FOOD INGESTION IN THE ESTUARINE TURTLE MALACLEMYS TERRAPIN: COMPARISON WITH THE MARINE LEATHERBACK TURTLE DERMOCHELYS CORIACEA

V.L. BELS*, J. DAVENPORT† AND S. RENOUS‡

*Hauta École Provinciale du Hainaut Occidental et de Charleroi, and Centre Agronomique de Recherches Appliquées du Hainaut (CARAH) rue Paul Pastur 11, B-7800 Ath, Belgium, †University Marine Biological Station, Mullport, Isle of Cumbrae, Scotland, KA28 0BC, ‡Laboratory of Comparative Anatomy, National Museum of Natural History, rue Buffon 55, URA-1137, 75205 Paris, France

This study sheds light on the evolution of aquatic and terrestrial feeding modes in vertebrates, using two aquatic turtles as models. The estuarine aquatic diamondback turtle Malaclemys terrapin has a feeding mechanism that is similar to the basic feeding mechanism of terrestrial tetrapods (jaw gape cycles, incorporate slow opening, fast opening, fast closing and slow closing phases). Strikes upon prey also involve neck extension and cycles of the forelimbs. Malaclemys terrapin modulate their feeding behaviour and jaw action in relation to the nature of the prey item. Mussels are approached by walking on the substratum, and limb cycles are of small amplitude during the strike. Crabs, whether encountered in mid-water or on the substratum, are approached by swimming, and the strikes are produced by vigorous upstrokes of the forelimbs, that occur simultaneously with neck extension. Crabs are dangerous prey, and the turtles often strike with the gape already at maximum, minimizing the time needed to bite a limb or other part of the crab. The tongue is not involved in food capture, but has a major role in food manipulation and transport prior to swallowing. Although transport cycles are similar to ingestion cycles, ingestion and transport are easily separable in the species. Malaclemys terrapin exhibit great distension of the throat during the strike, but this does not appear to generate adequate suction to aid capture of hard-shelled prey: it is suggested that throat distension reduces pressure in front of the advancing snout, thus preventing pressure waves displacing or alerting prey. The pelagic marine turtle Dermochelys coriacea, which specializes in gelatinous prey, relies heavily on suction for ingestion, which overlaps considerably with transport.

INTRODUCTION

Generally it is believed that there is a clear division between aquatic and terrestrial feeding modes amongst vertebrates (see Liem, 1990 for review), with the aquatic mode being constrained by the aquatic medium (and therefore primarily dependent upon suction), yet showing great diversity (Liem, 1984), while the terrestrial mode shows constancy of mechanism (involving slow jaw opening, tongue protrusion, fast jaw opening, prey transport by the tongue, fast jaw closure and slow jaw closure) across a range of tetrapods (Bramble & Wake, 1988; Reilly & Lauder, 1990; Bels et al., 1994). Liem (1990) hypothesized that aquatic suction feeding is associated with feeding versatility within species, while the terrestrial feeding mode is linked to dietary specialization.
Chelonians form a useful group for testing hypotheses concerning differences between terrestrial and aquatic feeding modes because they are descended from terrestrial reptiles, yet have had semiaquatic and fully aquatic members throughout their 200 million year history. Among living forms, the wholly-aquatic feeding sea turtles have a marine ancestry dating back at least to the Upper Cretaceous, yet have some affinities with emydidts (Ernst & Barbour, 1989; Ernst et al., 1994). They exhibit adult dietary specialization (Hendrickson, 1980), though hatchlings of all species have neustonic feeding habits involving capture of slow-moving prey, particularly medusae. The leatherback turtle Dermochelys coriacea (Vandelli, 1761) continues to eat medusae throughout its life.

Terrestrial turtles show a typical terrestrial feeding mechanism, with tongue involvement in food transport, but not clearly in food ingestion (Bels et al., 1997). There are data for mechanisms of food capture and handling in sea turtles, including involvement of the limbs (Davenport & Clough, 1985; Bels & Renous, 1992). Only two freshwater species have been studied, both predominantly sit and wait predators in which limb involvement is minimal. Food intake in the kinosternid musk turtle (Claudius angustatus Cope; taxonomically remote from emydids) is produced by strong suction generated by swift depression of the mouth floor according to Weisgram (1985). This hypothesis was not supported by film, and appears to stem from morphological inferences. Contrariwise, Launder & Prendergast (1992) described prey capture by the snapping turtle Chelydra serpentina (L.) (another non-emydid) in great detail. This omnivorous species has a varied diet, and Launder & Prendergast (1992) used goldfish and earthworms as prey. These were caught by ‘ram feeding’ in which the open jaws of the moving head engulf the prey with negligible involvement of suction; a food capture mechanism also characteristic of some fish (e.g. Ayuus; Lien, 1990). No tongue involvement was reported, but the snapping turtles could modulate their feeding mechanism, using a slower technique on worms than on fish. Launder & Lien (1981) and Launder & Prendergast (1992) used the relative positions of the predator and the food item with respect to a fixed background to determine whether aquatic vertebrates use ‘ram feeding’. In Chelydra, Launder & Prendergast (1992) concluded that suction is not used to draw living prey into the mouth because food only begins to move into the buccal cavity after the plane of the gape has been crossed and not before. Consequently, decrease in predator-prey distance prior to maximum gape angle is entirely produced by head movement towards the prey.

The estuarine diamondback emydid turtle Malaclemys terrapin (Schoepff, 1793), inhabits salt marshes and lagoons along the east coast of the United States and has a varied marine diet, but in anatomy differs little from its freshwater relatives (Carr, 1952; Pritchard, 1979). It eats shrimp, crabs, polychaetes, littorinid gastropods, clams and the mussel Mytilus edulis (Coker, 1906; Carr, 1952; Hurd et al., 1979). Davenport et al. (1992) demonstrated that adult diamondbacks selected small sizes of littorinids and mussels because jaw gape constrained consumption of larger mussels, but the turtles were able to exploit crabs (Uca, Callinectes, Cancerus) of a wide size range because they had a complex behavioural repertoire that involved visual assessment of crabs and consumption of limbs ('cropping') if the crab was too large or dangerous to deal with whole.

The primary aim of the present study was to determine the nature of the feeding mechanism of M. terrapin, mainly upon crab prey. Since it is a versatile aquatic feeder, reliance upon suction would be expected from the hypothesis of Lien (1990), with no tongue involvement. However, most of the food items eaten by diamondbacks are hard-shelled, dense benthic organisms against which a suckorial feeding mechanism might be ineffective; a variant of ram feeding was predicted. A second prey type (mussels) was offered for qualitative comparison. Food was offered on the substratum and mid-water to elicit further information about the flexibility of response, especially in terms of limb involvement. Attention was also paid to food transport, the process of moving food backwards from the mouth towards the oesophagus. Here it was predicted that the tongue would be involved, since M. terrapin is closely related phylogenetically to emydids that employ a terrestrial feeding mode (Bels et al., 1997).

Data are also presented for food capture by juvenile leatherback turtles (D. coriacea). Dermochelys coriacea shows a range of morphological and behavioural adaptations for its wholly pelagic life in the open ocean (Hendrickson, 1980; Davenport, 1987; Renous et al., 1989; Renous & Bels, 1993; Renous, 1995). It feeds exclusively upon gelatinous prey (Bleakney, 1969; Brongersma, 1969; Davenport & Balazs, 1991; Bjorndal, 1997).

**MATERIALS AND METHODS**

**Collection and maintenance**

Diamondback terrapins (11 males; 10.1-11.7 cm carapace length (CL)), were purchased from a supplier; details of their husbandry are in Davenport et al. (1992). They were fasted for 24 h before feeding experiments (Davenport & Ward, 1993). For filming they were held in a 2000×500×500 mm aquarium filled to a depth of 400 mm with seawater (25°C, salinity 33 psu) and marked with a 20×20 mm grid.

Four leatherback turtles (25–30 cm CL, reared in captivity were held in an aquarium (1500×3000×1500 mm) filled with seawater (25°C, salinity 32 psu) for filming. A 10×10 mm grid provided a framework for kinematic analysis (Belis et al., 1996).

Prey (crabs, Carcinus maenas; mussels, Mytilus edulis) used to compare feeding kinematics were collected from the shore in North Wales, or in Belgium. Both species are found on the east coast of the USA and eaten by diamondback terrapins.

**Filming**

Diamondbacks were filmed with a Beaulieu R16 camera placed 2 m in front of the aquarium at 32 and 64 frames s⁻¹ or with a Panasonic F10 video camera fitted with a 0.001 s shutter and connected to a Panasonic video recorder. In either case, 1000 W spotlights illuminated the aquarium.

Leatherbacks were filmed using a Beaulieu R16 camera placed 2 m in front of the aquarium, to view the entire volume. Two spotlights of 1000 W were set to obtain sufficient light to film without perturbing swimming behaviour. Filming was at 48 frames s⁻¹. More information was collected with a Sony 3000P video camera connected to a JVC video recorder.
Feeding

Diamondbacks were offered crabs (10-30 mm carapace width) free on the bottom of the aquarium, or tethered by fine monofilament nylon in mid-water. Whole mussels (5-10 mm shell length) were offered on the substratum only, though pieces of mussel flesh were allowed to drift downwards from the water surface to be captured in mid-water.

Sea turtles were fed on pieces of mussel flesh presented to the turtles in front of the jaws. This type of food was used because: (1) it has been used to rear young leatherbacks (Bels et al., 1988); and (2) juvenile leatherback turtles eat soft prey in their natural habitat (Ernst & Barbour, 1989; Ernst et al., 1994). The turtles were able to cut portions of flesh and transport them directly to the oesophagus or bite the prey several times prior to such transport.

Digitizing and analysis of film/vidoe tape

Feeding sequences consisted of series of movements of the head, the jaws, the hyolingual system, the neck and the limbs. For categorizing capturing and transport cycles, the food position relative to the jaw apparatus was used. Cyclic movements were assigned to 'ingestion' when the food was bitten and entered the buccal cavity, while cyclic movements were termed 'transport' when the food item, completely or partly held within the buccal cavity, moved posteriorly towards the oesophagus.

Sequences in both species were projected onto a digitizing table (AGMEE, ULg) using a NAC motion analyser and an IBM Computer at the Museum of Natural History of Paris. Selected points on the head, carapace, neck and forelimbs of specimens of Malaclemys terrapin were digitized to describe feeding behaviour and strategies (Figure 1). Vertical jaw displacements were obtained by computing the displacement of their anterior tips and gape angle corresponded to the angle between points 2-3-4 (Figure 1). Displacements of the tongue were estimated by computing the distance between the position of its anteriormost tip (point 6) as soon as it was visible between the jaws and the tip of the lower jaw (point 2). It is difficult to determine accurately hyoid displacements on film, and it was not possible to attach any markers on the throat skin of the turtles because turtles rub off the markers against the sides of the aquarium. However, when the gape was closed, we observed that the throat had a characteristic shape described kinematically using the vertical distances between points 7 and 8 (anterior portion of the throat) and between points 9 and 10 (posterior portion of the throat). Maximal throat depressions were measured from the frames and transformed as a percentage of the carapace length of the observed turtles.

Displacements of the neck were calculated as the distance between point 11 on the carapace and point 5. Point 5 (on the neurocranium) was selected as appropriate for this analysis since no intracranial kinetism was observed on dissected turtles. The vertical and horizontal displacements of the limbs were illustrated by the distance between points 11 (carapace) and 12 (placed on the extremitiy of the forelimb, between the digits). Displacement of the turtle toward the prey corresponded to the distance between a fixed point on the prey (1) and point 2. When this distance was negative, it indicated that the jaws slid on the crab, which was not captured. The data were stored in files as tables of bipolar (X and Y) coordinates, angles and lengths were analysed using a computer programme developed by P. Théate and V. Bels. Frame 1 for each sequence was arbitrarily selected as the first frame that showed an increase in gape angle. The coordinates were plotted against time to provide the point displacements in the kinematic graphs. All measures of distance are expressed in cm and angles in degrees. A reference grid (squares of 20x20 mm) placed behind the filmed turtles was used to standardize measurements.

Ten lateral feeding sequences in Dermochelys coriacea were used in this study. Food items were captured with negligible lateral head displacements (eye-snout distance did not change on the successive frames). Analysis followed that described for M. terrapin. Its purpose was to provide comparable data for gape angle and relative movements of jaws, neck and forelimbs. For this purpose, gape angle was calculated as for M. terrapin. Vertical throat movement was illustrated by measurement of the distance between a point on the throat (corresponding to point 8 in M. terrapin) and the tip of the mandible (=point 2). Limb movements were computed from horizontal and vertical displacements of a point on the shoulder and a point on the tip of the visible forelimb.

RESULTS

Malaclemys terrapin

Overview of feeding bouts

Prey type strongly influenced the mode of approach to the food in Malaclemys terrapin. For crabs placed in mid-water or walking on the bottom of the experimental tank, the turtles always approached the prey by swimming (Figure 2A). When mussels were introduced on the bottom of the tank, the turtle approached with a slow
Food Ingestion

Profiles of ingestion of crabs and mussels were similar. The quantitative data presented are for strikes on living crabs (Figure 3); only qualitative comparative data are reported for mussels. Gape cycles for both prey items were typically divided into four stages: slow opening (SO), fast opening (FO), fast closing (FC) and slow closing (SC). Gape increase was often divided into two successive stages (76% of the observed strikes; N=10): slow opening (SO) and fast opening (FO) (Figures 3 & 4). The mean duration of the gape cycle for crab striking was 300.0 ms; SD 48.9 ms.

The mean duration of SO represented 56.9 ±3.4% of the entire gape cycle (Figure 5). Fast opening was variable in duration (coefficient of variation, CV=32%) and represented 15.7 ±1.4% of the gape cycle. Decrease of gape (FC+SC) represented 26.9 ±3.1% of the gape cycle. Rate of lower jaw depression exceeded the rate of cranial elevation (Figures 3 & 4).

Depression of the hyoid-tongue complex occurred at the end of SO or beginning of FO, when it was clearly visible (Figure 4). The tongue retracted both horizontally and vertically (Figure 4B). Amplitude of throat depression was significantly related to the prey type and to the relative positions of the turtle and its prey (Figure 6; analysis by ANOVA and Tukey's pairwise comparison). Depression and expansion of the throat during strikes on crabs was significantly greater than that used during mussel ingestion. Depression was also significantly greater (mean ±SD 25.7 ±0.5%) when capturing crabs placed in mid-water than when attacking crabs walking on the substratum (mean 22.2 ±0.3%). Tongue retraction occurred before the onset of hyoid depression (Table 1). However, the difference between the mean times for these events was only about 22 ms, indicating that both structures moved posteriorly almost simultaneously.

 Strikes by M. terrapin were characterized by a large neck extension that propelled the opening jaws towards the prey (Figures 2–4). Jaw–prey distance decreased rapidly during neck extension, which continued after peak gape increase (Figures 3 & 4). Jaws surrounded a leg or other portion of the crab and then closed on it. As jaws began to close, the head was still being projected forward (Figure 2A). Mean time to maximum shell–snout distance (used to quantify neck extension) occurred after the time of maximum gape and time of maximum throat depression.

Maximum gape angle was achieved (mean 219.0 ±20.0°) when head extension was still increasing (maximal head extension occurred at a mean 249.5 ±28.9°). Retraction of the neck began at the end of the cycle. Compared with neck extension, retraction was slow (Figures 3 & 4).

Figure 2. (A) Four successive drawings of Malaclemys terrapin feeding on a crab suspended by a fine wire. Elapsed time in seconds is indicated for each frame. Elapsed time was measured from the first frame involving gape increase. Jaws were slightly open from 0 to 0.50 s (SO, slow opening). A sudden increase in gape angle (FO, fast opening) occurred at time 0.52 s. Maximum gape angle was reached at 0.65 s. (B) Four successive drawings of M. terrapin capturing a small mussel on the substratum. Elapsed time indicated in seconds on each frame. Frame 1 followed immediately after gape increase started. The head was rotated to the animal's left during most of the ingestion cycle.

Forelimbs were extensively used during the feeding cycle in M. terrapin (Figures 2A & 4). The only difference between cycles was in the amplitude of forelimbs' displacements. Forelimbs began to move posteriorly (upstroke) during the slow opening stage (Figure 4). Relationships between cyclic displacements of the limbs and the jaw cycle followed a similar pattern whether the turtle was approaching crabs by walking on the substratum, or by swimming in mid-water. Maximum forelimb backward displacement (upstroke phase of the limb cycle) occurred (mean 232.6 ±27.6°) about 15–20 ms before maximum head extension (mean 249.5 ±28.9°). Maximum gape was achieved 15–20 ms before maximum forelimb retraction (Table 1). The action of both forelimbs during strikes was simultaneous, so it is not a simple modification of normal eumydid locomotion which involves alternate limb movements (Davenport et al., 1984).
Food transport

After food ingestion, extensive intraoral manipulation occurred. Mussels were moved from side to side and backwards and forwards within the buccal cavity to permit crushing of the shell. The tongue played a major role during these cycles (Figure 7), particularly in positioning the mussel shell between the edges of the jaws. After crushing, pieces of shell were expelled and the flesh moved towards the oesophagus. When dealing with larger pieces of soft material from larger mussels, the turtle exhibited the same kinematic pattern as described for the strike (Figure 6).

The neck was protracted during gape increases and maximum throat depression occurred during SO. For food transport, we did not analyse kinematic data statistically, because turtles could rarely be viewed from the lateral position. In general, mussel flesh was transported further into the buccal cavity before maximal depression of the throat occurred, indicating that transport was achieved by a
mechanism other than simple hyoid depression. In some sequences, mussel flesh was clearly in intimate contact with the tongue and tongue retraction was always accompanied by retraction of the flesh into the buccal cavity.

During transport cycles, related cycles of the limbs and neck (Figure 6B) were similar to those described for ingestion. The forelimbs moved backwards as soon as the head was protracted and food material entered the buccal cavity during the gape cycle.

Table 1. Summary of kinematics of prey capture in Malaclemys terrapin feeding on crabs in mid-water.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Mean ±SD</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time of maximum gape (ms)</td>
<td>219 ±10</td>
<td>450-194</td>
</tr>
<tr>
<td>Time of maximum hyoid depression (ms)</td>
<td>242 ±27</td>
<td>340-141</td>
</tr>
<tr>
<td>Time of tongue retraction (ms)</td>
<td>184 ±22.5</td>
<td>150-230</td>
</tr>
<tr>
<td>Time of beginning of neck extension (ms)</td>
<td>108 ±14.8</td>
<td>147-98</td>
</tr>
<tr>
<td>Time of minimum prey-jaw distance (ms)</td>
<td>257 ±34</td>
<td>320-225</td>
</tr>
<tr>
<td>Time of maximum forelimb protrusion (ms)</td>
<td>90 ±11.6</td>
<td>180-50</td>
</tr>
<tr>
<td>Time of maximum forelimb retraction (ms)</td>
<td>232 ±27.6</td>
<td>282-208</td>
</tr>
</tbody>
</table>

Derocochelys coriacea

Overview of feeding behaviour

Feeding in Derocochelys coriacea consisted of successive jaw and hyo-lingual cycles from prey ingestion to subsequent swallowing (Figure 9). The leatherback stabilized its body by slow displacements of the forelimbs which were not closely related to the successive gape cycles as in M. terrapin (Figure 10). Forelimbs were extended laterally; only their tips exhibited slight movements compared with high amplitude downstrokes and upstrokes shown during active swimming (Davenport, 1987; Renous & Bels, 1993).
Clear separation of ingestion cycles from transport and swallowing cycles was not easy. Functionally, the progress of food from the exterior to the oesophagus was often nearly continuous in *D. carinata*. Feeding was recorded for small and large pieces of mussels free in the water column (10–20 cm from the water surface), or held in the hand of the experimenter. In the first case, the turtle approached the food and used one or two ingestion cycles until the food moved completely into the buccal cavity. After these cycles, the turtle transported the food item posteriorly within the buccal cavity. In the second case, the turtle closed its jaws on the soft material at the end of the first ingestion cycle, cutting off a small piece of food. These cycles were described as 'biting cycles' by Bels & Renous (1992). During the next cycle, the turtle attempted to ingest the food material again, whilst simultaneously transporting the first piece that was already within the buccal cavity. When the food material was completely ingested, the turtle continued to feed by transport cycles (termed 'true transport cycles' by Bels & Renous, 1992).

**Figure 7.** Three successive frames of manipulation of a mussel by *Malaclemys terrapin* showing the role played by the tongue (arrows) in moving the mussel within the buccal cavity.

**Figure 8.** (A) Three frames of a transport cycle in *Malaclemys terrapin* feeding on mussel flesh showing the related movements of the head, the throat, and the food in *M. terrapin* feeding on mussel flesh. (B) Three positions of limbs illustrate the role of the limbs during feeding on mussel flesh. The numbers correspond to frames (filmed at 50 frames s⁻¹) and the dashed lines to movements.

**Food ingestion and transport**

Ingestion cycles were accomplished in about 600 ms (Table 2). The gape cycle was divided into four stages: SO (SO I–SO II), FO, PC, SC (Figures 9 & 10). Mean duration of the gape increase (SO + FO) was about 450 ms, including a mean duration of SO of 360 ±170 ms (80% of gape cycle). Mean duration of the FO was 90 ±20 ms (20% of gape cycle), and time to maximal depression of the lower jaw was 340 ±140 ms (~360 ±170 ms to beginning of FO).

The mouth was opened by a combination of ventral depression of the lower jaw and dorsal elevation of the upper jaw. Maximal elevation of the upper jaw coincided with maximal depression of the lower jaw (Figure 10).
During SO and the first half of FO, the hyoid–tongue complex was elevated and protruded. This was indicated by a decreasing throat angle (as in *M. terrapin*) (Figure 10) and by a decrease in the vertical distance between the mandible tip (point 2) and the throat (point 8). At the same time, the horizontal distance between points 8 and 2 decreased during mouth opening, maximally at 10 ±1 ms prior to maximal gape opening (end of FO). The throat was then greatly depressed during the rest of FO and jaw closing. Food moved towards the buccal cavity during the end of SO and beginning of FO; it contacted the tongue but no manipulation of food by the tongue was seen.
Table 2. Comparison of features of jaw action in Malaclemys terrapin and Dermochelys coriacea.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Malaclemys terrapin</th>
<th>Dermochelys coriacea</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gape duration (ms)</td>
<td>Mean ±SD</td>
<td>Mean ±SD</td>
</tr>
<tr>
<td></td>
<td>300 ±154</td>
<td>615 ±196</td>
</tr>
<tr>
<td>Duration of SO (ms)</td>
<td>175 ±99</td>
<td>360 ±170</td>
</tr>
<tr>
<td>Duration of FO (ms)</td>
<td>43 ±17</td>
<td>90 ±20</td>
</tr>
<tr>
<td>Duration of FC (ms)</td>
<td>200 ±170</td>
<td>170 ±80</td>
</tr>
<tr>
<td>Time of maximum gape angle (ms)</td>
<td>219 ±20</td>
<td>420 ±121</td>
</tr>
<tr>
<td>Time of beginning of throat depression (ms)</td>
<td>63 ±5</td>
<td>70 ±5</td>
</tr>
<tr>
<td>Maximum gape angle (°)</td>
<td>62 ±11</td>
<td>60 ±16</td>
</tr>
</tbody>
</table>

1 This time was calculated from the time of maximum gape angle and corresponds to the time interval before the time of maximum gape angle, SO, Slow opening; FO, Fast opening; FC, Fast closing.

**DISCUSSION**

Comparison of feeding behaviour and kinematics

Unlike Dermochelys coriacea, kinematic profiles of ingestion cycles of Malaclemys terrapin show pronounced modulation. Both species exhibit basically similar profiles of gape, jaw displacements, throat–hyoid and tongue displacements (Figures 4 & 10). Division of gape profiles into SO, FO, FC and SC was not always clear in some of the capture cycles in M. terrapin (Figure 4). In Chelydra serpentina, Lauder & Prendergast (1992) reported a slow gape increase (<50%) before FO that lasted 500 ms. Mean duration of SO in D. coriacea is similar to C. serpentina, but that of M. terrapin, is much shorter, and greatly variable (Table 2). Our data suggest that feeding cycles in D. coriacea are more stereotyped than those of M. terrapin. Such differences may be related to the feeding strategies of the two species. M. terrapin exploits a large variety of food items with different escape and defence capabilities, and different structural properties (i.e., shell of mussels and chitin of crabs) while D. coriacea eats material from gelatinous animals that have little escape capability.

Maximum gape angles are similar in both turtles (Table 2). Time to maximum gape in C. serpentina is related to characteristics of the prey (e.g., shape, size, elusiveness) (Lauder & Prendergast, 1992). In M. terrapin feeding on crabs, the turtle may modulate the duration of gape to increase the probability of being able to bite a part of a crab, when predator and prey are moving relatively. Davenport et al. (1992) showed that cropping limbs of medium-sized crabs was as energetically profitable as eating small crabs whole. By opening the mouth before striking, and even maintaining it at near maximum gape (e.g., Figure 4A), the turtle is more assured of a successful attempt to bite a piece from a defending crab whilst circling around it to seek a safe opening. Our data do not allow us to compare the effect of crab size on the duration, amplitude and velocity of gape increase, but this may be an area where further modulation of feeding strategy is possible.

Aquatic vertebrates use a rapid stereotyped head mechanism to capture elusive and rapidly-moving prey (e.g., swimming fish and worms) (Wainwright & Lauder, 1986; Lauder & Prendergast, 1992a,b). Lauder & Prendergast (1992) were the first to suggest a relationship between strike output and prey type (e.g., C. serpentina). Our data for M. terrapin support their suggestion and indicate that aquatic turtles from marine and freshwater habitats that contain varied prey items have a flexible response to increase the efficiency of food acquisition. In contrast, D. coriacea, which feeds on slow-moving medusae or pyrosomas, has a longer and stereotyped FO stage (Table 2). Slower gape increase would probably not affect the efficiency of food gain in this turtle.

The ecological niche of chelonians has an important effect on the related limb and jaw motor output. Chelydra serpentina are primarily sit-and-wait predators feeding on elusive prey items such as fish, though they will sometimes pursue prey (e.g., Pritchard, 1979), while M. terrapin and D. coriacea are continuously active foragers on dispersed prey. However, the term ‘active foraging’ covers a wide variety of behaviours, and these are considerable differences between M. terrapin and D. coriacea in this respect. These differences have repercussions on motor output as illustrated by kinematics (Figures 2–10). In the pelagic leatherback turtle, the medusa prey are: (1) slow-moving and neutrally-buoyant; (2) found in large associations allowing the turtle to ‘graze’ without a true chase of the prey; and (3) composed of soft gelatinous material that offers little resistance to the sharp jaws of the turtles. The diamondback must deal with prey that is elusive (shrimps), aggressive and fast moving (crabs), or composed of hard chitinous or calcareous material (crabs, mussels, gastropods).

The difference in kinematic profiles of limbs may be clearly associated with foraging tactics. Behavioural characteristics of the strike of M. terrapin are related to the type of food. In the case of mussels or pieces of mussel flesh, the turtle walks on the substratum (Figure 2B), and uses the limbs to maintain itself on the substratum, providing a steady platform when the turtle pulls its attached prey from the seabed. The behavioural response of M. terrapin facing crabs is more complex because the turtle must deal with behaviour of the prey (Davenport et al., 1992; this study). Large crabs (<50 mm carapace width) are avoided and visual evaluation of medium-sized crabs (30–50 mm carapace width) must be carried out to avoid the risk posed by the crab’s chelipeds. One of the major behavioural tactics is to attempt to ingest one of the crab’s legs (Figure 2A). In the case of smaller crabs (10–25 mm carapace width), the turtle will even bite the chelipeds. In all cases, the turtle approaches crab prey by swimming and uses the forelimbs’ propulsive force to speed the strike (Figure 2A). After approaching the prey, D. coriacea only exhibits small displacements of the limbs during successive strikes (Figure 10). The hind limbs are mainly used to propel the turtle slowly towards the food, while the fore flippers contribute almost nothing to swimming. Any typical down- and up-strokes of the forelimbs of the leatherback during feeding would result in displacement of medusae away from the mouth, inhibiting feeding. Dermochelys coriacea has an inextensible neck, which consequently has no role in the strike.
Suction feeding and the role of the tongue

Earlier studies have generally suggested that aquatic turtles from marine and freshwater habitats use fluid suction for prey ingestion. All authors (see Lauder & Prendergast, 1992, for review) point out that sudden depression of the hyoid, and consequent distension of the throat, inevitably reduces pressure within the buccal cavity. However, Lauder & Prendergast (1992) re-evaluated the role of suction during prey ingestion in C. serpentina. They suggested that the effect of suction feeding is minimal and that this turtle relies principally on the acceleration of the head and rapid opening of the jaws to overcome and surround the prey in the mouth. They described C. serpentina as a typical ram feeder. Based on kinematic data, if the distance between the head of the predator and the prey decreases while the position of the prey remains fixed relative to the background, then suction has almost no effect on the prey. We kinematically studied predator and prey displacements and distance in M. terrapin and D. coriacea using different types of food. Furthermore, we compared the degree of throat depression exhibited in relation to different food items to see whether the turtles modulated hyoid depression.

In our study, with dense prey items, there was no evidence for suction in M. terrapin despite great distension of the throat (Figures 1–5). Figure 6 also shows that the throat was depressed far more when turtles attacked crabs (whether in mid-water or walking on the substratum) than it was when they ingested mussels. Is there an alternative reason for throat distension, and can this be related to food capture? Van de Vusse (1986) notes that crabs only feed on bottom dwelling, and in their model of suctorial feeding in fish, point out that a fish which did not suck would tend to displace the prey away from the snout (by a pressure wave generated by forward swimming) when it came close to the prey. This would make the prey less easy to catch, and, since many aquatic animals are sensitive to pressure, might also alert it. We propose that throat distension (with concomitant inflow of water), which parallels gaping and neck extension towards the prey, will minimize development of high pressures in front of the mouth, and so facilitate the capture of active prey such as crabs. Conversely, less throat distension would be needed to ingest mussels, which are incapable of escape, and would not be displaced by a pressure wave either.

In D. coriacea, the soft material presented to the turtle enters the buccal cavity suddenly during FO and the beginning of FC (Figure 10). At this time, the throat is more or less in the position of suctioning. The food therefore enters the buccal cavity with the help of suction (and moves relative to the background). As in M. terrapin, D. coriacea surrounds the floating food material with the lower and upper jaws (Figure 10). We therefore suggest that D. coriacea uses suction to ingest food far more than do any eurydids or chelodids turtles so far studied. This appears to be related to the nature of the turtle's gelatinous prey — which cannot move quickly to escape, and which are easily sucked in as the turtle opens its mouth wide and approaches slowly.

It is also interesting to note that the tongue plays a consistent role only after ingestion of food. In M. terrapin feeding on crabs (and D. coriacea feeding on mussels) the tongue does not have a functional role in food capture. For M. terrapin it might be expected that there would be a risk in using the tongue because it might be bitten by the chelipeds of the crabs. Our data indicate that the tongue is fully protracted during ingestion cycles (Figure 4B), though the tip of the tongue does not protrude quite far enough to contact the prey until the latter moves into the buccal cavity. However, once food items enter the buccal cavity, the tongue is actively involved in transport and manipulation, just as in other tetrapods and terrestrial turtles (Bramble & Wake, 1985; Reilly & Lauder, 1990; Belts et al., 1994, 1997). It seems that the tongue has a particularly important role, first to change the position of the food within the buccal cavity and then to transport it towards the throat for swallowing (Figures 4 & 7).

Conclusions

Data collected for these two chelonian species show: (1) that there is not a clear division between aquatic and terrestrial feeding modes, since the ingestion and transport cycles of M. terrapin and D. coriacea are similar to those of terrestrial turtles. (2) That suction (as employed by D. coriacea) is not necessarily associated with feeding versatility, because leatherbacks have a very specialized diet that they ingest and transport in a very stereotyped fashion. (3) That expansion of the throat during food capture may have a function other than simply generating suction. (4) That M. terrapin is a ram feeder, whether eating whole mussels, or attacking limbs of crabs.

The authors wish to thank the British Council, the Commissariat Général aux Relations Internationales de la Communauté Française de Belgique and FNRS (Belgium) for travel and subsistence funding. They acknowledge the Aquarium of the University of Liège for its help in maintenance of Dermochelys coriacea. Thanks are also due to two anonymous referees for helpful criticism.

REFERENCES


