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Diving behaviour of dugongs, *Dugong dugon*

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Abstract

The diving behaviour of 15 dugongs (*Dugong dugon*) was documented using time–depth recorders (TDRs), which logged a total of 39,507 dives. The TDRs were deployed on dugongs caught at three study sites in northern Australia: Shark Bay, the Gulf of Carpentaria and Shoalwater Bay. The average time for which the dive data were collected per dugong was 10.4 ± 1.1 (S.E.) days. Overall, these dugongs spent 47% of their daily activities within 1.5 m of the sea surface and 72% less than 3 m from the sea surface. Their mean maximum dive depth was 4.8 ± 0.4 m (S.E.), mean dive duration was 2.7 ± 0.17 min and the number of dives per hour averaged 11.8 ± 1.2. The maximum dive depth recorded was 20.5 m; the maximum dive time in water >1.5 m deep was 12.3 min. The effects of dugong sex, location (study site), time of day and tidal cycle on diving rates (dives per hour), mean maximum dive depths, durations of dives, and time spent ≤ 1.5 m from the surface were investigated using weighted split-plot analysis of variance. The dugongs exhibited substantial interindividual variation in all dive parameters. The interaction between location and time of day was significant for diving rates, mean maximum dive depths and time spent within 1.5 m of the surface. In all these cases, there was substantial variation among individuals within locations among times of day. Thus, it was the variation among individuals that dominated all other effects. Dives were categorised into five types based on the shape of the time–depth profile. Of these, 67% of dives were interpreted as feeding dives (square and U-shaped), 8% as exploratory dives (V-shaped), 22% as travelling dives (shallow-erratic) and 3% as shallow resting dives. There was systematic variation in the distribution of dive types among the factors examined. Most of this

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variation was among individuals, but this differed across both time of day and tidal state. Not surprisingly, there was a positive relationship between dive duration and depth and a negative relationship between the number of dives per hour and the time spent within 1.5 m of the surface after a dive.

Keywords: Diving behaviour; Dive depth; Dive duration; Dugong; *Dugong dugon*; Time–depth recorder

1. Introduction

The dugong (*Dugong dugon*) is one of four extant species in the mammalian order Sirenia, all of which are aquatic herbivores. The dugong is the only herbivorous mammal that is strictly marine and is a benthic-feeding, seagrass specialist (Marsh et al., 1982; Lanyon et al., 1989; Aragones and Marsh, 2000). The other sirenians, the manatees (genus *Trichechus*), are generalist herbivores, feeding on many vascular aquatic and semiaquatic plants, growing throughout the water column (Jefferson et al., 1993; Reynolds and Odell, 1991).

All sirenians have a large body size (adults generally 250–700 kg; Spain and Heinsohn, 1975; Jefferson et al., 1993) and hindgut fermenting digestive systems (Gallivan and Best, 1980; Lanyon and Marsh, 1995; Reynolds and Rommel, 1996). These features, combined with the relatively low nutrient and energy content of their aquatic plant food (e.g., Aragones, 1996; Lefebvre et al., 1999), suggest that they must spend a high proportion of their time feeding in order to meet their daily food requirements. It has been estimated that wild dugongs consume approximately 28–40 kg wet weight of seagrass per day (Preen, 1993; Aragones, 1996).

To date, the only studies on sirenian diving and feeding behaviours have been based on visual observations from boats or shoreline vantage points (Anderson and Birtles, 1978; Reynolds, 1981; Anderson, 1982, 1998; Marsh and Rathbun, 1990; Churchward, 2001; Whiting, 2002) or by filming from a hovering helicopter (Marsh et al., 1997) or blimp (Amanda Hodgson, personal communication). It is very difficult to obtain behavioural and diving data from aquatic animals that generally live in turbid water and only come to the surface briefly to breathe. The shapes of dives and other underwater behaviours cannot be clearly observed from shore or boats.

The data from these behavioural observations indicate that the daily activities of both dugongs and manatees predominantly take place in less than 3 m of water. However, maximum dive depths of 9 and 33 m (inferred from feeding scars) and dive durations up to 24 and 10 min, respectively, have been reported for manatees and dugongs, (Reynolds, 1981; Anderson and Birtles, 1978; Anderson, 1982; Marsh and Rathbun, 1990; Bruce Ackerman and Holly Edwards, personal communication).

The seagrasses eaten by dugongs and some manatees are found throughout tropical to subtropical coastal waters, predominantly in shallow water (generally less than 15 m but up to 58 m in clear water regions; Lee Long et al., 1996). Seagrass distribution and abundance are highly variable, both temporally and spatially (Lee Long et al., 1996). The distributions of dugongs are highly correlated with their seagrass food (Marsh et al., 2002).

Time–depth recorders (TDRs) have been widely used to measure the diving parameters and classify the diving behaviours of predatory marine mammals (i.e., cetaceans and pinnipeds; see for example Martin et al., 1998; Elsener, 1999; Arnould and Hindell, 2001; Frost et al., 2001). Some predatory marine mammals dive to depths in excess of 100 m, and their dives commonly last for tens of minutes (e.g., Hooker and Baird, 1999). In contrast, dugongs and manatees are believed to restrict their diving to the relatively shallow depths where their preferred forage occurs (Anderson and Birtles, 1978; Anderson, 1982, 1998; Marsh and Rathbun, 1990; Wells et al., 1999; Churchward, 2001). Thus, it has been inappropriate to use TDRs to study sirenian diving behaviour until recently because of the limited depth resolution (>1 m) of older instruments. Recent improvements in the capabilities of TDRs have enabled finer scale measurements.

This paper provides the first detailed description of sirenian diving behaviours recorded using TDRs. These instruments were deployed on 15 dugongs at three study sites across northern Australia. We describe dive profiles, identify basic dive types and quantify the relative amount of time dugongs spent performing dives of each type. We discuss the possible biological role of each dive type and investigate how the activities of dugongs vary with sex, location, time of day and tidal cycle as a basis for understanding their foraging behaviour.

2. Materials and methods

2.1. Study areas

2.1.1. Shoalwater/Hervey Bays, Queensland

Shoalwater Bay (Fig. 1) is a large semienclosed bay located in the Great Barrier Reef World Heritage Area in eastern Australia, 100 km north of Rockhampton (22°40′ S, 150°40′ E). It has a complex coastline made up of bays, channels and islands. Most of the bay is less than 10 m deep. The area has a tidal range up to 6.3 m, which creates strong currents resulting in resuspension of sediment and turbid water. This large tidal range combined with a gentle, shallow-water topography results in large intertidal areas. For this reason, most of the seagrass in Shoalwater Bay occurs on intertidal mud and sand flats. Most seagrass meadows are dominated by *Zostera capricorni* (narrow leaf morph), with *Halophila* spp. common in subtidal seagrass beds.

Even though two of the study animals were tagged in Shoalwater Bay, they both moved southward approximately 375 km (straight-line distance) to Hervey Bay (Fig. 1), a large (3800 km^2), sheltered embayment immediately south of the Great Barrier Reef World Heritage Area. Hervey Bay and the adjacent Great Sandy Strait support more than 2000 km^2 of seagrass in mostly mixed species meadows (McKenzie et al., 2000), extending from the intertidal and subtidal areas (2–10 m below MSL) to a depth of 32 m. *Z. capricorni*, *Halodule uninervis* and *Halophila ovalis* predominate in intertidal areas. *Halophila spinulosa* and *H. ovalis* predominate at depths of >10 m (McKenzie et al., 2000). The tidal range in Hervey Bay ranges to about 3.6 m. The

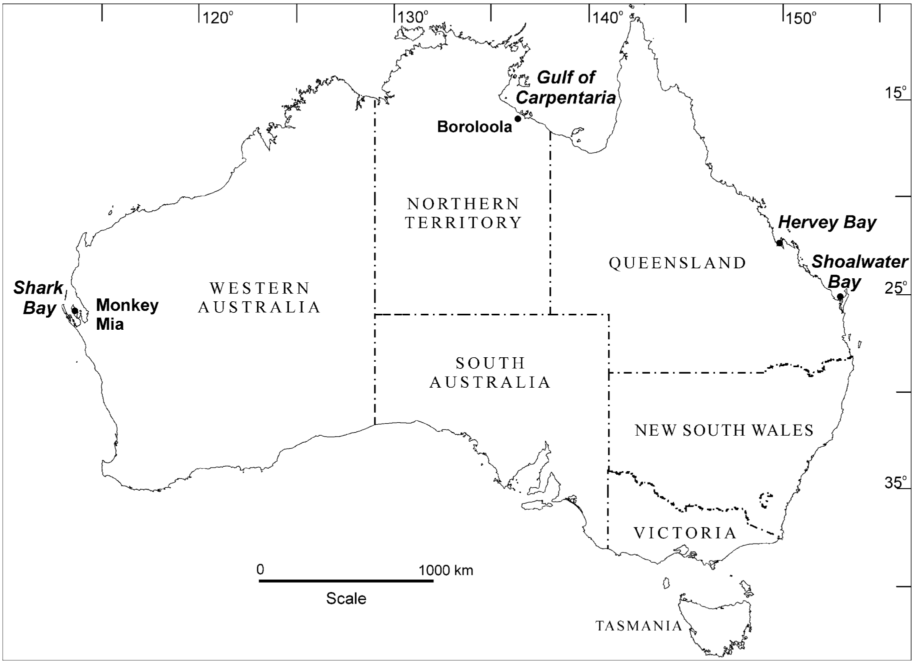

Fig. 1. Map of Australia showing locations mentioned in the text.

Burrum River discharges into Hervey Bay and the Mary River feeds into Great Sandy Strait. Floods from these rivers can have a serious impact on the seagrasses and dugongs in Hervey Bay (Preen and Marsh, 1995; Preen et al., 1995; McKenzie et al., 2000).

2.1.2. Shark Bay, Western Australia

Shark Bay is a large, semienclosed bay, located 800 km north of Perth, Western Australia. Peron Peninsula divides Shark Bay into two gulfs for much of its length. Our study site was located in the Eastern Gulf, near Monkey Mia (Fig. 1). The Eastern Gulf has a complex coastline including bays, channels, islands and a narrow peninsula. All areas are predominantly shallow, averaging approximately 10 m in depth, with a maximum depth of approximately 30 m. Shark Bay supports extensive shallow seagrass beds. No large rivers contribute to the marine system at this site. However, the tidal flows over shallows result in predominantly turbid waters. Maximum tidal variation is 1.2 m. Deeper subtidal seagrass beds are dominated by the temperate seagrass *Amphibolis antarctica*, however, species of *Halodule* and *Halophila* may be dominant in shallower waters. These latter two genera are generally considered to be preferred by dugongs (Marsh et al., 1982; Lanyon et al., 1989; Preen, 1995), although preliminary observations indicate that *Amphibolis* is eaten preferentially in winter in Shark Bay (Holley, personal observation; Churchward, 2001).

2.1.3. Southwestern Gulf of Carpentaria, Queensland

The coastal region of the southwestern Gulf of Carpentaria in northern Australia features a mangrove-lined coastline of low relief, the Sir Edward Pellew and Wellesley Islands and large mangrove-lined river systems. The coastal waters are less than 8 m deep. Maximum tidal variation is 2 m. The area experiences strong winds and, during the rainy season, high inputs of turbid floodwaters from the adjacent river systems. These two factors result in the inshore waters being almost continuously turbid. Most seagrass grows in the intertidal areas on shallow mud and sand flats. Seagrass beds are dominated by *Syringodium isoetifolium*; however, species of *Halophila* and *Halodule* are also common. The dugongs were tagged near Borroloola (Fig. 1).

2.2. Capture and deployment

All dugongs were caught using either a rodeo or hoop-netting technique similar to those described in Marsh and Rathbun (1990). Using a harness attachment technique basically similar to that described by those authors, a floating transmitter package was tethered to a tailstock harness by a 3-m tether. The transmitter packages contained a very high-frequency (VHF) transmitter. A platform transmitter terminal (PTT) satellite tag (ST-14 Telonics, Mesa, AZ, USA) was deployed on the animals caught in Queensland and the Northern Territory. The instruments connected to the dugongs caught in Shark Bay were GPS satellite units (Lotek, Newmarket, Ontario, Canada). The TDRs (MK4 and MK7, Wildlife Computers, Woodinville, WA, USA) were attached just above the harness, i.e., effectively on the dorsal aspect of the dugong's tailstock. Tags and harnesses were deployed intermittently between October 1994 and March 2001 on a total of 15 dugongs. All harness attachments were designed to release automatically from the animals for retrieval via either a corrodible link (units deployed in Shoalwater Bay and the Gulf of Carpentaria) or a remote radio-activated signal (Shark Bay). The MK4 TDRs (used on animals tagged in the Gulf of Carpentaria and Shoalwater Bay) sampled depth at 5-s intervals, with depth resolution of 40 cm, and were programmed to collect data on dive profiles for 1 day in every 5 or 10 days as detailed in Table 1. The MK7 TDRs (Shark Bay) sampled at 1-s intervals everyday, with depth resolution of 25 cm. Because of these difference between instruments, all data were analysed assuming a depth resolution of 40 cm. The minimum depth counted as a dive was set at 1.5 m to allow for (a) the TDR sensor resolution depth − 40 cm; (b) the location of the TDR tags on the tailstock which is commonly higher than the rest of the body, particularly while the dugong is feeding (Anderson, 1998); (c) fluctuations in the position of the tail as the dugong moves; and (d) drift in the zero depth reading and possible influences of wave action. Diving data were analysed using Multitrace (Jensen Software Systems Laboe, Germany) to produce summary statistics for each dive. Zero offset drift in the depth values for each tag was corrected manually within Multitrace.

2.3. Dive classification and data analysis

The shape of dive profiles (depth vs. time) was initially used to separate the dives manually into the five major dive type shapes [Square (S), U-shaped (U), V-shaped (V),

Table 1
Details of duty cycles of the various TDRS and the PTT locations where the TDR data were recorded for 15 dugongs

Dugong ID	Number of days of dive records	Sampling frequency	Summary of locations from which records available
92130	3	1 day in 10	Shoalwater Bay between 22.386°S and 22.523°S and 150.466°S and 150.519°S and Hervey Bay around 25.194°S and 152.642°E
92127	6	1 day in 10	Hervey Bay between 25.168°S and 25.230°S and 152.601°E and 152.806°E
091	13	daily	Shark Bay within 10 km of 25.85°S, 114.04°E water depth < 10 m
093	12	daily	Shark Bay within 10 km of 25.85°S, 114.04°E water depth < 10 m
435	12	daily	Shark Bay within 10 km of 25.85°S, 114.04°E water depth < 10 m
437	14	daily	Shark Bay within 10 km of 25.85°S, 114.04°E water depth < 10 m
8001	15	daily	Shark Bay between 25.58°S and 25.74°S and 113.59°E and 113.73°E
8002[a]	14	daily	Shark Bay between 25.74°S and 25.82°S and 113.73°E and 114.05°E
8003[a]	16	daily	Shark Bay between 25.50°S and 25.74°S and 113.57°E and 113.84°E
8004[a]	15	daily	Shark Bay between 25.52°S and 26.11°S and 113.21°E and 113.59°E
8005[a]	12	daily	Shark Bay in region of 25.56°S and 113.63°E in water < 5 m
92128[a]	7	1 day in 10	tagged in SW Gulf of Carpentaria, locality data not available
127[a]	6	1 day in 5	tagged in SW Gulf of Carpentaria, locality data not available
92129[a]	4	1 day in 10	tagged in SW Gulf of Carpentaria, locality data not available
93122[a]	7	1 day in 10	tagged in SW Gulf of Carpentaria, locality data not available
	10.4 ± 1.1		

These locations are approximate only as PTT position data were not available for the dugongs caught in the Gulf of Carpentaria or for all days on which the TDR data were recorded at the other study sites.

[a] PTT records not available for all days on which dive records obtained.

Erratic (E), and Resting (R)] for 13 dugongs (Fig. 1; Table 2; for definitions, see Results). Approximately 1500 of the 39,507 dives were classified into these five dive types using this method. An additional 4725 dives were then independently classified using both manual and numerical classifications as the basis for error comparisons. The remaining 33,282 dives were classified using the numerical dive type classifications alone (described in Results). As dugongs are obligate benthic feeders, we have interpreted the bottom section of the Square, U-shaped and V-shaped dives to represent the approximate depth of the water in which the dugong was located. Given the relative position of the bottom and the TDR on the dugong's tail stock, it is likely that some of these depths were underestimated by up to about 2 m.

All results are presented as means ± 1 S.E. Multinomial log-linear models were used to determine the relationship between the categorical variables: dugong sex, location (Shoalwater/Hervey Bays, Shark Bay and Gulf of Carpentaria), time of day (each day was divided into six 4-h periods starting at 0000 local time) and tidal cycle (each cycle was divided into four equal time periods: In High, Out High, Out Low, In Low) and the frequency of dives of the five major shapes for 13 of the dugongs (Table 2; for definitions see Results). Data from two dugongs were excluded from this analysis as no tidal information was available for dugong 127 and 8005 had unusually variable and therefore suspect TDR readings.

Table 2
Results of the multinomial log-linear analysis of the effects of dugong sex, location, time of day and tide on the relative frequency of the five dive types exhibited by 13 individual dugongs fitted with time–depth recorders

Model term	*df* × (*n* − 1 dive types)	Error term	Deviance	*F*	*p*
Location	8	ID(Location × Sex)	1860.00	0.651	0.7300
Sex	4	ID(Location × Sex)	1568.00	0.548	0.7030
ID(Location × Sex)	36	Error	2859.00	*	< 0.0001
Time of day	20	ID(Location × Sex) × Time of day	135.20	*	< 0.0001
Tide	12	ID(Location × Sex) × Tide	115.60	*	< 0.0001
Time of day × Tide	60	Error	267.30	*	< 0.0001
Location × Time of day	40	ID(Location × Sex) × Time of day	324.10	*	< 0.0001
Sex × Time of day	20	ID(Location × Sex) × Time of day	112.70	*	< 0.0001
Location × Tide	24	ID(Location × Sex) × Tide	15.86	*	0.9990
Sex × Tide	12	ID(Location × Sex) × Tide	55.73	*	< 0.0001
ID(Location × Sex) × Time of day	180	Error	1691.00	*	< 0.0001
ID(Location × Sex) × Tide	108	Error	577.10	*	< 0.0001
Error	680		2677.00		

*Analysis of deviance using chi-square.

We calculated the frequency of each of these five dive types at each combination of treatment levels for each individual and performed the analysis on the weighted frequency of dives of each type. The categorical response was dive type and the weight attached to each dive type at a given treatment combination was the number of times that dive type was observed for each individual for that combination of treatment levels. Square dives were recorded at 294 treatment combinations, U-shaped dives at 274 treatment combinations, V-shaped dives at 247 treatment combinations, ‘Erratic’ dives at 280 treatment combinations and ‘Resting’ dives at 213 treatment combinations.

The mean weight of dive types at given treatment combinations was 27 dives (median = 11, range 1–301).

The fitted model can be represented as

$$\text{Dive type}_5 \sim \frac{(\text{Location}_3 \times \text{Sex}_2)}{\text{ID}_{13}} \times \text{Time of day}_6 \times \text{Tide type}_4$$

where Location and Sex were crossed with Individual Dugong (ID) nested within the Location by Sex interaction. This component was crossed with the factors Time of day and Tide Type (which were crossed). There was substantial imbalance in the available data as all dive types were not recorded for all individuals at all treatment combinations (i.e., location × sex × time of day × tide). Accordingly, only first-order interactions among the predictors were examined.

The individual dugongs (ID) were considered a random sample from the larger population of individuals and therefore were represented as a random effect in the analysis. This inclusion of an ‘individual’ effect introduces a dependency within individuals in the analysis. The random effects also allow for the analysis of multilevel data with more than one error term. The appropriate error terms for each effect in the analysis are provided in Table 2. The significance of individual-dependent effects was examined using analysis of deviance (with test statistics distributed as chi-square) by comparing the change in mean deviance in dive type frequency attributable to the individual-dependent term when fitted second-last in the model to the mean deviance due to the individual term when fitted last. This approach enabled each effect to be examined when all other terms in the model (apart from the appropriate error term) had been taken into account. The significance of among-individual effects (i.e., location and sex) was examined using F-ratios by comparing terms as above.

The above analysis was repeated for 10 dugongs by omitting all the dugongs tagged in the Gulf of Carpentaria because of the uncertainties about the accuracy of the tidal data from this region and the exact locations of the dugongs because PTT locations were not available.

A weighted split-plot ANOVA model (Table 3) was used to examine variation in the mean maximum depth of dives, the mean duration of dives, the mean time spent in shallow water after dives and the mean number of dives per hour, both between and within individuals taking into account the effects of dugong sex, location, time of day and tidal cycle. The fitted model was the same as for the dive type frequency analysis above and included a random effect for individual dugong variation to account for the dependency between repeated observations on each individual. The model assumes a constant correlation structure among observations (i.e., dives) on each individual within the error structure ID(Location × Sex) × Time of day × Tide. Consequently, there were multiple random terms in the analysis, and appropriate error terms, some involving composite terms, for each effect are given in Table 3. Additionally, as a result of the imbalance in the data, the composite error terms were based on weighted proportions of the components of variance in each case constructed using Satterthwaite's (1946) method. The responses (mean maximum depth of dives, the mean duration of dives and the mean surface interval after dives) were natural log transformed. The mean number of dives per hour did not require transformation.

Variance components for the random effects were estimated using a restricted maximum likelihood method. The estimated mean square error was inflated due to the weighted analysis. Therefore, the other variance components were multiplied by the mean weight of the observations for comparison with the mean square error. The mean square error was the weighted variance estimate for the ID(Location × Sex) × Time of day × Tide interaction (i.e., the within-individual variance amongst the repeated terms). As outlined above and for the same reasons, the analysis was repeated, omitting all the dugongs tagged in the Gulf of Carpentaria.

2.4. Limitations

We estimated that we could analyse the diving behaviours of dugongs to a depth accuracy of 1.5 m. However, as this and other studies have shown, dugongs spend a considerable proportion of their time in less than 1.5 m of water, and can feed in very shallow water (Preen, 1993; Anderson, 1998). This limitation could be lessened in the

Table 3
Split-plot analysis of variance model used to examine the effects of dugong sex, location, time of day and tide on diving rates (dives per hour), mean maximum dive depths, durations of dives, and time spent in very shallow water (≤ 1.5 m)

Model term	*df*	Error term	Error *df* for each response[a]			
			Mean maximum dive depth	Mean dive duration	Mean number of dives per hour	Mean time in shallow water after dive
Location	2	ID(Location × Sex) + Error	10.39[b]	10.73	11.27[b]	11.94[b]
Sex	1	ID(Location × Sex) + Error	10.17	10.32	10.28	10.84
ID(Location × Sex)	10	ID(Location × Sex) × Time of day + ID(Location × Sex) × Tide − Error	48.49[c]	40.75[c]	35.13[c]	36.33[c]
Time of day	5	ID(Location × Sex) × Time of day + Error	104.49[b]	131.62	113.28	138.26
Tide	3	ID(Location × Sex) × Tide + Error	95.85	89.79	116.64	109.25
Time of day × Tide	15	Error	185.00	185.00	181.00	185.00
Location × Time of day	10	ID(Location × Sex) × Time of day + Error	84.76[c]	103.03	104.47[c]	107.75[c]
Sex × Time of day	5	ID(Location × Sex) × Time of day + Error	67.03	76.01	62.34	78.37
Location × Tide	6	ID(Location × Sex) × Tide + Error	70.40	66.65	105.90	79.23
Sex × Tide	3	ID(Location × Sex) × Tide + Error	44.51	43.19	44.97	47.64
ID(Location × Sex) × Time of day	50	Error	185.00[c]	185.00[c]	181.00[c]	185.00[c]
ID(Location × Sex) × Tide	30	Error	185.00[b]	185.00[b]	181.00	185.00

[a] Estimated degrees of freedom differ for each response variable reflecting the imbalance in the data. Degrees of freedom were calculated using Satterthwaite's method (see text).

[b] Indicates the term is significant for the given response at $\alpha = 0.05$.

[c] Indicates significance at $\alpha = 0.01$.

future by the consistent use of high-resolution, extended memory TDRs, development of a technique for affixing the TDR directly onto the animal, the inclusion of accurate animal locations (GPS and satellite positioning), detailed habitat description and combined visual/TDR observations.

TDRs measure depth vs. time in two dimensions. They provide no information on the movements of telemetered animals in three-dimensional water space (Stewart, 2002). Thus, the validity of our inferences about behaviour from TDR dive profiles is untested. For example, we had no means of distinguishing a dive in which a dugong was moving along the bottom from one in which an animal was stationary on the bottom. The use of crittercams (Marshall, 1998; Parrish et al., 2000) or geomagnetic, acceleration and velocity sensors (Mitani et al., 2003) would help distinguish between these activities.

The distributions of dugongs are affected by many environmental influences, including seasonal and storm- and flood-induced changes in distribution and abundance of seagrass, and seasonal changes in water temperature. These influences are also likely to affect dugong diving behaviour; however, we could not investigate them with the current data set.

3. Results

Information was collected from a total of 39,507 dives from 15 dugongs. The number of dives recorded per individual ranged from 501 to 5282 (mean 2634 ± 523, Table 6), and the average time for which data were available was 10.4 ± 1.1 days. Nine dugongs (6 ♀ and 3 ♂) were tagged in Shark Bay. For these animals, TDR information was collected for a mean of 13.7 ± 0.4 days per individual with a total of 28,917 dives recorded. Two female dugongs were tagged in Shoalwater Bay and moved to Hervey Bay (Table 1). An average of 4.5 ± 2.1 days of TDR information was obtained per individual for a total of 1833 dives. Data were collected from four dugongs (2 ♀ and 2 ♂) tagged in the southwestern Gulf of Carpentaria. An average of 6.0 ± 0.8 days of information was collected per individual with a total of 8757 dives monitored.

3.1. Dive shapes

The main shapes of the time–depth profiles were Square, U-shaped, triangular or V-shaped including those skewed to the left and to the right, erratic rectangular or triangular with shallow depths (E) and (R) shallow (resting) dives after > 5 min spent within 1.5 m of the surface (R) (Fig. 2). Although (E) and (R) dives had the same basic shapes, we distinguished them because the behaviour of the dugong prior to the dive was different, suggesting that these dives were associated with different behaviours.

Parameters were established for each dive type (Table 4). These parameters included maximum depth, bottom time relative to duration (bottom time equals the time spent at ≥ 75% of a dive's maximum depth), time prior to the dive spent within 1.5 m of the surface and presence of >1-m wiggles (>1 m discontinuity in water depth during the bottom phase of a dive). The comparison between manual and numerical dive type classifications indicated less than 10% error for the numerical classification of dive types. The error rate for each dive type was 7% for Square dives, 13% for U-shaped dives, 8% for V-shaped dives, 15% for 'Erratic' dives and 5% for 'Resting' dives. Most errors in numerical classifications resulted in a dive being classified in the category closest to its actual dive shape, e.g., 85% of the 7% of misclassified Square dives were classified as U-shaped dives; similarly, 85% of the 13% misclassified U-shaped dives were classified as Square dives.

All dives were classified into one of the five basic types. Overall, 55% of dives were classified as Square dives, 12% U-shaped dives, 8% Triangular, 22%, 'Erratic' dives and 3% shallow 'Resting' dives. Some dugongs maintained dives of the same shape without interruption for very long periods (Table 5). The longest such dive sequence was 212 Square dives lasting more than 20 h, nearly 17 h of which (81%) were spent more than 1.5 m below the surface.

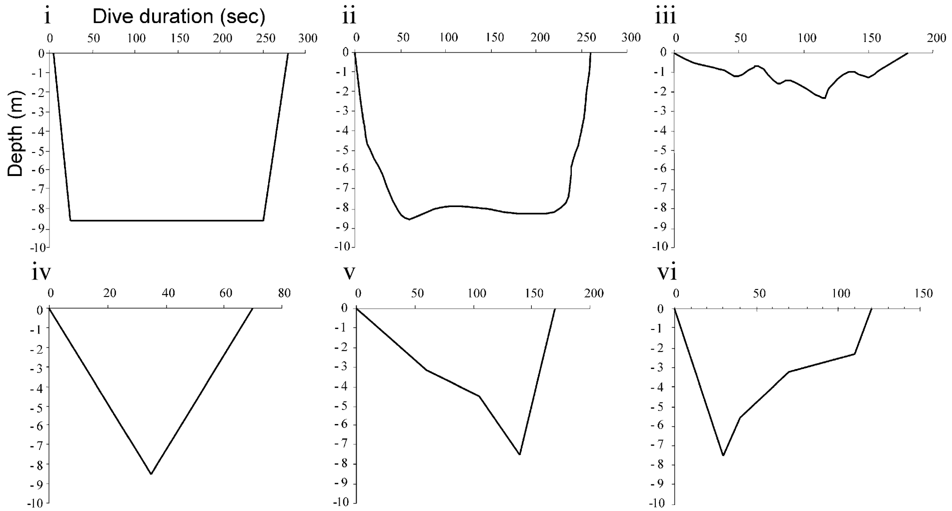

Fig. 2. Examples of dugong dive type profiles. Dive profiles are plotted from time–depth recorder data recorded every second. The five main dive types are (i) Square; (ii) U-shaped; (iii) 'Erratic' and 'Resting'—shallow dives following an extended period ≤ 1.5 m; (iv–vi) V-shaped or triangular, skewed left and right.

3.2. Factors influencing dive shape

There is evidence for systematic variation in the distribution of dive types (Fig. 2) among the factors examined (Table 2). Most of the variation is among individuals (ID) (note the large deviances) and this negates any meaningful inference about the other effects. However, there are differences among individuals across both time of day and tidal state (i.e., the error term in the analysis). There was significant variability in the distribution of dive types among the first-order interactions of all fixed terms (i.e., Time of day × Tide, Time of day × Location, Time of day × Sex, and Tide × Sex), except for Location × Tide. Omitting the animals tagged in the southwestern Gulf of Carpentaria made no substantive difference to the result.

Table 4
Characteristics of the five dive types recognised for dugongs

Dive type	Minimum/ maximum depth (m)	Proportion bottom time to total dive duration (%)	Dive contains wiggles[a] >1 m	Time within ≤ 1.5 m of surface
S-square	>1.5	>65	no	n.a.
U-shaped	>1.5	33 ≤ 65	possible	n.a.
V-shaped	>3.0	0	no	n.a.
E-erratic	1.5 ≤ 3.0	<33	possible	n.a.
R-erratic with long shallow-water period	1.5 ≤ 3.0	<33	possible	>5 min

[a] A wiggle refers to a >1 m discontinuity in water depth during the bottom phase of a dive.

Table 5
Longest sequence of dives of the same type recorded for each type of dive

Dugong ID	Sex	Location	Date day/month/year	Number of dives in sequence	Time at start of sequence	Time at end of sequence	Duration of sequence	Cumulative duration of dives	Time within ≤ 1.5 m of surface
Square (S)									
8002	M	Shark Bay	22/8/2000	212	2000	1612	20.4 h	16.6 h	3.8 h
8002	M	Shark Bay	26/8/2000	172	0450	2019	16 h	13.3 h	2.7 h
8002	M	Shark Bay	27/8/2000	160	0610	2023	14.4 h	10.6 h	3.8 h
8003	F	Shark Bay	29/8/2000	126	1928	0232	7 h	6.5 h	0.5 h
U-shaped									
8005	M	Shark Bay	20/8/2000	10	0058	0111	14.6 min	13 min	1.6 min
92129	M	Gulf of Carpentaria	9/6/1998	9	0749	0802	14.4 min	12.8 min	1.6 min
127	M	Gulf of Carpentaria	18/10/1994	9	1730	1744	16 min	11.9 min	4.1 min
Triangular(V)									
8001	M	Shark Bay	30/8/2000	14	2226	2304	41 min	36 min	5 min
92129	M	Gulf of Carpentaria	19/6/1998	11	0924	0935	11.7 min	8.4 min	3.3 min
Erratic (E)									
8004	F	Shark Bay	21/8/2000	40	1250	1419	91 min	50 min	41 min
8003	F	Shark Bay	28/8/2000	31	1750	1854	65 min	43 min	22 min

3.3. Submerged time, depth, duration and rate of diving

Overall, dugongs spent 53 ± 3% of their time more than 1.5 m below the surface (Table 6) and 72% of their time less than 3 m from the sea surface. The mean depth and duration of dives made by individual dugongs ranged from 2.1 ± 0.1 to 7.2 ± 0.1 m and 1.8 min ± 1 s to 4.2 min ± 1 s (Table 6). Means dive durations and depths across all individuals were 2.7 ± 0.17 min and 4.8 ± 0.4 m with maximums of 12.3 min and 20.5 m, respectively. Fifty percent of all dives were less than 4 m in depth and 3 min duration, while 90% of all dives were to less than 9 m and <5 min duration. The rate of diving (dives per hour) per individual ranged from 6.6 ± 0.4 to 22.5 ± 0.7 dives h^{-1}, with an overall mean across individuals of 11.8 ± 1.2 dives h^{-1} (Table 6). We could not relate dive depths to water depths because of the uncertainty of the locations of the dugongs, which were located by the satellite transmitters only about three times per day on average.

3.4. "Surface intervals": time spent <1.5 m below the surface

The TDR data for the time that the dugongs spent <1.5 m below the surface were interpreted with caution because of the 1.5-m limitation on dive measurements explained above. Overall, the maximum time spent continuously within 1.5 m of the surface was 12.7 h (excluding the questionable data from dugong 8005, Table 7). The mean time spent

Table 6
Summary statistics (± S.E.) for proportion of time within 1.5 m of surface, maximum dive depths and dive durations for 15 dugongs

Dugong	Sex	Study site[a]	Number of dives >1.5 m	Proportion of time submerged >1.5 m	Dives per hour	Mean depth ± S.E. (m)	Median depth (m)	Depth range (m)	Modal Depth (m)	Mean duration (min)	Median duration (min)	Duration range (s–min)	Modal duration (min)
92130	F	1	501	0.61	8.7 ± 0.9	3.9 ± 0.1	3.2	1.5–20	1.5	2.3 ± 0.07	2.0	7–8.8	1.9
92127	F	1	1332	0.40	9.7 ± 0.5	6.8 ± 0.1	5.9	1.5–12.2	2.2	3.2 ± 0.06	3.3	5–9.0	4.8
091	F	2	4542	0.49	15.8 ± 0.7	6.8 ± 0.1	7.0	1.5–10.7	8.2	2.2 ± 0.02	1.7	15–5.3	1.0
093	F	2	2086	0.46	9.2 ± 0.4	7.2 ± 0.1	8.0	1.5–10	8.2	3.6 ± 0.03	3.7	5–6.9	4.9
435	F	2	2695	0.31	9.6 ± 0.6	3.6 ± 0.1	2.5	1.5–12.9	1.8	1.8 ± 0.02	1.5	8–8.8	1.0
437	F	2	1725	0.61	6.6 ± 0.4	6.1 ± 0.1	6.5	1.5–15.6	8.2	3.1 ± 0.03	2.7	10–7.2	2.3
8001	M	2	2511	0.36	6.9 ± 0.4	4.2 ± 0.1	2.5	1.5–11.8	2.0	2.8 ± 0.02	2.3	15–8.9	2.2
8002	M	2	3920	0.75	10.8 ± 0.2	6.5 ± 0.1	7.0	1.5–18.2	7.5	4.2 ± 0.02	4.3	5–8.6	4.5
8003	F	2	5282	0.65	14.1 ± 0.5	4.6 ± 0.1	3.4	1.5–15.3	1.8	2.7 ± 0.02	2.5	13–8.2	2.9
8004	F	2	4807	0.55	13.5 ± 0.5	3.8 ± 0.1	2.8	1.5–9.8	2.1	2.5 ± 0.02	2.2	5–12.3	1.1
8005[b]	M	2	1349	*	*	3.7 ± 0.1	3.2	1.5–20.5	2.1	2.8 ± 0.03	2.6	15–7.4	1.8
92128	F	3	3502	0.62	22.5 ± 0.7	2.1 ± 0.1	2.1	1.5–4.8	2.4	1.8 ± 0.02	1.8	15–6.3	1.6
127	M	3	1595	0.53	10.6 ± 1.0	3.4 ± 0.1	2.9	1.5–9.7	2.2	2.9 ± 0.02	1.9	20–8.7	1.0
92129	M	3	1340	0.53	14.1 ± 1.1	4.0 ± 0.1	3.9	1.5–13.3	2.2	2.3 ± 0.03	2.1	20–8.5	1.6
93122	F	3	2320	0.48	13.6 ± 0.7	3.8 ± 0.1	2.4	1.5–6.9	1.7	2.1 ± 0.02	2.0	25–5.6	1.9
Overall[c]			2634 ± 376	0.53 ± 0.03	11.8 ± 1.2	4.8 ± 0.4	0.5	1.5–20.5		2.7 ± 0.17		5–12.3	

The effective limit of resolution of the TDRs on the dugongs was 1.5 m.

Dugong 8005 had highly variable TDR readings. This animal's dive data were interpreted with caution. Dive rate, proportion of time submerged and time spent within 1.5 m of the surface were not calculated.

[a] Location: 1 = Shoalwater/Hervey Bays, 2 = Shark Bay, 3 = Gulf of Carpentaria.

[b] Excludes animal 8005.

[c] Mean across the mean results of individual dugongs.

Table 7

Summary statistics for the time spent within 1.5 m of surface after dives for 15 dugongs

Dugong ID	Sex	Location[a]	Number of dives >1.5 m	Mean ± S.E. (min)	Median (s)	Mode (s)	Range (h)
92130	F	1	501	4.5 ± 1	35	5	0–4.8
92127	F	1	1332	3.1 ± 0.5	45	5	0–7.2
091	F	2	4542	1.4 ± 0.2	30	6	0–7.8
093	F	2	2086	4.2 ± 0.6	45	3	0–12.4
435	F	2	2695	4.4 ± 0.5	33	6	0–10.4
437	F	2	1725	6.8 ± 1.2	46	6	0–12.7
8001	M	2	2511	1.9 ± 0.4	24	7	0–10.4
8002	M	2	3920	1.4 ± 0.1	36	33	0–2.8
8003	F	2	5282	1.5 ± 0.2	18	5	0–7.9
8004	F	2	4807	2.1 ± 0.3	24	5	0–10.2
8005*	M	2	1349	*	18	5	0–30.5
92128	F	3	3502	0.8 ± 0.0	5	5	0–3.8
127	M	3	1595	2.6 ± 0.6	30	5	0–8.3
92129	M	3	1340	1.9 ± 0.4	15	5	0–4.5
93122	F	3	2320	1.4 ± 0.3	10	5	0–7.6
Overall			39,507	2.7 ± 0.4*			

*Dugong 8005 had highly variable TDR readings. This animal's dive data were interpreted with caution.

[+] Mean of means of individual animals.

[a] Location: 1 = Shoalwater/Hervey Bays, 2 = Shark Bay, 3 = Gulf of Carpentaria.

so close to the surface was highly skewed as can be seen by comparing the means, medians and mode for each individual in Table 7. The modal times dugongs spent within 1.5 m of the surface (~ 5 s) is probably closest to the actual surface interval, although this figure is likely to be positively biased for dugongs tagged in Shoalwater Bay and the Gulf of Carpentaria because those TDRs registered depth at 5-s intervals. We investigated the surface interval further by studying the modal time within 1.5 m of the surface for sequences of >10 Square dives for dugongs from Shark Bay only (data recorded every second). The mode was 6 s.

Table 8

Estimates of the components of variance (% of total) from the model used to analyse the effects of dugong sex, location, time of day and tide on diving rates (dives per hour), mean maximum dive depths, durations of dives, and time spent within ≤ 1.5 m of surface

Component	Variance component estimates			
	Mean maximum dive depth	Mean dive duration	Mean number of dives per hour	Mean time within 1.5 m of surfaces after dive
ID(Location × Sex)	11.53 (62)	4.94 (50)	56.87 (34)	26.45 (27)
ID(Location × Sex) × Time of day	2.45 (13)	1.05 (11)	27.05 (16)	12.41 (13)
ID(Location × Sex) × Tide	0.76 (4)	0.66 (7)	0.00 (0)	3.56 (4)
ID(Location × Sex) × Tide × Time of day (i.e., Error)	3.998 (21)	3.142 (32)	82.248 (50)	55.454 (56)

3.5. Individual variation in dive parameters

All the dive parameters measured varied significantly among individual dugongs for all four responses: mean maximum depth of dives, mean duration of dives, mean time spent within 1.5 m of the surface after dives, and mean number of dives per hour ($p < 0.0001$ for ID(Location × Sex) for all four responses). Although some fixed effects (Location and Time of day and/or their interaction) were significant ($p < 0.05$; Table 3) for some responses, there was always significant random variation among individuals within locations among times of day ID(Location × Sex) × Time of day ($p \leq 0.004$ in all cases; Table 3) which suggests that inference for these fixed effects is not meaningful. Random variation among individual dugongs averaged over the repeated effects plus the large within-individual variation among times of day explained at least 39% of the variance for all responses (Table 8). Omitting the data from the animals tagged in the Gulf of Carpentaria made no substantive difference to the results.

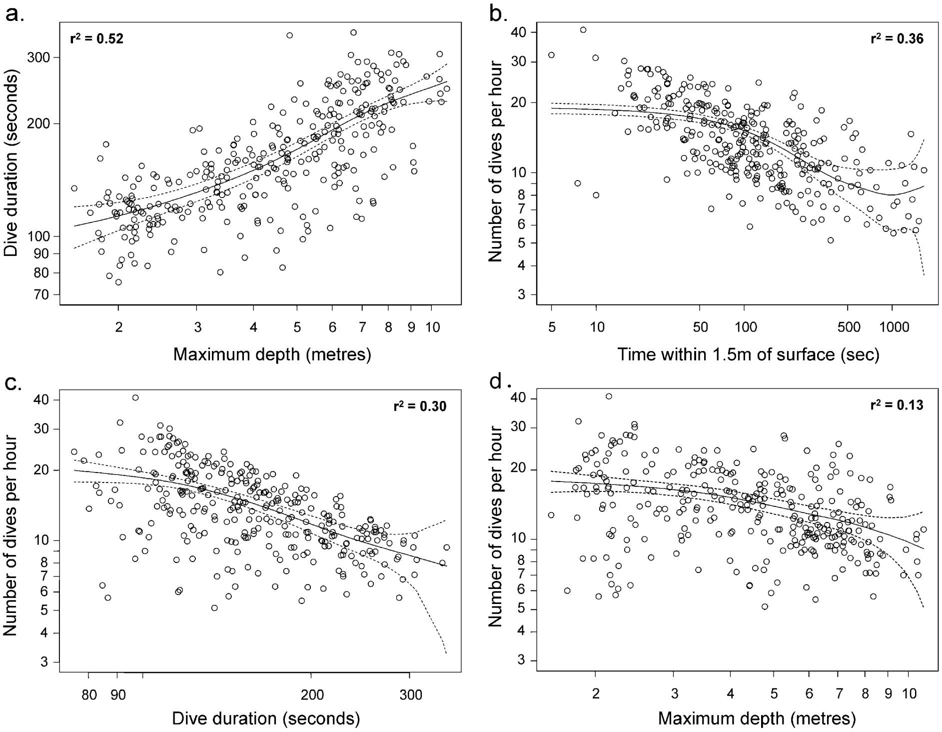

Fig. 3. Relationships between each of the four dive parameters recorded from individual dugongs undertaking more than five dives per hour and with dive durations of greater than 60 s. Solid lines represent fitted smoothing splines with degrees of freedom estimated by cross-validation; dotted lines represent approximate 95% confidence intervals or the fitted smoothing spline. The r^2 values indicate the proportion of variance explained by the smooth relationship.

3.6. Correlations between dive parameters

We explored the relationships between dive parameters using cubic smoothing splines with degrees of freedom estimated by cross-validation (Hastie and Tibshirani, 1990). The analysis was based on the subset of data for each individual where more than five dives per hour were recorded and for which the duration of dives was greater than 60 s as there was substantial variability in both duration and maximum depth of dives when very small numbers of dives per hour were recorded. There was a significant positive relationship between dive duration and maximum depth (Fig. 3a) and a negative relationship between number of dives in an hour and the time in water <1.5 m in the same hour (Fig. 3b). There is also some evidence for negative relationships between dive duration and dives per hour (Fig. 3c) and also between maximum depth and dives per hour (Fig. 3d).

4. Discussion

Our TDR records show that dugongs dive throughout the diel cycle, and that they are capable of making dives to deeper than 20 m and for up to 12 min. The longest dive durations reported previously were 10 min 58 s for a wild dugong (Whiting, 2002) and 8 min 26 s for a captive animal (Kenny, 1967). Overall, the 15 dugongs we studied spent 47% of their daily activities within ≤ 1.5 m of the water surface; 72% of their time within 3 m of the surface. Given that as herbivores dugongs must spend much of their time feeding, this suggests that, at least at our three study sites, the dugongs were highly dependent on the seagrasses growing in intertidal and shallow subtidal areas. This may restrict their access to forage at low tide, particularly in areas such as Shoalwater Bay where the tidal range is 6.3 m. Similar results have been recorded for West Indian manatees, *Trichechus manatus*, using both visual observation and TDRs (Reynolds, 1981; Holly Edwards and Bruce Ackerman, personal communication). Manatees' daily activities also predominantly take place in <3 m of water.

4.1. Diving parameters

There was significant individual variation among dugongs for all the dive parameters examined. Satellite tracking demonstrates that like Florida manatees (Deutsch et al., 2003), dugongs are very individualistic in their movements (Marsh and Rathbun, 1990; Marsh et al., 2002). This variation does not seem to be influenced by gender or life stage in either species, but some individual manatees behave in a very consistent manner in successive years, while others are more flexible. Comparable data are not available for dugongs. Deutsch et al. (2003) interpret movement polymorphism in manatees as an Evolutionary Stable Strategy that results in migrants and residents occurring in the same population. To explore the factors influencing the patterns of movements and diving in dugongs, it will be necessary to have data on the movements and diving behaviour from many more individual dugongs over several years, data on the individual attributes of the dugongs including their size and gender and reproductive status, and more spatially detailed information on environmental parameters.

The mean diving rate we recorded (11.8 ± 1.2 dives h^{-1}) is low in comparison with the 49–75 dives h^{-1} estimated from grand means of dive and surface durations by Anderson (1998) but similar to the 10 dives per hour recorded by Whiting (2002). Two factors will have influenced the difference between our results and Anderson's: (1) Anderson's dive rates were estimates based on grand means of dive and surface durations he recorded from visual observations of dugongs and therefore were considered overestimates of diving rates, and (2) our diving rates are restricted to dives to depths >1.5 m and therefore may underestimate of the true dive rate. Whiting's (2002) data set is based on observations of between 1 and 19 dives by an unknown number of individual dugongs in turbid water between 1 and 6 m deep.

Consistent with our lower dive rate, our estimates of the mean duration of dives are longer than most measurements based on visual observations [mean dive durations: present study 156 ± 5 s, Anderson and Birtles (1978) 73 ± 2.7 s, Anderson (1982) 54 ± 2.9 s, Anderson (1985) 94 ± 5 s, Marsh and Rathbun (1990) 80 ± 27 s, Anderson (1998) 71.8 ± 2.9 s]. However, Whiting (2002) recorded a mean submergence time of 360.4 + 131.7 s (standard deviation) for wild dugongs near Darwin in Northern Australia.

As explained above, we had difficulty measuring surface intervals using the TDRs. Our estimates were based on the modal time spent within 1.5 m of the surface: ~ 5 s overall and 3–6 s for consecutive bouts of >10 Square dives. Given the limitations of the TDRs which recorded depth at >1-s intervals, these figures approximate most mean "surface intervals" obtained by direct observation: 1.4 ± 0.1 s (Anderson and Birtles, 1978), 2.6 ± 0.56 s (Marsh and Rathbun, 1990), or from video recordings from a helicopter 1.8 ± 0.10 s (Marsh et al., 1997). Again, the dugongs observed by Whiting (2002) were exceptional. He measured mean surfacing intervals of 13.0 ± 9.9 s (standard deviation). At least some of these differences can be attributed to the way Whiting defined a surface interval.

4.2. Dive classifications and behavioural functions

Because the TDRs provide two-dimensional dive profiles only, our inferences about diving behaviour must be regarded as hypotheses which merit further testing. It is possible to classify diving behaviour using several methods (e.g., Schreer and Testa, 1996; Schreer et al., 1998; Lesage et al., 1999; Baechler et al., 2002). As this is the first analysis of sirenian diving profiles, we used a relatively simple technique to analyse dive profiles using visual and numerical descriptors to understand the structure and suggest possible behavioural functions of each dive. Five distinct dive types were identified using these methods (Fig. 2). The classification of all five dive types to a high level of accuracy across all three sites and both sexes emphasises the consistency of behaviour shown by dugongs and increases the validity of our dive classifications.

Despite its relatively shallow depth range, the diving pattern of the dugong shows strong similarities with the 12 species of pinnipeds and seabirds reviewed by Schreer et al. (2001). For example, Square dives were by far the most abundant dive type. In particular, the extended periods of bottom time relative to dive duration of both Square and U-shaped dives imply these dives have a feeding or resting function. These dive types are often considered to be primarily foraging dives during which various species of marine mammals and sea birds spend time in a food patch (e.g., Hindell et al., 1991; Martin et al., 1998; Lesage et al., 1999; Schreer et al., 2001; Baechler et al., 2002), although they presumably also have other functions such as exploring or travelling in some species (Schreer et al., 2001). Such dives are also considered to be foraging or resting dives for the green turtle (Hocheid et al., 1999), which, like the dugong, feeds on seagrasses. V-shaped dives are probably exploratory (testing water depth or bottom type) or possible predator/boat avoidance dives as has also been concluded for other species of marine mammals and sea birds (e.g., Schreer et al., 2001). It is possible that the variations of the dives (i.e., extended descent or ascent phases) could be related to travelling, following the sea floor, or resting behaviours as predicted for some seal species (e.g., Hindell et al., 1991; LeBoeuf et al., 1986). (R) and (E) dives are shallow and erratic, and we hypothesise that they represent travelling and resting behaviours, respectively. The predominant difference between these two dive types is the extended time (>5 min) spent within ≤ 1.5 m of the surface for (R) dives, which may indicate surface resting behaviours. It is possible, however, that there are several functions associated with these two dive types, particularly as (1) we could not classify dive types within the top 1.5 m of the water column, and (2) it is impossible to be certain when dugongs are travelling. Churchward (2001) observed that dugongs remain on or near the surface while resting or travelling regardless of water depth, increasing the validity of our interpretation of the potential biological function of these two dive types.

Square dives represent 55% of all dives, U-shaped dives 12% of all dive types. Together, these two dive types suggest that 67% of all dives may represent feeding activity or bottom resting. Churchward (2001) reported 58.3% of all observed dives were foraging dives ($n = 3947$) during daylight hours; Anderson (1998) suggested feeding dives made up 75% of all dives between 0600 and 1800 h, with feeding dives making up 100% of all dives between 0700 and 0800 h, >90% between 1500 and 1800 h and dropping to 57% between 1200 and 1300 h. Anderson and Birtles (1978) also noted that foraging dives were the most commonly observed activities of dugongs.

V-shaped dives made up only 8% of all recorded dives. Published descriptions of dugong diving do not record this behaviour, although it has been observed in clear shallow water while filming from a blimp (Amanda Hodgson, personal communication, 2003). Twenty-two percent of all dives were classified as ‘Erratic’ or possible travelling dives. Churchward (2001) reported 11.9% of all dives observed between 0600 and 1800 h were travelling dives. This is low relative to our estimate; however, 20% of the dives Churchward recorded were unknown behaviours, and her observations did not include night activity. We classified only 3% of all dives as ‘Resting’ dives compared with an estimated 9.9% by Churchward (2001). Consistent with our results, Anderson (1998) recorded resting behaviour only 18 times over 15 days, only when wind was < 17 km h^{-1} and only once at night. He noted that most resting behaviours took place between 1000 and 1300 h. The differences between the behavioural time budget estimates calculated from TDR dive profiles and those of Anderson (1998) and Churchward (2001) from visual observations of dugongs’ behaviours may be the result of the methodological differences. However, as discussed earlier, the limitations of most observational work—including the likelihood of confusing individuals, the inability to “see” the shape of a dive or behaviour of an animal underwater or to observe animals in turbid conditions or at night—place much greater limitations on behavioural observations than on TDR data. A combined visual and TDR study would help develop a greater understanding of these differences and the relationship between dugong dive profiles and behavioural functions.

There were differences in the dive parameters between each dive type (Table 4). The greatest mean maximum depths and durations were recorded for feeding and exploratory dives, while the longest time spent in very shallow water (equal to or less than 1.5 m) was by definition recorded for 'Resting' dives. Churchward (2001) reported that overall, foraging dives were significantly longer than travelling or resting dives for dugongs, particularly in water greater than 3 m deep (foraging 149.6 ± 5.9 s, resting 73.3 ± 6.3 s, travelling 53.7 ± 3.9 s). In contrast, Reynolds (1981) reported mean submerged times for adult Florida manatees, *T. manatus latirostris*, were greatest while resting (177.7 ± 6.2 s, $n = 203$), followed by foraging (136.5 ± 5.3 s, $n = 42$) and then travelling (116.4 ± 10.5 s, $n = 22$). These differences may be the result of different definitions of dive classifications and behaviours, or the biological differences between the two herbivores. Florida manatees feed on a much more diverse range of food types than dugongs and can feed throughout the water column in contrast to dugongs which are obligate bottom feeders (see Reynolds and Odell, 1991; Marsh and Beck, 1999).

4.3. Estimated time budget for foraging activities

Our preliminary interpretation of diving patterns and behavioural functions suggests that more than two-thirds of the diving behaviours of dugongs are related to feeding activities. This figure is likely to be an underestimate because behaviours within 1.5 m of the surface are excluded from our analysis. Preen (1993) and Anderson (1998) both recorded a high proportion of feeding behaviours in water less than 2.5 m. We combined two methods to estimate that dugongs spend at least about 16 h each day feeding: [7.43 dives h^{-1} feeding dives × mean dive duration of feeding dives 2.6 min = 7.7 h day^{-1}, plus 53% of the daily budget spent in >1.5 m and 67% of that time was involved in feeding behaviours; therefore, $24 \times 0.53 \times 0.67 = 8.2$ h] = 16.2 h. There have been no previous estimates of the total time dugongs spend in feeding behaviours each day.

5. Conclusion

The obligate benthic seagrass diet of dugongs influences their life history and behaviour (Kwan, 2002), including their diving behaviours. Although dugongs may be seen in waters up to 70 m deep and over 50 km offshore (Marsh and Saalfeld, 1989) and occasionally cross ocean tranches (Marsh et al., 2002), the dive patterns from this research show they spend the majority of their lives less than 3 m from the water surface. Further research is clearly needed on dugong's diving to such shallow depths.

Understanding the diving behaviours of dugongs and their relationships to daily cycles, tidal state and environmental variables is an important tool for the conservation and management of this species. Our results have application, not only because they increase understanding of the foraging behaviours of individuals, but also because they have the capacity to improve the calibration of population estimates based on aerial surveys. Understanding the relationships between surface and dive duration times of dives relative to behaviour and environment are critical to develop accurate correction factors to account for availability bias, the proportion of dugongs that are unavailable to observers during aerial surveys because of water turbidity. Accordingly, we have used the diving data obtained in this paper to improve our aerial survey estimates of dugong abundance.

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