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OBSERVATIONS OF GUT FUNCTION IN YOUNG GREEN TURTLES *CHELONIA MYDAS* L.

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ABSTRACT

Food consumption in post hatchling *Chelonia mydas* rises linearly between 18°C and 33°C. It is predicted that food intake will cease between 15°C and 16°C. The large intestine of post hatchlings is only half the length of the small intestine (c.f. 2.5 times the length of the small intestine in adults). The food of post hatchlings spend most of its transit time in the stomach and small intestine; that of yearlings (i.e. animals of 0.5-1.0 kg body wt) spends most time in the large intestine. The changes in gut proportions and in the residence time of meals in the large intestine during development are correlated with a shift from a carnivorous to a herbivorous diet. Yearling turtles are capable of digesting plant material, achieving an energy absorption efficiency of 68 per cent on a diet of *Zostera* (c.f. 87 per cent on a diet of cod flesh). Yearlings have the ability to move food to and fro in the large intestine; several meals reside in the large intestine at once and become mixed. Posthatchling and yearling *Chelonia mydas* can store food for short periods in the oesophagus.

INTRODUCTION

Over the past few years there have been several studies devoted to the nutrition and energetics of the sea turtle *Chelonia mydas* L. (e.g. Bjorndal, 1979, 1980, 1985; Wood and Wood, 1981; Mortimer, 1981; Davenport *et al.*, 1982; Hadjichristophorou and Grove, 1983; Davenport and Oxford, 1984). A major reason for the interest in *Chelonia mydas* is that adult green turtles, unlike other living sea turtles species, are predominantly herbivorous with a definite preference for seagrass (*Thalassia* supp.) and eelgrass (*Zostera* supp.), although they subsist on benthic algae in some areas (e.g. Ferreira, 1968). Bjorndal (1979) showed that adult animals possessed a cellulose-degrading gut microflora in the large intestine. Thompson (1980) has demonstrated that the large intestine of adult green turtles is more than twice as long as that of the carnivorous loggerhead turtle *Caretta caretta* (compared with the small intestine) and has related this to the green turtles' herbivorous diet.

Hatchling green turtles have rarely been seen in the wild after leaving their hatching beach, and the period between hatching and arriving on seagrass beds as fairly large animals (c. 2-5 kg) is obscure (the 'lost year' — Carr, 1967). In the Caribbean, where most studies have been carried out, it seems probable that young green turtles are associated with sargassum rafts (Carr and Meylan, 1980) during this period, and are opportunistic carnivorous that feed upon ctenophores, tunicates and sea anemones (Hirth, 1971; Booth and Peters, 1972). Sargassum rafts are unavailable to some populations of *Chelonia mydas*; Davenport and Oxford (1984) reported that hatchling green turtles from Cyprus were omnivorous and would readily consume algae, sponges, invertebrates and fish (being capable of chasing and catching the mobile species). Davenport and Oxford also reported that faeces of the young turtles contained gram negative rod bacteria capable of digesting cellulose, suggesting that they too are adapted to deal with plant material in their diet.

Hadjichristophorou and Grove (1983) and Davenport and Oxford (1984) studied gut clearance times in young green turtles, and found that these were prolonged. However, the latter authors suggested that the long recorded gut clearance times might be to some extent erroneous because of the large intestine acting as a fermentation reservoir, mixing material from 'old' meals, with 'new' meals, to spread label to material with which it was not originally associated. Although experiments with radio-opaque barium sulphate labelled food tended to support this hypothesis, their qualitative nature made firm conclusions impossible.

The study reported upon here was designed to yield quantitative data about residence times of meals in various parts of the gut of young *Chelonia mydas*; to determine whether the turtles sorted material in the gut, or moved material to and fro in the large intestine; to investigate the effect of temperature on food consumption; to measure the length of the large intestine in post hatchlings; and to measure absorption efficiency in animals fed plant and flesh diets.

MATERIALS AND METHODS

COLLECTION AND MAINTENANCE

Recently hatched specimens of *Chelonia mydas* were acquired from the Lara Reserve Turtle Project, Department of Fisheries, Cyprus. Initially they weighed between 31 g and 58 g. They were studied immediately and subsequently for about 3 months during which they grew to 80-150 g. Study was then interrupted until the turtles were about 8 months old (520-645 g). Work upon them continued until they

were 13 months old (740-980 g). At this point they were returned to Cyprus for release into the Mediterranean Sea. For the purpose of this study the animals up to 3 months old will be described as 'post hatchlings'; those 8-13 months old as 'yearlings'. Throughout, animals were held in circulating sea water (34 per cent) at 25±1°C unless otherwise stated. Routine feeding was upon floating commercial trout food (Omega trout pellets).

Effect of Temperature on Routine Feeding in Post Hatchlings

Two post hatchlings were held in sea water in each of five temperature baths set at the following temperatures: 18, 21, 25, 27 and 33°C. Trout pellet meals of known weight were offered to each of them daily for 9 days. Uneaten food was filtered, dried and weighed to allow the calculation of routine meal size.

Intestinal Proportions of Post Hatchlings

Single frozen specimens of post hatchling *Chelonia mydas* and *Caretta caretta* (loggerhead) were dissected and the lengths of the small and large intestines measured.

Movement of Material Along the Gut

Post hatchlings and yearlings were fed on a diet prepared in the following manner. Trout pellets were ground in a mortar with barium sulphate (5:1 by weight) to provide a basic barium meal to outline the gut during X-radiographic studies. Radio-opaque barium sulphate spheroids (ICI Ltd) were added and carefully mixed into the barium meal, so that a 2 per cent body weight meal would contain roughly 100 spheroids (each spheroid weighing 0.9 mg). This meal was then mixed with a hot solution of gelatin in water (40 g gelatin: 100ml water) and allowed to set in plastic dishes. When cool, the meal was cut into pieces of appropriate size to allow easy swallowing by the post hatchling or yearling being studied. The gelatin was needed to prevent spheroids falling out of the meal during feeding.

In each gut transit experiment, a turtle was fed meals of trout pellets mixed with gelatin for 2 days; it was then deprived of food for 30 h (post hatchlings) or 48 h (yearlings) before being offered a 2 per cent body weight meal of the barium sulphate/barium spheroid diet. The period of food deprivation was needed to ensure complete consumption of a rather unappetising meal. The turtle was X-rayed before the meal and at regular intervals thereafter. After the barium meal the animal was fed daily (1.5 per cent body weight meals being offered) upon trout pellets mixed with gelatin until the end of the experiment.

To confirm that the barium spheroids provided a true reflection of the rate of movement of food through the gut and were not sorted, single post hatchlings and yearlings were each fed a diet containing barium sulphate, barium spheroids and fine, varnish coated iron particles. The animals were X-rayed for several days to check that the barium shadows, spheroid images and iron particle images remained together throughout gut transit.

Iron Tag Experiment

Davenport and Oxford (1984) suggested that food might be moved to and fro in the hind gut of green turtles to aid microbial fermentation. To test this hypothesis, two yearlings were each fed a barium and spheroid labelled meal which also contained a 6mm long metal tag encased in soft, thin plastic. The barium meal was preceded by a 48 h period of food deprivation. Regular X-rays were taken after the tagged meal.

Absorption Efficiencies

Although adult green turtles are largely herbivorous (Bjorndal, 1980, 1985; Mortimer, 1982), they will take animals on occasion (Kooyman, 1972) and it is now clear that young green turtles, like the young of other sea turtle species, are predominantly carnivorous, though they will eat plant material if hungry (Booth and Peters, 1969; Witham, 1980; Davenport and Oxford, 1984). It was decided, therefore, to compare absorption efficiencies for energy in yearlings fed upon animal and plant diets. All six available yearlings were used, and ranged between 714 g and 981 g at the time of the experiments. The following experimental procedure was used. Fresh cod (*Gadus morhua*) was skinned and muscle tissue finely minced. Sea grass (*Zostera supp.*) was collected from small beds at Morfa Nefyn (Lleyn Peninsula, North Wales); it was finely chopped. Gelatin was used to bind the diets, and chromic oxide (2 per cent by weight) was thoroughly mixed with each. Batches of food without the chromic oxide label were also prepared. Three yearlings were fed for 7 days on label-free fish, then for 4 days on labelled cod. This feeding regime was followed by 7 days of feeding on label-free sea grass and 4 days on labelled sea grass before returning to the normal trout pellet diet for several days. During this whole procedure the turtles produced green, chromic oxide-laden faeces during two periods, each lasting several days. The faeces were all collected, but only those voided at the midpoint of each period were subsequently analysed. These latter faeces therefore correspond a) to the cod meals and b) to the meals of *Zostera*. The other three yearlings were handled in similar fashion, but were fed sea grass first and cod second.

Chromic oxide labelled food and faeces samples were oven dried at 45°C for 8 days and then stored in a desiccator until analysed. Chromic oxide content was analysed by wet oxidation to dichromate and subsequent spectrophotometric determination by the diphenylcarbazide reaction (McGinnis and Casting, 1964). Energy content of food and faeces was measured by bomb calorimetry.

RESULTS

Effects of Temperature on Food Consumption in Post Hatchlings

The effect of temperature on food consumption in post hatchlings is shown in Table I. It appears that food consumption and temperature are linearly related over this temperature range, and from the regression

equation derived from the data it may be calculated that food consumption will cease between 15°C and 16°C. The regression also indicates that Q_{10} for food consumption is much greater at lower temperatures:

Q_{10} 18-23°C = 9.64
Q_{10} 23-28°C = 2.82
Q_{10} 28-33°C = 1.97

Intestinal Proportions of Post Hatchlings

The ratio of the length of the large intestine to the length of the small intestine in post hatchling turtles can be compared with that in the adults measured by Thompson (1980):

	Chelonia	*Caretta*
Post hatchling	0.45	0.97
Adult	2.52	0.89

Turtle No.	Temperature (°C)	Mean Meal Size (% body wt d^{-1})
1.	18	0.13
2.	18	0.13
3.	21	0.33
4.	21	0.46
5.	25	0.59
6.	25	0.60
7.	27	0.64
8.	27	0.69
9.	33	0.99
10.	33	1.34

TABLE 1: Effect of temperature on routine food consumption (measured over 9 days) in post hatchling *Chelonia mydas*.

Regression analysis of above data shows that mean meal size (y % d^{-1}) is linearly related to temperature (x°C) by the following equation:

$y = 0.064x - 1$ $(R^2 = 0.92)$

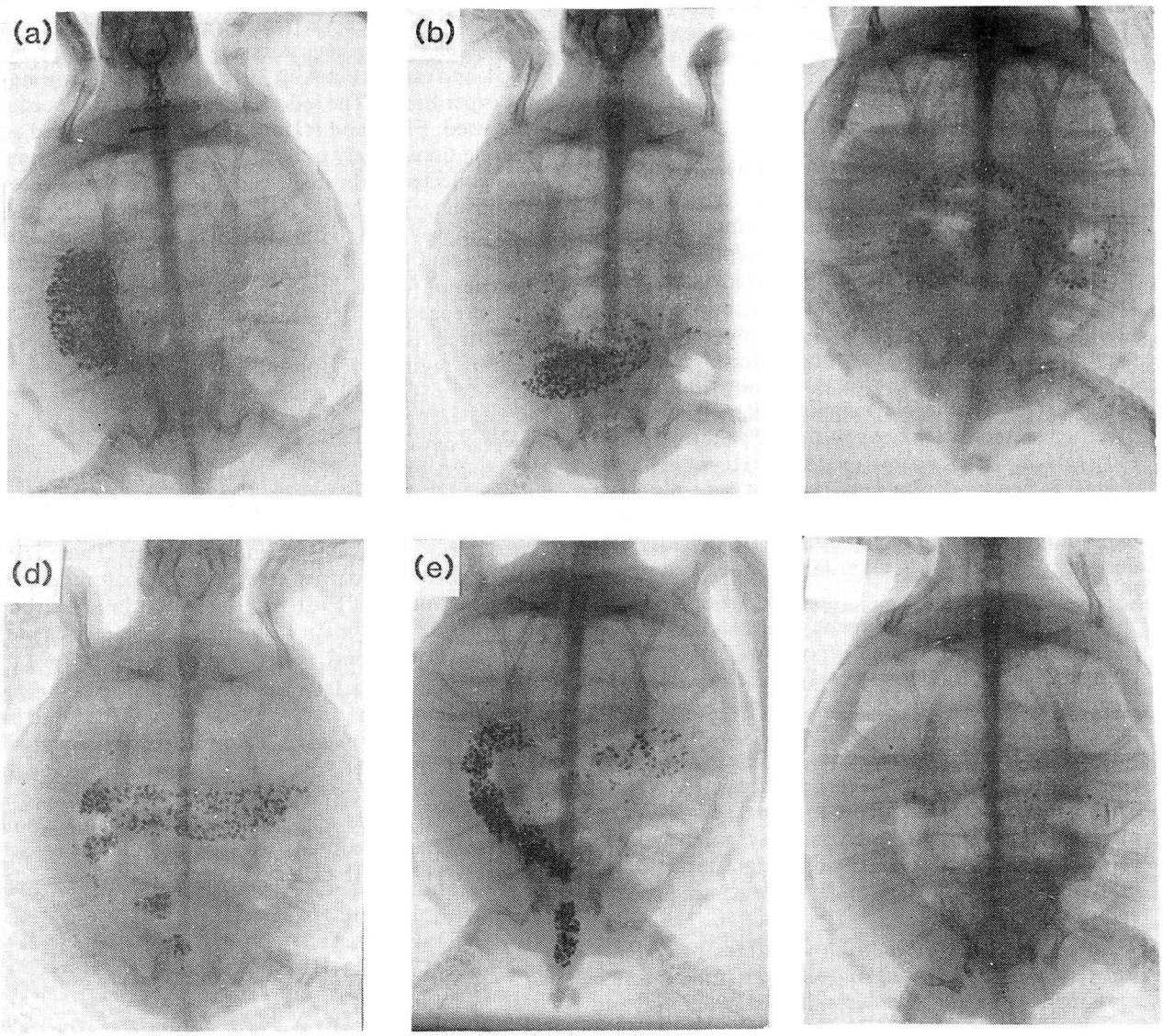

PLATE I. Progress of barium spheroid labelled meal through the gut of a post hatchling specimen of *Chelonia mydas*. (a) 15 min after meal. Note spheroids in oesophagus and stomach. A few (9) spheroids are scattered in the intestines and were apparently derived from reingested faeces. (b) 7 h after meal. Spheroids are entering duodenum. (c) 24 h after meal; spheroids mainly in small intestine. (d) 70 h after meal. Spheroids mainly in large intestine. (e) 71 h after meal. About to defaecate bulk of spheroids. (f) 97 h after meal. A few spheroids in large intestine.

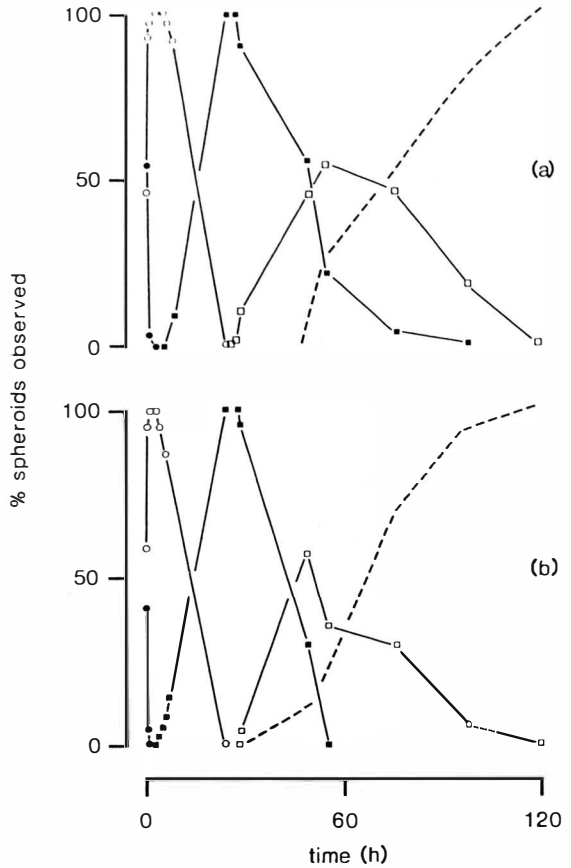

Fig. 1 Meal residence time in different parts of the gut of two posthatchling *Chelonia mydas*. Closed circles represent residence in oesophagus, open circles in stomach, closed squares in small intestine, open squares in large intestine. Dashed line represents defaecated spheroids.

Although post hatchling and adult *Caretta caretta* have similar ratios between the lengths of the large intestine and small intestine, with the large intestine being slightly the shorter, the situation for *Chelonia mydas* is different. While Thompson (1980) found that the adult green turtle has a large intestine more than twice the length of the small intestine, the post hatchling dissected in the present study possessed a large intestine less than half the length of the small intestine. Obviously more data collection would be desirable (though hardly from a conservation viewpoint !), but it seems likely that the relative size of the large intestine of *Chelonia mydas* increases substantially between hatching and maturity.

Movement of Material Along the Gut

Plate 1 illustrates the progress of barium sulphate spheroids through the gut of a post hatchling turtle and demonstrates their visibility. Figs. 1 and 2 show the residence times (at 25°C) of spheroid-labelled meals in different parts of the gut of post hatchlings and yearlings, respectively. These data demonstrate that gut function changes as *Chelonia mydas* grows. Firstly they indicate that total gut clearance time (TGCT) is rather longer in yearlings than in post hatchlings. Secondly, there are differences in the proportion of time that spheroids spend in different parts of the gut.

In post hatchlings there is some retention of food in the oesophagus, but within 15-30 min all of the meal is present in the stomach. The meal remains wholly within the stomach for at least 2-3 h and only after 5-7 h are significant numbers of spheroids transferred to the small intestine. By the time 24 h have elapsed all

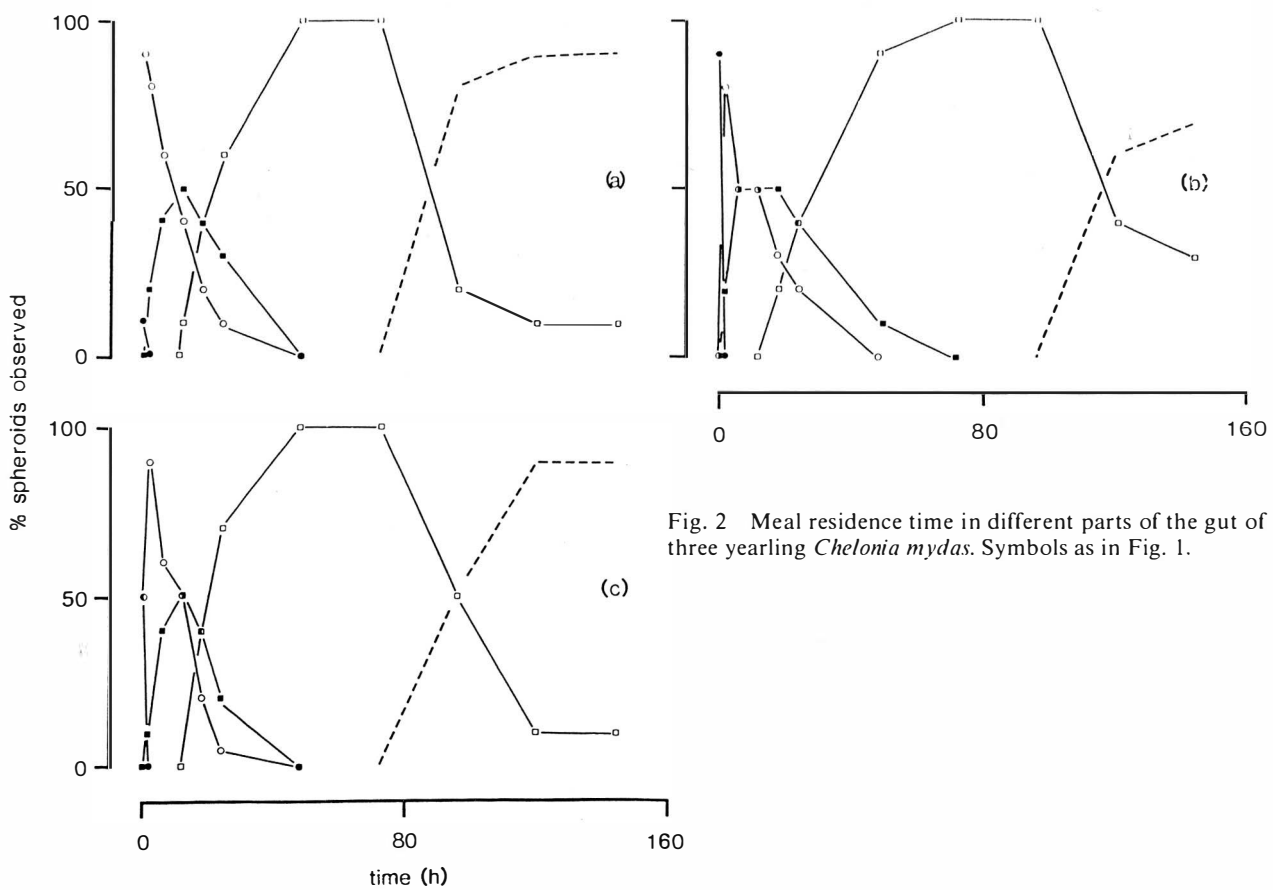

Fig. 2 Meal residence time in different parts of the gut of three yearling *Chelonia mydas*. Symbols as in Fig. 1.

of the meal is in the small intestine; small amounts start to move into the large intestine after 26-28 h. No more than 50-60 per cent of the spheroids are present in the large intestine at any one time as defaecation starts 48-72 h after ingestion of a meal. In post hatchlings it is evident that meals are accommodated in the anterior portions of the gut for most of their transit time.

In yearlings the oesophageal residence is again short (15-30 min), but by the time the last spheroids have moved from the oesophagus into the stomach, others have already entered the small intestine. In consequence, the meal is never wholly contained within the stomach. Residence time within the small intestine is relatively short and substantial quantities of spheroids reach the large intestine within 18 h. No more than 50 per cent of the spheroids are found inside the small intestine at any one time. The whole meal is held within the large intestine by the time 48-72 h have elapsed. Defaecation of the meal starts after 72-96 h, but was not complete at the end of the study period (terminated after 144 h) in any of the yearlings studied. It appears that the food of yearlings spends most of its gut residence time in the large intestine. The curves shown in Fig. 2 each represent the progress of a single meal in a sequence of daily meals. Since material from a labelled meal reaches the hind gut within 18 h, but is not fully defaecated by 144 h, the curves imply that parts of several daily meals are present in the large intestine at the same time.

The date derived from the experiments with iron tags were rather equivocal. In one yearling turtle the tag (which gave a very strong X-ray image) remained in the stomach for a while after the associated barium meal had left, but thereafter progressed steadily along the gut with no hint of to and fro movement. In the other yearling the tag moved steadily in one direction until it reached the descending colon of the large intestine, but was then left in a gas pocket before moving backwards into the loops of the large intestine. It is evidently possible for material to move to and fro in the hind gut as suggested by Davenport and Oxford (1984), but whether this happens because of two-way peristalsis or simply in association with the movement of gas bubbles is not yet clear.

During one of the iron tag experiments a yearling ate faeces containing spheroids; these spheroids 'caught up' in the large intestine with the spheroids of the previous labelled meal and mixed with them.

Absorption Efficiency (of Energy) in Yearlings

To calculate the absorption efficiency (energy) on plant and animal diets, the data shown in Table 2 were used with the following equation:

$$E = 100 \times 1 - \frac{(c^d/e^d)}{(c^f/e^f)}$$

Where E = absorption efficiency (%)
c^d = chromic oxide content of diet
e^d = energy content of diet
c^f = chromic oxide content of faeces
e^f = energy content of faeces

	Mean Chromic oxide content (mg g^{-1})	Mean Energy content (KJoules g^{-1})
(A) Foods		
1. Cod flesh	1.81	22.68
2. *Zostera spp.*	2.73	18.45
(B) Faeces		
1. Cod diet	9.09	14.73
2. *Zostera* diet	8.09	17.57

TABLE 2: Chromic oxide and energy contents of food and faeces of 6 yearling *Chelonia mydas* fed on plant and animal diets.

On a diet of cod yearlings had an absorption efficiency of 87 per cent; on a diet of *Zostera* the efficiency was 68 per cent.

DISCUSSION

The literature devoted to the thermal biology of sea turtles is extensive (see Mrosovsky, 1980 for review). Although the lower lethal temperatures of green and loggerhead hatchlings are below 10°C (Schwartz, 1978) there is abundant evidence to show that turtles do not grow at temperatures below 20°C and move away from coastal feeding grounds during winter when temperatures are low (Carr *et al.*, 1980), Bjorndal (1980) also found that absorption efficiencies became low and variable in green turtles at low temperatures (about 20°C). At about 15°C, the temperature at which we predict feeding will cease, there is evidence that green turtles become torpid, with some populations hibernating (Felger *et al.*, 1976). The upper lethal temperature for green turtles is not known though Bustard (1970) reported that hatchlings survived rectal temperatures of 36-40°C for 15 min. The temperature range employed in this investigation is therefore a fair reflection of the total thermal range over which feeding can take place. The steady rise in food consumption with increasing temperature is similar to that observed in young loggerhead turtles, but the maximum rate of food intake (c. 1 per cent body weight d^{-1}) is less than half that of post hatchling loggerheads (Birse and Davenport, 1987), Bjorndal (1981) suggested that adult green turtles have a low rate of food consumption rate because their sea grass diet requires a long gut residence time (thus limiting intake), but it seems that low food consumption is inherent in *Chelonia mydas* throughout life.

It is accepted that large juvenile and adult green turtles (8-66 kg) are predominantly herbivorous (e.g. Ferreira, 1968; Bjorndal, 1980), while recently hatched animals are believed to be opportunistic carnivores. The results presented in this study demonstrate that green turtles not only change their diet during development, but also alter their gut proportions and function. The large intestine of post hatchlings is less than half the length of the small intestine (this study), while that of adults is more than $2\frac{1}{2}$ times the small intestine length (Thompson, 1980). We have no

measured intestinal lengths for the yearlings investigated here, but qualitative observation of X-ray plates indicates a considerable lengthening of the large intestine (and increased convolution) in comparison with the post hatchlings. The lengthening of the large intestine is associated with a change in the pattern of gut residence; meals remain longest in the foregut of post hatchlings, but in the large intestine in yearlings. The TGCT values recorded in this study with barium spheroids are much shorter than those derived from observations of coloured food label in faeces. This is particularly true of hatchlings. Davenport and Oxford (1984) recorded TGCT values as high as 394 h (vs. 120 h in this study). We suspect that unnoticed faecal ingestion may have been partly responsible for the extreme values.

A capacious large intestine in which meals spend a long time has been correlated with herbivory as these features facilitate the breakdown of cellulose by microorganisms. Bjorndal (1980) demonstrated a cellulytic flora in adult green turtles; Davenport and Oxford (1984) obtained evidence (albeit not conclusive) that such microorganisms were present in post hatchlings too. The absorption efficiency data collected in the present study confirm that yearlings (i.e animals of about 0.7-1.0 kg) can readily digest plant material since 68 per cent of the energy content of meals of *Zostera* is absorbed — a value well within the range reported for large juvenile and adult animals feeding on sea grass (21-71 per cent at 20-35°C; Bjorndal, 1980). This indicates that effective herbivory develops earlier in the life of *Chelonia mydas* than previously recognised, perhaps indicating a phase during which more and more plant material is taken. The rather higher absorption efficiency on a diet of cod flesh (87 per cent) shows that the ability to digest plant material does not diminish the turtles' capacity for exploiting available animal food sources. Energy absorption efficiencies have rarely been reported for reptiles, especially herbivores, but the literature reviewed by Hamilton and Coe (1982) suggests that green turtles are as efficient in their digestion as herbivorous lizards (54.5-69.5 per cent) and markedly more efficient than Aldabran giant tortoises which only achieve 34.5 per cent.

The measured large intestine residence times, the results of the 'iron tag' experiments, and the observation of 'catch up' by spheroids from reingested faeces all indicate that material from several meals is present in the hind gut at the same time, and that mixing of meals takes place. This will be of advantage for digesting plant material, facilitating the inoculation 'new' material with microorganisms from 'old' meals.

Two interesting details of food movement in the gut were revealed by this study. Firstly, it is clear that both post hatchling and yearling green turtles can store food in a distended oesophagus. They do not often do so, and only for a limited period (15-30 min). This contrasts with the abilities of the loggerhead sea turtle *Caretta caretta* (Birse and Davenport, 1987) and the freshwater turtle *Mauremys caspica* (Davenport and Kjørsvik, 1988), both of which can store food in the oesophagus for more than an hour. However, all three cryptodiran species studied in these laboratories have shown oesophageal storage; Davenport and Kjørsvik suggested that such storage originated in chelonians capable of retracting the head into the shell (which sea turtles are not), possibly in response to the necessity for sudden head retraction during meals interrupted by predators.

Secondly, it was noticed that the food of yearlings often went straight through the stomach into the small intestine; there is little evidence of a sphincter guarding the duodenum. It is doubtful whether adult green turtles eat 'meals' as such in the wild; instead they browse on benthic algae or sea grass beds, in the latter case selecting the young leaves with least lignin (Bjorndal, 1981). Since most digestion takes place in the large intestine there will be little need to retain food in the stomach.

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