SYMPOSIUM

Kinematics of Terrestrial Capture of Prey by the Eel-Catfish
Channallabes apus

Sam Van Wassenbergh[1,*,†]

*Department of Biology, Ghent University, Ledeganckstraat 35, B-9000 Gent, Belgium; †Department of Biology, Universiteit Antwerpen, Universiteitsplein 1, B-2610 Antwerpen, Belgium

[1]E-mail: sam.vanwassenbergh@ugent.be

Synopsis In contrast to numerous studies on the function of the locomotor system used by fishes when moving between water and land, little knowledge is available about the biomechanical requirements to the capture and transport of food by fish in a terrestrial situation. This study focuses on the kinematics of terrestrial capture of prey by the eel-catfish (*Channallabes apus*: Clariidae), a behavior that was only recently discovered for this species. The analyses show that *C. apus* inclines its head downward at a significantly steeper angle during terrestrial feeding compared with benthic aquatic feeding. This suggests that placing the jaws above ground-based prey is important for successful prehension by the jaws. The increased inclination of the head resulted from accumulated dorsoventral flexion of the body more than one head-length behind the skull. Alternatively, this posture of the head was assumed by rolling to one side while bending the body laterally. The speed of buccopharyngeal expansion in air versus in water matched the predicted increase by a factor of 3, under the assumption that the velocity of muscular contraction for maximal output of power by *C. apus* is optimized to operate under a specific hydrodynamic loading, and shifts to an unloaded contraction regime when operating in air. Combining these insights with future studies on other extant amphibious fish species that perform terrestrial feeding may eventually allow us to pinpoint the adaptations to the feeding system that have led to the evolution of a terrestrial lifestyle in tetrapods.

Introduction

The radiation of ray-finned fishes (Actinopterygii) into the aquatic environment was very successful. This group is morphologically diverse and consists of about half of all currently described vertebrate species (Near 2012). The aquatic success of these fishes is, at least in part, due to the highly kinetic musculoskeletal system of their crania that generates flows of water to ventilate the gills during respiration and facilitates the capture or transport of prey during feeding (e.g., Alexander 1967). Such flows of water are produced by coordinated sequences of movements that result in anterior-to-posterior waves of expansion and contraction of the buccopharyngeal cavity (Hughes and Shelton 1962; van Leeuwen and Muller 1984; Lauder 1985). Drawing prey into the mouth and transporting it further intra-orally via

such anterior-to-posterior water flows is called suction-feeding. This behavior is considered to be the ancestral mode of feeding within this group (Lauder 1980), and is used by a large majority of extant species (e.g., Gibb and Ferry-Graham 2005). Morphological variation in this kinetic feeding apparatus has allowed ray-finned fishes to exploit nearly all types of aquatic food (e.g., Sibbing and Nagelkerke 2001).

Despite the dominance of obligatorily aquatic species in each of the orders of Actinopterygii, the capacity to capture ground-based terrestrial prey has evolved at least five times independently within this group. Records of terrestrial feeding exist for the reedfish, *Erpetoichthys calabaricus* (Polypteridae) (Sacca and Burggren 1982), the four-eyed fishes (Anablepidae) (Zahl et al. 1977), the eel-catfish,

Channallabes apus (Clariidae) (Van Wassenbergh et al. 2006a), blennies (Blennioidei) (Rao and Hora 1938; Nieder 2001), and mudskippers (Oxudercinae) (Stebbins and Kalk 1961; Sponder and Lauder 1981). Yet, these five groups are only a fraction of all amphibious fish species capable of performing terrestrial excursions (e.g., Gordon et al. 1969; Gillis 1998; Schoenfuss and Blob 2003; Sayer 2005; Hsieh 2010; Gibb et al. 2011). In addition to moving on land, this suggests that specific biomechanical adaptations are necessary to overcome the physical challenges to the capture of ground-based prey.

One of these challenges is that suction-feeding using flows of air is virtually impossible (Herrel et al. 2012). Since the density (ρ) of air is about 800 times less than that of water, a given buccopharyngeal expansion has to be 28 times faster (i.e., square root of 800) to produce a flow of air with the same kinetic energy ($E_{kin} = 0.5\ \rho V v^2$, with V fluid volume and v fluid speed). For species adapted to the aquatic environment, muscles involved in aquatic suction-feeding are assumed to work at one-third of their maximum unloaded contraction velocity (i.e., the optimal shortening velocity for generation of power) (Hill 1938). This means any reduced fluid loading as experienced during a transition to feeding in air would only result in an increase in speed of buccopharyngeal expansion by a factor of 3. This is an order of magnitude less than that needed to transfer sufficient kinetic energy to generate a flow of fluid sufficient to carry prey (with a mass similar to that of aquatic prey) toward the mouth. In addition, a flow of air over a prey item would generate relatively low frictional forces compared with water due a decrease in dynamic viscosity of air versus water of about 50-fold.

Aquatic suction-feeders making the transition to terrestrial feeding are thus forced to develop an alternative strategy for capturing and swallowing prey on land (Reilly and Lauder 1990). Since the force on prey due to Archimedes' principle is negligible in air compared with the gravitational force, most prey will be held against the substrate by gravity. Prey laying or crawling on the ground will probably require terrestrial feeders to position their oral jaws above the prey in order to effectively capture prey (Herrel et al. 2012). It can therefore be expected that the function of the oral jaws in terrestrial feeding in amphibious fishes is similar to that of aquatic feeders that feed on the substrate.

Terrestrial capture of prey was recently discovered in an anguilliform species of the air-breathing catfish family Clariidae: *C. apus* or the eel-catfish (Van

Wassenbergh et al. 2006a). In an aquatic environment, this species is a high-performance suction-feeder (Van Wassenbergh et al. 2007). When capturing terrestrial prey, the mouth opens and closes repeatedly from the instant of contact with the prey until the object is held firmly between the jaws. During this cyclical opening and closing of the mouth, the typical sequence of depression of the lower jaw, shortly followed by depression of the floor of the buccal cavity by the hyoid (as observed during aquatic feeding in this species, and in suction-feeding by ray-finned fish in general), and finally by abduction of the opercular bones and branchiostegal membranes, is maintained when capturing terrestrial prey. Given this conserved timing of movements of the cranial elements both when feeding underwater and on land, it was argued that relatively minor changes seem necessary in the higher-level control circuits that guide the capture of food (Van Wassenbergh et al. 2006a). In contrast to this conserved sequence of motion of the jaws and hyoid, the most notable kinematic aspect reported in this article was the remarkable posture of the eel-catfish: the head pitching steeply downward.

Several intriguing kinematic aspects of terrestrial versus aquatic feeding in *C. apus* call for a more detailed and elaborate analysis and discussion. My first goal is to describe the function and quantify of the functional consequences of the downward-tilted head posture of *C. apus* on the performance and kinematics of terrestrial feeding. How this downward-tilted head posture is achieved and whether this has consequences for neurocranial movement during prey-capture are currently open questions. A second goal is to further unravel the enigma of the remaining buccopharyngeal expansion, including an extensively depressing hyoid apparatus, despite the lack of utility that suction provides on land.

Materials and methods

High-speed video recording

Individuals of *C. apus* were wild-caught in Northern Gabon. The animals were first kept together for several months in a large aquarium where they were fed a wide variety of food items. The animals were then transferred to a separate aquarium (Fig. 1) for high-speed video recording sessions. From the start the animals readily fed terrestrially at night, suggesting that in the wild they are nocturnal feeders. However, because of the light requirements for high-speed videography, it was necessary that they fed by day; it was several months before they would do so.
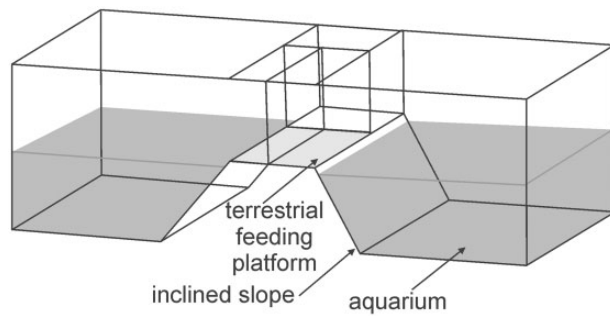
Fig. 1 Two-compartment aquarium used for recording videos of terrestrial capture of prey by *C. apus*. The slope toward the terrestrial part has an inclination of 45°. The length and width of the aquarium are 1.10 and 0.22 m, respectively.

High-speed videos (250 frames per second; Redlake Motionscope or Redlake MotionPro HS1000 camera; IDT, Tallahassee, FL) were recorded of *C. apus* during aquatic feeding on the bottom (two individuals, skull lengths of 17.7 and 24.5 mm, 10 sequences of prey capture each) and terrestrial feeding (three individuals; skull lengths of 17.7, 22.6, and 26.0 mm, respectively, 16, 5, and 2 sequences of prey capture). Only those sequences in which the sagittal plane of the catfish was approximately perpendicular to the symmetry axis of the camera lens (less than 15°) were used for analysis. This allowed us to retain only 1 out of 10 video recordings. The following prey were used in the experiments: (1) pieces of cod fillet (*Gadus morhua*) of about 0.5 cm^3 and (2) live beetles (*Tenebrio molitor*). Prey were always presented at the bottom of the aquarium or laying on the terrestrial section of the aquarium. Note that Coleoptera constitute the species' main prey, but Cypriniform fish also were found in stomachs of *C. apus* (Huysentruyt et al. 2004). We analyzed 18 and 5 sequences of terrestrial captures of fish and beetles, respectively. The 20 aquatic sequences of feeding on the bottom included only cod as prey.

Kinematic analysis

Specific anatomical landmarks, including the tip of the upper jaw (landmark '1'), the tip (symphysis) of the lower jaw (2), the jaw joint, which according to Devaere et al. (2001) lies at initial mid-height of the head at the level of the eye (3), the hyoid tip or, in case the hyoid is still elevated, the point on the floor of the head at the level of the posterior edge of the eye (4), the rostral tip of the skull's roof (5), and the center of the eye (6) were digitized frame-by-frame (Fig. 2) using Didge (version 2.2.0, AJ Cullum; Creighton University, NE). As the precise position of the caudal tip of the skull (needed to quantify
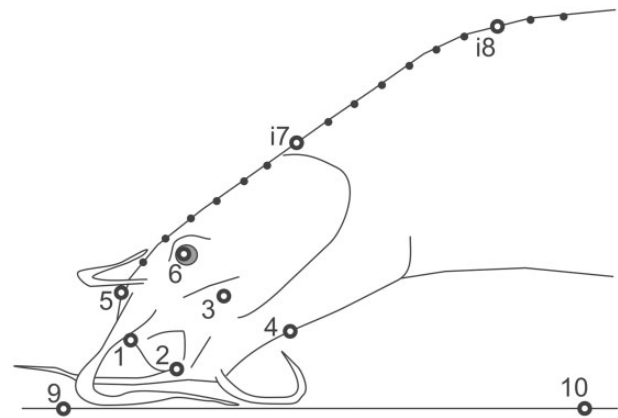

Fig. 2 Positions of the digitized anatomical landmarks described in the text (open circles 1–6), contour landmarks of the dorsal side of the skull and body (small full circles), length-interpolated landmarks (using these contour landmarks) at one and two head lengths posterior of the tip of the rostrum (i7 and i8), and two reference landmarks on the ground (9–10). The *xy*-coordinates of these landmarks were used to calculate the kinematic variables of interest.

inclination of the head) is not directly discernible on the video frames, the dorsal contour of the head and body was digitized with a finite series of landmarks (Fig. 2). For each series of contours, the caudal tip of the skull (i7) and the coordinate at one skull length behind this rostral tip (i8) were extracted using linear interpolations based on accumulating the distance between consecutive contour landmarks. Also, two remote landmarks on the substrate (9 and 10) were digitized in order to calculate the angle between the head and the substrate (Fig. 2).

The following four kinematic profiles were determined from the *xy*-coordinates of these landmarks: angle of gape (angle 1–2–3), angle of inclination of the head (angle between 5–i7 and 9–10), angle of head to body (angle 5–i7–i8), and distance from hyoid to eye (distance between 6 and 4). From these profiles, the following eight kinematic variables were determined: initial angle of gape (at the start of mouth opening when the jaws are close to the prey), maximal angle of gape, average velocity of mouth-opening (total change in the angle of gape divided by the duration of mouth opening), angle of inclination of the head (averaged over the feeding cycle), initial angle of head to body (at the start of mouth opening), neurocranial elevation (maximal change in angle of head to body), maximal hyoid depression (peak "minus" initial distance from hyoid to eye), average velocity of hyoid depression (maximal hyoid depression divided by duration of hyoid depression). To normalize for head size, distances of depression of the hyoid were expressed in head lengths. Head

length was defined as the distance from the tip of the rostrum to the caudal end of the occipital process.

Statistics

Since kinematic data of both terrestrial and aquatic feeding are available for only one of the four individuals used, with only two trials of terrestrial feeding for this individual, when testing for differences between aquatic and terrestrial feeding, it is not possible to account for differences between individuals in a statistically robust way. However, the following analysis suggests that it is very likely that the main kinematic differences in our data are effects of the different physical environments, and that the results will probably not be significantly affected by variation between the individuals that were randomly selected for this study. A principal-components analysis (PCA) on the eight kinematic variables described above (yielding two significant PCs explaining 64% of the total variance) showed that (excluding the two terrestrial data points for the individual with prey captures analyzed in both environments) each of the two individuals feeding terrestrially separated significantly from each of the two aquatically feeding individuals along the first principal component (Tukey HSD *post-hoc* test; $P < 0.05$), and did not differ among each other (Tukey HSD *post-hoc* test; $P = 0.75$). Although the two aquatic individuals also differed significantly from each other (Tukey HSD; $P = 0.047$), a plot of the principal-component scores showed that these individuals were both located away from the terrestrial species in the same direction in this 2D kinematic space (Fig. 3). The two data points of terrestrial feeding in the individual from which also 10 aquatic feeding sequences were analyzed also showed a notable shift toward the centroids of the terrestrial kinematics (Fig. 3; individual 3).

For the above reason, and due to statistical limitations, the most appropriate way to statistically analyze the original, biomechanically meaningful kinematic variables was to treat the terrestrial feeding sequences as if they were performed by a single individual (two small samples of $N = 2$ and $N = 5$ pooled with large sample $N = 16$). Consequently, variation between individuals in the terrestrial environment, which did not show statistical difference in the above PCA (Fig. 3), was not taken into further account. Next, differences in feeding kinematics between environment (terrestrial vs. aquatic) were tested with a one-way analysis of variance (ANOVA; pooled terrestrial feedings and two aquatic individuals; 1 degree of freedom), and if significant followed by Tukey *post-hoc* tests. No significant differences from normal distributions were found in the
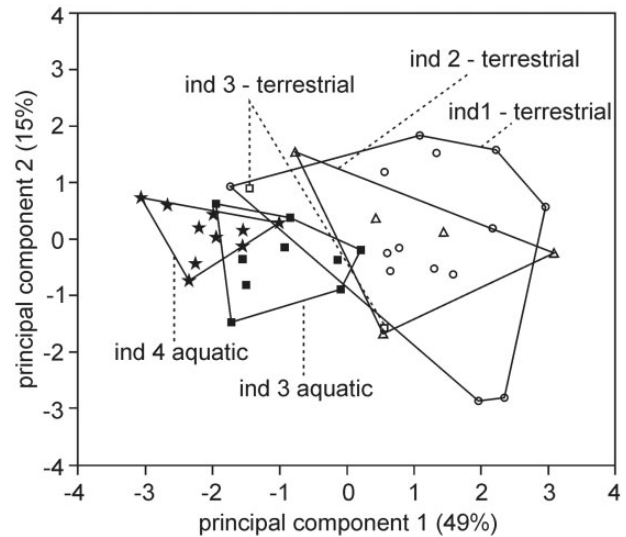

Fig. 3 Principal-component plot indicating the position of each individual (individuals 1–4), and feeding environment (open symbols = terrestrial; filled symbols = aquatic) in 2D kinematic space. This graph suggests that, despite kinematic differences between the two individuals feeding aquatically, a clear kinematic separation between the two environments occurred in our sample; this result is unlikely to be caused by inter-individual variation.

data within environments (Kolmogorov–Smirnov tests). Effects of prey type were not considered, since only a small fraction (about 20%) of the terrestrial observations were recorded using an alternative prey type, and their PC-scores from the above PCA did not differ significantly from the other type of prey (ANOVA, $F_{2,18} = 2.3$, $P = 0.13$). Following Moran (2003), sequential Bonferroni corrections for multiple statistical tests were not conducted; as recommended by Moran (2003), all *P*-values are reported.

Results

First, the prey-capture behavior of *C. apus* is described in a more complete and more quantitative way than in the previous publication on this topic (Van Wassenbergh et al. 2006a). Next, in relation to the central questions of the current article, the focus will be on the comparison between capture of prey on land and capture in water.

Terrestrial prey-capture kinematics

After propelling the anterior half of its body on the terrestrial section of the aquarium (Fig. 1), the eel-catfish scanned the surface of the ground for food. Generally, *C. apus* did this by moving the mouth and barbels over the ground with the front part of its body already lifted and the head bent downward. Sometimes, the head and body remained horizontal
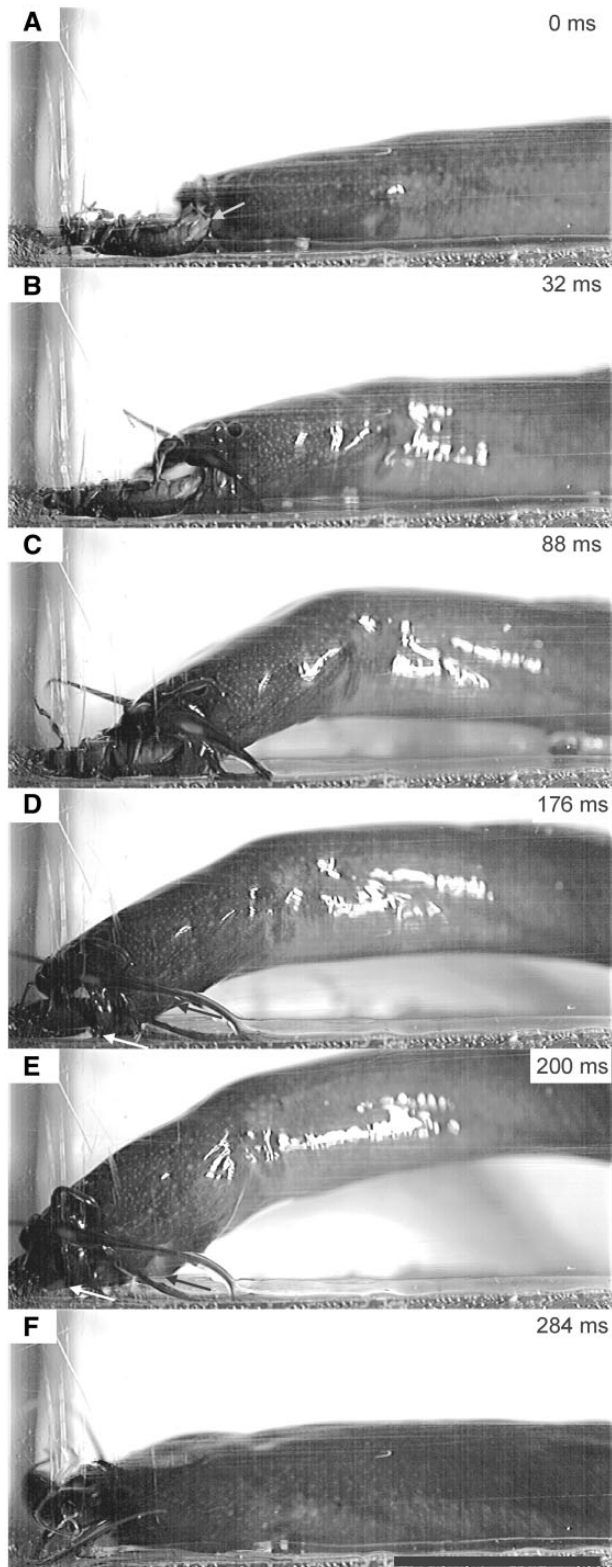
Fig. 4 Selected frames from a high-speed video of terrestrial feeding on a beetle by *C. apus*. The gray arrow in (**A**) shows the instant of contact between the maxillary barbell and the prey (gray arrow), which sequentially initiates turning toward the prey (**B**), lifting of the trunk and downward pitching of the head (**C**), further opening of the mouth (white arrow) and the start of hyoid depression (black arrow) (**D**). At frame (**E**), the mouth is

during this phase of searching for the food (Fig. 4A). In either case, the head yawed from side to side, and contact with one of its chemotactile barbels appeared to trigger prey-capture (Fig. 4B–F). When the head and body were still horizontal at the instant of barbel contact, a few degrees of yaw directed the head toward the prey (Fig. 4B) and was immediately followed by lifting of the trunk, and assuming of the characteristic head-down posture as described and illustrated by Van Wassenbergh et al. (2006a) (Fig. 4C). This posture is maintained until the prey is held firmly between the upper and lower jaws. The downward inclination of the head is either achieved by flexion of the body in the sagittal plane (Fig. 4), or by flexion in the frontal plane (i.e., lateral bending) combined with rolling of the head to one side (Fig. 5). Note that the kinematics of prey-capture during feeding sequences when there was lateral flexion of the body could not be analyzed due to the unfavorable perspective of the camera caused by this action.

The mouth was already open during searching for food (Fig. 4A–C). The average angle of mouth-opening at this time was $34 \pm 11^\circ$ (mean $\pm$ SD). Next, cyclical opening (beyond the initial opening) and closing of the mouth, together with abductive and adductive motions of the hyoid apparatus, branchiostegal membranes, and opercula were observed, which resulted in rostro-caudal expansion–compression waves of the buccopharyngeal cavity (Fig. 4D and E). Suction sounds were commonly produced during this phase. As illustrated in Fig. 5, the pieces of fish were sometimes sucked into the mouth cavity when the mouth was pressed down on this relatively large and soft item of food. In all other cases, the catfish abandoned the trunk-lifted posture as soon as the food was grabbed firmly between the jaws (Fig. 4F); the fish then slipped back into the water and transported the food farther back into the buccopharyngeal cavity. Videos illustrating the terrestrial feeding behavior of *C. apus* are available online (www.nature.com/nature/journal/v440/n7086/suppinfo/440881a.html).

Kinematics of aquatic capture of prey

The prey was approached closely, but in contrast to terrestrial feeding, *C. apus* leaves some distance

Fig. 4 Continued
closing (white arrow) whereas the hyoid reaches its point of maximal depression (black arrow). Finally, the trunk falls down on the ground and the catfish moves backward into the water, holding the beetle between its jaws. Scale bar, 20 mm.
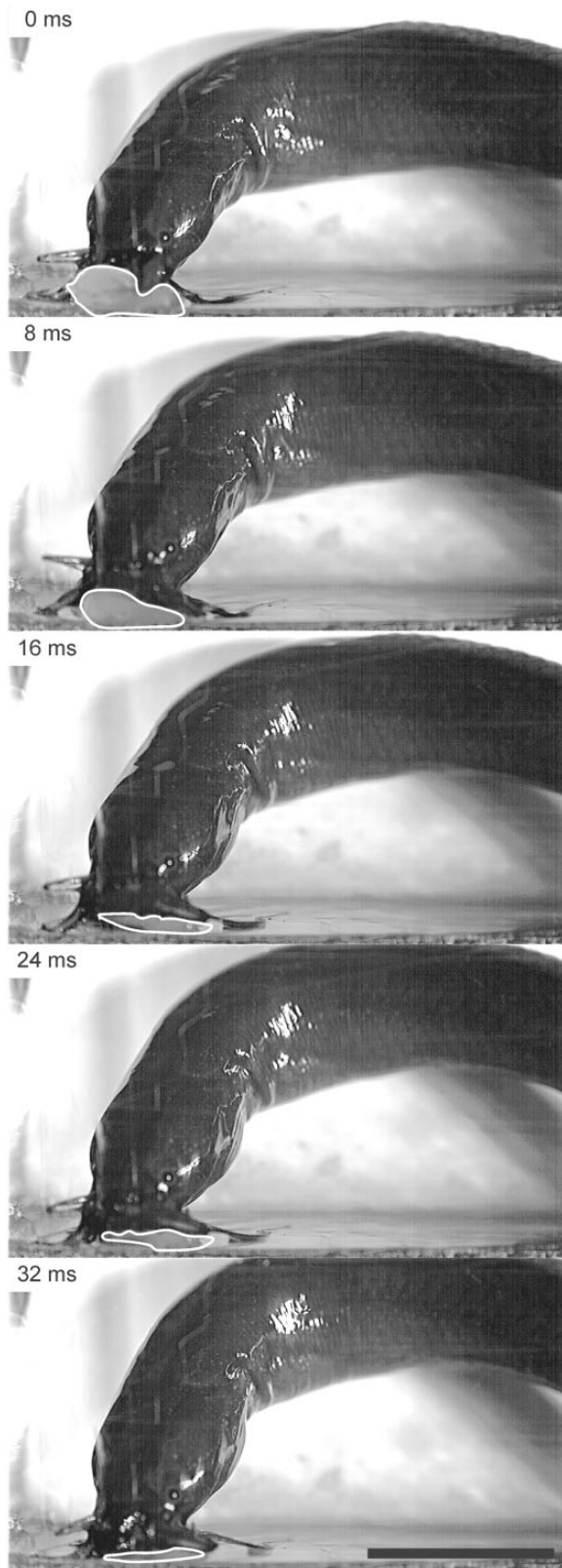
Fig. 5 High-speed video frames of terrestrial feeding in *C. apus* showing a piece of fish (contour highlighted by a white line) being sucked into the mouth. Scale bar, 20 mm.
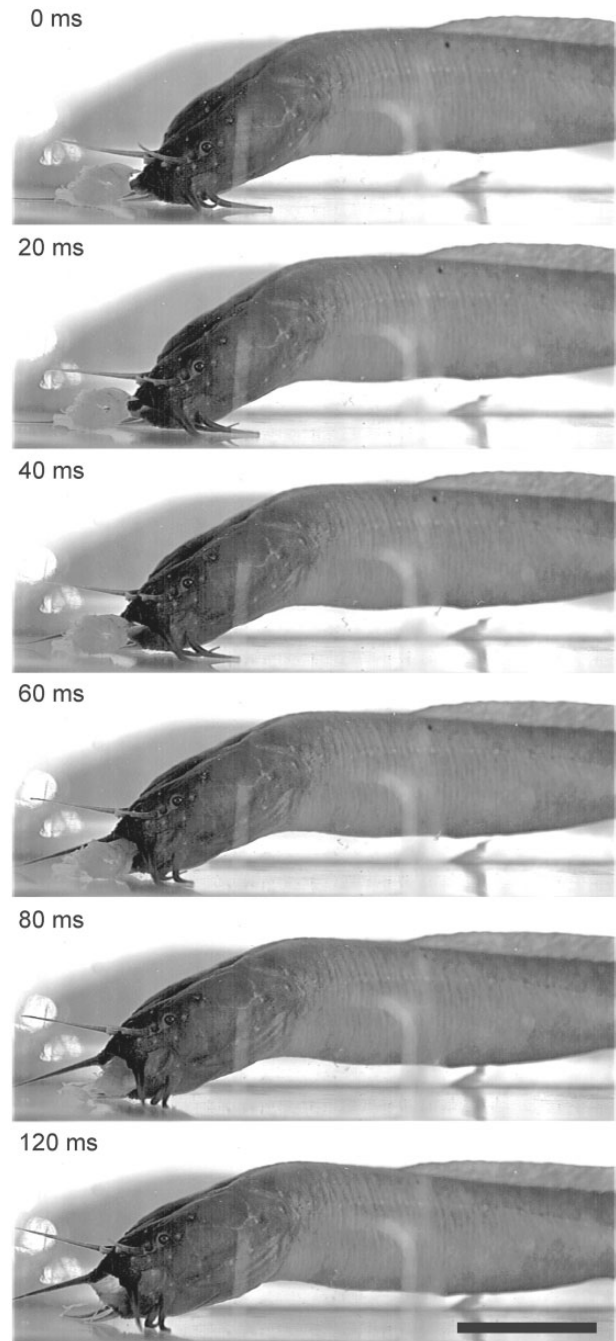

Fig. 6 High-speed video frames of aquatic, bottom feeding by *C. apus* on a piece of fish. Scale bar, 20 mm.

between the anterior tips of the jaws and the prey (Fig. 6). Suction-feeding is then initiated from a nearly standstill position. This suction caused the prey to be drawn into the mouth cavity. The head is always inclined downward prior to, and during, the actual capture (Fig. 6). Neurocranial rotation during benthic suction-feeding either occurs in the dorsal direction (i.e., elevation) or in the ventral direction (i.e., depression), as observed in other species of Clariidae (Van Wassenbergh et al. 2006b).

Terrestrial versus aquatic capture of prey

The eight kinematic variables were statistically compared among terrestrial and aquatic captures of prey (Table 1). As discussed earlier (see "Materials and Methods" section), differences are only considered significant if the pooled terrestrial data (Group 1 in Table 1) differ significantly (at $P < 0.05$) from both of the aquatically feeding individuals (Groups 2 and 3 in Table 1). Means, standard deviations, and standard error of each of the kinematic variables are displayed in Fig. 7.

The initial angle of the gape was significantly larger during terrestrial feeding (Table 1 and Fig. 7A). A difference in maximum angle of gape between feeding sequences in the two environments, however, could not be demonstrated. Although, the velocity of mouth opening did show an average tendency to be higher during terrestrial feeding (Fig. 7 and Table 1), this trend was not significant (Tukey post-hoc test; Table 1). The head was inclined at a much steeper angle with respect to the ground during terrestrial feeding. The mean angle of inclination was almost double that occurring during aquatic feeding (Fig. 7D), a significant difference (Table 1). The head-to-body angle, on the other hand, did not differ between the two feeding environments (Fig. 7E and Table 1). Although neurocranial elevation showed a tendency to be higher during terrestrial feeding, this trend was not significant (Table 1; $P = 0.07$ for Group 1 compared with Group 2). The magnitude of hyoid depression did not differ significantly between feeding on land and in the water (Fig. 7G and Table 1). The velocity of hyoid depression, on the other hand, was significantly higher when feeding terrestrially (Fig. 7H). If the velocity of hyoid depression during terrestrial feeding

was divided by 3 (see third paragraph of the "Introduction" section), no differences could be detected (Tukey HSD test; the minimal P was 0.31 between Groups 1 and 3, as defined in Table 1).

Discussion

Terrestrial capture of prey by the eel-catfish shows several kinematic aspects that differ from those of aquatic benthic feeding. These differences can either be a consequence of moving in a different fluid environment (air vs. water), or it can involve active modulation of musculoskeletal function. As gravity is now acting on the body, modulation of musculoskeletal recruitment seems necessary to maintain the head-down posture observed during hunting on land in *C. apus* (Van Wassenbergh et al. 2006a). In addition, the current analysis shows that the inclination of the head was significantly steeper when feeding on land (Fig. 7D). This is indicative of a crucial role for this characteristic posture.

How does the eel-like fish achieve this downward tilt of the head? Does this posture result from increased dorsoventral bending in the most anterior part of the body, as hypothesized earlier (Van Wassenbergh et al. 2006a)? The results showed that the considerably steeper inclination of the head with respect to the ground in terrestrial versus aquatic feeding (Fig. 7D) did not correspond with a difference in head-to-body angle (focusing on the region one head length behind the back of the skull; Fig. 2). This means that, although a certain amount of dorsoventral flexion in the anterior region of the vertebral column is employed both during terrestrial and aquatic feeding (Fig. 7E), the steeper inclination of the head is caused by accumulation of bending from more posterior regions of the body. This ability

Table 1 Results of the statistical analysis comparing the kinematics of terrestrial and aquatic capture of prey in *C. apus*

	Mean			Probability P			
					Tukey *post-hoc* test		
Kinematic variable	Group 1: terrestrial data (individual 1–2–3)	Group 2: aquatic (individual 3)	Group 3: aquatic (individual 4)	Between groups (ANOVA)	Group 1–2	Group 1–3	Group 2–3
Initial angle of gape (°)	34.0	17.3	24.7	**0.000032**	**0.00015**	**0.020**	0.16
Maximum angle of gape (°)	45.7	32.6	43.0	**0.0038**	**0.0028**	0.75	0.054
Mouth-opening velocity (°/s)	404	259	281	**0.036**	0.062	0.13	0.95
Inclination of head (°)	40.5	23.0	22.5	**0.000025**	**0.00051**	**0.00038**	0.99
Initial angle of head to body (°)	22.6	18.9	20.9	0.41	0.39	0.80	0.83
Neurocranial elevation (°)	4.63	−0.982	−3.52	**0.0039**	0.070	**0.0056**	0.66
Hyoid depression (CL)	0.197	0.106	0.186	**0.00032**	**0.00035**	0.86	**0.0063**
Velocity of hyoid depression (CL/s)	4.71	1.19	2.53	**0.000000**	**0.00012**	**0.0011**	0.11

Group 1, $N = 23$; Group 2, $N = 10$; Group 3, $N = 10$. CL = cranial lengths. ANOVA $df_1 = 1$, $df_2 = 40$. $P < 0.05$ are printed in bold.
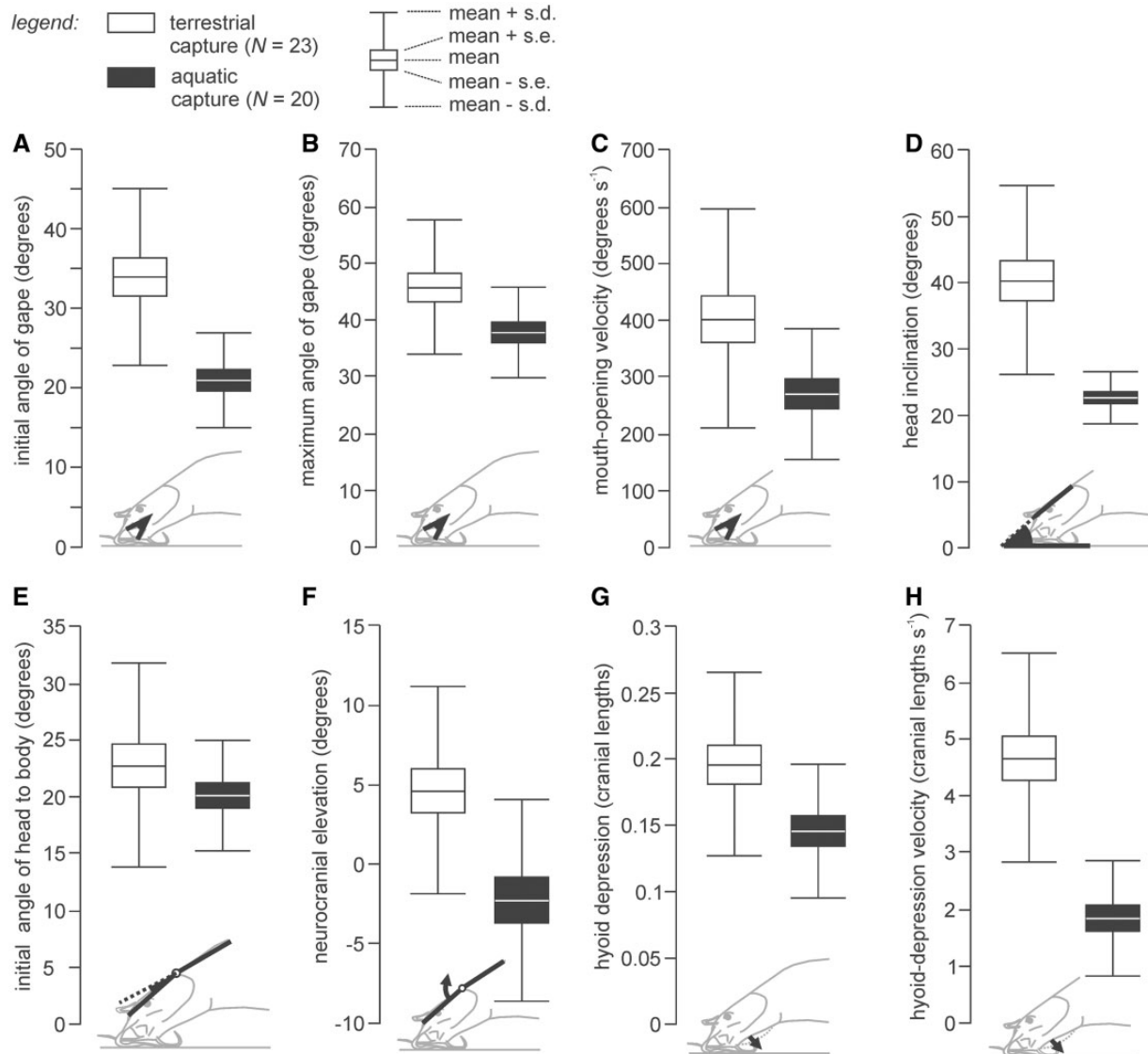
Fig. 7 Box and whisker plots comparing the means and variability in the kinematic variables for *C. apus* capturing prey on land and in the water (**A–H**). A legend of symbols is provided at the top. A significantly larger initial angle of gape (A), inclination of the head (D), and velocity of hyoid-depression (H) were found for capturing prey terrestrially. Although neurocranial elevation also showed this trend (although non-significant at $P = 0.07$; Table 1) (F), no significant differences were found for this or the other variables (B, C, E, and G).

can be attributed to the long, anguilliform body of *C. apus.*

It was observed that *C. apus* could achieve even steeper inclinations of the head by rolling to one side and laterally flexing the body (Fig. 5). Unfortunately, these videos could not be analyzed quantitatively due to problems of perspective. Nevertheless, these observations suggest that dorsoventral flexion in the vertebral column is not a prerequisite to feed on land via a steep angle between the head and the substrate, in contrast to previous suppositions (Van Wassenbergh et al. 2006a); lateral flexion of the body can be an equally good alternative. However, the scanning for food by left-to-right yawing of the head is nearly

always performed during dorsoventral flexion of the body.

Does the downward-tilted head posture have consequences for neurocranium movement during prey capture? Neurocranial elevation is a very common aspect contributing to buccopharyngeal expansion in fishes, and indirectly also to opening of the mouth (Gibb and Ferry-Graham 2005; Collar and Wainwright 2006). It would not be surprising if this cranial elevation would be compromised when the head needs to be tilted strongly downward. However, a small amount of neurocranial elevation does still occur when capturing terrestrial prey (Fig. 7F). In contrast, neurocranial elevation is rarely

employed during benthic, aquatic feeding (Figs. 6 and 7F). This behavior is similar to that of catfish species that are specialists in benthic feeding (*Corydoras splendens* and *Synodontis multipunctatus*); they generally suction-feed with a relatively stationary neurocranium (Van Wassenbergh et al. 2009). Consequently, neurocranial rotation in *C. apus* does not seem mechanically limited during feeding in the terrestrial environment. The support from the posterior part of the body and the tail appears to be sufficiently forceful to prevent the head from bobbing up and down when the animal is performing consecutive cycles of neurocranial elevation. Alternatively, the cycles of neurocranial elevation and depression may be too quick (duration of about 0.1 s) to result in significant losses of height due to gravity.

It is generally assumed that the capture and intra-oral transport of prey by moving the fluid that surrounds the prey does not function in air (Herrel et al. 2012). The fact that *C. apus* nearly always returned to the water to ''swallow'' prey held between the jaws by sucking water and the prey to the back of the buccopharyngeal cavity confirms this hypothesis. However, an alternative type of suction to draw the prey into the mouth did sometimes occur when this species fed on land on pieces of fish (Fig. 5); pushing the jaws onto this type of prey sealed the interface with the borders of the mouth, which in turn created a closed buccopharyngeal chamber. Next, expansion of this chamber due to depression of the hyoid inevitably creates a negative, intra-oral pressure that immediately causes the chamber's border surface with the least resistance to collapse inward. A biomechanical analog is, for example, the usage of the lips and thorax expansion in humans to suck in a boiled spaghetti noodle. This type of aerial vacuuming could be used by *C. apus*, for example, when scavenging large pieces of meat. However, it may not be used frequently in nature since the terrestrial prey in the diet of this species mainly consist of insects (Huysentruyt et al. 2004) of which the size and shape make it impossible to create a sealed interface with the mouth.

Why does the eel-catfish still perform such extensive expansions of the buccopharynx by depressing the hyoid apparatus despite the fact that the resulting suction of air is useless in either capturing or transporting its natural types of prey? First of all, it can be argued that, because of the strongly decreased fluid loading when feeding in air, the mechanical costs in terms of power or work for these movements probably are negligible. Consequently, there may not be a selective pressure for decreasing the magnitude or for cancelling movements that originally evolved as mechanisms of aquatic feeding, and that are still used for this purpose

in *C. apus*. Second, as Actinopterygii do not have a lower-jaw-depressor muscle linked to the neurocranium as in Sarcopterygii (musculus depressor mandibulae), depression of the hyoid has been shown to be indispensable for opening of the mouth during feeding, for example, in catfish (Adriaens et al. 2001; Van Wassenbergh et al. 2005). In the clariid catfish, *Clarias gariepinus*, for example, the ventral motions of the hyoid are coupled, via the protractor hyoidei muscles, to ventral motions of the lower jaw, which, even without shortening of this muscle, would be responsible for approximately 70% of the observed rotation of the lower jaw rotation (Van Wassenbergh et al. 2005). Turtles and salamanders, however, do show a decreased depression of the hyoid when feeding on land versus in water (Reilly 1996; Summers et al. 1998; Stayton 2011). This difference between ray-finned fishes and turtles may be linked to the role of the depressor mandibulae muscles in opening of the mouth in these amniotes. For ray-finned fishes, in contrast, it would probably require the evolution of a novel mouth-opening mechanism to open the mouth widely without using hyoid depression.

Previous research showed that *C. apus* performs aquatic suction-feeding as effectively as do obligatory aquatic feeders from the same family (e.g., *C. gariepinus*) (Van Wassenbergh et al. 2007). This means that the contractile properties of its feeding muscle are probably tuned to maximize power output under aquatic loading conditions. In that case, theory of muscle physiology (Hill 1938) predicts that upon maximal activation, muscles will be able to contract about three times faster when the resultant movement has negligible external resistance, such as working in air versus water. This relationship was indeed confirmed for the velocity of hyoid depression (Fig. 7H). Velocity of mouth opening, on the other hand, increased only by 50% (Fig. 7C), but this movement was not really comparable since the mouth started from an ''initially open'' position during terrestrial feeding (Fig. 7A). Terrestrial mouth opening on average involved a rotation of only $11.7°$, which probably lasted too short a time to be able to reach maximal velocity of contraction of the mouth-opening muscles.

This study focused on one of the few groups of actinopterygian fishes that managed to make the transition to capturing prey on land. It shows how the support and flexibility of an anguilliform body can be particularly useful for an effective capture of ground-based prey. Although the cycles of expansion and compression caused by these elements were considerably quicker when operating in air, the typical (i.e., aquatic) sequence of motion of the jaws and

hyoid were retained. In contrast, the animal's ability to assume and stably maintain its inclined head posture and flexed body in an environment where gravity is no longer cancelled by hydrostatic lift is probably the most impressive evolutionary achievement observed here. Since mudskippers also position their jaws over the prey by inclining the head downward (Sponder and Lauder 1981) so that the line connecting the tips of the upper and lower jaws approachs a parallel orientation with respect to the surface of the ground, this posture appears to be essential for terrestrial capture of ground-based prey by amphibious fish. However, it may be too early, given the limited amount of data at hand, to make a conclusive overview of what is morphologically or behaviorally required for fish to become successful terrestrial feeders. The profound morphological differences from the other groups of fishes performing terrestrial feeding prevent us from deducing general pattern of adaptations based solely on the data from the eel-catfish. Consequently, biomechanical and functional morphological information on the capture of terrestrial prey in groups other than air-breathing catfish would be very useful. Ultimately, with the help of these data, our biomechanical insight may allow us to develop and/or refine evolutionary scenarios of the evolution of terrestrial feeding in vertebrates.

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