Modulation and Variability of Prey Capture Kinematics in Clariid Catfishes

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ABSTRACT   Species with narrow or limited diets (trophic specialists) are expected to be less flexible in their feeding repertoire compared to species feeding on a wide range of different prey (trophic generalists). The ability to modulate prey capture kinematics in response to different prey types and prey position, as well as the overall variability in prey capture kinematics, is evaluated in four clariid species ranging from trophic generalist (*Clarias gariepinus*) to species with morphological specializations and a narrow diet (*Channallabes apus* and *Gymnallabes typus*). High-speed video recordings were made of prey captures on two prey that differ in shape, attachment strength and hardness. While the observed amount of strike-to-strike variability in prey capture kinematics is similar for all species and not influenced by prey type, only the two less specialized species showed the ability to modulate their prey capture kinematics in function of the presented prey types. All species did, however, show positional modulation during the strike by adjusting the magnitude of neurocranial elevation. These results indicate that the narrow dietary breadth of trophic specialists is indeed indicative of functional stereotypy in this group of fishes. Although most studies focussing on prey processing found a similar result, the present study is one of the few that was able to demonstrate this relationship when focussing on prey capture mechanics. Possibly, this relationship is less frequently observed for prey capture compared to prey processing because, regardless of prey type, the initial capture of prey requires a higher amount of variability. *J. Exp. Zool. 305A:559–569, 2006.*   © 2006 Wiley-Liss, Inc.

In evolutionary biology, it has been hypothesized that trophic breadth is correlated with behavioural and functional versatility or flexibility. Species with limited diets (trophic specialists) are expected to be less flexible in their feeding capacities compared to species that feed on a wide range of different prey (trophic generalists). Indeed, trophic generalists often have to switch from one prey to another and the ability of generalists to change their feeding behaviour in function of the type or position of the prey (i.e., modulation) is an important aspect of their success (e.g., Norton, '91, '95; Nemeth, '97a,b). In contrast, because trophic specialists restrict themselves to a limited range of prey for which they possess specific morphological and/or behavioural modifications (Ferry-Graham et al., 2002), the importance of being able to handle a wide variety of prey decreases. Although several experimental tests on fishes have supported the above hypothesis (Lauder, '83a,b; Sanderson, '91; Ralston and Wainwright, '97), other studies failed to demonstrate this suggested stereotypy of specialists compared to the flexibility of generalists (Sanderson, '88, '90) or even showed striking examples countering this hypothesis (Liem, '78, '80,'84; Norton, '91). Yet, the reason why support for this hypothesis is found in some cases and not in others remains unclear.

In this study, the variability and modulation of prey capture kinematics is studied in four catfish species of the family Clariidae (*Clarias gariepinus*, *Clariallabes longicauda*, *Gymnallabes typus* and *Channallabes apus*) that show clear differences in the diversity of their diet (Fig. 1). *Clarias gariepinus* is a typical example of a trophic generalist with a broad diet of different prey ranging in size from zooplankton to fishes half its own length (Groenewald, '64; Bruton, '79; Yalçin et al., 2001). This species feeds in a variety of habitats and in fluctuating marginal areas of lakes and rivers. *Clarias gariepinus* switches from one prey to another as prey availability (density and accessibility) changes (Bruton, '79). *Clarias gariepinus* is also known to use multiple feeding modes like foraging, shovelling, surface feeding and group hunting (Bruton, '79), and different structural adaptations can be linked to different feeding types ranging from filter feeding to piscivory (Groenewald, '64). Unlike *Clarias gariepinus*, the other clariid species used in this study (*Clariallabes longicauda*, *Gymnallabes typus* and *Channallabes apus*; Fig. 1) have developed unusually large (or hypertrophied) jaw adductors, and also lack elongated and numerous gill rakers
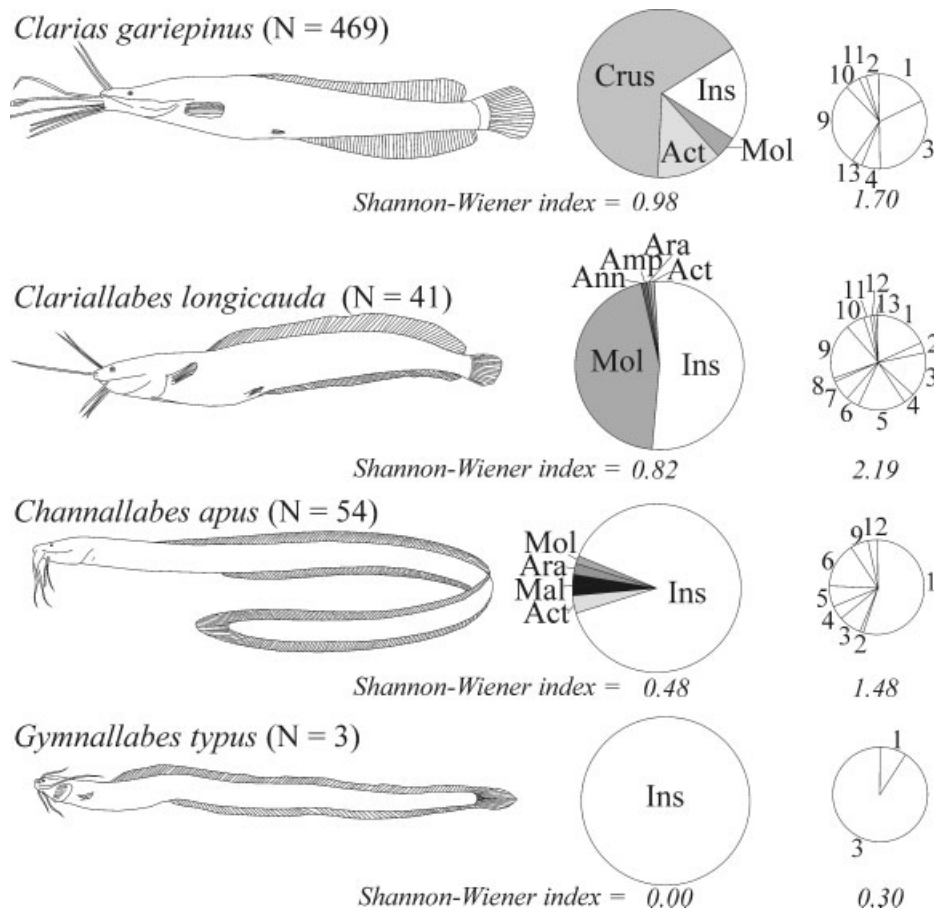

Fig. 1. Dietary composition of four species of Clariidae according to the literature (Bruton, '79 for *Clarias gariepinus*, Wyckmans, 2004 for *Clariallabes longicauda* and Huysentruyt et al., 2004 for *Channallabes apus* and *Gymnallabes typus*). The Shannon–Wiener index of dietary diversity was used to quantify the degree of specialization in each species, and is calculated by $\sum p_i \ln p_i$, where p_i is the numerical proportion of a particular prey category. The large pie-charts in the middle give broad taxonomic groupings (see legend below). The smaller pie-charts on the right side illustrate the numerical proportions of the most important groups of insects in the diet. Drawings of *Channallabes apus* and *Gymnallabes typus* are made after Teugels and Adriaens (2003). Legend: Act = Actinopterygii, Amp = Amphibia, Ann = Annelida, Ara = Arachnida, Crus = Crustacea, Ins = Insecta, Mol = Mollusca, 1 = Colleoptera, 2 = Dictyoptera, 3 = Diptera, 4 = Hemiptera, 5 = Hymenoptera, 6 = Isoptera, 7 = Lepidoptera, 8 = Mecoptera, 9 = Odonata, 10 = Orthoptera, 11 = Trichoptera, 12 = Ephemeroptera and 13 = others. N = number of stomachs analysed with content. Although the dietary data sample of *Gymnallabes typus* is small, similar results are found for *Gymnallabes alvaresi* (Huysentruyt et al., 2004). This species (closely related to *Gymnallabes typus*) ingests Coleopterans in high proportions and has a low Shannon–Wiener index of diet diversity.

(Cabuy et al., '99). While the diet of *Clariallabes longicauda*, a species with an intermediate degree of jaw adductor hypertrophy is still relatively diverse, the trophic diversity is strongly reduced in the anguilliform representatives *Channallabes apus* and *Gymnallabes typus* (Fig. 1). According to Herrel et al. (2002), modifications of the feeding system (i.e., jaw adductor hypertrophy) enable these species to exert much larger bite forces onto prey (bite forces for *Channallabes apus* are more than 10 times higher than *Clarias gariepinus* for a skull length of 39 mm). Given this increased bite performance, it was not surprising that dietary analyses showed an altered and more selective feeding pattern for species that possess hypertrophied jaw adductors with a special preference for coleopterans, which are indeed hard prey (Huysentruyt et al., 2004).

Here, we test whether the trophic generalists exhibit a greater ability to modulate their prey capture kinematics in response to different prey types when compared with the more specialized species. We also tested whether there is a relationship between the overall variability of the exhibited kinematic pattern and the degree of trophic specialization and whether the experimental prey types influence the variability of the kinematic patterns (see also Wainwright and Friel, 2000). Not only prey type, but also prey position can elicit alternative prey capture movements (Elshoud-Oldenhave and Osse, '76; Lauder and Liem, '80; Liem, '80; Lauder, '81). Therefore, we also tested the ability of these catfish species to adjust their head position with respect to the prey right before prey capture. As clariid catfishes are mainly nocturnal predators relying predominantly on chemotactile and electrical signals for prey detection (Bruton, '79; Hanika and Kramer, 2000), such positional "fine-tuning" during prey capture can be important in this group of fishes.

MATERIALS AND METHODS

Animals

Seventeen adult specimens (six *Clarias gariepinus*, four *Clariallabes longicauda*, four *Channallabes apus* and three *Gymnallabes typus*) were used in the experiments. The *Clarias gariepinus* specimens were aquarium-raised specimens of which larval stages were initially obtained from the Laboratory for Ecology and Aquaculture (Catholic University of Leuven). Specimens of *Clariallabes longicauda* and *Channallabes apus* were caught in Northern Gabon. *Gymnallabes*

typus was imported from Western tropical Africa. Cranial lengths (CLs) of the *Clarias gariepinus* specimens were 44.4, 44.7, 47.5, 47.5, 51.7 and 56.6 mm. The *Clariallabes longicauda* individuals had CLs of 32.4, 34.7, 35.7 and 49.0 mm. The measured CLs for *Channallabes apus* and *Gymnallabes typus* were respectively 22.6, 23.10, 24.2, 25.80 mm and 19.20, 20.8, 22.15 mm. CL was defined as the distance between the rostral tip of the premaxillary and the caudal tip of the occipital process. The animals were kept separate in 20 L test aquaria and were trained to capture the presented food inside a narrow, projecting feeding arena (25 cm length, 8 cm width, 15 cm water height) in the aquarium (which forced the animals to feed in a position perpendicular to the camera).

Prey

Two different prey types were used: (1) a piece of cod fillet (*Gadus morhua*) of about 3 cm³ and (2) a North Sea shrimp (*Pandalus borealis*) of approximately 4 cm in total length. Both prey types were attached to a thin, plastic-coated steel wire and were suspended about 5 cm above the bottom of the corridor. The cod was pinned onto the steel wire, while the shrimp was clipped around its middle (see Fig. 2). For both prey, we measured the force needed to detach the prey from its attachment (by pulling horizontally), the force needed to tear a piece from the prey, and force needed to penetrate the prey using a standard object (flat-tipped screw of 3 mm diameter) using a Kistler Force Transducer 9203 (range 0.1–500 N) and charge amplifier (type 5995).

These prey were selected because they differ in several physical properties. (1) Both prey types differ in shape: a spherical piece of fish vs. a more elongated shrimp. (2) The attachment strength of both prey types differs significantly ($P < 0.001$) implying that the piece of fish can be sucked easily from its attachment, while the firmly tied shrimp has to be pulled more forcefully from its attachment (Table 1). (3) Both prey types clearly differ in their hardness: While the fish can be easily penetrated, significantly ($P < 0.001$) higher forces are needed to pierce the shrimp (Table 1).

When feeding on attached prey types, clariid catfishes are known to use a combination of suction feeding (drawing the prey toward the mouth) followed by fast snapping of the oral jaws onto the prey (Bruton, '79; Van Wassenbergh et al., 2004). If the prey cannot be sucked directly from its attachment, they are detached by a lateral
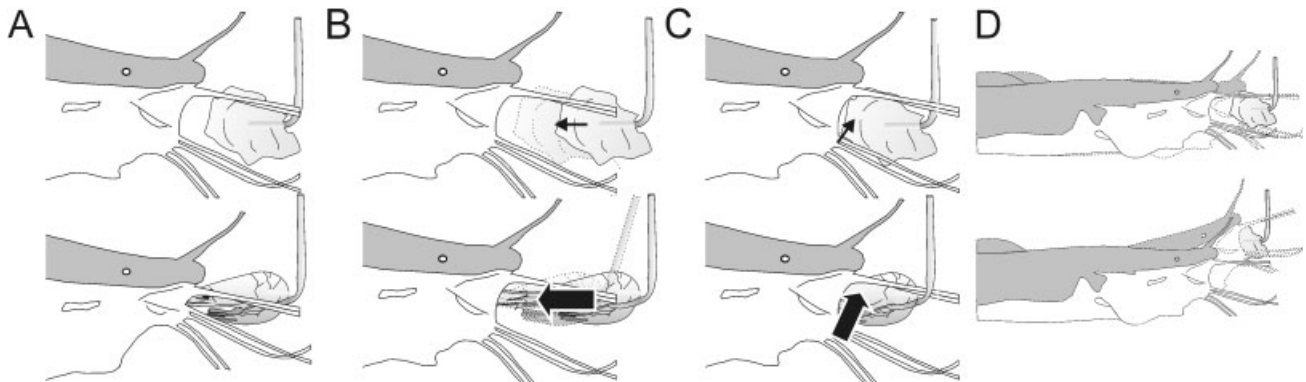
Fig. 2. Illustration of the four types of modulation that are expected to increase a clariid catfishes' capture performance on the prey used in this study (attached fish and shrimp). (**A**) Oral gape is adjusted according to the size of the prey. (**B**) An increased suction effort is shown when feeding on the more firmly attached shrimp. (**C**) The jaws are closed faster during captures on shrimp. Compared to the fish, this prey is harder to pierce the teeth into, and also needs a firmer grip to be detached during subsequent lateral head swings. While (A–C) are prey–type-related modulations, a ''positional'' modulation is shown in (**D**). In this, the magnitude of neurocranial elevation is adjusted according to the position of the prey.

TABLE 1. *Force (mean $\pm$ standard deviation) needed to detach, tear and pierce the presented prey types*

	Fish	Shrimp
Detach*	$0.4 + 0.1$	$1.8 + 0.6$
Tear	$2.1 + 1.1$	$2.0 + 0.6$
Pierce*	$2.1 + 0.8$	$4.6 + 0.8$

$N = 10$.
*Significant prey-type differences ($P < 0.05$).

head swing in which the prey is held tightly between the oral teeth (Van Wassenbergh et al., 2004). Prey processing usually only occurs after these catfishes have returned to their favoured, hiding places in the aquarium.

Given this feeding mode and the above-mentioned physical properties of both prey used in this study, several ways of modulation of prey capture kinematics in function of prey type can be expected (Fig. 2). The three types of modulation expected are: (1) modulation of gape in function of the shape and size of the prey (Fig. 2A). Reducing the oral gape as much as possible will increase prey capture performance, because it increases the suction-induced flow speed (Alexander, '70; Muller et al., '82) and also reduces the duration of the compressive phase. Note in this respect, that the depression of the hyoid apparatus in Clariidae is responsible for the largest increase in buccal volume (Van Wassenbergh et al., 2006) and a reduced mouth opening will therefore only have a smaller effect on the total volume of water sucked into the mouth. (2) Modulation of suction effort in function of the attachment strength of the prey (Fig. 2B). The increased attachment strength

of the shrimp makes it more difficult to draw it towards the mouth by suction feeding. Therefore, an increased magnitude and/or speed of buccal expansion are likely to increase the prey capture efficiency on this prey type. (3) Modulation of jaw closing speed in function of external texture and piercing strength of the prey (Fig. 2C). As the shrimp cannot be sucked directly from its attachment, a strong grip on this prey by the jaws prior to the lateral head swing will likely increase the prey capture success. A higher level of jaw adductor muscle activation when capturing the shrimp, resulting in faster jaw closing movements and higher biting forces at the moment of impact of the lower jaw with the prey, will most likely improve the piercing of the catfish's teeth into this type of prey.

Although both prey types are immobile food items, our observations show that both prey types are challenging for the catfish, which often needed several attempts to detach a single prey by suction, especially (but not only) during feeding on the firmly attached shrimps. The catfish sometimes even returned to their hiding places in the aquarium after failing to detach the food. We can therefore safely assume that high levels of performance are exhibited during feeding on these prey, and that the catfish are prompted to enhance their performance by showing prey-type modulation if they are capable to do so.

High-speed video recordings

High-speed video recordings (250 frames/s) were made from a lateral and ventral position, using a

Redlake Imaging Motionscope digital high-speed video camera (shutter 1/2,500). Lateral and ventral views of prey captures of eight individuals were recorded separately (different prey capture sequence for each recording). All other individuals were filmed simultaneously from a lateral and a ventral view using a mirror inclined at 45°. Two floodlights (600 Watt) provided the necessary illumination. Only those prey capture sequences that were approximately perpendicular to the camera lens were selected and retained for further analysis. To do so, lateral recordings in which skull roof, skull bottom or origin of the maxillary barbel of the opposite side of the fish were visible, as well as ventral recordings in which the side of the skull was visible, were discarded. For each individual, 10 lateral and 10 ventral recordings (each consisting of five fish and five shrimp captures) were analysed. For one *Clarias gariepinus* individual, however, only four (instead of five) ventral recordings with cod as prey could be analysed. Anatomical landmarks were digitized on the recorded images (Fig. 3) using Didge (version 2.2.0, Alistair Cullum), and the horizontal (x) and vertical (y) coordinates for each point were exported to a spreadsheet.

Kinematic variables

After digitization of the sequences, the coordinates of each point were used to calculate the variables of interest (Fig. 3). After data filtering (fourth-order, zero phase-shift Butterworth low-pass filter) and differentiation, peak velocities of jaw and hyoid movements were determined. Because for some individuals lateral and ventral views were not recorded simultaneously, the data sets of each recording view (lateral and ventral) had to be analysed separately.

For the lateral high-speed video recordings, the following kinematic variables were analysed: (1) maximum gape angle, (2) total lower jaw rotation (maximal angle minus starting angle) (3) total hyoid depression (maximal depression minus starting position), (4) total depression of the branchiostegal membrane (maximum depression minus starting position) and (5) total neurocranial elevation, (6) the maximal jaw opening velocity, (7) maximal jaw closing velocity and (8) maximal hyoid depression velocity.

From the ventral high-speed video recordings, the following kinematic variables were analysed: (1) maximal width of hyoids (angle), (2) maximal lateral expansion of the hyoids (angle, maximal
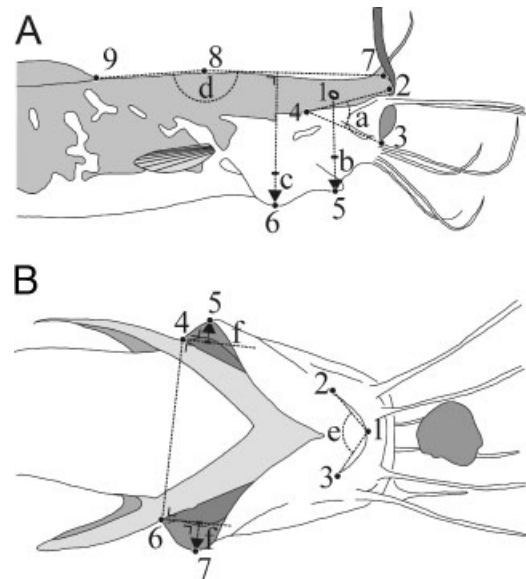

Fig. 3. Anatomical landmarks digitized with the calculated kinematic variables (dotted lines) on the lateral (A) and ventral (B) high-speed video images of *Clarias gariepinus*. Identical landmarks were digitized on images of the other species. (**A**) Lateral landmarks: (1) middle of the eye, (2) upper jaw tip, interior side, (3) lower jaw tip, interior side, (4) jaw articulation, (5) tip of the hyoid, (6) most ventrally positioned point of the branchiostegal membrane, (7) rostral tip of the skull roof, (8) caudal tip of the skull roof and (9) anterior tip of the caudal fin. The measured angular variables are: gape angle (a) and neurocranial elevation (d). The linear variables are: hyoid depression (b) and branchiostegal depression (c). (**B**) Ventral landmarks: (1) hyoid symphysis, (2,3) most caudally discernible points on the hyoid bars, (4,6) base of pectoral spine, (5,7) lateral tip of the branchiostegal membrane. The measured angular variable is the hyoid expansion (e). The measured linear variable is the branchiostegal expansion ((f, average between left and right).

width minus starting width) and (3) the lateral expansion of the branchiostegal membrane (maximal excursion minus starting position) and (4) average angular hyoid abduction velocity (see also Fig. 3)

Statistics

To evaluate the ability of each species to modulate its prey capture kinematics for the different experimental prey, the statistical approach of Ralston and Wainwright ('97) was used. First, two-way analyses of variance (ANOVAs) were used to test for each species the ability to alter the kinematic variables of interest when feeding on the two different prey types. In these ANOVAs, the ''individual'' factor (random effect) was crossed with ''prey type'' factor (fixed effect),

resulting in an individual-by-prey-type interaction. F-ratios for "prey type" effect were calculated with the prey mean squares in the numerator and the interaction-term mean squares in the denominator. If two-way interaction between "prey type" effects and "individual" effects occur, there are differences in the way individuals respond to the two different prey types. In this case, separate tests for "prey type" effects (one-way ANOVA) within each individual of the species were performed.

Second, the ability of each species to modulate its position with respect to the prey during the course of the strike was evaluated. Therefore, a Spearman rank correlation was used to test whether catfishes elevate the skull more when the head of the fish (when approaching the prey) was deeper under the prey. For each prey capture sequence, the frame preceding the start of the feeding event (mouth starts to open) was analysed. The position of the skull with regard to the prey at this moment was evaluated by extending the segment describing the position of the skull (landmarks 7 and 8 of Fig. 3A) towards the attached prey. The following scores were given: (1) skull segment above the prey, (2) skull segment intersects the upper part of the prey, (3) skull segment intersects the lower part of the prey (4) skull segment underneath the prey.

Third, principal components analyses (PCAs) were performed on the kinematic variables of (1) the lateral high-speed video recordings and (2) the ventral high-speed video recordings. To quantify the amount of variation exhibited, centroid distances were calculated (distance between unrotated PC scores for each prey capture and the mean position of all PC scores for the corresponding prey type in a three-dimensional representation) and we tested whether prey type influenced the variability of the kinematic patterns within each species (two-way crossed design ANOVAs described above, performed on centroid distances from separate PCAs for each species). When testing for interspecific differences in the overall variability in prey capture kinematics, a single PCA was performed including the data sets of all the species studied. In this, distances and linear velocities were scaled according to CL in order to exclude the influence of size. "Species" effects in centroid distances from the first three principal components were tested in one-way ANOVAs, followed by Spjotvoll–Stoline post hoc tests (only performed when the one-way ANOVA indicated overall statistical significance). Although this

approach is analogous to measuring the effect of "prey type" on the variance of each kinematic variable, the final interpretation is strongly simplified as a single parametric test can be used to test the significance of the results (Ralston and Wainwright, '97).

Although the significance level of $P = 0.05$ is used throughout the analyses, the results of applying a sequential Bonferroni correction (that adjusts the significance level according to the number of tests that were carried out) in case of consecutive univariate testing are also given whenever applicable. However, as the use of this method (and other multiple testing adjustments) in ecological studies has recently been questioned (Moran, 2003), we base the discussion on the unadjusted results (see also Ralston and Wainwright, '97). Nevertheless, as the sequential Bonferroni method has been used in several topic-related studies (e.g., Sanderson, '91), the comparative value of our results is increased by including this into the analysis.

RESULTS

Prey-type modulation

The two less specialized species (*Clarias gariepinus* and *Clariallabes longicauda*) showed significant modulation in response to the two prey types (Table 2). *Clarias gariepinus* decreases its maximal gape angle when feeding on shrimps compared to the larger pieces of fish (ANOVA, $F_{1,5} = 6.31$, $P = 0.0075$). After applying the more conservative statistical method described above (i.e., sequential Bonferroni correction), this modulation of mouth opening size in *Clarias gariepinus* is the only statistically significant modulation of the entire data set (Table 2). In general, no modulation in the magnitude or speed of the observed cranial expansion can be discerned for this species, although two out of the six individuals did show a significantly larger lateral expansion of the branchiostegal membranes during shrimp captures (ANOVA, $F_{1,8} = 6.31$, $P = 0.040$). In contrast to *Clarias gariepinus*, *Clariallabes longicauda* did not modulate its gape but showed larger hyoid depressions when feeding on the more firmly attached shrimps (ANOVA, $F_{1,2} = 17.9$, $P = 0.025$) as predicted. Also within *Clariallabes longicauda*, some individuals responded differently to the two types of prey (Table 2): while one individual increases its jaw closing speed when capturing shrimps (ANOVA, $F_{1,8} = 43.2$, $P = 0.00017$), another individual

TABLE 2. Means and standard errors of the analysed kinematic variables of prey capture

	Clarias gariepinus		Clariallabes longicauda		Channallabes apus		G. typus	
	Fish	Shrimp	Fish	Shrimp	Fish	Shrimp	Fish	Shrimp
(A) Gape								
Max. gape angle (°)	**35.4±1.4***	**30.8±1.1***	58.5±1.8	57.5±1.5	47.4±1.7	45.8±1.3	55.9±2.0	53.0±1.8
(B1) Buccal expansion magnitudes								
Lower jaw opening rotation (°)	25.9±1.1	23.2±0.8	28.5±1.5	27.3±1.6	20.9±1.5	20.1±1.2	26.5±2.0	24.3±1.5
Hyoid depression (mm)	7.55±0.30	7.36±0.29	**7.12±0.37**	**8.70±0.26**	5.20±0.22	5.28±0.20	5.11±0.21	5.23±0.15
Branchiostegal depression (mm)	6.96±0.39	6.06±0.30	3.78±0.27	4.06±0.20	2.63±0.12	3.21±0.19	2.85±0.16	3.27±0.31
Max. width of hyoids (°)	117.7±0.7	117.5±0.9	121.0±0.9	118.9±1.3	104.8±1.1	101.6±2.6	116.9±3.4	109.9±2.2
Lateral expansion of hyoids (°)	31.8±1.2	30.5±1.2	18.9±1.2	19.0±1.2	15.5±1.1	14.6±0.7	21.2±1.9	18.5±1.6
Lateral branchiostegal expansion (°)	3.38±0.29[1]	3.57±0.18[1]	2.97±0.13[1]	4.00±0.19[1]	1.96±0.13[1]	2.09±0.17[1]	1.83±0.15	1.64±0.19
(B2) Buccal expansion velocities								
Max. jaw opening velocity (°/s)	422±22	496±28	727±46	859±58	533±31	617±46	958±61	762±48
Max. hyoid depression velocity (mm/s)	125±6	144±7	165±8	250±14	126±9	160±10	151±8	163±8
Mean lateral hyoid abduction velocity (°/s)	377±18	430±26	364±43	329±33	265±32	287±30	457±42	361±33
(C) Jaw closing								
Max. jaw closing velocity (°/s)	411±23	451±25	402±32[1]	553±44[1]	455±37	492±25	688±60	680±33

Significant prey differences are printed in bold (two-way crossed design ANOVAs within each species, $P < 0.05$).
*Significant after sequential Bonferroni correction.
[1]Significant prey type-by-individual interaction.
See text for further information.

showed larger lateral expansion of the branchiostegal membrane when feeding on this prey type ($F_{1,8} = 16.7$, $P = 0.0035$).

However, no prey–type-related modulation could be demonstrated for the two most specialized species (*Channallabes apus* and *Gymnallabes typus*). A single exception was that, like some *Clarias gariepinus* and *Clariallabes longicauda* individuals, one out of the four *Channallabes apus* specimens showed a larger lateral expansion of the branchiostegal membrane (ANOVA, $F_{1,8} = 11.1$, $P = 0.010$). An overview of the results for all species is given in Table 2.

Positional modulation

For all species, differences in approach position are adjusted during the strike by altering the amount of neurocranial elevation (Fig. 4). More neurocranial elevation is shown if, while approaching the prey, the head was positioned deeper underneath the prey (Spearman rank correlation; *Clarias gariepinus*: $R = 0.52$, $N = 60$, $P < 0.001$; *Clariallabes longicauda*: $R = 0.36$, $N = 40$, $P = 0.023$; *Channallabes apus*: $R = 0.53$, $N = 40$, $P < 0.001$; *Gymnallabes typus*: $R = 0.67$, $N = 30$, $P < 0.001$). The largest neurocranial elevations were observed in *Clarias gariepinus* and *Clariallabes longicauda* (more than 25°). *Clarias gariepinus* and *Gymnallabes typus* even showed neurocranial depressions in about 10% of the analysed prey captures.

Variability of prey capture kinematics

Regardless of prey type, the species studied showed similar amounts of variation in their prey capture kinematics in lateral view (ANOVA on centroid distances, $F_{3,166} = 2.83$, $P = 0.040$; but Spjotvoll–Stoline post hoc test, $P = 0.099$ between the most distant species) and in ventral view (ANOVA, $F_{3,166} = 1.41$, $P = 0.24$). The experimental prey types also did not influence the variability of the kinematic patterns within each species. As shown in Table 3, the calculated average centroid distances of the PCA scores (quantifying the amount of variability in strikes) for each prey type are not significantly different in either of the clariid species.

DISCUSSION

The results of the present study generally support the hypothesis suggesting that trophic specialists have a reduced flexibility in their feeding mechanics in response to different prey
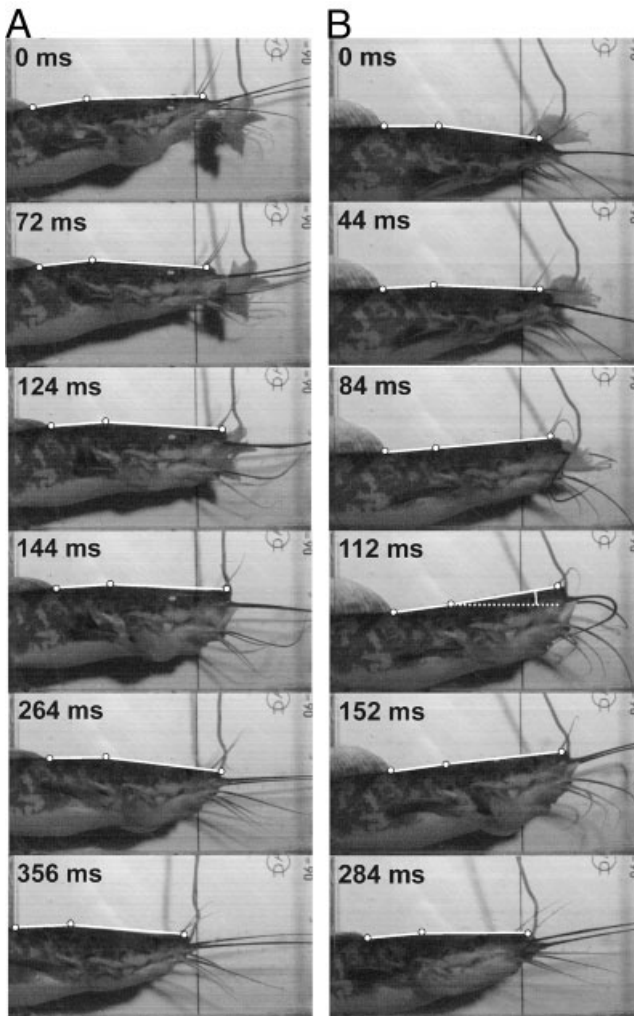
Fig. 4. Positional modulation in *Clarias gariepinus* feeding on a piece of fish. More neurocranial elevation is shown (compare (**B**) and (**A**)) when, just before the strike (see 0 msec frame), the head is positioned deeper underneath the prey. Neurocranial elevation is illustrated by the increase in skull-to-body-axis angle (white lines). The maximal angle of neurocranial elevation in sequence (B) is represented by the angle between the dotted and full line (112 msec frame). The same pattern of positional modulation is observed for all other species in this study.

types (or prey positions) compared to trophic generalists. Indeed, the species with the largest degree of trophic specialization in our study (*Channallabes apus* and *Gymnallabes typus*; Fig. 1), which have a narrow dietary range (Huysentruyt et al., 2004) and a morphologically modified jaw system (Herrel et al., 2002), show a reduced degree of modulation compared to the more generalist species (*Clarias gariepinus* and *Clariallabes longicauda*). More specifically, prey-type differences in prey capture kinematics could

be demonstrated only for *Clarias gariepinus* and *Clariallabes longicauda*, but not for *Channallabes apus* or *Gymnallabes typus* (Table 2). However, all other estimates of modulatory capacity and variability of kinematics are similar for all the species studied: they all show the ability to modulate position during the strike by adjusting the degree of neurocranial elevation (Fig. 4), show a similar amount of variability in prey capture kinematics, and the degree of variability is not influenced by the offered prey types (Table 3).

Apparently, dietary breadth of trophic specialists and the possession of specialized morphological features are correlated with functional stereotypy in clariid catfishes. However, many previous studies failed to demonstrate differences in modulation capacity for trophic generalists and specialists (Liem, '80, '84; Sanderson, '88, '90). In these studies, it was shown that species with morphological and dietary specialization still possess the ability to respond differently to a variety of prey types. This was the case, for instance, for the neuromuscular control of feeding in cichlid fishes (Liem, '80, '84), as well as for the muscle activity patterns (Sanderson, '88) and jaw movements (Sanderson, '90) of labrid fishes. On the other hand, and in accordance with our results, other experimental studies have confirmed the evolutionary hypothesis of reducing functional versatility with increasing degree of trophic specialization (Lauder, '83a,b; Sanderson, '91). A highly specialized snail-crushing sunfish, for example, showed a stereotyped muscle activity pattern of the pharyngeal jaws, also when processing prey other than snails (Lauder, '83a). Consequently, independent evolution towards trophic specialization apparently leads to a reduced functional flexibility or versatility in certain groups of fishes, while not in others. However, this still leaves us with the question "*why* does this evolve in some groups, but not in others?"

Interestingly, the results of a study by Ralston and Wainwright on pufferfishes ('97) supported the expected relationship between trophic breadth and functional flexibility for *buccal manipulation*, but the ability to modulate *prey capture* mechanics in function of prey type was limited for both generalists and specialists. Apparently, differences in the degree of modulatory capacity among closely related species are harder to demonstrate for prey capture when compared to prey processing. In fact, apart from the present study, only a single study investigating prey capture relation to differences in trophic breath (or degree of

TABLE 3. *Variability of prey capture kinematics, expressed as average centroid distances (with standard errors)*

Total variability[1]	Clarias gariepinus		Clariallabes longicauda		Channallabes apus		G. typus	
Lateral	1.19 + 0.08		1.47 + 0.09		1.36 + 0.09		1.58 + 0.17	
Ventral	1.28 + 0.08		1.39 + 0.12		1.49 + 0.12		1.57 + 0.17	
Variability within prey types[2]	Fish	Shrimp	Fish	Shrimp	Fish	Shrimp	Fish	Shrimp
Lateral	1.56 + 0.09	1.54 + 0.07	1.50 + 0.08	1.59 + 0.08	1.57 + 0.10	1.54 + 0.11	1.68 + 0.09	1.46 + 0.13
Ventral	1.58 + 0.09	1.52 + 0.10	1.44 + 0.11	1.57 + 0.10	1.34 + 0.12	1.66 + 0.13	1.53 + 0.09	1.50 + 0.17

[1]All species and both prey items pooled in the PCA.
[2]Separate PCAs for each species.
All results are not significant ($P > 0.05$; ANOVA).

specialization) found reduced modulatory capacity in specialized species when compared to closely related generalists (Sanderson, '91; but see Liem, '78, '80; Sanderson, '88, '90; Norton, '91; Ralston and Wainwright, '97). In contrast, all studies focussing on prey processing found support for the hypothesis on the reduced functional flexibility of specialists (Lauder, '83b; Ralston and Wainwright, '97).

Possibly, prey capture demands a higher minimal degree of variability/flexibility compared to prey processing, even for specialized species. Many factors can vary during prey capture that potentially influence the appropriate prey capture behaviour, even when always capturing the same prey (prey movement, prey position relative to the predator and approaching speed of the predator, etc.). Indeed, Aerts ('90) even showed a relationship between the degree of bucco-pharyngeal expansion and the precise moment of prey uptake within the expansion phase of an insectivorous cichlid (*Astatotilapia elegans*) under identical feeding conditions (i.e., same prey and prey attachment method). Once the prey, for which the species is specialized, is captured and held between the oral or pharyngeal jaws, the number of uncertainties in the system decreases. In this way, the evolution of a stereotyped and specialized pre-programmed prey processing pattern may be less constrained than developing a stereotyped and specialized initial prey capture pattern. This may be a possible explanation to the observed dichotomy in the amount of studies that did, or did not find support for the hypothesis of reduced feeding flexibility in trophic specialists.

An evolutionary explanation of ''Liem's paradox'' (referring specifically to cichlids with morphological specializations but still showing multiple, distinct prey capture mechanisms) has been proposed in population ecology (Robinson

and Wilson, '98). Based on optimal foraging theories, Robinson and Wilson ('98) suggested that species can develop specializations for non-preferred resources driven by competition, but still act as trophic generalists whenever the food availability rises. From this point of view, the flexibility of ''specialists'' would not be greatly compromised during evolution. The present result for Clariidae, in which the overall variability of prey capture kinematics is still very high in the most specialized species, in some way supports this theory. Due to the large variability in prey capture kinematics (regardless of prey type), even the specialized species will be able of performing successful prey captures on alternative, non-preferred prey. Yet, as the capacity to respond with altered capture kinematics in response to prey characteristics decreases, the specialized Clariidae will overall have a reduced prey capture success when feeding on a wide range of prey compared to the generalists. However, it is unknown how these differences in modulatory capacity affect the population ecology or competition in the natural environment of Clariidae.

The positional modulation by adjusting the magnitude of neurocranial elevation (Fig. 4) is an additional aspect of feeding versatility that has not been reported in previous studies. This capacity seems to be a general feature for Clariidae. Although it has been observed in other fishes that prey position (e.g., at the bottom, in midwater or at the water surface) can result in changes in capture kinematics (Liem, '80; Lauder, '81), prey were always suspended at the same distance from the bottom of the aquarium in the present study. However, they were not always approached in the same way. Prey were approached by the catfish with the head at the same level, underneath or slightly above the prey. By modifying the degree of neurocranial elevation,

the catfish were capable of adjusting the position of the head during suction feeding. More neurocranial elevation was shown in strikes with the head positioned deeper underneath the prey during the approach, when compared to strikes in which the head was positioned at a higher level with respect to the prey (Fig. 4). Such positional modification through neurocranial elevation can be of great use, especially for predator species that need to locate prey from a short distance. While hunting, catfish mainly use tactile, chemical and electrical signals to locate the prey (Alexander, '65; Bruton, '79; Hossain et al., '99; Hanika and Kramer, 2000; Pohlmann et al., 2001). Visual signals are also used, but are considered less important, as these catfishes have small eyes, and are mainly nocturnal predators. The exact position of the prey is detected by touching the food (active or passive) with the barbels that extend from the mouth in the form of a widening cone (Bruton, '79). As this predatory strategy locates prey from a short distance, the ability to elevate the skull to a greater or lesser extent (according to the position of the prey) during suction feeding, will most likely be important, and may beneficially influence prey capture success.

Finally, it should be noted that the range of prey used in the experiments of our study (Fig. 2) is inevitably, relatively narrow compared to the total diversity of prey included in the diet of some of the species studied (Fig. 1). We therefore cannot conclude that the trophically specialized species *Channallabes apus* and *Gymnallabes typus* are completely unable of modulation in function of prey type. For example, modulation could still be observed if highly evasive prey had been included in our study. Nevertheless, the difference in shape, hardness and attachment strength between the prey used in the present study were enough to elicit modulation in the trophic generalists (*Clarias gariepinus* and *Clariallabes longicauda*), and thus provided a situation in which these catfish could distinguish both prey and adjust prey capture kinematics accordingly.

In conclusion, the present study on prey capture kinematics of a range of clariid species with increasing degree of specialization found a reduced flexibility in response to differences in prey type for the more specialized species. Modulation in function of prey position relative to the fish's head and the variability of prey capture kinematics, however, are independent of the level of trophic specialization. This result supports the notion that ecological and morphological speciali-

zation are linked with functional versatility of the feeding system in fishes, as hypothesized previously (see Liem, '84). In contrast to studies on prey processing, the present study is one of the few that was able to demonstrate the functional stereotypy of specialists compared to generalists when focussing on prey capture mechanics. The fact that the hypothetical relationship between the degree of trophic specialization and the degree of flexibility of the feeding behaviour is harder to observe for prey capture compared to prey processing, is possibly due to a higher demand on variability, needed for the initial capture of prey.

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