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Behaviour and buoyancy control in a shallow diving marine mammal, the dugong (*Dugong dugon*)

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Shallow diving air-breathing animals face the challenge of maximising oxygen stores to extend dive duration while being subject to rapid pressure changes, especially in the first 10 m. Buoyancy control is integral to managing the physiological and physical challenges of shallow water diving. Dugongs (*Dugong dugon*) are shallow diving megaherbivores and must spend extended periods foraging on shallow benthic seagrass communities. Thus, balancing the locomotor activity associated with diving and limited oxygen stores is critical for dugongs, making the dugong a valuable model for investigating buoyancy control in shallow diving marine mammals. We used multi-sensor tags to investigate the buoyancy control of seven mature dugongs (three female, four male; deployments lasting 10–35 hours) in New Caledonia, 2019 (n=2) and the Exmouth Gulf, Western Australia, 2021 (n=5). Our study demonstrates that dugongs regulate their buoyancy by controlling their inhaled lung volume prior to diving, a strategy that contrasts with some other deeper diving marine mammals (e.g. phocid seals), which dive on exhalation. For the dugongs, the depth at which gliding commenced, a proxy for the animal's buoyancy shifting from positive to negative, increased with maximum dive depth during descent and ascent. This is a strong indication for inhaled air volume increasing with maximum dive depth. Body angle, fluke beat frequency and activity during descents and ascents increased in unison. This evidence suggests that dugongs utilise lung-mediated buoyancy control to maximise the time spent at depth, while minimising the locomotory costs associated with buoyancy while diving.

KEYWORDS
acceleration, biologging, buoyancy, dive depth, diving, dugong

1 Introduction

Air-breathing aquatic animals must divide their time between diving for resources and surfacing to breathe, while facing the physiological challenges associated with an aquatic lifestyle, including buoyancy control and hydrodynamic drag (Miller et al., 2004). These animals need to maximise the time spent underwater between breaths. However, taking a full breath to maximise oxygen stores while diving will increase the upward buoyant force acting on the animal (Hays et al., 2004). The buoyant force will be positive when the animal is less dense than water, and negative when the animal is denser than water (Watanabe et al., 2006). Thus, the buoyant force is greater than the gravitational force for positive buoyancy, the reverse is true for negative buoyancy (Beck et al., 2000; Davis, 2019; Wilson et al., 1992). Air-breathing marine animals are usually positively buoyant at the surface of the water due to inspired air within the lungs and the air trapped within the pelage (Davis, 2019; Miller et al., 2004; Yeates et al., 2007). Adipose tissue also significantly contributes to overall buoyancy, and seasonally changing body composition can affect buoyancy in marine mammals (Davis, 2019; Watanabe et al., 2006; Webb et al., 1998). Changes in lung volume will affect the buoyant force acting on the animal, which is reflected in locomotor activity (Okuyama et al., 2012; Watanabe et al., 2006).

Buoyancy plays a pivotal role in the locomotory activity of air-breathing marine animals. When animals are swimming in the opposing direction to their overall buoyancy, locomotor activity must be increased to swim at a given velocity, and when buoyancy assisted, locomotor activity can be decreased or cease altogether (Beck et al., 2000; Watanabe et al., 2006; Yasuda and Arai, 2009). For example, positively buoyant animals must actively swim to descend from the surface, but are able to float to return to the surface (Beck et al., 2000; Minamikawa et al., 1997; Sato et al., 2002; Watanuki et al., 2003; Wilson et al., 1992). Locomotory activity affects the rate at which oxygen stores are depleted: high locomotory activity during a descent, due to positive buoyancy, will deplete oxygen stores faster because of increased swimming effort (Davis, 2019; Sato et al., 2003; Yasuda and Arai, 2009). Therefore, an animal's ability to utilise its buoyancy to reduce locomotory activity while diving will aid in extending aerobic diving duration (Sato et al., 2002). Thus, minimising locomotory activity during a dive will improve diving efficiency, extending the time spent at the bottom of a dive by lowering oxygen demand (Fossette et al., 2010; Hays et al., 2004; Sato et al., 2002; Yasuda and Arai, 2009). However, an animal's buoyancy changes while diving due to hydrostatic pressure; consequently, locomotor activity will vary accordingly (Fossette et al., 2010; Hays et al., 2004; Sato et al., 2002; Watanabe et al., 2006).

In accordance with Boyle's law, hydrostatic pressure increases with depth, compressing the volume of airspaces in the animal's body, most prominently the lungs, proportionally to the change in ambient pressure (Davis, 2019; Minamikawa et al., 1997). Subsequently, the resulting reductions in buoyant force lead to decreases in locomotory activity (e.g. fluke or wing beats) with increasing depth (Sato et al., 2002). Typically, a transition from positive buoyancy near the surface to negative buoyancy at greater depths will occur and translate into a transition from active propulsion to passive gliding, with the opposite being observed during ascent (Kooyman and Ponganis, 1998; Mitani et al., 2009; Sato et al., 2002; Webb et al., 1998; Williams et al., 2000; Yasuda and Arai, 2009). As previously mentioned, the rate of oxygen consumption is linked to locomotor activity, thus reductions in buoyancy and consequently locomotor activity while descending or ascending can further extend diving duration (Hays et al., 2004; Watanabe et al., 2006; Webb et al., 1998).

Air-breathing marine animals have evolved physiological and behavioural adaptations to cope with the forces encountered during diving, thereby extending diving duration. Behavioural adaptations include gliding during descents and ascents when buoyancy assisted (Fossette et al., 2010; Sato et al., 2002; Williams et al., 2000), and regulating lung volume by controlling the amount of inspired air (Davis, 2019). An animal's ability to control its lung volume, and thus regulate buoyancy with respect to depth, is pivotal in maximising its use of limited oxygen stores (Davis, 2019; Fossette et al., 2010; Sato et al., 2013). Exhalent divers (divers that typically dive with largely empty lungs) are usually deep diving animals that encounter physiological risks related to the effects of pressure on the body (e.g. shallow water blackout and nitrogen narcosis) (Hooker and Fahlman, 2015; Kooyman and Ponganis, 1998; Ponganis, 2011). Deep diving animals such as phocid seals, are reported to utilise negative buoyancy to glide for extended periods during descents, to conserve oxygen and increase their aerobic dive duration (Davis, 2019; Kendall-Bar et al., 2023; Mitani et al., 2009; Webb et al., 1998; Williams et al., 2000). Meanwhile, inhalant divers such as penguins, marine turtles and otariids are comparatively shallow divers (with notable exceptions), and are reported to adjust the volume of air inhaled with the targeted dive depth to maximise aerobic diving duration (Davis, 2019; Fossette et al., 2010; Sato et al., 2002; Zellmer et al., 2021). A problem for shallow diving animals occurs when the combined volume of gasses in their lungs and pelage/plumage is too large and they experience excessive positive buoyancy during the bottom phase of a dive. This situation requires high locomotory activity to operate at fixed depths (such as feeding on the benthos) and will deplete oxygen stores faster, therefore curtailing the dive (Sato et al., 2002; Yasuda and Arai, 2009). Considering this, shallow divers should be stringent when regulating their buoyancy to maximise their aerobic diving duration to ensure longer, more sustainable dives with a short recovery (Bird et al., 2024; Costa and Favilla, 2023; Sato et al., 2002).

Morphological and physiological adaptations also contribute to prolonging the duration of aerobic diving. Such adaptations include but are not limited to: body size and shape, lung size and blood oxygen stores (Davis, 2014; 2019; Kooyman and Ponganis, 1998; Marshall et al., 2022). Shallow divers typically have a larger lung volume-to-body size ratio than deep divers, meaning they can hold a larger volume of air in their lungs relative to their body size (Davis, 2019; Zellmer et al., 2021). For shallow divers, large lungs suggest that aerobic diving is sustained through reliance on air, rather than oxygen bound to myoglobin or haemoglobin (Kooyman, 1973). The large lungs add buoyancy, thus increasing locomotory activity at the start of the dive. Still, they allow the animal to sustain aerobic diving for longer when at depth and negatively buoyant, i.e., more time can be spent foraging or resting (Davis, 2019; Hays et al., 2000a, 2007; Minamikawa et al., 1997; Sato et al., 2002; Zellmer et al., 2021). Deep diving animals have evolved to store the majority of their oxygen in haemoglobin and myoglobin rather than in inspired air, allowing sustained aerobic dives following exhalation (Hays et al., 2004; Kooyman and Ponganis, 1998; Ponganis, 2011; Schreer et al., 2001). Exhalation prior to submersion in deep diving marine mammals suggests that morphological factors, specifically the amount of adipose tissue an individual stores, rather than inspired air, dictate buoyancy at depth. It is not known whether buoyancy control in shallow diving marine mammals, such as sirenians (dugongs and manatees), is more akin to that of deep diving marine mammals or to other taxa that typically dive to shallow depths.

Dugongs (*Dugong dugon*) are diving marine mammals that conduct hundreds of relatively short and shallow dives daily (Hagihara et al., 2014). Dugongs spend most of their time in depths of less than five metres foraging on seagrass, a relatively low energy food source (Chilvers et al., 2004), though have been recorded to dive as ‘deep’ as 36.5 m (Sheppard et al., 2006). As megaherbivores, dugongs must balance the need to forage for extended periods at the seafloor with the cost of moving between the surface and seafloor. However, for dugongs, controlling buoyancy while maximising oxygen stores can be challenging due to rapid pressure changes in the top 10 m of water. This is because, dugongs have relatively large lungs relative to their body size, a feature that adds buoyancy. Remaining near the seafloor in shallow waters, where a dugong’s predominant food source grows, will be costly for a positively buoyant animal. Dugongs have morphological adaptations that make them denser than seawater, including dense skin (Kipps et al., 2002) and pachyosteosclerotic bones (Domning and de Buffrénil, 1991; Taylor, 2000). These adaptations offset the positive buoyancy contributed by large lungs that span the length of their torso (Marsh et al., 1978; Rommel and Reynolds, 2000) and a large digestive tract (Marshall et al., 2022), enabling them to control their buoyancy in shallow waters by changing their lung air volume accordingly. Buoyancy control in a shallow diving megaherbivore such as the dugong may be more developed than in other shallow diving animals as they must forage for extended periods at the seafloor by undertaking repeated dives. Therefore, the dugong should be a valuable model for understanding buoyancy control in shallow diving marine mammals.

Here, we sought to quantify, for the first time, the buoyancy control of a shallow diving marine mammal, the dugong, to understand how they adjust their buoyancy and behaviour to the physical constraints of diving in shallow waters, using multi-sensor tags. We investigated the lung-regulated buoyancy control of dugongs from two different locations; New Caledonia and Exmouth Gulf, Western Australia to: (1) determine whether dugongs control their buoyancy by regulating their inspired air volume according to dive depth; (2) describe the trade-off between buoyancy and locomotor activity during diving; and (3) compare the relationship between dive duration and maximum depth with those of other marine animal species.

2 Methods

2.1 Study sites

The western coast of the main island of New Caledonia (-21.14301°, 164.72916°) supports a range of habitats, from shallow seagrass meadows to diverse reef structures and deep channels, and experiences a tropical climate (Cleguer et al., 2024). Exmouth Gulf (-22.15501°, 114.25090°) is a large and shallow embayment on the eastern side of the North West Cape peninsula in Western Australia experiencing a semi-arid to arid, sub-tropical climate (Environmental Protection Authority, 2021). The eastern shores of the Gulf, where our fieldwork took place, are characterised by extensive mud and sand flats with well-developed mangroves (Environmental Protection Authority, 2021).

2.2 Tagging process

Field work was conducted in October 2019 along the western coast of New Caledonia and in July 2021 in the eastern side of Exmouth Gulf, Western Australia. Dugongs were closely followed and captured using the ‘*Rodeo*’ technique as described by Lanyon et al. (2006). Permits to pursue by boat, rodeo and tag the dugongs in the North provinces of New Caledonia were obtained (N°609011-52/2019/DEPART/JJC) and approved by Murdoch University Animal Ethics Committee (R3169/19). Permits for Exmouth Gulf were approved by Murdoch University (RW3324/21) and the Western Australian Department of Biodiversity, Conservation and Attractions (FO25000344). Once the dugong was captured, a skin sample for genetic analysis was taken, and the morphometric features of the dugong were measured and/or recorded including total length (snout to fluke notch), sex and presence of tusks and/or mammary glands (Spain and Heinsohn, 1975). As a final step, the dugong was tagged with either a suction-cup multi-sensor mini-diary CATs (Customised Animal Tracking Solutions, Australia) tag (22 cm X 10 cm X 5 cm, 318 g) or a camera diary CATs tag (25 cm X 14 cm X 5 cm, 758 g), hereafter referred to as mini-diary or camera diary tags respectively, and then released.

Mini-diary and camera diary tags were equipped with multiple sensors, including a tri-axial accelerometer, a magnetometer and gyroscope, pressure (as a measure of depth), temperature, and a Global Positioning System (GPS). The camera diary had an additional camera sensor, that was not used here. The sensors were programmed to record at 50 Hz. Both the mini-diaries and camera diaries were equipped with a VHF transmitter (model F1840B, Advanced Telemetry Solutions). The camera diary packages incorporated a SPOT-258 satellite tag (Wildlife Computers) to aid retrieval via ARGOS satellite locations. Tags were attached to the dorsal side of the dugong, on the upper back behind the neck of the animal, using three (mini-diary) or four (camera diary) suction cups attached to the base of the tag. Each tag featured a Galvanic Timed Release (GTR) to facilitate timely release of the tag from the dugong. Tags were located for retrieval using a VHF receiver and 3 element folding Yagi antenna (Receiver model R410, Advanced Telemetry Systems).

2.3 Analysis

Multi-sensor data downloaded from the tags were analysed using IGOR Pro version 9.0.2.4 (Igor Pro, Wavemetrics, Lake Oswego, Oregon, USA) and the "Ethographer" package (Sakamoto et al., 2009). Zero-offset calculations were used to adjust for sensor drift when present, with a three-to-five-minute running minimum, based on the maximum dive duration per dugong. Once corrected, the raw depth values were smoothed over 201 points using the Savitzky-Golay method in the second order, a type of least squares polynomial smoothing (Savitzky and Golay, 1964). Vertical Velocity (VV) was calculated by taking the difference between successive smoothed depth data points at a one second interval (Andrzejaczek et al., 2018; Miller et al., 2004).

Raw tri-axial acceleration for the three orthogonal body axes (surge: anterior-posterior movement, heave: dorsal-ventral movement, sway: lateral movement – Figure 1) were used to calculate the gravitational (also often referred to as static acceleration) and dynamic acceleration. Static acceleration reflects body posture relative to Earth's gravity, and dynamic acceleration is the change in velocity due to body movement (Shepard et al., 2008). Static and dynamic acceleration were separated using a 4-second box smoother, as outlined in Shepard et al. (2008). Overall Dynamic Body Acceleration (ODBA) was used as a proxy for energy expenditure related to locomotor activity (Gleiss et al., 2011), and was calculated using the following equation adapted from Wilson et al. (2020);

$$ODBA\ \ (g) = \ dynX_{abs} + dynY_{abs} + dynZ_{abs}$$

Body angle was calculated from the static components of the surge, heave and sway acceleration using the following equation adapted from Bidder et al. (2015), where S_x= static surge, S_y= static heave and S_z= static sway;

$$Body\ \ Angle\ \ (\,^{\circ}\,) = atan2(S_x, (\sqrt{S_y{*}S_y +\ \ S_z{*}S_z}))*\frac{180}{\pi}$$

Positive body angles mean that the dugong's body was angled upwards; negative body angles downwards (Figure 1). Body angle, ODBA, VV and depth were resampled from 50 Hz to 1 Hz intervals using the resampling with replacement (Bootstrap) function in IGOR Pro to downsample the data.

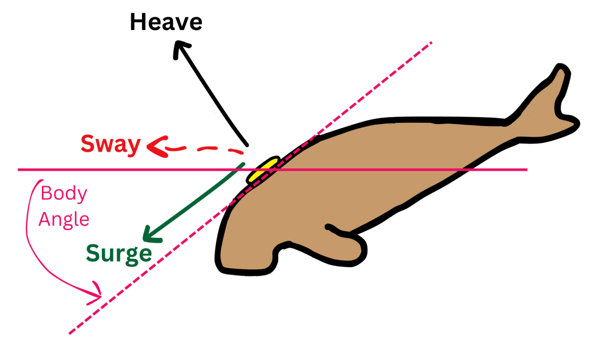

FIGURE 1
Schematic showing a dugong with annotated surge, heave and sway acceleration axes measured by the mini-diary tags and how they relate to the calculated body angle of the dugong *Tag not to scale.

To account for any post-capture stress, the first two hours of every deployment were omitted. This threshold was determined by using ODBA as a proxy for activity. Plotting ODBA against the time since deployment for individual dugongs, revealed that ODBA declined over the first two hours post deployment, after this time the ODBA for each dugong did not significantly change. The remaining data were imported into the *R* statistical environment (v2024.04.2, R Core Team, 2024), where all statistical analyses were conducted. Individual dives, their respective phases (descent, bottom phase and ascent) and corresponding statistics were identified using the "*createTDR*" and "*calibrateDepth*" functions within the "*diveMove*" package in R (v1.6.2, Luque, 2007), and a 0.1 m dive threshold. Dive phases were identified from changes in vertical rate using a "*smooth spline*" cubic spline model within the "*calibrateDepth*" function. The smoothing parameter was set to 0.5 and was selected after testing values from 0.05 to 1.0, increasing in increments of 0.05. A dive was determined to have started once the dugong was below 0.1 m. The 0.1 m threshold was chosen to demonstrate the ability of the depth sensor within the mini-diary tags to resolve very shallow and short dives. Threshold suitability was assessed following a procedure similar to that of Hagihara et al. (2011), in which the appropriate dive threshold was selected after testing thresholds from 0.05 m to 1.0 m, increasing by 0.05 m intervals. The most appropriate threshold was 0.1 m as it suitably removed very short and shallow dives. Later, a subset was created to remove dives that were less than five seconds in duration, this removed any dives with short duration that were likely the dugong dipping its head below the surface in between breaths rather than diving.

2.3.1 Buoyancy regulation

The transition from positive to negative buoyancy during dives is typically characterised by a concomitant change from active swimming to gliding during descent and vice-versa during ascent (Fossette et al., 2010; Sato et al., 2002). Quantifying the buoyancy transition (gliding depth) allows inferences about buoyancy control, since changes in inhaled air volume are expected to shift the depth at which buoyancy transitions occur. For dugongs, fluke beats can be visualised in the dorso-ventral heaving axis, the primary movement axis for these animals. The dominant cycle frequency of dugong fluke beats (Fluke Beat Frequency, hereafter referred to as FBF) was identified using the continuous wavelet transformation function (Spectrum Analysis; MinCycle= 0.25, MaxCycle= 6, ω_0 = 10) in Ethographer, within Igor Pro Wavemetrics (Sakamoto et al., 2009). Spectrum analysis was used to characterise dive descents and ascents and to visually identify the point during descent or ascent at which fluke beats stopped and gliding began (hereafter referred to as gliding depth). Descent and ascents were characterised as: entirely active, fluke beats present the entire phase; entirely passive, no fluke beats detected during the phase; active and passive, fluke beats initially present then become absent. The latter group includes more complex kinematics such as active-passive-active ascents (10 dives) where a gliding depth, therefore buoyancy transition, occurred. Gliding in dive descents and ascents was indicated where the cycle could not be detected, visually identified by a lack of amplitude in the spectrogram (Fossette et al., 2010). From this, the gliding depth (if present) and time gliding commenced was recorded. The gliding depth in each dive was visually identified by one person – RL, to reduce the risk of interobserver differences. The gliding depth separated active and passive descents and ascents into four subphases: active descent, gliding descent, active ascent, and gliding ascent, as per Fossette et al. (2010). When calculating means per dive phase for VV, FBF, ODBA and body angle, the mean per variable was calculated between the start and end time of each subphase.

To investigate the buoyancy regulation of dugongs, the relationships between maximum dive depth and gliding depth in dives with a buoyancy transition (active and passive descents or ascents) were tested using linear mixed effect models. Models were fitted using maximum likelihood, with the final model reported using restricted maximum likelihood (REML) in the package "*lme4*" in R (Bates et al., 2015). Linear mixed effect models included dugong ID as a random effect to account for any individual variation that might be present. To identify an appropriate transformation for the data (if required) histograms of the variables were plotted and compared between untransformed and transformed data. Where necessary, variables were transformed. To address any skewness in the data, log transformations were applied in the model during the regression analysis and compared with the model without any transformation to assess the effect on the QQ plot (to test normality) and the distribution of residuals and identify the most appropriate model for the data. When a transformation did not improve the model, the untransformed model was chosen. The same process was followed when investigating the relationships between maximum dive depth and mean body angle, ODBA, FBF, and VV during active descents and ascents of dives with active and passive kinematics. Models were assessed by obtaining the difference in AIC (ΔAIC) between the model and null model (model without a fixed effect) fitted using maximum likelihood. Models were further assessed by obtaining the conditional R^2 using the package "*MuMIn*" in R (v1.48.11, Barton, 2025). To investigate the probability of a descent or ascent featuring a kinematic transition from active to passive with increasing maximum dive depth, we used generalised linear regression models: specifying family as "binomial" and we used the default link as "logit".

If dugongs were to regulate their lung volume according to dive depth, and inhaled air volume increases with increasing maximum dive depth, we anticipate that dugongs will need to increase their FBF at the beginning of descents to deeper depths over those to shallower depths, as a result of increased buoyancy. To test this, we investigated the relationship between FBF, instantaneous depth, and buoyancy throughout dive descents and ascents. The mean FBF was calculated for binned instantaneous depth during descents or ascents. Descents and ascents with the active and passive kinematics were included. Dives were split into groups according to maximum dive depth; 0–2 m, 2–5 m, 5–7 m and 7 m +. Dives deeper than seven metres were excluded as there was only one dugong that dived deeper than seven metres.

2.3.2 Buoyancy and locomotor activity trade-off

Dives with higher locomotor activity will consume oxygen stores faster (Yeates et al., 2007). We would therefore expect dive duration to decrease with increasing ODBA. However, if maximum dive depth and inhaled air volume increase concomitantly, then we would expect the dive duration of deeper dives to be longer than that of shallow dives with similar mean ODBA. To investigate the relationship between dive duration, maximum dive depth and ODBA per dive we conducted a multiple linear mixed effect model with Dugong ID as a random effect. Mean dive ODBA was binned into three groups; 0.0-0.1 g (low), 0.1-0.2 g (medium) and 0.2 g+ (high), hereafter binned ODBA and treated as a factor. The latter binned ODBA group (0.2 g+) is larger as this group included outliers from the exploratory boxplot (right hand side tail). The analysis was conducted on dives that were less than seven metres in maximum depth, because only one dugong from New Caledonia dove deeper than seven metres. To visualise the relationship between dive duration, maximum depth and ODBA, maximum dive depth was binned into one metre intervals (from 0 to 7 m), hereafter binned depth. For every binned ODBA group and binned depth interval, the mean dive duration was calculated per dugong. Following this, the mean and standard error of dive duration were calculated across individuals for binned ODBA and binned depth intervals. Not every individual contributed data to every binned depth and ODBA group (see Supplementary Table 1).

2.3.3 Comparisons with other species

If dugongs dive on inhalation, in contrast to some other marine mammal species, we expect the relationship between maximum dive depth and dive duration to feature a larger slope value. To compare the relationship between maximum dive depth and dive duration of dugongs with other marine animals (pinnipeds and seabirds), we followed Schreer et al. (2001). Unlike Schreer et al. (2001), we included dives shallower than five metres, as they comprised the majority of dugong dives. Furthermore, we chose not to discriminate dives by shape, as dugong diving is not well described by shape dichotomies (Hagihara, 2015). Instead, we chose to pool dugong dives and compare the slope to the slopes of pooled dives for the study species in Schreer et al. (2001). To ensure the slopes of the data were comparable, dive duration was converted from seconds to minutes; no transformation was applied within the model as per Schreer et al. (2001), and the model was run on the pooled dives. However, for the dugong data the underlying assumption for homoscedasticity was not satisfied in linear regression, therefore, to obtain robust standard errors, t- and p-values we used the "*coeftest*" function specifying type "HC3" within the "*lmtest*" and "*sandwich*" packages in the statistical program R (Zeileis, 2004; Zeileis and Hothorn, 2002). Slope values describing the relationships between maximum dive depth and dive duration for pooled dives for species reported in Schreer et al. (2001) were extracted using the "*digitize*" package in R (v0.0.4, Poisot, 2011).

3 Results

3.1 General dive characteristics

Multi-sensor tags were successfully recovered from eight dugongs (n=2 mini-diaries, New Caledonia, 2019 and n=6; four mini-diaries and two camera diaries, Exmouth Gulf, 2021) (Table 1). Deployment duration ranged between 2 and 35 hours of data for each dugong. Due to truncation of the first two hours, a total of 1186 dives and one dugong (Ddu_06) were omitted from the analysis. This dugong was excluded as the deployment duration lasted less than two hours. Post truncation, a combined total of 6117 dives were analysed from seven dugongs (Table 1). The median dive duration was 68 ± 41.5 s (MAD) (range; 6–401 s) and the median maximum dive depth across different dugongs was 1.13 ± 0.8 m (MAD) (range; 0.1-22.9 m) (Table 1). 77% of all dives had a maximum depth of <2 m and 97% were <4 m. 77% of dives lasted <100 s. Log-log linear regression revealed that dive duration increased with maximum dive depth for all dugongs (Supplementary Table 2).

Dugongs exhibited three different descent and ascent kinematics while diving: entirely active, entirely passive, and active and passive (Figure 2). For pooled dive descents, the entirely active, entirely passive, and active and passive descents accounted for 77%, 20% and 3% of dives respectively. While entirely active ascents characterised 62% of pooled dives, entirely passive ascents accounted for 22% of pooled dives and 16% of pooled dive ascents were active and passive. Across the seven study dugongs, dives featured all combinations of descent and ascent kinematics (e.g. dives with an entirely active descent could have an entirely active, entirely passive, or active and passive ascent; Supplementary Table 3). From pooled dives, dives with an entirely active descent and entirely active ascent were the most common (53.2% of total dives: Supplementary Table 3); followed by dives with an entirely active descent and an active and passive ascent (13.8%: Supplementary Table 3); and then dives that have an entirely passive descent and an entirely passive ascent (12.7%: Supplementary Table 3). Dives with an active and passive descent were in the minority (Supplementary Table 3).

3.2 Buoyancy regulation

In 1109 dives (18.3% of total) a transition from positive to negative buoyancy was recorded during the dive (active and passive descent and/or ascent) and was used to quantify changes in buoyancy. From these dives: 5.7% contained active and passive phases in both the descent and ascent (e.g. Figure 2C), 12.3% only contained a kinematic transition in the descent and 82.0% featured a kinematic transition in the ascent phase only (e.g. Figure 2B). Descents that featured a kinematic transition from active to passive began with higher FBF that decreased during the active portion before ceasing during the gliding portion until the end of descent (Figure 2C). Ascents that featured a kinematic transition from active to passive typically began with higher FBF during the active portion, before ceasing during the gliding portion; as the animal passively ascended to the surface (Figures 2B, C). The median gliding depth across all dugongs was 1.51 ± 0.92 m (MAD) in the descent, and 0.99 ± 0.58 m (MAD) in the ascent (Table 1). The probability of active and passive kinematics during descent or ascent increased with increasing maximum dive

TABLE 1 Summary of truncated dugong data for dugongs tagged in New Caledonia 2019 (n=2) and Exmouth Gulf, Western Australia 2021 (n=5).

		Ddu_01	Ddu_02	Ddu_03	Ddu_04	Ddu_07	Ddu_08	Ddu_09
Sex		F	F	M	M	M	M	F
Date tagged		04/10/19	09/10/19	06/07/21	07/07/21	10/07/21	10/07/21	10/07/21
Location		NC	NC	EX	EX	EX	EX	EX
Deployment duration (hours)		32.6	29.2	25.8	27.1	8.1	1.5	10.7
Length (nose to fluke notch) (m)		2.36	2.23	2.40	2.40	2.20	2.30	2.20
Total number of dives		1647	1272	1065	1166	406	75	526
Median maximum depth (m)		0.8 ± 0.5	1.6 ± 1.1	0.9 ± 0.5	1.9 ± 0.8	2.0 ± 1.4	0.8 ± 0.1	1.0 ± 0.4
Maximum dive depth range (m)		0.1 – 7.0	0.1 – 22.9	0.1 – 5.0	0.2 – 4.5	0.2 – 4.1	0.4 – 1.3	0.2 – 2.9
Median dive duration (s)		53.0 ± 40.0	67.0 ± 43.0	80.0 ± 34.1	73.0 ± 46.0	71.5 ± 45.2	65.0 ± 22.2	66.5 ± 33.4
Number of dives (proportion) with an Active and Passive descent and/or ascent		288 (0.17)	289 (0.23)	109 (0.10)	256 (0.22)	125 (0.31)	NA	41 (0.08)
Median maximum depth (m) for dives with Active and Passive descent/ascent	Descent	1.4 ± 0.8	2.3 ± 0.9	3.5 ± 1.4	2.5 ± 0.7	3.6 ± 0.4	NA	1.1 ± 0.5
	Ascent	1.0 ± 0.4	2.5 ± 1.8	1.1 ± 0.3	2.2 ± 0.7	2.2 ± 1.1	NA	1.1 ± 0.3
Median dive duration (s) for dives with Active and Passive descent/ascent	Descent	63.0 ± 25.2	126.0 ± 99.3	141.0 ± 71.2	106 ± 50.4	129 ± 46.0	NA	85.5 ± 15.6
	Ascent	48.0 ± 25.2	75.0 ± 38.5	71.0 ± 91.3	63.0 ± 22.2	65.0 ± 28.2	NA	74.5 ± 34.1
Median gliding depth: descent (m)		0.9 ± 0.3	1.9 ± 1.7	2.9 ± 1.8	1.7 ± 0.6	2.5 ± 0.5	NA	1.0 ± 0.6
Median gliding depth: ascent (m)		0.6 ± 0.2	0.9 ± 0.5	0.9 ± 0.2	1.6 ± 0.4	1.7 ± 0.5	NA	1.0 ± 0.2

NC, New Caledonia; EX, Exmouth Gulf. Values are median ± median absolute deviations.
All uncertainty intervals are median absolute deviations. The information from Ddu_06 is not included as explained in the text.

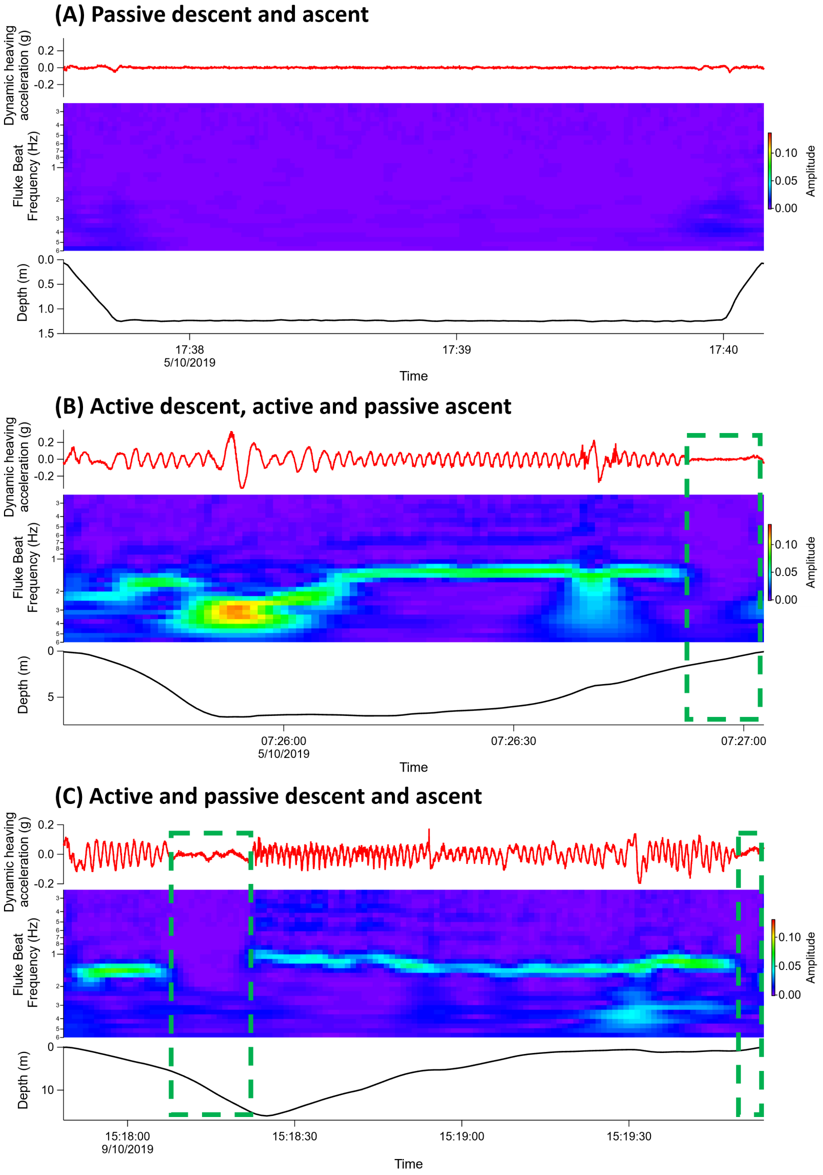

FIGURE 2
Representation of the diversity of descent and ascent kinematics of dugong dives (passive, active, active and passive). The gliding phase for dives with 'active and passive' kinematics during the descent and/or ascent is identified by a dashed green box. For each dive, upper panel (red) is the dynamic heaving acceleration, corresponding to dugong fluke beats, lack of movement (e.g. flattening of the line) is indicative that the animal is gliding. Middle panel: fluke beat frequency throughout each dive (amplitude and cycle from a spectrogram). Bottom: dive depth (black) Dive examples are from New Caledonia Dugongs; Ddu 01 **(A, B)** and Ddu 02 **(C)**.

depth. The probability of an active and passive descent, increased by 42.2% for every one metre increase in maximum dive depth (β=0.352 SE = 0.03, z=12.29, p<0.05). For ascents, the probability of an active and passive ascent, increased by 38.5% with every one metre increase in maximum dive depth (β=0.326, SE = 0.02 z= 13.91, p<0.05).

3.2.1 Gliding phases of 'active and passive' descents and ascents

In general, the depth that the gliding phase in a dive began increased with maximum dive depth for both the descent and ascent phases (Figure 3). There was an increasing relationship between maximum dive depth and the depth at which gliding began during the descent (β = 0.92, SE = 0.032, t=28.40, conditional R^2 = 0.87; Figure 3, Supplementary Table 4). Mean duration of gliding phase in the descent was 9.8 ± 4.9 s (S.D). Depth that the gliding phase in the ascent commenced increased with increasing maximum dive depth (β=0.49, SE = 0.02, t=31.23, conditional R^2 = 0.73; Figure 3, Supplementary Table 4). Only one dugong in the truncated dataset, Ddu_02 a female tagged in New Caledonia, performed dives >10m (n=13). These deeper dives were not highly influential: there were no values >0.5 when assessing Cook's distance. Mean duration of gliding in the ascent phase of dives was 4.9 ± 2.7 s (S.D).

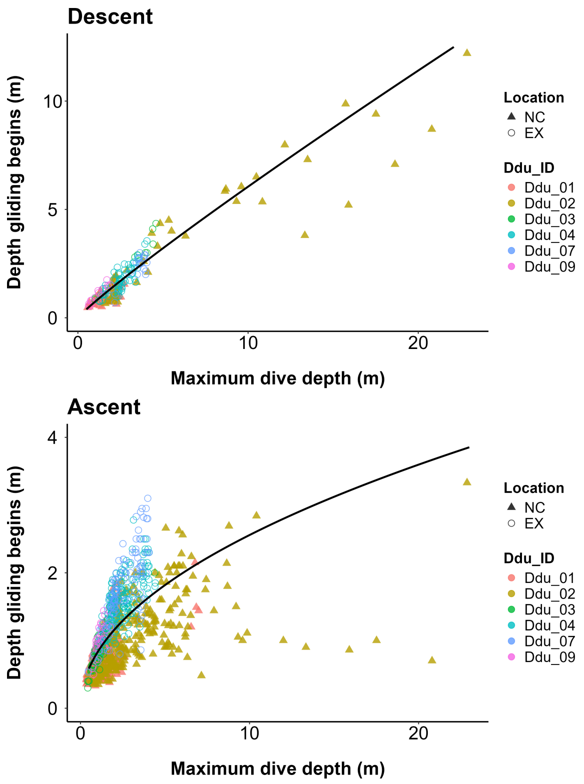

FIGURE 3
Relationships between maximum dive depth and depth gliding commenced in the descent and ascent phase of the dives. Top: Depth that gliding in the descent begins increases with increasing maximal dive depth (β=0.92, SE = 0.032, t=28.40). Bottom: Depth that gliding commenced in the ascent increases with increasing maximal dive depth (β=0.49, SE = 0.02, t=31.23). Variable depth that gliding in the descent and ascent begins indicates that dugongs can dive with variable lung volumes that increase as maximal dive depth increases i.e. Dugongs take a larger inhale prior to diving to deeper depths. Descent: y= exp(0.92*log(x)-0.31); Ascent: y=exp(0.49*log(x)-0.19).

3.2.2 Active phases of 'active and passive' descents and ascents

3.2.2.1 Descent: active phase

The active phase of the descent typically accounted for between 11% and 91% of the total descent time. The mean duration for the active phase of the descent was 9.3 ± 6.0 s (S.D) for dugongs. In general, the mean body angle, FBF, ODBA and VV in the descent phase increased with increasing maximum dive depth (Supplementary Figure 1). Mean body angle during the active descent phase was -14.7 ± 14.3° (S.D). Body angle during the active portion of the descent increased with increasing maximum dive depth (β=-5.7, SE = 1.1, t=-5.0, conditional R^2 = 0.70; Supplementary Figure 1, Supplementary Table 5). Mean FBF through the active descent phase was 0.44 ± 0.11 Hz (S.D). FBF during the active portion of the descent increased with maximum dive depth (β=0.2, SE = 0.03, t=6.3, conditional R^2 = 0.40; Supplementary Figure 1, Supplementary Table 5). Mean ODBA during the active descent phase was 0.16 ± 0.06 g (S.D). ODBA during the active descent phase increased with maximum dive depth (β=0.2, SE = 0.04, t=4.59, conditional R^2 = 0.56; Supplementary Figure 1, Supplementary Table 5). Mean VV during the active descent phase was 0.21 ± 0.13 m/s^{-1} (S.D). There was an increasing relationship between VV in the active descent phase and maximum dive depth (β=0.12, SE = 0.01, t=12.62, conditional R^2 = 0.72; Supplementary Figures 1, 2, Supplementary Table 5).

3.2.2.2 Ascent: active phase

The active portion of ascents typically accounted for between 3% and 94% of the ascent time. The mean duration of the ascent active phase was 13.5 ± 8.3 s (S.D). Mean body angle, FBF, ODBA and VV during the ascent phase all had a positive relationship with increasing maximum dive depth (Supplementary Figure 2). Mean body angle during the active ascent phase was 8.9 ± 4.9° (S.D), body angle during the active ascent phase became steeper with increasing maximum dive depth (β=3.1, SE = 0.26, t=11.8, conditional R^2 = 0.32; Supplementary Figure 2, Supplementary Table 5). Mean FBF throughout the active ascent phase was 0.56 ± 0.15 Hz (S.D). FBF in the active ascent phase increased with maximum dive depth (β=0.05, SE = 0.008, t=6.3, conditional R^2 = 0.31; Supplementary Figure 2, Supplementary Table 5). Mean ODBA during the active ascent phase was 0.14 ± 0.04 g (S.D). ODBA during the active ascent phase increased with maximum dive depth (β=0.18, SE = 0.01, t=12.88, conditional R^2 = 0.45; Supplementary Figure 2, Supplementary Table 5). Mean VV ascent rate during the active ascent phase was -0.07 ± 0.06 m/s^{-1} (S.D), there were higher VV values during the active ascent phase at deeper maximum dive depths (β=-0.06, SE = 0.002, t=-28.11, conditional R^2 = 0.60; Supplementary Figure 2, Supplementary Table 5).

3.2.3 Fluke beat frequency during descents and ascents

FBF varied throughout descent and ascent. For dives with maximum depth between 0 m and 7 m, the mean FBF decreased as the descent progressed (Figure 4). Mean FBF was highest at the start of the descent phase for every depth group. There are clear differences in FBF throughout the descent phase for each depth group, dives to deeper maximum depths (e.g. group 5–7 m) had higher mean FBF at each instantaneous depth interval for the entirety of the descent phase (Figure 4). For ascents of dives with maximum depth between 0 m and 7 m, the mean FBF decreased as the ascent progressed. FBF is highest at the start of the ascent phase for dives <2 m and 5–7 m (Figure 4). Ascent for dives with deeper maximum depth (5–7 m) had the highest initial FBF; this is followed by the middle-depth group (2–5 m) and then the shallowest maximum-depth group (<2 m) (Figure 4). In general, for all three depth groups, as the ascent progressed the FBF decreased as the distance to the surface (instantaneous depth) decreased. However, the FBF in the two deepest groups (2–5 m and 5–7 m) slightly increased after start of the ascent before continuing to

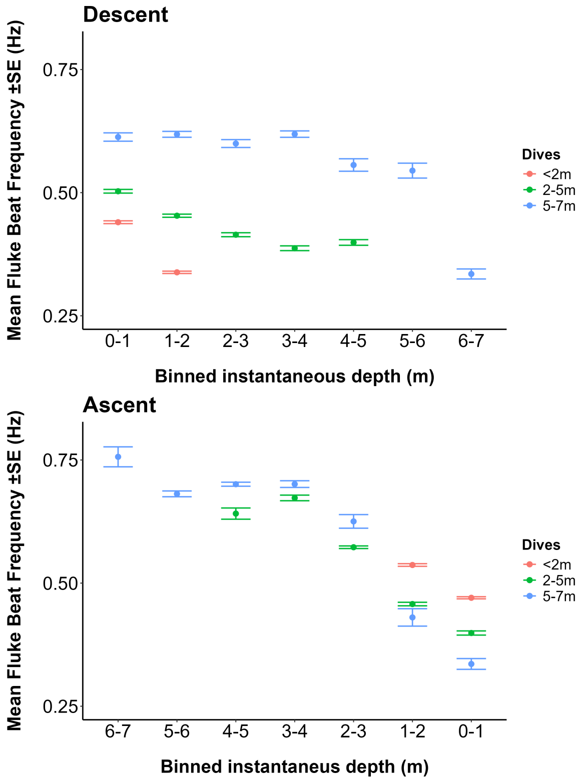

FIGURE 4
Top: Mean fluke beat frequency over instantaneous depth throughout dive descents by depth group. Fluke beat frequency reduces as the descent progresses for each depth group. Fluke beat frequency is higher at the start of descent for all depth groups suggesting that dugongs have increased buoyancy due to increased lung volume when diving to deeper depths i.e. Dugongs take a larger inhalation prior to diving to deeper depths. Bottom: Mean fluke beat frequency over instantaneous depth throughout dive ascents, grouped by depth. In general, fluke beat frequency decreases for each depth group as the ascent phase progresses, this indicates that dugongs work harder at the start of the ascent to overcome negative buoyancy.

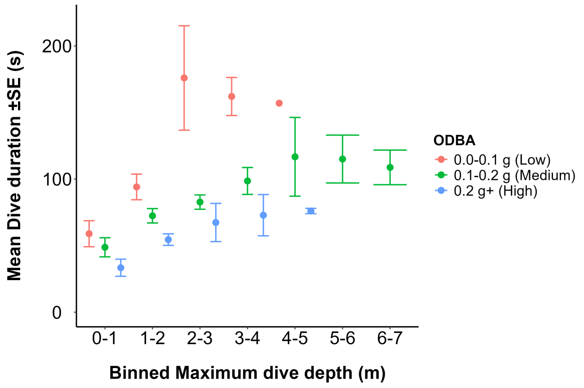

FIGURE 5
Mean of individual means dive duration (s) (± SE) as a function of depth (m) for three different locomotory activity groupings (ODBA: Overall Dynamic Body Acceleration). Number of individuals contributing to each point detailed in Supplementary Table 1. As dive depth increases, dive duration increases concomitantly. Dugong dive duration decreases as activity increases i.e., the more active the dugong is, the faster the oxygen stores in the dugong's lungs are consumed therefore dive duration is reduced.

decrease (Figure 4). At the closest distance to the surface (0–1 m) the deepest dive group (5–7 m) had the lowest FBF, followed by group 2–5 m and the shallowest group (<2 m) had the highest FBF (Figure 4).

3.3 Buoyancy and locomotor activity trade-off

Dive duration generally decreased with increasing ODBA as maximum dive depth increased, with every 1% increase in maximum dive depth there is an increase in dive duration by 1.95% (SE = 0.01) for the lowest ODBA group, 1.29% (SE = 0.02) for the mid-range and a 0.88% (SE = 0.04) for the highest ODBA group (Figure 5, Supplementary Table 6). Shallow, long dives tended to have the lowest ODBA (group: 0.0-0.1 g), whereas shallow, short dives had higher associated ODBA (group: 0.2 g+) (Figure 5). Dives with a mean ODBA between 0.0 g and 0.1 g had a higher mean dive duration at every binned depth interval they occurred in (Figure 5). Deeper dives were typically associated with mid-range ODBA values (group: 0.1-0.2 g) (Figure 5).

3.4 Relationship for comparison with other species

Dive duration increased with maximum depth for dugongs (Multiple R^2 = 0.13, SE = 0.01, t=16.97, $F_{(1,6115)}$ = 932, $P < 0.05$; Figure 6). The slope for the relationship between dive duration and maximum dive depth for dugongs was 0.203.

4 Discussion

Our study provides compelling evidence that dugongs regulate their lung volume by varying the inhaled air volume before diving. To the best of our knowledge, this is the first study to quantify the buoyancy control of a sirenian, which are amongst the shallowest

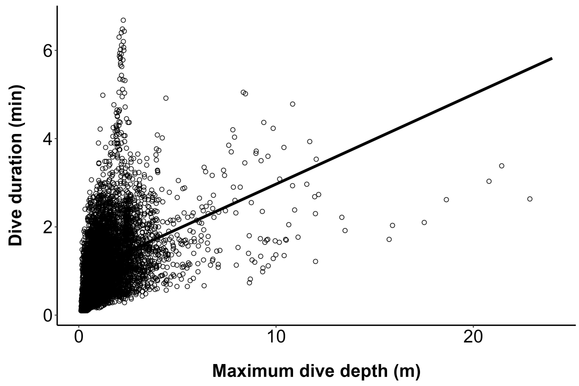

FIGURE 6
The relationship (slope) between dive duration and maximum dive depth increases with increasing maximum dive depth (Multiple R^2 = 0.13, $F_{(1,6115)}$= 932, n= 6117), for pooled dives for dugongs from Exmouth Gulf (n=5) and New Caledonia (n=2). Regression line is shown on graph: y=0.932 + 0.203(x).

diving clades of fully aquatic tetrapods. We found that dugongs utilise several descent and ascent kinematics when diving in shallow waters. We suggest this is because dugongs control their buoyancy in association with dive function to maximise their breath-hold duration while minimising locomotor activity resulting from buoyant forces in shallow waters, thereby allowing them to exploit shallow waters efficiently.

4.1 Buoyancy regulation

The transition from positive to negative buoyancy, approximated by the gliding depth, can be considered a proxy for lung volume, because greater lung volumes result in a transition to negative buoyancy at a deeper depth (Sato et al., 2002). The relationship between maximum dive depth and the buoyancy transition indicates that deeper dives coincide with larger lung volumes in dugongs and suggests that dugongs regulate their buoyancy through inspiration prior to diving. Further, the positive relationships between maximum dive depth and mean body angle, vertical velocity, ODBA and fluke beat frequency during the active phase of descents and ascents suggest dugongs dive at larger angles with higher activity when diving to deeper depths with larger lung volumes. This inference is further supported by the negative relationship between fluke beat frequency and instantaneous depth throughout descents and ascents. As in other inhalant divers, air spaces in the body represent the major contributors to buoyancy and therefore the physical forces an individual has to overcome (Lovvorn and Jones, 1991; Sato et al., 2002; Yasuda and Arai, 2009). Consequently, when dugongs experienced high positive buoyancy due to greater lung volumes prior to deeper dives those greater forces must be overcome by increased locomotor activity at the start of the descent, which reduce once the positive buoyancy progressively reduces in line with increasing ambient pressure compressing the lung (Fossette et al., 2010; Sato et al., 2002; Wilson, 2003; Yasuda and Arai, 2009).

Inhalant divers therefore trade their oxygen stores for reduced oxygen consumption at shallow depths by partial inhalation (Hays et al., 2004; Minamikawa et al., 2000; Sato et al., 2002). This phenomenon has been documented in king and adelie penguins (Sato et al., 2002), green turtles (Hays et al., 2004; Hazel et al., 2009) and loggerhead turtles (Hochscheid et al., 2003; Minamikawa et al., 1997), and equally seems to hold for dugongs. While partial inhalation may appear counterintuitive for a breath-hold diver, given that it invariably reduces oxygen stores during submersion, it increases dive duration at a given depth as a result of reduced locomotor activity (Hazel et al., 2009; Sato et al., 2002). Indeed, excessive positive buoyancy during the bottom phase of dives, in particular, will substantially increase locomotor activity, resulting in rapid depletion of oxygen stores (Davis, 2019; Hays et al., 2004; Hazel et al., 2009). Contrary to most other marine mammals but consistent with previous studies, dugongs spent nearly all their time in very shallow waters, in our case less than four metres (Chilvers et al., 2004; Hagihara et al., 2014; Keith-Diagne et al., 2022). Given the physical and physiological challenges posed by diving in such shallow water, it is not surprising that dugongs, and presumably manatees, have evolved behavioural strategies to adapt to their unique lifestyle. Dugongs carefully adjust their buoyancy by controlled inhalation according to dive depth, akin to other divers, such as marine turtles and some species of penguin that mostly perform shallow dives (Hays et al., 2004; Sato et al., 2002). This strategy contrasts with that of most other marine mammals, which dive on exhalation and do not adjust their respiratory volume according to dive depth to the same extent, thereby making maximal dive depth play a lesser role in descent and ascent kinematics (Davis, 2019).

4.2 Buoyancy and locomotor activity trade-off

Our finding that dive duration increased with dive depth but decreased with increasing locomotor activity reveals an expected trade-off between buoyancy and locomotor activity for dugongs. The positive relationship between maximum dive depth and mean dive duration, irrespective of activity, indicates two key findings. First, the oxygen stores available while diving increase with depth, thereby increasing the animal's buoyancy at the start of a dive, as discussed previously. Second, in dives to the same maximum depth, oxygen stores are consumed more slowly when activity is lower due to reduced locomotory activity, a result that is consistent with previous studies (Halsey et al., 2009, 2011; Keith-Diagne et al., 2022; Okuyama et al., 2012; Reynolds, 1981; Wilson et al., 2006). For example, studies of shallow diving green and loggerhead turtles recorded longer resting dives when dives were deeper (Hays et al., 2000b; Minamikawa et al., 1997; Okuyama et al., 2012; Yasuda and Arai, 2009). It follows that like shallow diving turtles and penguins, dugongs maximise their oxygen stores for a given dive by regulating buoyancy prior to diving, a critical adaptation that allows them to exploit shallow waters for extended periods (Hays et al., 2004; Sato et al., 2002).

While dugongs appear to control their buoyancy similarly to other inhalant divers, their proportions of descent and ascent kinematics did not resemble the stereotypical sequences found in other species studied to date, in which active propulsion gives rise to passive gliding once respiratory volumes are sufficiently compressed to result in negative buoyancy during descent, or positive buoyancy during ascent (Beck et al., 2000; Davis et al., 2001; Fossette et al., 2010; Mitani et al., 2009; Webb et al., 1998; Williams et al., 2000). While gliding is thought to provide significant savings in oxygen stores, allowing elephant seals to extend dive duration (Webb et al., 1998), the absence of gliding in most dugong dives suggests that conserving oxygen stores during descent or ascent may not be the primary goal. Alternatively, the changes in buoyancy experienced in a given dive are insufficient to provide the necessary forces to replace locomotor activity. Especially during shallow dives, inhalation is expected to be minimal, permitting entirely passive descents, meaning that the overall change in the buoyant forces with increasing depth is equally small. This hypothesis is supported by our data, as the probability of descents and ascents with a pronounced gliding phase (active and passive kinematics) increased with dive depth. However, there was considerable variation in this relationship, suggesting that other factors not quantified here also play an important role.

Dugongs in this study exhibited a diversity of descent and ascent kinematics, possibly a result of different dive functions (e.g. travelling vs foraging vs resting dives), driving the animal's buoyancy control. For instance, while it would be beneficial for a foraging dugong to be negatively buoyant to avoid expending energy to remain at the seafloor while foraging (indicated by entirely passive or active and passive kinematics), the buoyancy of a travelling dugong is less critical, since travel mainly occurs in shallow to midwater (Churchward, 2001; Hagihara, 2015). Foraging dives are expected to have entirely passive or active and passive kinematics with larger body angles in descents and ascents and consequently higher vertical velocities in benthic dives to maximise time during the bottom phase. In contrast, travelling dives are expected to feature active kinematics with smaller body angles in descents and ascents and lower vertical velocities to maximise the horizontal distance covered during a dive. Furthermore, the diversity of kinematics in descents and ascents of dives greater than 20 m could be expected to differ across dive functions as observed in other species that spend extended periods gliding during the descent phase (Davis et al., 2001; Mitani et al., 2009; Williams et al., 2000). Thus, the way that buoyancy impacts locomotion is likely context specific. Therefore, it is conceivable that the function of the dive influences dugong buoyancy control and resultant diving kinematics. This matter should be explored further.

4.3 Comparisons with other species

Sirenians differ considerably in their evolutionary history and ecology from other endothermic breath-hold divers (Davis, 2019; Keith-Diagne et al., 2022; Marsh et al., 2011). Their herbivorous diet means they are almost exclusively found in shallow to very shallow environments where seagrass, their predominant food source grows (Marsh et al., 2018). Furthermore, the relatively low energy content of their food source compared with predatory endothermic breath-hold divers with diets of greater energy density (e.g. fish, krill) also likely means that substantially more time feeding is required to satisfy their daily energy expenditure (Keith-Diagne et al., 2022; Lanyon et al., 2025; Preen, 1992). These combined constraints suggest that dugongs may rely more heavily on behavioural and physiological mechanisms that maximise foraging time, including the greater ability to adjust their buoyancy. The relationship between dive duration and dive depth has previously been used as an indicator of lung-regulated buoyancy control, with steeper slopes indicating greater ability to extend dive duration through variable lung volume (Hays et al., 2004). For example, the depth-duration slope for green turtles (1.65), which are ectothermic herbivores, was greater than slopes reported for U-shaped dives performed by endothermic divers (Hays et al., 2004). Because the metabolic rate in ectotherms such as turtles is strongly temperature dependent, their rate of oxygen consumption is typically lower, therefore increasing their dive duration at a given depth (Hazel et al., 2009), and thus endothermic species such as dugongs would be expected to feature shallower depth-duration slopes.

Our results indicate that, when considering dives of all shapes, dive duration in dugongs increases more rapidly with depth than has been reported for other endothermic breath-hold divers (Figure 7). However, this comparison should be interpreted cautiously as the studies summarised by Schreer et al. (2001) are restricted to dives exceeding five metres, whereas our study focuses on this depth range. In addition, most dives deeper than seven metres in our dataset were performed by a single individual, highlighting the need for further data on deep dives to confirm this pattern.

Despite these limitations, the comparatively steeper slope observed for dugongs (0.203: Figure 7) suggests that lung volume may play a greater role in sustaining dive duration than in many other endothermic divers. For example, Adelie penguins exhibit a much shallower slope compared to dugongs (0.024: Figure 7), reflecting their greater reliance on blood oxygen stores. Despite their smaller lung volume, Adelie penguins have greater blood oxygen stores, with blood myoglobin approximately five to six times larger than sirenians, thus a change in lung volume will not affect dive duration as substantially (Kooyman and Ponganis, 1998; Ponganis et al., 2015; Weber et al., 1974). A similar pattern is evident in phocid seals (Davis, 2019). For example, southern elephant seals (*Mirounga leonina)* predominantly rely on blood oxygen stores to sustain aerobic diving. They have higher myoglobin concentrations and smaller lungs than another sirenian, the Florida manatee (*Trichechus manatus latirostris)*, at 10.8 and 0.54 times, respectively (Davis, 2019). As a result, variation in lung volume has relatively little influence on dive duration in these taxa.

Given that dugongs have large lungs like manatees, we infer that they are more reliant on their lung oxygen stores to sustain diving than deeper diving marine mammals. Similar to turtles, their lungs will play an important role in both buoyancy control and oxygen storage (Hays et al., 2004; Hochscheid et al., 2003). Large lungs permit increased intake and storage of oxygen during diving, thereby extending breath-hold duration in shallow waters and enabling them to maximise time spent benthically feeding on seagrass while diving aerobically (Davis, 2019). Their greater ability to control buoyancy through inhaled lung volume, thereby reducing external forces acting on the lungs during shallow diving, allows dugongs to reduce locomotor activity in response to changing buoyancy, further extending dive duration, as discussed earlier. Thus, the dual role of dugong lungs for buoyancy control and oxygen storage, is likely a key evolutionary adaptation that allows dugongs, like marine turtles, to exploit shallow waters efficiently (Hochscheid et al., 2003; Marshall et al., 2022).

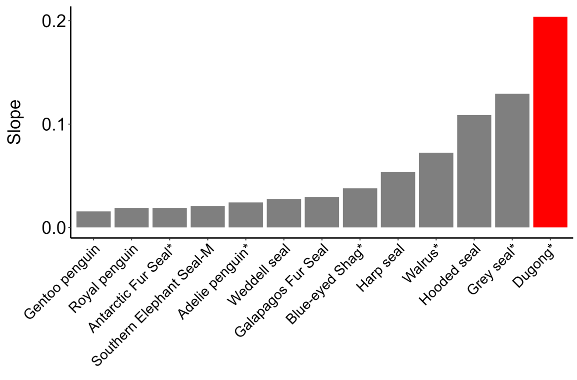

FIGURE 7
The relationship (slope) between dive duration and maximum dive depth for air-breathing diving birds and marine mammals. Values are taken from Schreer et al. (2001), refer to Schreer et al. (2001) for details on individuals, with the addition of the slope describing the relationship between dive duration and maximum dive depth for dugongs from Figure 6. Asterisks (*) next to the species name denotes a species with a mean dive depth <30 m as reported by Schreer et al. (2001), or in this study for the dugong.

5 Conclusions

This study provides evidence that dugongs are inhalant divers that utilise lung-regulated buoyancy control, a critical adaptation that enables them to exploit the shallow water habitats of a seagrass community specialist. Unlike other marine mammals studied to date, dugongs in this study did not exhibit stereotypical descent and ascent kinematics, presumably because of their extensive use of shallow water, which results in only relatively small changes in buoyancy due to dugong's regulating their inhaled lung volume with depth (i.e. when the dugongs dive shallow, they take a smaller inhalation). Diving on inhalation seems to be an adaptation that allows dugongs to adjust their buoyancy with the intended dive depth and maximise the time they spend aerobically diving. Thus, dugongs appear to be better adapted to control their buoyancy more like other shallow diving vertebrates such as marine turtles than other marine mammals.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to Renae Lambourne, renae.lambourne@my.jcu.edu.au.

Ethics statement

The animal study was approved by Murdoch University Animal Ethics Committee. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

RL: Conceptualization, Data curation, Writing – original draft, Writing – review & editing, Formal analysis. HM: Conceptualization, Writing – review & editing. CC: Conceptualization, Writing – review & editing, Funding acquisition. MH: Writing – review & editing. AG: Conceptualization, Writing – review & editing.

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