Feeding patterns of *Chelus fimbriatus* (Pleurodira: Chelidae)

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Summary

The kinematics of feeding on fish have been studied in the aquatic feeding specialist *Chelus fimbriatus*, the fringed turtle, to provide a basic description of complete feeding cycles. Anatomical findings supplement the kinematic results. High-speed video (500 frames s^{-1}) recordings and X-ray film (150 frames s^{-1}) are used to analyse the kinematic variables characterizing head, hyoid, oesophageal and prey movements. The high velocities, especially of mouth opening, the forward thrust of the head and suction of the prey, are unique among turtles and comparable with those of aquatic salamanders and certain fishes (unidirectional feeders, in contrast to *Chelus fimbriatus*). The expandability of the pharynx and the anterior half of the oesophagus enables a specific type of unidirectional flow, at least during the early stages of the feeding cycle. This considerably improves the feeding performance compared with that of other aquatic turtles. The streamlined shape of the skull, the large hyoid apparatus, the highly reduced tongue and the extremely distensible oesophagus support the kinematics to a great extent, making *C. fimbriatus* a specialized suction feeder that can be regarded as one endpoint in the feeding evolution of aquatic reptiles.

Key words: kinematics, feeding, suction, anatomy, turtle, fringed turtle, *Chelus fimbriatus*.

Introduction

Turtles are of special interest for investigations of functional morphology and the evolution of aquatic feeding mechanisms. The large number of aquatic turtles provides us with a group of vertebrates that developed aquatic feeding convergently with anamniote feeding systems. Turtles are therefore highly suitable for testing hypotheses regarding the morphological and functional patterns associated with aquatic feeding in lower vertebrates. Most previous studies on feeding kinematics have involved fishes and amphibians (for a review, see Reilly, 1995), while turtles have been somewhat neglected (Bels et al., 1997; Bramble, 1973, 1978; Lauder and Prendergast, 1992; Lemell and Weisgram, 1997; Summers et al., 1998; Van Damme and Aerts, 1997; Weisgram, 1985; Wochesländer et al., 1999).

Chelus fimbriatus, the matamata or fringed turtle, is often described as a suction feeding specialist (e.g. Ernst and Barbour, 1989; Pritchard, 1979; Pritchard and Trebbau, 1984). A few studies have concentrated on the ethology and statistics of prey capture in this species (Formanovic et al., 1989; Hartline, 1967; Holmstrom, 1978, 1991; Wise et al., 1989). The present study analyses the kinematics of complete feeding cycles of the aquatic feeding specialist *C. fimbriatus* using high-speed video recordings and X-ray film sequences. We describe the kinematics of the head, hyoid, oesophagus and prey during complete feeding cycles to provide a basic description of food uptake and transport in this species. These data are supplemented by a morphological description. Furthermore, special features of the matamata are characterized and the findings are compared with other aquatic feeding turtles.

Materials and methods

The fringed turtle *Chelus fimbriatus* Schneider is a purely aquatic freshwater turtle that is widely distributed in the Amazon and Orinoco systems of South America as well as in Trinidad. It prefers slow-moving blackwater streams, oxbows, muddy lakes, stagnant pools, marshes and swamps, where it remains at shallow depths (Ernst and Barbour, 1989; Pritchard and Trebbau, 1984). *C. fimbriatus* is a carnivorous ambush predator, feeding on aquatic invertebrates and fish. The animals investigated were maintained in an aquarium (110 cm×70 cm×60 cm, 7–14 cm water depth, approximately 27 °C water temperature and high humidity between 80 and 90 %) with a 12 h:12 h light:dark photoperiod.

Anatomy

The morphology of the feeding apparatus – skull, hyoid, jaw and hyoid musculature – was studied in five subadult specimens. Three were frozen individuals (carapace length 10–15 cm) from the 'House of the Sea' in Vienna, the other two (carapace length approximately 11 cm) were obtained commercially. The animals were killed by intraperitoneal injection of sodium pentobarbital (Nembutal) and fixed in an 8 % formaldehyde solution for 3 days prior to dissection.

Computer tomographic pictures were obtained using a CT pace, third-generation from G.E. (General Electric Medical Systems) in sagittal slices (layer thickness and distance 2 mm) and reconstructed in the 'bone window' of Advantage Windows AW 2.0.20.

Film recordings

Three similarly sized specimens (carapace length approximately 12 cm) were selected for detailed analysis of kinematic patterns. For filming, they were fed with dead fish 2–4 cm in total length. Feeding was recorded at 500 frames s^{-1} with a NAC colour HSV 1000 frames s^{-1} high-speed video recorder. Recordings were made in a 40 cm×16 cm×25 cm aquarium with a background grid (grid squares 1 cm×1 cm). The aquarium was illuminated by two Dedocool halogen spotlights (maximum 1250 W) and two Kobold lights (300 W). Prior to filming, the turtles were trained for several weeks to feed in the strong light necessary for filming. Two 45 ° mirrors, one in front of and the other underneath the aquarium, were used to measure the gape perimeter and the total oesophageal volume. Fish were suspended on a string in the water to simulate both moving and non-moving prey.

X-ray films were taken with a Philips Optimus M200 (maximum 150 frames s^{-1}) using a Kodak CFE film. The same sequences were recorded simultaneously with a U-matic videorecorder (Sony VO-5800PS, maximum 50 frames s^{-1}). The contrast of the prey fish in the X-ray recordings was enhanced with the X-ray contrast medium Gastrografin (Schering). One day prior to filming, lead markers were glued to the turtles' skull (two at the level of the tympanum, one behind the nose, one on the upper jaw and one on the lower jaw) and underneath the hyoid body. The latter marker turned out to be of no use because of skin movement.

General patterns of feeding behaviour

Twenty video sequences from a total of 46 (three specimens with five, seven and eight recordings, respectively) were suitable for the description of the general patterns of feeding kinematics (the selection criterion used was that the turtle's head moved parallel to the background grid). One entire feeding cycle was recorded on X-ray film, and eight further sequences were taken from X-ray video (U-matic). The latter sequences were used for analysing intraoral transport and swallowing. To calculate kinematic
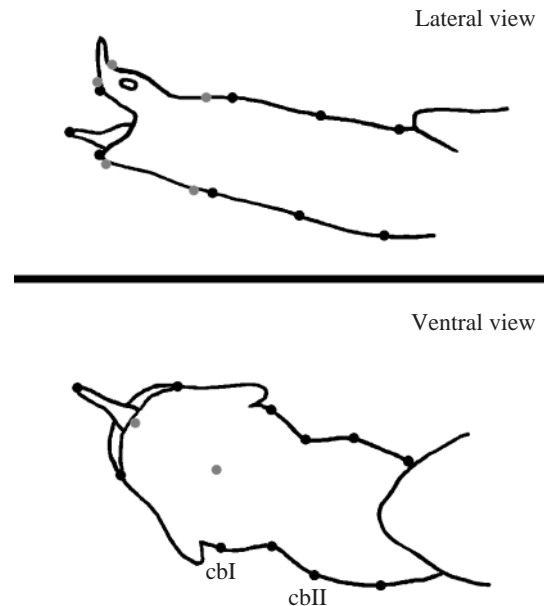

Fig. 1. Schematic representation of a high-speed video frame of *Chelus fimbriatus* during prey capture. Dots mark the points digitized from recordings (for details see Materials and methods); grey dots mark lead markers for X-ray film. cbI, cornu branchiale I; cbII, cornu branchiale II.

variables, only data derived from the NAC video sequences were used.

Kinematic analyses

The film sequences were digitized and analysed using AviDigitiser (© P. Snelderwaard). The frame immediately before mouth opening was defined as time zero.

A series of distance and timing variables was measured from each gape cycle to describe the movements of the jaws, hyoid apparatus, oesophagus and prey and to allow comparisons with other selected turtle species. The following distance variables were measured from the digitized points (Fig. 1): prey parameter, the distance between the prey and a fixed point on the background grid; snout parameter, the distance between the tip of the snout and a fixed point on the background grid; gape distance, the distance between the most ventral point of the anterior surface of the premaxilla and the most dorsal point of the anterior surface of the mandibular symphysis; hyoid depression, the perpendicular distance between a line along the dorsal border of the cranium and the most ventral point visible externally on the hyoid apparatus; and neck dimensions, dorso-ventral and transverse distances at the level of the second branchial horn and just in front of the shell (to locate the position of each point correctly, we used landmarks on the turtle's neck).

From these data, timing variables (Table 1) and oesophageal volume (the volume of water inhaled) during prey capture were calculated. The oesophageal volume was calculated from the measured areas of the gape and four neck segments (see Fig. 1).

Table 1. *Means of 23 statistical variables digitized from the kinematic profiles of* Chelus fimbriatus *feeding on fish*

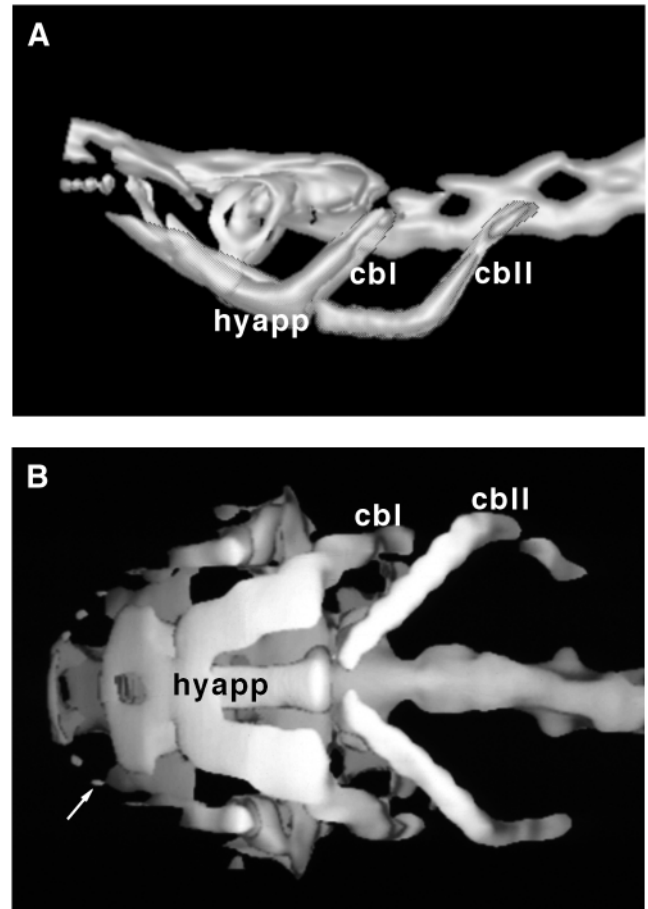| Variable	
Mean velocity of stalking (cm s^{-1})	0.36±0.30
Time between start of gape and start of approach (ms)	5.94±1.89
Mean velocity of forward thrust of head (cm s^{-1})	70.47±15.81
Maximum velocity of forward thrust of head (cm s^{-1})	177.97±48.64
Gape cycle duration (ms)	83.35±19.90
Time to maximum gape (ms)	20.30±4.59
Mean velocity of gape (cm s^{-1})	75.46±14.96
Maximum velocity of gape (cm s^{-1})	151.15±40.72
Mean velocity of mouth closure (cm s^{-1})	25.46±8.13
Maximum velocity of mouth closure (cm s^{-1})	88.46±33.30
Delay between start of hyoid depression and maximum gape (ms)	11.10±2.77
Delay between maximum hyoid depression and maximum gape (ms)	46.55±10.78
Time to maximum hyoid depression (ms)	54.00±10.92
Mean velocity of hyoid depression (cm s^{-1})	29.70±6.59
Maximum velocity of hyoid depression (cm s^{-1})	93.93±27.24
Mean velocity of prey (suction) (cm s^{-1})	144.33±70.30
Maximum velocity of prey (suction) (cm s^{-1})	282.59±166.76
Delay between start of oesophageal distension and hyoid depression (ms)	6.50±3.36
Duration of oesophageal distension (ms)	1340.00±219.10
Time to first peak of oesophageal distension (ms)	43.95±9.25
Duration of distension (ms)	218.90±85.14
Mean velocity of oesophageal distension (cm s^{-1})	39.40±11.63
Maximum velocity of oesophageal distension (cm s^{-1})	103.48±28.07
Ram-suction index	+0.36±0.23

Values are means ± S.D. (*N*=20).

Fig. 2. Computer tomographic photographs of the skull of *Chelus fimbriatus*. (A) Lateral view; (B) ventral view. The arrow in B indicates the lower jaw, which is too thin to be reconstructed correctly. Note the enlarged ventral area of the hyoid apparatus (hyapp); cbI, cornu branchiale I; cbII, cornu branchiale II.

The ram-suction index (RSI), introduced by Norton and Brainerd (1993) to describe the feeding mechanisms of fishes, was determined:

$$RSI = (D_{pred} - D_{prey})/(D_{pred} + D_{prey}),$$

where D_{pred} and D_{prey} are the net distance moved by the predator and the prey, respectively, between the moment the mouth first begins to open and the moment the prey disappears or is seized by the jaws. RSI ranges from +1, indicating a pure ram strike in which only the predator moves, to –1, indicating a pure suction strike in which only the prey moves.

Results

Anatomy

The anatomy of the skull of *Chelus fimbriatus* has been well described (Gaffney, 1979). The head including the lower jaw (Fig. 2A) is orientated at an acute angle (35°) to the horizontal.

The posterior half of the lower jaw is used for the muscle insertions of the adductor complex and the depressor; the anterior part is composed of thin dentaries (arrow in Fig. 2B).

Depression of the mandible during prey capture enables a maximum mouth opening of approximately 80°, which is unique for turtles.

The hyoid apparatus is one of the largest in aquatic feeding turtles. From the breadth of its anterior part [hyoid body and branchial horn I (cbI); see Fig. 2B], it is obvious that depression and expansion of the buccal chamber will incorporate a larger volume than in other aquatic feeding turtles.

The main muscle systems of the jaws and hyoid apparatus are shown in Fig. 3. In contrast to other aquatic feeding turtles, the jaw adductors except the adductor mandibulae externus are poorly developed. The external adductor is covered anteriorly by a half-folded skin overlayed by mucus, which acts as a lubricant. This may be necessary, since a cartilago transiliens is missing. This cartilage, which is present in all cryptodires and pleurodires, is usually embedded within the external tendon and facilitates gliding of the external adductor over the trochlear process of the quadrate (cryptodires) or the pterygoid bone (pleurodires). The skin unfolds during mouth opening,

functioning as a cheek, which is obviously advantageous for suction feeding. For optimal functioning of jaw adduction, the muscles of the external, internal and posterior complex must work together (Fig. 3A). The horizontal traction of the external complex is transformed into a vertical force by the external tendon, enabling the lower jaw to be lifted by retraction. The muscles of the internal and posterior complex and the medial part of the external adductor form a muscular crescent in the lower temporal fossa. The pterygoid muscle forms the topographic equivalent to the externus complex (protraction). The fibres of the posterior adductor run vertically, producing a mainly medial traction. The medial part of the external

adductor produces slight retraction close to the jaw articulation. Protraction and retraction combine to lift the lower jaw. These components act synergistically in closure, reducing horizontal stresses at the articulation. Since the posterior muscles and the medial part of the external complex closely adjoin the articulation, they are responsible for fixation of this joint. Medial traction is a result of all the jaw muscles working together.

The function of the major visceral muscles is indicated in Fig. 3B. The hyoid apparatus is retracted by the well-developed coracohyoideus. At the same time, three muscles are responsible for hyoid depression. These are the branchiomandibular and the two geniohyoid muscles. The main work is done by the branchiomandibular, which encloses the more rigid cbI in a sheathlike manner. Compression of this muscle alone would depress the hyoid and pull it forwards, but in association with retraction caused by the coracohyoideus, the hyoid apparatus moves posteroventrally. Both geniohyoid muscles are mainly responsible for the lateral distension of the branchial horns, but also for their depression in combination with the retraction.

The tongue of *C. fimbriatus* is very small. Thus, it neither occupies space within the oral cavity that could otherwise be utilized for volumetric expansion and suction nor acts as an impediment to high-velocity fluid flow, which would increase the force and energy requirements of suction feeding.

Description of the strike kinematics
Prey capture

Before the strike, a very slow stalking motion of approximately $0.4\ \mathrm{cm\ s^{-1}}$ (see Table 1) towards the prey occurs
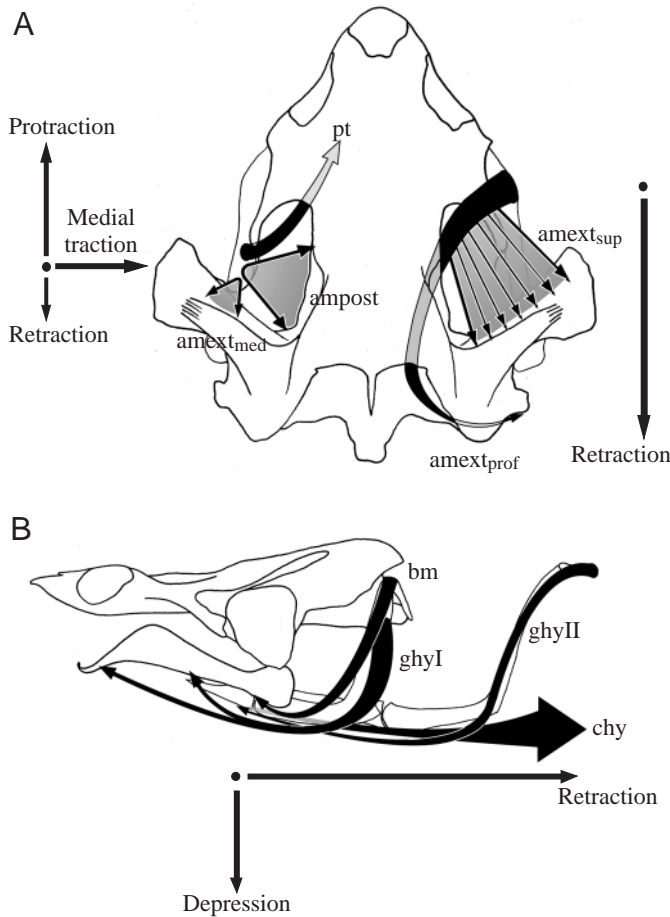

Fig. 3. (A) Dorsal view of skull of *Chelus fimbriatus*. The arrows indicate the directions of forces produced during contraction of the jaw adductor muscles, the shaded areas indicate the extent of the muscles and the thickness of the arrows reflects the relative forces of the muscles; the resulting forces produced by the muscles shown on each side are indicated next to the skull. amext$_{med}$, pars medialis of external adductor; amext$_{prof}$, pars profunda of external adductor; amext$_{sup}$, pars superficialis of external adductor; ampost, posterior adductor; pt, pterygoid muscle (internal adductor). (B) Lateral view of the skull. The courses of the major visceral muscles connected to the hyoid are shown by arrows. The resulting forces produced during contraction of the muscles are shown at the bottom. bm, branchiomandibular muscle; chy, coracohyoid muscle; ghyI and ghyII, geniohyoid muscles I and II.
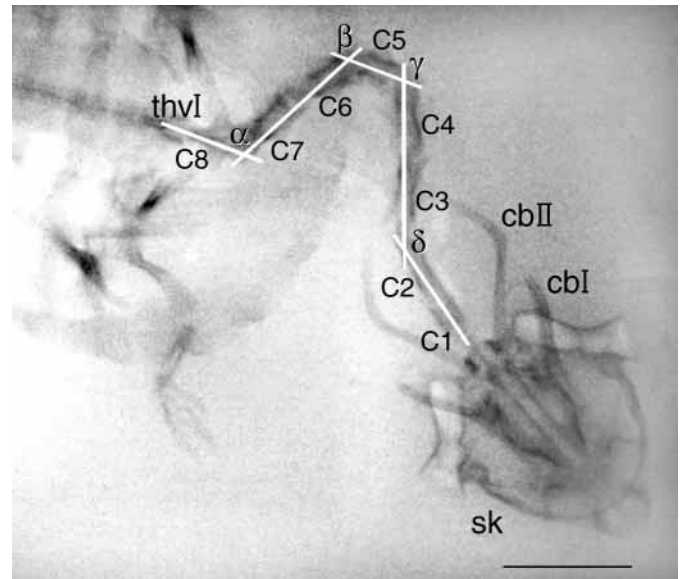

Fig. 4. X-ray photograph of *Chelus fimbriatus* showing the characteristic neck position before a strike. α–δ represent the angles between segments of neck vertebrae; C1–C8, cervical vertebrae; cbI, cornu branchiale I; cbII, cornu branchiale II; sk, skull; thvI, first thoracal vertebra. Scale bar, 1 cm.
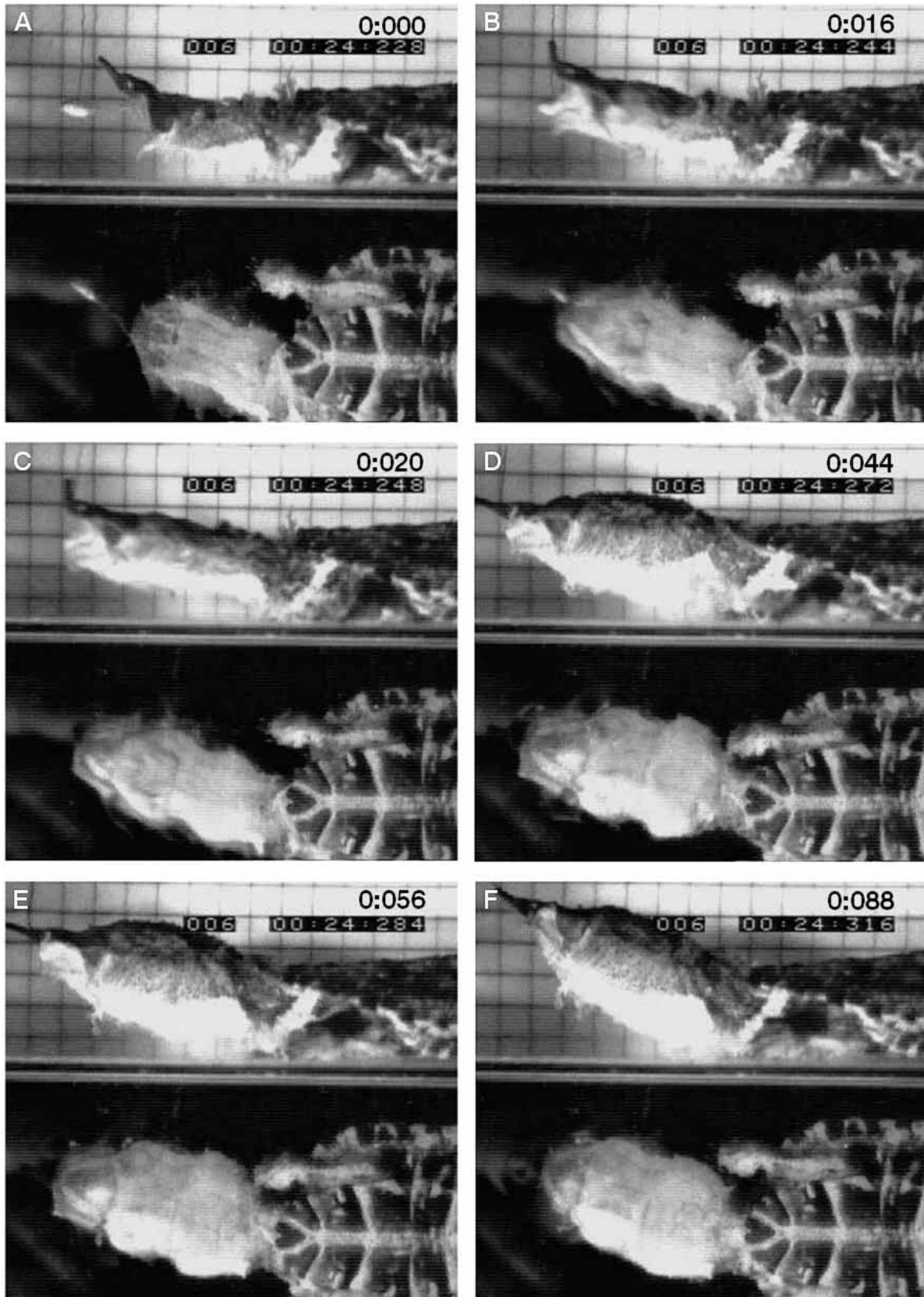
Fig. 5. Six single frames of a high-speed video recording (500 frames s^{-1}) showing a *Chelus fimbriatus* capturing a fish. Each frame shows a side view (upper) and a ventral view (lower) recorded *via* a 45° mirror below the tank. The real time (s:ms) is specified above the NAC-generated time code. Grid size is 1 cm×1 cm.
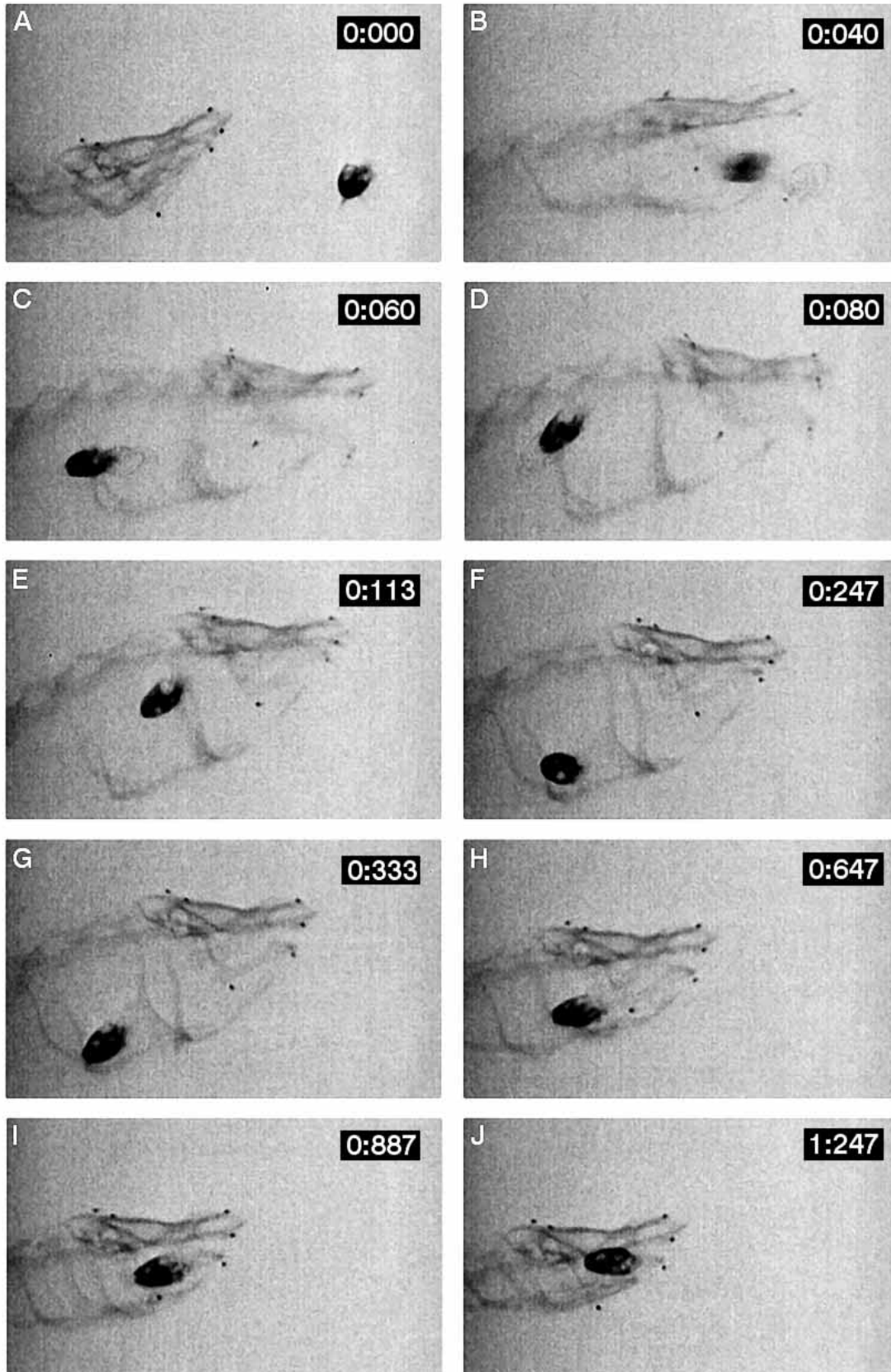
Fig. 6. Ten single frames of a high-speed X-ray film sequence (150 frames s^{-1}) showing a lateral view of *Chelus fimbriatus* capturing a fish. The real time (s:ms) is specified in the top right corner of each frame. The prey item appears dark because of the X-ray contrast medium; the positions of lead markers on the turtle's skull can be seen clearly.

Fig. 7. Eight single frames of a high-speed X-ray film sequence (150 frames s^{-1}) showing a lateral view of *Chelus fimbriatus* during intraoral transport before swallowing. The real time (s:ms) is specified in the top right corner of each frame. The prey item appears dark because of the X-ray contrast medium; the positions of lead markers on the turtle's skull can be seen clearly.
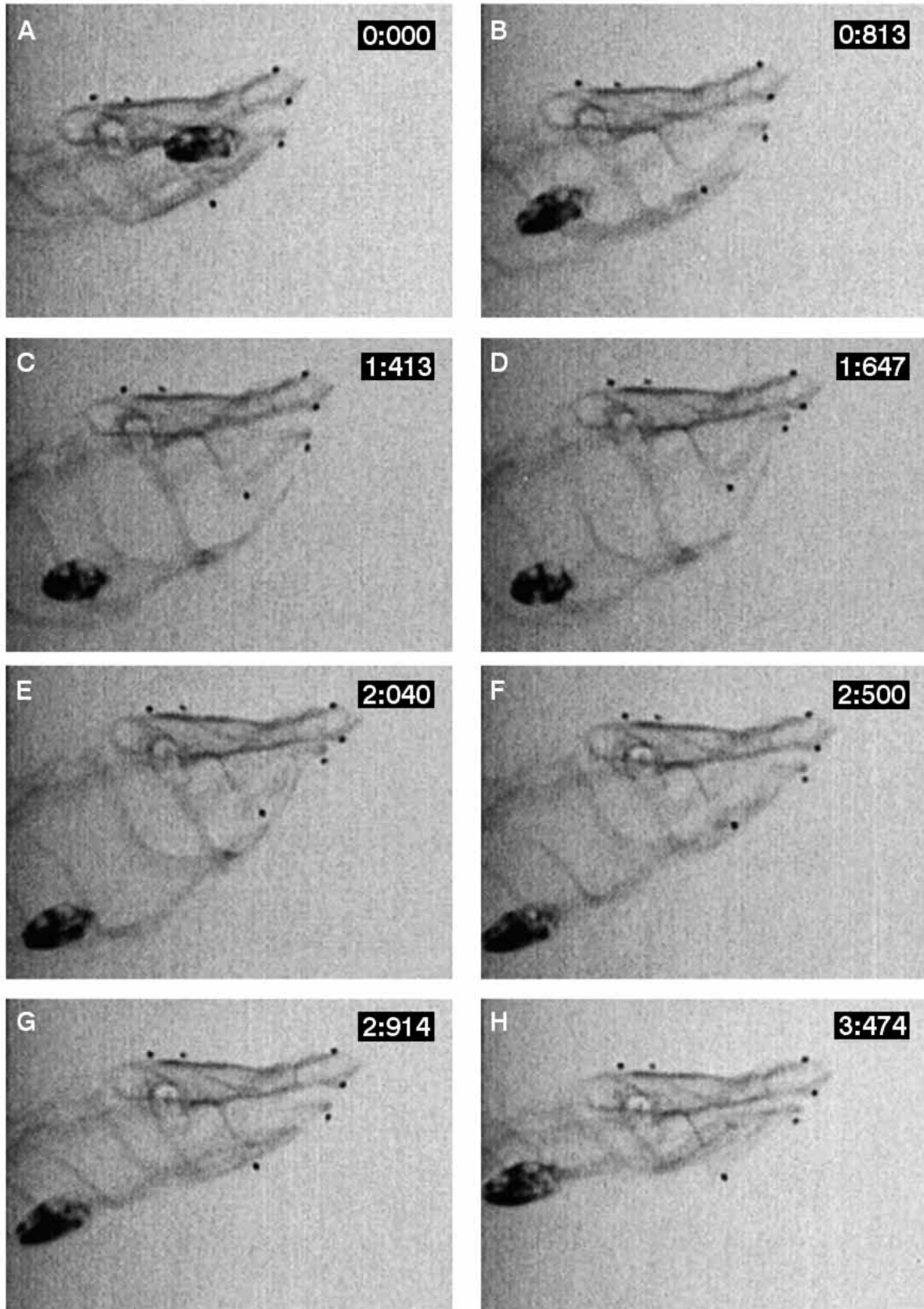
until the tip of the snout is approximately 2 cm away from the fish. During this approach phase, the head and cranial half of the cervical vertebrae show very little vertical or horizontal motion with respect to the shell. The first two cervical vertebrae (C1, C2) are typically aligned with the skull (Fig. 4). C3–C7 are arranged in a half-elipsoid curve: angles α–γ (the angles between more-or-less straight vertebral segments of C3/C4, C5, C6/C7 and C8; see Fig. 4) lie within a very small range (115–120°). The curved neck allows forward expansion of one-third of the total neck length during the strike.

Figs 5A and 6A show the turtle just before the capture sequence begins. After this time, the direction of the forward thrust of the head is fixed, and the head traces a straight line from the starting position towards the prey. During the strike, no vertical adjustments of the head direction take place. The fast forward thrust of the skull and neck towards the prey item does not start until approximately one-third of the maximum gape has been reached. Approximately 20 ms later, the gape is at its maximum (Figs 5B, 6B). At this point, hyoid depression has just begun and the neck is nearly fully stretched. The fish has not yet moved, but 4 ms later (Fig. 5C) it disappears within the mouth. The neck reaches maximum extension with all cervical vertebrae aligned with the skull, and the geniohyoid musculature begins to pull apart the hyoid horns. In Fig. 5D, the forward motion of the head has stopped and the head then moves slightly upwards (Fig. 5E) before being retracted. The neck is still completely extended, the hyoid has reached its maximum depression and the horns are maximally distended laterally. The oesophagus is filled with the large amount of water sucked in during the gape cycle until the mouth is closed (Fig. 5F).

Prey movement through the mouth cavity can be clearly followed in the X-ray film sequences: the prey is sucked inwards (Fig. 6B) and then floats just above the hyoid up to the level of the second branchial horn (cbII) (Fig. 6C). It drifts upwards in a half-circle and then forwards to the level of cbI (Fig. 6D,E). After the mouth has been closed (Fig. 6F), the prey sinks down to floor of mouth (the hyoid apparatus). The neck is retracted slightly, bringing cervical vertebrae C8–C5 into their prestrike positions; C4–C1 remain aligned with the skull. Shortly thereafter, the mouth is again opened slightly to expel the excess water by returning the hyoid apparatus to its starting position (Fig. 6G–J). The fish is retained by the jaws.

Intraoral transport and swallowing

Before the transport phase, 2–3 very slight hyoid movements (depression of approximately 3 mm) take place. This results in a small amount of water being sucked in and blown out again. Two different kinematic patterns can then be used to bring the prey into position for swallowing. The first, used in 75 % of the filmed events, is slow suction. The hyoid is depressed slightly (depression of approximately 5 mm); then, after the mouth has been opened enough to release the prey from the jaws, the fish floats further inwards up to the end of the cbII, where it is held by the horizontal part of the rods (compare with Fig. 2). The gape cycle during this transport phase takes between 250 and 600 ms.

In the second transport pattern (Fig. 7), the prey is also sucked in very slowly, but hyoid depression is of the same extent as during prey capture. The anterior part of the oesophagus increases in volume slowly (1–1.5 s; Fig. 7A–D) so that the fish can be held between the second branchial horns (Fig. 7E). By expelling the water very slowly (Fig. 7E–G), the turtle keeps the prey at the posterior end of the hyoid apparatus (Fig. 7H).

When the prey has been positioned at the end of the second branchial horn, it is swallowed by contractions of the constrictor musculature supported once again by a slow water flow.

Special features during feeding

The first important feature of the feeding of *Chelus fimbriatus* is the almost pressure-wave-free prey capture. Any moving mass in a liquid produces wave-like disturbances in the surrounding medium that must be compensated for by a predator.

The matamata is able independently to lift its skull or depress its lower jaw. The strategy it chooses depends on the position of the prey (Table 2). A fish on the ground is taken up by a straight forward thrust of the head, the lower jaw is maximally depressed to bring it into position under the prey. When the prey is immediately in front of the head, the skull is slightly lifted before gape begins (20–25°; see Fig. 5A). During the forward thrust, a small increase in the skull angle is observed. A fish lying above a fictitious horizontal line from the turtle (a line from the skull to the carapace) is stalked with a head angle of approximately 45°. This angle decreases during the subsequent capture phase, reaching approximately

Table 2. *Head angles and lower jaw depression of* Chelus fimbriatus *for three prey positions*

Fish position	Head angle (degrees)			Lower jaw depression with respect to the background (cm)
	Before gape	During maximum gape	At end of forward thrust	
On substratum	2.4±1.7	2.35±1.14	2.35±1.16	1.59±0.19
In front of head	23.9±3.39	33.3±2.58	2.25±1.59	0.87±0.21
Above head	44.3±2.75	33.95±2.35	2.3±1.59	0.5±0.14

Values are means ± S.D. (*N*=20).
Head angles were measured during three different stages of the forward thrust.

0° at the end of the thrust phase. The lower jaw is opened to one-third of its maximum gape (approximately 0.5 cm) and is then thrust forward in a straight line. These patterns suggest that the turtle tries to avoid the production of pressure waves that would affect the prey.

The second notable feature is the enormous increase in oesophageal volume. Although the true oesophageal volume cannot be calculated from the film sequences, the proportional volume increase may be estimated by measuring the changes in overall neck dimensions. During the first 10 ms, the volume remains more-or-less constant. During the forward thrust phase, the volume increases up to twofold as a result of stretching of the neck and oesophagus. During the closing phase, the volume of the oesophagus is further increased by the inflow of water. By mouth closure, the oesophagus has expanded to approximately four times its starting volume.

Ram-suction index

For the feeding sequences recorded here using fish prey, the calculated RSI during prey capture was always positive (0.071–0.664). No correlation between RSI and prey item length was found. Over the whole cycle, the ram component was predominant, in contrast with previous findings.

Fig. 8A shows changes in D_{pred} and D_{prey} over time. RSI calculated using these values is given in Fig. 8B. This approach provides quantitative information on the change from ram to suction feeding. Following a pure ram phase (RSI=+1),
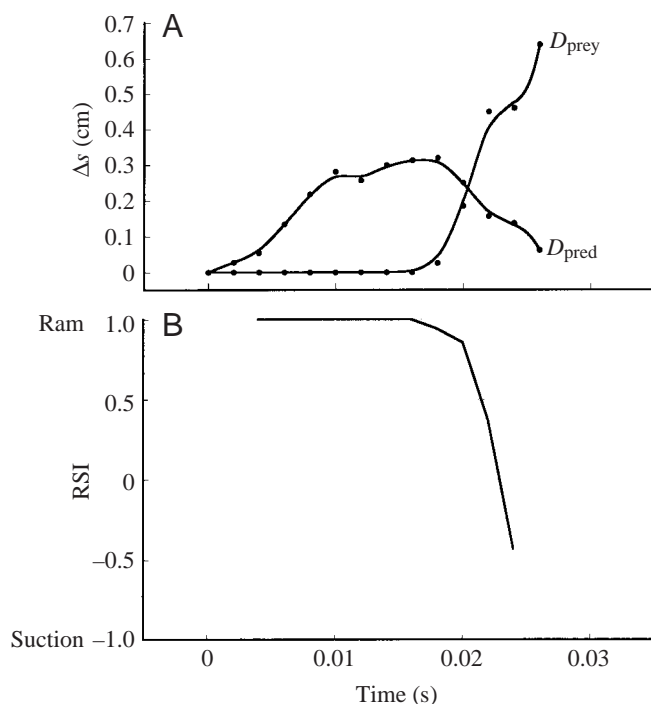

Fig. 8. (A) Distances covered between each frame (Δs) for predator and prey. (B) Ram-suction index (RSI) calculated for each frame of one representative feeding sequence of *Chelus fimbriatus*. D_{pred} and D_{prey} are the net distance moved by the predator and the prey, respectively.

suction starts in the last third of the feeding cycle and becomes predominant only during the final stages of the capture process. Suction and movement of the prey start when the turtle's head reaches its highest velocity (0.3 cm in 2 ms at t=0.02 s; Fig. 8A). After suction has started, the speed of the forward thrust decreases, and the animal stops moving forwards after a few milliseconds. The rapid increase in suction shortly before the prey disappears (thereby determining the end point of the calculation of RSI) means that values up to –0.8 are reached.

Discussion

Anatomical peculiarities

The characteristic anatomical features of aquatic feeding vertebrates (see Bramble and Wake, 1985) are a large, relatively rigid and well-ossified hyoid apparatus with massively developed musculature, a small tongue with a simple surface topography and a relatively short gape that is restricted laterally. All these features are found in *Chelus fimbriatus*, accompanied by some special characteristics.

The extremely flattened skull is comparable with that of certain representatives of Tryonichidae (e.g. *Chitra* spp., *Cyclanorbis* spp.). Its streamlined shape leads to an almost pressure-wave-free capture strike – useful for an ambush predator. The shape of the lower jaw is also unique for turtles. From the high speed of mouth opening, two different opening mechanisms can be postulated: muscular power alone or muscles aided by the forward thrust of the head. In the first case, the power necessary to open the mouth would have to be maintained over the whole period of mouth opening, while in the second case only a small gape – and therefore a short period of muscle activity to initiate the opening, together with the water resistance due to the forward thrust of the head – would extend the gape to its maximum value. An analysis of the present recordings indicates that the motion of the lower jaw is linked directly to the head's forward motion. Mouth closure occurs at one-third of the opening velocity and starts after maximum neck extension has been reached. Since, at that time, a considerable inward flow is occurring, the movement of the jaw is presumably aided by forces resulting from Bernoulli's law. The power requirements of the jaw musculature during prey capture are therefore probably minimised.

The hyoid apparatus is one of the largest known in turtles. It covers the whole floor of the mouth up to the start of the oesophagus. This development, together with its rigidity, allows a large suction force, comparable only with the feeding performance of *Chitra indica* (R. Gemel, personal communication), to be generated.

The musculature of matamatas exhibits some peculiarities. The lack of a cartilago transiliens – at least in the subadult individuals studied here (adult specimens were not available for investigation) – and the line of action of the external adductor, which is closely connected to the cheek, are unusual for turtles. The typical line of action of the external adductor in pleurodires is from the mandible over the trochlear process to the supraoccipital bone (Lemell et al., 2000). In *C.*

fimbriatus, as in other turtles, this muscle is divided. The pars profunda is particularly well-developed, changing its direction three times. This is a unique situation in turtles, but is presumably necessary because of the enormous water pressure exerted on the lower jaw during feeding. Since the mouth is closed while the turtle is still moving forwards, the more usual lever system with one vertical and one horizontal arm would have to be very large to produce sufficient force. This, however, would be difficult to accommodate in a flattened skull shape. Therefore, in *C. fimbriatus*, a type of pulley block with three changes of direction has been developed to facilitate adduction of the lower jaw. In such a lever system, the musculature can be kept small while generating the same or even higher muscle forces than in other aquatic feeding turtles with well-developed adductor musculature.

This species has a reduced tongue to allow more space for volumetric expansion of the oral cavity. The development of a 'cheek' is also very useful for a suction feeding species. During mouth opening, this cheek bounds the lateral side of the mouth from just behind the eyes. This allows a suction force similar to that of fish and aquatic amphibians to be developed.

The anterior half of the oesophagus has a large lumen that can be distended to four times its original volume. Such a distensible oesophagus – a feature of most Chelidae – is a prerequisite for a suction feeding specialist that uses a bidirectional flow system (Lauder and Shaffer, 1986, 1993). The bidirectional system becomes functionally unidirectional by greatly delaying the reverse flow of water out of the mouth until the jaws seize the prey. The larger the inner volume of the oesophagus, the larger the period of suction that can be applied.

Strike kinematics

The traditional characterization of feeding in lower vertebrates involves a terminology used to define the different phases of prey capture in ray-finned fishes: preparation or slow opening (SO), expansion or fast opening (FO), compression or fast closing (FC) and recovery or slow closing/power stroke (SC/PS) (for reviews, see Lauder, 1985; Bramble and Wake, 1985). The SO phase in fishes and salamanders is used mainly to decrease the buccal cavity volume prior to mouth opening by medial compression of the suspensorium, protraction of the hyoid apparatus and adduction of the lower jaw. This phase can also be found in some aquatic feeding turtles such as *Pelusios castaneus* (Lemell and Weisgram, 1997) and *Terrapene carolina* (Bels et al., 1997; Summers et al., 1998) in which the mouth is opened slowly to generate low pressure within the mouth cavity by protraction of the hyoid. The kinematic patterns during the FO phase used by turtles and by fishes and salamanders are quite similar. Rapid mouth opening is immediately followed by a postero-ventral movement of the hyoid apparatus, and peak hyoid depression follows peak gape. During the FC phase, the hyoid apparatus remains depressed until the mouth is closed. It is usually brought back into its

Table 3. *Selected kinematic variables of three aquatic feeding specialists,* Chelus fimbriatus, Chelodina longicollis *and* Chelydra serpentina, *and two aquatic feeding generalists,* Pelusios castaneus *and* Terrapene carolina

Variable	*Chelus fimbriatus,* suction feeder	*Chelodina longicollis,* suction feeder	*Chelydra serpentina,* ram feeder	*Pelusios castaneus,* ram-suction feeder	*Terrapene carolina,* ram-suction feeder
Food/prey	Fish	Pieces of meat	Fish/worm	Fish/snail	Mealworm
Time to maximum gape (ms)	20	≈60	30 (f) 60 (w)	90 (f) 50 (sn)	400 (S) 530 (B)
Gape cycle duration (ms)	80	110	80 (f) 100 (w)	300 (f) 150 (sn)	610 (B)
Maximum gape velocity (cm s^{-1})	150	≈30	120 (f) 50 (w)	30 (f) 50 (sn)	≈15 (S+B)
Maximum velocity of forward thrust (cm s^{-1})	180	24	150 (f) 50 (w)	10 (f) 50 (sn)	≈10 (S)
Time to maximum hyoid depression (ms)	50	≈40	60 (f) 110 (w)	120 (f) 50 (sn)	470 (S)
Maximum velocity of hyoid depression (cm s^{-1})	90	≈40	120 (f) 50 (w)	15 (f) 50 (sn)	≈25 (S)
Maximum prey velocity (cm s^{-1})	280	80	≈50	10 (f) 110 (sn)	–
RSI	+0.4 to –0.5 (during suction phase)	–	≈+0.7	+0.4 (f) –0.3 (sn)	–

Data are taken from Van Damme and Aerts (1997), Lauder and Prendergast (1992), Lemell and Weisgram (1997), Bels et al. (1997) and Summers et al. (1998).

≈ indicates values not specified in the publications but that could be calculated approximately from pictures or graphs.

RSI, ram-suction index; f, fish; w, worm; sn, snail; B, Bels et al. (1997); S, Summers et al. (1998).

starting position during the SC phase. Our observations suggest that *C. fimbriatus* also uses these typical aquatic feeding patterns.

Certain features, however, are notable. In contrast to fishes, aquatic salamanders and some turtles, no slow opening phase was observed in our video sequences. The morphology of *C. fimbriatus* makes this phase unnecessary: at rest, the hyoid apparatus lies just underneath the palate, establishing a permanent 'waterless' space. Compared with *Chelydra serpentina* (Lauder and Prendergast, 1992), a ram feeding specialist, and with *Chelodina longicollis* (Van Damme and Aerts, 1997), a suction feeder, the FO phase (time to maximum gape) of *C. fimbriatus* is faster (see Table 3). This phase is faster in aquatic salamanders and fishes (for reviews, see Lauder and Shaffer, 1986, 1993) and substantially slower in less-specialized aquatic feeding turtles.

Another difference from other aquatic feeding vertebrates is the duration of the closing phase. In *C. fimbriatus*, this phase is approximately four times longer than the opening phase, while in *C. serpentina* and *C. longicollis*, the closing phase is approximately twice as long as the opening phase (Table 3). From our qualitative observations, matamatas seem to use a relatively constant closing velocity with no clear separation into FC and SC phases. In addition, no crushing of the prey and, therefore, no power stroke during the SC phase take place, although there is a recovery phase between single gape cycles. In Table 3, the kinematics of three feeding specialists including *C. fimbriatus* are compared with that of feeding generalists such as *P. castaneus* (Lemell and Weisgram, 1997), a purely aquatic feeding turtle, and *T. carolina* (Bels et al., 1997; Summers et al., 1998), an emydid turtle that is able to feed both on land and in water. The very long opening phase of *T. carolina* can be attributed to its extended SO phase: *T. carolina* uses a terrestrial feeding style in water. In general, the velocities of all the cephalic elements of the feeding generalists are slower than those of specialists.

The term 'compensatory suction' was introduced by Van Damme and Aerts (1997) to describe the active compensation by the predator for the production of a pressure wave at the position of the prey due to the fast forward thrust of the head during a strike. This term should also ensure that the term 'ram feeding' is reserved for feeding events with continuous through-flow. In *C. serpentina* and *C. longicollis*, the production of a pressure wave is mainly compensated by depression of the hyoid apparatus during the forward thrust of the head. In *C. fimbriatus*, compensatory suction is not needed: no noticeable pressure wave was detected at the position of the prey. To illustrate the mechanism better, the skull and lower jaw can be compared with two ships sailing apart at a small angle. The bow waves of these ships make an acute angle and meet somewhere behind their bows. The effects on the position of the prey are neglible at this point and they will be compensated by the onset of suction (see Fig. 8). Although the large volume of water entering the mouth during the fast forward thrust of the head is accommodated by enormous enlargement of the oesophagus

to up to twice its initial volume, it is important to note that, in contrast to active compensation as defined above, no substantial hyoid depression and therefore no suction was recognizable.

Ram-suction index

The RSI allows the ratio of ram to suction to be assessed in individual strikes of aquatic predators. However, its applicability to the feeding performance of *C. fimbriatus* is questionable: matamatas have often been described as a clear example of suction feeding (e.g. Ernst and Barbour, 1989; Pritchard, 1979; Pritchard and Trebbau, 1984). The mean RSI calculated here was +0.36±0.23 (mean ± S.D., *N*=20), which indicates a dominant contribution from head motion. The equation used for RSI will tend to overestimate the ram component because, particularly for fish feeding (for which this index was initially introduced), even pure suction will lead to forward thrust due to momentum conservation, and an RSI of –1 will therefore never be obtained.

For turtles such as the matamata, a feeding mechanism based mainly on the conservation of momentum has been proposed by Van Damme and Aerts (1997). They suggested that the large volume of water sucked in during feeding causes the head to be thrown forward. This mechanism would reduce the use of the turtle's neck musculature solely to aiming the head towards the prey. To test this hypothesis, we calculated head velocity and water flow rate through the turtle's mouth. Using the model of Van Damme and Aerts (1997) with input data taken from our recordings (volume changes of the turtle's oesophagus and the area of the gape), the mass of the head at any time during the strike can be calculated assuming conservation of momentum. Instead of remaining constant during the strike, the mass varied by up to two orders of magnitude, indicating the existence of additional forces acting on the turtle's head. Although our model includes crude simplifications because of lack of information about the complex interplay between head, neck and other parts of the turtle's body, it suggests that, although suction will certainly increase the final velocity of the head, an important contribution to the forward thrust comes from the neck musculature.

It is clear from our X-ray film that the intake of the prey occurs largely by suction. A strong suction force will extend the effective capture range and increase the potential size of prey.

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