CSIRO PUBLISHING

www.publish.csiro.au/journals/wr *Wildlife Research*, 2004, **31**, 283–290

Change in abundance of dugongs in Shark Bay, Ningaloo and Exmouth Gulf, Western Australia: evidence for large-scale migration

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Abstract. The third in a series of five-yearly aerial surveys for dugongs in Shark Bay, Ningaloo Reef and Exmouth Gulf was conducted in July 1999. The first two surveys provided evidence of an apparently stable population of dugongs, with ~1000 animals in each of Exmouth Gulf and Ningaloo Reef, and 10000 in Shark Bay. We report estimates of less than 200 for each of Exmouth Gulf and Ningaloo Reef and ~14000 for Shark Bay. This is an apparent overall increase in the dugong population over this whole region, but with a distributional shift of animals to the south. The most plausible hypothesis to account for a large component of this apparent population shift is that animals in Exmouth Gulf and Ningaloo Reef moved to Shark Bay, most likely after Tropical Cyclone Vance impacted available dugong forage in the northern habitat. Bias associated with survey estimate methodology, and normal changes in population demographics may also have contributed to the change. The movement of large numbers of dugongs over the scale we suggest has important management implications. First, such habitat-driven shifts in regional abundance will need to be incorporated in assessing the effectiveness of marine protected areas that aim to protect dugongs and their habitat. Second, in circumstances where aerial surveys are used to estimate relative trends in abundance of dugongs, animal movements of the type we propose could lead to errors in interpretation.

Introduction

The dugong, *Dugong dugon*, is an internationally recognised threatened species. Coastal marine habitats around northern Australia remain the last substantial stronghold. Even within these waters, declines in dugong populations have been recorded in some areas (Marsh *et al.* 1996), anthropogenic pressures being a likely contributor (Marsh 2000). Aerial surveys designed to estimate dugong abundance have become the primary tool to quantify the spatial and temporal characteristics of dugong populations and to determine trends in population fluctuations.

Shark Bay supports an internationally significant population of dugongs. Two methodologically standardised aerial surveys (following Marsh and Sinclair 1989*a*, 1989*b*) conducted during the winter months of 1989 and 1994 resulted in minimum population estimates of 10146 ± 1665 (s.e.) and 10529 ± 1464 respectively (Marsh *et al.* 1994; Preen *et al.* 1997). Both surveys reported a density of 0.71 ± 0.12 dugongs km^{-2}, the highest recorded for any areas in which similar surveys had been undertaken. The proportion of dugongs classed as calves was higher in both surveys than recorded elsewhere: 19% (Marsh *et al.* 1994) and 16.6% (Preen *et al.* 1997). These survey data indicate that during the winter months Shark Bay supports a large, apparently stable and reproductively active dugong population. Whilst there has been no equivalent aerial survey conducted during the summer months when the shallow waters of Shark Bay warm up, more limited data and observations indicate a substantially different distribution (Anderson 1982, 1986). These distributional changes are probably driven by the dugongs' energy budget, influenced by both water temperature and the ephemeral nature of their forage species. The patterns of dugong seasonal movements within Shark Bay are not understood and are the subject of current investigations utilising radio-telemetry and satellite GPS technology. One crucial question is whether or not dugongs move from Shark Bay on a seasonal basis, and whether the abundance estimates of dugongs in winter

10.1071/WR02073 1035-3712/04/030283

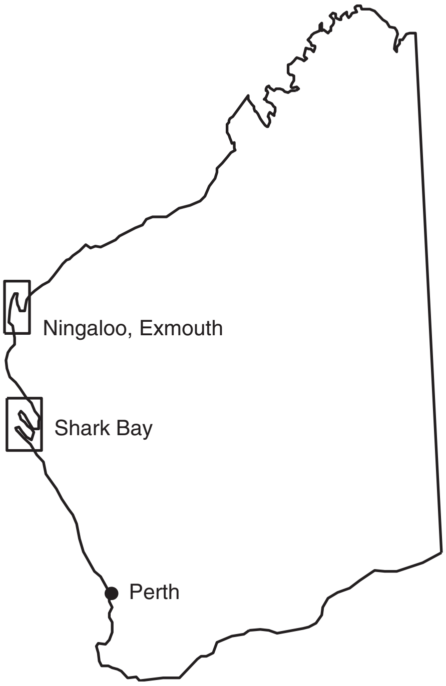

Fig. 1. Regional area and locations of surveys.

represent the entire Shark Bay population. During the 1989 and 1994 aerial surveys of Shark Bay (Marsh *et al.* 1994; Preen *et al.* 1997), waters to the north of Shark Bay, comprising the inshore waters of Ningaloo Reef and Exmouth Gulf (Fig. 1), were also surveyed for dugongs and other marine megafauna. Whilst the Ningaloo Reef flight paths in 1989 and 1994 were different, the estimates for dugong abundance were ~1000 dugongs in each of these two areas (Preen *et al.* 1997). It is not known to what degree, if any, the Shark Bay, Ningaloo Reef and Exmouth Gulf dugong populations mix.

In order to monitor trends in dugong populations from aerial surveys, Marsh and Saalfeld (1989) recommended a five-year gap between surveys. We report on the results of an aerial survey conducted in July 1999, representing the third in the series of five-yearly winter surveys for the Shark Bay, Ningaloo Reef and Exmouth Gulf dugongs.

Methods

A description of the study areas (Fig. 1) is provided by Preen *et al.* (1997). For a description of the survey design and counting procedures see Marsh *et al.* (1994).

The three aerial surveys were conducted between 8 and 16 July 1999. Previous surveys were conducted at similar times (4–11 July 1989 and 21–30 June 1994: Marsh *et al.* 1994; Preen *et al.* 1997). The strip-transect survey design used in this study replicated as closely as possible that undertaken during the previous surveys of this area. The transects flown in Shark Bay and Exmouth Gulf were identical to previous surveys (Fig. 1). Earlier surveys of Ningaloo Reef varied in transect design. In this survey we followed Preen *et al.* (1997) in the selection of 43 east–west Ningaloo Reef transects, but selected the 20-m depth contours as the westerly end of each transect. West of this depth was across the fringing reef crest into open ocean, where the water rapidly deepened and dugongs were not expected to be found.

All transects were east–west oriented. In Shark Bay transects were set every 2.5′ of latitude (4.63 km) apart, except for transects at the very southern ends of the eastern and western half of Shark Bay. In southern Shark Bay transects were every 5′ of latitude (9.26 km) because few, if any, dugongs were expected in these cool waters during winter.

A Partenavia 68B aircraft equipped with aviation-approved pseudowing-struts (transect markers) was used for the survey (Marsh 1995). Flights were conducted during good weather only (Beaufort sea state ≤ 3) and at times that minimised glare (mid-morning and/or mid-afternoon). Flying times were limited to a maximum of ~3.5 h (based on fuel capacity and mass of aircraft load). When weather conditions permitted, two flights were conducted each day. The survey altitude was 137 m (450 ft) flown at 185 km h^{-1} (100 kn). At this survey altitude, the transect markers delineated a 200-m-wide transect on the water surface on either side of the aircraft. The survey crew comprised the pilot-navigator, survey leader/data recorder and four observers organised as two tandem teams (as per Marsh and Sinclair 1989*a*, 1989*b*). The same survey crew and pilot were used for each survey, with all observers experienced in aerial survey techniques. Counting procedures and data recording followed Marsh and Saalfeld (1989). Observers recorded, in order of priority, the numbers of dugongs (including calves), other large marine vertebrates, as well as sighting conditions.

Data handling and analysis were similar to those used in previous dugong surveys (Marsh and Sinclair 1989*a*, 1989*b*; Marsh *et al.* 1994; Preen *et al.* 1997; Caughley and Grigg 1981). Since the transects varied in area, the ratio method (outlined in Marsh and Saalfeld 1989) was used to estimate the population size for each survey. The population estimates were corrected for the sampling fraction and adjusted to incorporate errors associated with availability and perception correction factors (after Marsh and Sinclair 1989*a*, 1989*b*). Errors were calculated according to Caughley and Grigg (1981) for the variance due to the population estimate derived by the ratio method and Marsh and Sinclair (1989*a*, 1989*b*) for the variance of the availability and perception factors and the total variance.

For availability correction factors, untested assumptions are made that the proportion of time spent at the surface will not vary with depth, time, location and dugong behaviour, and that the water visibility and depth regime for the surveys recorded here was similar to that in Moreton Bay. Whilst these assumptions may be invalid, this calculation offers an appropriately standardised method for comparing surveys conducted in the same locations at similar times, which was the case with this set of surveys.

To avoid overestimation of dugong, herds (groups of >10 dugongs) were stratified out prior to calculating background density, then added in later to produce population and density estimates per zone. This is as per previous dugong-survey calculations (Marsh and Sinclair 1989*a*).

During each flight, a GPS downloaded track data in the form of locations every two seconds into a laptop computer. Latitude and longitude coordinates were converted to UTM values (Eastings and Northings) and the track smoothed using a running, second-order curve-fitting process. The smoothed aircraft UTM coordinates were then used to derive the area surveyed and the exact location of each group of dugongs sighted. In Shark Bay the total survey region was assumed to be 14239 km^2, based on the estimate of Marsh *et al.* (1994), who used a digitising tablet on a 1:250000 map of the area. The area of Exmouth Gulf was assumed to be 3180 km^2, based on the estimate from Preen *et al.* (1997). Digitised bathymetry data (Australian Chart series AUS 331) were used to interpolate the depth of water in which each dugong was sighted.

Results

Shark Bay

The sightings data and transect locations for the Shark Bay surveys are shown in Fig. 2. Details of sightings for each survey are shown in Table 1. The area surveyed was 1186 km^2, which represented 8.31% of the overall Shark Bay survey area. We counted 534 dugongs in 356 groups. Two herds of 41 and 35 dugongs were encountered. The distribution of group sizes is shown on Fig. 3. The mean group size, excluding the two largest groups, was 1.294 ± 0.089 (95% confidence limit). In all, 26 calves were sighted in 23 groups, representing 4.87% of the total number of animals. Calves tended to occur in groups of several animals, with the mean group size containing calves at six, and the median at two (note that the two large herds of 35 and 41 animals each had two calves present and are included in these calculations). Single dugongs represented 83% of all group sightings. The distribution of group sizes shows a strong skew towards a group size of one.

Data on group size and correction factors are presented in Table 2. Using these values, the overall dugong population in Shark Bay was estimated to be 13929 ± 1652 (s.e.). This gives a density of 0.98 dugongs km^{-2}. This population estimate was calculated using the same methods as per the previous Shark Bay surveys (Marsh *et al.* 1994; Preen *et al.* 1997). We found that a crucial factor in determining the final population estimate was the determination of group size. The calculations as defined by Marsh and Sinclair (1989*a*) are made on groups, not individual dugongs. Hence the availability and perception corrections are calculated on groups, and these are then translated to an estimate of number of groups in the survey area. The choice of correction factor, to then convert estimated groups in the survey area to numbers of dugongs, is then crucial. From Fig. 3 it can be seen that the size distribution of dugong groups is highly skewed to a group size of one. Using a group size of one (the median group size with or without the two groups of >10 animals) in the calculations gave a population estimate of 10766 ± 1284 (s.e.) dugongs, whereas using the mean group size of 1.500 ± 0.301 (95% confidence limits) by including all groups in the calculation of the mean group size, gave a population estimate of 16149 ± 1919 (s.e.) dugongs. These are significantly different from the estimate of 13929 ± 1652 dugongs calculated using the mean group size for groups <10, and indicate that the population estimate is highly sensitive to the method used to estimate group size.

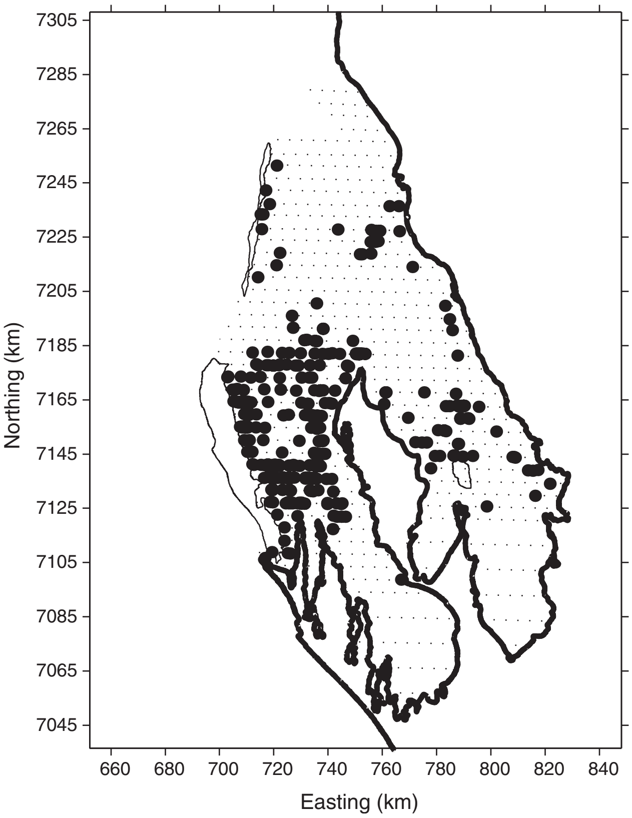

Fig. 2. Locations of dugong groups sighted within Shark Bay and the transects flown (dotted lines).

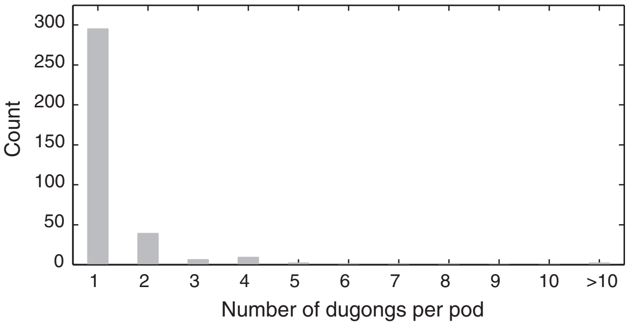

Fig. 3. Distribution of dugong group sizes for Shark Bay sightings.

The depth distribution of groups in Shark Bay is shown on Fig. 4. The mean water depth for each dugong group was 8.4 ± 0.5 (95% confidence limits) m. The distribution is slightly skewed towards shallow water. Dugong observations relative to sea surface temperatures (SST) are shown in Fig. 5. The SST image data were obtained from an Advanced Very High Resolution Radiometer (AVHRR) image taken on 9 July 1999. The mean water temperature for all dugong groups was 18.7 ± 4.1°C.

Ningaloo Reef and Exmouth Gulf

The sighting details for Ningaloo Reef and Exmouth Gulf are shown on Table 1, while the calculated availability and perception factors and their coefficients of variation are shown in Table 2. No calves were sighted along Ningaloo reef or in Exmouth Gulf. The maximum group size for Ningaloo sightings was two, to give a mean group size of 1.278 ± 0.229. All groups sighted in Exmouth Gulf were of single animals. The sample sizes for these surveys were too

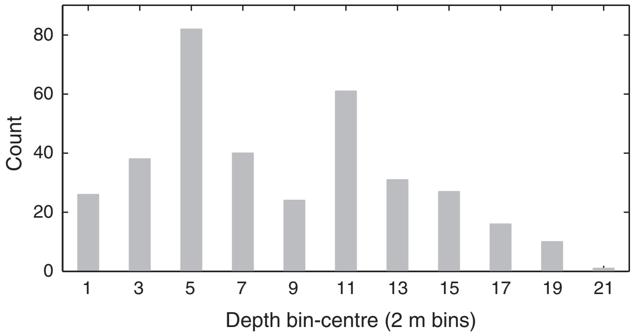

Fig. 4. Depth distribution of Shark Bay groups.

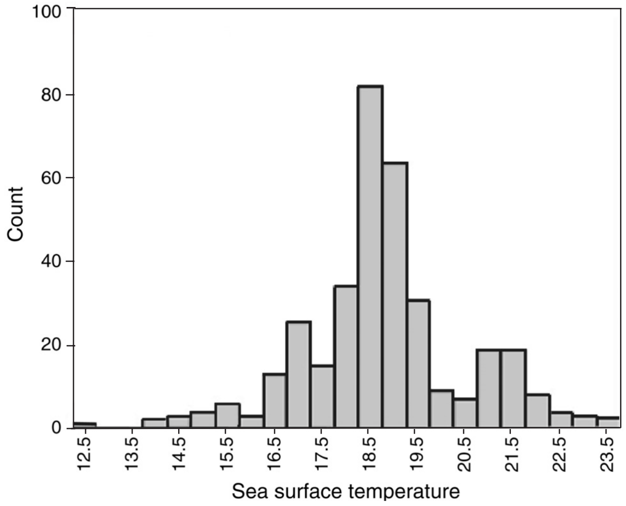

Fig. 5. Distribution of dugongs in relation to sea surface temperature.

low to give meaningful perception and availability factors, or their variability.

Using the respective mean group size, the estimated population of the Ningaloo Reef area was 163 ± 148 (s.e.) dugongs and for Exmouth Gulf, 174 ± 82 dugongs. Dugong densities were estimated at 0.040 km^{-2} and 0.055 km^{-2} for Ningaloo and Exmouth respectively.

Discussion

We report substantial changes from earlier surveys in the dugong abundance estimates of the three regions surveyed. The Shark Bay dugong population was estimated to be ~10 000 in 1989 and 1994 (Marsh *et al.* 1994; Preen *et al.* 1997). Using the same techniques, our estimate of 13 929 represents a 40% increase from these previous estimates. Further, the estimates for abundance in the Ningaloo Reef and Exmouth Gulf regions by Marsh *et al.* (1994) and Preen *et al.* (1997) were of ~1000 dugongs at each location (allowing for different coverage of the Ningaloo region between surveys). These 1999 stock size estimates of 163 and 174 for Ningaloo Reef and Exmouth Gulf respectively suggest an approximate 6-fold reduction in stock size compared with 1989 and 1994. We propose three possible hypotheses to explain these changes:

(1) the changes in abundance estimates were an artefact of errors in survey design and implementation and/or the use of correction factors;
(2) the changes in abundance estimates were real, and result from changes in fecundity and/or survival in the dugong populations in the three regions; or,
(3) the changes in abundance estimates were real, and reflect large-scale movements of dugongs between the regions surveyed and possibly regions further north.

Hypothesis 1

If the differences in estimates of dugong abundance were an artefact of methodological error, they must arise from factors to do with observer performance, environmental conditions (e.g. sea state, turbidity or tidal regime) or from assumptions associated with the availability correction factor. The abundance estimates are sensitive to changes in the correction factors. All other aspects of the methods were essentially identical for the three sets of aerial surveys.

All surveys used observers experienced in aerial survey, with an initial training period specifically to sight dugongs prior to the formal survey. The reliability of the observers can be assessed by the degree to which the mid- and rear-seat

Table 1. Details of sightings for the three aerial surveys

	Shark Bay	Ningaloo Reef	Exmouth Gulf
Total groups (port/starboard)	356 (161/195)	18 (10/8)	6 (1/5)
Total dugongs (port/starboard)	534 (293/241)	23 (14/9)	6 (1/5)
Groups port – forwards only	17	0	0
Groups port – rear only	18	2	0
Groups port – both	126	8	1
Groups starboard – forwards only	36	0	3
Groups starboard – rear only	10	3	0
Groups starboard – both	149	5	2
Transect flown	69	43	19
Total area searched (km^2)	1186	570	273

Table 2. Mean perception and availability factors for each survey, using dugong group sizes of <10

Survey	Groups observed	Groups available	Perception correction	Perception c.v.	Availability correction	Availability c.v.
Shark Bay						
Port	161	163	1.0151	0.0024	2.5714	0.1287
Starboard	195	197	1.0124	0.0021	2.4149	0.1288
Both	356	360	1.0152	0.0017	2.4891	0.1021
Ningaloo Reef						
Port	10	10	1	0	0.4286	0.969
Starboard	8	8	1	0	0.6667	0.9483
Both	18	18	1	0	0.5217	0.174
Exmouth Gulf						
Port	1	1	1	0	2.4891	0.0908
Starboard	5	5	1	0	2.4891	0.0908
Both	6	6	1	0	2.4891	0.0908

observers make dual sightings, as opposed to sightings made by only one member of the port- or starboard-side pair (Marsh and Sinclair 1989*a*). As the level of observer concurrence increases, the perception correction factor will approach unity. Values of 1.02–1.20 have been reported for multiple surveys in Queensland (Marsh and Sinclair 1989*a*), and these values encompass those reported during the 1989 (1.03) and 1994 (1.04–1.11) dugong surveys in Shark Bay, Ningaloo Reef and Exmouth (Marsh *et al.* 1994; Preen *et al.* 1997). We report values of 1.015 and 1.012 for the port and starboard perception correction factors. These correction factors are lower than the earlier values and indicate a high level of observer precision. Greater observer precision has the effect of slightly lowering the abundance estimate. For example, if we use the higher perception correction factors from the previous surveys for the Shark Bay estimates they have the effect of increasing the estimate by 1–2%.

The survey we report was flown during a similar mid-winter season as the previous surveys. Sea surface temperatures were comparable to those previously reported. Sea state conditions were consistently below Beaufort level 2 or 3 (as in previous surveys) and the mid-morning, mid-afternoon flight times would be expected to have been flown in times of similar glare conditions. Indeed, it appears that glare had no significant effect on dugong sightings as the number of animals seen on the glare-affected northern view from the aircraft (starboard side when flying west, port side when flying east) was not significantly different from the number of animals seen on the relatively glare-free southern view (Mann–Whitney rank sum test: t = 4795.5, P = 0.998).

Water turbidity is a factor that affects dugong visibility. This variable is incorporated into the calculation of the availability correction factor that accounts for the proportion of dugongs on the surface compared with those seen below the surface, and should compensate for turbidity differences. Nevertheless, it might be expected that biases in abundance estimates, or at least in estimates of their coefficients of variation, could result with surveys conducted at times of significantly different turbidity. This argument is based on the principle that reducing the availability of animals (through turbidity) to a mark–recapture-based population- estimate model (as in this case) will decrease the accuracy of the estimate. It is not possible to quantify turbidity from the air in surveys such as these. However, if, for example, the survey waters were less turbid during our survey (compared with the previous two), we would expect to sight relatively more animals below the surface, and hence calculate a lower availability correction factor. For Shark Bay, our calculated availability correction factor was 2.49 (c.v. = 0.10), which was in close accord to the 2.45 (0.12) calculated from the 1989 survey (Marsh *et al.* 1994), but was indeed substantially lower than the 3.35 (0.12) calculated for the 1994 survey (Preen *et al.* 1997). As Preen *et al.* (1997) reported seeing about the same number of animals as reported by Marsh *et al.* (1994), then the higher availability correction factor must have resulted from seeing more animals on the surface. This may have resulted from differences in viewing conditions (turbidity in this case), or from differences in diving behaviour of the animals. Consequently, differences in turbidity may have contributed to some of the abundance comparisons between this and the 1994 survey, but probably not between this and the 1989 surveys.

Water depth and tidal regime may also account for some of the differences between this and the 1989 and 1994 surveys. Dugongs observed during this survey were in waters generally <10 m deep (Fig. 4) compared with the 1989 survey, in which 57% of dugongs sighted were in depths of more than 12 m (Marsh *et al.* 1994). No data are available on distribution of dugongs relative to tidal fluctuation during these surveys, however Lanyon (unpublished data) found a 43% decrease in dugong population estimate during a low-tide survey of Moreton Bay banks compared with a high-tide survey on the same day under otherwise identical conditions. If these Shark Bay surveys varied in timing of tides so that a different proportion of the population was in deep versus shallow waters, this may presumably account for at least some of the variation in population estimate. At low tide (e.g. in Moreton Bay) a greater proportion of a dugong's dive time is spent at greater depths and for longer durations than at high tide, i.e. the proportion of dugongs visible in surface waters during low tide decreases (J. Lanyon, unpublished data).

The assumptions associated with the calculation of the availability correction factor are not tested, and hence may present problems in predicting trends from comparison of abundance estimates. In particular, the assumption that the proportion of time a dugong spends on the surface will not vary with depth, time, location and behaviour is likely to be false. Additionally, it is wrongly assumed that dugongs feeding in clear, shallow water in Moreton Bay will display typical surface interval behaviour for all scenarios (J. Lanyon, unpublished data). Basic foraging theory tells us that dive capability (and hence surface availability for sighting) is constrained by physiology, and that the behaviour within these limits is determined by aspects of the animal's ecology such as the distribution, abundance, depth, and energy content of the forage (e.g. Costa 1991), as well as the animal's reproductive ecology and interactions with predators. Currently, no data exist to control for these complex variables and the pragmatic use of the availability correction factor is appropriate. Indeed, research is underway to control for aspects of depth and turbidity. Nevertheless, we acknowledge that the differences we report between our abundance estimates and those of the previous surveys may result from the survey being conducted at a time when dugongs' diving behaviour was fundamentally different to that at the time of the previous surveys, and that the inputs for the calculation of the availability correction factor may not have been sufficient to account for this difference. A decrease of ~28% in our availability correction factor to ~1.8 (i.e. if we had seen either 28% fewer animals at the surface, or 28% more animals overall, of which none of the extra animals were at the surface) would result in an abundance estimate of ~10000 dugongs (i.e. similar to the previous surveys). A figure of 1.8 is within the range of 1.06–3.08 reported by Marsh and Sinclair (1989*a*) for surveys in Queensland.

Although no measurements of water visibility were taken, the water clarity in Shark Bay is generally good, at least along the western side of the Bay (authors' observations), where most animals were seen. In shallow clear water it is probable that a high proportion of animals would be visible. We consider it unlikely that an extra 28% of animals above those already sighted under water were missed.

Hypothesis 2

This hypothesis assumes that the abundance estimates reflect real trends in the dugong populations and that the demographic changes occurred within what are assumed to be functionally closed populations (i.e. insignificant movements of animals between Shark Bay, Ningaloo Reef and Exmouth Gulf). For this hypothesis to be satisfied, the Shark Bay dugong population would have required a population increase of ~7.0% per annum to achieve the overall 40% increase in the five years between the surveys of 1994 and 1999. Alternatively, if we determine that the comparison between the 1989 and 1999 surveys is more legitimate (based on the fact that the calculated correction factors for both surveys were almost the same, which assumes similar surface availability of dugongs) then an annual growth rate of ~3.4% would be required. However, the 1994 survey returned an identical population size to the 1989 survey, suggesting that during 1989–94 there had been a low growth rate.

Dugongs are long-lived animals with a low reproductive rate and a long generation time, investing considerable time in raising each offspring (Marsh *et al.* 1984). Population models predict low potential annual rates of population increase (Marsh *et al.* 1984; Marsh 1995). A maximum asymptotic rate of increase of only 6.3% is predicted (with a 95% confidence interval of 1.5–6.3%) with the most optimistic combination of life-history parameters. The model is particularly sensitive to changes in survival and birth interval (Marsh *et al.* 1984), and if the less optimal life-history parameters determined from a dugong study in Daru, New Guinea, are used, an annual rate of increase of only 2.4% is predicted (Marsh 1995). The dugong populations of Shark Bay, Ningaloo Reef and Exmouth Gulf are not known to be subject to substantial threatening processes. Hunting is limited to indigenous communities and is thought to be responsible for perhaps only tens of animals being killed each year (N. Gales, unpublished data). Dugongs are not known as a by-catch of any fisheries in the area, and significant sea grass degradation resulting from human activities has not been identified in the areas. Indeed, Preen *et al.* (1997) commented that the low level of human impact on this large population made it unusual. Consequently, an annual growth rate of 3.4% would be a reasonable proposition. The rate of 7% that would account for the 40% increase in a five-year period is approximately twice that postulated for a population in optimal growth.

During the previous surveys, the proportion of calves sighted in Shark Bay and the calculated dugong densities were among the highest reported for this species (Marsh *et al.* 1994; Preen *et al.* 1997). Our survey determined an even higher dugong density of 0.98 dugongs km^{-2} (cf. 0.71 dugongs km^{-2} in the previous surveys), but substantially fewer calves, comprising 4.9% in this Shark Bay survey compared with 19% in 1989 and 16.6% in 1994. The consistently high dugong densities in Shark Bay suggest that the area is more productive than other areas in their range and has a higher carrying capacity. This 'optimal' environment may well support high population-growth rates. The substantially lower proportion of calves sighted during this survey is curious. Calves were defined as being 'substantially smaller and in close association with another animal'. This loose definition may lead to some imprecision in interpretation, but is unlikely to account for the 3–4-fold difference in the proportion of calves we report. Breeding and calving seasons for dugongs in the Shark Bay area have not been well defined. Neonates have been seen in the South Passage region in winter (Fig. 2) (C. and J. Shankland, personal communication), and the Faure Sill region in summer (Anderson 1997). As the timing of the three surveys was consistent, it appears that the under-yearling cohort in 1999 was substantially less than that of the previous two surveys. This may reflect a decrease in annual growth rates, or may be part of normal fluctuations in birth rates or calf survival.

If the dugong populations of Shark Bay, Ningaloo Reef and Exmouth Gulf are separate, and if we assume that the 1994 estimate is inaccurate, then it is possible for the population to have grown to the current estimates in the inter-survey period. But, for the Shark Bay population, the growth rate necessary for this would suggest optimal environmental and ecological conditions, the full reproductive capacity of the species utilised and low mortality. The low number of calves observed suggests this had not happened.

Hypothesis 3

This hypothesis varies from Hypothesis 2 in that the principal factor responsible for the population growth is suggested to be migration between regions. Indeed, it predicts that an influx of up to 4000 dugongs into Shark Bay has occurred from areas to the north within the past five years. In Western Australia, spatial aspects of dugong stocks have not been determined by genetic or other means and tracking studies are still in their infancy. Initial tracks of dugongs in Shark Bay (1999–2002) have documented movements restricted to the Bay region, with no flux north to Ningaloo Reef or Exmouth Gulf (N. Gales, D. Holley and I. Lawler, unpublished data). However, movements over several hundreds of kilometres have been recorded for radio-tagged dugongs in the southern Great Barrier Reef (A. Preen, unpublished data), and the small sample size of animals tagged in Shark Bay, and the limited temporal span of the deployments, cannot preclude that such movements may occur.

Our study estimated that there were fewer than 400 dugongs in the Ningaloo/Exmouth region at the time of the survey, compared with ~2000 during the previous two surveys (Marsh *et al.* 1994; Preen *et al.* 1997). If these estimates are reasonably accurate, then more than 75% of the earlier population has either moved away from the area, or has perished. If these dugongs have moved south, including to Shark Bay, then our estimated population size for the whole Exmouth/Ningaloo/Shark Bay region would be only ~18% higher than that of previous estimates. Such a population change is within plausible ranges of growth over the 5-year (since the 1994 survey) or 10-year (since the 1989 survey) period.

Dugong populations to the north-west of Exmouth Gulf have been comprehensively surveyed only once, in 2000 (R. Prince, unpublished data). During this survey, Prince sighted only 54 dugongs in an extensive coastal strip (coast to 20 m isobath) of 23 700 km^2 between North West Cape and the Port Hedland region. Dugong densities (0.10 km^{-2}) were about one-tenth of those we report for Shark Bay. Previous, anecdotal accounts of dugong sightings along this coastline suggest that it supports only small, relatively isolated areas of dugong habitat. Given this extended region of habitat that is likely to support only low dugong densities, the Shark Bay/Ningaloo Reef/Exmouth Gulf region would appear to be largely isolated from other rich dugong habitats lying to the north in the Kimberley region and beyond.

In March 1999 a severe (Category 5) tropical cyclone (Tropical Cyclone Vance) passed down through Exmouth Gulf, causing widespread regional damage. Episodic events of this nature can give rise to widespread damage to seagrass beds and subsequent large-scale movements of dugongs (e.g. Preen and Marsh 1995). We estimated dugong densities in Exmouth Gulf and Ningaloo Reef to be 0.04 km^{-2} and 0.05 km^{-2} respectively. The Exmouth Gulf density in 1999 is almost an order of magnitude less than the estimates for Exmouth Gulf in 1989 and 1994 (0.33 km^{-2} and 0.33 km^{-2} respectively: Marsh *et al.* 1994, Preen *et al.* 1997). The differences between the 1999 and earlier dugong densities in the Ningaloo Reef region are even greater (1.14 km^{-2} in 1989 and 1.11 km^{-2} in 1994). Dugong numbers in Exmouth Gulf were still low in April 2000, when only one dugong was seen in the area surveyed (R. Prince, unpublished data). The evidence from the four surveys, and the likely large-scale ecological disruption wrought by Tropical Cyclone Vance in the Exmouth Gulf region, support an interpretation that a large-scale migration of dugongs from the Exmouth Gulf area is likely to have occurred. Given the substantial increase in dugong abundance in Shark Bay, and the relatively low dugong abundance in the region to the north of Exmouth in April 2000 (R. Prince, unpublished data), we believe that it is likely that a southern migration has occurred and this has, at least in part, contributed to the 1999 estimate of the Shark Bay population.

Summary and conclusions

Our estimate of dugong abundance in Shark Bay in 1999 represents an increase of ~40% on previous estimates. We also report the opposite trend of substantially lower estimates of dugong abundance in the Ningaloo Reef/Exmouth Gulf region. Determining whether these opposing trends result from survey/estimate error, natural changes in discrete population demographics, or large-scale dugong movements is difficult.

We demonstrate that abundance estimates are highly sensitive to calculations of group size, and that group size data are highly skewed to unity. We further note the potential problems of incorporating untested assumptions of dugong behaviour into the survey estimate design. Whilst these methodological constraints have been applied to all the surveys with which we compare our survey data, it is clear that the degree to which they may bias each survey will vary in response to the determinants of dugong behaviour at the site and time of each survey. Such biases may account for some of the possible regional trends in dugong abundance we report.

We discuss that, without immigration, natural population growth is unlikely to have led to a 40% population increase in Shark Bay in the past five years. Some increased fecundity may have contributed to the changes in abundance estimates, in concert with methodological errors in this and/or previous surveys, and/or with movements between the populations we measured. We argue that the changes in regional dugong abundance we report are likely to primarily reflect a significant movement of dugongs from the Ningaloo Reef/Exmouth Gulf region into Shark Bay in response to changes in forage availability, in this case as a possible consequence of a storm event.

Our evidence of large-scale movements of dugongs on a population scale has important management implications. The Shark Bay World Heritage Area was established in part to protect its uniquely large and apparently secure dugong population. Preen *et al.* (1997) noted that during the winters of 1989 and 1994, over 50% of sighted dugongs were in waters to the north of the established Marine Park boundaries. If there is a flux of dugongs along the Western Australian coast from Shark Bay to the waters to the north, which move in response to large-scale, natural habitat changes, then isolated protected marine areas may not provide the degree of protection for which they were designed (Preen 1998).

Our findings highlight the importance of appropriate scaling of dugong surveys. A good understanding of the scale, frequency, magnitude and determinants of dugong movements, and of the genetic structure of Australia's coastal dugong populations is required to adequately interpret spatially discrete aerial surveys. Without such knowledge we are likely to miss detecting important trends in populations. Dugong surveys are expensive and time consuming. Few appropriate aircraft are available in Australia. The surveys published to date effectively reflect the realistic spatial limits that can be achieved. Given these constraints, future dugong research could fruitfully be directed at measuring dugong behaviour in relation to its habitat, and at determining the genetic make-up of dugong populations.

Acknowledgments

Gail Nolan-Neylan, John Riley and Roxane Shadbolt are thanked for their excellent efforts as observers. Eddie Malatesta piloted the aircraft with great skill, maintaining air speed, altitude and transect position with great precision. Funding was provided by the Commonwealth World Heritage Funding Program. Helene Marsh and Ivan Lawler are thanked for comments on the manuscript.

References

Anderson, P. K. (1982). Studies of dugongs at Shark Bay, Western Australia. I. Analysis of population size, composition, dispersion and habitat use on the basis of aerial surveys. *Australian Wildlife Research* **9**, 69–84.

Anderson, P. K. (1986). Dugongs (*Dugong dugon*) of Shark Bay, Australia: seasonal migration, water temperature, and forage. *National Geographic Research* **2**, 473–490.

Anderson, P. K. (1997). Shark Bay dugongs in summer. I: Lek mating. *Behaviour* **134**, 433–462.

Caughley, G., and Grigg, G. C. (1981). Surveys of the distribution and density of kangaroos in the pastoral zone of South Australia, and the bearing of the feasibility of aerial survey in large and remote areas. *Australian Wildlife Research* **8**, 1–11.

Costa, D. P. (1991). Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds. *American Zoologist* **31**, 111–130.

Marsh, H. (1995). Fixed-width aerial transects for determining dugong population sizes and distribution patterns. In 'Population Biology of the Florida Manatee'. (Eds T. J. O'Shea, B. B. Ackerman and H. F. Percival.) National Biological Service Technical Report No. 1, pp. 56–62.

Marsh, H. (2000). Evaluating management initiatives aimed at reducing the mortality of dugongs in gill and mesh nets in the Great Barrier Reef World Heritage Area. *Marine Mammal Science* **16**, 684–694.

Marsh, H., and Saalfeld, W. K. (1989). The distribution and abundance of dugongs in the Northern Great Barrier Reef Marine Park. *Australian Wildlife Research* **16**, 429–440.

Marsh, H., and Sinclair, D. F. (1989*a*). An experimental evaluation of dugong and sea turtle aerial survey techniques. *Australian Wildlife Research* **16**, 639–650.

Marsh, H., and Sinclair, D. F. (1989*b*). Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. *Journal of Wildlife Management* **53**, 1017–1024.

Marsh, H., Heinsohn, G. E., and Marsh, L. M. (1984). Breeding cycle, life history and population dynamics of the dugong, *Dugong dugon* (Sirenia: Dugongidae). *Australian Journal of Zoology* **32**, 767–788.

Marsh, H., Prince, R. I. T., Saalfeld, W. K., and Shepherd, R. (1994). The distribution and abundance of the dugong in Shark Bay, Western Australia. *Wildlife Research* **21**, 149–161.

Marsh, H., Corkeron, P., Lawler, I., Lanyon, J., and Preen, A. (1996). The status of the dugong in the southern Great Barrier Reef Marine Park. Great Barrier Reef Marine Park Authority Research Publication No. 41.

Preen, A. (1998). Marine protected areas and dugong conservation along Australia's Indian Ocean coast. *Environmental Management* **22**, 173–181. doi:10.1007/S002679900094

Preen, A., and Marsh, H. (1995). Response of dugongs to large-scale loss of seagrass from Hervey Bay, Queensland. *Australian Wildlife Research* **22**, 507–519.

Preen, A. R., Marsh, H., Lawler, I. R., Prince, R. I. T., and Shepherd, R. (1997). Distribution and abundance of dugongs, turtles, dolphins and other megafauna in Shark Bay, Ningaloo Reef and Exmouth Gulf, Western Australia. *Wildlife Research* **24**, 185–208.

Manuscript received 19 August 2002; accepted 24 July 2003