Estimation of Water Turnover Rate in
Captive Dugongs (*Dugong dugon*)

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Abstract

Water turnover rate was measured for two captive dugongs (*Dugong dugon*) using deuterated water. Body water content of 69.5% in a dugong was high compared to other marine mammals. A water turnover of 257.2 ml kg^{-1} day^{-1} measured in one dugong was almost twice as high as the highest rates measured in studies of captive West Indian manatees (*Trichechus manatus*) and was high compared to those measured in carnivorous marine mammals. The other dugong's estimated water turnover rate of 134 ml kg^{-1} day^{-1} was comparable to the highest rates in manatees. Two alternative explanations are offered for the high water turnover: (1) the incidence of mariposia or voluntary drinking of sea water by the dugong or (2) a metabolic rate that is significantly higher than predicted, based on its phylogeny.

Key Words: Dugong, *Dugong dugon*, water turnover, deuterium, metabolism, mariposia

Introduction

Dugongs (*Dugong dugon*) are marine mammals that spend their entire lives in the marine system. In contrast, their closest relatives range from the strictly freshwater Amazonian manatee (*Trichechus inunguis*) to the West Indian (*T. manatus*) and West African (*T. senagalensis*) manatees that move freely between fresh and salt water (Husar, 1975; Ortiz et al., 1998). Water turnover rates for the West Indian manatee are highest in those animals residing in fresh water rather than marine systems, suggesting an increased rate of drinking fresh water and a lack of mariposia (spontaneous drinking of sea water) (Ortiz et al., 1998, 1999; Ortiz, 2001; Ortiz & Worthy, 2006).

Unlike manatees, the dugong is physiologically independent of fresh water (Marsh, 1989).

Its unusual nonlobulated kidney structure is different from the manatee's (Batrawi, 1953, 1957), but its structure suggests that it probably has the ability to conserve water through concentration of urine (Ortiz et al., 1998). Since the extent to which animals have achieved independence from external water sources is reflected in the amount of water they process through their bodies each day (i.e., water flux or turnover), water flux rates in dugongs are expected to be low.

Since extracting physiologically useful water from sea water is energetically costly, drinking sea water is probably minimal. Water turnover rates in dugongs may be lower than in manatees that actively drink fresh water. In a major review of water influx data, Nagy & Peterson (1988) presented an allometric equation for herbivorous mammals. The predicted daily water influx for a 116 kg herbivorous mammal is 65 ml kg^{-1}; however, there are large errors associated with this predicted value, 16.5 to 254 ml kg^{1} (95% CI).

We report herein the first trial to measure water turnover rates in the dugong. Water turnover rate and total body water pool size were estimated for two captive dugongs using deuterated water, a nonradioactive water isotope. Similar isotopic methods have been used to estimate water turnover rates for a variety of terrestrial and marine mammals (Nagy & Costa, 1980; Nagy & Peterson, 1988; Nagy, 1989; Ortiz, 2001), including the West Indian manatee (Ortiz et al., 1999; Ortiz & Worthy, 2006). Estimation of water turnover is a necessary first step to metabolism studies using doubly labeled water.

Materials and Methods

Water turnover trials were performed on two captive female dugongs (D1 and D2) at Jaya Ancol Oceanarium in Jakarta, Indonesia. This represented

50% of only four dugongs held captive worldwide at the time of this study. Judging by body sizes, both dugongs were subadults (D1: body length, 2.03 m; weight, 116 kg; D2: body length, 1.99 m, weight, 126 kg) (Table 1). The dugongs were held together in a round tiled seawater pool (diameter, 7 m; maximum depth, 2.6 m). The pool was drained and refilled each morning with filtered seawater from the Java Sea, with no added chemicals. Water was at ambient temperature (28 to 29° C). The dugongs were fed twice daily: in the morning before 0900 h and soon after 1530 h. Throughout the trial period (and for many months prior to this period), the diet remained constant. The fresh seagrass offered to the dugongs consisted mainly of *Syringodium isoetifolium* with negligible amounts of *Cymodocea rotundata* and *Halophila ovalis*. These seagrasses all form part of the dugong's natural diet with *S. isoetifolium* being a frequently consumed item in many parts of their range (Marsh et al., 1982; Supanwanid & Lewmanomont, 2003; Preen, pers. comm.). At each feed, the dugongs fed from seagrass floating on the water surface (a daily combined total offering of 30 to 40 kg wet weight seagrass). Most of the seagrass was consumed within a couple of hours, with negligible amounts lost to the filter. Despite the dugongs being slightly underweight for their size (according to Spain & Heinsohn, 1975), they appeared to be otherwise healthy and had been subject to routine weekly veterinarian checks since being brought into captivity. Further, the long habituation time of these dugongs in captivity (> 5 y) meant that the dugongs were placid when handled. These dugongs did not have access to fresh water during the course of the experiment, mimicking the wild situation.

Dugongs were weighed to the nearest 0.5 kg in a sling suspended from the roof above the pool at the start of the trial, and again at the end of the trial. Dugongs did not change body mass over the course of the 4-d trial period. Two, 4-ml blood samples were collected from the anterior palmar surface of the pectoral flipper between the distal parts of the ulna and radius using a 21-gauge, 3.6-cm needle and syringe. All blood samples were held in sealed syringes until they could be processed. Initial blood samples were taken from each animal to measure natural background levels of deuterium (background levels = B). Immediately after the B blood sample was collected, 100% deuterated water was injected intraperitoneally into the mid-dorsal body wall of each dugong just posterior to the rib cage at a dosage of 0.15 ml kg^{-1} body weight (17 ml for D1 and 18.9 ml for D2). The accuracy of the injection volumes was determined gravimetrically (i.e., by weighing the syringe to the nearest 1 mg before and after injection). After administration of the isotope, the

holding pool was refilled to half volume (~1.5 m depth), and the animals were free to swim. Food was withheld from the dugongs at this time. Curatorial staff would not allow the dugongs to be held out of the water for the equilibration period, however. We had to operate under the assumption that dugongs (like fully marine cetaceans and pinnipeds) would be unlikely to drink water (Ortiz et al., 1999).

After equilibration periods of 3.76 h and 4.12 h (D1 and D2, respectively), the pool was drained and a second blood sample was collected from each dugong (equilibration blood sample = E). This equilibration time was based on studies of other marine vertebrates—for example, southern elephant seals (*Mirounga leonina*) have a minimum E time of 1 to 3 h (Hindell, pers. comm.); fur seal (*Arctocephalus* spp.), E = 1.5 to 3 h (Costa, 1987; Costa et al., 1989); emperor penguins (*Aptenodytes fosteri*), E = 2 h (Robertson & Newgrain, 1992); and terrestrial mammals of similar body size (Nagy, 1989). The initial dilution of the deuterium isotope that occurs during the equilibration period provides an estimate of the total body water (TBW) pool.

The isotope turnover trial was run over 3 and 4 full days for D1 and D2. During this period, the pool was filled to capacity, and the dugongs were free to swim and feed. Final blood samples (F) were taken at the end of the trial period. The dilution of deuterium isotope in the blood during this period is determined by water influxes (e.g., food water, metabolic water, drinking water) and water effluxes (e.g., pulmo-cutaneous exchange, excretion, defecation) and is assumed to occur by simple Newtonian exponential decay (Lifson & McClintock, 1966).

Sealed syringes of blood were kept in an air-conditioned laboratory (~24° C) until processing. B blood was processed 26 h after collection, and E and F blood within 3 h of collection. Ten subsamples of each blood sample were drawn up into nonheparinised haematocrit tubes and one end heat-sealed. Haematocrit tubes were then placed in glass pasteur pipettes, and both ends of the pipette were heat-sealed to exclude moisture and prevent evaporation of the samples. Samples were returned to Australia in this form. Water was extracted from blood by distillation under vacuum (Wood et al., 1975). Deuterium concentration in the distillate was measured in an Isotope Ratio Mass Spectrometer (VG Optima) (Gessaman et al., 2004). Water influx was calculated using equation (3) of Nagy & Costa (1980).

Samples of the dugongs' main food item, *S. isoetifolium*, were desiccated at 60° C to determine water content, which was then used to estimate the possible contribution of dietary water to water

influx. Dietary water intake was estimated as the product of the amount of food eaten and its water content. Food consumed was averaged for the two animals in the single tank and dietary water was expressed as ml H_2O kg^{-1} body mass per day.

Results

Total body water (TBW) for D2 was 69.5%. Unfortunately, all of the pipettes containing the equilibration (E) samples for D1 sustained tiny cracks during transit to Australia. We assumed that the mean mass-specific body water content for D1 was similar to D2 and calculated water influx by the single sample method (Webster & Weathers, 1989).

Absolute and mass-specific water turnover rates for each dugong are summarized in Table 1. Neither of the dugongs changed body mass over the trial period, so water turnover rates were calculated from a constant pool size. The water turnover rate for D2 was 257 ml kg^{-1} day^{-1}, and water

turnover rate for D1 was about half this value, 134 ml kg^{-1} day^{-1}. Since the E sample for D1 was estimated, this turnover rate may be erroneous. D1 had a similar body length to D2, but weighed 8% (10 kg) less; D1 probably had relatively less body tissue (muscle and fat) in relation to skeletal material. A decrease in body condition of dugongs is reflected in reduction of subcutaneous and visceral body fat and also in body wall muscle mass (JML, unpubl. data). The poorer body condition is reflected in a higher mass specific body water pool. If the pool size for D1 was increased by 10%, the initial estimated counts would decrease by 10%, and the calculated daily water influx would be about 120 ml kg^{-1}.

The two dugongs were offered between 30 and 40 kg wet weight of seagrass per day. After the two daily feeds, there was no seagrass remaining. The water content of the dietary seagrass *S. isoetifolium* was 77.43 ± 0.56% dry matter (*n* = 4). Assuming that each dugong equally shared the seagrass offered each day, and based on the maximum offering of 40 kg per day (i.e., 20 kg seagrass per dugong per day), absolute daily dietary water influx was estimated as 20 kg x 0.77 = 15.4 kg water day^{-1}. Based on these figures, mass-specific dietary water was estimated at 132 and 122 ml kg^{-1} day^{-1} for D1 and D2, respectively.

Discussion

The 69.5% body water content measured in one of these dugongs was high compared to other marine mammals (Table 2). Since the proportion of body mass that is water is inversely related to the proportion of fat (Pace & Rathbun, 1945), marine mammals with their higher fat and blubber content generally have a body water content lower than the greater than 60% body water content of terrestrial mammals (Richmond et al., 1962). In contrast, sirenians generally have thinner blubber layers than cetaceans and pinnipeds (Bryden

Table 1. Body mass, total body water, and rates of water turnover of captive dugongs, D1 and D2

	Dugong D1	Dugong D2
Body length (m)	2.03	1.99
Initial body mass (kg)	116.00	126.00
Total body pool (l)	80.62[a]	87.57
Final body mass (kg)	116.00	126.00
Total body water (TBW) (%)	69.50[b]	69.50
Absolute water turnover l day^{-1}	15.52	32.41
Mass-specific water turnover ml kg^{-1} day^{-1}	133.80	257.20
Dietary water (ml kg^{-1} day^{-1})	132.75	122.22
Trial / release period (d)	3	4

[a] Total body pool estimated for D1
[b] TBW for D1 assumed to be similar to D2 (see "Results")

Table 2. Percent total body water content and water turnover (influx) rates (ml kg^{-1} day^{-1}) of free-living marine mammals, including cetaceans, pinnipeds, and sirenians

Species	Water content (%)	Water turnover (ml kg^{-1}day^{-1})	Source
New Zealand sea lions	66.0	--	Costa & Gales, 2000
Common (harbour) seals	55.0-64.0	85*	Reilly & Fedak,1991
Grey seals	--	48.8*	Reilly & Fedak, 1991
Common dolphin	37.0	77.00	Hui, 1981
Fat Antarctic fur seal	50.0	--	Costa et al., 1989
Lean Antarctic fur seal	73.0	169.00	Costa et al., 1989
West Indian manatees	--	145 ± 12	Ortiz et al., 1999
Dugongs	69.5	196 (mean)	This study

* Expressed as ml kg$^{-0.8}$ day^{-1}

et al., 1998), and dugongs have thinner blubber than manatees (Nichols, 2005). The body condition of these dugongs suggests that they did not have high body fat content.

The rates of water turnover for the dugongs in this study were higher than anticipated. A water turnover of 257.2 ml kg^{-1} day^{-1} is almost twice as high as the highest rates measured in captive West Indian manatees (Ortiz et al., 1999) and is high compared to those measured in other marine mammals (Table 2). Even the estimate of 134 or 120 ml kg^{-1} day^{-1} for D1 is comparable to the highest rates in manatees (i.e., 145 ± 12 ml kg^{-1} day^{-1}) (Ortiz et al., 1999), although it should be noted that this lower value may be unreliable since it assumed similar body water content in the two dugongs.

Water influx in marine mammals consists of food water, metabolic water, drinking water, and absorption of water across the skin, each to varying degrees (Ortiz, 2001). The combined daily water influxes were 15.52 + 32.41 l or more likely, 13.92 + 32.41 l. This may also be a slight overestimate (about 4%) because pool size is overestimated by the hydrogen isotope dilution technique. It is also most likely that the food was not consumed in equal proportions by the two dugongs, with the relatively fatter D2 possibly consuming twice as much as D1 during the experimental period. In this study, preformed water accounted for 69% (i.e., 30.8/44.55) of water influx. The remaining 31% of water influx may be explained by the production of metabolic water and/or mariposia (voluntary drinking of sea water). Although Hui (1981) suggested that skin may be a major avenue of water flux in dolphins, this is unlikely in the dugong given its relatively thick subcutaneous dermal layer and lack of superficial subdermal vascularisation.

Mariposia has not been described in dugongs. Ortiz et al. (1999) suggested that West Indian manatees do not drink sea water under natural conditions, but they will drink fresh water when available. With few exceptions, drinking salt water is not a common practice in fully marine mammals or marine birds (Ortiz, 2001). For example, in common dolphins (*Delphinus delphis*), up to 16% of the water flux is from drinking (Hui, 1981), while in penguins (*Pygoscelis papua*), the intake of water from drinking is usually less than 5% of water influx (Robertson et al., 1988). In other fully marine mammals, water balance is maintained by metabolic and dietary water, while incidental ingestion of salt water may maintain electrolyte balance. The fully marine habits of the dugong suggest that it may similarly have little need to drink salt water; however, its herbivorous diet and fermentative digestive strategy presumably require high water content for efficient functioning, which is in line

with other herbivorous mammals (Green, 1989) and in contrast to carnivorous marine mammals. Certainly, the dugong's kidney structure (Batrawi, 1953, 1957) suggests it has the capacity to drink sea water, and its feeding habit of ingesting large quantities of seagrass per feeding dive (Lanyon, 1991) could presumably result in considerable incidental ingestion of salt water. It is interesting to speculate on the dugong's ability to actively consume sea water and gain free water, and its capacity to excrete excess Na^+ and Cl^- should this occur. A comparison of renal structures of dugongs and manatees may reflect differences in their respective marine and freshwater habitats (Ortiz, 2001).

An alternative explanation for the high rate of water turnover may be that dugongs have a higher metabolic rate than manatees, hence a higher flux of metabolic water. Sirenians are tropical to subtropical animals and appear to be sensitive to changes in water temperature, moving into warmer waters when temperatures drop below about 20° C in the case of Florida manatees (Irvine, 1983; Reynolds & Wilcox, 1986) or 18 to 19° C in the case of dugongs (Anderson, 1986; Preen, 1993; Lanyon, 2003). Compared to cetaceans and pinnipeds, sirenians have only thin blubber layers, and it appears that manatees at least may have a limited ability to increase their metabolic rate to compensate for heat loss during cold weather (Gallivan et al., 1983). Furthermore, studies of manatee metabolism suggest that the basal metabolic rate of manatees may be low compared to that predicted for a terrestrial mammal of similar body size, that is, 15 to 22% of the predicted level for Florida manatees (Irvine, 1983) and 36% for Amazonian manatees (Gallivan & Best, 1980). Metabolic rate has not been measured in dugongs; however, it has been assumed that dugongs have similarly low metabolic rates, based largely on phylogeny, but also through thermal considerations.

A difference in basal metabolic rate may help explain some of the anomalies in growth and reproductive rates between dugongs and manatees. Although sirenians in general have slow and variable reproductive rates, dugongs have a significantly protracted reproductive cycle compared to manatees (Marsh, 1995). First, the prepubescent phase in dugongs is long so that, throughout most of their range, the minimum pre-reproductive phase for both sexes is 9 to 10 y. Further, many females do not reach sexual maturity until 15 to 17 y, compared to 3 to 4 y for West Indian manatees (Marmontel, 1995). Second, the intercalving period of the dugong is a long and variable 3 to 7 y (Marsh, 1995), while female manatees tend towards calves every 3 y (Marmontel, 1995). The reasons for these differences have been unclear.

Dugongs also appear to be faster and more active than manatees (J. P. Reid, pers. comm.; JML, pers. obs.). High activity patterns coupled with higher metabolism, but a restricted diet of low nutrient seagrass, may suggest that the growth and reproductive patterns of the dugong are limited by energetic and nutritional factors. Results from this study suggest that an investigation into the metabolism and energetic requirements of the dugong is warranted.

Acknowledgments

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