Diet composition in relation to morphology in some African anguilliform clariid catfishes

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ABSTRACT. Genera of the catfish family Clariidae that have an extreme anguilliform body shape (e.g. *Dolichallabes*, *Gymnallabes* and *Channallabes*) are also characterized by an extreme hypertrophy of the jaw closing muscles. Whereas it has been demonstrated that the hypertrophy of these muscles results in increased bite performance, the adaptive significance of these enlarged jaw muscles remains unclear. Given that hypertrophied forms bite harder it was suggested that the hypertrophy of the jaw adductors might be correlated with changes in diet or an altered feeding pattern. To test this hypothesis, stomach contents were analysed from specimens of a few more anguilliform species, as well as in a limited set of specimens from some of the less anguilliform clariid species. The results show that specimens with a more anguilliform body-shape have a different feeding pattern with a special preference for coleopterans. However, the absence of bite-marks on the prey retrieved from the stomachs indicated that jaw morphology and bite performance are not likely to be related to the dietary composition in the species with hypertrophied jaw adductors.

KEY WORDS : anguilliformity, Clariidae, diet, ecomorphology, Siluriformes.

INTRODUCTION

Members of the Clariidae, one of the 35 presently recognised families of catfishes (DE PINNA, 1998), mainly occur on the African continent, but can also be found in Minor Asia, the Indian subcontinent and southeast Asia (TEUGELS, 1996). Clariids are primarily freshwater fishes, but they also tolerate brackish water. Together with their ability to utilize atmospheric air through a suprabranchial organ and to "walk" on land, this tolerance partially explains their large area of dispersion (ROBERTS, 1975; TEUGELS, 1996). Clariids, and many other families of Siluriformes, are also characterized by a more benthic and/or nocturnal life-style, combined with morphological adaptations for such a life-style (ALEXANDER, 1965). These alterations are mainly : (1) small eyes, in combination with a highly specialised Weberian apparatus, and the presence of oral barbels, and (2) the dorso-ventral flattening of the head (as an adaptation towards a more benthic life-style) (FINK & FINK, 1981; ADRIAENS & VERRAES, 1997).

Within the Clariidae, both genera with a more fusiform and genera with a distinct anguilliform body shape exist, as well as intermediate forms. The more anguilliform genera show several transformations within the cranial morphology associated with hypertrophy of the adductor mandibulae complex (CABUY et al., 1999; DEVAERE et al., 2001). Although it has been shown that the hypertrophy of the jaw adductors results in an increased bite performance (HERREL et al., 2002), the question remains whether this is an actual adaptation or simply the result of the miniaturization of the skull (DEVAERE et al., 2001).

As the hypertrophy of the jaw adductors results in an increase in bite force, an often suggested and plausible explanation would be that this is an adaptation to a dietary specialisation involving the crushing of hard prey. This explanation can be tested by comparing the diet of hypertrophied forms with that of non-hypertrophied ones. Whereas the diet of some more fusiform genera that show no hypertrophy of the jaw adductors (e.g. *Clarias* sp., SCOPOLI, 1777) has been well investigated (SPATARU et al., 1987; FAGBENRO et al., 1991), little or no information is available concerning the diet of the genera with more hypertrophied jaw adductors.

Thus, the aims of this study were : (1) to determine, based on stomach-content analysis, the overall composition of the diet of different clariid species, (2) to investigate whether the species with hypertrophied jaw adductors show changes in diet compared to species with less hypertrophied jaw adductors and (3) to examine whether the hypertrophy of the jaw adductors can be linked to shifts in diet.

MATERIAL AND METHODS

Sampling

For this study, a total of 306 specimens from six species of clariids were examined, focussing largely on the species with the most extreme hypertrophy of the jaw

adductors : *Channallabes apus* (Günther, 1873) (173 specimens), *Gymnallabes alvarezi* Roman, 1970 (85 specimens) and *Gymnallabes typus* Günther, 1867 (25 specimens). For comparative purposes, the diets of some of the intermediate species of clariids, were also examined : *Platyallabes tihoni* (Poll, 1944) (13 specimens), *Clariallabes melas* (Boulenger, 1887) (five specimens) and *Clariallabes longicauda* (Boulenger, 1902) (five specimens). However, certain geographically distinct populations of *C. apus* and *G. alvarezi* might be in need of transfer from one species to the other. For the purpose of the present paper, however, this issue is of minor importance as the main objective was to determine whether the species with strongly hypertrophied jaw adductors such as *C. apus*, *G. alvarezi*, *G. typus* and *D. microphthalmus*, have specialized diets that might be related to the observed hypertrophy of the jaw adductors. Some of the specimens used were obtained from the Koninklijk Museum voor Midden-Afrika / Musée Royal de l'Afrique Centrale (MRAC), Tervuren, Belgium and some from an expedition to Gabon in September 2000. Due to the scarcity of material, no conclusions as to seasonality or locality of the diet could be made. From all specimens the content of the stomach was removed, sorted and identified up to the level of order.

To assess whether animals actually selected certain prey, several pitfall traps were placed at two distinct sites in Gabon where the fish (half of the *C. apus* specimens and almost all *G. typus* specimens) were collected. These sites were chosen in such a way that they reflected the overall composition of the habitat of the anguilliform clariid species. Pitfalls were placed, for 48 hours, in the swamp area where fish were collected, and randomly arranged at each site. Four aluminium guides were placed perpendicularly around each pitfall to increase capture success. The contents of the traps were sorted and identified as mentioned above.

As it was expected that animals with hypertrophied jaw adductors would preferentially feed on harder prey, the hardness of the prey collected in the pitfalls was determined. By comparing prey in the stomach of the fishes with the hardness data of the available prey we were able to determine whether fish actually selected for harder prey. Prey hardness was measured using a Kistler force transducer (type 9203, Kistler, Zwitserland), connected to a Kistler charge amplifier (type 5058A, Kistler, Zwitserland) and a PC equipped with an electronic measuring board (PC-Scope T512, IMTEC, Germany), as described in HERREL et al. (1999). A screw with narrow pointed tip was attached to the transducer and slowly pushed onto the prey until failure of the exoskeleton of the hardest part of the body (usually the head and prothorax). The maximal force recorded just before failure of the prey was considered to be the hardness of that prey. Differences in prey hardness between dietary categories were compared by means of pairwise Mann-Whitney U tests.

As the formaldehyde solution used to preserve arthropods in the pitfalls might affect hardness, we experimentally tested the effects of preservation on the hardness of two prey types : mealworms and crickets. Thirty house crickets (*Acheta domestica*) and twenty large mealworms (*Tenebrio molitor*) were selected for testing. Each prey group was randomly subdivided in half, and euthanised. One half of the prey groups was subsequently preserved in a 10% aqueous formaldehyde solution for five days. The other half of each group was measured (length and width) using Mitutoyo (type CD 20DC) electronic callipers, and weighed to the nearest 0,001 gram using a Denver Instruments (M220) electronic balance. Next, prey hardness was measured for each individual prey item using a Kistler (type 9203) force transducer attached to a portable Kistler charge amplifier (type 5995) as described in HERREL et al. (2001). Preserved prey were taken out of the formaldehyde, rinsed, blotted dry and measured, weighed and crushed as described above. Two-way analysis of variance was used to estimate the effects of preservation and prey type on prey hardness (SPSS v. 10.05).

Data analysis

To describe and compare diets among species, several indices per food item were calculated :

– Relative importance index (PINKAS et al., 1971) :

$$IRI = (\%N + \%V) \cdot \%Oc$$

where %N and %Oc are, respectively, numeric abundance and the frequency of occurrence, and %V is the volumetric percentage of the prey type. In this research the %V was replaced by %DW as suggested by KONÉ (2000). In addition, %IRI was calculated, being the proportion of IRI of each prey type in relation to the total IRI value.

– Electivity index (KOHLER & NEY, 1982) :

$$E_i = (\%N - \%N_{pit}) / (\%N + \%N_{pit})$$

where %N and %N$_{pit}$ are as mentioned above. This index compares the abundancies of the prey items as found in the stomachs with those in the pitfalls, thus providing an indication of the degree to which the diet is selective.

In addition, the diets from the two species with the largest sample size, *C. apus* and *G. alvarezi*, were compared using a randomisation test designed by MANTEL (1967) and used by PATTERSON (1986) and SEVENSTER & BOUTON (1998) for the comparison of diets. This procedure uses the mean percentage overlap as a test statistic. The percentage overlap between two individuals *a* and *b* is calculated as :

$$O_{ab} = \sum_i \min(p_{ai}, p_{bi})$$

where p_{ai} is the proportion of prey type *i* used by specimen *a* and min (p_{ai}, p_{bi}) is the smallest of p_{ai} and p_{bi}. The statistic for interspecific overlap is the mean of the overlaps in all possible heterospecific pairs of individuals, and the statistic for intraspecific similarity is the mean of the overlaps in all possible pairs of individuals of the same species (SEVENSTER & BOUTON, 1998).

RESULTS

The dietary results are summarized below and are sorted per species as they were defined by POLL (1942).

Species diet

Table 1 shows the results of the stomach content analysis. For *C. apus* the table shows that Coleoptera is the species' main prey type (%IRI = 89,31). In comparison with the number of Coleoptera found in the pitfalls the species

shows actual selection for the given prey item ($E_i = 0,69$), which also seemed to be the case for Isoptera ($E_i = 0,75$). The latter value is, however, of little significance and will be dealt with further in the discussion. Hymenoptera ($E_i =$ -0,66) and also Hemiptera, Diptera and Araneae are underrepresented. Furthermore, *C. apus* has a high vacuity index and a low Shannon-Wiener index or small diet breadth.

TABLE 1

Diet composition in C. apus and G. alvarezi

Prey category	N	%IRI	%Pit	E_i	N	%IRI	%Pit	E_i
Mollusca								
Gastropoda	3	0.36	-	-	-	-	-	-
Malacostraca								
Isopoda	2	0.7	-	-	-	-	-	-
Arachnida								
Araneae	5	1.90	7.80	-0.27	-	-	-	-
Insecta								
Ephemeroptera	3	0.21	-	-	-	-	-	-
Odonata	6	2.01	-	-	1	0.96	1.00	0.41
Dictyoptera	1	0.34	0.49	0.30	-	-	-	-
Isoptera	15	0.51	1.95	0.75	-	-	-	-
Hemiptera	5	1.24	9.76	-0.37	1	0.09	4.81	-0.35
Diptera	8	1.84	9.76	-0.15	5	1.86	3.85	0.50
Hymenoptera	7	1.23	31.22	-0.66	1	0.12	37.50	-0.88
Coleoptera	54	89.31	8.78	0.69	34	96.97	31.73	0.43
Actinopterygii								
Cypriniformes	2	0.65	-	-	-	-	-	-
Aves								
Sp.	-	-	-	-	1	-	-	-
No. of stomachs examined			173				85	
Vacuity index		68.79				75.29		
Shannon-Wiener index			0.57				0.16	

Also for *G. alvarezi* Coleoptera form the majority of the diet (%IRI = 96,97) and a positive selection towards this prey type is present (E_i=0,43). Other results have little significance, since the absolute numbers of prey eaten were low. Remarkable, however, is the small bird found in one of the *G. alvarezi* stomachs. The results also show a high vacuity index and low Shannon-Wiener index.

Table 2 combines the results of the other species examined. The numbers of prey found in these analyses were, however, so low that no significant conclusions could be made. Nevertheless the data are presented for comparison and can be considered as indicative. The high percentage of dipteran larvae and Ephemeroptera is remarkable for *G. typus* and *P. tihoni*. The high abundance of fish prey in the analysis of *C. melas* is another interesting point of possible divergence compared to the two diets previously mentioned. The results for *C. longicauda*, however, only show Coleoptera within the diet.

Prey Hardness

Fig. 1 shows the results obtained on the relative hardness of different prey types that occur within the habitat of the investigated species. These results were analysed by means of pairwise Mann-Whitney U tests, from which the respective p-levels are given in Table 3. This table shows that Hymenoptera are significantly harder than all other investigated prey types, followed by Coleoptera and Hemiptera, which in turn are significantly harder than all remaining prey, except for Dictyop-

TABLE 2

Diet composition in *G. typus*, *P. tihoni*, *C. melas* and *C. longicauda*

Species	Prey Category	N	%N
G. typus	*Insecta*		
	Diptera	10	90.91
	Coleoptera	1	9.09
Vacuity index = 88,0 %			
P. tihoni	*Insecta*		
	Ephemeroptera	5	71.43
	Diptera	2	28.57
Vacuity index = 76,9 %			
C. melas	*Insecta*		
	Odonata	2	40.00
	Diptera	1	20.00
	Actinopterygii		
	Gonorhynchiformes	2	40.00
Vacuity index = 40,0 %			
C. longicauda	*Insecta*		
	Coleoptera	3	100.00
Vacuity index = 60,0 %			

tera. Gryllidae, Araneae and Decapoda are in turn significantly softer than all other prey items, except for Dictyoptera. Supplementary tests also showed that effects of preservation on prey hardness were present but had no influence on the relative proportions of prey hardness.
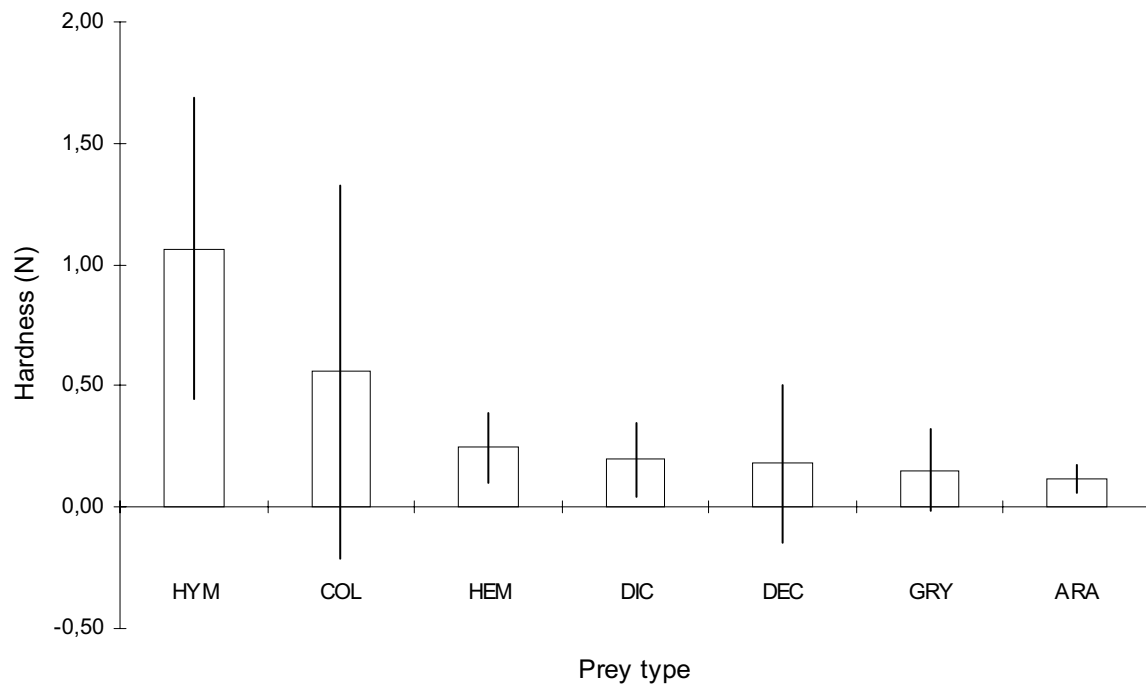
Fig. 1. – Comparison of hardness of prey from pitfalls (HYM : Hymenoptera; COL : Coleoptera; HEM : Hemiptera; DIC : Dictyoptera; DEC : Decapoda; GRY : Gryllidae; ARA : Araneae) The column height displays the average, the whiskers indicate standard deviation.

TABLE 3

Pairwise comparison of U-values (bottom) and p-levels (top) in Mann-Whitney U test concerning relative hardness of possible prey types. (DEC : Decapoda; ARA : Araneae; GRY : Gryllidae; DIC : Dictyoptera; HEM : Hemiptera; HYM : Hymenoptera; COL : Coleoptera) *p < 0.05; ** p < 0.005.

	DEC	ARA	GRY	DIC	HEM	HYM	COL
DEC		0,136	0,096	0,148	*	**	**
ARA			0,835	0,440	*	**	*
GRY				0,250	*	**	*
DIC					0,444	*	0,353
HEM						**	0,372
HYM							**
COL							

Dietary overlap

The Schoener index mainly indicated dietary overlap between *C. apus* and *G. alvarezi*, a hypothesis that was further tested in a randomisation test, of which the results are represented in Table 4. The table shows that the diets

TABLE 4

Observed (Obs.) and expected (Exp.) overlaps, and estimated significance, based on 1000 simulations.

Overlap	Obs.	Exp.	Significance	
Between groups	36.8	31.5	p = 1.000	(100.0% of simulations < observed)
Within *C. apus*	22.6	31.3	p = 0.001	(0.1% of simulations > observed)
Within *G. alvarezi*	60.6	31.7	p = 1.000	(100.0% of simulations > observed)

of *C. apus* and *G. alvarezi* do not differ significantly (p = 1.00). The results also show a high intraspecific overlap in *C. apus* (p = 0.001) and a low intraspecific overlap in *G. alvarezi* (p = 1.000).

DISCUSSION

This study indicates that both *C. apus* and *G. alvarezi* mainly feed on Coleoptera and that their diets in general do not differ significantly. This is indicated by the Schoener index as well as in the randomisation test. The latter, however, reveals a much higher intraspecific overlap in *C. apus* than in *G. alvarezi*, which could imply that *G. alvarezi* is a more specialised feeder, whereas *C. apus* has a more generalised feeding habit (SEVENSTER & BOUTON, 1998). The fact that the abundance of Coleoptera was lower in the pitfalls than in the stomachs of both species nevertheless indicates that both species tend to have a preference for Coleoptera (E_i = 0.69 and 0.43). The fact that both diets are characterized by a rather low Shannon-Wiener index demonstrates that the diet is highly specialised (LABROPOULOU et al., 1997), which is confirmed in the randomisation test for *G. alvarezi* but not for *C. apus*. Feeding intensity and frequency are negatively related to the number of empty stomachs, thus the high vacuity index that was found in *C. apus* as well as in *G. alvarezi* indicates that in both species intensity and frequency of feeding are very low (BOWMAN & BOWMAN, 1980). In addition, feeding intensity and frequency are directly correlated with meal size and digestion time (FANGE & GROVE, 1979). All these observations suggest that both species mainly feed on large or relatively indigestible food (*e.g.* hard prey), which tallies with the observation that mainly Coleoptera are eaten. On the other hand, Table 3 showed that not only Coleoptera but also

Hymenoptera and Hemiptera were significantly harder than most other preys. The latter two prey types, however, were underrepresented in the stomachs, and thus a negative preference towards both prey types seems to be present. This is also confirmed by the E_i of both prey types in *C. apus* as well as in *G. alvarezi* (Table 1). As to Hymenoptera, it may be mentioned that they were mainly ants; ants produce venom, which makes them less attractive (TAYLOR et al., 2002). The same may be suggested for Hemiptera, since eight of the ten families of Hemiptera that are considered aquatic have specialised glands that emit pungent, protective secretions against potential predators (SCRIMSHAW & KERFOOT, 1987). Within the Coleoptera, however, no species are known to be venomous (BLUM, 1981).

The results in other clariids, discussed below, have to be considered with care since data on these were few, although they provide some interesting indications.

In *G. typus*, for instance, the results show a different feeding pattern. The vacuity index is very high (Table 2), so the species may also feed on large or hard prey items. The data on the stomach contents, however, do not confirm this, since mainly small Diptera were eaten (Table 2). For *P. tihoni* the vacuity index is again very high (Table 2). Again little or no evidence of a diet of large and/or relatively indigestible prey is found. In both *Clariallabes*-species, again relatively high vacuity indices were found. Also in *C. longicauda* large and relatively indigestible prey were found, comparable to *C. apus* and *G. typus*, which is also indicated by a high Schoener index between the latter two species and *C. longicauda* (Table 2).

The data of *C. apus* and *G. alvarezi* seem to confirm the assumption that the hypertrophy of the main jaw muscles in these anguilliform species is an actual adaptation towards dietary changes, which is to a high extent confirmed by the data on relative prey hardness. However, when examining the prey items that were found within the stomachs, it was noticed that most of them were intact and had no bitemarks. This indicates that both species swallow their prey whole without prior oral or pharyngeal processing, apart from buccal transport. The swallowing movements are mainly accomplished by hyoid depression and through the action of protractor hyoidei, hyohyoideus inferior and sternohyoideus (SCHAEFER & LAUDER, 1986; LAUDER, 1980). In conclusion it can be stated that the current analysis of the diet does not support the hypothesis that hypertrophism of the musculus adductor mandibulae complex is an adaptation to feeding on larger or harder prey. Yet, these hypertrophied muscles may enable the fish to occasionally eat larger or harder preys, as in the example of the small bird that was eaten by one of the *G. alvarezi* specimens. The fact remains, however, that the diet of both *C. apus* as *G. alvarezi* is very selective towards coleopteran prey, since intensive feeding on Coleoptera is not widespread among teleosts. Even when regarding the diet of an other eel-shaped freshwater teleost such as *Chendol keelini* KOTTELAT & LIM, 1994 (Chaudhuriidae), the number of coleopteran prey only represented an average of 2.3 % of the diet (KERLE et al., 2000). Also in data on diets of other Clariidae as *Heterobranchus bidorsalis* GEOFFROY ST. HILAIRE, 1808 and *Clarias gariepinus* (BURCHELL, 1822) low numbers of coleopteran prey are found. In *Clarias gariepinus* a figure of 6.8 % (FAGBENRO et al., 1991) is mentioned and in *Heterobranchus bidorsalis* an exact number of coleopteran prey was not given but the total number of insect prey only added up to an average of 19.2 % of the diet (SPATARU et al., 1987).

As far as the diet results of *G. typus* are concerned, a different diet was found, mainly consisting of mosquito-larvae. However, the high vacuity index found in the specimens examined precludes justifiable interpretation of these results.

In conclusion, this study shows that the diet of both *C. apus* and *G. alvarezi* is a very selective one. Both species mainly feed on Coleoptera, which are generally harder than other prey items. Although these results could indicate that the main jaw muscles are extremely enlarged as an adaptation towards an altered and specialized feeding pattern, the absence of bite marks on hard prey items suggests that both species presumably feed by swallowing rather then biting. This suggestion is further confirmed by the results of VAN WASSENBERGH (2003), who stated that features in favour of an increased biting force (such as enlarged jaw muscles) have consequences on suction feeding mechanisms. As a consequence, this still leaves the question on the functional significance of these altered jaw muscles open, which could confirm the hypothesis by DEVAERE et al. (2001) that they could well be just the result of the miniaturization of the skull.

REFERENCES

ADRIAENS, D. & W. VERRAES (1997). Some consequences of transformations in siluriform chondrocrania : a case study of *Clarias gariepinus* (Burchell, 1822) (Siluriformes : Clariidae). *Neth. J. Zool.*, 47 : 349-363.

ALEXANDER, R.M. (1965). Structure and function in the catfish. *J. Zool. Lond.*, 148 : 88-152.

BLUM, M.S. (1981). *Chemical defenses in arthropods*. Academic Press, New York.

BOWMAN, R.E. & E.W. BOWMAN (1980). Diurnal variation in the feeding intensity and catchability of silver hake (*Merluccius bilinearis*). *Can. J. Fish. Aquat. Sci.*, 37 : 1565-1572.

CABUY, E., D. ADRIAENS, W. VERRAES & G.G. TEUGELS (1999). Comparative study on the cranial morphology of *Gymnallabes typus* (Siluriformes : Clariidae) and their less anguilliform relatives, *Clariallabes melas* and *Clarias gariepinus*. *J. Morphol.*, 240 : 169-194.

DE PINNA, M.C.C. (1998). Phylogenetic relationships of Neotropical Siluriformes (Teleostei : Ostariophysi) : Historical overview and synthesis of hypotheses. In : MALABARBA, L.R., R.E. REIS, R.P. VARI, Z.M. LUCENA & C.A.S. LUCENA

(eds), *Phylogeny and classification of Neotropical fishes*. Edipucrs, Porto Alegre : 279-330.

DEVAERE, S., D. ADRIAENS, W. VERRAES & G.G. TEUGELS (2001). Cranial morphology of the anguilliform clariid *Channallabes apus* (Günther, 1873) (Teleostei : Siluriformes) : are adaptations related to powerful biting? *J. Zool. Lond.*, 255 : 235-250.

FAGBENRO, O.A., T.S. OLANIRAN & A.O. ESAN (1991). Some aspects of the biology of the catfish, *Heterobranchus bidorsalis* Geoffrey Saint-Hilaire, 1809 (Clariidae) in river Ogbese, Nigeria. *Rev. Zool. Afr.*, 105 : 363-372.

FANGE, R., & D. GROVE (1979). Digestion. In : HOAR, W.S., D.J. RANDALL & J.R. BRETT (eds), *Fish physiology Vol VIII. Bioenergetics and growth*. Academic Press, New York : 162-260.

FINK, S.V., & W.L. FINK (1981). Interrelationships of the ostariophysan fishes (Teleostei). *Zool. J. Linn. Soc.* 72 : 297-353.

HERREL, A., M. VERSTAPPEN, & F. DE VREE (1999). Modulatory complexity of the feeding repertoire in scincid lizards. *J. Comp. Physiol.*, 184 : 501-518.

HERREL, A., R. VAN DAMME, B. VANHOOYDONCK, & F. DE VREE (2001). The implications of bite performance to diet in two species of lacertiid lizards. *Can. J. Zool.*, 79 : 662-670.

HERREL, A., D. ADRIAENS, P. AERTS, & W. VERRAES (2002). Bite performance in clariid fishes with hypertrophied jaw adductors as deduced by bite modeling. *J. Morphol.*, 253 : 196-205.

KERLE, R., R. BRITZ, & P.K.L. NG (2000). Habitat preference, reproduction and diet of the earthworm eel, *Chendol keelini* (Teleostei : Chaudhuriidae). *Env. Biol. Fish.*, 57 : 413-422.

KOHLER, C.C., & J.J. NEY (1982). A comparison of methods for quantitative-analysis of feeding selection of fishes. *Env. Biol. Fish.*, 7 : 363-368.

KONÉ, T. (2000). *Régime alimentaire et reproduction d'un tilapia lagunaire (Sarotherodon melanotheron Rüppel, 1852) dans la rivière bia et le lac de barrage d'ayamé (Côte D'Ivoire)*. Unpublished Phd-thesis, KULeuven, Leuven.

LABROPOULOU, M., A. MACHIAS, N. TSIMENIDES, & A. ELEFTHERIOU (1997). Feeding habits and ontogenetic diet shift of the striped mullet, *Mullus surmuletus* Linnaeus, 1758. *Fish. Res.*, 31 : 257-267.

LAUDER, G. V. (1980). Evolution of the feeding mechanism in primitive Actinopterygian fishes : a functional anatomical analysis of *Polypterus*, *Lepisosteus*, and *Amia*. *J. Morphol.*, 163 : 283-317.

MANTEL, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Res*, 27 : 209-220.

PATTERSON, G. B. (1986). A statistical method for testing dietary differences. *New. Zeal. J. Zool.*, 13 : 113-115.

PINKAS, L., M.S. OLIPHANT, & I.L.K. IVERSON (1971). Food habits of Albacore, Bluefin Tuna, and Bonito in California waters. *Cal. Fish Game Fish. Bull.*, 152 : 1-105.

POLL, M. (1942). Description d'un genre nouveau de Clariidae originaire de Congo Belge. *Rev. Zool. Bot. Afr.*, 36 : 96-100.

ROBERTS, T.R. (1975). Geographical distribution of African freshwater fishes. *Zool. J. Linn. Soc.*, 57 : 249-319.

SCHAEFER, S.A. & G.V. LAUDER (1986). Historical transformation of functional design : evolutionary morphology of feeding mechanisms in Loricarioid catfishes. *Syst. Zool.*, 35 : 489-508.

SCRIMSHAW, R.W. & W.C. KERFOOT (1987). Chemical defenses of freshwater organisms : beetles and bugs. In : KERFOOT W. C. & A. SIH. (eds), *Predation : direct and indirect impacts on aquatic communities*. University Press of New England, Hanover : 240-262.

SEVENSTER, J.G. & N. BOUTON (1998). The statistical significance of diets and other resource utilization patterns. *Neth. J. Zool.*, 48 : 267-272.

SPATARU, P., J.A.R. VIVEEN & M. GOPHEN (1987). Food composition of *Clarias gariepinus* (= *C. lazera*) (Cypriniformes, Clariidae) in Lake Kinneret (Israel). *Hydrobiol.* 144 : 77-82.

TAYLOR, W.A., P.A. LINDSEY & J.D. SKINNER (2002). The feeding ecology of the aardvark *Orycteropus afer*. *J. Arid Env.*, 50 : 135-152.

TEUGELS, G.G. (1996). Taxonomy, phylogeny and biogeography of catfishes (Ostariophysi, Siluroidei) : an overview. *Aq. Liv. Res.*, 9 : 9-34.

VAN WASSENBERGH, S., A. HERREL, D. ADRIAENS & P. AERTS (2003). Effects of jaw adductor hypertrophy on buccal expansions during feeding of air breathing catfishes (Teleostei, Clariidae). *Zoomorph.*, *in press*.