Analysis of Stomach Contents of Dugongs from Queensland

Helene Marsh, Peter W. Channells, George E. Heinsohn and Janice Morrissey
Zoology Department, James Cook University of North Queensland, Townsville, Qld 4811.

Abstract
Quantitative analysis of samples of the stomach contents of 95 north Queensland dugongs (63 from the Townsville area, 30 from the Mornington Island area and two from the Torres Strait area) and one dugong from south Queensland indicates that the diet of most consisted almost entirely of seagrasses of all available genera. Halodule was found in 95% of stomachs, followed by Halophila (89%), Cymodocea (61%) and Thalassia (39%). Seagrass rhizomes were present in all stomachs examined including that of a neonatal calf. The generic composition of the stomach contents probably reflects that of the seagrass beds in the areas where the dugongs were captured and is not necessarily indicative of discrimination in selecting food. Non-epiphytic algae occurred in 51% of the stomachs, usually in small amounts. When seagrasses are abundant, dugongs appear to eat algae often but only in very small amounts (<2% of food volume). Dugongs do not appear to be well adapted to utilize algae as food and probably usually consume them incidentally with seagrasses. Many of the dugongs which drowned in the shark nets near Townsville in the year after a cyclone had severely damaged the seagrass beds in the area had eaten more of the seagrasses Cymodocea and Thalassia, less of the seagrasses Halodule and Halophila, and more algae than animals which died in other years.

Introduction
The dugong, Dugong dugon (Müller), the only truly marine mammalian herbivore, feeds predominantly on seagrasses (Prater 1928; Gohar 1957; Jones 1959, 1976; Jarman 1966; Kingdon 1971; Heinsohn and Birch 1972; Lipkin 1975; Wake 1975; Johnstone and Hudson 1981). Some dugongs also eat algae (Annandale 1905; Hirasaka 1932; Mani 1960; Spain and Heinsohn 1973; Johnstone and Hudson 1981), especially if seagrasses are scarce (Spain and Heinsohn 1973; Heinsohn and Spain 1974). Mangrove, Avicennia marina, has been found in the mouth of one dugong (Johnstone and Hudson 1981). Invertebrates are also sometimes taken (Hirasaka 1932; Asano 1938; Harry 1956; Pfeffer 1963; Spain and Heinsohn 1973; Lipkin 1975; Wake 1975), presumably incidentally with seagrasses.

Although seagrasses are now undisputed as the dugong's major food, there have been few detailed and comprehensive studies. Gohar (1957) qualitatively examined the stomach contents of 15 dugongs caught over a 13-year period in the Red Sea and concluded that they feed exclusively on Halodule uninervis (cited as Diplanthera uninervis). Heinsohn and Birch (1972) qualitatively examined the stomach contents of the first 15 of the Townsville dugongs used in this study and reported that dugongs feed selectively on certain genera of seagrasses. In contrast, Wake (1975)
compared the composition of the seagrasses in the stomachs of three Townsville
dugongs with that of the plants available at the time and place of capture. She
concluded that dugongs did not feed selectively with regard to species of seagrasses
eaten, but fed in accordance with their availability. Her conclusions were supported
by Lipkin (1975), who examined the gut contents of six dugongs from the Gulf of
Elat at the head of the Red Sea. However, Wake (1975) and Anderson and Birtles
(1978) did observe that dugongs fed on small, sparsely distributed Zostera capricorni
in preference to dense old stands of the same species in adjacent areas of Shoalwater
Bay (22°21'S., 150°30'E.). Johnstone and Hudson (1981) determined the plant
species and their relative abundance in 61 food samples recovered from the mouths
of 276 dugongs killed for traditional commerce in the Maza Wildlife Area, Western
Province, Papua New Guinea. They concluded that the seagrass species eaten by
dugongs appeared to be related to the abundance, ecological distribution and
energy value of the species.

We report on the quantitative analysis of the stomach contents of 95 dugongs
from three localities in northern Queensland and of one animal from southern
Queensland.

Materials and Methods

Source and Collection of Material

The following north Queensland dugongs were sampled between May 1968 and August 1978: 65,
most of which were accidentally drowned in nets (usually shark nets set for swimmer protection) near
Townsville (19°15'S., 146°45'E.); 28, speared and drowned for food by Aboriginals in the Mornington
I. area (16°30'S., 139°38'E.); two similarly killed by Torres Strait Islanders at Thursday I. (10°35'S.,
142°14'E.).

Each carcass was sexed, measured, and dissected. The age and reproductive status were determined,
as outlined by Marsh (1980). A sample of digesta, approximately 600 ml in volume, was collected from
the cardiac region of the main sac of the stomach (Marsh et al. 1977), where the food is least digested,
and preserved in 10% seawater formalin.

The stomach contents only, of one dugong drowned in the shark net near Bundaberg (24°52'S.,
152°21'E.), were also sampled and preserved as above.

Analysis of Stomach Contents

As dugong stomach contents are extensively macerated, the leaves and stems of seagrasses were
identified to genus mainly on the basis of the size and shape of the epidermal cells, by means of a
reference collection of north Queensland species. We could not readily identify to species by this
method. Generic identification of rhizomes and algae was also not practicable, but they were recorded
as separate categories.

The identification of and distinction between three genera, Cymodocea, Thalassia and
Thalassodendron, presented a major problem. We could not distinguish Cymodocea rotundata from
Thalassia hemprichii, or Cymodocea serrulata from Thalassodendron ciliatum on the cell features used.
However, T. ciliatum and C. rotundata occur rarely in the localities where the dugongs were collected,
in contrast to T. hemprichii and C. serrulata, which are both found very abundantly. In view of these
ecological differences we decided to refer all specimens of this group to either Thalassia or Cymodocea.

Quantitative Technique

The relative volumes of the leaves plus stems of each genus of seagrass, the total rhizomes, and the
total algae present in each stomach were estimated by means of a Weibel graticule (Schaefer 1970) and
the principles of stereology, as follows. Eight slides were prepared from each stomach by spreading a
separate sample of well mixed digesta evenly over each slide with a spatula. The slides were then scanned
qualitatively to determine which seagrasses were present. Ten sites on each slide were then examined
quantitatively with the Weibel graticule in a compound microscope at ×40. The first sample site was
selected by placing the slide on the microscope stage and moving it to a pre-determined coordinate. Subsequent sites were selected at pre-defined points along two parallel transects. A higher power (×100) was used when necessary to aid identification. The degree of fragmentation and ease of identification of the contents of each stomach were also recorded. The technique is described in detail by Channells and Morrissey (1981).

Data Analysis

Statistical analyses of the data were performed with BMDP (Brown 1977). Each dugong was classified using the percentage volume of each seagrass genus, rhizome, algae, and unidentified material in its stomach. Classification was carried out on untransformed data with the Clustan IC package (Wishart 1978). The sorting strategy used was Ward’s method (error sum of squares) (option 6 in procedure HIERARCHY). The similarity measure used was the squared Euclidean distance (option 1 in procedure CORREL).

The means and standard deviations of these attributes and details of other data not used in generating the classification, such as places and dates of death, sexes, ages of the dugongs, were printed by the diagnostic procedure RESULT. Study of the dendrogram (Fig. 4) and of the diagnostic procedure, together, provided the means of defining the groupings of dugongs on the basis of the composition of their stomach contents and the attributes which characterized each group.

Fig. 1. Frequency histogram showing the number of dugongs sampled in each calendar month at each location. All animals collected in north Queensland from 1969 to 1978 are included. Open bars, Townsville; hatched, Mornington I.; solid bars, Thursday I.

Results

The 65 Townsville dugongs whose stomach contents were studied included healthy juveniles and adults of both sexes. Few juvenile dugongs and no pregnant females were obtained from Mornington I., probably due to a hunting bias (Marsh et al. 1981).

The monthly distribution of the dates of death of the dugongs sampled is shown in Fig. 1. Specimens from Townsville were obtained in all months of the year; the small number of animals caught in June–July is a result of the removal of the shark nets at that time (Heinsohn 1972; Heinsohn and Spain 1974). The peak period of dugong hunting activity at Mornington I. is in July–August, the major period when an observer was on hand to collect specimens (Marsh et al. 1981).
The stomach contents of most dugongs consisted almost entirely of seagrasses. Seven genera of seagrasses are known to be available in the shallow waters off Townsville (Heinsohn and Birch 1972). Six of these were identified in the stomachs of Townsville dugongs, the exception being *Syringodium*. This genus has, however, been found in stomach contents of two dugongs killed at Mornington I. in November 1976.

From two to four genera of seagrasses were found in the stomachs of most dugongs (Fig. 2). Five dugongs, three from Townsville and two from Mornington I., had eaten seagrasses from five genera. Three Townsville dugongs had stomachs containing only one genus (*Halophila*, *Halodule*, or *Cymodocea*), and one from Bundaberg in southern Queensland contained *Halophila* exclusively.

Table 1. Generic composition of the leaves and stems in the stomach contents of 95 dugongs from north Queensland

<table>
<thead>
<tr>
<th>Genus</th>
<th>Percentage of samples in which present</th>
<th>Percentage by volume of non-rhizomatous material</th>
<th>Mean</th>
<th>Range</th>
<th>Modal class interval</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Halodule</em></td>
<td>95</td>
<td>44.0</td>
<td>0.1-99.5</td>
<td>10-15</td>
<td></td>
</tr>
<tr>
<td><em>Halophila</em></td>
<td>89</td>
<td>29.0</td>
<td>0.1-89.5</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td><em>Cymodocea</em></td>
<td>61</td>
<td>23.2</td>
<td>0.3-95.5</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td><em>Thalassia</em></td>
<td>39</td>
<td>13.5</td>
<td>0.1-69.2</td>
<td>5-10</td>
<td></td>
</tr>
<tr>
<td><em>Enhalus</em></td>
<td>8</td>
<td>14.8</td>
<td>0.4-92.0</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td><em>Zostera</em></td>
<td>3</td>
<td>39.1</td>
<td>6.6-69.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Syringodium</em></td>
<td>2</td>
<td>-</td>
<td>3.3-38.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unidentified</td>
<td>67</td>
<td>3.2</td>
<td>0.1-18.1</td>
<td>0-5</td>
<td></td>
</tr>
</tbody>
</table>

*Halodule* was present in 95% of stomachs, followed by *Halophila* (89%), *Cymodocea* (61%), and *Thalassia* (39%). All these genera occurred in widely ranging proportions (Table 1). *Enhalus* was eaten by only seven dugongs and constituted a high proportion (92% of the volume) of the leaf plus stem material in the stomach contents of only one animal, an old male from Thursday I. Only two dugongs had eaten *Zostera* in substantial amounts (41.2 and 69.4% of the volume of stomach contents).
contents). Both were obtained from Townsville shark nets in October 1972, 10 months after Cyclone Althea had severely damaged the littoral and sublittoral communities in the area (Heinsohn and Spain 1974). *Syringodium* made up a substantial proportion (38.5%) of the volume of the stomach contents of only one dugong. The generic composition of the leaves and stems of the seagrasses in the stomach contents is summarized in Table 1.

The percentage volume of unidentified leaf plus stem material was generally small. Rhizomatous material was present in the stomachs of all dugongs examined, including a neonatal calf, in proportions ranging from 6.5 to 86% of contents. A high proportion of the volume of the stomach contents of animals feeding on *Halophila* and *Halodule* usually consisted of rhizomes. In these genera, the biomass of the rhizomes plus roots is greater than that of the leaves plus stems (Wake 1975). In contrast, dugongs do not appear to eat the rhizomes of *Enhalus acoroides*, which is a large and fibrous species.

![Fig. 3. Bar diagram showing the number of stomachs in which each genus of seagrass was recorded as more than isolated fragments, and the predominant size of the fragments of each genus in each stomach. *Syringodium*, which was found in only two stomachs, is not included.](image)

Non-epiphytic algae were found in 51% of the stomachs, usually in small amounts. However, algae made up more than 2% (by volume) of the stomach contents of 19 of the 23 dugongs drowned in shark nets near Townsville during 1972, the year after Cyclone Althea. The three animals which had eaten algae (mainly *Sargassum* sp.; Spain and Heinsohn 1973) in the largest amounts (73–89%), were all drowned in August–September 1972. When seagrasses are abundant, dugongs appear to eat algae often but only in very small amounts (<2% of food volume). Under such circumstances algae are probably eaten incidentally.

Most dugongs chewed their seagrass food into small (0–50 mm long) fragments (Fig. 3). The majority of seagrass pieces in the stomachs of four animals were unusually large (>75 mm). One of these animals was a neonate in which premolars 2 and 3 (Marsh 1980) were the only cheek teeth in wear; another was an adult with exceptionally small cheek teeth, in which the crown and central cross-sectional areas of molars 2 and 3 were substantially less than those of other dugongs of approximately the same age (Marsh 1980) that we have examined. The algal fragments observed in dugong stomachs were often large and appeared not to have been chewed adequately.
Cluster Analysis

The dendrogram (Fig. 4) resulting from the cluster analysis of the contents of all stomachs from north Queensland dugongs suggests six principal groupings (numbered 1-6). Similar analysis of data from Townsville dugongs alone yielded identical groupings, except for one animal which was relocated from group 1 to group 2. Of the 10 variables used in generating Fig. 4, six were sufficiently common to be of value in the characterization of the groups. They are summarized for each group in Table 2. Animals in groups 1-3 had been eating large quantities of Halophila and Halodule, including large amounts of rhizomes. Cymodocea was the major constituent of the stomach contents of dugongs in group 4. Group 5 was a rather heterogenous grouping with no dominant genus. Group 6 consists of the three dugongs which had consumed large amounts of algae.

![Fig. 4. The classification of the 95 north Queensland dugongs on the basis of the (untransformed) type and proportion of their stomach contents by Ward's method (error sum of squares; option 6 in procedure HIERARCHY in the Clustan IC package) (Wishart 1978). The scale on the left indicates the similarity measure (the squared Euclidean distance: option 1 in procedure CORREL) at each fusion. The main characteristic which caused each major group of dugongs to cluster together is indicated. C, Cymodocea, A, algae.]

Dugongs which were caught close together in space and time were often grouped close together in the dendrogram, as summarized in Table 3. Seventeen of the 21 dugongs in groups 4-6 died in the Townsville shark nets during 1972, the year after Cyclone Althea. The other eight animals that died in the first five months after the cyclone had a high proportion of rhizomes in their stomach contents and were in group 2, and the remaining three 1972 animals, which had consumed mostly Halophila (group 3), all died in the latter part of the year (August-November) (Table 3). In years other than 1972, stomach contents were obtained from at most
seven dugongs from Townsville. As the sample from Mornington I. is seasonally restricted (Fig. 1), we can make no comment on the effect of seasonality on forage choice by dugongs.

Table 2. Occurrence and percentage composition by volume of food items in stomachs of dugongs arranged in groups extracted by cluster analysis

For details of groups, see Fig. 4. Values in parentheses are percentages of the number of stomachs in the group. An asterisk indicates the dominant constituent of the stomach contents in a group. Means and ranges of contents refer only to those stomachs in which the item concerned was present

<table>
<thead>
<tr>
<th>Group</th>
<th>Group</th>
<th>Group</th>
<th>Group</th>
<th>Group</th>
<th>Group</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Total No. of dugongs</td>
<td>16</td>
<td>41</td>
<td>17</td>
<td>3</td>
<td>15</td>
</tr>
<tr>
<td>No. from Townsville</td>
<td>9</td>
<td>23</td>
<td>12</td>
<td>3</td>
<td>13</td>
</tr>
<tr>
<td>No. from Mornington I.</td>
<td>6⁸</td>
<td>18</td>
<td>5</td>
<td>0</td>
<td>1⁸</td>
</tr>
</tbody>
</table>

**Rhizomes**

<table>
<thead>
<tr>
<th>No. of stomachs</th>
<th>Mean content</th>
<th>Range of contents</th>
</tr>
</thead>
<tbody>
<tr>
<td>16 (100)⁹</td>
<td>36.8</td>
<td>19-53</td>
</tr>
</tbody>
</table>

**Halodule**

<table>
<thead>
<tr>
<th>No. of stomachs</th>
<th>Mean content</th>
<th>Range of contents</th>
</tr>
</thead>
<tbody>
<tr>
<td>16 (100)*⁹</td>
<td>50.0</td>
<td>29-71</td>
</tr>
</tbody>
</table>

**Halophila**

<table>
<thead>
<tr>
<th>No. of stomachs</th>
<th>Mean content</th>
<th>Range of contents</th>
</tr>
</thead>
<tbody>
<tr>
<td>16 (100)⁹</td>
<td>90</td>
<td>0.1-28</td>
</tr>
</tbody>
</table>

**Cymodocea**

<table>
<thead>
<tr>
<th>No. of stomachs</th>
<th>Mean content</th>
<th>Range of contents</th>
</tr>
</thead>
<tbody>
<tr>
<td>9 (56)</td>
<td>4-9</td>
<td>0-2-27</td>
</tr>
</tbody>
</table>

**Thalassia**

<table>
<thead>
<tr>
<th>No. of stomachs</th>
<th>Mean content</th>
<th>Range of contents</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.3</td>
<td>0.03-13</td>
<td>1-2-9</td>
</tr>
</tbody>
</table>

**No. seagrass genera present**

<table>
<thead>
<tr>
<th>Mode</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>2-4</td>
</tr>
</tbody>
</table>

**Algae**

<table>
<thead>
<tr>
<th>No. of stomachs</th>
<th>Mean content</th>
<th>Range of contents</th>
</tr>
</thead>
<tbody>
<tr>
<td>17 (44)</td>
<td>1.3</td>
<td>0.04-3</td>
</tr>
</tbody>
</table>

⁸ One member of the group was from Torres Strait.

Discussion

This study confirms that seagrasses are the principal food of dugongs but indicates that small amounts of algae are often eaten.

Eight genera of seagrasses occur in north Queensland waters (den Hartog 1970). Thalassodendron, the only genus not recorded in the 95 dugong stomachs we examined from this area, was probably eaten, but not detected for the technical reasons outlined above. Small amounts of T. ciliatum were found by Lipkin (1975) in the
stomach of a dugong thought to have been captured near Dahab in the Gulf of Elat. Although some genera of seagrasses were found in a much higher proportion of dugong stomachs than others (Table 1), all the seagrass genera we recorded were eaten in substantial amounts by at least one dugong.

Den Hartog (1970) records 10 genera of seagrasses within the total range (Bertram and Bertram 1973) of the dugongs. Species of the two genera which do not occur in North Queensland, Amphibolis antarctica (cited as Cymodocea antarctica) and Posidonia australis, are the two most common seagrasses in Shark Bay, W.A. (24°30'–26°40'S., 113°35'E.) (Logan and Cebulski 1970) which has recently been identified as an area of major dugong habitat (Prince et al. 1981). The stomach contents of the dugongs in Shark Bay have not been studied, but animals in the area of Dirk Hartog I. have been most often observed feeding in beds of A. antarctica (Anderson 1982), which probably constitutes their major food at this location. It seems likely, therefore, that dugongs consume whatever species are most readily accessible.

Even local differences in dietary intake indicated by this study (Table 1) and by Gohar (1957), Heinsohn and Birch (1972), Lipkin (1975) and Johnstone and Hudson (1981) may be, at least partly, an unavoidable artefact of the sampling techniques. Despite assertions that dugongs move inshore to feed mainly at night (Jonklaas 1961; Jarman 1966), recent aerial surveys (Heinsohn et al. 1976, 1979; Heinsohn 1981) and shore-based observations (Anderson and Birtles 1978) demonstrate that diurnal, inshore feeding is normal (at least for north Queensland dugongs) and it is likely that feeding is their predominant activity (Anderson and Birtles 1978). Hence, the food present in the cardiac region of the stomach (or

Table 3. Details of the dugongs which died relatively close together in space and time and which were grouped together on the basis of similarity of stomach contents

For details of the groups, see Fig. 4. Locations: Forsyth I. and Mornington I. are both in the Wellesley Group

<table>
<thead>
<tr>
<th>Group No.</th>
<th>No. in group</th>
<th>No. collected close together</th>
<th>Location</th>
<th>Collection details</th>
<th>Time span</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>16</td>
<td>2^A</td>
<td>Magnetic I., nr Townsville</td>
<td>26.xi.1970</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>41</td>
<td>3</td>
<td>Townsville mainland</td>
<td>18-27.vii.1977</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>17</td>
<td>3</td>
<td>Government Bay, Forsyth I.</td>
<td>1-2.vii.1976</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>2</td>
<td>Magnetic I., nr Townsville</td>
<td>19.i-11.v.1972</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>15</td>
<td>12</td>
<td>Townsville</td>
<td>3-27.viii.1977</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>3</td>
<td>3</td>
<td>Wellesley Is</td>
<td>30.vi-6.vii.1976</td>
<td></td>
</tr>
</tbody>
</table>

^ACow and accompanying neonatal calf.
mouth) of a dugong carcass is likely to have been consumed soon before the animal died and to reflect the composition of the seagrass beds close to the time and place of its capture. This was shown in detail for three dugongs by Wake (1975). Lipkin (1975) also concluded that the stomach contents of the six dugongs he examined from Sinai agreed with the seagrasses available in the area of capture, although there were indications that one animal had last grazed outside the bay in which it was taken.

Detailed collection data were not consulted during our analysis of the stomach contents of the north Queensland dugongs. The fact that dugongs caught close together in space and time were often classified together on the basis of their stomach contents (Table 3) not only confirms the reliability of our analytical technique but also supports our assertions that the analysis of stomach contents from opportunistically collected dugong carcasses reflects the food available when and where they happened to be caught. It is not, therefore, necessarily a reliable indication of their discrimination in selecting food.

The Townsville shark nets (Heinsohn 1972; Heinsohn and Spain 1974) are set about 12 km or more from the south-east corner of Cleveland Bay, the most important dugong habitat area in the vicinity (Marsh and Heinsohn 1981), and the dugongs sampled from Mornington I. were all caught in one of the frequently used hunting areas which constitute only a small proportion of the dugong habitat in the Wellesley Is (Marsh et al. 1981). Thus the samples we have analysed are not necessarily representative of the seagrasses eaten by even the Townsville and Mornington I. populations of dugongs.

Study of the species composition of the seagrass beds where large aggregations of dugongs have been observed may be a more reliable indicator of their dietary preferences. Such data indicate that dugongs select habitats within the available plant communities (the basis for habitat selection is not known) but also support the thesis that they eat a wide range of seagrasses. Thus the Shark Bay aggregations tend to be associated with seagrass communities dominated by *A. antarctica* (Anderson 1982); those in Shoalwater Bay (Wake 1975; Anderson and Birtles 1978) and Missionary Bay (18°15'S., 146°00'E.) (Wake 1975) with communities dominated by *Z. capricorni*. *Halophila ovalis* is the most common seagrass in the favoured, sheltered, south-east corner of Cleveland Bay, near Townsville (Wake 1975), but the large herds of dugongs in Moreton Bay near Brisbane (Heinsohn et al. 1978; M. M. Bryden and R. J. Lear, unpublished data) are frequently seen on the sandbanks of the north-western end of North Stradbroke I., which are covered with *Z. capricorni*, *H. ovalis* and *H. uninervis* (Young and Kirkman 1975).

Data collected in this study support and extend the observations of Spain and Heinsohn (1973) of changes in the diet of Townsville dugongs following Cyclone Althea, which occurred in December 1971. Seventeen of the 21 animals classified in groups 4, 5 and 6 (Fig. 4) died in the Townsville shark nets during 1972. Animals in these groups had less *Halophila* and *Halodule* and more *Cymodocea*, and/or *Thalassia* and/or algae in their stomachs than the remaining 74 north Queensland dugongs, in groups 1–3 (Table 2). Despite the limitations of the analysis of stomach contents discussed above, these cyclone-associated feeding changes are probably real. All but two (which were permanently removed) of the shark nets were replaced in the same places after the cyclone (Heinsohn and Spain 1974), so that the sampling technique remained essentially the same.
The remaining eight animals that died in the first five months after the cyclone were in group 2 (Fig. 4; Table 3), which indicates that they had eaten a high proportion of rhizomes. This suggests, not unexpectedly, that seagrass rhizomes may survive cyclones better than the leaves and stems. Three dugongs which died towards the end of 1972 had eaten mostly *Halophila* (Table 3). *H. ovalis* is considered to be eurybiontic and a good pioneer species (den Hartog 1970) and would be expected to have recovered more rapidly from the cyclone than species such as *C. serrulata*, *C. rotundata*, and *T. hemprichii*. Seagrasses propagate mainly by vegetative means [W. R. Birch, quoted by Heinsohn and Spain (1974)] and take a long time to regenerate if destroyed (Moore 1963). Presumably, after the dugongs had overgrazed what was left of their usual feeding grounds following the cyclone (see Table 3 for the group 2 animals that died between 19 January and 11 May 1972), they were forced to seek seagrass communities which had not been damaged and to supplement their diet with algae. They would have moved around more than usual in search of food, which would explain the exceptionally high dugong mortality in the shark nets during this period (Heinsohn and Spain 1974).

Although 51% of all the north Queensland dugongs we examined had eaten some algae, this was usually in small amounts (<2% by volume) and was probably eaten incidentally with seagrasses. In contrast, algae comprised 73–89% of the volume of the stomach contents of three dugongs which died in August–September 1972, 9 months after the cyclone.

Anderson (personal communication) reports that at least one dugong was seen to eat algae by another diver and himself in an area of Shark Bay where there were no seagrasses in the immediate vicinity. During their analysis of the mouth contents of 61 dugongs, Johnstone and Hudson (1981) also found two samples consisting entirely of algae.

Although they may resort to eating large amounts of algae, dugongs do not appear to be well adapted to utilize them as a food source. We agree with Annandale (1905) and Lipkin (1975), who reported that the algal fragments they observed in dugong stomachs were generally larger than those of the seagrasses and appeared not to have been adequately chewed. Lipkin (1975) observed that the algae consumed by the dugongs he examined were not digested at all, even in the large intestine. Hartman (1979) reported that algae do not figure significantly in the diet of manatees, *Trichechus*, unless vascular vegetation is unavailable. In contrast, the recently extinct sirenian, Steller's sea cow *Hydrodamalis*, utilized algae as its major food source (Domning 1976).

The dugong chews its seagrass food into small pieces (Fig. 3) using its cheek teeth, possibly assisted by the horny pads which oppose each other anterior to the teeth in each jaw. A total of six cheek teeth erupt in each quadrant during a lifetime and, although no new teeth erupt after an animal is 7–9 years old, tooth loss and wear are encountered principally by the continued axial growth of molars 2 and 3 and the radial growth of molar 3 (Marsh 1980). Although the neonatal dugong we examined had consumed seagrasses as well as milk, its complement of two small premolars in wear in each quadrant made it less efficient than older dugongs at chewing seagrasses.

Like the Red Sea dugongs studied by Lipkin (1975) and the southern Papua New Guinea animals examined by Johnstone and Hudson (1981), all the Queensland dugongs examined had eaten some rhizomes. The amount of rhizome eaten varied
with the type of seagrass, being greatest with *Halodule* and *Halophila*. The rhizomes of *Enhalus acoroides*, a large fibrous species, were not eaten. Anderson (1982) has observed that dugongs also do not eat the robust (den Hartog 1970) rhizomes and tough stalks of *Amphibolis antarctica* in Shark Bay, WA.

Dugong tusks wear quickly on the outer surface after eruption (Marsh 1980). This wear presumably occurs when the animal uses its snout to grub seagrasses from the bottom. This action forms a feeding trail, as described by Anderson and Birtles (1978). However, erupted tusks cannot be essential equipment for digging up rhizomes, as tusks are unerupted in almost all females and in young males, both of which were well represented in group 2 (Fig. 4). D. Magor (personal communication) reports that Caribbean manatees *Trichechus manatus* (which have no tusks), feeding in a seagrass meadow in Puerto Rico, removed up to 100% of the seagrass biomass down to at least 20 cm from the surface. Ease of removal of rhizomes, however, is undoubtedly strongly dependent on bottom type.

Conflicting statements have been made about the nutritive value of seagrasses, and further studies are required before they can be compared with terrestrial plants as food for herbivores (Birch 1975; Wake 1975; Murray et al. 1977; Johnstone and Hudson 1981). However, experience with captive animals indicates that a dugong is able to consume 30-40 kg of seagrasses per day (Tas'an et al. 1981). Animals feeding in areas where small species, such as *H. ovalis* and *H. uninervis*, predominate may need to dig up rhizomes to obtain enough food, in contrast to those feeding on larger species such as *A. antarctica* and *E. acoroides*. It seems unlikely that seagrass rhizomes contain nutrients not provided by the leaves and stems; they are, however, a rich source of starch (Birch 1975) and for most species have a higher calorific value than the leaves (Birch 1975; Johnstone and Hudson 1981).

The rhizomes of *E. acoroides* and *A. antarctica* and the tough stalks of *A. antarctica* may be avoided because they are extremely fibrous and therefore relatively low in nutrients. Dugongs have been shown to avoid dense, old stands of *Z. capricorni* in preference to smaller, sparser stands of the same species (Wake 1975; Anderson and Birtles 1978). The latter are probably easier to digest as they have a higher soluble organic content (Wake 1975).

**Acknowledgments**

Dugong research at James Cook University is financed by the Australian National Parks and Wildlife Service and the Australian Research Grants Commission. We acknowledge the assistance of the many people, particularly Dr A. V. Spain and Mr B. R. Gardner, who have helped in collecting dugong specimen material since 1969. We also thank Dr T. J. Done for his assistance with the cluster analysis, Ms J. Hart for her help with seagrass identification, and Professors J. M. Taylor, P. K. Anderson and D. Domning for critically reading the manuscript, which was completed while the senior author was a visiting investigator at the University of British Columbia.

**References**


Manuscript received 16 February 1981; accepted 8 May 1981