

THE ROLE OF THE MIDGUT CAECUM AND LARGE INTESTINE IN THE DIGESTION OF SEA GRASSES BY THE DUGONG (MAMMALIA: SIRENIA)

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Abstract—1. Digesta samples were obtained within 30 min of death from 16 sites along the alimentary canal of an adult female dugong, *Dugong dugon*, captured off Townsville, Australia.

2. The ingesta consisted of the sea grasses, *Halophila ovalis* (98.8%) and *Halodule uninervis* (1.2%).

3. The apparent digestibilities, using lignin as an indigestible marker were 70%, 63%, 84% and 82% for nitrogen, phosphorus, neutral detergent fibre and acid detergent fibre respectively.

4. Total volatile fatty acid concentrations in the stomach and small intestine were low (16 and 18 mM/l respectively). The mean concentrations within the caecum and large intestine were high (183 and 236 mM/l respectively).

5. Although the volatile fatty acid concentrations in the caecum and large intestine were considered unnaturally high, it is obvious that the contribution of the hindgut to the digestion of the dugong is considerable.

INTRODUCTION

The dugong, *Dugong dugon* (Müller), is the only existing herbivorous mammal which is exclusively marine. Although the dugong is presently considered rare over most of its range (Bertram & Bertram, 1973), considerable populations still exist in the shallow seas around tropical Australia (Heinsohn, 1972; Heinsohn *et al.*, 1976). The dugong feeds on tropical and subtropical seagrasses and algae (Heinsohn & Birch, 1972; Spain & Heinsohn, 1973) and as such it fills a unique and most significant ecological niche.

Previous studies on digestion in the dugong have been restricted to the anatomy and histology of the digestive tract (Home, 1820; Owen, 1838; Osman-Hill, 1945; Meinertz, 1956) and have almost invariably been based on inadequate material. Recent anatomical and histological work at this university (Kenchington, 1972; Spain & Heinsohn, 1975; Marsh *et al.*, in press and in preparation) suggests that the dugong has a postgastric fermentative digestive system similar to many terrestrial herbivores, such as the horse and the elephant.

The present study was undertaken to determine the major sites of digestion of the main food fractions of sea grasses by the dugong.

MATERIALS AND METHODS

The animal

A dugong was netted specifically to obtain fresh samples of blood, tissues and digesta (Heinsohn *et al.*, 1976). The animal thus obtained, an adult female (body length 2.68 m) drowned while being removed from the net.

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Sampling

Samples of blood were collected from severed jugular and carotid vessels into heparinized centrifuge tubes, capped and stored in ice for 24 hr and then at 4°C until analysed for plasma inorganic phosphorus (P) and urea.

Digesta samples were obtained as quickly as possible from 16 labelled sites along the alimentary tract. The exact position of each site was determined later. The digesta samples were collected into 25 ml bottles, several (6–7) drops of concentrated H₂SO₄ were added to prevent any further digestive or fermentative action, and then stored in ice for 24 hr, thereafter at 4°C; until analysed for volatile fatty acid (VFA) concentrations. Up to 500 g samples were obtained from 7 of the sites for proximate analysis.

A sample of ingesta was taken from the oesophageal end of the stomach and preserved in 10% seawater formalin for subsequent microscopic examination to determine the foods eaten using the technique of Wake (1975).

All specimens were obtained within 30 min of death.

Chemical analyses

Blood. Plasma was obtained by centrifugation. Proteins were precipitated using 10% trichloroacetic acid and centrifugation. The supernatant was analysed for inorganic P by the method of Fiske & Subbarow (1925). Plasma urea was determined on an aliquot of the protein-free supernatant by the oxime method (Varley, 1967).

Digesta. Dry matter (DM) was determined on the proximate samples by drying in a forced draft oven at 80°C for 24 hr. Organic matter (OM) was determined by ashing at 550°C for 3 hr. The nitrogen (N) content of the DM was determined by steam distillation and titration following Kjeldahl digestion (A.O.A.C., 1960), while the same digest was used for P determination (Fiske & Subbarow 1925). Neutral detergent fibre (NDF), acid detergent fibre (ADF) and lignin content of the DM was analysed using the method of Van Soest (1963). Digesta fluid was obtained by centrifugation and analysed for total VFA concentration by steam distillation and titration (Annison, 1954) and for individual VFA by gas chromatography (Erwin *et al.*, 1961).

Calculation of digestibility

Digestibility was calculated with the marker ratio technique (Crampton & Harris, 1969) using lignin as the internal marker. Several assumptions have been made in the estimation of digestibility: that the digesta sample from the oesophageal region of the stomach was representative of the ingesta; that the digesta sample from the posterior rectum was representative of faeces; and that the plant lignin was indigestible.

RESULTS

Blood

Inorganic phosphorus was 7.8 mg P/100 ml plasma, while plasma urea nitrogen levels were 5.5 mg urea/100 ml.

Composition of food

Two species of sea grasses and one species of diatom were identified by Wake (1975) in the food sample taken from the oesophageal end of the stomach.

Most (98.8%) of the sea grass was *Halophila ovalis* (R.Br.) Hook. f. The remainder was *Halodule uninervis* (Forsk.) Aschers. The sea grasses in this food sample were similar in species and proportion to those found on the sea grass beds in the area where the dugong was caught (Wake, 1975).

Large numbers of the diatom *Cocconeis* spp. were observed, often as a heavy crust on the surface of the sea grass. This may contribute to the relatively high ash level (14%) found in the ingesta.

Volatile fatty acids

The digesta was quite gelatinous and spongy throughout the digestive tract and some difficulty was experienced in obtaining fluid from most samples. Total VFA concentrations (Table 1) in the stomach and small intestines were low (16 and 18 mM/l respectively); however, the mean concentrations within the caecum and large intestines were very high (193 and 236 mM/l respectively). The proportions of individual acids present are shown in Table 1. Acetic acid was predominant in the areas of low concentrations of total VFA (stomach and small intestines) and there was considerable increase in butyric acid and some increase in propionic acid in the caecum and large intestine.

Digestibility

Ingesta from the oesophageal region of the stomach contained 3.1 g N, 0.61 g P, 36 g NDF, 29 g ADF and

3.0 g lignin/100 g DM (Table 2). The OM content was 84% of DM. Rectal samples of digesta contained 17.9 g lignin/100 g DM and the apparent digestibilities of the N, P, NDF, and ADF were 70%, 63%, 84% and 82% respectively.

Table 2 shows the relative disappearance or increase of each food constituent throughout the gut.

DISCUSSION

The stomach contents containing the sea grasses, *Halophila ovalis* and *Halodule uninervis* on which this dugong was grazing are of high nutritive value containing 19% crude protein and 36% NDF. The alimentary tract of the dugong is well adapted to digest this material, and apparent digestibilities of all principal areas of the diet were high. The disappearance of the fibre fraction of the diet were found to be the midgut caecum and large intestine. The high concentrations of VFA that occurred in this area of the gut would support this argument.

It is also significant to note that in an adult dugong the large intestine is about 30 m long and the weight of the midgut caecum and large intestine plus contents is about 10% of total body weight. The weight of the dugong stomach plus contents is about 5% of total body weight (Marsh, unpublished data). In contrast, the contents alone of the rumen-reticulum of most ruminants constitute 10–15% of body weight (Hungate *et al.*, 1959).

Thus, the dugong belongs to that group of non-ruminant herbivores which have a greatly enlarged hindgut with a rich microflora. It is almost certain that the other modern Sirenians, the manatees, which have a digestive system very similar to that of the dugong (Harrison & King, 1965) and which are also herbivorous, also belong to this group as do the other members of the Superorder Paenungulata, the elephants and the hyraxes (Bernard, 1973).

Blood levels of urea and inorganic P are within the normal ranges for these parameters in non-ruminant terrestrial herbivores.

The spongy consistency of the digesta was surprising and may have been due to the presence of gelatinous compounds within the marine grasses. That this remained a feature of the digesta throughout the digestive tract was even more surprising. Despite the high dry matter content of the digesta, difficulty was experienced in obtaining fluid from the samples. A further complication of the nature of the digesta would have been poor

Table 1. Mean concentration of total volatile fatty acid (VFA) in mM/l and the errors of the mean (S.E.) plus the proportions of individual acids (%). The number of observations is shown in brackets after the mean concentration of total VFA

Site	Mean total VFA	S.E.	Proportions			Standard deviation or VFA
			Acetate	Propionate	Branched chain Butyrate	
Stomach	16 (4)	2	82	6	12	—
Small intestine	18 (3)	2	84	6	10	—
Caecum	183 (2)	10	57	17	25	1
Large intestine	236 (7)	14	50	17	32	1

Table 2. Dry matter (DM) content (%) and the composition (g/100 g DM) of the dry matter of digesta samples from various sites along the alimentary tract, plus the proportion of each constituent apparently digested before each site (%)

	Composition of dry matter							Proportion of constituent apparently digested (%)			
	DM	OM	N	P	NDF	ADF	Lignin	N	P	NDF	ADF
Stomach (near oesophageal entrance)	13	84	3.1	0.61	36	29	3.0	—	—	—	—
Anterior small intestine	8	81	1.8	0.37	30	30	2.0	7	0	-27	-54
Posterior small intestine	10	83	3.0	0.59	33	32	3.0	1	1	10	-9
Midgut caecum	15	88	2.0	0.32	40	33	3.2	46	56	-5	-5
Anterior large intestine	16	76	4.5	1.00	36	32	10.2	49	42	72	68
Mid large intestine	20	71	4.4	1.40	31	30	15.9	63	39	84	81
Posterior large intestine	27	77	4.8	1.16	34	32	17.9	70	63	84	82

mixing of the sulphuric acid throughout each sample, thus delaying inhibition of fermentation, or failing to prevent microbial action. The VFA values recorded from the caecum and large intestines are much higher than would be expected from the hind-gut of horses (Hintz *et al.*, 1971), pigs (Farrell & Johnston, 1970), sheep (Faichney, 1969) or kangaroos (Kempton *et al.*, 1976), or from the rumen of sheep (Leng, 1970), cattle (Rumsey *et al.*, 1971) or the stomach of kangaroos (Kempton *et al.*, 1976).

Although further work with more sophisticated techniques is needed to extend our knowledge of digestion by the dugong, it is obvious that the contribution of the hind-gut to the nutrition of the dugong is considerable.

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