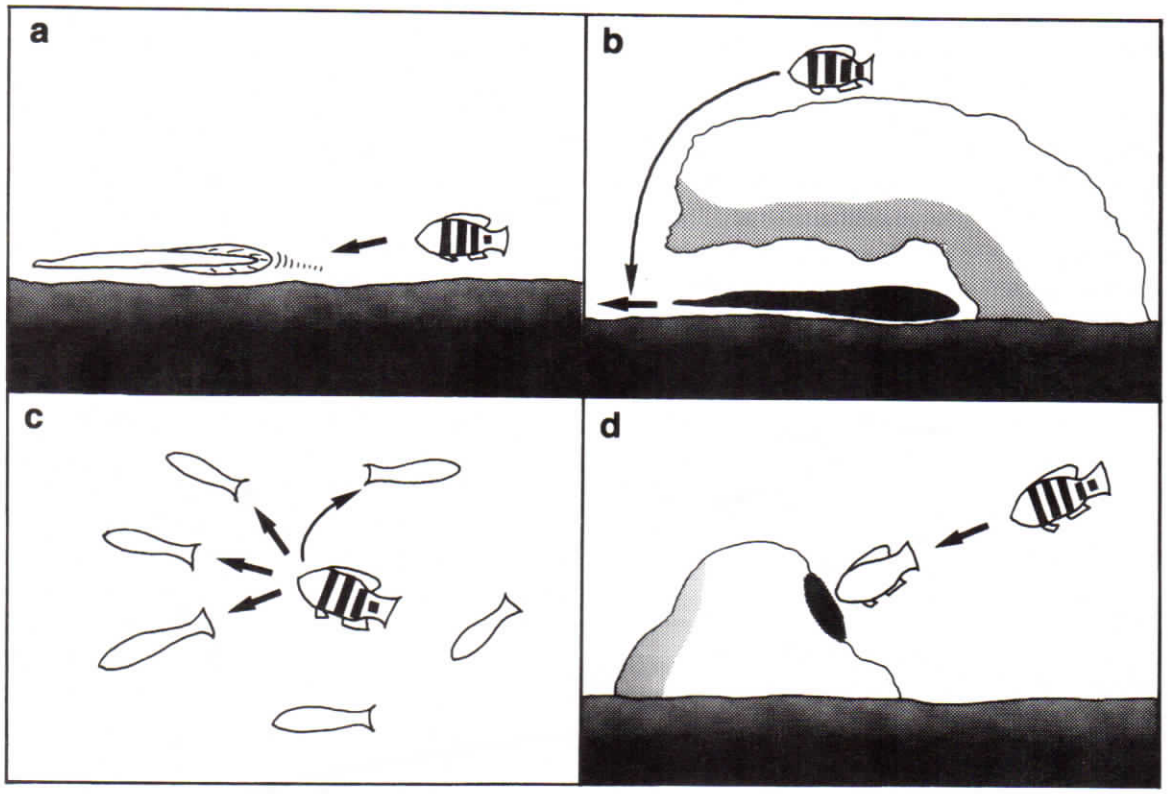


Fig. 1. Four hunting techniques of *Plecodus straeleni*, pursuing (a), waiting (b), mingling (c) and aiming (d). Arrows indicate the direction of attacks.

viduals within a class) and N_1 and N_2 the numbers of total attacks by them.

Results

Time budgets

Foraging behavior of *P. straeleni* was mainly composed of cruising and the use of hunting techniques. Five distinct hunting techniques were recognized and designated as pursuing, waiting, mingling, aiming and stealthy approaching (see below). The cruising time amounted to 3/4 of the total time (Table 1). One bout of cruising ranged from 3 to 514 sec. The cruising time did not differ among adult males, adult females, subadult males and subadult females (ANOVA, $F_s = 2.48$, $p > 0.05$). Substrate-cruising was more common than midwater-cruising in both adults and subadults, although the time spent on midwater-cruising by adults was significantly longer than by subadults ($F_s = 14.34$, $p < 0.05$).

P. straeleni stopped cruising when it was attracted by a fish or a group of fish. Then it started one of the five hunting techniques (Fig. 1). (The time of stealthy approaching could not be recorded and was therefore included in the cruising time.) Pursuing is the behavior in which a scale-eater followed a target fish or a group of fish at a much higher speed than during cruising. Waiting is the behavior during which a scale-eater stayed on the substrate, waiting for a known fish to appear from a shelter, or watching a sequence of behaviors of a target fish in order to seize a favorable opportunity for attacking. This behavior usually lasted more than 10 sec. Mingling is the behavior during which a scale-eater mixed with a school of other fish before it attacked members of the school. Aiming is the behavior during which a scale-eater kept motionless at a certain site above the substrate or in midwater for a moment,

usually directing its head at a fish. (The duration of aiming was often difficult to measure. The aiming time in Table 1 includes the time when the scale-eater stayed on the substrate before and after aiming.)

About 20% of the time was devoted to these hunting techniques (Table 1). Waiting was more common than the others in adult males and females, whereas the mingling time was longer in subadult males and the aiming time longer in subadult females. The remaining time (about 1%) was spent in the following activities: chasing of conspecific fish, being chased by other conspecific and prey fishes, picking some matter from the substrate or from midwater.

Cruising

Adults foraged in a deeper water (21.2 m ± 5.62 SD, N = 10 for males; 11.1 ± 4.25, N = 20 for females) than subadults (8.7 m ± 4.47 SD, N = 16 for males; 8.0 ± 4.42 SD, N = 20 for females). Both adults and subadults cruised nearly parallel to the shoreline. The cruising distance in 1 h exceeded 200 m (275, 433, 506 m for adults and 400 and 430 m for sub-

Table 2. The frequency (per hour) and mean bout length of five hunting techniques of *Plecodus straeleni* against main prey species.

Prey fish	Adult male (N = 10)	Adult female (N = 20)	Subadult male (N = 18)	Subadult female (N = 21)	Mean bout length (sec)
Pursuing					
Afromastacembelus moorii	6.1	1.5	1.2	0.6	17.5
Cyathopharynx furcifer	0.3	0.2	0.2	0.1	16.6
Lamprologus callipterus	0.0	0.7	0.2	0.6	18.4
Lates angustifrons	0.7	0.0	0.0	0.0	10.5
Chrysichthys sp.	0.6	0.0	0.0	0.0	5.0
Total (species)	9.6	6.7	2.6	2.3	19.6
Waiting					
Cyathopharynx furcifer	0.0	5.4	0.5	3.6	43.3
Afromastacembelus moorii	4.4	0.8	0.5	0.2	53.8
Chrysichthys sp.	1.0	0.0	0.0	0.0	70.3
Lates augustifrons	0.6	0.0	0.0	0.0	26.0
Synodontis multipunctatus	0.4	0.1	0.0	0.0	36.6
Total (species)	6.7	6.6	2.0	4.1	45.2
Mingling					
Neolamprologus brichardi	0.0	0.5	5.0	4.1	46.4
Cyprichromis microlepidotus	2.9	0.0	3.4	0.1	71.7
Lepidiolamprologus elongatus	0.1	1.8	0.0	0.0	74.8
Petrochromis spp. (mixed school)	0.0	0.2	0.0	0.8	46.8
Cyathopharynx furcifer	0.0	0.1	0.0	0.1	24.0
Total (species)	3.1	2.9	8.6	5.7	63.2
Aiming					
Cyathopharynx furcifer	0.3	1.1	0.3	0.8	–
Neolamprologus brichardi	0.8	0.0	1.7	0.6	–
Petrochromis polyodon	0.0	0.7	0.3	1.0	–
Petrochromis orthognathus	0.0	0.6	0.5	0.6	–
Tropheus moorii	0.0	0.3	0.1	1.4	–
Total (species)	2.7	5.0	8.1	8.5	–
Stealthy approaching					
Cyathopharynx furcifer	0.2	0.2	0.1	0.8	–
Petrochromis trewavasae	0.2	0.1	0.3	0.0	–
Lepidiolamprologus elongatus	0.1	0.1	0.3	0.3	–
Ophthalmotilapia ventralis	0.2	0.0	0.1	0.0	–
Total (species)	1.3	1.8	4.5	4.4	–

adults). Their foraging areas overlapped with one another. Strict territorial behavior was not seen among them, although one usually lightly chased off the other when two individuals encountered. Nevertheless, they seemed to have more or less fixed home ranges, because they turned back at a certain site and repeated the nearly same cruising route.

During cruising, body color frequently changed in females, whereas no detectable color changes occurred in males. About 70 percent of females (14/20 adults and 14/21 subadults) changed color between the faintly banded beige pattern and the nonbanded dark one (see Yanagisawa et al. 1990) at least once in 1 h. The mean frequency of the color changes per hour was 9.3 (n = 11) for adult females and 15.6 (n = 12) for subadult females. The color change from the former pattern to the latter often occurred when females moved from the midwater to the rocky substrate and the opposite change occurred in the opposite situation.

Hunting techniques

Each of the five hunting techniques was directed toward some particular prey species (Table 2). This selectivity seems to be determined by the life styles of prey species.

Pursuing was more often done by adults than by subadults (Tables 1, 2). This behavior was most frequently directed toward a large spiny eel, *Afromastacembelus moorii* (Mastacembelidae) (about 30–60 cm total length in adults). An eel would hide under a rock except when it moved along the substrate between rocks. When *P. straeleni* found a crawling eel, it pursued the eel, which fled for up to 45 sec. Pursuing usually ended with a successful attack or hiding of the eel under a rock. Two other large non-cichlid fishes, *Chrysichthys* sp. (Bagridae) (about 100 cm TL in adults) and *Synodontis multipuncatus* (Mochokidae) (about 25 cm TL in adults), were also pursued when they left their hiding places and swam over the substrate. Cichlid fishes pursued by *P. straeleni* were usually in a school: e.g., foraging adults of *Lamprologus callipterus* (see Hori 1983) and foraging subadults of algae eaters *Petrochromis* spp. and *Tropheus moorii* on the substrate and resting subadults of *Cyathopharynx furcifer* in midwater.

Waiting was performed in three different situations. First, *P. straeleni* waited for a target fish hiding under a rock or in a hole to emerge. In this case, target fishes were three non-cichlid fishes – *Mastacembelus moorii, Synodontis multipunctatus* and *Chrysichthys* sp. (Table 2). The former two hid under a rock, and the latter sheltered in a big horizontal hole with a diameter of about 0.5 m and a length of 1.5–2 m where parents brooded the young. When waiting for *Chrysichthys* sp. showing its face from the entrance of its nesting hole, *P. straeleni* sometimes slipped into the hole and compelled it to leave, probably by poking the body of the prey. Second, the scale-eater waited near a crater-like sand bower of *Cyathopharynx furcifer* to plunder the eggs of a spawning pair (see Nshombo 1991). Third, the scale-eater waited on the substrate to seize an opportunity for attacking a fish. The target fishes

Table 3. The numbers of successful and unsuccessful attacks of *Plecodus straeleni* by five hunting techniques and at sudden encounter. The numbers of hunting techniques accompanied by attacks and the total numbers of hunting techniques observed are shown in parentheses. More than one attack often occurred during pursuing and mingling (for details see text).

		Hunting techniques					Sudden encounter
		Pursuing	Waiting	Mingling	Aiming	Stealthy approach	
Adult male	(N = 10)	47 + 0(20/ 96)	7 + 0 (7/ 67)	12 + 8(16/ 31)	18 + 9	12 + 1	2 + 1
Adult female	(N = 20)	24 + 6(18/ 67)	28 + 0(28/133)	32 + 10(15/ 59)	73 + 27	30 + 7	3 + 1
Subadult male	(N = 18)	14 + 0(11/ 48)	6 + 0 (6/ 37)	134 + 35 (38/156)	129 + 18	68 + 13	19 + 1
Subadult female	(N = 21)	13 + 3(16/ 49)	29 + 3(32/ 88)	50 + 16(26/121)	136 + 44	68 + 26	1 + 1
Total	(N = 69)	98 + 9(65/260)	70 + 3(73/325)	228 + 69(95/367)	360 + 98	178 + 47	25 + 4

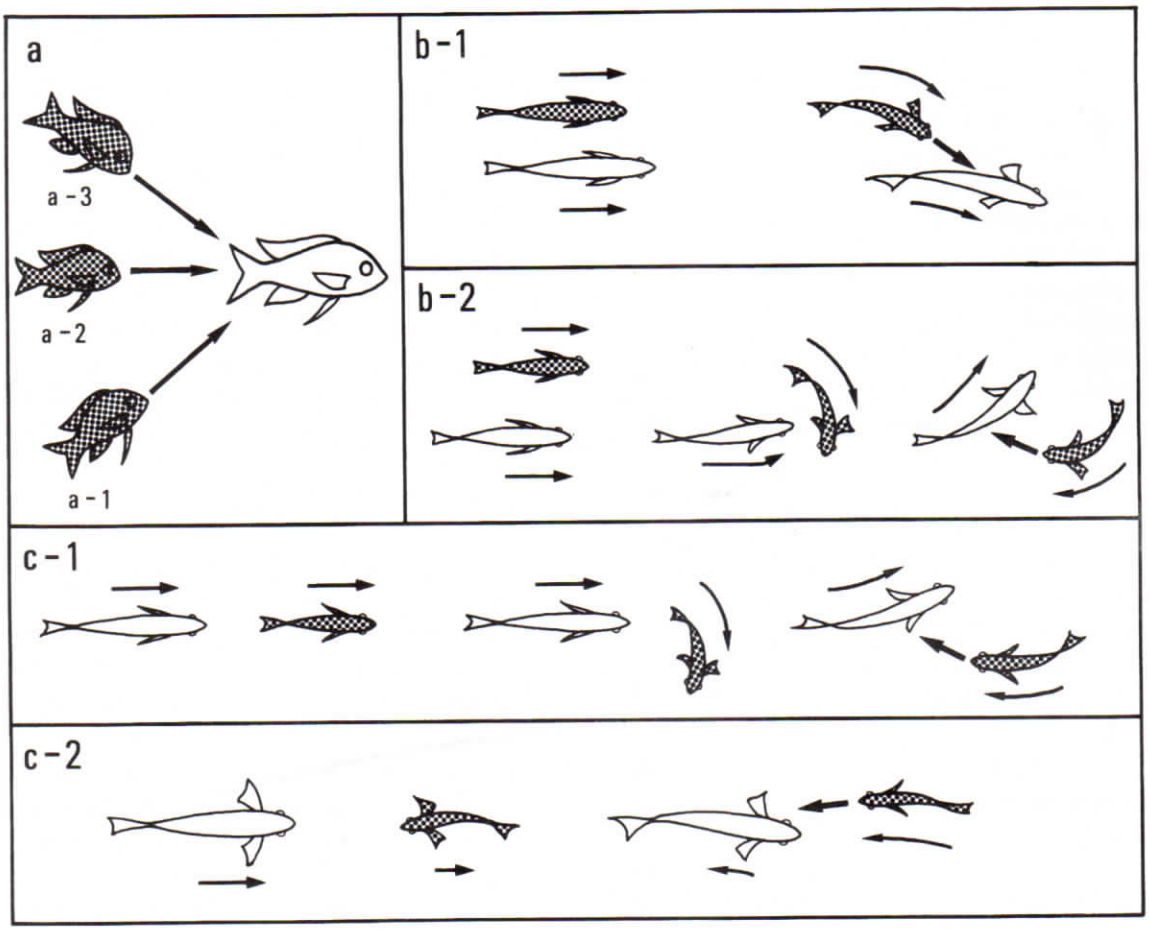


Fig. 2. Schematic presentation of dash styles in *Plecodus straeleni*. Shaded and blank fishes represent scale-eaters and prey fishes, respectively. Thick arrows show the direction of attacks and thin arrows the movement of fishes. a-1 = upward dash, a-2 = horizontal dash, a-3 = downward dash, b-1 = sidewise dash A, b-2 = sidewise dash B, c-1 = counterattack A, c-2 = counterattack B. See text for details.

were subadults of the snook *Lates angustifrons* (Centropomidae) (about 40 cm TL) and some large cichlids such as *Ophthalmotilapia nasutus* and *Petrochromis* spp. (about 20 cm TL).

Waiting for hiding non-cichlid fishes was more often performed by adults, especially males, than by subadults. On the other hand, waiting for a spawning *C. furcifer* was nearly exclusively done by females (Table 2, also see Nshombo 1991). Waiting for a snook was done by adult males and that for cichlid fishes mainly by subadult males and females.

Mingling was most often adopted by subadult males (Table 3). The scale-eater slowly approached schools of other fishes and mixed with them. Within a school, fish which became close to *P. straeleni* kept away from it or sometimes charged it but most of other members were indifferent to its presence. The most frequently mingled were schools of the planktivores *Neolamprologus brichardi* and *Cyprichromis microlepidotus*, which have the largest populations in water shallower and deeper than 10 m, respectively. The scale-eater stayed in one school for about 1 min on average (Table 2).

Aiming was the simplest and most common hunting technique. Since I could not identify this behavior definitely when its duration was short, only bouts of aiming that resulted in attacking prey were counted (Tables 2, 3). Aimed fishes, mostly cichlid fishes, were often engaged in activities of courtship display, spawning, feeding and territorial behavior.

Attacking behavior

Forty-one percent of pursuing, 22% of waiting and 81% of mingling were followed by attacking dashes on the prey (Table 3); in the other cases, scale-eaters stopped the hunting techniques and left the target fishes. Attacks by the hunting techniques including aiming and stealthy approaching amounted to 97% of total attacks observed. The other 3% of attacks occurred without a hunting technique, when the scale-eater suddenly came close to a territorial fish which drove away intruders and when it happened to encounter a fish at the corner of a rock.

In 81% of total attacks observed, *P. straeleni* succeeded in striking a prey's body. The attacking success ratio was relatively low when it attacked during mingling or by stealthy approaching (Table 3). When *P. straeleni* attacked *Chrysichthys* sp. by pursuing or waiting, several bites were quickly repeated until the prey took refuge into a hole. During one bout of mingling, attacks were made upon up to 9 different fish within the school.

Dashes of *P. straeleni* were categorized into three types according to the situation and relative position of the attacker and its prey: straight dash, sidewise dash and counterattack dash (Fig. 2). Before a sidewise dash, a scale-eater swam or hovered side by side with a prey. Then, it struck the near side of the prey's body (sidewise dash A) or the opposite side (sidewise dash B) (Fig. 2b). In the latter dash, a scale-eater suddenly swam round the prey's nose to reach the opposite side of the prey, so that the prey was obliged to stop swimming or to change its swimming route. A counterattack dash (Fig. 2c) occurred when a scale-eater was chased by other fish. While being chased, the scale-eater suddenly turned around and attacked in the flank of the chaser (counterattack dash A). Or, after a short retreat the scale-eater suddenly rushed to the chaser to strike its flank (counterattack B).

Two thirds of attacks (777/1189) were done by straight dashes, of which 2/3 were horizontal ones (Table 4). *Chrysichthys* sp. was attacked only by upward dashes; when this fish swam out from its nesting hole, a scale-eater which had waited near the hole rushed upwards on it to tear off the skin of its flank or ventral fin. In contrast, *Afromastacembelus moorii*, which crawled on the substrate, was mostly attacked by downward dashes. While biting the body surface of these two non-cichlid fishes, *P.*

Table 4. The numbers of dash styles used by *Plecodus straeleni* to attack various prey fishes in a total of 69 h observation time.

Prey species	Straight dash			Sidewise dash		Counter attack dash		Total
	Upward dash	Horizontal dash	Downward dash	A	B	A	B	
Neolamprologus brichardi	18	90	2	68	3	26	10	217
Cyathopharynx furcifer	15	46	8	21	2	12	12	116
Cyprichromis microlepidotus	9	26		32	1	3	1	72
Afromastacembelus moorii	3	10	55					68
Petrochromis polyodon	10	34	1	9	1	5	2	62
Petrochromis orthgnathus	6	35	3	10	2	2	2	60
Telmatochromis temporalis	3	32	3	12	3	3		56
Lepidiolamprologus elongatus	10	26	4	3	3	6		52
Tropheus moorii	7	30		5	1		3	46
Neolamprologus mondabu	1	14	5	6		10	7	43
Petrochromis trewavasae	3	17	2	14		2	1	39
Lamprologus callipterus	1	12	8	5	2	2	1	31
Lobochilotes labiatus	4	16	3	3			2	28
Limnotilapia dardennii	8	12		5	2			27
Chrysichthys sp.	26							26
Others	20	106	33	37	6	31	13	246
Total	144	506	127	230	26	102	54	1189

Table 5. Percentage of attacks upon prey fishes by *Plecodus straeleni* in each sex and size class.

	Adult male	Adult female	Subadult male	Subadult female
No. of 1 h observations	10	20	18	21
Attacking rate per hour	11.7	12.1	24.3	18.8
Prey species				
Cichlid fishes				
Neolamprologus brichardi	6.9	4.6	32.4	14.2
Cyathopharynx furcifer	1.7	15.3	2.8	16.4
Cyprichromis microlepidotus	16.3		11.9	0.2
Petrochromis polyodon		6.7	1.7	9.9
Petrochromis orthognathus	0.9	7.9	3.9	5.9
Telmatochromis temporalis		1.7	7.8	4.6
Lepidiolamprologus elongatus	3.4	10.3	3.2	2.2
Tropheus moorii		3.0	1.3	8.3
Neolamprologus mondabu		1.2	7.6	1.8
Petrochromis trewavasae	1.7	3.8	3.0	3.9
Lamprologus callipterus		3.8	1.9	3.6
Lobochilotes labiatus	0.9	3.8	1.3	3.0
Neolamprologus toae		2.0	2.2	3.2
Limnotilapia dardennii	7.7	2.4	1.7	1.2
Ophthalmotilapia ventralis	1.7	2.0	2.2	2.0
Petrochromis fasciolatus		2.0	1.3	3.0
Lamprologus lemairii		3.8	1.0	2.6
Petrochromis famula	0.9	3.8	0.7	2.0
Xenotilapia flavipinnis	1.7	0.9	1.1	1.0
Neolamprologus savoryi	0.9	0.4	1.3	0.8
Neolamprologus tretocephalus	0.9	0.9	1.1	0.6
Tropheus duboisi	0.9	1.2	0.4	0.6
Ophthalmotilapia nasutus		0.9	1.1	0.2
Julidochromis marlieri		0.4	1.0	0.2
Gnathochromis pfefferi			0.7	0.8
Haplotaxodon microlepis	0.9		0.2	0.6
Neolamprologus niger		0.4	0.2	0.6
Lepidiolamprologus attenuatus		0.9		0.6
Perissodus microlepis			1.1	
Lepidiolamprologus profundicola	0.9		0.4	
Pseudosimochromis curvifrons			0.2	0.6
Simochromis diagramma				0.8
Neolamprologus furcifer		0.9		
Ctenochromis horei		0.4	0.2	
Altolamprologus compressiceps				0.6
Cyphotilapia frontosa	0.9			
Telmatochromis bifrenatus			0.2	
Tanganicodus irsacae				0.2
Non-cichlid fishes				
Afromastacembelus moorii	22.2	12.9	1.9	0.8
Chrysichthys sp.	22.2			
Synodontis multipunctatus	2.6	0.8	0.4	0.2
Lamprichthys tanganicanus		0.8	0.2	1.0
Lates angustifrons	0.9			1.0
Lates mariae		0.4		1.0
Malapterurus electricus	3.4			

Table 6. The similarity index, C, of prey between sex and size classes of *Plecodus straeleni.*

	AM	AF	SM	SF
Adult male (N = 10)		0.397	0.360	0.172
Adult female (N = 20)			0.341	0.755
Subadult male (N = 18)				0.611
Subadult female (N = 21)				

straeleni usually twisted their body to tear a piece of skin and muscle off. Sidewise dashes mainly occurred when *P. straeleni* was in a school of prey species such as *Neolamprologus brichardi* and *Cyprichromis microlepidotus.* Most counterattack dashes were directed to territorial fishes (e.g., males of *Cyathopharynx furcifer* with a spawning bower and females of *Neolamprologus mondabu* guarding the young) and schooling fishes (e.g., *Neolamprologus brichardi*).

In all, *P. straeleni* attacked 45 prey species, including 38 cichlid fishes and 7 non-cichlid fishes (Table 5). These included nearly all fish species that occurred in considerable numbers in the study area. Half of attacks by adult males were upon 5 non-cichlid fishes. These non-cichlid fishes, excepting *Lates angustifrons*, are scaleless (*Chrysichthys* sp., *Synodontis multipunctatus* and *Malapterurus electricus*) or have embedded minute scales (*Afromastacembelus moorii*). (The name scale-eater is therefore inappropriate at least for adult males.) Adult females attacked many cichlid species, especially *Cyathopharynx furcifer, Lepidiolamprologus elongatus* and *Petrochromis* spp.. They also often attacked the non-cichlid fish *Afromastacembelus moorii.* Subadults, both males and females, mainly attacked cichlid fishes. In subadult males, attacks upon schooling fishes *Neolamprologus brichardi* and *Cyprichromis microlepidotus* were most frequent. For subadult females, *Cyathopharynx furcifer* near the bowers, a schooling fish *N. brichardi* and algal eaters *Petrochromis* spp. and *Tropheus moorii* were the main prey.

The attacking rate was higher in subadults than in adults (Table 5); the difference was significant between adult and subadult males (Mann-Whitney U test, $U = 23$, $N_1 = 10$, $N_2 = 18$, $p < 0.05$), between adult and subadult females ($U = 95.5$, $N_1 = 20$, $N_2 = 21$, $p < 0.05$), between adult males and subadult females ($U = 53.5$, $N_1 = 10$, $N_2 = 21$, $p < 0.05$) and between adult females and subadult males ($U = 41.5$,

Table 7. The number of attacks by one scale-eater upon each prey species during the 1 h observation time and percentage of attacks made successively upon it. Sixteen main prey species are shown.

Prey species	Individuals which attacked the prey species	No. of attacks by one individual (× + SD)	No. of total attacks	Successive attacks (%)*
Neolamprologus brichardi	30	7.2 + 7.2	217	48.8
Cyathopharynx furcifer	36	3.2 + 2.6	116	38.3
Cyprichromis microlepidotus	7	10.2 + 7.8	72	73.6
Afromastacembelus moorii	29	2.3 + 1.8	68	45.6
Petrochromis polyodon	26	2.3 + 1.7	62	17.7
Petrochromis orthognathus	29	2.0 + 1.3	60	21.6
Telmatochromis temporalis	25	2.2 + 1.8	56	16.1
Lepidiolamprologus elongatus	28	1.8 + 3.1	52	23.0
Tropheus moorii	19	2.4 + 2.9	46	23.9
Neolamprologus mondabu	16	2.6 + 1.9	43	11.6
Petrochromis trewavasae	25	1.5 + 0.8	39	5.1
Lamprologus callipterus	18	1.7 + 0.8	31	16.1
Lobochilotes labiatus	23	1.2 + 0.4	28	7.4
Neolamprologus toae	16	1.7 + 1.0	28	3.6
Limnotilapia dardennii	14	1.9 + 1.7	27	14.8
Chrysichthys sp.	2	13.0 + 6.0	26	88.5

* (attacks upon a prey species following or preceding an attack upon the same species)/ (total attacks) × 100.

$N_1 = 20$, $N_2 = 18$, $p < 0.05$). The average value of Simpson's index of concentration on prey species was higher in adult males (0.53) than in adult females (0.28), subadult males (0.31) and subadult females (0.25), suggesting that prey preference of adult males is most strict. The prey body size positively correlated with the body size of scale-eaters ($r = 0.795$, $p < 0.001$, $N = 28$ for males; $r = 0.635$, $p < 0.001$, $N = 41$ for females). The prey similarity was high between the adult and subadult females and between the subadult male and female but lowest between the adult male and the subadult female (Table 6).

Individual variation in foraging behavior

Foraging behavior and prey preference of *P. straeleni* varied not only with sex and size but even among consexuals of similar body sizes. The prey similarity between adult males and between adult females was lower than that between subadult males and between subadult females: the mean value of the similarity index, C, between two individuals within a class was 0.224, 0.255, 0.358 and 0.323 for respective classes. This means that adults are more individualized in prey preference than subadults.

Many individuals, either adults or subadults, successively attacked a certain prey species. This trend was remarkable when a scale-eater attacked two non-cichlid fishes *Chrysichthys* sp. and *Afromastacembelus moorii* by pursuing or waiting, two schooling cichlid fishes *Neolamprologus brichardi* and *Cyprichromis microlepidotus* by mingling and a cichlid fish *Cyathopharynx furcifer* near bowers by waiting or aiming (Table 7). A great specialization in prey preference was seen when *P. straeleni* attacked these species (Table 8).

Some prey species tended to be attacked together by the same individual of *P. straeleni* during a 1 h observation period. The most remarkable pair of prey species was *Lamprologus callipterus* and *Lo-*

Table 8. Attack sequences for *Plecodus straeleni* which concentrated their attacks upon a few prey species (> 0.50 in the Simpson's index of concentration).

Individuals	No. of attacks	Prey species
Adult male		
AM1	4	am-am-am-me
AM2	7	ch-ch-ch-ch-ch-ch-ch
AM3	19	cm-cm-cm-cf-cm-cm-cm-cm-cm-cm-cm-cm-cm-cm-cm-cm-cm-am-cm
AM4	27	ch-ch-ch-ch-ch-ch-ch-ch-ch-ch-ch-ch-ch-hm-am-am-ch-ch-ch-ch-ch-ch-ch-am-am-am-am-am
Adult female		
AF1	8	am-cy-cy-cy-ll-cy-cy-cy
AF2	9	cy-am-cy-cy-cy-cy-cy-cy-am
AF3	10	tm-am-am-am-le-am-cy-am-am-am
Subadult male		
SM1	8	cm-cm-cm-nb-cm-cm-cm-cm
SM2	25	cm-cm-cm-cm-cm-le-cm-lc-cm-cm-cm-cm-cm-cm-cm-cm-cm-cm-cm-nb-cm-cm-nb-nb-cm
SM3	26	lp-cm-cm-cm-cm-cm-cm-cm-cm-le-cm-cm-nb-cm-cm-cm-cm-sm-cm-nb-cm-cm-cm-cm-cm-nb
SM4	43	td-tt-nb-on--nb-nb-nb-nb-nb-nb-nb-nb-nb-xf-nb-nb-nb-nb-nb-nb-nb-nb-nb-nb-po-nb-nb-tt-nb-nb-nb-nb-nb-nb-nb-nb-nb-nb-td-nb-lp-nb-nb
Subadult female		
SF1	7	cy-cy-cy-cy-cy-cy-am
SF2	12	xf-cy-cy-lb-cy-cy-pp-cy-cy-cy-cy-cy
SF3	18	nb-on-nb-nb-cy-nb-nb-nb-nb-nb-nb-nb-hm-nb-nb-nb-ov-lb

am: *Afromastacembelus moorii*, cf: *Cyphotilapia frontosa*, ch: *Chrysichthys* sp., cm: *Cyprichromis microlepidotus*, cy: *Cyathopharynx furcifer*, hm: *Haplotaxodon microlepis*, lb: *Lobochilotes labiatus*, lc: *Lamprologus callipterus*, le: *Lepidiolamprologus elongatus*, ll: *Lamprologus lemairii*, lp: *Lepidiolamprologus profundicola*, me: *Malapterurus electricus*, nb: *Neolamprologus brichardi*, on: *Ophthalmotilapia nasutus*, ov: *Ophthalmotilapia ventralis*, po: *Petrochromis orthognathus*, pp: *Petrochromis polyodon*, sm: *Synodontis multipunctatus*, td: *Tropheus duboisi*, tt: *Tropheus moorii*, xf: *Xenotilapia flavipinnis*.

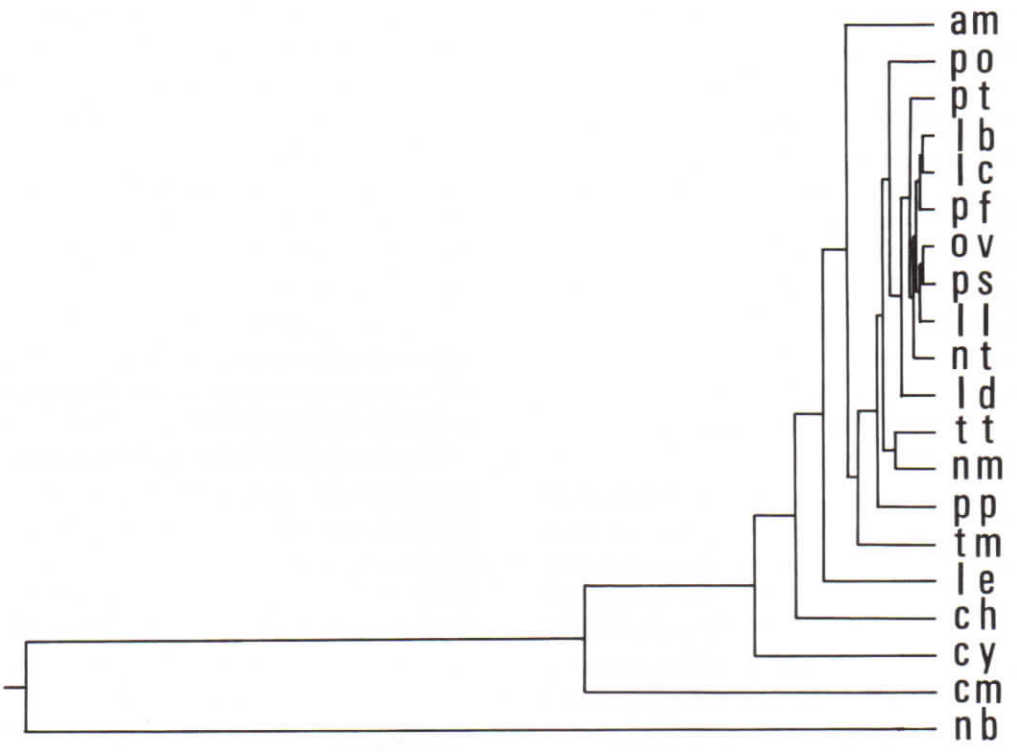


Fig. 3. Dendrogram of the similarity of attackers among the main 20 prey fishes of *P. straeleni*, produced by UPGMA. am = *Afromastacembelus moorii*, ch = *Chrysichthys* sp., cm = Cyprichromis microlepidotus, cy = *Cyathopharynx furcifer*, lb = *Lobochilotes labiatus*, lc = *Lamprologus callipterus*, ld = *Limnotilapia dardennii*, le = *Lepidiolamprologus elongatus*, ll = *Lamprologus lemairii*, nb = *Neolamprologus brichardi*, nm = *Neolamprologus mondabu*, nt = *Neolamprologus toae*, ov = *Ophthalmotilapia ventralis*, pf = *Petrochromis famula*, po = *Petrochromis orthognathus*, pp = *Petrochromis polyodon*, ps = *Petrochromis fasciolatus*, pt = *Petrochromis trewavasae*, tm = *Tropheus moorii*, tt = *Telmatochromis temporalis*.

bochilotes labiatus. Attacks by 12 scale-eaters which attacked both of these species amounted to 77% (22/31) and 57% (16/28) of total attacks upon them, respectively. Another remarkable pair was *Telmatochromis temporalis* and *Neolamprologus mondabu*. Fifty-five percent (31/56) and 72% (31/43) of total attacks upon them respectively, were made by 11 scale-eaters which attacked both species. In both pairs, the two species are bottom-feeders with a similar life style: *L. labiatus* and *L. callipterus* often formed a mixed species foraging school, and *T. temporalis* and *N. mondabu*, having the similar body shape and pinkish color, often foraged boundary zones between rocks and sand. In general, when scale-eaters attacked benthic cichlid fishes (e.g., *Petrochromis* spp., *Tropheus moorii*, *Neolamprologus toae* and *Lamprologus lemairii*), their prey preference was less strict (Fig. 3). In other words, scale-eaters did not center their attacks on one or a few particular species among these cichlid fishes.

Discussion

A scale-eater is defined in a narrow sense as a fish feeding on scales taken from other living fishes (Keenleyside 1979). If a prey fish is scaleless, however, the material obtained from the fish is only skin or skin and muscle. Therefore, the term skin-eater may be more appropriate wording than the term scale-eater. In this paper, the term scale-eater was conventionally held but was defined as a fish subsisting on pieces of materials removed from trunk surfaces of other living fishes. Fin-eating (Sazima & Machado 1990), specialists of which are found among African characoid fishes in the family Ich-

thyboridae (Keenleyside 1979), may be the closest feeding habit to scale-eating.

The observation of the foraging behavior of *Plecodus straeleni* in this study and the examination of its stomach contents (Yanagisawa et al. 1990) show that both adults and subadults of this species take all food from other living fishes except for occasional egg-eating by some females (Nshombo 1991). Such a high degre of specialization is also known in another scale-eater, *Perissodus microlepis,* in Lake Tanganyika (Nshombo et al. 1985) but is rare among scale-eaters in other regions. Most scale-eaters take food items other than materials from fishes (for review see Sazima 1983).

Scale-eaters have a large repertoire of hunting techniques (Fryer & Iles 1972, Keenleyside 1979, Sazima 1983, Hori 1988, Sazima & Machado 1990). Ambush using a cover, stealthy approaching and disguise (aggressive mimicry) are the main feeding techniques (Sazima 1983). In *P. straeleni,* pursuing, waiting, mingling, aiming and stealthy approaching were recognized. Aiming is the simplest behavior, which may be common to all scale-eaters and other mutilating predators (see Sazima & Machado 1990). Mingling or joining prey schools, which is often associated with aggressive mimicry, has been observed in many scale-eaters of characoids, cichlids, carangids, teraponids and blenniids (see Sazima 1983, Sazima & Machado 1990). Pursuing and waiting seem to be peculiar to *P. straeleni* as far as I know. Pursuing by *P. straeleni* is different from rushing by the characoid *Exodon paradoxus* and the theraponid *Therapon jarbua* that is done in a group attack (Roberts 1970, Whitfield 1979, Sazima 1983). Waiting of *P. straeleni* is different from ambush common to scale-eaters, since *P. straeleni* waits or watches a known fish to seize an opportunity for attacking it, but other scale-eaters ambush to attack fish which accidentally pass nearby (Sazima & Machado 1990, Nshombo et al. 1985, Hori 1988).

The color patterns of some scale-eaters have been discussed in relation to their foraging behavior (Roberts 1970, Whitfield & Blaber 1978). In *P. straeleni*, two basic color patterns are linked to sexes. Males, which have a striped color pattern conspicuous from a distance, show remarkable resemblance to two unimportant prey cichlids, *Cyphotilapia frontosa* and *Neolamprologus tretocephalus,* instead of mimicking preferred prey fishes as do some other scale-eaters (Trewavas 1947, Major 1973, Sazima 1977, 1983, Brichard 1978, Sazima & Uieda 1980). *P. straeleni* may thus gain access to other prey due to a camouflaging effect by these models (Yanagisawa et al. 1990). On the other hand, a beige or dark chocolate coloration of females is cryptic. They seem to have more chances of approaching prey along the substrate without being noticed. This may be the reason why only females often waited on the substrate for courting *Cyathopharynx furcifer* to spawn (Nshombo 1991).

The foraging behavior and prey preference more fundamentally differed between adults and subadults than between males and females. Subadults, either males or females, mainly attacked cichlid fishes in the shallower water, whereas adults, especially adult males, frequently attacked large non-cichlid fishes in the deeper water. This agrees with a general tendency among scale-eating species that smaller individuals attack smaller prey and larger ones larger prey (e.g., *Perissodus microlepis,* Nshombo et al. 1985). For subadults, to approach large piscivorous non-cichlid fishes such as *Chrysichthys* sp. and *Afromastacembelus moorii*, which often counterattacked scale-eaters, may involve risks. Even if not so, their tough skin may be beyond subadults' biting power. In contrast, *Chrysichthys* sp. and *A. moorii* seem to be the most preferred prey of adults. When adult *P. straeleni* noticed these non-cichlid fishes passing nearby, they nearly always stopped their present activities to pursue them. They persistently waited for these fishes, although their waiting bouts rarely resulted in successful attacks (Table 3). The most extreme case of persistent waiting has been observed in an adult male which constantly placed himself near the entrance of a big hole of *Chrysichthys* sp. for at least two weeks (Yanagisawa personal communication). Adults prefer these non-cichlid fishes probably because much larger pieces can be torn off from them than from cichlid fishes in single attacks, as the examination of stomach contents suggests (Yanagisawa et al. 1990). Attacking chances upon these non-cichlid fishes are probably limited by their cryptic life style and low population density.

Individual variation in foraging behavior and prey preference was striking. Many individuals centered their attacking activities on one or a few prey species and used the same hunting techniques through a 1 h observation period. They showed no interest in other potential prey fishes which passed nearby. A typical case of neglect of other fishes was observed when scale-eaters used the tactic of mingling. They often moved a long distance from one school of a prey species to another school without attacking other fish on the way. This suggests that *P. straeleni* keep their favorite feeding techniques for a long time, although it obviously must be demonstrated by a field observation of marked individuals.

It has been assumed that variations in feeding tactics among members of a population are derived from physiological, behavioral and morphological sources (Ringler 1983). For *P. straeleni,* the behavioral source seems to be important, although studies on morphology and physiology in relation to foraging behavior of this fish are needed. Their potential prey fishes have an enormous diversity of life styles and behaviors. Specialization of prey and establishment for each individual of favorite feeding techniques by learning may be essential to increase the hunting efficiency.

Acknowledgements

Y. Yanagisawa of Ehime University is especially thanked for supervising this work and reviewing the manuscript. I thank A. Mori for his drawing and N. Mizuno, K. Omori and I. Bambang of Ehime University for their kind advice. Thanks are extended to M. Kohda of Osaka City University, N. Abe of Osaka Women's University, M. Hori of Wakayama Medical Colloge, H. Kawanabe and M. Yuma of Kyoto University and M.M. Gashagaza of CRSN/ Uvira for their helpful comments on the manuscript. This work was supported by CRSN, JICA and the Ministry of Education, Science and Culture, Japan (Nos. 63041080, 02041058, 04041078, 04044088).

References cited

Brichard, P. 1978. Fishes of Lake Tanganyika. T.F.H. Publications, Neptune City. 448 pp.

Fryer, G. & T.D. Iles. 1972. The cichlid fishes of the Great Lakes of Africa, their biology and evolution. Oliver & Boyd, Edinburgh. 641 pp.

Hori, M. 1983. Feeding ecology of thirteen species of *Lamprologus* (Teleostei; Cichlidae)) coexisting at a rocky shore of Lake Tanganyika. Physiol. Ecol. Japan. 20: 129–149.

Hori, M. 1988. Mutualism and commensalism in a fish community in Lake Tanganyika. pp. 219–239. *In:* S. Kawano, J.H. Connell & T. Hidaka (ed.) Evolution and Coadaptation in Biotic Communities, University of Tokyo Press, Tokyo.

Keenleyside, M.H.A. 1979. Diversity and adaptation in fish behaviour. Springer-Verlag, Berlin. 208 pp.

Liem, K.F. & D.J. Stewart. 1976. Evolution of the scale-eating cichlid fishes of Lake Tanaganyika: a generic revision with a description of a new species. Bull. Mus. Comp. Zool. 147: 319–350.

Major, P.F. 1973. Scale-feeding behavior of the leatherjacket, *Scomberoides lysan* and two species of the genus *Oligoplites* (Pisces: Carangidae). Copeia 1973: 151–154.

Nshombo, M. 1991. Occasional egg-eating by the scale-eater *Plecodus straeleni* (Cichlidae) of Lake Tanganyika. Env. Biol. Fish. 31: 207–212.

Nshombo, M., Y. Yanagisawa & M. Nagoshi. 1985. Scale-eating in *Perissodus microlepis* (Cichlidae) and change of its food habits with growth. Japan. J. Ichthyol. 32: 66–73.

Poll, M. 1956. Poissons Cichlidae. Explor. Hydrobiol. Lac Tanganyika (1946–1947), 3 Fasc. 5B: 1–619.

Ringler, N.H. 1983. Variation in foraging tactics of fishes. pp. 159–171. *In:* D.L.H. Noakes, D.G. Lindquist, G.S. Helfman & J.A. Ward (ed.) Predators and Prey in Fishes, Dr W. Junk Publishers, The Hague.

Roberts, T.R. 1970. Scale-eating American characoid fishes, with special reference to *Probolodus heterostomus.* Proc. Calif. Acad. Sci. 38: 383–390.

Sazima, I. 1977. Possible case of aggressive mimicry in a neotropical scale-eating fish. Nature 270: 510–512.

Sazima, I. 1983. Scale-eating in characoids and other fishes. Env. Biol. Fish. 9: 87–101.

Sazima, I. & F.A. Machado. 1990. Underwater observations of piranhas in western Brazil. Env. Biol. Fish. 28: 17–31.

Sazima, I. & V.S. Uieda. 1980. Scale-eating behavior in *Oligoplites saurus* and records of scale-eating in *O. palometa* and *O. saliens* (Pisces, Carangidae). Revta. bras. Biol. 40: 701–710. (In Portuguese).

Takamura, K. 1983. Interspecific relationship between two Aufwuchs eaters *Petrochromis polyodon* and *Tropheus moorei* (Pisces: Cichlidae) of Lake Tanganyika, with a discussion on the evolution and functions of symbiotic relationship. Physiol. Ecol. Japan 20: 59–69.

Takamura, K. 1984. Interspecific relationships of Aufwuchs-eating fishes in Lake Tanganyika. Env. Biol. Fish. 10: 225–241.

Trewavas, E. 1947. An example of 'mimicry' in fishes. Nature 160: 120.

Whitfield, A.K. 1979. Field observations on the lepidophagous teleost *Terapon jarbua* (Forskål). Env. Biol. Fish. 4: 171–172.

Whitfield, A.K. & S.J.M. Blaber. 1978. Scale-eating habits of the marine teleost *Terapon jarbua* (Forskal). J. Fish Biol. 12: 61–70.

Yamaoka, K. 1982. Morphology and feeding behavior of five species of genus *Petrochromis* (Teleostei: Cichlidae). Physiol. Ecol. Japan 19: 57–75.

Yamaoka, K. 1983. Feeding behaviour and dental morphology of algae scraping cichlids (Pisces: Teleostei) in Lake Tanganiyka. Afr. Stud. Monogr. 4: 77–89.

Yanagisawa, Y., M. Nshombo, M. Nishida & Y. Niimura. 1990. Sexual dichromatism and food habits of the scale-eater *Plecodus straeleni* (Cichlidae, Teleostei) in Lake Tanganyika. J. Ethol. 8: 25–28.