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Source: African Zoology, 45(1):32-40. 2010.

Published By: Zoological Society of Southern Africa

DOI: 10.3377/004.045.0117

URL: <http://www.bioone.org/doi/full/10.3377/004.045.0117>

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# Diversification of prey capture techniques among the piscivores in Lake Tana's (Ethiopia) *Labeobarbus* species flock (Cyprinidae)

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Received 16 September 2009. Accepted 31 October 2009

Lake Tana harbours the only known intact species flock of large cyprinid fishes (15 *Labeobarbus* spp.). One of the most curious aspects of this species flock is the large number (8) of piscivorous species. Cyprinids are not well designed for piscivory (i.e. small slit-shaped pharyngeal cavity, lack of teeth in the oral jaws, lack of a stomach), which raises the question how well adapted these labeobarbs actually are to function as piscivores? In this study we analyse the kinematics of prey capture (by varied combinations of suction, swimming and jaw protrusion) among Lake Tana's piscivorous labeobarbs. Suction feeding kinematics were similar to values reported for other piscivorous fish species. A detailed analysis of several *Labeobarbus* species displayed distinct types of techniques (overswimming, velocity/volume suction with jaw protrusion) suited to capture elusive prey in different macro-habitats. Lake Tana's *Labeobarbus* species evolved a wide range of piscivorous predation techniques, a unique scenario for cyprinid fishes.

**Key words:** adaptive radiation, evolution, functional morphology, predation, trophic segregation.

## INTRODUCTION

The Cyprinidae are the most species-rich (>2000 species; Nelson 1994) and widespread among all freshwater fish families. Despite the enormous abundance of cyprinid fishes throughout the world's lakes and rivers, the *Labeobarbus* species of Lake Tana (Ethiopia) form the only known remaining intact species flock of large cyprinid fishes, since the one in Lake Lanao in the Philippines has almost disappeared due to anthropogenic activities (Kornfield & Carpenter 1984). One of the most intriguing aspects of Lake Tana's presumably young (c. 15 000 years old; de Graaf *et al.* 2007; Lamb *et al.* 2007) *Labeobarbus* species flock is the large number of piscivorous species (8 of 15). Piscivory is rare amongst the highly successful but predominantly benthivorous cyprinid fishes. Cyprinids seem not well designed for piscivory; they lack teeth in the oral jaws, have a small slit-shaped pharyngeal cavity and all lack a stomach with low pH for digesting large prey.

Owing to the seemingly lack of proper tools for piscivory and the young age of the species flock, the question arises how well adapted these

labeobarbs actually are to piscivory? For example, de Graaf *et al.* (2008) showed that average prey size of Lake Tana's piscivorous *Labeobarbus* is small (predator-to-prey length ratio (PPR) mean 0.15, max 0.25) compared to non-cyprinid freshwater piscivores (mean 0.25–0.40 PPR, max 0.40–0.70 PPR; van Ooijen 1982; Winemiller & Kelso-Winemiller 1994; Mittelbach & Persson 1998).

Suction feeding through a rapid expansion of the head volume leading to a negative pressure inside and resulting in water and prey being drawn into the mouth, is probably the most common feeding mode among bony fishes (Osse 1969; Lauder 1980; Muller & Osse 1984). Muller & Osse (1984) described a series of feeding types based on differences in the timing of opercular valve opening, relative contribution of forward motion, absence or presence of jaw protrusion and shape of the flow. Many of Lake Tana's *Labeobarbus* species have evolved unique anatomical features, presumably adaptations to different food resources, since the radiation of Lake Tana's barbs was hypothesized to be driven by trophic resource partitioning (Sibbing *et al.* 1998). Based on predictions from food properties and functional morphology (Food Fish Model) Sibbing & Nagelkerke (2000) suggested that some of Lake Tana's

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piscivores were likely to use different predation strategies (e.g. ambush hunters versus pursuit hunters). In this study we investigated in detail prey capture kinematics among Lake Tana's piscivorous *Labeobarbus* species to determine the extent of ecological segregation in predation techniques. Our objectives were to (1) determine the diversity in the kinematics of head expansion during suction feeding following Muller & Osse (1984); (2) describe the feeding strategies that have evolved among the piscivorous labeobarbs; and (3) discuss the abilities and limitations of Lake Tana's *Labeobarbus* to function as piscivores compared to non-cyprinid piscivores.

## METHODS

### Collection of fish

Three species of piscivorous *Labeobarbus* were caught using hook-and-line, fish traps or bottom trawl in Lake Tana and its affluent rivers. The fish were acclimatized for at least one month before starting any of the experiments. Predators were housed in 250 l tanks (90 × 45 × 45 cm). Each 250 l tank was partitioned by a PVC-slate into two equal parts and one predator was held per section (45 × 45 × 45 cm). Predators were fed live prey fish (*B. humilis*), which were captured daily, sorted according to size and held in 250 l tanks. Prey fish were fed commercial flake food (Trouvit, Trouw, Putten). *Barbus humilis* was used as prey in all feeding performance experiments as it is by far the most common prey species in Lake Tana and forms a significant part of the diet of all piscivorous *Labeobarbus* species (de Graaf *et al.* 2008). The 16 indoor 250 l tanks were part of a semi-closed system; c. 10% of the water was replaced every day by water pumped directly from the lake. The aquarium room was not illuminated by artificial light, but followed the natural light cycle.

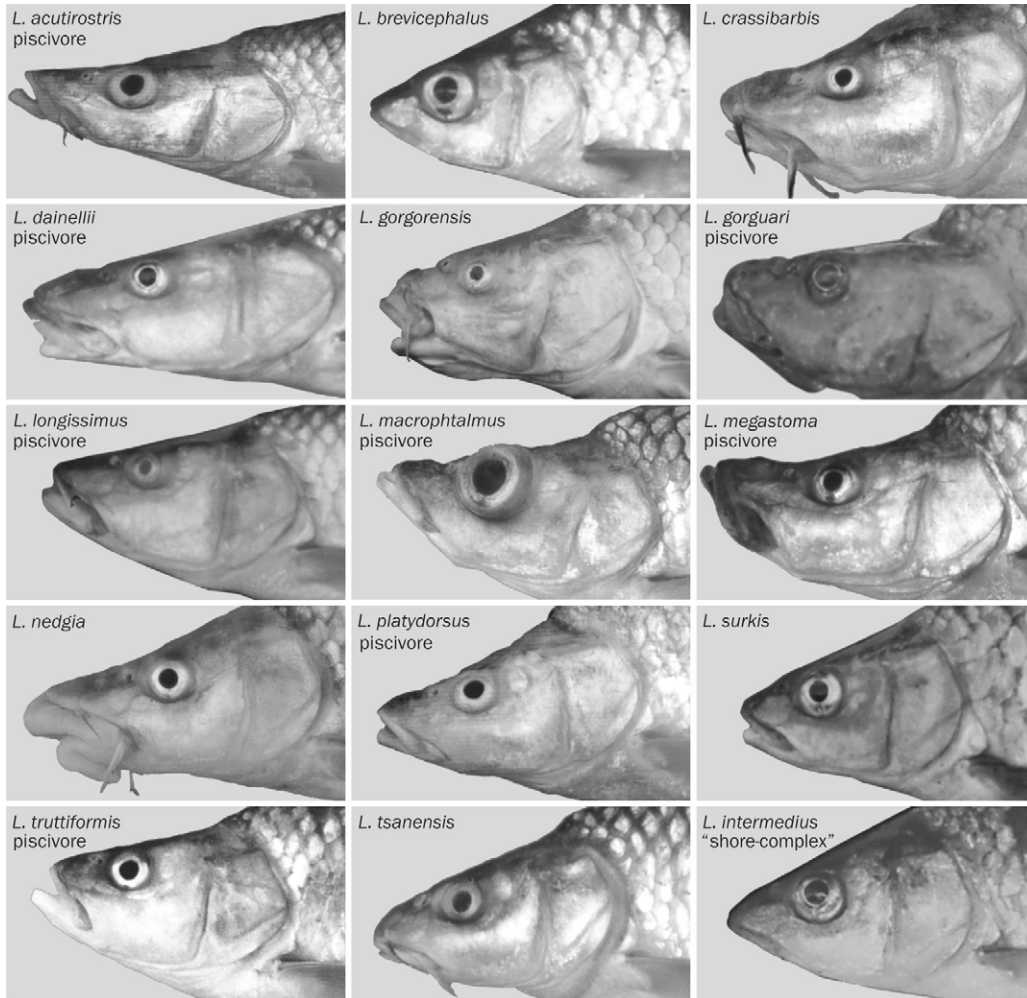
### Predation techniques

After introduction in the experimental tank (90 × 45 × 45 cm), a predator was trained until it foraged willingly despite the regular disturbances associated with conducting the feeding trials. Prey capture events were recorded at 200 images/s with a digital camera (JVC GR-DVL9700) using daylight. A mirror was placed at 45° directly below the position where prey was presented to the predator to obtain an additional ventral view of the capture sequence showing the opening of the opercular valves. Both lateral and ventral views

were recorded in the same image. The back and the bottom of the experimental tank were marked with a 2.5 cm grid. Additional markers were placed at the front of the tank near the bottom. A freshly killed prey fish (*B. humilis*, PPR 0.07–0.25) was presented in a fixed horizontal position 5 cm of the bottom of the tank. A thin thread (0.08 mm diameter) was attached to the body of the prey fish just in front of the dorsal fin, in such a way that when captured by a predator it could be easily dislodged. Offering prey fish in such a way standardized the prey capture for comparison among individuals and species. To quantify the movement of the prey and predator, the images were analysed frame by frame using Media100 for Macintosh and Motion Analyst. Around 20 frames (100 ms total elapsed time) were analysed for each feeding sequence. Several landmarks on the predator (lateral view: the anterior tip of both the upper and lower jaw, the nasal opening as a reference for upper jaw protrusion, the centre of the eye as a reference for the position of the hyoid below; ventral view, posterior tips of the operculi), six points on the prey (ventral/lateral views: anterior end of the head, middle of the body (estimated), posterior end of the tail) and three reference points of the grid at the back of the tank, were digitized. For all sequences,  $T_0$  (time 0) was determined as the time at which the mouth first began to open. After the frames had been digitized, the  $x$  and  $y$  coordinates of 16 landmarks in the lateral and ventral view of the predator and prey were used to calculate the parameters of interest. In total nine kinematic parameters (five related to timing and four related to displacement) were analysed: (1)  $T_{ogmax}$  = time (ms) to maximum oral gape, (2)  $T_{op}$  = time (ms) of opercular valve opening and forming of opercular slits, (3)  $T_{opmax}$  = time (ms) of maximum opercular abduction, (4)  $T_{in}$  = time (ms) that the centre of the prey passed into the oral gape aperture, (5)  $T_{cl}$  = time (ms) to closure of the oral gape, (6)  $D_{og}$  = oral gape opening, distance between upper and lower jaw (Fig. 2a), (7)  $D_{hy}$  = depression of the hyoid (Fig. 2a), (8)  $D_{pr}$  = upper jaw protrusion (in % standard length (SL), Fig. 2a), and (9)  $D_{op}$  = opercular abduction. Morphological characteristics (Fig. 2b) related to predation techniques were measured in 10 specimens of each of the eight piscivorous *Labeobarbus* species.

## RESULTS

The piscivorous labeobarbs were difficult to obtain alive in the field and proved to be easily stressed



**Fig. 1.** Heads of the 15 *Labeobarbus* species of Lake Tana.

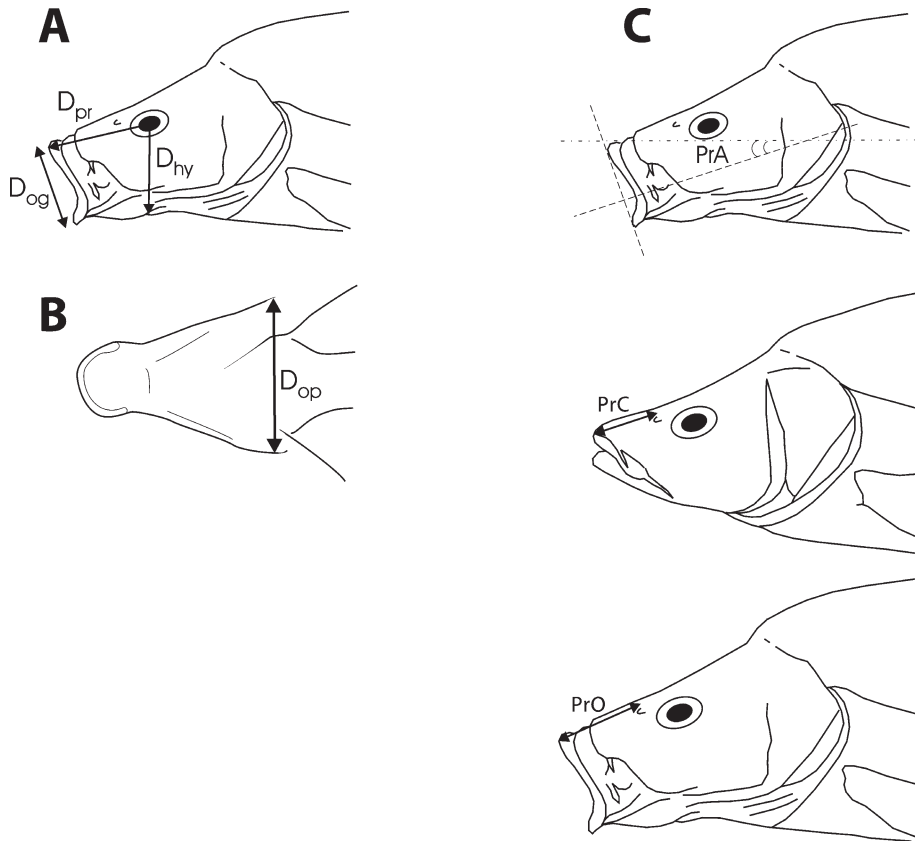
during handling in the laboratory, resulting in the refusal to eat for days or even weeks. Owing to these constraints, successful prey capture events were recorded for only two individuals each of *L. macrophthalmus*, *L. megastoma* and *L. truttiformis*. However, these three piscivorous species have a similar diet and co-occur near the surface in sub-littoral and offshore zones in Lake Tana (de Graaf *et al.* 2008). The observations on prey capture kinematics provided a good opportunity to determine whether these three co-occurring species were possibly segregated along a behavioural dimension, i.e. predation technique.

The patterns of displacement and timing of the head structures during prey capture were highly similar in *L. macrophthalmus* and *L. megastoma* (Table 1; Fig. 3a,b). The timing of maximum oral

gape and maximum opercular abduction ( $T_{ogmax}$  and  $T_{opmax}$ ) did not differ between the three species, but the timing of opercular valve opening and prey intake ( $T_{op}-T_{in}$ ) and the contribution of jaw protrusion (Table 2) deviated markedly in *L. truttiformis* compared to the two other species. In *L. truttiformis*, the opercular slits opened earlier, in many events even before the prey had passed the oral gape (negative values in Table 1) and jaw protrusion contributed little in prey capture (Fig. 3c, Table 2).

## DISCUSSION

Four of Lake Tana's eight piscivorous species occur predominantly near the surface in the sublittoral-pelagic area. *Labeobarbus truttiformis*, *L. megastoma* and *L. macrophthalmus* occur predominantly in the



**Fig. 2.** Position of the displacement variables on the lateral (A) and ventral (B) side of the head measured using prey capture events ( $D_{og}$  = oral gape opening,  $D_{hy}$  = depression of the hyoid,  $D_{pr}$  = upper jaw protrusion,  $D_{op}$  = opercular abduction) and (C) position of morphological measurements (PrA = protrusion angle, PrC = protrusion chain length closed, PrO = protrusion chain length open, and protrusion length (PROT) = PrO-PrC).

offshore areas while *L. longissimus* can also be found in littoral areas (de Graaf *et al.* 2008). All four species forage high in the water column, which explains the high proportion (40–75%, de Graaf *et al.* 2008) of the small pelagic, zooplanktivore *B. tanapelagius* and the almost complete lack (<5%) of benthic *Garra* in their diet. Furthermore, all four species have a very small protrusion angle (2–6°), hence a nearly terminal mouth opening in comparison with the four benthic feeding piscivores (Table 2). Two different predation techniques are deployed by these pelagic piscivores. *Labeobarbus truttiformis* is a typical pursuit hunter using overswimming (e.g. *Oncorhynchus mykiss*; Muller & Osse 1984; Table 1), characterized by the early opening of the opercular valves during prey capture (Table 1) and small protrusion (Table 2). Although no prey capture events for *L. longissimus* were recorded, its similarity in (trophic) morphology to *L. truttiformis* (Table 2; Nagelkerke & Sibbing

2000; Sibbing & Nagelkerke 2001), its distribution in the lake and its diet composition strongly suggest that *L. longissimus* is also a pursuit hunter using overswimming. Pursuit hunting by overswimming is restricted to the open water (Muller & Osse 1984) and is not suitable to capture prey in an environment with high structural complexity, i.e. between rocks or in dense vegetation. The smaller specimens (200–300 mm FL) of *L. longissimus* that do occur in the littoral zone, forage therefore high in the water column. Their diet consists of *B. humilis* and *B. tanapelagius*, the bottom-dwelling *Garra* consequently is rare in their diet. Based on the analysis of the high-speed recordings of prey capture events and their ecology (Table 2), *L. megastoma* and *L. macrophtalmus*, are 'pelagic' ambush hunters using velocity suction with protrusion (cf. *Pterois russelli*; Muller & Osse (1984), Table 1) in Lake Tana's turbid water. Their capture events are characterized by a shorter duration of the whole



**Table 1.** A comparison of kinematic variables for piscivorous *Labeobarbus* (Cyprinidae) with typical representatives (Muller & Osse 1984) of the different types of suction feeding: velocity suction with protrusion in *Pterois russelli*, overswimming with little suction in *Oncorhynchus mykiss* and volume suction in *Gadus morhua*. SL = standard length,  $T_{ogmax}$  = time (ms) to maximum gape,  $T_{opmax}$  = time (ms) to maximum opercular abduction,  $T_{op}$  = time (ms) of opercular valve opening and forming of opercular slits,  $T_{in}$  = time (ms) that the centre of the prey passed the oral gape aperture, Min = minimum value, S.D. = standard deviation,  $n$  = number of successful capture events recorded per individual.

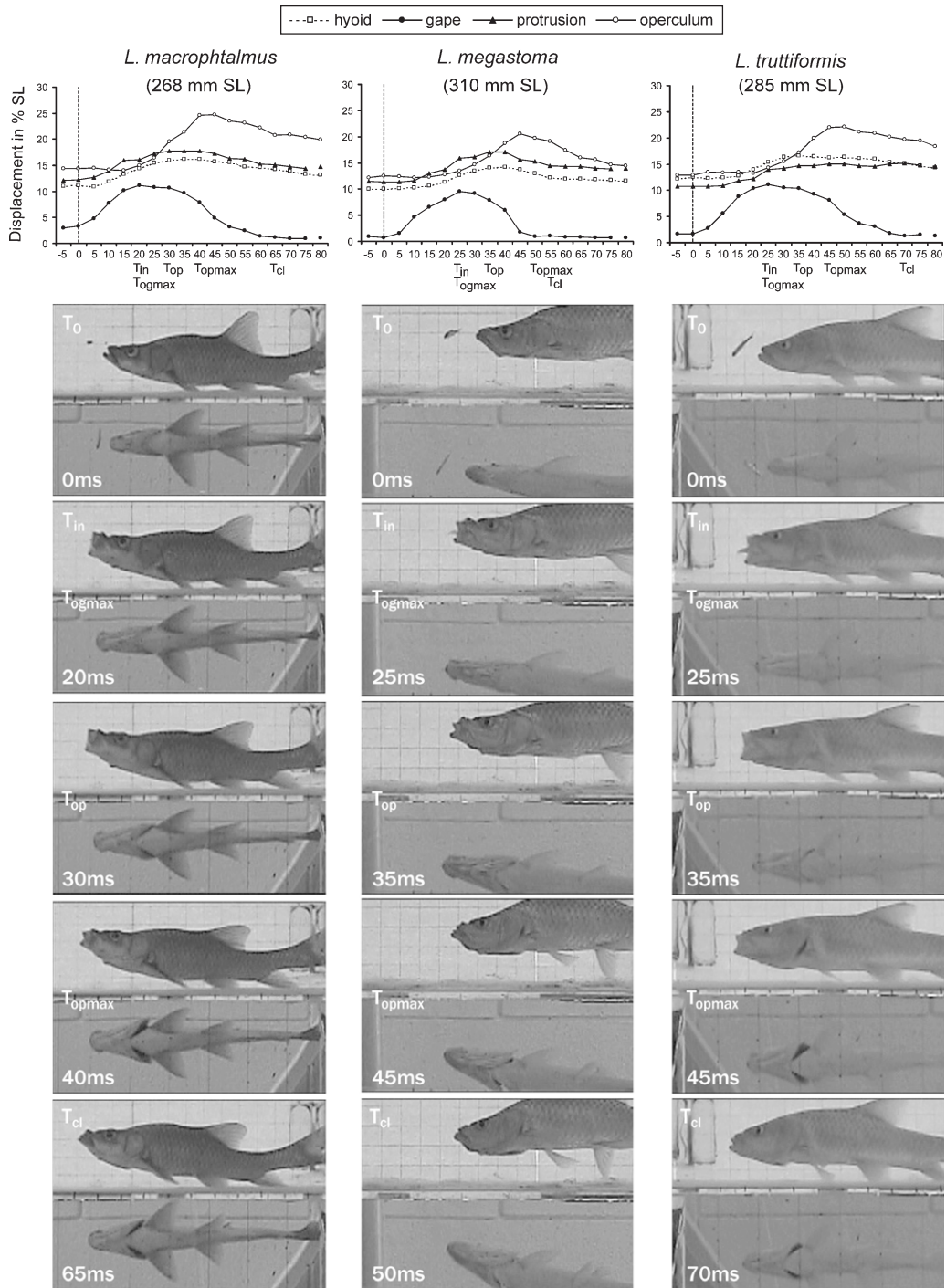
Species	SL (mm)	Prey	$T_{ogmax}$ (ms)			$T_{opmax}$ (ms)			$T_{op}-T_{in}$ (ms)			$n$
			Min	Mean	S.D.	Min	Mean	S.D.	Min	Mean	S.D.	
<b>Velocity suction with protrusion</b>												
<i>L. macrophthalmus</i>	273	Fish	25	39.5	11.3	50	70.5	16.7	10	16.4	6.7	11
<i>L. macrophthalmus</i>	268	Fish	20	33.1	7.8	45	58	11.0	0	9.4	6.0	27
<i>L. megastoma</i>	310	Fish	30	50.6	9.0	50	82.8	11.8	10	16.5	6.1	33
<i>L. megastoma</i>	283	Fish	30	40.0	8.2	65	86.3	39.7	0	27.5	22.5	4
<i>L. gorguari</i> <sup>4</sup>	350	Fish							7	9.5	3.5	2
<i>Pterois russelli</i> (Scorpaenidae) <sup>2</sup>	138	Fish	15	24.4	7.6	23	40	12.3	-1	6.2	5.1	7
<b>Overswimming</b>												
<i>L. truttiformis</i>	285	Fish	30	56.1	16.7	55	89.4	28.2	-25	4.2	12.7	18
<i>L. truttiformis</i>	263	Fish	60	97.8	19.5	110	143	23.6	-35	1.9	12.8	18
<i>Aspius aspius</i> (Cyprinidae) <sup>3</sup>	348	Fish	30			75			-18			
<i>Oncorhynchus mykiss</i> (Salmonidae) <sup>1</sup>	345	Meat	55			70			-17			
<b>Volume suction</b>												
<i>L. dainellii</i> <sup>5</sup>	254	Fish	55	119	37.6	120	210.3	35.1	0	43.3	18.8	21
<i>L. acutirostris</i> <sup>5</sup>	254	Fish	25	53.6	22.1	55	100	34.8	10	25	19.1	7
<i>L. acutirostris</i> <sup>5</sup>	250	Fish	25	67.5	44.3	50	146	77.9	15	26	13.9	5
<i>L. acutirostris</i> <sup>4</sup>	250	Fish							50			1
<i>L. acutirostris</i> <sup>4</sup>	268	Fish							33			
<i>Gadus morhua</i> (Gadidae)	375	Meat	28	32.1	3.6	79	91	10.6	60	65.1	5.2	3

<sup>1</sup>van Leeuwen (1984), <sup>2</sup>Muller & Osse (1984), <sup>3</sup>van Oostenbrugge (unpubl. data), <sup>4</sup>van de Weerd *et al.* (1999), <sup>5</sup>van de Weerd (unpubl. data).

event ( $T_{opmax}$ ), later opening of the opercular valves and a larger protrusion distance (Tables 1 & 2) compared with pursuit hunting *L. truttiformis*. Again the lack of the bottom-dwelling *Garra* in the diet of smaller (200–300 mm FL) *L. megastoma* in the littoral zones shows that their specialization (pelagic ambush hunting using velocity suction with protrusion, terminal oral gape) comes at a cost, i.e. the inability to capture elusive prey from the bottom.

The four benthic predators *L. dainellii*, *L. gorguari*, *L. acutirostris* and *L. platydorsus* are characterized by their downward protrusion (large protrusion angles, 10–44°; Table 2) and the lack of the surface-dwelling *B. tanapelagius* in their diets (de Graaf *et al.* 2008). *Labeobarbus dainellii* and *L. gorguari* both occur in habitats with high structural complexity, rocky shores (both species) and between the stems of submerged vegetation (*L. gorguari*) at the edge of the lake (de Graaf *et al.* 2008). Both environ-

ments are unfavourable for pursuit hunting using overswimming (Muller & Osse 1984). Among the eight piscivorous *Labeobarbus*, the type of suction feeding of *L. dainellii* showed the most resemblance with *Gadus morhua*, volume suction (Table 1). On average the duration of the whole capture event is long and the opercular valves open late. Volume suction (with protrusion) might enable *L. dainellii* to capture prey between rocky substrate, e.g. 'sucking' *Garra* from crevices below its body without the need for a vertical position that would impede a fast escape in this shallow area for predators (e.g. birds). The stationary *L. gorguari* is an ambush hunter using velocity suction with protrusion (Tables 1 & 2). *Labeobarbus acutirostris* and *L. platydorsus* both occur predominantly above sandy/muddy substrates in littoral and sublittoral/pelagic zones, respectively. Based on their diet (*L. acutirostris* ~65% *B. humilis*; *L. platydorsus* ~45% *Garra*), habitat (sandy bottom



**Fig. 3.** Kinematic profiles of four parameters and selected video frames (200 frames/s) from a prey capture event for *Labeobarbus macrophthalmus*, *L. megastoma* and *L. truttiformis*.  $T_0$ , the onset of mouth opening is indicated by a vertical dashed line. Displacement is expressed in percentage standard length.  $T_{ogmax}$  = time (ms) to maximum oral gape,  $T_{in}$  = time (ms) that the centre of the prey passed the oral gape,  $T_{op}$  = time (ms) of opercular valve opening and forming of opercular slits,  $T_{opmax}$  = time (ms) of maximum opercular abduction,  $T_{cl}$  = time (ms) to closure of the oral gape.

**Table 2.** Hypothesized main predation techniques of the eight piscivorous *Labeobarbus* species. Predictions by the Food-Fish Model (FFM) (fig. 7 in Sibbing & Nagelkerke (2000): ++ = good, + = fair, 0 = neutral abilities. Spatial distribution of the particular species: LR = littoral rock, LM = littoral mud, SLB = sublittoral benthic, SLP = sublittoral pelagic, OB = offshore benthic, OP = offshore pelagic, (definitions in de Graaf *et al.* 2008). Diet: G = *Garra* (benthic), H = *B. humilis* (whole water column, except offshore pelagic), T = *B. tanapelagius* (top layer water column). Morphology: PrA = protrusion angle in degrees (see Fig. 2), PROT = protrusion length in percentage standard length (SL) (see Fig. 2).

Species	Predicted FFM <sup>1</sup>		Observed			Type of suction feeding	Predation technique
	Ambush	Pursuit	Distribution <sup>2</sup>	Diel <sup>2</sup>	PrA mean ± 95% CI		
<i>L. dainellii</i>	++	++	LR	G/H	44 ± 4.3	4.1 ± 0.5	Ambush volume suction (with protrusion)
<i>L. gorguari</i>	+	+	LR/LM	G/H	10 ± 4.9	2.5 ± 0.7	Ambush velocity suction with protrusion
<i>L. acutirostris</i>	0	++	LM	H	17 ± 2.8	1.9 ± 0.2	Pursuit/ambush intermediate volume/velocity suction
<i>L. platydorsus</i>	++	0	SLB/OB	G/H	17 ± 3.9	2.0 ± 0.3	Ambush/pursuit intermediate volume/velocity suction
<b>Benthic</b>							
<i>L. macrophthalmus</i>	0	0	SLP/OP	T/H	6 ± 2.0	3.4 ± 0.3	'pelagic' ambush velocity suction with protrusion
<i>L. megastoma</i>	0	++	SLP/OP	T	2 ± 1.3	2.8 ± 0.3	'pelagic' ambush velocity suction with protrusion
<i>L. longissimus</i>	+	++	LR/SLP	T/H	4 ± 3.2	1.5 ± 0.4	Pursuit overswimming
<i>L. truttiformis</i>	+	0	SLP/OP	T	3 ± 1.2	1.5 ± 0.2	Pursuit overswimming
<b>Pelagic</b>							

<sup>1</sup>Sibbing & Nagelkerke (2001), <sup>2</sup>de Graaf *et al.* (2008), <sup>3</sup>van de Weerd *et al.* (1999), <sup>4</sup>van de Weerd (unpubl. data).



with no structural complexity), intermediate protrusion (Table 2) and intermediate type of suction feeding (*L. acutirostris*, Table 1), both predators are probably behavioural opportunists possibly switching between ambush and pursuit hunting with intermediate volume/velocity suction with protrusion. The agile *L. acutirostris* seems to lean more towards pursuit hunting, while *L. platydorsus* probably leans more towards ambush hunting (FFM, Table 2).

Suction feeding in fishes is the result of a highly coordinated explosive expansion of the oropharyngeal and opercular cavity, together with the internal head volume, that results in a rapid drop in pressure (Osse 1969). Prey is drawn into the mouth by a flow of water that is generated by this expansion (Muller & Osse 1984; van Leeuwen 1984). Elusive prey elicit a more powerful prey capture act, i.e. strikes with a larger and faster reduction in pressure, than non-elusive prey (Elshoud-Oldenhave 1979; Nemeth 1997). Because escape speed ('elusiveness') of prey increases with body size (Lundvall *et al.* 1999), the maximum prey size that can be captured by a predator is therefore strongly related to its capacity to develop negative pressure and the orientation of the water flow during suction feeding. The amount of negative pressure that can be generated by a predator is dependent on the dynamics of head expansion and the resultant rate of change in the internal head volume (Muller & Osse 1984). The highest speed of the opening of the oral gape ( $T_{ogmax}$ ) is similar (c. 30ms) among the piscivorous *Labeobarbus* of Lake Tana and representatives of piscivores of other fish families (Table 3; large mouth bass, Svanbäck *et al.* 2002; nurse shark, Motta *et al.* 2002). Therefore, based on acceleration and velocity rates related to prey capture during suction feeding, no differences are expected in prey size between labeobarbs and non-cyprinid piscivores. Further experiments on predation performance (capture success, predation rate), trophic morphology (oral/pharyngeal gape limitations, internal head volume) and predator-prey interactions will need to be undertaken to determine what is constraining prey size in Lake Tana's piscivorous *Labeobarbus*. Lake Tana's *Labeobarbus* species flock is a fascinating example of adaptive radiation and rapid diversification of piscivorous predation techniques, that unexpectedly originated from an ancestral benthivorous design common among African labeobarbs today.

## ACKNOWLEDGEMENTS

We thank the Amhara Regional Agricultural Research Institute of the Amhara National Regional State, Ethiopia for facilitating the *Labeobarbus* project. Furthermore we would like to thank Frew, Elias, Andalemew, Solomon, Kinde, Tadessa, Tassara, Eshetu and Zewde for their fishing efforts and assistance in the laboratory. Erika Nentwich for her support in Ethiopia, the Netherlands and Australia. The research was funded by the Netherlands Foundation for the Advancement of Tropical Research, NWO-WOTRO project W 82-231 (de Graaf) and Schure-Beijerinck-Popping Fonds SBP/JK/2001-44 (van de Weerd).

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Responsible Editor: O. Weyl