Breeding Cycle, Life History and Population Dynamics of the Dugong, *Dugong dugon* (Sirenia: Dugongidae)

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Abstract

Study of the gonads of 108 dugongs from north Queensland indicates that neither females nor males are continuously in breeding condition. The gonadal activity of males in a population is not synchronized. Ovaries tend to be active in the latter half of the year. There is no evidence for females coming into oestrus soon after giving birth but conception can occur during lactation. In the Townsville–Cairns area, dugongs calve from August–September through December. Neonates are between 1.0 and 1.3 m long and weigh 20–35 kg. Dugongs of both sexes less than 2.2 m long are likely to be immature, those over 2.5 m long are probably mature, and the status of animals between 2.2 and 2.5 m long is uncertain. The pre-reproductive period seems to be very variable but is a minimum of 9–10 years for both sexes. The gestation period is about 1 year and lactation can last at least 1.5 years. The usual litter size is one. The secondary and tertiary sex ratios are 1:1. Estimates of the calving interval based on pregnancy rates, the rate of accumulation of placental scars, and calf counts from aerial surveys and photographs, range from 3 to 7 years for various populations. A simple population model has been used to calculate the relationship between calving interval and adult mortality rate for stationary populations with different pre-reproductive periods and juvenile mortality rates. Even the most optimistic schedule of reproduction and juvenile mortality demands an adult survivorship of about 90% per year for population maintenance.

Introduction

As reviewed by Marsh et al. (1978), information on reproduction in the dugong *Dugong dugon* (Müller) has, to date, been largely anecdotal or the result of incidental observations. However, the results of the gross and histological examination of the reproductive organs of 59 male and 49 female dugongs from north Queensland have been documented in companion papers (Marsh et al. 1984a, 1984b). The ages of almost all these animals were estimated from counts of dentinal growth layers in tusks (Marsh 1980).

These investigations, supplemented by data both from other people and from other sources such as aerial surveys, have produced new data on the breeding cycle and life history of the dugong, as detailed in this paper. The resultant estimates of parameters such as longevity, pre-reproductive period, calving interval and mean litter size must be regarded as preliminary, but they present fewer problems than the development of a realistic mortality schedule for dugongs.

An age frequency distribution can provide life-table information and hence survivorship curves, but only when it is drawn from a population with a stable age distribution, and a known rate of increase (Caughley 1977). Given that the age frequency data for the Townsville dugongs (Marsh 1980) was obtained over a 9-year period shortly after a massive increase in mortality caused by the introduction of shark nets in 1964 (Heinsohn 1972), it is unrealistic to assume that this population was stable, and we have no knowledge of its rate of change. Further, the age frequency data for males are unsuitable for such analysis because the
tusks of mature males erupt and wear, with consequent loss of an unknown number of growth layers. Thus only minimum age estimates are available for mature males (Marsh 1980). The number of females from the Mornington Island population for which age estimates are available (27) is too small for life-table analysis (see Caughley 1977), and the rate and direction of demographic change in this population are not known.

Despite the above, if certain simplifying assumptions are made it is possible to calculate for various combinations of reproductive parameters the mortality schedules which will be necessary to maintain a population of dugongs at a zero rate of increase. A simple population model has been developed along these lines. The implications of this model for the conservation and management of the dugong, which is currently considered to be vulnerable to extinction (Thornback and Jenkins 1982), are also discussed.

Materials and Methods

Carcass Analysis

The animals studied and the methods used in the carcass analysis are detailed by Marsh et al. (1984a, 1984b). In addition, thin longitudinal ground sections were prepared from unworn cheek teeth (premolars 3 or 4, both of which are present at birth: Marsh 1980) from seven dugongs of body length 1.4 m or less, by Dr T. Kasuya, Ocean Research Institute, University of Tokyo. Dr Kasuya counted fine layers present in these sections using polarized light and without knowledge of the dates of death or body lengths of the dugongs. These fine layers are considered to be laid down at approximately monthly intervals (Kasuya and Nishiwaki 1978; Kasuya, personal communication 1983). The putative monthly layer counts were subsequently used to estimate age in months and hence date of birth.

Table 1. Criteria used for classifying dugongs according to reproductive maturity

<table>
<thead>
<tr>
<th>Sex</th>
<th>Stage</th>
<th>Criteria</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females</td>
<td>Immature</td>
<td>Ovaries and uterus small and undeveloped and without ovulatory and placental scars</td>
</tr>
<tr>
<td></td>
<td>Maturing</td>
<td>Ovaries and uterus larger than immature but without ovulatory and placental scars; large (&gt;3 mm diameter) Graafian follicles may be present</td>
</tr>
<tr>
<td></td>
<td>Mature</td>
<td>At least one corpus luteum or corpus albicans present^A</td>
</tr>
<tr>
<td></td>
<td>Parous</td>
<td>At least one placental scar in uterus</td>
</tr>
<tr>
<td>Males</td>
<td>Immature</td>
<td>Each testis weighs less than 20 g and is histologically immature^B</td>
</tr>
<tr>
<td></td>
<td>Approaching puberty (maturing)</td>
<td>Each testis weighs less than 30 g but is histologically mature^B and has many Leydig cells; no spermatozoa in epididymides</td>
</tr>
<tr>
<td></td>
<td>Mature</td>
<td>Each testis weighs more than 30 g; tests may be regressed, resting, intermediate, recrudescent or fully spermatogenic^B but have mature histology^B; spermatozoa may or may not be present in epididymides</td>
</tr>
</tbody>
</table>

^A Described in Marsh et al. (1984a).
^B Described in Marsh et al. (1984b); also see text.

Aerial Surveys

The aerial survey technique has been described by Heinsohn et al. (1979) and Heinsohn (1981). In addition, vertical aerial photographs were obtained of a dugong herd in Moreton Bay (27°25'S., 153°20'E.) on 12 May 1982, on Kodak Plus X 2404 Emulsion 245-2 film with a yellow filter. The camera was a Wild RC10 No. 1234 equipped with a 152.02-mm (6 in.) focal length lens, mounted in the floor of a Cessna 406 operated by a commercial photogrammetry firm. Photographs were taken at a scale of approximately 1:2000. (This scale could not be determined precisely as the aircraft was fitted with a pressure altimeter only.) Weather conditions were excellent. The sea was smooth (almost glassy) and the water visibility was very good (seagrasses were clearly visible on the bottom).

Other Sources

Because of the paucity of data on dugong reproductive behaviour we have also included in the 'Results' section of this paper pertinent but previously unpublished incidental observations made by various people.
Results

Criteria for Determining Reproductive Status

The criteria used for classifying the 59 male and 49 female dugongs studied according to their reproductive maturity are outlined in Table 1.

Incidence of Gonadal Activity

(i) Females

The ovarian condition of all the cycling and/or mature female dugongs which were not pregnant or recently pregnant is summarized in Fig. 1. Females were classified into one of four categories as follows:

Regressed. Non-atretic large (> 3 mm diameter) Graafian follicles, and corpora lutea absent. Hilar fat scanty in spite of large amounts of abdominal fat.

Resting. Non-atretic large, Graafian follicles and corpora lutea absent.

Follicular. Several non-atretic large, Graafian follicles (> 3 mm diameter) present.

Luteal. One or more corpora lutea present.

In the Townsville sample, the six females examined in February–April, one of the three in August and one of the two in September had resting or regressed ovaries. Females with large...
ovarian follicles were observed in August (two dugongs), October (one) and December (two). Well developed corpora lutea were present in the ovaries of two animals, one in August and one in September. Although the sample is too small for statistical analysis, the data suggest that ovaries tend to be active in the latter half of the year.

Although information from Mornington I. is seasonally restricted, it is reasonably consistent with that from Townsville. Animals from Mornington I. with large non-atretic ovarian follicles were observed in July (one dugong) and August (one); animals with large follicles and newly forming corpora lutea in July (one) and August (one); dugongs with rests or regressed ovaries were observed in June (one), July (one), August (three) and November (one).

The four females whose ovaries were inactive in August (Fig. 1) were all estimated to be more than 40 years old and had ovaries classified as regressed (see also Marsh et al. 1984a). The five, younger maturing and mature females (aged 13–27 years) sampled in August had active ovaries. These observations suggest that ovarian activity may be reduced in some old females. Another old female (No. 192, aged 42 y) was pregnant with a large foetus.

As summarized in Marsh et al. (1984a, table 2 and fig. 8), few or no macroscopic follicles were present in the ovaries of Nos 20 and 89 (each of which was pregnant with a large foetus), No. 18 (mother of a neonate) or No. 185 (which had probably given birth a few weeks before dying). As oestrus is preceded by the enlargement of many follicles (Marsh et al. 1984a, figs 4B, 8), these observations suggest that oestrus is not usual during the immediate post-partum period. Oestrus can, however, occur during lactation, as evidenced by animals No. 149 (with a 1.5-year-old calf) and No. 5 (with a calf of unknown age).

(ii) Males

The gonadal activity of adult male dugongs and those approaching puberty sampled in each calendar month is shown in Fig. 1. Each male was classified into one of five categories according to the following criteria ('predominant phase in testes' as detailed by Marsh et al. 1984b):

<table>
<thead>
<tr>
<th>Predominant phase in testes</th>
<th>No. of spermatozoa in epididymides</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regressed</td>
<td>-4</td>
</tr>
<tr>
<td>Resting</td>
<td>-3</td>
</tr>
<tr>
<td>Intermediate</td>
<td>-2</td>
</tr>
<tr>
<td>Recrudescent</td>
<td>-1, 0, 1-5</td>
</tr>
<tr>
<td>Fully spermatogenic</td>
<td>1-5 or 6</td>
</tr>
</tbody>
</table>

The Townsville data are from 19 animals collected from 1969 to 1981. Animals with fully spermatogenic gonads were observed in May (two individuals), August (one) and October (three). Animals with inactive (regressed, resting, intermediate) testes were sampled in February (three individuals), March (four), June (one), September (one); recrudescent males were observed in August (two animals), October (one) and November (one).

It is clear that the breeding season is not sharply defined, but at least some males are not continuously in breeding condition as discussed by Marsh et al. (1984b).

The sample from Mornington I. is seasonally restricted and does not permit the determination of male reproductive seasonality. Again it is obvious that at least some dugongs are not breeding continuously. Study of the testes and epididymides of the 17 males that died in July–August in 1976, 1977 and 1979 (Fig. 1; Table 2) indicates that reproductive activity is not synchronized in this population.

The testes of three dugongs (Nos 66, 80, 127), all of which were estimated to be old (see Marsh et al. 1984b), were regressed (majority of tubules at phase -4), suggesting that these animals may have been for long periods or even permanently aspermiogenic.
Gestation and Birth

(i) Incidence of births

The data on foetuses and young calves (<1·4 m long) accumulated since 1966 (Table 3) suggest that calving is diffusely seasonal in the Townsville–Cairns area. Apparently near-term foetuses were observed in July (one individual), September (one) and December (one). A smaller (13·5 kg) foetus (No. 89) was also measured in July. Dugongs that had apparently recently given birth or aborted a very large foetus were examined in August (one) and September (one).

Calves less than 1·3 m long have been measured in September (two animals), October (one), November (three), January (one) and March (one). One of the calves measured in September (No. 190) was probably born prematurely. It weighed much less than the others and no neonatal line could be found in tooth sections. As detailed in Table 3, two calves born in November (Nos 19 and 164) were definite neonates. Each had one putative monthly dentinal layer. One calf measured in January (No. 167) was a minimum of 5 weeks old and had two putative monthly dentinal layers. Using putative monthly dentinal layer counts (Table 3) we estimate that No. 24 was born about September, No. 44 about November and No. 53 about October.

(ii) Gestation Period

The gestation period of the West Indian manatee, *Trichechus manatus*, is estimated to be 13 months (Hartman 1979). Given this fact, our observation that Townsville dugongs tend to have active ovaries in the second half of the year (Fig. 1) and to calve in August–September through December (Table 3), suggests that the gestation period is also about a year or a little more.

(iii) Size at birth

The data in Table 3 and Bertram and Bertram (1973) indicate that neonatal dugongs are about 1·1–1·25 m long and that they weigh about 27–35 kg. P. K. Anderson (personal communication 1981) examined a 1·0-m-long dugong carcass in Shark Bay, W.A. (26°07'S.,
Table 3. Details of dugong foetuses and young calves from Townsville-Cairns area

<table>
<thead>
<tr>
<th>Acc. No.</th>
<th>Date</th>
<th>Place</th>
<th>Body length (m)</th>
<th>Body weight (kg)</th>
<th>Putative monthly dentinal layer count</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>89</td>
<td>19.vii.1975</td>
<td>Townsville</td>
<td>1-07A</td>
<td>13</td>
<td></td>
<td>Foetus</td>
</tr>
<tr>
<td>—</td>
<td>31.vii.1966</td>
<td>Townsville</td>
<td>1-14</td>
<td></td>
<td></td>
<td>Foetus measured by shark-netting contractor (Heinsohn 1972)</td>
</tr>
<tr>
<td>148</td>
<td>18.viii.1977</td>
<td>Townsville</td>
<td>1-09</td>
<td></td>
<td></td>
<td>Reproductive tract of dead mother indicates recent abortion of large foetus</td>
</tr>
<tr>
<td>—</td>
<td>10.ix.1967</td>
<td>Townsville</td>
<td>1-12</td>
<td>15-5+</td>
<td>0</td>
<td>Calf measured by shark netting contractor (Heinsohn 1972)</td>
</tr>
<tr>
<td>190</td>
<td>17.ix.1981</td>
<td>Townsville</td>
<td>1-12</td>
<td></td>
<td>0</td>
<td>Calf (body weight and lack of neonatal line in dentine suggest premature birth)</td>
</tr>
<tr>
<td>185</td>
<td>18.ix.1979</td>
<td>Townsville</td>
<td>1-12</td>
<td></td>
<td></td>
<td>Reproductive tract of mother indicated recent birth</td>
</tr>
<tr>
<td>192</td>
<td>27.ix.1981</td>
<td>Townsville</td>
<td>1-21</td>
<td>29-6</td>
<td></td>
<td>Mother washed up with aborted large foetus</td>
</tr>
<tr>
<td>1</td>
<td>20.x.1968</td>
<td>Townsville</td>
<td>1-23</td>
<td></td>
<td></td>
<td>Calf</td>
</tr>
<tr>
<td>—</td>
<td>30.x.1976</td>
<td>Lucinda Point</td>
<td>1-14</td>
<td>30B</td>
<td></td>
<td>Three very small calves with mothers, + dugong apparently giving birth, +5 adults in shallow sandbank area (seen during repeated circling on aerial survey)</td>
</tr>
<tr>
<td>180</td>
<td>02.xi.1979</td>
<td>Cardwell</td>
<td>1-23</td>
<td>35-3C</td>
<td>1</td>
<td>Calf (A. Thorsbourne, personal communication)</td>
</tr>
<tr>
<td>164</td>
<td>10.xi.1979</td>
<td>Townsville</td>
<td>1-25</td>
<td></td>
<td>1</td>
<td>Calf (neonate, stump of umbilicus present)</td>
</tr>
<tr>
<td>20</td>
<td>01.xii.1970</td>
<td>Townsville</td>
<td>1-25</td>
<td>34+</td>
<td>4</td>
<td>Near-term foetus</td>
</tr>
<tr>
<td>24</td>
<td>01.i.1971</td>
<td>Townsville</td>
<td>1-25</td>
<td></td>
<td>4</td>
<td>Calf</td>
</tr>
<tr>
<td>167</td>
<td>08.i.1979</td>
<td>Townsville</td>
<td>1-29</td>
<td>27</td>
<td>2</td>
<td>Calf (ectoparasitic barnacles at least 5 weeks old. R. Monroe and M. Draper, personal communication)</td>
</tr>
<tr>
<td>44</td>
<td>23.ii.1977</td>
<td>Townsville</td>
<td>1-39</td>
<td>54-6</td>
<td>3</td>
<td>Calf</td>
</tr>
<tr>
<td>53</td>
<td>06.iii.1972</td>
<td>Townsville</td>
<td>1-28</td>
<td>54+</td>
<td>5</td>
<td>Calf</td>
</tr>
<tr>
<td>157</td>
<td>23.iii.1978</td>
<td>Cairns</td>
<td>1-28</td>
<td>69C</td>
<td></td>
<td>Calf</td>
</tr>
</tbody>
</table>

*aMeasurement taken along curvature of back and therefore not strictly comparable.  
*bEstimated.  
*cAfter several days without food.
113°25'E); its premolar 3 was worn, suggesting that this animal had fed on solid food and was not stillborn. Jones (1967) measured a female which had a body length of 1.06 m and weight 20 kg. We conclude that the size of dugong neonates must be quite variable within a length range of 1.0-1.3 m and a weight range of 20-35 kg.

(iv) **Parturition**

As the only published description is that of Macmillan (1955) we include the following account by F. Griffin (personal communication 1981) a medical practitioner who watched nearby as a dugong was born on a sandy beach at Townsville in about 1950.

It was in warm weather and in the early morning. The female dugong was almost completely out of the water, making writhing movements which I, at first, mistook for efforts to re-float herself, but on observation, the movements were rhythmic and she was obviously in labour. Within a few minutes, she delivered herself of the foetus with a remarkable twist to the right, enabling her to bring her offspring on to her chest, where it became attached to her right nipple, while she nuzzled and cleaned it. It was only a minute or so, and not I would think coincidental, when the tide had come in far enough for mother dugong and baby to float off the beach with barely any effort. A few moments later, they disappeared under the water and out towards Magnetic Island.

(v) **Pregnancy rate**

All but one of the 18 mature females from Townsville were parous. However, only four were pregnant when examined, including two (Nos 148, 192) which had probably aborted about the time of their deaths. Three others were lactating. Most of the Townsville animals were caught in shark nets (Heinsohn 1972; Heinsohn and Spain 1974), which are likely to be unselective, suggesting that at any one time a substantial proportion of the parous female dugongs in the Townsville population is not pregnant or lactating.

None of the seven parous females examined from Mornington Island was pregnant or lactating. This sample, which may reflect a fishing bias against catching pregnant females (Marsh et al. 1981), contained three females (Nos 142, 144, 204) estimated to be more than 40 years old, with regressed ovaries.

Low pregnancy rates have also been reported in other populations of dugongs. Bertram and Bertram (1973) reported that only 28 of the 86 females over 2.29 m in length (the size of the smallest pregnant female) examined at Numbulwar were pregnant. In addition, only 25 of the 160 mature females examined at Daru, Papua New Guinea (9°3'S., 143°13'E.) were pregnant (Marsh and B. E. T. Hudson, unpublished).

(vi) **Litter size**

The two intact pregnant females examined from Townsville each contained one foetus, as did the 25 examined at Daru (Marsh and B. E. T. Hudson, unpublished) and the five in Torres Strait (M. Gibuma, personal communication 1975). Reports of the occasional occurrence of twin foetuses (Norris 1960; Jarman 1966; Thomas 1966; Bertram and Bertram 1968) are vague and unsubstantiated. The mean litter size must be close to one.

(vii) **Calving interval**

Because of the inadequate sample sizes and sampling periods the following estimates of mean calving interval must be viewed as very approximate, especially as this parameter is likely to vary considerably between populations and possibly also between years. Several estimates have been calculated based on independently derived data.

*Estimates based on the apparent pregnancy rate.* The calving interval can be estimated by means of the following formula: (No. pregnant females/Total No. adult females) = (Gestation period in years/Calving interval in years). There are at least three problems with the use of this method:
(1) It assumes that the sample is not biased, i.e. the probability of catching a given female does not change when she is pregnant.

(2) It requires an accurate knowledge of the gestation period.

(3) The probability of detecting a pregnancy increases as pregnancy progresses. This is a serious problem if a seasonally restricted sample coincides with the birth pulse. Fortunately, sampling was not seasonally restricted for any of the populations for which dugong pregnancy rate data are available.

Estimates of calving interval based on the pregnancy rate (Table 4) range from about 3 years (Numbulwar population) to about 7 years (Daru population). No data obtained by this method are available from Mornington Island as no pregnant females have been examined.

Table 4. Estimates of the calving interval of several populations of dugongs, based on data from carcass salvage programs or aerial survey

Source of data: Numbulwar population, Bertram and Bertram 1973; Daru, Marsh and Hudson, unpublished; Moreton Bay count, Heinsohn et al. 1978; Burrum Heads, Heinsohn and Marsh 1980; Starcke River area, Heinsohn 1976; Shark Bay, Anderson 1982; others, this study

<table>
<thead>
<tr>
<th>Population or location</th>
<th>Coordinates</th>
<th>Total No of dugongs and calves sighted</th>
<th>No. of mature females</th>
<th>Calving interval (y) 12-month 13-month gestation</th>
</tr>
</thead>
<tbody>
<tr>
<td>TownsvilleA</td>
<td>19°15'S. 146°15'E.</td>
<td>18</td>
<td>4.5 4.9</td>
<td></td>
</tr>
<tr>
<td>Numbulwar</td>
<td>14°17'S. 135°44'E.</td>
<td>86</td>
<td>3.1 3.3</td>
<td></td>
</tr>
<tr>
<td>Daru</td>
<td>9°3'S. 143°13'E.</td>
<td>160</td>
<td>6.4 6.9</td>
<td></td>
</tr>
<tr>
<td>Based on accumulation rate of placental scars</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TownsvilleA</td>
<td>19°15'S. 146°15'E.</td>
<td>13</td>
<td>6.6</td>
<td></td>
</tr>
<tr>
<td>Mornington Island A</td>
<td>16°30'S. 139°30'E.</td>
<td>7</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Based on photographs taken during aerial surveys in clear waterB</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moreton Bay</td>
<td>27°25'S. 153°20'E.</td>
<td>63, 7</td>
<td>4.5</td>
<td></td>
</tr>
<tr>
<td>Based on counts during aerial surveys in clear waterB</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moreton Bay</td>
<td>27°25'S. 153°20'E.</td>
<td>154, 15</td>
<td>5.1</td>
<td></td>
</tr>
<tr>
<td>Burrum Heads</td>
<td>25°11'S. 152°37'E.</td>
<td>97, 11</td>
<td>4.4</td>
<td></td>
</tr>
<tr>
<td>Starcke River area</td>
<td>14°49'S. 144°58'E.</td>
<td>209, 23</td>
<td>4.5</td>
<td></td>
</tr>
<tr>
<td>Shark BayC</td>
<td>26°07'S. 113°25'E.</td>
<td>1537, 177</td>
<td>4.3</td>
<td></td>
</tr>
</tbody>
</table>

*a Crude estimate only, due to small sample.

*b Assuming a 1:1 sex ratio and that half the females are parous.

*c Results of several surveys.

Estimates based on number of placental scars. If the placental scars persist throughout life—and the fact that up to nine have been counted in one dugong (unpublished data from Daru) suggest that they persist for a considerable time—the low number observed even in some in very old animals (Marsh et al. 1984a, fig. 13) suggests that fecundity is low and calving interval long. The regression of age (t) on the number of scars (s) of parous dugongs is given by: \( t = as + b \). The slope (a) is an estimate of the mean calving interval (Laws 1967) as follows:
Fig. 2. Aerial photograph of a dugong herd in Moreton Bay. The cow–calf pairs (identified by examining enlargements of two successive photographs of this herd) have been arrowed. Scale, 1:1300 (approximately).
Townsville population: \( t = 6.6s + 6.9 \), \((s > 1) (r = 0.89)\), giving a mean calving interval of 6.6 y (Table 4). The difference of the mean ages of the 1- and 2-scar groups is also 6.6 years.

Mornington I. population: \( t = 4.04s + 16.7 \), \((s > 1) (r = 0.83)\), suggesting a mean calving interval of 4 y (Table 4).

*Estimates based on aerial survey data.* Although calves are probably undercounted during most aerial surveys, we consider that reasonably accurate counts can be obtained during surveys in which large numbers of dugongs are counted in clear water and in good weather.

The most reliable calf counts will be from vertical aerial photographs of dugongs taken under these conditions. The herd photographed in Moreton Bay in May 1982 (Fig. 2) comprised 63 dugongs, seven of which were identified as calves by their small size and the proximity of each to a larger animal (presumably the mother). The calf body length estimates obtained from two successive photographs of this herd ranged from about 1.4 to 2 m (assuming a scale of 1:2000). Admitting the errors inherent in using a pressure altimeter to measure aircraft height, these data are consistent with those obtained from the shark-meshed dugongs from Townsville where a 1.72-m calf (estimated age 1.5 years based on dentinal growth layer counts) was caught in the net with her lactating mother (No. 149). Thus it is likely that dugongs up to at least 2 y old are counted as calves in an aerial survey. Thus (assuming low neonatal mortality), the number of calves born per year will be about half the number observed. The calving interval can then be estimated (Table 4) assuming a 1:1 sex ratio (which is likely, see below) and that half the females are parous (as were 24 of the 48 females examined from Townsville and Mornington I.). (The second assumption is more doubtful as this parameter is likely to vary considerably from one population to another.) On these assumptions the estimated mean calving interval for the Moreton Bay herd photographed in May 1982 is 4.5 y.

No suitable calf counts are available from aerial surveys of the Townsville and Mornington I. dugong populations, as the water is too muddy in these locations. However, estimates for other Australian populations where conditions are more suitable (summarized in Table 4) suggest calving intervals of 4-5 y.

(viii) **Length of lactation**

A calf estimated to be 1.5 years old (on the basis of dentinal growth layer counts) was caught in a Townsville shark net with its presumed mother who was still lactating. This suggests that lactation can last at least 1.5 years even though dugongs start eating seagrass soon after birth (Marsh *et al.* 1982).

**Sexual Maturity**

(i) **Age of sexual maturity in females**

The ovaries and uterus of all females less than 8 y old were small and undeveloped, while those of Nos 23 and 67 (8 y) and Nos 22, 69, 71, 84, 143 (9 y) showed some enlargement which suggested approaching maturity. Macroscopic follicles were present in the ovaries of Nos 23 and 84 (Marsh *et al.* 1984a, table 2).

The youngest female to have ovulated was a 9.5-y-old Townsville dugong (No. 55) with no macroscopically visible follicles but 66 corpora albicantia in the ovaries, even though she was nulliparous with no placental scars. All females from Townsville 10 y old or older were parous with one or more placental scars (Marsh *et al.* 1984a, table 2).

The youngest parous female from Mornington I. was No. 107, aged 14.5 y with one placental scar. However, three females (Nos 201, 203, 206) from Mornington I., aged 15.5-17.5 y, were nulliparous even though they had large ovarian follicles. In addition, No. 206 had four young corpora lutea, and No. 201 two corpora albicantia (Marsh *et al.* 1984a, table 2).
From this evidence it is suggested that in the Townsville population females usually start to ovulate at 9 or 10 y, but that follicular maturation and ovulation first occur several years later in at least some animals from Mornington I. Further, some animals caught in Townsville appear to have matured late. For example, only one placental scar could be seen in the uterus of No. 5, which was 24.5 y old and lactating (Marsh et al. 1984a, table 2). There is obviously considerable plasticity in the age at which female dugongs become sexually mature.

(ii) Age of sexual maturity in males

Attempts to estimate the age of sexual maturity have been hampered by the following: (1) the asynchronous, discontinuous male breeding pattern; (2) our inability to distinguish pubertal males (those approaching first spermiogenesis) from recrudescent males on the bases of testicular histology (Marsh et al. 1984b); (3) the paucity of material from young animals from Mornington I. (only seven males less than 20 y old); (4) the absence of specimens from Townsville aged between 6.5 and 8.5 y inclusive.

If sexual maturity is defined as the age at which the epididymides first contain copious amounts of spermatozoa, then three Townsville dugongs (Nos 38, 146, 156: Marsh et al. 1984b, table 3) aged 9-10.5 y were mature, even though their tusks had not yet erupted. Two other Townsville males were also in this age group. The testes of No. 39 were entering the phase of active spermatogenesis and those of No. 131 were classified as resting (Marsh et al. 1984b, table 3). All Townsville males 12 y old or older had mature testes and erupting or erupted tusks. Thus most male dugongs from Townsville probably become sexually mature when they are about 9 or 10 y old.

Sexual maturity certainly occurred later in the sample from Mornington I. Four immature dugongs from this population were estimated to be 10.5-15.5 y old (Marsh et al. 1984b, table 1).

(iii) Size of sexually mature females

Three parous females with body lengths of less than 2.4 m were examined. One (No. 58, 2.34 m long) was from Townsville, two (No. 129, 2.36 m, and No. 102, 2.38 m long) from Mornington I. No. 55 (from Townsville), nulliparous but with corpora albicantia in her ovaries, was 2.35 m long. The smallest pregnant female of the 433 dugongs examined at Numbulwar (Bertram and Bertram 1973) was 2.29 m long. Two nulliparous females from Mornington I. with active ovaries (Nos 201 and 203) were 2.4 and 2.5 m long respectively.

The range of dugong body lengths for a particular age is considerable (Marsh 1980), and using body length as an indication of age is unsatisfactory except for young animals. However, it seems that female dugongs from northern Australia less than 2.2 m long are almost certainly non-parous, and those larger than 2.5 m are likely to be parous. The reproductive status of animals with body lengths between 2.2 m and 2.5 m is uncertain.

(iv) Size of sexually mature males

The size at which male dugongs reach sexual maturity is very variable. The largest immature male was 2.49 m long (No. 191 from Townsville), and the body lengths of the 41 pubertal and adult males examined ranged from 2.19 to 2.8 m.

The five mature Townsville dugongs less than 2.4 m long (Nos 39, 86, 131, 156, 179: Marsh et al. 1984b, table 3) were all estimated to be younger than 18 y, but two animals with body lengths of 2.26 m (No. 127 from Torres Strait) and 2.27 m (No. 136 from Mornington I.) were aged at more than 33 y and 21.5 y respectively (Marsh et al. 1984b, table 4). It seems that male dugongs from northern Australia less than 2.2 m long are likely to be immature, but those larger than 2.5 m are probably mature. The reproductive status of males with body lengths between 2.2 and 2.5 m is uncertain.
Young sexually mature males are usually smaller than older animals. They also tend to have smaller testes (Marsh et al. 1984b, table 5) which probably produce fewer spermatozoa. Their tusks may have not yet erupted (see below). This may diminish their ability to compete with other males and they are probably less likely to breed than older males.

(v) **Tusk eruption**

**Females.** A female with erupted tusks is likely to be more than 40 y old (Marsh et al. 1984a, table 2; and unpublished data).

**Males.** As summarized in fig. 2 and tables 3 and 4 of Marsh et al. (1984b), the tusks of four males from Townsville (Nos 36, 50, 86, 87, aged 12-15.5 y) and one male from Mornington I. (No. 154, aged 15 y) were in the process of erupting. Nos 42 and 45 (from Townsville) had erupted and worn tusks at minimum ages of 13 y and 14.5 y respectively. In contrast, the tusks of Nos 99, 112 and 117 from Mornington I. were still unerupted at 14-15.5 y. The data from Nos 38, 146 and 156 indicate that in the male dugong testicular competence precedes eruption of the tusks. It is probably reasonable to assume that a male with erupting or erupted tusks is sexually mature.

**Sex Ratio**

The data from Mornington I. are not suitable for this analysis, as there may be a bias against hunting pregnant females (Marsh et al. 1981).

Out of a total of 89 dugongs examined from the Townsville area 45 were female and 44 male. Almost all of these animals died in shark nets, which are assumed to be non-selective. Seven females and six males were estimated to be less than 2 y old. Assuming that there are no sex differences in mortality during this period (while they were still accompanying their mothers), these results suggest that the sex ratio at birth is 1:1. Of the mature animals (estimated to be 10 y old and older), 22 were females and 23 males, indicating a tertiary sex ratio of 1:1 as well.

**Survival and Mortality**

(i) **Survivorship necessary for maintaining a stationary population**

In order to examine the relationships between pre-reproductive period, calving interval and mortality which are required to maintain stationary dugong populations, we have made the following assumptions:

1. The reproductive rate \( \lambda \) is independent of age during the reproductive part of a female’s lifespan.
2. The force of mortality (Pollard 1973) has the constant value \( \mu_1 \) for the first \( c \) years of life and the constant value \( \mu_2 \) for the remainder of life. [This is undoubtedly an oversimplification. In mammals the mortality rate typically follows a U-shaped trend with age (Caughley 1977).]
3. Females cease to bear calves at age 50. [Increasing this age has a minimal effect on the results (see Hanks and McIntosh 1973).]
4. The secondary sex ratio is 1:1.

In a continuous model, a constant force of mortality \( \mu \) is related to the probability \( l_x \) of survival to age \( x \) by the equation: \( l_x = \exp(-\mu x) \). For any \( x \), \( l_{x+1}/l_x = \exp(-\mu) \), and if \( \mu \) is small, then the mortality rate \( q_x \) equals \( 1-(l_{x+1}/l_x) = \mu \). For the values of \( \mu_1 \) and \( \mu_2 \) considered here, this approximation is adequate. We have:

\[
P(\text{surviving to age } c) = \exp(-\mu_1 c);
\]
\[
P(\text{surviving to age } x > c) = \exp[-\mu_2(x-c)] \cdot \exp(-\mu_1 c).
\]

If the reproductive rate \( \lambda \) is constant over the reproductive lifespan \((a, \beta) \) and \( c < a \), then for a stationary population (Pollard 1973):
Assuming a 1:1 sex ratio at birth, the quantity $\frac{1}{2}\lambda$ is the mean calving interval. Thus the last equation enables the relationship between birth rate (or calving interval) and mortality for stationary populations of this type to be investigated.

The three graphs in Fig. 3 show the relationship between calving interval and adult mortality $p_2$ for three different values of $\mu_1$, the mortality during the first 4 years of life (i.e. $c = 4$). On each graph, three different curves are drawn, one for each of three different ages of first breeding: $\alpha = 10\,\text{y}, 12\,\text{y}$ and $18\,\text{y}$ respectively.

From the graphs it can be seen that even for the most optimistic reproductive schedule (i.e. first calf at age 10 y, calving interval of 3 y) and the lowest level of juvenile mortality (5% per year), adult mortality must be about 9% per year to maintain a stationary population, i.e. about 90% of females older than 4 years need to survive each year. If the pre-reproductive period or calving interval is longer than these values, or if the level of juvenile mortality is higher, the adult mortality rate needs to be lower (Fig. 3). Fig. 3 also illustrates the major importance of the mortality rate, particularly the juvenile mortality rate, for maintenance of dugong populations.

(ii) Causes of mortality in young calves

The circumstances surrounding the death, stranding or capture of 13 dugongs estimated to be less than 1 y old are summarized in Table 5. In five instances the mother was known to have died also. There have been three reports (Table 5) of dugongs of neonatal size being
stranded on beaches; two near Darwin, N.T. (12°27'S., 130°15'E.) (M. Elliott, personal communications 1980, 1981) and one near Cardwell, Qld (18°16'S., 146°01'E.) (A. Thorsbourne, personal communication 1979). On two separate occasions, a neonate was found alive in shallow water near Townsville without its mother (Table 5).

Birth complications such as a retained placenta may also cause death of a neonate, as discussed in Marsh et al. (1984a) with reference to the pathology of No. 185.

Table 5. Circumstances resulting in the measurement of very young dugongs

<table>
<thead>
<tr>
<th>Circumstance</th>
<th>Number of young dugongs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
</tr>
<tr>
<td>Caught in net with mother</td>
<td>3</td>
</tr>
<tr>
<td>Caught in net alone</td>
<td>3</td>
</tr>
<tr>
<td>Found alive in shallows without mother</td>
<td>2</td>
</tr>
<tr>
<td>Washed up on beach alive</td>
<td>3⁴</td>
</tr>
<tr>
<td>Washed up on beach dead</td>
<td>2</td>
</tr>
</tbody>
</table>

⁴ Two animals stranded near Darwin (M. Elliott, personal communication); one near Cardwell (A. Thorsbourne, personal communication).

Discussion

Reproductive Behaviour

Study of reproductive organs salvaged from dugong carcasses provides valuable information on each animal's terminal reproductive state and, in the case of a female, her reproductive history. Knowledge of dugong reproductive behaviour would greatly enhance our ability to interpret these data but, to date, our information is restricted to incidental surface observations.

Australian Aborigines (e.g. Roughsey 1971) report the presence of 'whistlers' which they have told us they regard as dominant males, although a male role in integrating social structure has never been identified.

Dugongs exhibit little sexual dimorphism. The asymptotic length of females may be slightly longer than that of males (Marsh 1980). Male dugongs have tusks [illustrated by Marsh (1980)] which erupt several years after gonadal maturity but never protrude more than a few centimetres from the gums. Pairs of parallel scars [illustrated by Anderson and Birtles (1978)] were conspicuous on many of the dugong carcasses examined. Such scars were present on both males and females. The spacing of these scars suggested that they might be from tusk wounds. Agonistic behaviour has rarely been observed; however, E. Deemal, a dugong hunter from Hopevale, Qld (15°18'S., 145°07'E.), recalled seeing two dugongs inflicting bleeding tusk wounds on each other while apparently fighting (personal communication 1982).

Although dugongs have no elaborate display organs comparable to those of some terrestrial herbivores, the males may engage in simple displays such as 'rushing', described by Anderson and Birtles (1978). Presumed courtship and/or mating behaviour has occasionally been described (Roughsey 1971; Anderson and Birtles 1978).

There have been consistent reports of calving in shallow and/or sheltered areas (Macmillan 1955; Jarman 1966; Hughes and Oxley-Oxland 1971; Kingdon 1971; Table 4; F. Griffin, quoted above). Griffin's account is strikingly similar to that of Macmillan (1955). In both instances the mother was effectively aground when giving birth. Unfortunately neither Griffin nor Macmillan mentions the expulsion of the placenta. These reports suggest that dugongs may seek special areas for calving, presumably to reduce shark predation. This factor should be considered when management initiatives are being developed, especially as a low juvenile mortality rate is clearly very important for population maintenance (Fig. 3).
The little that is known about dugong reproductive behaviour suggests many similarities with that of the West Indian manatee, *Trichechus manatus*, which has been extensively observed underwater, principally by Hartman (1979) in Florida, at the northern limit of its range. For example, Roughsey (1971) described how sometimes five or six male dugongs will chase one female, who will seek refuge in very shallow water. Hartman (1979) described almost identical manatee behaviour. Many of the elements of the dugong sexual interactions detailed by Anderson and Birtles (1978) were also similar to Hartman's descriptions. West Indian manatees, like dugongs, seek the safety and seclusion of sheltered backwaters to give birth. Both dugong (Marsh *et al.* 1982) and manatee (Hartman 1979) calves start to nibble on vegetation at an early age even though lactation apparently lasts 1–2 y in both species.

These similarities are interesting especially as manatees and dugongs are adapted to rather different aquatic environments. The West Indian manatee occurs primarily in riverine and estuarine areas and appears to require fresh water (Hartman 1979), but the dugong is strictly marine even though it occurs in coastal waters. Also manatees and dugongs have been separated for a considerable period. Immunological distance determinations time the trichechid–dugongid separation at 30 My ago (V. Sarich, personal communication 1980). Palaeontological evidence suggests even earlier separation of the two lineages (in the Eocene), even though trichechid origins are obscure (D. Domning, personal communication 1980).

**The Pattern of Breeding**

The level of gonadal activity in the 38 mature male dugongs that we have examined from Townsville and Mornington I. was very variable. Even though individual males are apparently not continuously in breeding condition, there is no sharply defined male breeding season (Fig. 1) and reproductive activity within a population is not synchronized (Table 2). We therefore consider it more appropriate to describe the male dugong as a discontinuous rather than a seasonal breeder.

Examination of the ovaries of 26 maturing and mature females from the same populations, which were not pregnant or recently pregnant, suggests that ovarian activity tends to concentrate in the second half of the year (Fig. 1). A larger sample would probably extend this period, as presumed courtship and/or mating activity has been observed at Mornington I. from May to August (Roughsey 1971). Given that male dugongs are discontinuous breeders, it is not surprising that the females do not cycle continuously. There is no known species of mammal in which the females can breed through the year and do not do so because the males are seasonally aspermatogenic, although there are many species in which the males are always fertile and the females seasonal (Weir and Rowlands 1973).

**Seasonality of Calving**

Although assessments based on the questioning of local residents or fishermen in northern Australia (Bertram and Bertram 1973; Anderson and Heinsohn 1978) have suggested that dugongs calve all the year round, the data presented in Table 3 strengthen the evidence that breeding is diffusely seasonal. Like the Amazonian manatee, *Trichechus inunguis*, (Best 1982), the dugong apparently calves over several months, in the Townsville–Cairns area most doing so from August–September through December (Table 3). Heinsohn (1972), with many fewer data, concluded that most births in this area occurred in August–September.

Why should calving be seasonal in this tropical marine mammal? One advantage of giving birth in spring in the Townsville–Cairns area would be to reduce the chance of the calf's being thermally stressed. Although dugongs are not known to suffer cold-related mortality like the West Indian manatee (Hartman 1979), water temperature does appear to limit their distribution (Heinsohn *et al.* 1977) and a 20–35-kg neonate (Table 3) would certainly find it harder to maintain its body temperature than an adult weighing 250–400 kg.
There is an annual unimodal fluctuation of about 8°C in surface seawater temperature off Townsville, reaching a minimum in July when temperatures may be as low as 19.3°C (Walker 1981). The occurrence of most births from August–September to December inclusive would maximize the period before young calves are exposed to the mid-year low water temperatures.

Howard Campbell (quoted by Hartman 1979) had data based on the recovery of newborn carcasses that suggest that natality of West Indian manatees may increase in the spring in Florida. Hartman interpreted this as a strategy that is evolving to prevent calves being exposed to the potentially dangerous water temperatures that occur in this area during the winter.

**Nutrition and the Timing of Reproduction**

(i) **Seagrasses as food for dugongs**

Conflicting statements have been made about the nutritive value of seagrasses (Birch 1975; Wake 1975; Murray et al. 1977; Johnstone and Hudson 1981) and further studies are required before they can be properly evaluated as food for herbivores. However, most evidence indicates that their nutritive value is low. Birch (1975) found that seagrasses collected near Townsville had the lowest calorific content of any vascular vegetation so far analysed. Nitrogen and phosphorus contents were also low, comparable to those in poor terrestrial pasture. Biomass levels of northern Australian seagrass communities are also often low. Wake (1975) sampled seagrasses in six major dugong feeding areas and obtained biomass values ranging from 1.37 to 278 g dry weight per square metre. Dugong feeding activities are curtailed by the tide in many areas (e.g. Shoalwater Bay: Anderson and Birtles 1978). Thus dugongs are not always able to compensate for low food quality and availability by eating more. Under these conditions it seems likely that dugongs will time their reproduction to take advantage of temporal changes in food supply, which we postulate will prove very important for the breeding of dugongs in north Queensland waters.

Rainfall in this area is strongly seasonal and tends to be the dominant climatic characteristic. A wet summer of variable but short duration and variable intensity is followed by a generally dry remainder of the year (Oliver 1978). The rains wash nutrient-rich soils from the land via the rivers, with concomitant reduction in the clarity of inshore waters. We expect these environmental variables to influence the growth of the seagrasses eaten by dugongs, but this has not been documented in north Queensland. Welsby (1967), who chronicled the experiences of himself and others as dugong hunters in Moreton Bay in southern Queensland, considered that the food supply of the dugong is ‘entirely influenced’ by the summer rains. Whenever there was a summer freshet or a flood in the local rivers the dugong feeding grounds were fertilized with a fine slimy silt which caused a vigorous sprouting of the seagrasses.

(ii) **Probable effects of nutrition on the female**

Dugong calves may be born in the spring (August–September through December) to take advantage of the nutritional as well as the thermal conditions. Observations of an intertidal seagrass bed near Townsville from January through September 1983 revealed marked changes in the density of the two seagrass species present (*Halodule uninervis* and *Halophila ovata*). Density decreased through to June and July, leaving the area with only a sparse patchy cover of old leaves. Regrowth commenced in August and within several weeks a clear increase in seagrass density was evident (Hall 1983; H. Marsh, personal observation).

A similar pattern was observed by Masini (1982) in a temperate environment, the Swan–Canning River estuary in Western Australia (31°57'S., 115°51'E.), where the biomass of *Halophila ovalis* fell significantly in the winter, most noticeably in the leaves. The non-structural carbohydrate content of the plants also fell during winter but increased markedly in late winter and spring.
Best (1982) reported on the estimated birth dates of 24 neonatal Amazonian manatees in the region about Manaus, Brazil (03°08′S., 60°02′W.). With only one exception, the births occurred between December and July inclusive, with 63% in the months February–May, the period of rising river levels. The aquatic plants on which the manatee feeds are most nutritionally valuable at this time, with many new shoots which are low in fibre and high in digestible carbohydrates.

As the gestation period of sirenians is about 1 year, oestrus and calving occur in approximately the same season. As Best (1982) points out, there are potential advantages of synchronizing oestrus and calving with optimal nutritional conditions. If oestrus is controlled by nutritional status, then in poor food years many of the females would avoid the energy demands of a long pregnancy and lactation. This may explain the high numbers of parous dugongs, observed in north Queensland populations, which are not pregnant or lactating. Timing calving to coincide with the start of the period of maximum plant productivity would serve the greatly increased energy demands of the offspring during late pregnancy and early lactation. Finally, as the calves begin feeding on plants soon after birth (Marsh et al. 1982), they could take advantage of the abundant new shoots available.

Unwashed seagrasses as consumed by dugongs contain 30 times more sodium and 15 times more chloride than most terrestrial pasture plants (Birch 1975). As far as is known, dugongs do not seek fresh water. The water-balance stress of lactation is likely to be considerable. We do not know whether cows can become pregnant while nursing a very young calf. Oestrus can certainly occur during the later stages of lactation (e.g. No. 149 who was nursing an 1.5-year-old calf). Welsby (1967) related how he caught a pregnant lactating female with a large calf, confirming that a lactating female can conceive.

(iii) Probable effects of nutrition on the male

The testes of some old males (Nos 68, 80, 127) were regressed, with a majority of tubules without spermatoocytes, spermatids or spermatozoa (phase -4; Marsh et al. 1984b), which suggests that these animals had been aspermatogenetic for a long period. This reproductive inactivity may have been solely due to advanced age, but it may also be relevant that the stomach contents of Nos 68 and 127 were markedly different from those of most of the other 93 north Queensland dugongs examined (Marsh et al. 1982). No. 127 was the only dugong to have consumed large quantities of Enhalus acoroides, the largest and most fibrous seagrass occurring in north Queensland waters. No. 68 was the only male which had consumed large quantities of algae, presumably because seagrasses were scarce 9 months after Cyclone Althea (Spain and Heinsohn 1973; Heinsohn and Spain 1974; Marsh et al. 1982). Dugongs seem to be ill-adapted to utilize algae as their major food source, as they apparently have difficulty in chewing and digesting them (Annandale 1905; Lipkin 1975; Marsh et al. 1982).

Nietschmann and Nietschmann (1977, 1981) report that the Torres Strait Islanders distinguish between ‘wati dangal’, lean dugongs with poor-tasting fat and meat which they consider almost inedible, and which are found around island margins and nearby reefs, and ‘malu dangal’ ('deep' water dugong), which are actively hunted for their highly esteemed fat and meat. The preliminary analysis of stomach samples taken from both types suggest that wati dangal consume more algae than the largely seagrass-feeding malu dangal (Nietschmann and Nietschmann 1977). Although it had eaten mainly Enhalus rather than algae, No. 127 was a wati dangal. The Islanders who caught this animal were most reluctant to kill it, and tethered it to a mangrove while they hunted for other dugongs, only returning to butcher it when they failed to find others. If most wati dangal are reproductively inactive for long periods or post-reproductive, it is regrettable from the viewpoint of conservation that the Islanders prefer to kill the malu dangal.

However, we consider it unlikely that mature males fail to produce sperm only when they are nutritionally stressed. For example, three (Nos 42, 50 and 52) of the males with resting
testes (phase -3 predominant; Marsh et al. 1984b) died in February-March 1972. Although these animals were examined less than 3 months after Cyclone Althea damaged seagrass beds in the Townsville area, they were judged in good condition at necropsy and No. 52 had excessive epicardial fat (U. Rowlatt, personal communication 1981). It is thus unlikely that these animals were failing to produce spermatozoa because they were stressed by food shortage.

The low nutritive value of tropical seagrasses and their often low biomass means that a dugong must spend a major proportion of its time feeding. Under these conditions we suggest that selection is likely to favour discontinuous sperm production, even though there is no evidence that sperm production per se is energetically expensive. Male reproductive behaviour can be demanding of time and energy. For example, the activity budgets of red deer stags, Cervus elaphus, show a rapid change during the rut. The proportion of daytime spent grazing falls from 44% to 5%, and some individuals lose as much as 20% of their body weight over the 2-month rutting period (Clutton-Brock et al. 1982). Geist (1974) pointed out that in the tropics the overall cost of social life for male ungulates with breeding seasons of several months or more should be higher than those of temperate species where the rutting season is much shorter. The males of tropical forms are not free to idle and grow fat but must be ready over an extended period to seek and compete for oestrous females. Geist postulated that mechanisms may evolve to ration rutting for each male in ungulates that live close to carrying capacity and breed all the year round.

The breeding season of the dugong apparently lasts for several months (Table 3). At least some females seem to undergo a number of sterile cycles before conceiving (Marsh et al. 1984a). The discontinuous and asynchronous male breeding pattern may be an energetically efficient means of ensuring the presence of fertile males in the population over an extended period, while minimizing the energy expended in reproduction by an individual male. A relatively short annual rut would allow an individual to recuperate from his reproductive activities and increase his life expectancy. This would, in the long run, allow him to sire more offspring than if he were in rut continuously and died young.

**Sexual Maturity**

The minimum pre-reproductive period for dugongs from Townsville appears to be about 9-10 years for both sexes. In contrast, maturity is delayed in some animals of both sexes from Mornington I. until they are more than 15 years old.

On the basis of captive animal growth curves, Odell et al. (1981) tentatively concluded that the West Indian manatee matures at 8-10 years of age. However, Rathbun and Powell (1982) have found, as a result of their longitudinal studies of known individuals in north Florida, where abundant food is usually available, that the minimum age at first parturition for West Indian manatees is 5 years. Manatee food plants such as *Hydrilla* have erupted to nuisance levels in this area within the last 20 years (Hartman 1979).

The age of reproductive maturity is known to be density-dependent in at least 15 species of large mammals, eight of these being marine (Fowler et al. 1978). Sexual maturity in the Mornington I. dugong population may be delayed by density-dependent nutritional and social stresses as has been suggested from some African elephant populations (Laws 1969).

As illustrated in Fig. 3, changes in the juvenile and/or adult mortality rates are much more important than changes in the length of the pre-reproductive period in determining dugong population dynamics. However, comparison of the age of reproductive maturity between different populations of the same species is likely to be an indicator of population conditions (Eberhardt and Siniff 1977). Although, we do not know the age of maturity in an unexploited dugong population, the apparent delay in the age of sexual maturity of dugongs from Mornington I. suggests that the native fishery was not over-exploiting this population at the time the specimens were collected (1976-79).
Implications for Conservation

This paper extends the dugong life-history work of Marsh (1980). Both papers provide evidence that the dugong is a long-lived mammal with a lifespan of 50-60 years and a minimum pre-reproductive period of 9-10 years for both sexes, which bears one calf at a time at intervals of 3-7 years. As shown in Fig. 3, both juvenile and adult female mortality rates must be low even to maintain a population. These results are not unexpected. As Goodman (1981) points out, large mammals have a particular sort of life table. Survival rates are high, fecundity rates are low, and fecundity is usually late. Several cetaceans have life-spans similar to that of the dugong (see Sacher 1980). The life history of the dugong is also very similar to that of the elephant (see Croze et al. 1981).

Even though we lack information on the mortality schedule of any dugong population, the use of a marking program to obtain such information should not be attempted without a careful cost-benefit analysis. Artificially marking a dugong will almost certainly involve chasing it in a speedboat, which may cause it to suffer the potentially lethal effects of capture myopathy (Anderson 1981; Marsh and Anderson 1983). Thus a large-scale dugong tagging program has the potential to increase mortality in a species which is already considered to be vulnerable to extinction.

Our lack of detailed knowledge of dugong population dynamics need not prevent the initiation of programs to reduce mortality. Long-lived mammals with a low reproductive rate, a long generation time and a large investment in each offspring must sustain a high survival rate to maintain population numbers. Even though some Australian Aboriginal and Torres Strait Islander dugong hunters have told us that they can sex a dugong before spearing it, sexual dimorphism is slight, so protection based on a selective fishery for males would seem impractical. It is obvious that if dugong numbers are to be maintained in an area, man-induced mortality must be minimized.

It is important that measures which are adequate to protect dugongs and their specialized habitats be implemented before numbers are further substantially reduced.

Acknowledgments

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References


Oliver, J. (1978). The climatic environment of the Townsville area. In 'Geographical studies of the Townsville Area'. (Ed. D. Hopley.) (James Cook University of North Queensland: Townsville.)


*Note Added in Press*

Anthropologist John Bradley (*in litt.* 1984) saw the birth of two dugongs in the Port McArthur area (15°48'S., 136°40'E.) of the Gulf of Carpentaria, in the course of his work with the people of the Yanyuwa tribe. In early December 1979, a lone female was observed giving birth; the calf was born tail first. The second female gave birth in October 1982, and was accompanied by another large dugong and a small one. Both births took place in about 1 m of water in a sandbar area near the mouth of the McArthur River. Each female lay on her side to give birth and then pushed the calf to the surface. Bradley also reported seeing a neonatal-sized dugong being attacked by a tiger shark, in mid-August 1982 in the same general area. This dugong was in a feeding herd; the rest of the animals quickly dispersed. The calf was subsequently found dead with most of its snout eaten away.

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