



Temporal variability in the life history and reproductive biology of female dugongs in Torres Strait: The likely role of sea grass dieback

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ABSTRACT

The extensive sea grass meadows in Torres Strait enable it to be a globally important habitat for the dugong, *Dugong dugon*, a marine mammal of cultural and dietary significance to Torres Strait Islanders and the basis for the substantial island-based fishery in the Torres Strait Protected Zone. Torres Strait sea grass communities are subjected to episodic diebacks which are now believed to be largely natural events. Information on dugong life history was obtained from specimens obtained from female dugongs as they were butchered for food by Indigenous hunters at two major dugong hunting communities in Torres Strait: Daru (9.04°S, 143.21°E) in 1978–1982 (a time of sea grass dieback and recovery) and Mabuiag Island (9.95°S, 142.15°E) in 1997–1999 (when sea grasses were abundant). Dugongs sampled in 1997–1999 had their first calf at younger ages (minimum of 6 cf. 10 years), and more frequently (interbirth interval based on all possible pregnancies 2.6 ± 0.4 (S.E.) yr cf. 5.8 ± 1.0 yr) than the dugongs sampled in 1978–1982. Pregnancy rates increased monotonically during 1978–1982, coincident with sea grass recovery. The age distribution of the female dugongs collected in 1997–1999 also suggested a low birth rate between 1973 and 1983 and/or a high level of mortality for animals born during this period. These results add to the evidence from other regions that the life history and reproductive rate of female dugongs are adversely affected by sea grass loss, the effect of which cannot be separated from a possible density-dependent response to changes in dugong population size. Many green turtles in Torres Strait were also in poor body condition coincident with the 1970s sea grass dieback. The impacts of future sea grass diebacks need to be anticipated when management options for the traditional Torres Strait fisheries for dugongs and green turtles are evaluated.

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1. Introduction

The dugong, *Dugong dugon*, occurs along much of the tropical and sub-tropical coast of Australia from Shark Bay in Western Australia to Moreton Bay in Queensland. Torres Strait (Fig. 1) is the most important area within this region supporting the largest population of dugongs in Australian waters and probably the world (Marsh et al., 1997, 2002). On the basis of wet-weight landings, the dugong fishery is the largest island-based fishery in the Torres Strait Protected Zone (Fig. 1; Harris et al., 1994). Torres Strait Islanders, Papuan coastal villagers, and Aboriginal residents of the Northern Peninsula Area and the Inner Islands hunt dugong and green turtles as part of their traditional way of life and livelihood, which is protected by the *Torres Strait Treaty* between

Australia and Papua New Guinea and these fisheries are listed as Article 22 fisheries under the Treaty.

Green turtles feed on both algae and sea grasses in Torres Strait (André et al., 2005). Dugongs are sea grass community specialists (Heinsohn and Birch, 1972; Marsh et al., 1982; Lanyon et al., 1989; André et al., 2005) and the estimated 13,425 km² (Coles et al., 2003) to 17,500 km² (Poiner and Peterken, 1996) of sea grass in Torres Strait enable the region to be globally important dugong and green turtle habitat. Torres Strait sea grass communities are subjected to episodic diebacks. Such diebacks are probably caused largely by light deprivation resulting from sediment resuspension from two major depocentres on either side of the strait (Saint-Cast, 2008). Prolonged periods of monsoon winds and/or extreme weather events enhance sediment resuspension.

Johannes and MacFarlane (1991) present extensive oral history and some scientific evidence for a widespread and prolonged sea grass dieback in both intertidal and deepwater areas of Torres Strait during the early 1970s. Both the causes and precise dates of this dieback are uncertain. Some Islanders linked the event to pollution resulting from the grounding of the oil tanker, *Oceanic*

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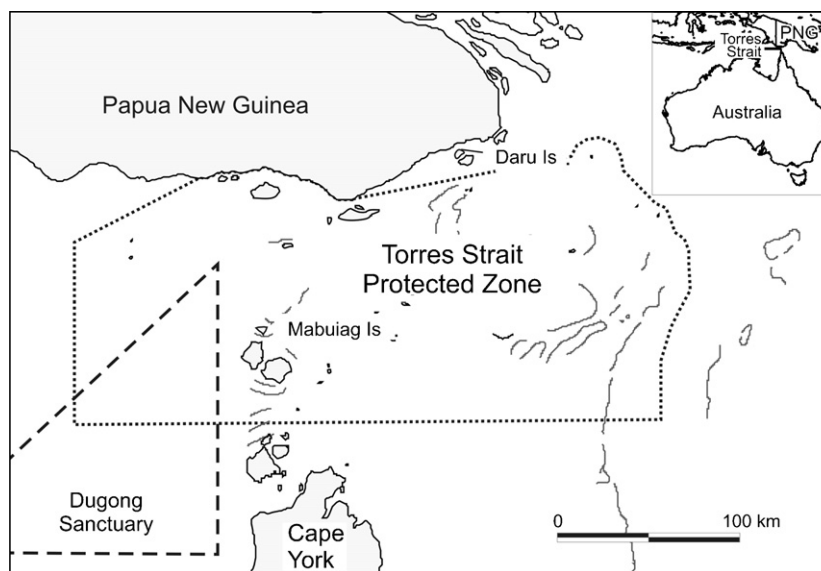


Fig. 1. Map of Torres Strait showing the locations of the Torres Strait Protected Zone, the Dugong Sanctuary and the place names mentioned in the text. The inset figure shows the position of Torres Strait relative to Australia and Papua New Guinea.

Grandeur, in 1970; the limited scientific information about the spill does not support this explanation but it cannot be ruled out (Johannes and MacFarlane, 1991). Nietschmann (1977 unpublished cited by Johannes and MacFarlane, 1991) attributes this dieback to overgrazing by an unusually large numbers of dugongs and green turtles. Both deep and shallow water sea grasses were reportedly affected by the dieback and to have recovered by the early to mid 1980s (Johannes and MacFarlane, 1991).

Subsequent diebacks appear to have been more localized and to have occurred largely in north-western Torres Strait. For example, Poiner and Peterken (1996) report the loss of several hundred km² in north-western Torres Strait in 1991–1992, which they tentatively attribute to high turbidities from flooding of the Mai River in Papua New Guinea. Marsh et al. (2004) provide anecdotal evidence of another dieback event in the Orman Reef area north-east of Mabuiag Island (9.95°S, 142.15°E) in 1999–2000.

Hunters based in Daru (9.04°S, 143.21°E) did not record any pregnant dugongs in the 35 females caught between October 1976 and July 1977 (Hudson, 1986). The observations of Bernard and Judith Nietschmann who spent a year on Mabuiag Island (9.95°S, 142.15°E) studying dugongs from July 1976 (Nietschmann and Nietschmann, 1981, Nietschmann, 1984) and the oral history evidence recorded by Johannes and MacFarlane (1991) indicate that a high proportion of dugongs caught in Torres Strait during the 1970s were lethargic with limited and poor-tasting fat. These 'wati dangal' tended to occur around the shallow lee-sides of islands. The Islanders attributed this unusually high proportion of 'wati dangal' to inadequate food availability (Johannes and MacFarlane, 1991). This conclusion is supported by the oral history evidence of Islanders and the empirical observations of Nietschmann (1984) that the stomach contents of the 'wati dangal', which he collected, contained larger amounts of brown and green algae than the largely sea grass eating 'malu dangal' (deep water dugong which are fatter and considered good eating by Islanders). Evidence from other areas suggests that dugongs eat algae in greater quantities when sea grass is in short supply (Spain and Heinsohn, 1973) and that, in contrast to green turtles, dugongs are not well adapted to using algae as a food source (Marsh et al., 1982).

The objectives of this paper are to (1) review the evidence for temporal variability in life histories and reproductive biology of

dugongs in Torres Strait in the context of information on the changes in the status of its sea grass habitats, and (2) explore the implications of this variation for management of the Indigenous fisheries of Torres Strait and their habitats, especially the dugong fishery.

2. Methods

2.1. Specimen collection and examination

Specimens for life history and reproductive analysis were obtained from dugongs as they were butchered for food by Indigenous hunters at two major dugong hunting communities in Torres Strait: Daru (9.04°S, 143.21°E) in 1978–1982 (Hudson, 1986 and Marsh, 1995) and Mabuiag Island (9.95°S, 142.15°E) in 1997–1999 (Kwan, 2002) (Fig. 1). The body length of each animal was measured according to the protocol outlined in Eros et al. (2000). Age determination using growth layer groups in the tusks followed the technique outlined in Marsh (1980). The entire reproductive tract and/or the ovaries of each dugong were examined macroscopically when fresh, and macroscopically and histologically when formalin-fixed according to the protocols developed by Marsh et al. (1984a). Assessment of the reproductive status of females was generally based on macroscopic examinations of the uterus and ovaries using criteria described by Marsh et al. (1984b) and Boyd et al. (1999). Differences between years in the proportion of pregnant females from Torres Strait were based on the comparative period for which data were available: 1 July to 30 June, in the years 1978–1979, 1979–1980, 1980–1981, 1981–1982 and 1998–1999.

In 1997–1999 only, fat tissue was collected from each of five standard sites on each dugong: three from the dorsal surface and two from the ventral surface as outlined in Kwan (2002). The samples were refrigerated for an hour before the fat depth was measured with a ruler correct to 0.1 cm.

2.2. Sampling biases

Kwan (2002) evaluated the potential biases of sampling from subsistence fisheries in Torres Strait on the basis of her interviews

with hunters and personal observations. The most obvious potential bias of the dugong fishery is the reported Islander preference for meat of fatter females, particularly pregnant animals (Nietschmann and Nietschmann, 1981; Raven, 1990; Johannes and MacFarlane, 1991; Kwan, 2002). However, Kwan's empirical evidence from 1997 to 1999 suggests that most captures of dugongs at that time were opportunistic in terms of sex and size of the catch, although there may have been some indirect selection based on the differential habitat use of different age/sex classes of dugongs (Kwan, 2002). Without more data, we consider that it is impossible to establish whether there were any significant biases in the sampling regime or whether these biases differed in the two sampling periods.

2.3. Statistical analyses

Logistic regression models (generalized linear models with logit link and binomial variance function) were fitted with the proportion of pregnant females (apparent pregnancy rate) as the response weighted by the total number of females examined in the sampling period with the year effect as the independent variable. Likelihood ratio (χ^2 tests) were then used to examine the nested model defined by dropping the year term from the model to test for differences between years.

Mixed effects statistical models were used to determine the differences between reproductive classes in the mean depth of fat from the standard sites. Individuals within each reproductive class were expected to vary randomly about the reproductive class mean and repeated samples were taken from each individual. Mixed models were fitted with a fixed term for average differences in fat depth between the reproductive classes and a random intercept term for individual variation about the reproductive class mean. The random variation between observations on the same individual was the residual. Data are presented as means \pm standard errors (S.E.).

3. Results

3.1. Age composition

The tusks of male dugongs erupt and wear after puberty making age determination using this technique inaccurate for mature male dugongs (Marsh, 1980). Information on sex is not available for many of the tusks collected in 1978–1982 making an

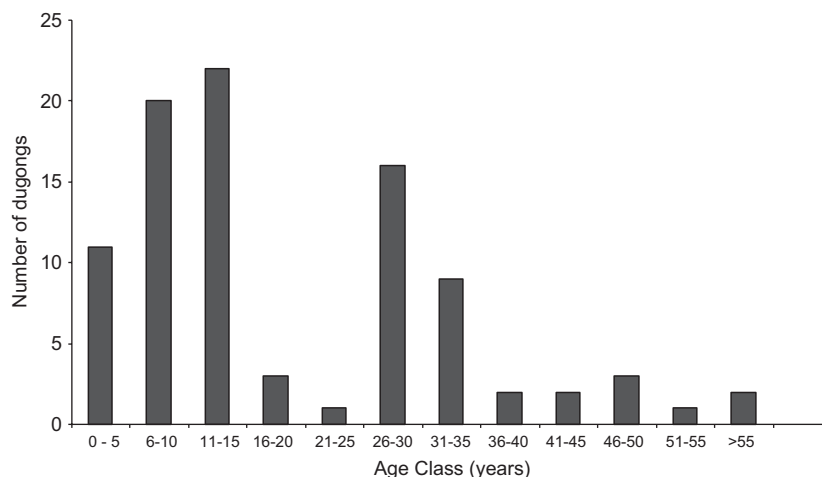


Fig. 2. Age–frequency histogram of 92 female dugongs sampled from landings from the Indigenous fishery at Mabuiag Island in 1997–1999. The females were aged on the basis of the Growth Layer Groups in their tusks.

age–frequency histogram uninformative. The most unexpected feature of the age distribution of the female dugongs collected in 1997–1999 was the low number of animals ($n = 4$) aged between 16 and 25 years in comparison with the numbers aged between 26 and 35 years ($n = 25$) (Fig. 2). This result suggests a low birth rate between 1973 and 1983 and/or a high level of mortality for animals born during this period. The relative low number of animals in the 0–5 and 5–10 age classes presumably reflects the hunters' tendency to avoid small dugongs (Nietschmann and Nietschmann, 1981) because they are not as fat as larger, mature animals (Fig. 3).

3.2. Age and size at first reproduction

Because of the relatively low number of dugongs for which both age and reproductive data are available, especially for the samples collected between 1978 and 1982, we present the data as ranges of ages. The data in Table 1 provide additional evidence of

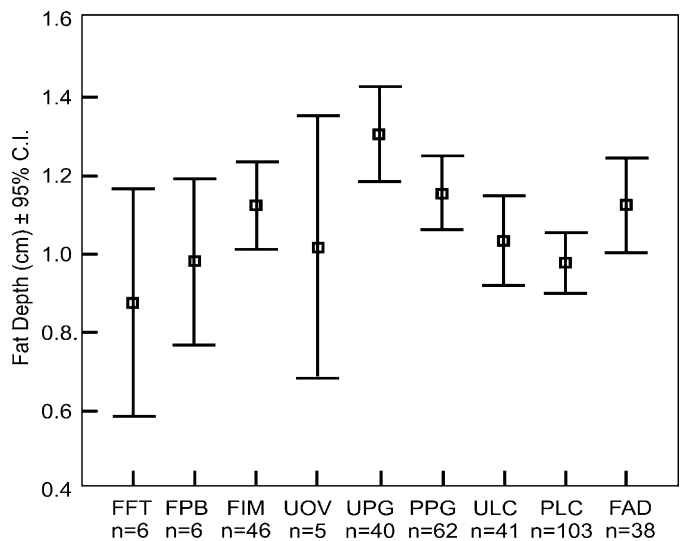


Fig. 3. The mean fat tissue depth collected at standard sites in different reproductive classes of female dugongs sampled from landings from the Indigenous fishery at Mabuiag Island in 1997–1999. Legend: FFT = foetus, FPB = prepubescent, FIM = immature maturing; UOV = primigravid ovulating, UPG = primigravid pregnant, PRG = pregnant (parity unknown), PPG = multiparous pregnant, ULC = uniparous lactating, PLC = multiparous lactating, FAD = adult (no other information available).

Table 1

Comparison of ages of female dugongs of different reproductive status sampled from two Indigenous fisheries in Torres Strait: Daru 1978–1982 and Mabuiaig 1997–1999

	1978–1982 (N = 28)	1997–1999 (N = 105)
Oldest nulliparous (yr)	12	11
Youngest primiparous or primigravid (yr)	13	7
Range ages primiparous/primigravid animals (yr)	13–18	7–14
Youngest with two placental scars (two advanced pregnancies/births)	n/a	8 yr

substantial individual variation in the age of the first pregnancy in dugongs. These data also suggest that (1) dugongs were reproducing at substantially younger ages in 1997–1999 than in 1979–1982; and (2) the dugongs sampled at Mabuiaig in 1997–1999 were breeding several years earlier (≤ 6 yr cf. 10 yr) and at smaller body lengths (minimum size of ~ 2.27 m cf. 2.34 m) than in any other dugong population studied (Boyd et al., 1999).

3.3. Pregnancy rate

The annual pregnancy rate was 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). Calculation of the annual pregnancy rate assumes that (1) the length of gestation is accurately known; (2) all pregnancies are detected; (3) there are no biases as a result of seasonal birthing; and (4) the distribution of reproductive status in the sample is representative of the population (Perrin and Reilly, 1984). Given the possible sampling biases discussed above and the lack of precision of estimates of the gestation period (Boyd et al., 1999), none of these assumptions is likely to be true for this study and so the figures presented here are approximate only. However, the temporal differences should be robust given that both sample sets are from Indigenous fisheries with similar sampling constraints.

We calculated the annual pregnancy rate assuming a gestation period of 14 months (the approximate mid-point of estimates for the gestation period in dugongs, Kwan, 2002) based on confirmed pregnancies (all females with a fetus *in utero*) ranged from 0.15 ± 0.03 in 1978–1982 to 0.33 ± 0.05 in 1997–1999. Pregnancy rates based on all possible pregnancies (all females with corpora lutea in their ovaries irrespective of presence of a fetus) ranged from 0.17 ± 0.03 in 1978–1982 to 0.40 ± 0.06 in 1997–1999.

We also calculated the apparent pregnancy rate (proportion of pregnant females uncorrected for gestation period) based on (1) the proportion of pregnant females based on confirmed pregnancies only, and (2) all possible pregnancies. The apparent pregnancy rate for 1998–1999 was 0.38 ± 0.06 for confirmed pregnancies and 0.46 ± 0.06 for all possible pregnancies significantly higher than the corresponding figures for 1978–1982 (Table 1), both for confirmed ($\chi^2 = 19.9$, d.f. = 4, $p < 0.001$) and all possible pregnancies ($\chi^2 = 25.6$, d.f. = 4, $p < 0.0001$). For all possible pregnancies, repeated contrasts demonstrated that 1978–1979 differed significantly from 1979–1980 ($z = 2.102$, $p = 0.036$), and that no other year differed significantly from the preceding year. As the proportion of pregnant females was lowest in 1978–1979, the above result suggests all years differed significantly from 1978–1979. The corresponding tests for confirmed pregnancies indicated that 1979–1980 ($z = 1.53$, $p = 0.125$) and 1980–1981 ($z = 1.92$, $p = 0.06$) did not differ from 1978–1979. However, 1981–1982 ($z = 2.59$, $p = 0.01$) and 1998–1999 ($z = 3.88$, $p < 0.001$) differed from 1978–1979. These data suggest

Table 2

Comparison of reproductive parameters of mature female dugongs sampled from two Indigenous fisheries in Torres Strait: Daru 1978–1982 and Mabuiaig 1997–1999

Year	N	Confirmed pregnancies	All possible pregnancies
Apparent pregnancy rate \pm S.E.			
1978–1979	75	0.09 ± 0.03	0.11 ± 0.04
1979–1980	47	0.19 ± 0.06	0.26 ± 0.06
1980–1981	29	0.24 ± 0.08	0.28 ± 0.08
1981–1982	17	0.35 ± 0.12	0.35 ± 0.12
1998–1999	73	0.38 ± 0.06	0.46 ± 0.06
Annual pregnancy rate \pm S.E. assuming 14-month gestation			
1978–1982	168	0.15 ± 0.03	0.17 ± 0.03
1997–1999	105	0.33 ± 0.05	0.40 ± 0.06
Calving interval \pm S.E. assuming 14-month gestation			
1978–1982	168	6.8 ± 1.3	5.8 ± 1.0
1997–1999	105	3.1 ± 0.4	2.6 ± 0.4

that the pregnancy rate increased in the early 1980s coincident with the recovery of the sea grass reported by Johannes and MacFarlane (1991).

3.4. Interbirth interval

The interbirth interval is the reciprocal of the annual pregnancy rate. We estimated the calving interval using the following formula:

$$C = G \times \frac{T}{P},$$

where C is the mean interbirth interval, G is the gestation period (assumed to be 14 months) in years, T the total number of mature females in the sample, and P the number of pregnant females (Perrin and Reilly, 1984). The interbirth intervals of dugongs for 1997–1999 based on both confirmed pregnancies (3.1 ± 0.4 yr) and all possible pregnancies (2.6 ± 0.4 yr) were the shortest recorded for dugongs (Boyd et al., 1999) and less than half the corresponding figures for 1979–1982 (Table 2).

3.5. Body condition

The mean fat depth differed significantly among female reproductive classes for the material collected in 1997–1999 ($F = 3.273$, d.f. = 87, $p = 0.0018$) (Fig. 3). The mean was significantly greater than average for primigravid pregnant females ($t = 3.9972$, d.f. = 87, $p = 0.0001$) and approached significance of multiparous pregnant females ($F = 1.8326$, d.f. = 87, $p = 0.0703$) indicating that pregnant females were fatter than the other reproductive classes, empirical confirmation of Islander traditional knowledge (Nietschmann and Nietschmann, 1981; Johannes and MacFarlane, 1991).

4. Discussion

4.1. Reasons for temporal variability in the life histories of dugongs in Torres Strait

Studies of large terrestrial herbivore populations have shown that their population dynamics, particularly age at first breeding and breeding frequency, may be strongly influenced by stochastic variation in the environment and population density (Saether, 1997; Gaillard et al., 2000). Delaying breeding is a common

response of long-lived iteroparous species to adverse environmental conditions and/or high population density (Gaillard et al., 2000). Variation in the age at first reproduction is one of the most important population regulatory mechanisms in large mammals, including marine mammals (Fowler, 1984) and terrestrial herbivores (Gaillard et al., 2000) and is thus a useful index of changes in the reproductive potential of populations (DeMaster, 1981). Age at first reproduction is ultimately determined by phylogenetic and life history traits such as body growth, development and longevity (Harvey and Zammuto, 1985; Flowerdew, 1987). Nonetheless, nutrition and thus body condition affect the onset of sexual maturity in several mammal species (Flowerdew, 1987; Saether, 1997) and the fecundity of young females shows strong variation with changes in environmental conditions and population density (Gaillard et al., 2000).

Nonetheless, the variation we observed in the life history parameters of dugongs in Torres Strait could be the result of one or more of three factors: (1) genetic differences between individuals and populations; (2) a density-dependent response to changes in population size; and (3) density-independent factors (i.e., environmental conditions that alter the food supply in space and time). Each of these mechanisms is evaluated below.

4.1.1. Genetic differences

Genetic differences between dugongs landed in Daru and Mabuiag Island are unlikely, even though dugong hunters from Mabuiag and Daru generally capture animals from regions some 100 km apart. McDonald (2006) has demonstrated using mitochondrial DNA and microsatellite markers that dugong populations in Australian waters are not structured at this relatively fine spatial scale. Sheppard et al. (2006) demonstrated by satellite tracking 70 dugongs between 5 and 551 days on the east coast of Australia that movements over the spatial scale of Torres Strait are common. Twenty percent of the males and females they tracked (including cows with calves) made movements of > 100 km and up to 560 km during the tracking period; a further 40% of tracked individuals made movements of between 15 and 100 km. Aerial surveys (Marsh et al., 1997, 2004) also provide evidence of large-scale dugong movements between surveys. Furthermore, the oral history evidence of Islanders (Nietschmann and Nietschmann, 1981; Nietschmann, 1984; Raven, 1990; Johannes and MacFarlane, 1991) suggest that dugongs in Torres Strait also make extensive movements between areas as well as local-scale movements in response to tidal fluctuations,

4.1.2. Density-dependent influences

The temporal variability in life history parameters of dugongs in Torres Strait could also be a density-dependent response in a population reduced by exploitation. There have been ongoing concerns that dugongs are over-harvested in the Torres Strait region since at least the 1980s (Hudson, 1986; Marsh, 1986; Johannes and MacFarlane, 1991; Marsh et al., 1997). Heinsohn et al. (2004) and Marsh et al. (2004) used two independent modeling techniques which suggest that the present levels of anthropogenic mortality of dugongs in Torres Strait are unsustainable.

The changes in the life history parameters of dugongs in Daru during 1978–1982 (Sections 3.2–3.4; Table 2) were coincident with the collapse of the Daru dugong fishery, suggesting that these changes may be density-dependent responses to population decline. Fecundity in dugongs from Daru increased monotonically from 1978 to 1982 (Table 2). The size of the catch went from 66 in 1978, peaking to 212 in 1979 then to 70 in 1981 and 18 in 1982 (Hudson, 1986). The fishery was closed as a result of a ban on the sale of dugong meat in 1984. Thus a density-dependent response cannot be ruled out for the change in fecundity observed in

1978–1982. Nonetheless, the significant increase in dugong fecundity between 1978–1979 and 1979–1980 may be too rapid to be explained by a density-dependent response to population decline in the absence of simultaneous environmental effects on food availability and/or quality.

The differences between the reproductive parameters of the dugongs sampled at Mabuiag between 1997–1998 and those from Daru in 1979–1982 (Sections 3.2–3.4 and Table 2) and other dugong populations (Boyd et al., 1999) also lend support to the hypothesis that the temporal variation in dugong life history and reproductive rates in Torres Strait is influenced by changes in dugong population density. However, this hypothesis is impossible to prove or disprove, especially given the aerial survey evidence from Torres Strait and other areas (Preen and Marsh, 1995; Gales et al., 2004; Marsh et al., 2004) that some dugongs move in response to sea grass dieback, effectively changing the size of the dugong population dependent on various sea grass meadows, so that population density and environmental variation are confounded.

4.1.3. Density-independent influences: sea grass dieback

The observed difference between dugong life history parameters between 1978–1982 and 1997–1999 may also have been a response to fluctuations in environmental conditions, especially the difference between the widespread and prolonged sea grass dieback in the 1970s (for references, see Johannes and MacFarlane, 1991) and the abundance of sea grass in the late 1990s (Long and Poiner, 1997; Taranto et al., 1997). When their food supply fails, individual dugongs variously exhibit one of two functional responses: (1) move from the affected area as explained in Section 4.1.2 above; and/or (2) stay and consume low quality food such as algae and less nutritious sea grass genera. Such plants have also been reported in the stomachs of dugongs following the loss of sea grass pastures in other parts of their range (Spain and Heinsohn, 1973; Marsh et al., 1982; Preen and Marsh, 1995). For example, following severe damage to sea grass beds in Townsville caused by a cyclone in 1971, unusually high proportions of algae and the sea grasses *Cymodocea* and *Thalassia* were recorded in the stomachs of many dugongs drowned in shark nets in the following year of the cyclone (Spain and Heinsohn, 1973; Marsh et al., 1982).

The sea grass *Thalassia* constituted a high proportion (30–50%) of stomach contents of dugongs killed by Indigenous hunters from Mabuiag both during the period of extensive sea grass dieback in Torres Strait in the 1970s ($n = 16$; Nietschmann and Nietschmann, 1981) and in 1997–1999 ($n = 128$; André et al., 2005). Thus, *Thalassia* appears to be a staple food for the dugongs which are accessible to hunters in Torres Strait, despite its not being favored by dugongs in the Townsville region. The biggest difference in the sea grass consumed by dugongs in the two sampling periods was the consumption of *Enhalus acaroides*. *E. acaroides* comprised 35.6% of the stomach contents of the 16 dugongs which died in March–June 1977 (Nietschmann and Nietschmann, 1981) but was only consumed in trace amounts (<0.3%) by the dugongs caught in 1997–1999, despite its abundance at that time in the Orman Reef area where most of the dugongs were caught (André et al., 2005). Dugongs seem to be ill-adapted to feed on *E. acaroides*, a large and fibrous species, and apparently do not eat *E. acaroides* rhizomes (Marsh et al., 1982).

Taken together, the evidence presented here suggests that the environmental conditions affecting dugongs in Torres Strait in the 1970s were widespread: (1) Daru hunters reported that no pregnant females were landed in 1976–1977 (Hudson, 1986); (2) the pregnancy rates reported in Table 2 are the lowest ever recorded for dugongs (see also Boyd et al., 1999); (3) lethargic, thin and poor-tasting 'wati dangal' were unusually abundant

(Johannes and MacFarlane, 1991); and (4) the age structure of female dugongs sampled at Mabuiag Island in 1997–1999 suggests a low recruitment in age classes of animals born from about 1972 to 1983 (Fig. 2), a period which includes the period of documented low fecundity of dugongs landed at Daru (Table 2).

Dugongs in poor condition are unlikely to breed. The Islanders claim that the females in the best condition are either pregnant or those seen mating, feeding or traveling with a male (Nietschmann and Nietschmann, 1981). The data in Fig. 3 which indicate that pregnant females were fatter than the other reproductive classes, provide empirical confirmation of Islander traditional knowledge (Nietschmann and Nietschmann, 1981; Johannes and MacFarlane, 1991).

The high fecundity of the dugongs sampled in Torres Strait in 1997–1999 may not be as exceptional as the data presented by Boyd et al. (1999) suggest. The life history parameters reported from dugongs from two other localities in northern Australia, Townsville in 1969–1981 (Marsh et al., 1984b) and Mornington Island in 1976–1977 (Marsh et al., 1984b), also reflect periods where there were substantial losses of sea grass beds caused by extreme weather events: cyclone damage in Townsville (Marsh et al., 1982; Heinsohn and Spain, 1974) and large-scale flooding of the Gulf of Carpentaria in 1973–1974. Sea grass loss has been associated with a reduction in the proportion of dugongs seen during aerial surveys that are classified as calves in Hervey Bay (Preen and Marsh, 1995) and in the Orman Reef region of Torres Strait in 2001 (Marsh et al., 2004).

We consider the most likely reason for the differences between the life history parameters observed in dugongs from Daru in 1978–1982 and Mabuiag Island in 1997–1999 was the large-scale sea grass dieback in the 1970s, possibly exacerbated by a density dependent response to reduced competition for food by a population reduced by harvesting. In large-herbivore populations, environmental variation and density dependence co-occur and have similar effects on various fitness components (Gaillard et al., 2000). As demonstrated in ungulate species, obtaining quantitative evidence to determine the relative importance of density dependence and environmental stochasticity on population dynamics is very difficult (see Aanes et al., 2000). Comparing the effects of both harvesting and natural processes operating simultaneously on population dynamics is even more difficult (Solberg et al., 1999).

4.2. A comparison with the effect of the sea grass dieback on green turtles

Dugongs and green turtles tend to be hunted together using similar equipment in Torres Strait (Marsh et al., 1997). Green turtle life history traits such as growth and breeding rates also vary with environmental factors (Limpus and Nicholls, 1988; Chaloupka et al., 2004). For example, the number of green turtles that breed each year increases 1.5 years following an El Niño event (Limpus and Nicholls, 1988). Green turtles show strong site fidelity to particular foraging areas, and recent studies have found significant spatial and temporal differences in proxies of both body condition and growth (Chaloupka et al., 2004; Hamann et al., 2002, 2005).

Therefore, it is not surprising that Nietschmann and Nietschmann (1981), Nietschmann (1984) and Johannes and MacFarlane (1991) report the presence of 'gatau waru', lethargic and poor-tasting green turtles with thin black fat, during the 1970s concurrently with the large numbers of 'wati dangal'. There were four La Niña years between 1971 and 1975, producing conditions unfavorable for green turtles preparing to breed. Johannes and MacFarlane (1991) disputed that green turtles could have been

affected by the sea grass dieback *per se* because of evidence that green turtles in Torres Strait mainly eat algae. However, Johannes and MacFarlane's argument was based on data collected in years with low sea grass abundance. Nietschmann (1981) reported that the stomach contents of the six green turtles he collected in 1976–1977 contained 90–100% algae, 5–10% sea grass. Algae also constituted 90% of the food in the stomachs of the 44 green turtles collected from Torres Strait in 1979 (Garnett et al., 1985). However, both these data sets from the second half of the 1970s could reflect large-scale sea grass dieback and annual variation in regional climatic drivers such as the Southern Oscillation. In contrast, in 1997–1998, a strong El-Niño year, the stomach contents of 26 green turtles collected at Mabuiag during 1997–1998, contained a mixture of algae and sea grasses, especially *E. acaroides* and *Thalassia hemprichii* (André et al., 2005). Collectively, these results suggest that green turtles eat more sea grass when it is abundant and that their condition was also adversely affected by the 1970s sea grass dieback with consequent impact on the traditional fisheries of Torres Strait.

4.3. Implications for managing the marine environment of Torres Strait

The data presented here add to the evidence that dugongs respond to large-scale sea grass dieback by using at least two strategies: (1) move away from the affected area, and/or (2) postpone breeding. As episodic sea grass diebacks occur relatively frequently in Torres Strait, it will be imperative to consider them in marine planning and fisheries management.

Habitat protection needs to focus on maintaining habitats containing high quality forage for dugongs and green turtles (see Sheppard et al., 2007; Sheppard et al., 2008). The impact of sea grass dieback events can be exacerbated by poor land-use activities (Preen and Marsh, 1995; Preen et al., 1995). Herbicides including diuron (associated with agricultural land use, primarily sugarcane production) found in nearshore sediments along the eastern coast of north Queensland (Haynes et al., 2000a) have the potential to impact local sea grass communities (see Haynes et al., 2000b) and human health. Co-operation between Australia and PNG will be essential to ensure that future land use in the region does not compromise water quality in Torres Strait. This matter and the associated potential impacts on human health are of long-standing concern to Islanders, (e.g. Dight and Gladstone, 1993).

4.4. Implications for managing the traditional fisheries of Torres Strait

The 'National Partnership Approach' to the management of Indigenous hunting of turtles and dugongs in Australia (<http://www.deh.gov.au/coasts/species/turtles/national-approach.html>) is being implemented by the Australian Department of the Environment, Water, Heritage and the Arts in cooperation with the relevant Australian state and territory governments and Indigenous organizations, including the Torres Strait Regional Authority. The Regional Activity Plan for Torres Strait developed to guide the implementation of activities under this project includes four key components: community management plans, monitoring programs, catch sharing, and education and awareness-raising.

The methods to be used by Torres Strait communities to implement these components of the Regional Activity Plan have yet to be negotiated. It will be important to consider management options in the context of the high likelihood of further sea grass dieback events and their impact on dugong and green turtle populations in the region. For example, if fisheries output controls such as total allowable catches are favored, they will need to take

the impact of sea grass dieback into account as demonstrated by Heinsohn et al. (2004) and Marsh et al. (2004). Alternatively, if Islander communities are interested in spatial management tools such as area closures or designated hunting areas, these options will need to be evaluated in the context the high likelihood of substantial dugong movements in response to sea grass dieback and recovery (Marsh et al., 2004) which can alter the accessibility of dugongs to hunters. For example, the recovery of the sub-tidal sea grass beds in the 1980s (Johannes and MacFarlane, 1991) may have contributed to the collapse of the Daru dugong fishery. The Daru hunters tended to hunt on the top of Warrior Reef (Hudson, 1986). If the dugongs dispersed as the sub-tidal sea grass beds recovered, they would have been less accessible to the hunters. Kwan (2002) reports changes in the spatial pattern of hunting effort in 2001 in response to dugongs moving close to the main urban areas of Torres Strait, possibly in response to sea grass dieback in the Orman Reef region.

As Islander fishermen are likely to be the first to observe sea grass dieback and the associated increase in 'wati dangal', a community-based GIS system to enable them to record their observations and share them with other communities would be a very valuable education and management tool. Management and monitoring clearly need to be coordinated across the region at ecologically relevant scales. Community management plans should not be developed in isolation by individual communities. The simultaneous occurrence of large numbers of 'gatau waru' and the sea grass dieback in the 1970s suggest that these factors will also need to be taken in to account when developing management plans for the green turtle fishery.

5. Conclusions

In Torres Strait, episodic sea grass diebacks are natural events which significantly decrease dugong reproductive rates and cause some dugongs to move from affected areas. Community-based management options for the dugong and green turtle fisheries need to be developed with the expectation that the diebacks will continue to occur. Management of these fisheries needs to anticipate sea grass dieback in a manner conceptually similar to the need to 'drought proof' terrestrial primary industries in drought-prone regions.

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