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FEEDING AND DIGESTION IN THE OMNIVOROUS ESTUARINE TURTLE *BATAGUR BASKA* (GRAY)

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ABSTRACT

The emydid river terrapin *Batagur baska* (colloquially known as the tuntong) lives in rivers and estuaries of S.E. Asia. The species is omnivorous, but predominantly herbivorous from the hatchling stage onwards. Young river terrapins (3-4 months; 140-200 g body wt) from a headstarting programme in western Malaysia were studied. Appetite on a plant diet (kangkong; *Ipomoea aquatica:* Convolvulacea) was extremely high (16% body wt d^{-1} on fresh wt basis); river terrapins spend long periods of browsing, using the double serrations of the upper beak to cut up plant material. The serrations also function in ratchet like fashion to allow large leaves to be progressively moved into the oesophagus without the turtle losing contact with the food. *Batagur baska* readily eats water hyacinth (*Echornia crassipes*), a plant which often chokes tropical waterways.

River terrapins fed on trash fish move a meal through the gut more quickly (total gut clearance time, TGCT = 5 days) than do those fed upon kangkong (TGCT = 6 days). The gut features a large stomach, a small intestine of moderate length but large diameter and a capacious large intestine. The gut does not sort material. Assimilation efficiency on a diet of fish (mean assimilation of dry mass = 91.6%, of energy (joules) = 90.5%, of protein = 97.4%) is much greater than on a diet of kangkong (43.2%, 38.6% and 66.0% respectively). It is recommended that headstarted animals are regularly fed on fish to improve growth rates. River terrapins readily eat plant material in salinities between 0 and 19.8‰, but refuse to eat in water of 23.1‰ or more, presumably to avoid the incidental drinking of water with a higher ionic content than their blood.

INTRODUCTION

The river terrapin, *Batagur baska*, is a large emydid turtle (< 25 kg, 59 cm carapace length) once common in the lower reaches of the large river systems of S.E. Asia, but now much reduced in numbers. Known as tuntong by Malays (though this term is also applied to the related *Callagur*), river terrapins (Iverson, 1985) have also been referred to as batagurs in the older scientific literature. River terrapins are amongst the few reptiles that exploit the brackish waters of estuaries. Outside the breeding season they often forage in estuaries and mangroves (Maxwell, 1911; Moll, 1978) and are occasionally seen in sea water (Gunther, 1864), though Davenport & Wong (1986) demonstrated that their physiological ability to cope with a saline environment is limited, and that river terrapins largely survive by deploying behavioral osmoregulatory responses.

Batagur baska is an endangered species, its numbers having fallen by a combination of habitat loss and direct exploitation of adults and eggs for human food. Headstart programmes were established in Malaysia in the early 1970s and have been described by Moll (1980) in his comprehensive study of the biology of the species.

River terrapins are true omnivores and readily eat invertebrates, fish or carrion as well as plant material. However, from the study of Moll (1980) it appears that they are predominantly herbivorous, browsing upon floating and riverside vegetation as well as eating fruit (including the fruit of mangrove trees). He found that 45% of the volume of faecal samples was composed of the remains of leaves and stems, 25% of fruit (overwhelmingly mangrove fruit) and 30% of mollusc shells (pelecepods of unidentified species). Before their numbers were reduced by human exploitation river terrapins were probably of considerable importance ecologically since they break up and recycle large quantities of plant material.

Many aquatic chelonians are omnivores, but in early life most of such species are characterised by predominantly carnivorous feeding (e.g. green sea turtles, *Chelonia mydas* (Hirth, 1971; Booth & Peters, 1972), the freshwater pond slider *Trachemys scripta* (Clark & Gibbons, 1969)) and it seems that a high protein diet is needed to sustain the high growth rate of hatchlings and juveniles. Only river terrapins, the pleurodiran river turtles of South and Central America (*Podocnemys sp.*) and *Dermatemys* appear to be able to grow quickly from the earliest stages on a diet rich in plant material. The first objective of the study reported here was to determine whether tuntong are particularly efficient in assimilating nutrients from vegetation, or simply process unusually large quantities of food. A second objective was to compare food processing and assimilation in river terrapins fed either on plant or fish diets. Thirdly, because river terrapins spend much of their time in estuaries, especially mangroves, but are known not to feed when held in sea water (Davenport & Wong, 1986), it was decided that the effect of environmental salinity on feeding should be investigated. The final task was to observe and analyse the feeding mechanism of river terrapins, particularly in *Batagur baska* browsing on floating vegetation - a challenging proposition from a biomechanical point of view.

MATERIALS AND METHODS

COLLECTION AND MAINTENANCE

Twenty young (3-4 months; 140-200 g body weight) river terrapins were borrowed from a hatchery/headstart station at Sungar Pinang near Alor Setar, N.W. Malaysia. Individual animals were identified by numbering the carapace with typewriter correction fluid. The river terrapins were held in fresh water at the temperature employed throughout this study (30±2°C) and fed daily upon kangkong (*Ipomoea aquatica* Forsk : Family Convolvulacea) until used in experiments. Kangkong was used as the basic food for several reasons. First, although widely eaten as an inexpensive vegetable in Malaysia, kangkong grows wild, especially by the side of rivers. It is therefore a likely food item of wild river terrapins, though not specifically mentioned by Moll (1980) who was unable to identify the leaves and stems whose remains made up 45% of faecal volume in Perak river specimens. Secondly, kangkong is the main item of food fed to river terrapins reared at the two river terrapins hatcheries in Malaysia, at Sungar Pinang and at Bota Kanan in the state of Perak. Hatchling and juvenile river terrapins are now fed almost exclusively on kangkong, with only occasional supplementation with banana. This contrasts with earlier reports by Moll (1980) that they were regularly fed on fish. The hatcheries still feed older animals (5-7 years old) on a mixed diet of kangkong and trash fish (i.e. fish of no commercial value or undersized commercial fish - species unknown). Finally, pilot experiments revealed that kangkong maintains a constant weight when held in fresh water for periods of many hours, thus allowing accurate estimates of appetite (see below).

Feeding Behaviour

Four river terrapins were held for 24 hr without food and then placed in a large, well lit, glass aquarium marked out on three sides and the bottom with a 1 cm inked grid. The subsequent actions were videorecorded with a Panasonic camera and videorecorder (AG6200). The camera incorporated a 0.001 s shutter, allowing blur-free field-by-field analysis. The river terrapins were offered two food items; kangkong and water hyacinth (*Echornia crassipes*). To supplement the videotape data, 35 mm photographs and drawings of the jaws of the turtles were made. Animals feeding on trash fish were observed but not filmed.

Effect of Salinity on Feeding

Two animals were placed in each of 11 aquarium tanks containing water of the following salinities: 0, 3.3, 6.6, 9.9, 13.2, 16.5, 19.8, 23.1, 26.4, 29.7, and 33‰. The animals were allowed to settle down for one hour and were then offered intact leaves of kangkong (5 leaves per aquarium). The tanks were inspected after 1, 6 and 24 hr and the number of leaves consumed (or showing evidence of bites) counted.

Measurement of Appetite

The satiation ration for river terrapins eating kangkong was assessed in the following manner. Three animals were deprived of food for 48 hr and then each was offered a preweighed 'meal' of kangkong leaves (not stems as they hold liquid water and cannot be weighed accurately) in a separate aquarium. Weighing of kangkong was performed after drying in paper towels. Each animal was left with its 'meal' for 24 hr, then all remaining pieces of plant material were collected and reweighed. In pilot experiments it had been established that 50 g of kangkong could be weighed repeatedly with an accuracy of 0.2-0.5 g over 24 hr periods. Several examples of kangkong were weighed and dried to constant weight in an oven at 40°C. The mean water content of kangkong was 93% by weight. When eating vegetation, river terrapins are browsers, often feeding intermittently for several hours before satiation; this explains the rather unusual method of assessing appetite.

Gut Transit

Movement of food through the gut was studied by monitoring the progress of chromic oxide-labelled meals, and by X-radiography. Firstly, total gut clearance times (TGCTs) were established. Three river terrapins were fed daily on trash fish for seven days ('fish diet'); three other turtles were fed on kangkong for a similar period ('plant diet'). Each group was then fed on an appropriate single chromic oxide-labelled meal followed at daily intervals by normal unlabelled meals. Terrapins on the fish diet were fed a labelled meal made up by mincing 100 g trash fish fillets mixed with 5 g chromic oxide. The meal was bound together with agar. River terrapins eating the plant diet were fed on an agar-bound mixture of minced kangkong (100 g) and chromic oxide (10 g). The turtles were held in separate tanks which were inspected daily for the presence of chromic oxide-labelled faeces. During each inspection faeces were broken up and inspected with a low power binocular microscope.

X-radiography was performed on two river terrapins which had previously been fed on kangkong for more than two weeks. Each was deprived of food for 48 hr and then offered a meal made up in the following fashion. 100 g kangkong was finely minced and thoroughly mixed with 2 g barium sulphate powder. A few hundred barium/polystyrene spheroids (1 mm diameter; ICI Ltd) were stirred into the mixture, followed by several thousand lead glass beads (ca. 0.1 mm diameter). Warm agar solution was added and the mixture stirred until it began to set (thus preventing settlement of the spheroids and beads). When setting was complete the food was cut into pieces and offered to the river terrapins. Both ate voraciously for about 10 min. Feeding intensity then fell and the animals were transferred to another tank which contained floating kangkong. The animals were X-rayed at the following intervals after the labelled meals: 1, 7, 25, 31, 49 and 97 hr. Fresh kangkong was available to the turtles throughout this period and faeces were removed several times per day to avoid reingestion of labelled material.

Absorption/Assimilation Efficiency

To determine the efficiency of absorption of energy and protein in river terrapins fed upon plant and animal diets, two groups of three turtles were fed exclusively on one or other diet for two weeks. They were then fed for eight days on chromic oxide-labelled food (prepared as described above for gut transit experiments). Samples of food and freshly-voided faeces were then collected from each animal, frozen, freeze-dried and stored in a freezer at -25°C until analysed. Chromic oxide content was measured by the method of McGinnis & Kasting (1964). Energy content was determined by the wet oxidation method of Ivlev (1935); appropriate corrections for unreacted protein were applied to the data. Protein content was estimated by measuring total nitrogen (micro-Kjeldahl technique).

RESULTS

Feeding Behaviour

When feeding on trash fish the behaviour of river terrapins was similar to that of other emydid turtles. Small pieces of flesh were swallowed whole; large items were torn apart by combined action of jaws and forelimbs. Typically a turtle would bite

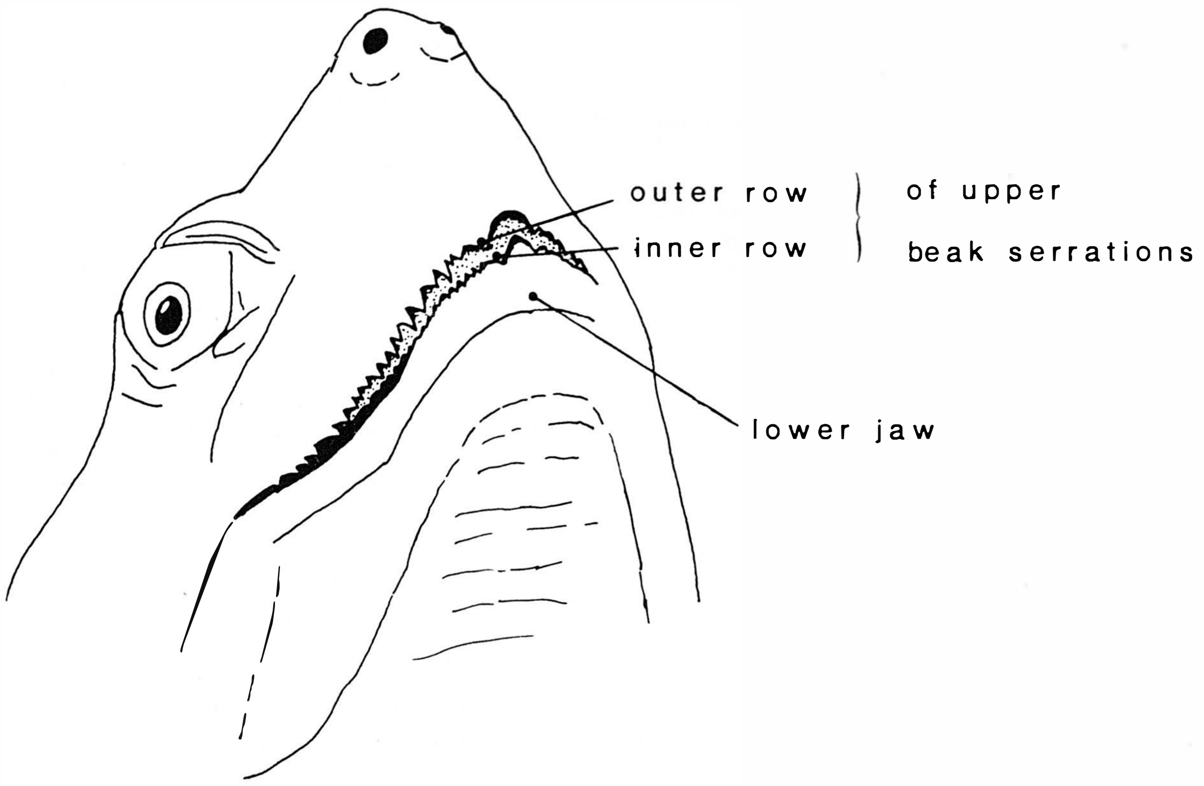

Fig. 1. Drawing of head of young *Batagur baska* to show serrations of beak. Note that the two visible rows of serrations are both on the upper jaw in this view (i.e. the stippled area is the lateral surface of the inner row of serrations). Because the jaws are firmly closed the edge of the lower beak is not visible as it is overlapped by the twin rows of serrations on the upper jaw. A *camera lucida* drawing made from a 35 mm photographic slide.

into a piece of fish with the beak and then push the food item forwards by simultaneous action of the forelimbs - until the piece of fish broke to leave a morsel in the mouth. At the onset of this pushing the forelimbs were extended and rotated medially so that the plantar surfaces of the forefeet were in contact with the prey, and the two sets of claws directed towards one another. River terrapins have extensively webbed forelimbs and relatively small claws. The claws appear to give purchase on prey items rather than being actively used to shred tissue.

When feeding on plant material, the beak structure of the river terrapins assumed great importance. From Fig. 1 it may be seen that the upper jaw is lined by a double row of recurved serrations which are more pronounced anteriorly. At the front of the upper jaw the two most medial pairs of inner and outer serrations are separated by curved central gaps. Serrations on the lower jaw are rather less pronounced, but anteriorly, in the midline, the lower jaw features a pronounced, curved and sharp hook which fits inside the gap in the serrations of the upper beak when the jaws are closed. When eat-

	Elapsed time (h)		
Salinity ‰	1	6	24
0.0	5	-	-
3.3	5	-	-
6.6	5	-	-
9.9	5	-	-
13.2	1	5	-
16.5	5	-	-
19.8	5	-	-
23.1	0	0	0
26.4	0	0	0
29.7	0	0	0
33.0	0	0	0

TABLE 1. Effect of salinity on feeding in river terrapins. Data show number of kangkong leaves (out of 5) showing evidence of browsing.

	Time after meal labelled with chromic oxide (days)						
	1	2	3	4	5	6	7
Plant diet							
Animal 1	-	-	-	xx	x	x	-
2	-	-	-	xx	x	x	-
3	-	-	-	xx	x	x	-
Fish diet							
Animal 4	-	-	xx	xxx	x	-	-
5	-	-	xx	xxx	x	-	-
6	-	-	x	xxx	x	-	-

x = trace quantities of label in faeces (only visible by microscopic inspection)
xx = noticeable quantities of green label
xxx = copious labelled faeces
\- = no label in faeces

TABLE 2. Gut transit times of contrasting meals in young *Batagur baska* at 30°C.

	Observed no. of radio-opaque particles					
Hours after labelled meal	1 hr	17 hr	25 hr	31 hr	49 hr	97 hr
I. Gut section						
A. Stomach						
barium spheroids	34	30	3	-	-	-
glass beads	103	93	3	-	-	-
B. Small Intestine						
barium spheroids	-	4	29	20	4	-
glass beads	-	10	100	68	6	-
C. Large Intestine						
barium spheroids	-	-	2	6	22	-
glass beads	-	-	-	10	62	-
II. Defecated						
barium spheroids	-	-	-	8	8	34
glass beads	-	-	-	25	25	103

TABLE 3. Progress of radio-opaque material along the gut of young *Batagur baska* fed on kangkong.

	Assimilation rate (%)		
	dry mass	energy (joules)	protein
Plant diet (n=3)			
mean	43.2	38.6	66.0
S.D.	23.9	21.1	17.9
Fish diet (n=3)			
mean	91.6	90.5	97.4
S.D.	1.5	0.9	0.9

N.B. For all three nutrient categories, a t-test indicates that there was a significant difference between mean assimilation efficiencies on plant and fish diets (P<0.05).

TABLE 4. Assimilation of nutrients from contrasting diets in young *Batagur baska* at 30°C.

Nutrient	A. Dry weight basis		B. Wet weight basis	
	1. kangkong 93% water	2. fish 80% water	1. kangkong 93% water	2. fish 80% water
protein (mg g^{-1})	276	583	19.3	117
energy (Kjoules g^{-1})	27.6	25.8	1.9	5.2

TABLE 5. Protein and energy content of kangkong and trash fish.

ing plant material the terrapin used the limbs to achieve a stable shell position in the water column, so that the head, substantially retracted, was very close to the food item. The turtle then struck at the plant, simultaneously extending the neck and gaping the jaws widely. As the jaws snapped shut, the floor of the buccal cavity was depressed so that the food was sucked into the mouth. In some cases the sharp serrations sliced through the leaf structure cleanly and the portion of plant material was then swallowed. On other occasions, particularly when eating long kangkong leaves, the river terrapins used the beak serrations in a ratchet-like fashion, repeatedly striking and swallowing the plant material, but without breaking pieces off, so that the whole leaf was progressively moved into the oesophagus, the beak serrations stopping material escaping between bites. When feeding on water hyacinth, the river terrapins climbed onto the raft of floating plants and browsed continuously for periods of up to 30 min. The finding that river terrapins will readily eat water hyacinth is interesting as Moll (1980) reported that specimens of the species were often found in association with water hyacinth, but he was unable to confirm that they ate it.

Effect of Salinity on Feeding

From the data shown in Table 1 it is evident that river terrapins fed readily at salinities of 19.8‰ and below, but completely refused to feed at salinities of 23‰ and above.

Appetite

Young river terrapins (145-192 g body wt) consumed considerable quantities of plant material on a fresh weight basis (mean±SD = 15.9±0.42% body wt d^{-1}). Even when allowance is made for the high water content of kangkong (93%), the mean feeding rate is equivalent to 11.5 g dry matter per kg live body weight per day - more than three times the ingestion rate reported for a range of herbivorous/omnivorous marine, freshwater and terrestrial turtles by Bjorndal (1985).

Gut Transit

Total gut clearance time (TGCT) for river terrapins fed on a diet of kangkong was 6 days (see Table 2), although most labelled faeces were voided on the 4th day (the first day on which labelled faeces were seen). TGCT on a trash fish diet was shorter, the first labelled faeces being seen on day 3 and all animals having cleared the gut of label within 5 days.

X-radiography was successful in the case of one of the two animals studied (the other vomited part of its meal, leaving too little material for analysis). The first X-radiograph, taken 1 hr after the meal, showed that all of the meal was contained within the stomach and that the animal had swallowed 34 barium spheroids and 103 glass beads as well as the barium-labelled kangkong. From Table 3 it may be seen that material had started to move out of the stomach after 7 hr. The stomach image was much reduced in size, indicating that some fluid reabsorption had taken place. After 25 hr there was still some material in the stomach, but most had moved into the small intestine. After 49 hr most labelled material was in the large intestine or had been defecated. All label had disappeared by the time 97 hr had elapsed. The transit time recorded with the radio-opaque diet was significantly shorter than for turtles given chromic oxide labelled kangkong. Two factors may have caused this: the 48 hr period of food deprivation before the radio-opaque meal and frequent handling for X-radiography.

The X-ray images showed that river terrapins do not exhibit prolonged oesophageal storage of food, unlike the carnivorous emydid *Mauremys caspica* (Davenport & Kjõrsvik, 1988). The stomach is large and there is no evidence of a powerful pyloric sphincter. The small intestine is of moderate length, but is of much wider diameter than in carnivorous turtles. The large intestine is fairly short, but capacious. There was no evidence of sorting by the gut; spheroids, glass beads and barium powder all moved along the gut together.

Absorption/Assimilation Efficiency

Assimilation efficiencies were calculated as described by Maynard & Loosli (1969) and are presented in Table 4. Despite the shorter gut transit time on a diet of trash fish, it may be seen that nutrients were absorbed from this diet with much greater efficiency than from the diet of kangkong; the difference is statistically significant (*t*-test for small samples). Table 5 gives the protein and energy content of the two diets. On a dry weight basis kangkong has a similar energy content to trash fish, but less than half the protein. However, on a wet weight basis the discrepancy between the diets is much greater, with the trash fish containing 6.1 times as much protein and 2.7 times as many joules.

DISCUSSION

The lower reaches of the river systems of S.E. Asia are enormously productive habitats. Input of energy from the forests surrounding the rivers is great (in the form of leaves, fruit, flowers etc.), but is matched in the tidal parts of the systems by the primary productivity of the marshes and mangroves, benthic algae and epiphytes. There is a superabundance of organic material, much of which is exported to the neighbouring continental shelf in the form of fish, invertebrates and detritus. Estuaries of this type are emphatically not food-limited ecosystems; predation and abiotic environmental influences (particularly salinity) are more important controllers of populations. From the data presented in this study it would seem that river terrapins eat unusually large quantities of plant material which pass through the gut in about the same time (6 days) as in young green turteles, *Chelonia mydas* (Davenport *et al.*, 1989), although comparisons of this type are difficult because of difference in holding temperature. Little information is available about protein assimilation rates in herbivorous reptiles, but the mean rate of assimilation of energy from kangkong by river terrapins (38.6%) is within the range reported for green turtles feeding on sea grass (Bjorndal, 1980) and similar to that reported for giant Aldabran tortoises (*Geochelone gigantea*) eating terrestrial vegetation by Hamilton & Coe (1982), i.e. 34.5%. Zimmerman & Tracy (1989) have summarized energy assimilation data for a range of herbivorous and carnivorous reptiles (especially lizards). These workers reported that the energy assimilation efficiency of herbivorous Testudinata ranged between 34 and 69%. There is therefore no indication that river terrapins are especially efficient at assimilating material from a plant diet; they fuel their growth by voracious feeding on a virtually unlimited resource. In this respect their nutritional physiology is consistent with the hypothesis of Sibly (1981), that animals in a food-limited ecosystem need to maximise assimilation efficiency to get the most out of units of food, whereas animals in a food-rich ecosystem should maximise ingestion rate and process food relatively quickly.

When feeding on trash fish, river terrapins show very high assimilation efficiencies (mean values of 91.6% for dry mass, 90.5% for energy and 97.4% for protein), similar to those exhibited by estuarine crocodiles, *Crocodylus porosus* (Davenport *et al.*, 1990). Few data for carnivorous emydid turtles are available and again the problem of comparability arises because of different thermal conditions, but Kepenis & McManus (1974) reported an assimilation rate (joules) of 80% for young painted turtles (*Trachemys picta*), while Davenport & Kjõrsvik (1988) recorded an assimilation efficiency for energy of 46% in adult Caspian terrapins, *Mauremys caspica*. This finding, that an omnivorous species can be more efficient in assimilating energy and protein from a diet of fish than its carnivorous relatives was unexpected. However, the total gut clearance time for *Batagur baska* fed on fish (TGCT=120 hr) is much longer than those reported for *Trachemys* (TGCT=59 hr) or *Mauremys* (TGCT=72 hr), so it is likely that the long gut residence times contribute to the high level of assimilation efficiency.

The high water content and low protein content of kangkong, when combined with the much poorer assimilation efficiency shown by river terrapins fed on plant rather than animal material, have implications for the rearing/conservation programmes in Malaysia. Roughly speaking, a river terrapin will have to eat six times as much kangkong as trash fish (on a wet weight basis) to absorb the same amount of energy, and nine times as much kangkong as fish to assimilate the same amount of protein. Given these differences it would appear that reliance on kangkong feeding alone for the youngest of river terrapins is unwise. Moll (1980) reported that growth of hatchlings in the hatchery was much faster than in the wild (a desirable feature in any headstarting operation), but he was reporting data collected at a time when hatchlings were regularly fed fish. Although kangkong is inexpensive, it is probable that weekly feeding on fish (in addition to daily feeding on kangkong) would improve growth rates considerably, thereby reducing the headstarting period. However, more study in this area is clearly desirable.

The finding that river terrapins will not feed at salinities below about 20‰ is consistent with the earlier findings of Davenport & Wong (1986) who found that *Batagur baska* would drink water of 8.7‰ but not 17.5‰. Dunson & Mazzotti (1989) have recently categorized the responses of estuarine/brackish water reptiles. They point out that the simplest adaptation needed to allow a freshwater turtle to cope with saline conditions is for the animal to avoid drinking the external medium when the latter is hypersosmotic to the blood. They also suggest that a reptile which eats numerous relatively small food items, rather than a few large items, must also avoid eating when the external salinity is high because of incidental intake of salty water with the food. This categorization fits *Batagur baska* perfectly. It can and does exploit the productivity of estuaries, but only eats and drinks when the salinities are below about 15-20‰. River terrapins also tend to exploit bankside vegetation rather than floating vegetation when carried into mangrove channels by the flooding tide (Moll, 1980). Although these behavioural responses appear simple, they do require a degree of neurophysiological adaptation; Dunson & Mazzoti report that freshwater reptiles will usually drink saline water if they are thirsty, a quite inappropriate and ultimately lethal response.

REFERENCES

Bjorndal, K. A. (1980). Nutrition and grazing behaviour of the green turtle *Chelonia mydas*. *Marine Biology* **56**, 147-154.

Bjorndal, K. A. (1985). Nutritional ecology of sea turtles. *Copeia* **1985**, 736-751.

Booth, J. & Peters, J. A. (1972). Behavioral studies on the green turtle in the sea. *Animal Behaviour* **20**, 808-812.

Clark, D. B. & Gibbons, J. W. (1969). Dietary shift in the turtle *Pseudemys scripta* (Schoepff) from youth to maturity. *Copeia* **1969**, 704-706.

Davenport, J. & Kjörsvik, E. (1988). Observations on gut function in *Mauremys caspica caspica* (Gmelin). *Herpetological Journal* **1**, 272-275.

Davenport, J. & Wong, T. M. (1986). Observations on the water economy of the estuarine turtles *Batagur baska* (Gray) and *Callagur borneoensis* (Schlegel and Muller). *Comparative Biochemistry and Physiology* **84A**, 703-707.

Davenport, J., Antipas, S. & Blake, E. (1989). Observations of gut function in young green turtles (*Chelonia mydas L.*). *Herpetological Journal* **1**, 336-342.

Davenport, J., Grove, D. J., Cannon, J., Ellis, T. R. & Stables, R. (1990). Food capture, appetite, digestion rate and efficiency in hatchling and juvenile *Crocodylus porosus* Schneider. *Journal of Zoology* **220**, 569-592.

Dunson, W. A. & Mazzotti, F. J. (1989). Salinity as a limiting factor in the distribution of reptiles in Florida Bay: a theory for the estuarine origin of marine snakes and turtles. *Bulletin of Marine Science* **44**, 229-244.

Gunther, A. (1864). *The reptiles of British India*. London: Ray Society Publications.

Hamilton, J. & Coe, M. (1982). Feeding, digestion and assimilation of giant tortoises (*Geochelone gigantea* (Schweigger)) on Aldabra atoll. *Journal of Arid Environments* **5**, 127-144.

Hirth, H. F. (1971). Synopsis of biological data on the green turtle (*Chelonia mydas* (Linnaeus) 1758). *FAO Fisheries Synopsis* **No 85** Rome.

Kepenis, V. & McManus, J. J. (1974). Bioenergetics of young painted turtles, *Chrysemys picta*. *Comparative Biochemistry and Physiology* **48A**, 309-317.

Iverson, J. (1985). Checklist of the turtles of the world with English common names. *SSAR Herp. Circular* No. 14.

Ivlev, V. S. (1935). Eine mikromethode zur bestimmung des kaloreinghalts von nahrstoffen. *Biochem. Z.* **275**, 49-55.

McGinnis, A. J. & Kasting, R. (1964). Comparison of gravimetric and chromic oxide methods for measuring percentage utilization and consumption of food by phytophagous insects. *Journal of Insect Physiology* **10**, 989-995.

Maxwell, F. D. (1911). *Reports on inland and sea fisheries in the Thongwa, Myaungmya, and Bassein districts and turtle banks of the Irrawaddy Division*. Rangoon: Rangoon Government Printing Office.

Maynard, L. A. & Loosli, K. J. (1969). *Animal Nutrition. 6th Edition*. New York: McGraw Hill Book Co.

Moll, E. O. (1978). Drumming along the Perak. *Natural History* **87**, 36-43.

Moll, E. O. (1980). Natural history of the river terrapin, *Batagur baska* (Gray) in Malaysia (Testudines: Emydida). *Malaysian Journal of Science* **6A**, 23-62.

Sibly, R. M. (1981). Strategies of digestion and defecation. In *Physiological ecology: an evolutionary approach to resource use*, 109-139. Townsend, C. R. & Calow, P. eds. Sunderland, Mass.: Sinauer Associates.

Zimmerman, L. C. & Tracy, C. R. (1989). Interactions between the environment and ectothermy and herbivory in reptiles: *Physiological Zoology* **62**, 374-409.