

Digesta Passage Times in the Dugong

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Abstract

The retention times of particulate digesta were measured in two captive dugongs, *Dugong dugon* (Muller 1776) using inert plastic markers. The mouth-to-anus retention times (146–166 h) were similar to those of the West Indian manatee, and much longer than those of most other herbivorous mammals. This slow gut passage rate may be explained by the dugong's long digestive tract, the low fibre level of the diet and the low food intake. Like the manatee, the dugong appears to have a digestive strategy that is atypical of hindgut fermenters: low-fibre material is retained for extended periods within the long hindgut and almost completely digested.

Introduction

The efficiency of chemical digestion of food depends on the rates of both nutrient extraction and passage through the digestive tract (Van Soest 1982). The relationship between these two factors may be an important determinant of how well an animal uses a particular food. Both factors have been found to influence food choice in several groups of herbivores (e.g. Milton 1981). Generally, the longer the food remains in the gut, the greater the degree of chemical digestion (Van Soest 1982).

In herbivorous mammals, digestion of dietary fibre by microbial enzymes increases with prolonged retention in the fermentation chamber (McLeod and Minson 1969; Parra 1978; Cork and Warner 1983). Some hindgut fermenters of small body size and relatively high mass-specific energy requirements derive most of their nutrients from the cell content fraction of the digesta. In these species, the coarse fibre fraction passes through the gut rapidly, allowing time for only minimal fermentation and providing the opportunity to maximise intake of the more digestible cell contents. Some other small hindgut fermenters also maximise fibre digestibility through coprophagy and selective retention of small particulate fibrous portions of the ingesta within the gut, for example, the rabbit (Hörnigke and Björnhag 1980) and the ringtail possum (Chilcott and Hume 1985).

Like small cell-content-feeding animals, some large hindgut fermenters also concentrate on cell contents. These herbivores [e.g. the horse and elephant (Janis 1976; Clemens and Maloiy 1982; Foose 1982)] also tend to have a relatively rapid digesta passage rate, sacrificing maximum fibre digestion for increased intake of total digestible nutrients. An exception to this pattern is the koala which has a very long digesta retention time despite the small contribution of fibre towards its overall energy balance (Cork 1981; Lanyon 1982; Cork and Warner 1983).

The dugong, *Dugong dugon*, is a large hindgut fermenter. If it fits the general pattern of other large hindgut fermenters, we might expect the greater proportion of its energy requirements to be met by digestion of unfermented cell contents but with a significant contribution from the fermentation of fibre and digestion of the end-products.

Murray *et al.* (1977) have reported high fibre digestibilities (84% neutral-detergent fibre digestibility) in the hindgut of the dugong. Indeed, these values were sufficiently high compared with those obtained for other herbivores (even foregut fermenters) to lead Murray (1981) to express concern about possible problems with his methodology. However, fibre digestibilities of similar magnitude have been reported for other sirenians, for example, the West Indian manatee, *Trichechus manatus* (Burn 1986). Lomolino and Ewel (1984) suggested that this high rate of nutrient extraction or high digestive efficiency may be due to the inordinately long passage time of digesta through the gut of the manatee (mean retention time 146 h). This digesta retention time has been questioned (Burn 1986). If the fibre digestibilities measured by Murray *et al.* (1977) are accurate and if gut passage rate has a bearing on the rate of fibre digestion, we would expect a similarly long digesta retention time in the dugong.

This paper describes an experiment in which the passage rate of particulate digesta through the gut of the dugong was measured in an attempt to provide an insight into its digestive strategy.

Materials and Methods

This experiment was performed on two dugongs at Jaya Ancol Oceanarium in Jakarta, Indonesia, one of only two places in the world to hold captive dugongs. Both animals had been in captivity for 26 months. Judging by their body sizes, both dugongs were immature (Marsh *et al.* 1984: length of male 2.05 m, weight 147 kg; length of female 1.86 m, weight 114 kg).

The growth rate of both animals over the preceding nine months had been slow: the male's weight had not changed and the female had grown 3 cm in length and gained 8 kg.

The dugongs were kept together in a single circular sea-water pool (7 m in diameter, maximum depth of 2.6 m). The pool water was at ambient temperature. The pool was emptied and refilled on most mornings. The water circulated through a pressure filter from approximately 0800 to 2200 hours daily, entering the pool through two inlet pipes at the pool sides and leaving via a central outlet on the pool floor. A strainer placed over the outlet pipe was designed to prevent seagrass and other debris from entering the filtration pump.

The species composition of the dugongs' diet had been stable for at least the preceding nine months, and was not altered during the course of the experiment. The seagrass was harvested in west Java and delivered to the Oceanarium every two days. The seagrass consisted mainly of the leaves of *Syringodium isoetifolium*, with negligible amounts of *Cymodocea serrulata* and *Enhalus acoroides*. Due to the requirements of the Oceanarium, the dugongs were fed twice daily, in the morning and late afternoon. Once the seagrass was introduced, the dugongs fed almost continuously until it was finished, generally within a couple of hours. The wet weight of seagrass available to the two dugongs at each feed prior to and during the experimental period was determined to the nearest 0.2 kg. Any uneaten seagrass remaining the following morning was also weighed. The neutral detergent fibre (NDF) levels of the seagrass fed to the dugongs were determined using the procedures of Van Soest and Wine (1967) and Goering and Van Soest (1970).

Inert cylindrical polythene beads measuring 3 mm in length and 1 mm in diameter were used to estimate the retention time of the particulate phase of the digesta. The marker beads were dyed with a colour-fast food contact pigment and had a specific gravity of 1.005, close to that of seagrass (1.01) and only slightly lower than Warner's recommended optimum of 1.1 (Lintermans 1979). The beads were administered in gelatin capsules (35 pellets per capsule). The gut passage rates of individual animals were distinguished by administering pulse doses of differently coloured marker beads. The dugongs were hand-fed bundles of *S. isoetifolium* in which the capsules were secreted, as per the schedule outlined in Table 1.

To recover the marker beads, 49 faecal collections were made over the 13-day experimental period. The dugongs tended to defecate in bursts after feeding, and whilst the pool was being drained each morning. Faeces were collected before the pool was drained (this collection included faeces eliminated at night whilst the filter was turned off), during draining and refilling, before the afternoon feed, as late as possible each evening and at other times when possible.

The beads dispersed homogeneously throughout the faecal pellets. They were recovered by wet-sieving each faecal collection through a 75- μ m mesh sieve. Washings from the sieve were also checked for presence of beads in case some beads had been broken or deformed during transit through the gut. Marker recovery was expressed as the number of beads recovered per faecal collection. Mean retention times for each pulse of markers were calculated according to Coombe and Kay (1965).

Limitations of the Methodology

Jaya Ancol Oceanarium imposed the following methodological constraints on the experiment. Plastic markers was the only acceptable method of measuring digesta passage times. From a review of marker methods, Warner (1981) suggested that inert plastic markers may give a good approximation of passage rate, particularly if there is close resemblance between the specific gravity and size of the plastic markers and the digesta particles they are to follow. In contrast, other workers have suggested that inert markers (i.e. those that do not closely adhere to particles) may be an unreliable index of the passage of digesta (e.g. Udén *et al.* 1980). A variety of marker methods including mordanted, radioactive or dyed particles have been recommended as being possibly superior to the plastic-marker method (e.g. Van Soest *et al.* 1978). However, these methods also have problems in fulfilling the requirements of closely following particles whilst not affecting digestive processes. The retention times measured here are probably reasonable approximations to retention times of digesta particles of similar size and specific gravity.

Dugong feeding times were dictated by the Oceanarium routine. The amount of food offered to the dugongs each day was also beyond our control. Ideally, the dugongs should have been fed *ad libitum*. In addition, faecal collection was constrained by the times we were allowed access to the Oceanarium and by the design and operation of the filtration system.

Results

Seagrass Intake

The total wet weight of seagrass offered to the two dugongs each day ranged from 26.0 to 47.5 kg (mean \pm s.e. 41.3 ± 1.9 kg; $n = 13$ days). There was never any seagrass remaining in the pool prior to drainage. Apparently, it was all either consumed or lost to the filtration system. Since between 0.25 and 2.2 kg of seagrass was collected from the strainer each morning, the dugongs were probably consuming a combined average of 40.34 ± 1.86 kg per day. There were no trends in the net amount of food apparently consumed by the two dugongs prior to and during the experiment. Although the strainer was supposed to retain debris, it is likely that an unknown quantity of seagrass was lost through the strainer; hence, the estimated consumption was likely to be an overestimate.

Both animals reingested faeces on several occasions before and during the experiment, especially after all of the seagrass had been consumed. This behaviour was commonly observed whilst the pool was being refilled after draining. The dugongs consumed faeces from the bottom of the pool opportunistically and indiscriminantly.

Gut Passage Rate

There was an overall low recovery rate of markers during the experimental period (Table 1). The yellow and green markers first appeared at 118 and 122 h, respectively, after administration. The appearance of a single blue marker, at 52 h, may have been an artefact,

Table 1. Details of the administration and recover of the coloured digesta markers in the gut passage rate experiment

Dugong	Bead colour	Estimated intake	No. of beads recovered	First appearance after administration (h)	Mean retention time (h)
♀	Yellow	300–400	29	118	163.3
♀	Buff	525 administered	0	None recovered	
♂	Buff	to both dugongs, most eaten by ♀			
♀	Blue	200	27	122 ^A	166.4
♂	Green	50	7	148.3	145.7

^AA single bead was collected on the outside of faeces at 52 h.

since it was on the outside of the faecal pellet, suggesting that it may have been picked up by and became attached to the pellet after defecation. The next blue bead was not collected until 148 h after administration.

The cumulative total of marker beads recovered (of each colour) was plotted against hours after administration (Fig. 1). In the female, the mean retention times of the two pulse doses were close (164 h, yellow beads; 166 h, blue beads). The mean retention time for the green marker beads in the male was shorter (146 h).

Seagrass NDF Levels

The NDF level in *S. isoetifolium* leaves was measured at $32 \pm 0.7\%$ ($n = 3$) of dry matter.

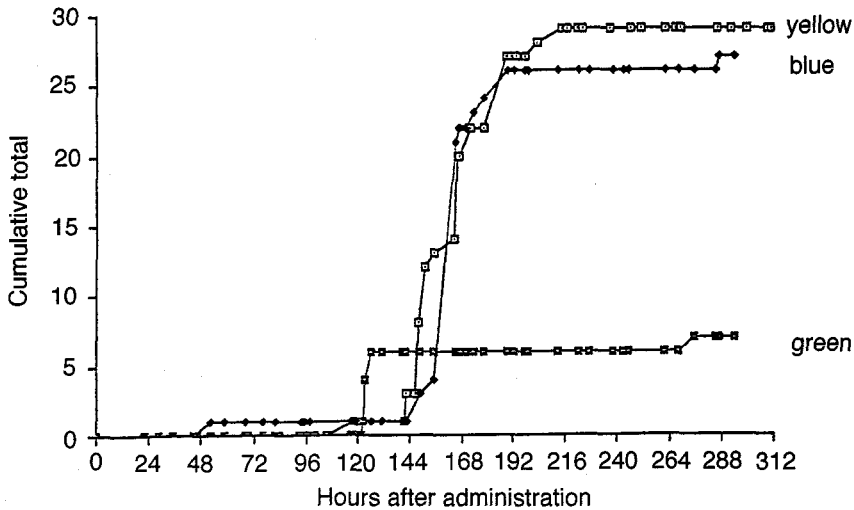


Fig. 1. Cumulative excretion of the particulate markers in the faeces after passage through the digestive tracts of the captive dugongs. Yellow and blue markers passed through the gut of the female; green markers passed through the male.

Discussion

The digesta retention times of 145–166 h (6–7 days) for particulate digesta through the digestive tract of dugongs feeding on low-fibre leaves of *S. isoetifolium* were long, especially when compared with other, even much larger, hindgut fermenting herbivores (Table 2). However, these times were similar to those measured for the West Indian manatee feeding on low-fibre water hyacinth (120–168 h; 5–7 days; Lomolino and Ewel 1984). The agreement between the retention times for dugongs and manatees may lend some credence to the validity of the manatee results. These particulate digesta retention times indicate that dugongs and manatees have the slowest gut passage rates yet measured in a mammal, with the exception of the sloth (200–300 h; 8–12 days) (Montgomery and Sunquist 1978).

The pattern of digesta marker recovery as suggested by the rapid rise of the cumulative excretion curve (Fig. 1) suggests that food moves through the gut of the dugong as a bolus rather than mixing substantially with flanking meals. The long time until first appearance of the marker is consistent with a long transit time. However, the overall low recovery of marker beads ($\leq 14\%$) during this experiment places doubt on an estimation of mean retention time of particulate digesta.

Table 2. Digesta passage time through the digestive tracts of dugongs and other herbivores
 Values for mean retention times (h) of particulate digesta in dugongs were based on the number of marker beads recovered

	Mean retention time (h)		Marker method	Source
	Particulate	Fluid		
Hindgut fermenters				
Dugong	146-66	-	Inert beads	This study
West Indian manatee	120-68	-	Change in diet	Lomolino and Ewel (1984)
Elephant	22-26	-		Foose (1978); Hackenburger and Atkinson (1982)
Horse	23	18		Udén <i>et al.</i> (1980)
Hyrax	72-96	-		Best (1981)
Ringtail possum	26-46	50-70	51Cr/103Ru-P	Chilcott and Hume (1985)
Greater glider	46	50	51CR/103Ru-P	Foley and Hume (1987)
	23	-	Cr mordant	Foley and Hume (1987)
Brush-tail possum	71	64	51CR/103Ru-P	Wellard and Hume (1981)
	51	49	51CR/103Ru-P	Foley and Hume (1987)
Koala	69-135	95-414	51CR/103Ru-P	Cork (1981); Cork and Warner (1983)
Foregut fermenters				
Cattle	48-65	18-20	51CR/103Ru-P	Udén <i>et al.</i> (1980)
Sheep	57	26	51CR/103Ru-P	Udén <i>et al.</i> (1980)
	25	21		Dellow (1982)
Eastern grey kangaroo	30	14		Dellow (1982)
Sloth	200-300	-	Glass beads	Montgomery and Sunquist (1978)

There are two possible reasons for the overall low recovery of marker beads.

(1) *Coprophagy.* Frequent coprophagy as practised by these two dugongs would serve to recycle at least some of the marker beads through the gut. If coprophagy was the major cause of the low recovery of marker beads, we would expect that the unrecovered beads were still moving through the gut as a bolus at the termination of the experiment. If the experiment could have continued for longer, we presume that elimination of the marker beads would have occurred in pulses, the intervals between which would have corresponded to the initial transit times. In theory, a true estimation of mean retention time would have to take these subsequent eliminations into account. Hence, in the presence of coprophagy (as in this case), mean retention times would be underestimated.

The reason why the captive dugongs practised coprophagy is unclear but may have been an artefact of the captive situation, especially their inadequate diet. Coprophagy is frequently practised by manatees, including those in the wild (Hartman 1979) and this is thought to serve as a dietary supplement (Best 1981). Coprophagy has not been observed in wild dugongs. Coprophagy may have contributed to the low marker recovery but cannot explain the long time before the first marker beads were recovered.

(2) *Loss of faeces and markers to the filtration system.* The mesh size of the strainer on the outlet pipe was possibly too large to retain the plastic marker beads. The Oceanarium curators would not permit us to erect a fine mesh screen over the outlet pipe, fearing that faeces would be trapped in the strainer. Although the filter was turned off at night to minimise loss when collection was impossible, it is likely that some faecal loss did occur between daylight faecal collections. It is particularly likely that marker beads on the outside of the faeces would have been lost. If most markers were lost to the filter system, real mean retention time probably lay somewhere between initial appearance of markers and the plateau of the cumulative excretion curve (Fig. 1) but cannot be estimated with accuracy.

It is possible that marker beads were lost through a combination of the above. For future studies of gut passage rate, prevention of coprophagy and loss of markers is necessary. The zero recovery of the buff beads is puzzling but was probably also due to the above factors. Although a cryptic colour, it is likely that we would have distinguished these beads from the faecal material, were they present.

The mechanism of digesta retention in the dugong was not examined. The long retention times in the dugong and the manatee may be at least partly attributable to their extremely long digestive tracts (Lomolino and Ewel 1984). The dugong digestive tract is up to 46 m long in an adult with the large intestine accounting for up to 30 m (65%) (Marsh 1977; Murray *et al.* 1977). This compares with the manatee large intestine that has been measured at between 18 m (Quiring and Harlan 1953) and 20 m (Snipes 1984) or greater (Reynolds 1980). Sirenians have long hindguts in comparison with other large hindgut fermenting herbivores [e.g. elephant 10 m (Clemens and Maloiy 1982) and horse 8 m (Sisson 1953)].

Our measurements suggest a gut passage rate of 0.17 m h⁻¹ in a 2-m juvenile dugong (calculated from Spain and Heinsohn 1975). This rate may be faster in the dugong than in the slightly larger manatee which has a shorter gut. Reynolds (1980) described colonic ridges running perpendicular to the direction of digesta passage within the West Indian manatee, and suggested that these would tend to slow passage through this region of the gut. No such histological feature has been reported for the dugong colon as yet. Kenchington (1972) described muscular gastric ridges in the stomach as possible impediments to the direct passage of ingesta from the oesophagus to the duodenum.

Other possible mechanisms regulating the rate of passage of digesta through the tract may include the low food intake of the captive dugongs, since digesta retention time tends to increase as a consequence of lowered food intake (Van Soest *et al.* 1978; Van Soest 1982). Wild dugongs stranded in pools without seagrass for up to one week after a cyclone were found with their stomachs and intestines still full of seagrass (Marsh *et al.* 1986), suggesting that the passage of digesta is very slow or even ceases when dugongs are not feeding. This fact may cast some doubt on whether our measurements of digesta retention times are representative of those in wild dugongs. However, Best (1981) suggests that wild dugongs probably have a low food intake relative to most hindgut fermenters.

The relatively low fibre level of the dugongs' diet in the Oceanarium (32% NDF) may also have contributed to the long digesta retention time, as has been found in other hindgut fermenters (Van Soest 1982). The long digesta passage times recorded for manatees were also measured on animals feeding on a low-fibre, low-lignin diet (Lomolino and Ewel 1984; Burn 1985). Seagrass species that may form part of the dugongs' diet in the wild range between 32 and 64% NDF (Lanyon 1991). However, as dugongs selectively feed on low-fibre seagrasses when possible (Lanyon 1991; Preen 1993), we consider that, if low-fibre were the cause of the long retention times, these times are likely to be realistic. After slow passage through the long digestive tract, such low-fibre seagrasses are almost completely digested and are relatively more digested than high-fibre seagrasses (Lanyon 1991).

Measurements of the apparent digestibility of dry matter in sirenians are high: 83% in *D. dugon* (Murray *et al.* 1977), 83–91% in *T. manatus* (Lomolino 1977; Lomolino and Ewel 1984) and 44–68% in *T. inunguis* (Best 1981). Fibre digestibilities in both manatees and dugongs have also been reported as extremely high compared with other large hindgut fermenting herbivores, falling within the range of ruminants (Murray *et al.* 1977; Burn 1986) that are very efficient fibre digesters (Udén and Van Soest 1982) (Table 3).

Lomolino and Ewel (1984) and Burn (1985, 1986) have suggested that the high fibre digestibility in the manatee may be at least partially accounted for by the long retention time in the hindgut, since fibre digestibility increases with fermentation time (McLeod and Minson 1969). If the fibre digestibilities in Murray *et al.* (1977) are accurate, they too may result from slow passage through the very long hindgut of the dugong and the low-fibre, low-lignin nature of the ingested seagrasses (Lanyon 1991).

Table 3. Apparent fibre digestibilities in sirenians (dugongs and manatees) compared with other herbivorous mammals
NDF, neutral detergent fibre

	Apparent digestibility (%)		Source
	Cellulose	NDF	
Hindgut fermenters			
Dugong	–	84	Murray <i>et al.</i> (1977)
West Indian manatee	64–89	–	Burn (1986)
Amazonian manatee	45–78	57–80	Best (1981)
Asian elephant	42–46	–	Foose (1982)
African elephant	45–56	–	Foose (1982)
Horse	33–66	–	Fonnesbeck (1969); Hintz <i>et al.</i> (1978)
Rabbit	16	–	Slade and Hintz (1969)
Ringtail possum	–	27–45	Chilcott and Hume (1984); Foley and Hume (1987)
Greater glider	–	34	Foley (1987)
Koala	31	25	Cork <i>et al.</i> (1983)
Foregut fermenters			
Cattle	–	69–83	Colburn <i>et al.</i> (1968)
Sheep	–	50–67	Keys <i>et al.</i> (1969)
Hippopotamus	55–71	–	Van Soest (1982)

Conclusions

The dugong, like the manatee, appears to have a digestive strategy that is atypical for hindgut fermenters. It retains low-fibre material for very extended periods within its long tubular hindgut, almost completely digesting the fibrous component (at least when feeding on some seagrass species). Like the manatee (Burn 1986), fibre digestibilities in the dugong are greater than those for other hindgut fermenters. The dugong also has a low food intake in contrast to other hindgut fermenters including the manatee (Best 1981). This digestive strategy is related not only to the functional morphology of the dugong's gut, but also to the nature of its seagrass diet.

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