The Life History, Pattern of Breeding, and Population Dynamics of the Dugong

by

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Abstract. The literature and recent unpublished data on the breeding cycle and life history of the dugong (*Dugong dugon*) are summarized. The studies were based on the analysis of carcasses from animals accidentally drowned in shark nets or killed by native hunters in northern Australia and in Papua New Guinea. Age was estimated by counting the dentinal growth-layer groups in the tusks, the deposition rate deduced from the seasonal pattern of growth-layer group deposition. The maximum estimated age was 73 years, and the minimum pre-reproductive period was 9 or 10 years in both sexes. The pre-reproductive period was variable and ranged to 15–17 years in some animals. Neither males nor females were continuously in breeding condition and breeding was diffusely seasonal. A single calf was usually born after an estimated gestation period of about 13 months. Calves suckled for at least 18 months. Estimates of mean interbirth interval based on pregnancy rates and placental scar counts ranged from 3 to 7 years in various samples. Variation between years was marked in the proportions of breeding males and females. Reliable data on age-specific fecundity or mortality are not available. Population simulations indicated that, with even the most optimistic combination of life history parameters and a low rate of mortality, a dugong population probably does not increase at more than about 5% or 6%/year.

Key words: Dugong, *Dugong dugon*, life history, reproduction, age determination, population dynamics.

The life history of the dugong (*Dugong dugon*) has been studied in northern Australia and in southern Papua New Guinea as part of the development of conservation and management of this species. However, data from known-age animals are not available. No longitudinal information comparable to that about wild Florida manatees (*Trichechus manatus latirostris*; O'Shea and Hartley 1995; O'Shea and Langtimm 1995; Rathbun et al. 1995) is available about dugongs. In addition, unlike manatees, dugongs have rarely been maintained in captivity and have never bred in captivity. All information has been obtained from the analysis of carcasses of animals that were either killed in native fisheries (Bertram and Bertram 1973; Nietschmann 1984; Hudson 1986) or opportunistically collected when animals incidentally drowned in shark nets set for the protection of bathers (Heinsohn 1972).

In this paper, I summarize the current understanding of dugong life history and breeding ecology to provide a comparative perspective of these features of manatee biology.

My assessment is based on previously published accounts (Marsh 1980, 1986; Marsh et al. 1984a, 1984b, 1984c) and my emphasis is on aspects of dugong life history that are relevant to the parallel research on manatees in Florida.

Life-history Parameters

Sex Ratio

Dugongs from a native fishery at Numbulwar (Northern Territory, Australia) sampled by Bertram and Bertram (1973) had a preponderance of females (88:143). In contrast, a sex ratio close to parity is indicated by other large samples from native fisheries (267:237, Western Islands of the Torres Strait, Australia, Nietschmann 1984; 218:235, Daru near the Papua New Guinean coast in the central Torres Strait, Hudson 1986) and from incidentally drowned animals in shark

nets at Townsville, northern Queensland, Australia (44:45, Marsh et al. 1984c).

Maximum Age

The absolute ages of 75 (Mitchell 1976) and 160 (Marsh 1980; H. Marsh, James Cook University, unpublished data) dugongs from various locations in northern Australia and of 96 dugongs from Daru (H. Marsh and B. Hudson, James Cook University, unpublished data) were estimated. The ages were estimated from the number of dentinal growth-layer groups in the tusks (Fig. 1); the seasonal layer deposition indicates that one growth-layer group is deposited per year (Marsh 1980). Estimated minimum ages ($\leq$34.5 years) are available only of adult male dugongs because their tusks erupt and wear after puberty (Marsh 1980). Some more-than-40-year-old females also have erupted and worn tusks so that their ages are underestimated because of wear. The estimated age of the oldest examined female was 73 years (H. Marsh, James Cook University, unpublished data). However, less than 1.5% of females whose absolute ages were estimated were older than 60 years.

Age at Attainment of Sexual Maturity

Females

Dentinal-layer counts and reproductive organs are available from 47 females from Townsville and Mornington Island (Queensland, Australia) and from 28 females from Daru. These data are appropriate for estimating the range of ages at which sexual maturity occurs but are insufficient for estimating the age at which 50% of the females are mature or for quantifying age-related changes in fecundity.

The ovaries and uteruses of all less-than-8-year-old females were small and undeveloped. Those of two 8-year-old and four 9-year-old animals from Townsville showed some enlargement that suggested approaching maturity; macroscopic follicles were present in the ovaries of two of the animals (Marsh et al. 1984c).

The most accepted definition of sexual maturity in females is that the animal has ovulated at least once. The youngest female with corpora lutea or corpora albicantia in the ovaries was a 9.5-year-old nulliparous female from Townsville. All 10-year-old or older females from Townsville were parous and had one or more placental scars in the uterus (Marsh et al. 1984a, 1984c). However, data from Mornington Island and Daru suggested that the age at which females bear their first calves is variable; three females from Mornington Island were still nulliparous at 15–17 years (Table 1). Two of the animals were sexually mature because their ovaries contained small numbers of corpora lutea or corpora albicantia (Marsh et al. 1984c). One 18-year-old female from Daru had recently had her first calf.

Males

What constitutes sexual maturity in males is complex. Attempts to estimate the age of sexual maturity in male dugongs have been hampered by the asynchronous, discontinuous pattern of male sexual activity (Marsh et al. 1984b); difficulties with distinguishing the testicular histology of pubertal males (those approaching first spermiogenesis) from that of mature males with recrudescent testes (Marsh et al. 1984b); and small sample sizes in the pubertal age range. The data suggested a pre-reproductive
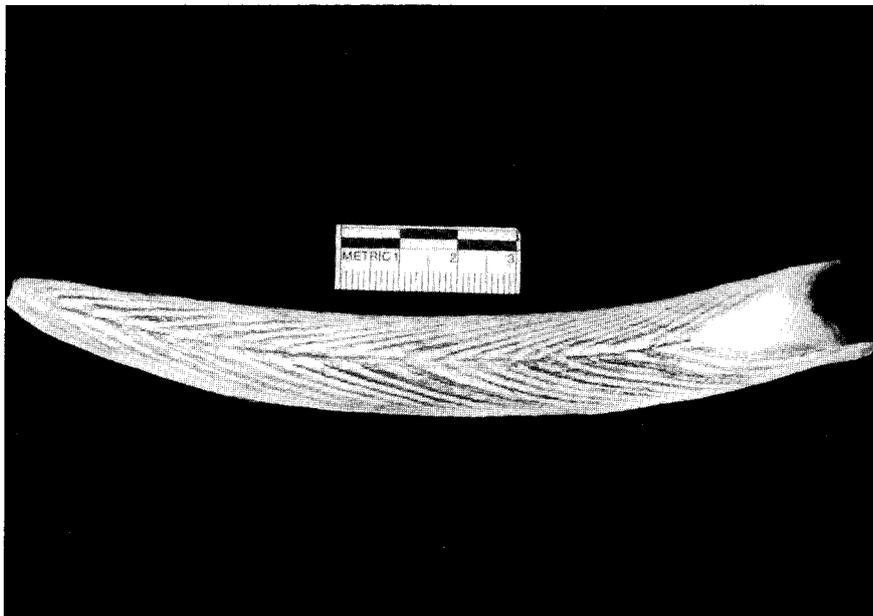

Fig. 1. A longitudinally bisected tusk of a female dugong (*Dugong dugon*) prepared for age determination. One dark band and one light band are laid down each year, indicating that this animal was 21 years old when it died.

Table 1. Pre-reproductive periods of female dugongs (*Dugong dugon*) from various areas.

Location	Youngest female with placental scar	Oldest female without placental scar	Source of data
Townsville	10	9.5	Marsh et al. (1984c)
Mornington Island	14.5	17.5	Marsh et al. (1984c)
Daru	13	12[a]	Marsh (1986)

[a] One 18-year-old female had recently given birth to her first calf.

period similar to that of females. Most male dugongs from Townsville were sexually mature when they were about 9 or 10 years old, and all 12-year-old or older males from Townsville had erupting or erupted tusks. However, some dugongs from Mornington Island and Daru that were as old as 16 years were immature and their tusks had not erupted (Table 2).

Size at Sexual Maturity

Marsh (1980) developed growth curves of male and female dugongs. The range of body lengths of dugongs of a particular age is considerable, and body length as an indicator of age is unsatisfactory except for young animals. Similarly, the size at which dugongs mature sexually is variable of animals of both sexes. The data of Marsh et al. (1984c) suggested that less-than-2.2-m-long male and female dugongs from northern Australia were immature, whereas those longer than 2.5 m were probably mature. Dugongs with body lengths between 2.2 and 2.5 m may be either immature or mature. There is some evidence (Marsh 1980) that the asymptotic body length of females is slightly greater than that of males.

Size at Birth

Nine fetal and nine postnatal dugongs had body lengths between 100 and 130 cm. The data are insufficient for the 50% interpolation method of estimating size at birth recommended by Perrin and Reilly (1984). Accordingly, I estimated the mean birth length as 115 cm from the lengths of the postnatal animals. With this method, size at birth tends to be overestimated (Perrin and Reilly 1984); however, three fetuses were longer than 115 cm.

Gestation Period

I estimated a gestation period of 13.9 months with the method of Huggett and Widdas (1951) and Laws (1959) and data on the body lengths and dates of deaths of 26 fetuses from Daru (Fig. 2). As a result of the small sample size and the diffusely seasonal breeding pattern of the dugong, the 95% confidence interval for this estimate was so imprecise, it was meaningless. However, the estimated mean was in good agreement with the estimated 12–14 month gestation period of captive Florida manatees. (*[1]Odell et al. 1992; Qi Jingfen 1984).

Length of Lactation

Data on length of lactation are sparse, especially because of the ban on taking females with attendant calves in the Daru fishery. A calf of an estimated age of 1.5 years (on the basis of dentinal-layer counts) and its presumed mother who was still lactating were caught in a shark net. This suggested that lactation can last at least 1.5 years (Marsh et al. 1984c), even though dugongs start eating seagrass soon after birth (Marsh et al. 1982). Pregnancy can occur during lactation. I noted one lactating female with a 41-cm-long fetus at necropsy (Marsh 1989).

Litter Size

One fetus was found in each of the 34 pregnant females that scientists examined in recent years. Reports of the occasional occurrence of twin fetuses (Norris 1960; Jarman 1966; Thomas 1966; Bertram and Bertram 1968) are

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[1] An asterisk denotes unpublished material.

Table 2. Pre-reproductive periods of male dugongs (*Dugong dugon*) from various areas.

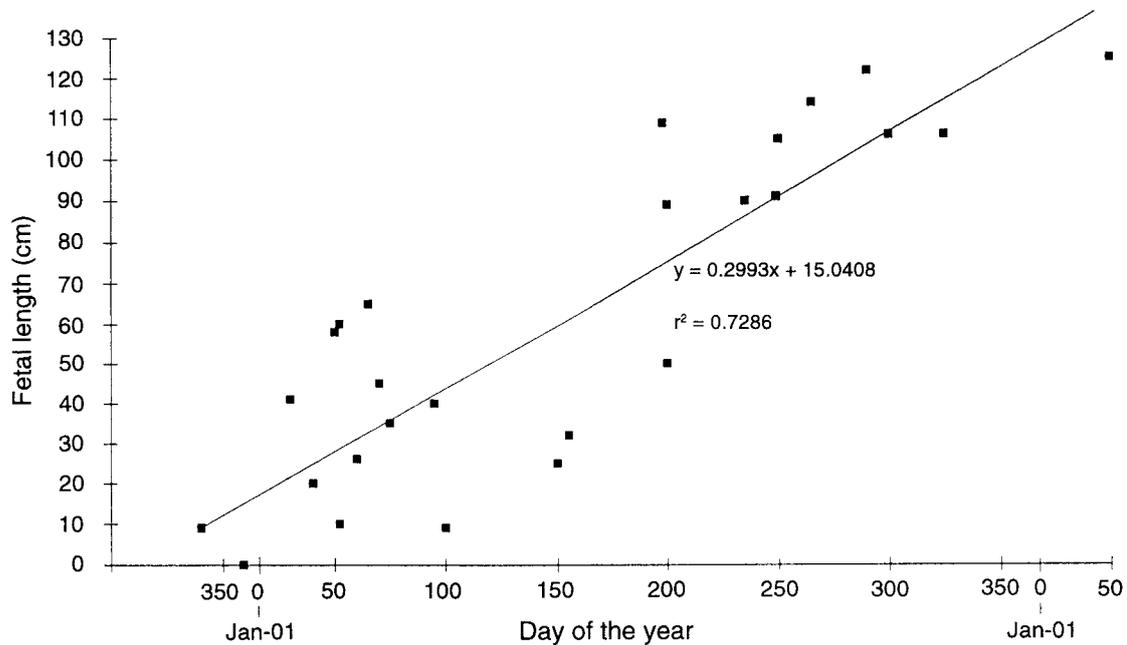| Location	Youngest male with mature testes	Oldest male with immature testes	Oldest male with unerupted tusks	Source of data
Townsville	9	6	10.5	Marsh et al. (1984c)
Mornington Island	15	15.5	15.5	Marsh et al. (1984c)
Daru	11	16	18	Marsh (1986)

Fig. 2. The relation between fetal length and day of the year (January 1 is day 1) in dugongs (*Dugong dugon*) from Daru in the Torres Strait. Data from H. Marsh and B. Hudson (James Cook University, unpublished data).

vague and unsubstantiated. The mean litter size must be close to one as in Florida manatees whose twin calves account for a low proportion of the total births (Marmontel 1995; O'Shea and Hartley 1995; Rathbun et al. 1995).

Pregnancy Rate and Interbirth Interval

The annual pregnancy rate is usually estimated as the percentage of mature pregnant females (including those pregnant and lactating) divided by the length of gestation in years (Perrin and Reilly 1984). The interbirth interval is the reciprocal of the annual pregnancy rate. Calculation of the annual pregnancy rate requires accurate knowledge of the length of the gestation period. Accordingly, I used the apparent pregnancy rate (proportion of pregnant females uncorrected for the length of gestation) in the following discussion and three estimates of the gestation period (12, 13, and 14 months) in the estimates of interbirth intervals based on pregnancy rates.

Apparent pregnancy rates of three series of dugong carcasses are available: 86 mature-sized females from the native fishery at Numbulwar (Bertram and Bertram 1973), 18 mature females from the Townsville shark nets (Marsh et al. 1984c), and 168 mature females from the native fishery in Daru (H. Marsh and B. Hudson, James Cook University, unpublished data). The females from Townsville and Daru were classified as mature by the appearances of their ovaries.

The probability of detecting a pregnancy increases as gestation progresses because of the size of the fetus, and

some small embryos may have been overlooked, especially in examinations in the field. Accordingly, I estimated the pregnant proportion based on only confirmed pregnancies (which tends to provide an underestimated pregnancy rate) and on possible pregnancies from females with corpora lutea in their ovaries. This tends to provide an overestimated pregnancy rate because not all corpora lutea are associated with pregnancy (Marsh et al. 1984a). Irrespective of the gestation period used in the model or whether the pregnancy rate was based on confirmed or possible pregnancies, all estimated interbirth intervals are long, ranging from about 3 to 7 years (Table 3). These estimates are generally higher than those of manatees (Marmontel 1995; O'Shea and Hartley 1995; Rathbun et al. 1995; Reid et al. 1995). The biases in the dugong samples on which these estimates are based are unquantified. However, the sample from Daru was probably biased in favor of pregnant females. These were regarded as a delicacy (Hudson 1986), and there was a ban against taking females with young calves (*Hudson 1981). Thus, the estimated pregnancy rates of the Daru sample are probably high.

A maximum of nine placental scars has been counted in the uterus of a dugong (Marsh et al. 1984a). The interbirth interval can also be estimated by regressing the number of placental scars against age of parous dugongs if persistence of the scar is assumed. These estimates also suggested that the interbirth interval was long: 6.6 years in Townsville dugongs and 4 years in Mornington Island

Table 3. Estimates of the interbirth interval of various dugong (*Dugong dugon*) populations based on the annual pregnancy rate and three possible gestation periods of 12, 13, and 14 months. Estimates are based on confirmed pregnancies (a) and all possible pregnancies (b).

Location	Number of mature females	Estimated interbirth interval for three possible gestation periods ($\pm$ S.E.)			Source of data
		12 months	13 months	14 months	
Numbulwar	86[a]	3.07 ± 0.47[a]	3.32 ± 0.55[a]	3.58 ± 0.62[a]	Bertram and Bertram
		2.69 ± 0.38[b]	2.91 ± 0.43[b]	3.14 ± 0.49[b]	(1973)
Townsville	18	4.50 ± 1.98	4.88 ± 2.26	5.25 ± 2.55	Marsh et al. (1984c)
Daru	168	5.79 ± 0.98[a]	6.28 ± 1.11[a]	6.76 ± 1.25[a]	H. Marsh and B. Hudson
		4.94 ± 0.76[b]	5.35 ± 0.86[b]	5.76 ± 0.97[b]	(James Cook University, unpublished data)

dugongs (Marsh et al. 1984c). The sample sizes on which these estimates are based are too small for meaningful associated confidence intervals. The difference in the mean ages of the dugongs from Townsville with one and two placental scars is also 6.6 years. Placental scars do not persist in manatees and cannot be used to estimate the number of parities (Marmontel 1995).

Evidence from Daru suggested marked temporal fluctuations in the apparent pregnancy rate. Hudson (1986) presented anecdotal evidence that none of the 35 females caught between October 1976 and July 1977 was pregnant. Carcasses were collected during the succeeding 4 years (1978–82). The proportion of mature females that was pregnant increased monotonically from 0.09 to 0.35 during this time (Table 4). The difference between years was significant (Table 4) and was paralleled by a significant increase in the proportion of males with active testes between 1978 and 1981 (Table 5), suggesting that a common factor was affecting female and male reproduction during this period. Anecdotal reports (Johannes and MacFarlane 1991) suggested a major die-back of seagrasses in the Torres Strait in the mid-1970's, and Nietschmann (1984) reported that seagrasses were overgrazed in the Torres Strait during 1976–77. Nietschmann and Nietschmann (1981) observed that

wati dangal (lean dugongs with poor-tasting meat) were quite common in the Torres Strait during this period.

Incidence of Breeding

The samples from Townsville (Marsh et al. 1984c) and Daru (H. Marsh and B. Hudson, James Cook University, unpublished data) indicated that neither male nor female dugongs are continuously in breeding condition. The ovaries of non-pregnant females probably contain follicles or corpora lutea in the second half of the year. Sterile cycles seem to be common (Marsh et al. 1984a) and may occur also in Florida manatees (Marmontel 1995, Rathbun et al. 1995).

Mature male dugongs do not continuously produce spermatozoa (Marsh et al. 1984b). Histological examination of the testes of 41 pubertal and mature males from northern Queensland and 141 mature male dugongs from Daru showed that more than half the males in each sample were infertile at the time of sampling. Some of these males had regressed testes (sensu Marsh et al. 1984b), suggesting long-term or permanent sterility (Marsh et al. 1984b). Animals with developed testes (fully spermatogenic or recrudescent testes sensu Marsh et al. 1984c) were a significantly higher proportion of the sample from Daru

Table 4. Differences between years (July 1978–June 1982) in the apparent pregnancy rate of dugongs (*Dugong dugon*) sampled at the Daru fishery in Papua New Guinea. Data from H. Marsh and B. Hudson (James Cook University, unpublished data).

Year[a]	Number of mature females	Apparent pregnancy rate $\pm$ S.E.	
		Confirmed pregnancies	All possible pregnancies
1978–79	75	0.093 ± 0.034[b]	0.107 ± 0.036[c]
1979–80	47	0.191 ± 0.057[b]	0.255 ± 0.064[c]
1980–81	29	0.241 ± 0.079[b]	0.276 ± 0.083[c]
1981–82	17	0.353 ± 0.116[b]	0.353 ± 0.116[c]

[a] 1 July through 30 June.

[b] Difference between years $G = 8.0001$, 3 df, $P = 0.046$.

[c] Difference between years $G = 8.677$, 3 df, $P = 0.034$.

Table 5. The numbers (%) of mature male dugongs (*Dugong dugon*) with active and inactive testes between February and May and between June and January, sampled at the Daru fishery each year between July and June 1978–1981 (H. Marsh and B. Hudson, James Cook University, Townsville, Australia, unpublished data). Animals with regressed testes were omitted from the table because they may have been permanently sterile (Marsh et al. 1984b).

| | February–May | | June–January | |
| | Active testes | Inactive testes | Active testes | Inactive testes |
Year				
1978–79[a]	5 (20)	20 (80)	12 (71)	5 (29)
1979–80	7 (37)	12 (63)	25 (83)	5 (17)
1980–81	6 (46)	7 (54)	14 (93)	1 (7)

[a] The effects of year, season, and testicular activity were not independent ($G_7 = 42.92$, $P < 0.001$); the effect of year was independent of season and of testicular activity ($G_5 = 10.07$, $P = 0.074$); testicular activity was dependent on season ($G_1 = 32.86$, $P < 0.001$).

between June and January than between February and May (Table 5). This seasonal pattern of gonadal activity overlaps that in females. Spermatogenesis also decreased in male manatees in Florida in winter (Hernandez et al. 1995), and the behavior of mating herds also revealed seasonal shifts in frequency (Rathbun et al. 1995).

Births also seem to be diffusely seasonal in dugongs in northern Australia. In the Townsville-Cairns area, dugongs give birth from August–September through November (Marsh et al. 1984c). Dugongs with near-term fetuses (>110 cm body length) were sampled at Daru between July and February (Fig. 2). Seasonal parity has been reported of Florida manatees (Marmontel 1995; O'Shea and Hartley 1995; Rathbun et al. 1995).

Natural Mortality

Reliable data on natural mortality in dugongs are not available. 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 change (Caughley 1977). The age-frequency data from dugongs at Townsville and Daru are not suitable for this analysis. The rates of population change were not known, and the assumption that the populations were stable was not valid. The sample from Townsville was obtained as a result of a massive increase in mortality from the introduction of shark nets. The sample from the Daru fishery was obtained during a time of rapidly changing harvest levels (Hudson 1986) and was not representative because of the ban on taking females with attendant calves. An additional problem was that minimum-age estimates are available only of mature male dugongs because of the loss of growth layers when the tusks wear (Marsh 1980). Admitting these limitations, a crude estimate of the mortality rate calculated from the age-frequency distribution of females drowned in the Townsville shark nets (Marsh 1980) was 0.08 with a 95%

confidence interval of 0.06–0.10 (H. Marsh, James Cook University, unpublished data).

In the absence of reliable natural mortality schedules of dugongs, Marsh (1986) constructed a simple population model by using two mortality schedules based on those developed for population models of another paenungulate, the African elephant (*Loxodonta africana*), by Hanks and McIntosh (1973). This model was extended to three mortality schedules (Table 6). The typically U-shaped mammalian mortality curve (Caughley 1966) was modeled as a step function with levels that corresponded to four different age groups.

Population Dynamics

For each mortality schedule, I constructed population models to determine the annual rate of increase of stable dugong populations for various combinations of pre-reproductive periods and interbirth intervals, chosen to span the range of estimates of pre-reproductive periods and interbirth intervals obtained from carcass analysis (Tables 1 and 3 unpublished data).

The models were based on six simplifying assumptions: (1) the reproduction rate is independent of age during the reproductive part of the female's life span, (2) females cease to bear calves at age 50 or 60 (this age has a minimal effect on the results; Fig. 3), (3) no females live

Table 6. Mortality schedules used for the population models of dugongs (*Dugong dugon*). Mortality is expressed as % of population in various age categories dying per year.

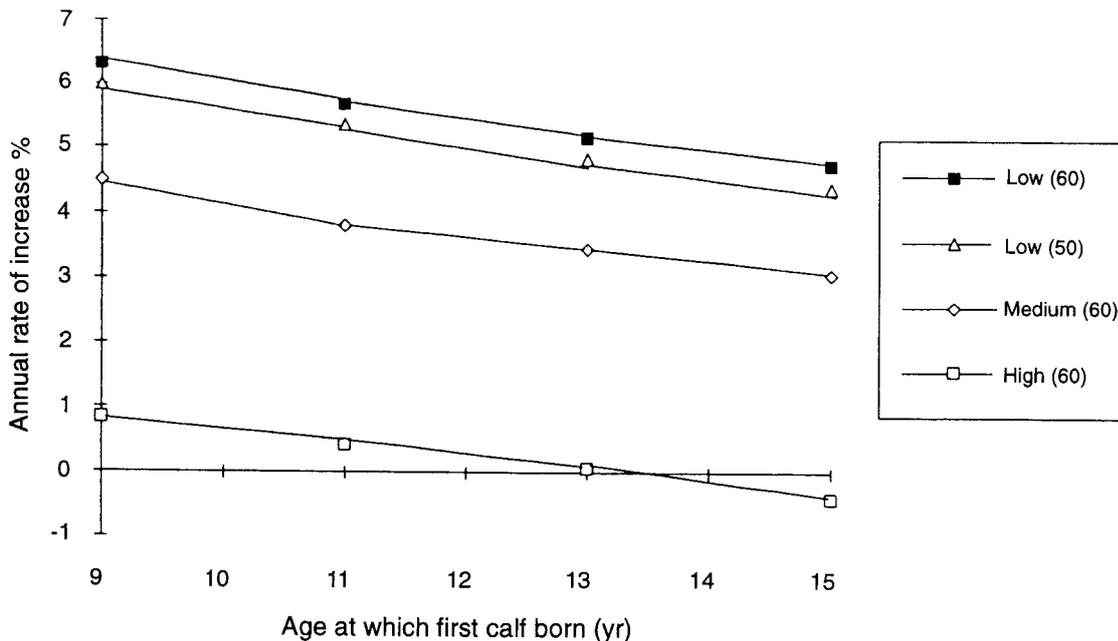| | Age in years | | | |
	0–4	5–45	45–55	55–60
Low mortality	5	1	5	50
Medium mortality	10	2	5	50
High mortality	20	4	5	50

Fig. 3. The effects of the mortality schedules defined in Table 6 and age at which the first calf is born at the annual rate of increase of a dugong (*Dugon dugon*) population with a mean interbirth interval of 3 years. The two graphs of the low mortality schedule show the effect of changing the age at which females bear their last calves at ages 50 to 60. For the medium and high mortality schedules, the graphs are based on the assumption that females bear their last calves at age 60.

Implications for Conservation

beyond age 60 (only 1.5% of females of which absolute age estimates are available were older than 60 years), (4) the sex ratio at birth is 1:1, (5) immigration and emigration do not occur, and (6) the anthropogenic mortality is zero.

Each asymptotic rate of increase was determined by executing the appropriate Leslie matrix model over a 100-year period with an approximate initial stable age distribution that was determined from an analogous continuous model (Pollard 1973). The resultant asymptotic rates of increase were confirmed by using them to modify the conditions of the simulation model.

The models indicated that the expected maximum asymptotic annual rate of increase of an unharvested dugong population is only 6.3% even with the most optimistic combination of life-history parameters derived from the carcass samples and a schedule of low mortality. If the parameters suggested by the Daru sample apply (pre-reproductive period 12 years, interbirth interval 6 years), the estimated annual rate of increase is only 2.4%. The simulations of Marsh et al. (1984c) and Marsh (James Cook University, unpublished data) also indicate the sensitivity of the models to changes in survivorship, particularly adult survivorship, and interbirth interval (Fig. 3; Table 7). The models are less sensitive to changes in the age at first reproduction (Table 7). These patterns are consistent with those predicted by Eberhardt and Siniff (1977) in marine mammals and by Packard (*1985) and Eberhardt and O'Shea (1995) in manatees.

Despite the limited sample sizes, the analyses of specimens from dugong carcasses from various locations in northern Australia and Papua New Guinea indicated that the dugong is a long-lived mammal with a low reproduction rate. The data suggested plasticity in the age and size at which dugongs mature sexually, but the causes of such variation are not known. Neither mature males nor females are continuously in breeding condition, and breeding is diffusely seasonal (Marsh et al. 1984a, 1984b, 1984c). The data from Daru suggested considerable differences between years in the proportions of breeding males and

Table 7. Annual rate of increase of a stable dugong (*Dugong dugon*) population at various combinations of pre-reproductive period and interbirth interval; the assumed mortality schedule is age 0–4 years (5%), 5–45 years (1%), 46–55 years (5%), 56–60 years (50%), and females are assumed to reproduce until they die.

Mean pre-reproductive period (year)	Mean interbirth interval		
	3	5	7
9	6.3	3.7	2.2
11	5.6	3.3	2.0
13	5.1	3.0	1.7
15	4.7	2.7	1.5

females. Anecdotal evidence links these fluctuations in breeding with changes in food availability.

Goodman (1981) pointed out that large mammals have a particular life table; survival is high, fecundity is low, and sexual maturity is usually late. The dugong is an even more extreme example of this life-history strategy than the Florida manatee (Eberhardt and O'Shea 1995; Marmontel 1995). If dugongs are to be conserved, survivorship must be high and anthropogenic mortality, low.

As explained by Marsh (1995), the range of the dugong in Australia extends over a vast area in which all causes of anthropogenic mortality cannot be prevented. Such prevention is unacceptable because it would not allow traditional hunting. A more practical approach is to provide a high level of protection in areas that support large numbers of dugongs. This protection must extend to the seagrass habitat and to the dugongs. Such a policy of zonal ecosystem management exists in the Great Barrier Reef Marine Park (*Great Barrier Reef Park Authority 1983, 1985) and is being extended to other regions by the Australian Government's Oceans 2000 program to establish a national system of protected marine areas.

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[2] An asterisk denotes unpublished material.

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